



Temporal facilitation for moving stimuli is independent of changes in direction

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Received 28 September 1999; received in revised form 4 July 2000

Abstract

A flash that is presented aligned with a moving stimulus appears to lag behind the position of the moving stimulus. This flash-lag phenomenon reflects a processing advantage for moving stimuli (Metzger, W. (1932) *Psychologische Forschung* 16, 176–200; MacKay, D. M. (1958) *Nature* 181, 507–508; Nijhawan, R. (1994) *Nature* 370, 256–257; Purushothaman, G., Patel, S.S., Bedell, H.E., & Ogmen, H. (1998) *Nature* 396, 424; Whitney, D. & Murakami, I. (1998) *Nature Neuroscience* 1, 656–657). The present study measures the sensitivity of the illusion to unpredictable changes in the direction of motion. A moving stimulus translated upwards and then made a 90° turn leftward or rightward. The flash-lag illusion was measured and it was found that, although the change in direction was unpredictable, the flash was still perceived to lag behind the moving stimulus at all points along the trajectory, a finding that is at odds with the extrapolation hypothesis (Nijhawan, R. (1994) *Nature* 370, 256–257). The results suggest that there is a shorter latency of the neural response to motion even during unpredictable changes in direction. The latency facilitation therefore appears to be omnidirectional rather than specific to a predictable path of motion (Grzywacz, N. M. & Amthor, F. R. (1993) *Journal of Neurophysiology* 69, 2188–2199). © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Motion; Facilitation; Latency; Direction change; Flash lag; Extrapolation

1. Introduction

A flash that is presented adjacent to a moving stimulus appears to lag behind the position of the moving stimulus (Metzger, 1932; MacKay, 1958). According to some, this illusion is evidence that the visual system compensates for the neural delays involved in processing moving stimuli by extrapolating the expected current physical location of a moving stimulus along its trajectory. The stimulus is thereby seen at the location it is expected to be, given its motion (i.e. at its actual location; Nijhawan, 1994, 1997; Khurana & Nijhawan, 1995). The flash, however, is perceived where it was presented, and thus appears to lag behind the moving stimulus.

Although the extrapolation model is intuitively pleasing, recent studies (Whitney & Murakami, 1998; Bren-

ner & Smeets, 2000; Eagleman & Sejnowski, 2000; Whitney, Murakami, & Cavanagh, 2000) have shown that, when there are changes in the velocity of the moving stimulus, such as an acceleration, a stop, or a reversal, the magnitude of the illusory flash lag is inconsistent with predictions made by extrapolation. Alternatively, we have proposed that the illusory flash lag is due to a shorter neural latency for moving than for flashed stimuli. Consistent with this suggestion, when the luminance contrast of the flash is increased sufficiently (thereby reducing the neural latency for the flash), the flash is not perceived to lag behind the bar, but to lead the bar (Purushothaman, Patel, Bedell, & Ogmen, 1998; cf. Roufs, 1974).

Despite the growing literature on the flash-lag phenomenon, the stimuli used to study the illusion have been restricted to movement along linear or predictable trajectories. These types of motion have been adequate to support the differential latency hypothesis, yet the mechanism by which such a hypothesis would operate remains elusive. After all, the suggestion that there is a

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processing difference between moving and flashed stimuli is counterintuitive: considering that flashed objects have motion energy in all directions, they must stimulate many of the same directionally selective detectors that respond to the moving stimulus. The flash and the moving stimulus do differ, nevertheless, in the continuity of their motion energy. One mechanism that may underlie the latency advantage for moving objects is facilitatory connections along the expected path of motion (Grzywacz & Amthor, 1993). Such path-dependent facilitation would lead one to expect that either predictable, or at least locally linear, trajectories of motion would have the greatest reduction in latency, or the maximum flash-lag effect.

In the following experiments, we test whether the latency advantage for moving stimuli is omnidirectional or specific to the established path of motion. To investigate which of these alternatives holds, we presented a flash adjacent to a moving stimulus that changed direction at a random position. In the first experiment, the moving stimulus was a pair of translating dots that created a three-dot vernier task when the flash was presented between them. To control for the anisotropic nature of this stimulus, the second experiment used a single moving dot, while the flash was a hollow ring. The response latency to a flash (of fixed luminance) will be constant irrespective of the trajectory of the moving stimulus. A change in the illusory flash lag at different points along the trajectory must therefore reflect a change in the latency of the response to the moving

stimulus as it changes direction (see Fig. 1 for an example of a 90° direction change).

2. Experiment 1: orthogonal direction change using a three-dot vernier

2.1. Methods

One naïve subject, and one of the authors (DVW) 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 monitor that had a refresh rate of 66.7 Hz. A pair of vertically aligned white (34.5 cd/m^2) squares translated vertically upwards (see Fig. 1 for a representative trial). Each square subtended 0.54° . The distance between the squares (1.26°) was constant, and they moved concurrently at 11.84 s^{-1} . The horizontal position where the squares (also referred to as a ‘bar’) appeared and began to move was randomly generated within a 4.32° window. When the vertically moving bar reached a randomly generated position, within a 1.8° vertical window, it abruptly made a 90° turn leftward or rightward (determined randomly); the squares remained vertically aligned. The average vertical distance between the fixation point and the turning point was 3.64° . A white (34.5 cd/m^2) fixation point was provided above the trajectory of motion (within 6.49° of the turning point). Because the point of motion initiation and the turning point were randomly varied, the fixation point was located in a different location relative to the motion of the bar in each trial. The background was dark (0.01 cd/m^2).

In each trial, a small white (34.5 cd/m^2) disk subtending 0.18° 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. When the flash is presented between the moving squares during linear continuous motion, the flash appears to trail behind the squares. To measure the degree of perceived lag, the flash was presented ahead of the moving squares. In this experiment, however, the moving squares change from vertical to horizontal motion. Therefore, the flash might appear to lag behind the squares in two-dimensional space. That is, as the moving squares change from vertical to horizontal motion, we might expect the flash to appear to lag vertically and horizontally behind the moving squares.

In order to measure where the flash appears aligned with the moving squares when they change direction (i.e. the degree of illusory flash offset), two separate conditions were necessary: the first to measure the apparent horizontal offset of the flash, and the second

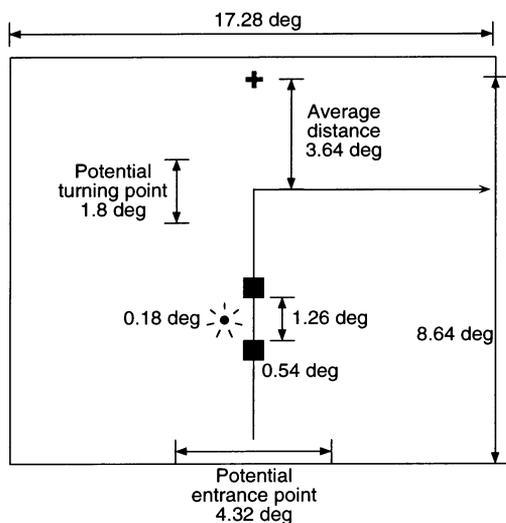


Fig. 1. Stimulus used in the first experiment. A moving bar (two vertically aligned squares) translated vertically before turning randomly rightward or leftward. The initiation of the bar’s motion was randomly assigned to a location within 4.32° . The turning point was also randomly determined. The location of the fixation point was therefore not predictive of the bar’s trajectory. The two bold lines that form a right angle indicate the bar’s trajectory, but were not presented during the experiment.

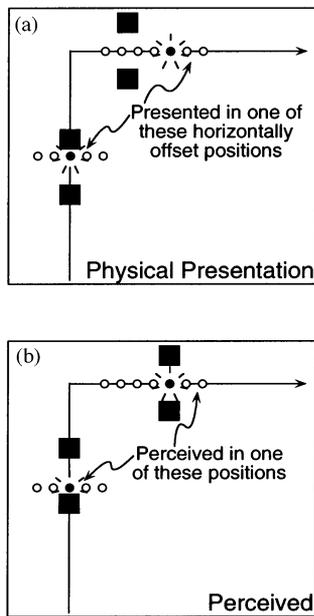


Fig. 2. In the first of two experimental conditions, a flash was presented before or after the bar at various horizontal offsets (potential flash locations indicated by hollow circles). The two bars (two pairs of squares) indicate that the flash could be presented during the bar's vertical or horizontal motion; only one bar was shown on each trial, however. The subject judged whether the flash appeared spatially offset to the right or left of the bar (2AFC task). By calculating a psychometric function, the location of the flash (solid circle) that appeared aligned with the bar was found.

to measure the apparent vertical offset of the flash. The method of constant stimuli was used in both conditions.

In the first condition, the flash was presented between the vertically aligned moving squares and offset by varying degrees to the right or left of them (Fig. 2a). The subject's task was to judge whether the flash appeared spatially offset to the right or left of the vertically aligned squares. A psychometric function was calculated for a given time (before or after the bar's abrupt change in direction) that yielded a horizontal setting of perceived alignment. This is the horizontal offset required to make the flash appear vertically aligned with the moving squares (Fig. 2b).

In the second condition, the flash was presented adjacent to the vertical midpoint between the vertically aligned squares (separated by 0.72° ; Fig. 3a). The position of the flash was then offset vertically from this midpoint. The subject's task was to judge whether the flash appeared above or below the midpoint between the vertically aligned squares. By varying the degree of vertical offset between the flash and the midpoint, a psychometric function was calculated that estimates the vertical point of perceived alignment. This is the vertical offset required to make the flash appear horizontally aligned with the midpoint of the moving squares

(Fig. 3b). When combined, the data for the two experimental conditions (Figs. 2 and 3) reveal the locations of the flash that appeared aligned with the bar as it traveled along its two-dimensional path.

For each condition, there were at least 20 trials for each of six positions of the flash relative to the bar. Data for the leftward motion of the bar were flipped and merged with that for the rightward motion. 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 (either vertically or horizontally depending on the condition). Positions of the flash that appear aligned with the moving bar were measured for each of 14 video frames (210 ms) around the velocity change.

2.2. Results

The flash alignment settings indicate where the flash is presented for it to appear aligned with the moving bar. These locations therefore trace out the perceived trajectory of the bar, and estimate the amount of time that the flash must precede the bar at a particular location.

Fig. 4a and Fig. 5a show the stimulus trajectory in an X - Y plot for two observers. Each video frame is sig-

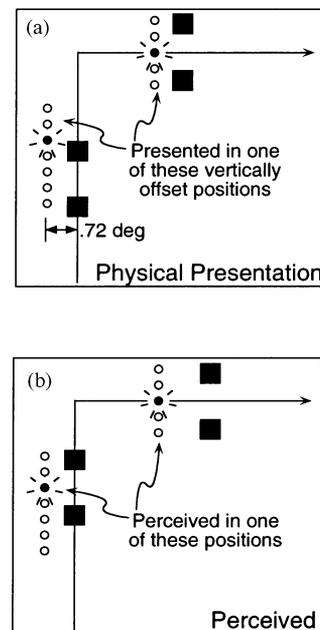


Fig. 3. In the second experimental condition, the flash was presented before or after the bar at various vertical offsets. As in the first experimental condition, only one bar was presented on each trial. The subject judged whether the flash appeared spatially offset above or below the bar (2AFC task). By calculating a psychometric function, the location of the flash that appeared aligned with the bar was found. When taken with the first experimental condition (Fig. 2), the combined data show the locations of the flash that appeared aligned with the bar as it traveled along its two-dimensional path.

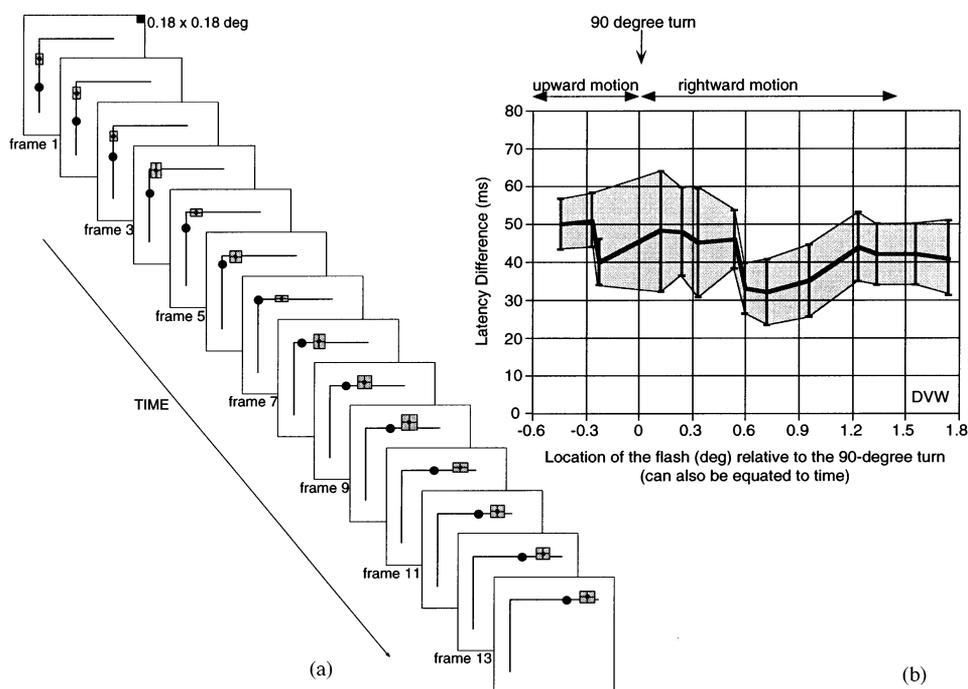


Fig. 4. (a) Space–space (X – Y) plots of the data for subject DVW across time. The moving bar and flash are represented by the large and small filled circles, respectively. Each video frame is represented by a single large square image. The two bold lines that form a right angle indicate the bar's trajectory, but were not presented during the experiment. The gray rectangular area around the small filled circle (flash) represents a 99% confidence interval. (b) In order to visualize the differential latency over the course of the stimulus motion, the data from (a) are graphed, showing the amount of time that the flash must precede the bar to perceptually align the two, i.e. the differential latency, at various locations relative to the direction change. (The abscissa of the graph shows the location of the flash relative to the turn, and can therefore be equated to the time of the bar before or after its turn.) The gray area on the graph represents the 99% confidence interval from (a). Notice that the differential latency is always greater than zero, indicating that the flash must precede the moving bar at all locations, despite the presence of an unpredictable direction change.

nified by a single square image. Data were gathered for 14 frames in total and, therefore, 14 positions of the moving bar. The solid large circle and smaller dot represent the moving bar and the flash that appeared aligned with the bar, respectively. The aligned flash is plotted with X as the horizontal alignment obtained in one condition and with Y as the vertical alignment obtained in the other condition. The width and height of the gray rectangles indicate the horizontal and vertical alignment setting 99% confidence intervals, respectively. If there is temporal facilitation for the moving bar (i.e. differential latency), we would expect that the flash must precede the bar at any location by some amount of time. If there is no facilitation for the moving bar, the flash should be presented at the same location as the bar for it to appear aligned.

The data in the X – Y plots of Figs. 4 and 5 reveal two important facts. First, the perceptually aligned flash (small dot) does not deviate from the motion trajectory. This finding rejects an explanation of the flash-lag phenomenon in terms of a predictive response, such as spatial extrapolation, because the moving bar should have appeared to overshoot the unpredictable point where it changed direction. Rather, this finding

supports our hypothesis that the perceptual difference between the flash and the moving bar is only a matter of latency. Second, and more importantly, there is relatively little variation in the amount of time that must separate the presentation of the bar and flash in order to align the two perceptually. This suggests that facilitation does not transiently disappear following an abrupt change in direction.

To analyze this more closely, we have calculated the amount of time that the flash must precede the bar at each of the flash's locations. For example, the data in Fig. 4a show that the flash in the first frame, and the moving bar in the fourth or fifth frame appear at the same time and the same place, thus their latency difference is roughly three to four video frames. In other words, the distance between the bar (large circle) and the flash (small dot) in the first frame is about 0.54 – 0.72° (which equals 45 – 60 ms). This value corresponds to the amount of time that the flash in the first frame must precede the moving bar at the same location to appear aligned.

Performing this calculation at each of the flash's locations provides a visualization of the change in the differential latency as a function of the motion trajec-

tory (Fig. 4b). For example, the first data point in Fig. 4b shows that, at the position of the flash in the first frame, the differential latency is about 50 ms (as earlier). Strikingly, Fig. 4b and Fig. 5b show that there is little variation in the differential latency at the point of direction change. If the temporal facilitation for moving objects were contingent on linear trajectories, we would expect that, at the time of direction change or one video frame after, the differential latency would be reduced significantly, if not completely eliminated, before recovering. These results tentatively support the idea that there is a differential latency for moving and flashed stimuli that exists regardless of the moving stimulus' history or direction.

One interesting facet of the data for subject DVW in Fig. 4b is that the differential latency decreases slightly about four frames ($\sim 0.72^\circ$) after the 90° turn. Although the differential latency does not decay entirely, the dip is clear, and is visible in the data of subject ELV about 75 ms after the bar's change in direction. This transient decrease in the differential latency is certainly tied to the direction change in some way, but concluding that there is path-dependent facilitation at the moment of a direction change is unwarranted because the dip in facilitation occurs well after the actual change in direction. Indeed, the least facilitation for the moving bar occurs after it has moved about 1° away from the point of direction change. There are several possible explanations for the transient dip in facilitation:

it could be evidence of path-dependent facilitation, a luminance artifact in the form of increased motion blur, or persistence at the unpredictable direction change (Hogben & Di Lollo, 1974; Watamaniuk, 1992), attentional shifts, or an artifact of the anisotropic stimulus used in the experiment. To control for the stimulus in the first experiment, the second experiment uses a more isotropic moving target and flash. The alternatives will be examined further in Section 5.

3. Experiment 2: orthogonal direction change using isotropic stimuli

3.1. Methods

The methods in the current experiment were identical to those of the first experiment, except that the moving stimulus (bar) was a single white (34.5 cd/m^2) moving disk (0.54° diameter). Just as in the first experiment, the moving bar (disk) translated vertically upwards before abruptly turning 90° left or right at an unpredictable location. To reduce the possibility of screen persistence or a luminance artifact, the speed of the moving disk was reduced in this experiment to $\sim 4.8^\circ \text{ s}^{-1}$. The flash was a white (34.5 cd/m^2) ring-shaped stimulus (1.8° diameter, 0.072° thick ring; see Fig. 6). The procedure and instructions to the subject were identical to those in the first experiment.

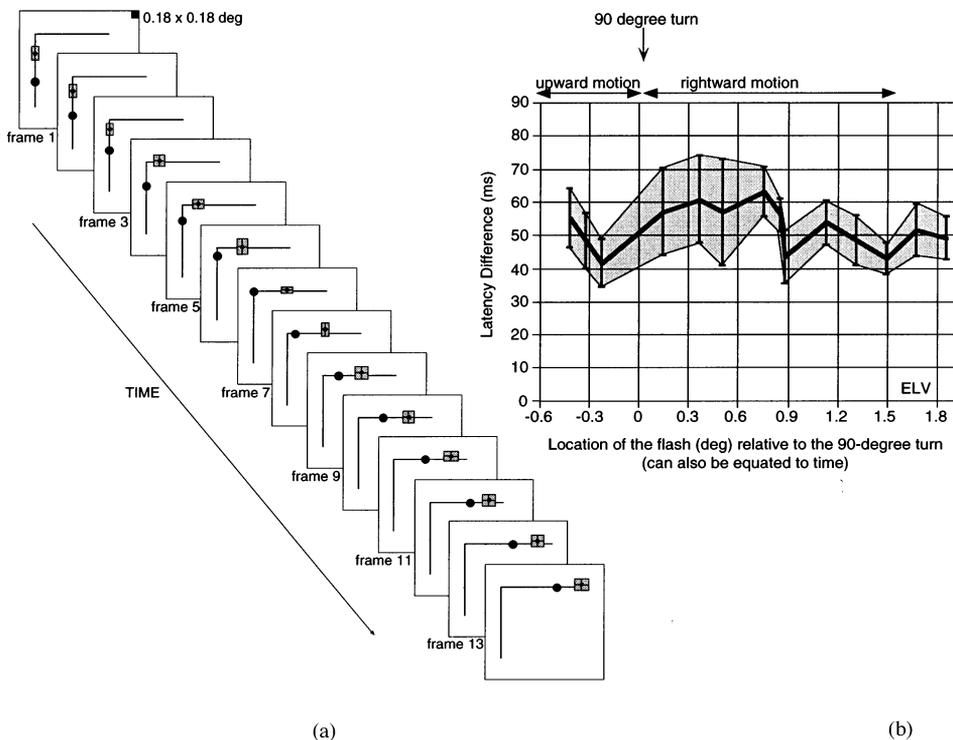


Fig. 5. (a) and (b) As Fig. 4 but for subject ELV.

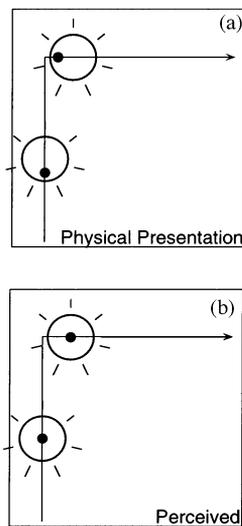


Fig. 6. Stimulus used in the second experiment. Methods were identical to those in the first experiment; only the stimulus was altered. A single bar (black disk) translated vertically, then turned 90° rightward or leftward. A circular ring was flashed for one video frame at a random point along the moving bar's trajectory. The two bars indicate that the flash could be presented during the bar's vertical or horizontal motion; only one bar was shown on each trial, however. Subjects were asked to judge the location of the flash relative to the bar.

3.2. Results

As with the first experiment, the flash alignment settings indicate where the flash is presented for it to appear aligned with the moving bar. These settings trace out the perceived trajectory of the bar, and estimate the amount of time that the flash must precede the bar at a particular location in order to appear aligned.

The differential latency between the flash and the bar is graphed in Fig. 7, as it was in Fig. 4b and Fig. 5b for experiment 1. The results are very similar to those of the first experiment. There is more noise in the data, however, which justifies the use of a three-dot vernier task in the first experiment. Although the speed of the moving disk was reduced in this experiment, the differential latency is similar to that in the first experiment; this is consistent with the velocity independence of the differential latency previously reported (Whitney et al., 2000). Unlike the first experiment, however, there is little or no transient dip in the differential latency around 40–60 ms after the direction change for subject DVW. Thus, it is possible that, in the first experiment, either the asymmetrical nature of the stimulus or the added luminance transients from faster motion caused the characteristic dip in the data.

Before concluding that there is constant facilitation around the direction change, however, it should be noted that there is a declining differential latency trend in the data: the average differential latency for subjects

DVW and ELV before the direction change was ~ 6 ms higher than that after the direction change. This dip is not dramatic, but is roughly consistent with the first experiment and raises the possibility that there is an anisotropic sensitivity to horizontal as opposed to vertical motion. If the subjects were more sensitive to vertical motion, we would expect a larger differential latency for vertical than horizontal motion, and a decreasing trend in the data in Fig. 4b, Fig. 5b, and Fig. 7. To address this possibility, a third experiment measured the differential latency for vertical and horizontal motion.

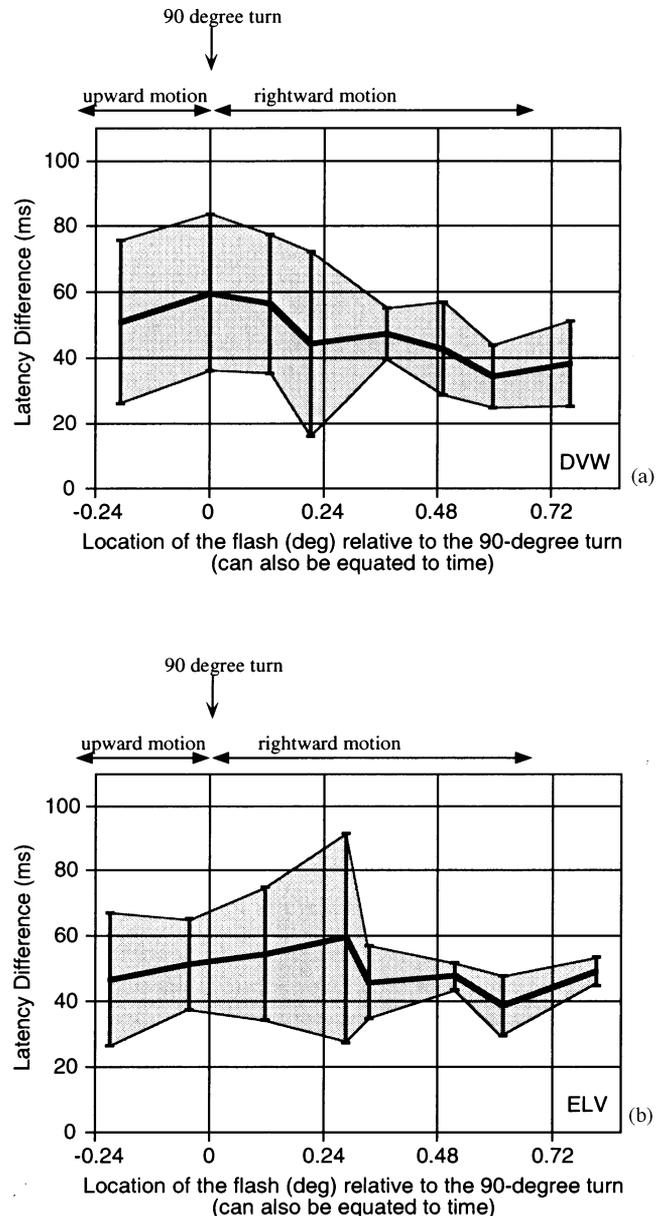


Fig. 7. Results of the second experiment. The differential latency is plotted as a function of the moving bar's position for subjects DVW and ELV, as in Fig. 4b and Fig. 5b. The graphs show the amount of time that the flash had to lead the bar at each of the flash's locations in order to appear aligned with the bar.

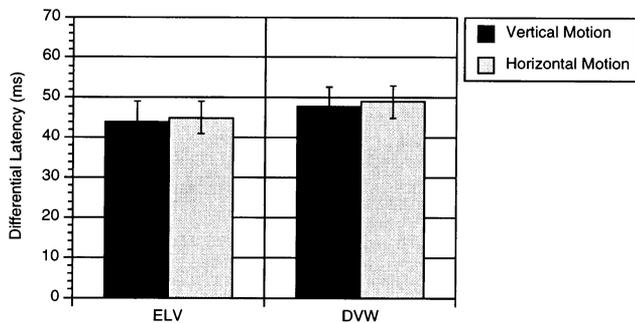


Fig. 8. Results of the third experiment. The differential latency for moving and flashed stimuli is plotted as a function of direction of motion. The graph indicates that there is not a significant difference between horizontal and vertical motion, suggesting that directional anisotropy in sensitivity is not responsible for the existence of a differential latency immediately after the 90° turn in the first and second experiments.

4. Experiment 3: horizontal versus vertical facilitation

4.1. Methods

The stimulus from the first experiment was also used here, except that no direction changes were employed and the moving bar (pair of aligned squares) moved only along vertical or horizontal trajectories.

Two subjects participated in the experiment (both of whom had participated in the first experiment). In each trial, two moving squares (bar) were randomly presented as either moving horizontally (left to right or right to left) or vertically (top to bottom or bottom to top). On the vertical motion trials, the squares were aligned horizontally, and on the horizontal motion trials, the squares were aligned vertically. The two squares were oriented vertically or horizontally to allow for more precise vernier discriminations (Beck & Schwartz, 1979). At a random point along the bar's trajectory, a flash was presented ahead of or behind the bar. The subjects were asked to judge whether the flash appeared spatially offset to the right or left if there was horizontal motion, and above or below if there was vertical motion.

4.2. Results

As the results in Fig. 8 show, the differential latency did not differ significantly between the conditions with only vertical motion or only horizontal motion (the most significant difference was for subject DVW: $t_{(20)} = 0.412$, $P > 0.05$). The differential latency measured in this experiment is consistent with that measured in the first experiment, and also with that reported in previous papers using similar stimuli (Whitney & Murakami, 1998; Whitney et al., 2000) This suggests that the slight drop in differential latency (~ 6 ms) after the direction

change is not an artifact of detectors that are differentially sensitive to the direction of motion.

5. General discussion

The first and second experiments showed that the differential latency for flashed and moving stimuli persists even during and after abrupt changes in direction. The fact that the flash-lag phenomenon was present at all points along the trajectory of motion, despite the abrupt change in direction, rules out such predictive mechanisms as spatial extrapolation (Nijhawan, 1994), and path-dependent motion facilitation.

An extrapolation mechanism is unable to account for the results because the motion was unpredictable. Since there were no predictive cues about the moving bar's trajectory, the extrapolation hypothesis requires that the perceived position of the bar continue to be extrapolated beyond the turning point. Yet, the perceived trajectory of the bar closely followed the actual trajectory (Fig. 4a and Fig. 5a), thereby reducing the likelihood of extrapolation's contribution to the flash-lag phenomenon.

The results also counter most models of path-dependent facilitation. If the latency advantage for moving stimuli followed a typical motion facilitation mechanism, such as those proposed for detection threshold where increasing the duration of the stimulus increases its detectability (Sekuler, Sekuler, & Sekuler, 1990), or spatial or temporal recruitment (Lappin & Bell, 1976; Nakayama & Silverman, 1984; Snowden & Braddick, 1989a,b; Watamaniuk, Sekuler, & Williams, 1989; Festa & Welch, 1997), one might expect that the facilitation observed in these experiments would fall off as a function of the angle between the initial and subsequent directions of motion (e.g. motion inertia or angular momentum; Anstis & Ramachandran, 1987). However, the results cannot be explained by such models of linear path facilitation because the reduced latency for moving stimuli is constant even during abrupt right-angle turns. This is somewhat surprising, for motion in the world is, by nature, locally continuous and often linear, at least over brief durations. The intuitive, path-dependent models already mentioned are based on this property.

The results do support a temporal facilitation mechanism (reduction in neural latency) that is insensitive to changes in the direction of motion. This type of omnidirectional facilitation is not commonly reported, but mechanisms could exist to serve such forms of unpredictable motion, either at the retinal level (Berry, Brivanlou, Jordan, & Meister, 1999) or even at higher stages of visual processing, where the continuity of moving stimuli would garner them an advantage that flashed stimuli do not have, i.e. although you do not

know where a moving stimulus will be, if it is undergoing continuous motion, the number of possible future locations are far fewer than for an unpredictable flash. Thus, omnidirectional facilitation may be as ecologically valid as the path-dependent forms of facilitation.

Although the third experiment demonstrated that there is no difference in sensitivity to horizontal and vertical motion, there could be a difference between vertical and horizontal motion with respect to the fixation point in the first two experiments. Previous studies have shown a greater sensitivity to motion toward than away from the fovea (Mateeff & Hohnsbein, 1988; Mateeff, Bohdanecky, Hohnsbein, Ehrenstein, & Yaki-moff, 1991; Mateeff et al., 1991). During the first vertical segment of the bar's trajectory, the bar moved roughly toward fixation, whereas immediately after the change in direction, there was an equal proportion of motion toward and away from fixation. This differential sensitivity could explain the slightly decreasing slope in the data shown in Fig. 4b, Fig. 5b, and Fig. 7, but it is consistent with the conclusion that there is maintained temporal facilitation at changes in direction.

5.1. Turning sharp corners

There are two questions about the abrupt change in direction used in the first two experiments. First, why was the three-dot stimulus used in the first experiment? Second, what caused the absence of spatio-temporal blurring of the sharp change in the direction of motion?

It is important to address the seemingly counterintuitive use of vertically aligned squares as the stimulus in the first experiment. When the squares move vertically, one trails behind the other, whereas when they are moving horizontally they are separated in space and never occupy the same location. This creates a kind of anisotropic stimulus that could have influenced the data.

There was a purpose for using such a stimulus, however. The two moving squares in the first experiment were vertically aligned so that it was easier to judge the flash's location when the squares were moving horizontally just after the 90° turn. When the flash was presented (or perceived) during this segment of the squares' motion, a three-dot vernier task was effectively created. Vernier acuity is significantly better for three-dot than two-dot configurations when the location of the center dot is manipulated (Beck & Schwartz, 1979; cf. Hadani, Meiri, & Guri, 1984). This should hold especially true for relatively high speeds, where traditional two-line vernier acuity degrades (Westheimer & McKee, 1975; Welch & McKee, 1985). Therefore, since we were primarily interested in the differential latency just at, or after, the change in direction, we chose to use a stimulus that would reduce error during the horizontal segment of the squares' motion.

A related question is why there is no blurring or rounding of the perceived trajectory of motion near the 90° turn. The flash alignment settings indicate the perceived trajectory of motion, and yet, if there were spatio-temporal filtering of the moving bar's trajectory (Whitney & Murakami, 1998; Whitney et al., 2000), one would expect this to be reflected in the flash alignment settings. It turns out that the stimulus configuration employed in the first experiment intentionally contributes to the lack of rounding near the turn. As Figs. 4 and 5 show, there is less error in the data in the first experiment than in the second, which used a different stimulus (Fig. 7). So, creating a three-dot vernier task seems to have improved the perception of the flash's position near the bar's turning point.

The perception of a sharp change in direction in the first experiment (Fig. 4a and Fig. 5a) also challenges a possible explanation for the relatively constant differential latency around the direction change. Spatio-temporal averaging of the moving bar's trajectory could have caused a smoothing of the differential latency and, in turn, the absence of any significant dip in the differential latency in Fig. 4b, Fig. 5b, and Fig. 7. For example, in the 'postdiction' model (Eagleman & Sejnowski, 2000), the moving bar's positions are integrated only after the flash, which naturally gives rise to a perceived position for the bar that is ahead of the flash. Another possibility is a slow averaging (~600 ms) of the moving bar and a persistent representation of the flash, which could lead to a difference in the perceived positions of the two stimuli (Lappe & Krekelberg, 1998; Krekelberg & Lappe, 1999, 2000). In both cases, integrating over the moving bar's trajectory should cause it to appear as if it were turning a rounded corner, rather than a sharp one. This was not the case, as the perceived bar trajectories in Fig. 4a and Fig. 5a show.

5.2. Previous research

Relatively few studies have investigated the effect of an abrupt change in direction on the detectability of a moving stimulus. Some studies have used reaction time (Sekuler et al. 1990; Sekuler & Sekuler, 1993), and others have used threshold duration for detection (Hohnsbein & Mateeff, 1998). Comparisons with these studies should be made with caution, however, because detection of a change in a moving stimulus does not necessarily imply detection of the position (or even direction) of the moving target (Levinson & Sekuler, 1975; cf. Watson, Thompson, Murphy, & Nachmias, 1980). However, aspects of previous research do merit discussion in the context of the present experiments.

For example, Sekuler et al. (1990) have used abrupt direction changes to measure the effect of predictability on the reaction time (RT) to motion onsets and direction changes. In their experiments, a small disc trans-

lated in a predictable or unpredictable direction and then abruptly changed direction by varying degrees to a predictable or unpredictable trajectory. Although their studies are different in that only a change in a moving target (rather than its position) needed to be detected in order to respond, the manipulations of predictability in their studies are also an inherent issue in the current study.

According to Sekuler et al. (1990), the predictability of a direction change improves its detectability (cf. Sekuler & Ball, 1977; Ball & Sekuler, 1980). They found that, even with a predictable initial trajectory, if the subsequent direction of motion was unpredictable, there was a significant increase in RT. This seems to contradict our result if RT is also taken as a measure of visual latency. Although in a strict sense the direction change was unpredictable in the current study, in that the moving bar could turn rightward or leftward, the number of possible directions were far fewer than in the studies by Sekuler et al. (1990). Indeed, as these authors point out when comparing their study with that of Watson et al. (1980), there is less uncertainty with fewer possibilities, and this could lead to less increase in RT. In addition, Sekuler et al. found that RT to an unpredictable change in direction decreased with increasing initial stimulus duration. Since the initial duration of the moving bar in the present experiment was relatively long (particularly in the second experiment), the effect of predictability was reduced.

A possible explanation for the increase in RT in the direction change experiments of Sekuler et al. (1990) is that there are attentional shifts in the presence of stimulus changes (cf. Baldo & Klein, 1995; Aschersleben & Müsseler, 1999). According to such a hypothesis, there would be a delay in the processing of the moving bar just after an unpredictable, abrupt direction change. This is comparable with the phenomenon that occurs when smoothly pursuing an object that is moving unpredictably; it is impossible to make predictive eye movements, which results in erroneous tracking that necessitates corrective saccades. If there were attentional shifts, we would expect not only an increase in RT, but a commensurate decrease in the differential latency. This was not observed in the first experiment, however, which suggests that, although attentional shifts were probably present, they did not dramatically affect the processing of the moving bar. On the other hand, the dip in the differential latency already noted in the first experiment could potentially be a result of such attentional shifts.

Another series of related studies involves a proposed model for the detection of changes in speed (Dzhafarov, Sekuler, & Allik, 1993). According to these authors, there is evidence that the detection of a change in velocity is carried out by a 'subtractive normalization' process, whereby a change in velocity from V_0 to V_1 is

actually equal to an onset of motion with a speed of $V_1 - V_0$. This is an interesting idea and has been applied not only to changes in velocity, but also to changes in direction (Dzhafarov et al., 1993; Hohnsbein & Mateeff, 1998; Mateeff, Genova, & Hohnsbein, 1999).

Could the results of the first experiment reported in this paper be due to a mechanism that detects the change in direction of motion as an onset of motion? This would imply that there is both a motion termination (vertical motion stops) as well as a motion initiation (horizontal motion starts). Although the results of Dzhafarov et al. (1993) and Hohnsbein and Mateeff (1998) are not directly comparable with the present study because the methodologies differ, other workers have conducted experiments on the effect of motion initiation on the apparent location of an adjacent flash (Nijhawan, 1992; Khurana & Nijhawan, 1995; Eagleman & Sejnowski, 2000), and concluded that when a flash is presented simultaneous with a motion onset, the flash appears to spatially lag behind the moving stimulus. The mechanisms responsible for the illusory flash lag at a motion initiation have been long debated, and could include a variation in the neural delay at motion initiation due to attentional shifts (Müsseler & Neumann, 1992; Müsseler & Aschersleben, 1998; Aschersleben & Müsseler, 1999), a predictive neural response at the instant of motion onset, a low level contrast gain mechanism (Berry et al., 1999), or a cognitive judgment bias in the direction of motion (Fröhlich, 1929; Roufs, 1974). Regardless of the mechanism involved in the motion initiation illusion (Fröhlich effect), the fact that the apparent initial location of a moving stimulus is biased in the direction of motion is consistent with the facilitation observed just after the change in the bar's direction in the present study.

This does not imply that a direction change is equivalent to a motion initiation, however. If this were the case, then the end of the vertical motion segment in the first and second experiments should have been taken as a motion termination; and a flash that is presented adjacent to the termination of a moving stimulus does not appear to lag behind the moving stimulus (Eagleman & Sejnowski, 2000; Whitney et al., 2000). Yet, in the first experiment, a flash-lag effect was perceived at every point around the direction change. So, although the results of the direction change experiment resemble those predicted by a subtractive normalization mechanism or a simple addition of motion termination and initiation responses, there is not enough evidence to support such a model in these experiments.

5.3. Neural mechanisms

Recently, physiological findings have suggested that there is a contrast gain mechanism in the retina that

effectively allows for the ‘anticipation of moving stimuli’ (Berry et al., 1999). This mechanism is thought to produce or contribute to the general flash-lag phenomenon because ganglion cells in rabbit and salamander retinæ have peak responses when moving stimuli first cross their receptive fields. In other words, neural activity is shifted forward in the direction of motion. It is not clear, however, how this mechanism would function in the presence of an abrupt change in direction.

Although anticipatory ganglion cell responses may contribute to the flash-lag phenomenon in some situations, they cannot give rise to flash-lag effects that do not involve retinal motion (Schlag, Cai, Dorfman, Mohempour, & Schlag-Rey, 2000; Sheth, Nijhawan & Shimojo, 2000); likewise, all other mechanisms based on retinal motion must be ruled out. The omnidirectional facilitation that we report, however, does not depend on retinal motion. Motion can be recovered from pursued objects that are stationary on the retina (Newsome, Wurtz, & Komatsu, 1988; Komatsu & Wurtz, 1988), and differential latencies could arise at these higher stages (e.g. speeded MT responses).

In fact, there is evidence that neural latencies are relatively short for moving stimuli. For example, the latency of the population receptive field response is shorter for moving than for stationary flashed stimuli (Jancke, Erlhagen, Schöner, & Dinse, 1997), reaction times to apparently moving stimuli are faster than those to flashing stimuli (Allik & Kreegipuu, 1998), and the latency of area MT’s response to rapidly moving stimuli is faster than the response of area V1 (Ffytche, Guy, & Zeki, 1995).

According to many authors, peak sensitivity to direction change occurs between 4 and 64° s⁻¹ (Ball & Sekuler, 1982; Orban, de Wolfe, & Maes, 1984; Pasternak & Merigan, 1984; Ball & Sekuler, 1987; DeBruyn & Orban, 1988). The velocity of the moving bar in the present experiments was well within this range, raising questions about whether the latency facilitation would occur in the presence of abrupt direction changes when velocity is outside peak sensitivity. If the latency advantage for moving stimuli depends on velocity in the same way that direction discrimination, similar mechanisms might subservise both direction discrimination and localization of position. In other words, if direction discrimination is necessary for the detection of a moving stimulus’ position, then sensitivity to direction might influence the temporal facilitation mechanism proposed in this study.

6. Conclusions

The experiments reported in this paper support previous findings that there is a temporal facilitation for moving stimuli in the form of reduced neural processing

delays. Common forms of motion facilitation are based on the statistical property that, within a short enough time window, a moving object will continue along its established trajectory. Contrary to these intuitive and well-supported forms of linear trajectory facilitation, the latency advantage for moving stimuli that we report is independent of changes in the direction of motion.

Acknowledgements

This work was supported by AFSOR 970407 and JSPS Research Fellowships for Young Scientists.

References

- Allik, J., & Kreegipuu, K. (1998). Multiple visual latency. *Psychological Science*, *9*, 135–138.
- Anstis, S., & Ramachandran, V. S. (1987). Visual inertia in apparent motion. *Vision Research*, *27*, 755–764.
- Aschersleben, G., & Müsseler, J. (1999). Dissociations in the timing of stationary and moving stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 1709–1720.
- Baldo, N., & Klein, S. (1995). Extrapolation or attention shift? *Nature*, *378*, 565.
- Ball, K., & Sekuler, R. (1980). Models of stimulus uncertainty in motion perception. *Psychological Review*, *87*, 435–469.
- Ball, K., & Sekuler, R. (1982). A specific and enduring improvement in visual motion discrimination. *Science*, *218*, 697–698.
- Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research*, *27*, 953–965.
- Beck, J., & Schwartz, T. (1979). Vernier acuity with dot test objects. *Vision Research*, *19*, 313–319.
- Berry, M. J. I. I., Brivanlou, I. H., Jordan, T., & Meister, M. (1999). Anticipation of moving stimuli by the retina. *Nature*, *398*, 334–338.
- Brenner, E., & Smeets, J. B. J. (2000). Motion extrapolation is not responsible for the flash-lag effect. *Vision Research*, *40*, 1645–1648.
- DeBruyn, B., & Orban, G. A. (1988). Human velocity and direction discrimination measured with random dot patterns. *Vision Research*, *28*, 1323–1335.
- Dzhafarov, E. N., Sekuler, R., & Allik, J. (1993). Detection of changes in speed and direction of motion: reaction time analysis. *Perception & Psychophysics*, *53*, 733–750.
- Eagleman, D. M., & Sejnowski, T. J. (2000). Motion integration and postdiction in visual awareness. *Science*, *287*, 2036–2038.
- Festa, E. K., & Welch, L. (1997). Recruitment mechanisms in speed and fine-direction discrimination tasks. *Vision Research*, *37*, 3129–3143.
- Ffytche, D. H., Guy, C. N., & Zeki, S. (1995). The parallel visual motion inputs into areas V1 and V5 of human cerebral cortex. *Brain*, *118*, 1375–1394.
- Fröhlich, F. W. (1929). *Die empfindungszeit*. Jena: Verlag von Gustav Fischer.
- Grzywacz, N. M., & Amthor, F. R. (1993). Facilitation in ON–OFF directionally selective ganglion cells of the rabbit retina. *Journal of Neurophysiology*, *69*, 2188–2199.
- Hadani, I., Meiri, A., & Guri, M. (1984). The effects of exposure duration and luminance on the 3-dot hyperacuity task. *Vision Research*, *8*, 871–874.

- Hogben, J. H., & Di Lollo, V. (1974). Perceptual integration and perceptual segregation of brief visual stimuli. *Vision Research*, *14*, 1059–1069.
- Hohnsbein, J., & Mateeff, S. (1998). The time it takes to detect changes in speed and direction of visual motion. *Vision Research*, *38*, 2569–2573.
- Jancke, D., Erlhagen, W., Schöner, G., & Dinse, H. R. (1997). Population receptive fields (PRFs) derived from moving stimuli recorded in cat visual cortex show reduced latencies compared to the stationary condition. *Society for Neuroscience*, *23*, 456.
- Khurana, B., & Nijhawan, R. (1995). Extrapolation or attention shift? *Nature*, *378*, 566.
- Komatsu, H., & Wurtz, R. H. (1988). Relation of cortical areas MT and MST to pursuit eye movement. I. Localization and visual properties of neurons. *Journal of Neurophysiology*, *60*, 580–603.
- Krekelberg, B., & Lappe, M. (1999). Temporal recruitment along the trajectory of moving objects and the perception of position. *Vision Research*, *39*, 2669–2679.
- Krekelberg, B., & Lappe, M. (2000). A model of the perceived relative positions of moving objects based upon a slow averaging process. *Vision Research*, *40*, 201–215.
- Lappe, M., & Krekelberg, B. (1998). The position of moving objects. *Perception*, *27*, 1437–1449.
- Lappin, J. S., & Bell, H. H. (1976). The detection of coherence in moving random-dot patterns. *Vision Research*, *16*, 161–168.
- Levinson, E., & Sekuler, R. (1975). The independence of channels in human vision selective for direction of movement. *Journal of Physiology*, *250*, 347–366.
- MacKay, D. M. (1958). Perceptual stability of a stroboscopically lit visual field containing self-luminous objects. *Nature*, *181*, 507–508.
- Mateeff, S., & Hohnsbein, J. (1988). Perceptual latencies are shorter for motion towards the fovea than for motion away. *Vision Research*, *28*, 711–719.
- Mateeff, S., Bohdanecy, Z., Hohnsbein, J., Ehrenstein, W., & Yakimoff, N. (1991). A constant latency difference determines directional anisotropy in visual motion perception. *Vision Research*, *31*, 2235–2237.
- Mateeff, S., Genova, B., & Hohnsbein, J. (1999). The simple reaction time to changes in direction of visual motion. *Experimental Brain Research*, *124*, 391–394.
- Mateeff, S., Yakimoff, N., Hohnsbein, J., Ehrenstein, W., Bohdanecy, Z., & Radil, T. (1991). Selective directional sensitivity in visual motion perception. *Vision Research*, *31*, 131–138.
- Metzger, W. (1932). Versuch einer gemeinsamen theorie der phänomene fröhlich und hazelhoff's und kritik ihrer verfahren zur messung der empfindungszeit. *Psychologische Forschung*, *16*, 176–200.
- Müsseler, J., & Aschersleben, G. (1998). Localizing the first position of a moving stimulus: the Fröhlich effect and an attention-shifting explanation. *Perception & Psychophysics*, *60*, 683–695.
- Müsseler, J., & Neumann, O. (1992). Apparent distance reduction with moving stimuli (Tandem Effect): evidence for an attention-shifting model. *Psychological Research*, *54*, 246–266.
- Nakayama, K., & Silverman, G. (1984). Temporal and spatial characteristics of the upper displacement limit for motion in random dots. *Vision Research*, *24*, 293–300.
- Newsome, W. T., Wurtz, R. H., & Komatsu, H. (1988). Relation of cortical areas MT and MST to pursuit eye movement. II. Differentiation of retinal from extraretinal inputs. *Journal of Neurophysiology*, *60*, 604–620.
- Nijhawan, R. (1992). Misalignment of contours through the interaction of apparent and real motion systems. *Investigative Ophthalmology and Visual Science*, *33*(suppl), 974.
- Nijhawan, R. (1994). Motion extrapolation in catching. *Nature*, *370*, 256–257.
- Nijhawan, R. (1997). Visual decomposition of colour through motion extrapolation. *Nature*, *386*, 66–69.
- Orban, G. A., de Wolfe, J., & Maes, H. (1984). Factors influencing velocity coding in the human visual field. *Vision Research*, *24*, 33–39.
- Pasternak, T., & Merigan, W. (1984). Effects of stimulus speed on direction discriminations. *Vision Research*, *24*, 1349–1355.
- Purushothaman, G., Patel, S. S., Bedell, H. E., & Ogmen, H. (1998). Moving ahead through differential visual latency. *Nature*, *396*, 424.
- Roufs, J. A. (1974). Dynamic properties of vision — V. *Vision Research*, *14*, 853–869.
- Schlag, J., Cai, R., Dorfman, A., Mohempour, A., & Schlag-Rey, M. (2000). Extrapolating movement without retinal motion. *Nature*, *403*, 38–39.
- Sekuler, R., & Ball, K. (1977). Mental set alters visibility of moving targets. *Science*, *198*, 60–62.
- Sekuler, A. B., & Sekuler, R. (1993). Representational development of direction in motion perception: a fragile process. *Perception*, *22*, 899–915.
- Sekuler, A. B., Sekuler, R., & Sekuler, E. B. (1990). How the visual system detects changes in the direction of moving targets. *Perception*, *19*, 181–195.
- Sheth, B. R., Nijhawan, R., & Shimojo, S. (2000). Changing objects lead briefly flashed ones. *Nature Neuroscience*, *3*, 489–495.
- Snowden, R. J., & Braddick, O. J. (1989a). The combination of motion signals over time. *Vision Research*, *29*, 1621–1630.
- Snowden, R. J., & Braddick, O. J. (1989b). Extension of displacement limits in multiple-exposure sequences of apparent motion. *Vision Research*, *29*, 1777–1787.
- Watamaniuk, S. (1992). Visible persistence is reduced by fixed-trajectory motion but not by random motion. *Perception*, *21*, 791–802.
- Watamaniuk, S. N. J., Sekuler, R., & Williams, D. W. (1989). Direction perception in complex dynamic displays: the integration of direction information. *Vision Research*, *29*, 47–59.
- Watson, A. B., Thompson, P. G., Murphy, B. J., & Nachmias, J. (1980). Summation and discrimination of gratings moving in opposite directions. *Vision Research*, *20*, 341–347.
- Welch, L., & McKee, S. (1985). Colliding targets: evidence for spatial localization within the motion system. *Vision Research*, *25*, 1901–1910.
- Westheimer, G., & McKee, S. (1975). Visual acuity in the presence of retinal image motion. *Journal of the Optical Society of America*, *65*, 847–850.
- Whitney, D., & Murakami, I. (1998). Latency difference, not spatial extrapolation. *Nature Neuroscience*, *1*, 656–657.
- Whitney, D., Murakami, I., & Cavanagh, P. (2000). Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flashed stimuli. *Vision Research*, *40*, 137–149.