Reducing magnocellular processing of various motion trajectories tests single process theories of visual position perception

Mark Chappell Applied Cognitive Neuroscience Research Unit, Griffith Health Institute, and School of Applied Psychology, Griffith University, Brisbane, Australia

Zach Potter Applied Cognitive Neuroscience Research Unit, Griffith Health Institute, and School of Applied Psychology, Griffith University, Brisbane, Australia

Trevor J. Hine Applied Cognitive Neuroscience Research Unit, Griffith Health Institute, and School of Applied Psychology, Griffith University, Brisbane, Australia

Kathy T. Mullen McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Canada

James Shand Applied Cognitive Neuroscience Research Unit, Griffith Health Institute, and School of Applied Psychology, Griffith University, Brisbane, Australia

Spatial projection and temporal integration are two prominent theories of visual localization for moving stimuli which gain most of their explanatory power from a single process. Spatial projection theories posit that a moving stimulus' perceived position is projected forwards in order to compensate for processing delays (Eagleman & Sejnowski, 2007; Nijhawan, 2008). Temporal integration theories (Krekelberg & Lappe, 2000) suggest that an averaging over positions occupied by the moving stimulus for a period of time is the dominant process underlying perception of position. We found that when magnocellular (M) pathway processing was reduced, there were opposite effects on localization judgments when a smooth, continuous trajectory was used, compared to when the moving object suddenly appeared, or suddenly reversed direction. The flash-lag illusion was decreased for the continuous trajectory, but increased for the onset and reversal trajectories. This cross-over interaction necessitates processes additional to those proposed by either the spatial projection or temporal integration theories in order to explain the perception of the position of moving stimuli across all our conditions. Differentiating our onset trajectory conditions from a Fröhlich illusion, in a second experiment, we found a null Fröhlich illusion under normal luminance-defined conditions, significantly smaller than the corresponding flash-lag illusion, but significantly increased when M processing was reduced. Our data are most readily accounted for by Kirschfeld and Kammer's (1999) backward-inhibition and focal attention theory.

Introduction

Agreement has not been reached as to how the human visual system localizes moving stimuli (e.g., Eagleman & Sejnowski, 2007; Nijhawan, 2008). We here test the generality of a number of proposed theories of visual localization by manipulating both the amount of magnocellular (M) pathway (Lee, Martin, & Valberg, 1989; Livingstone & Hubel, 1987) processing the stimulus induces and the type of trajectory the moving stimulus follows. Localization performance was tested using the *flash-lag illusion* (Nijhawan, 1994)

Citation: Chappell, M., Potter, Z., Hine, T. J., Mullen, K. T., & Shand, J. (2013). Reducing magnocellular processing of various motion trajectories tests single process theories of visual position perception. *Journal of Vision, 13*(10):16, 1–12, http://www.journalofvision.org/content/13/10/16, doi:10.1167/13.10.16.

doi: 10.1167/13.10.16 Received August 28, 2012; published August 28, 2013 ISSN 1534-7362 © 2013 ARVO

whereby a flashed stimulus presented adjacent to a moving stimulus is perceived to be behind it. Before describing our studies, we briefly review two versions of the spatial projection theory and a temporal integration theory of visual localization, as well as the motion trajectories that have been used to test them (for reviews see Krekelberg & Lappe, 2001; Nijhawan, 2008; Whitney, 2002).

Trajectories, theories, and the magnocellular visual pathway

The three trajectories that have been utilized to test theories of visual localization are the continuous trajectory, which is smooth and continuous around the time the position judgment is made; the onset trajectory, in which the moving stimulus suddenly appears as the flash appears; and the reversal trajectory, in which the moving stimulus suddenly reverses direction along the same path and the position judgment is made at or about the reversal point (e.g., Chappell, Hine, Acworth, & Hardwick, 2006; Eagleman & Sejnowski, 2000; Shen, Zhou, Gao, Liang, & Shui, 2007; Whitney, Murakami, & Cavanagh, 2000). Comparing across trajectories, the flash-lag illusion with onset trajectory has generally been found to be of similar magnitude to that with a continuous trajectory (Eagleman & Sejnowski, 2000; Gauch & Kerzel, 2008), or slightly, but significantly, larger (Chappell et al., 2006; Müsseler, Stork, & Kerzel, 2002; Öğmen, Patel, Bedell, & Camuz, 2004). Patel, Öğmen, Bedell, and Sampath (2000), however, found a much bigger difference using a bright flash and a dim moving stimulus. They reported a significant flash-lag illusion for the onset trajectory and a null illusion with the continuous trajectory. In contrast, Linares, Lopez-Moliner, and Johnston (2007) have reported conditions where the illusion with onset trajectory was significantly smaller.

Eagleman and Sejnowski (2000) also found the illusion with reversal trajectory to have the same magnitude as the others, whereas Chappell et al. (2006) found it to be similar to that with a continuous trajectory, but smaller than that with an onset trajectory. The illusion with the reversal trajectory is found to be in the final direction of motion, so that perception undershoots the reversal point, rather than overshooting it. Taken together, these results constrain localization theories, and we turn to these now.

Nijhawan (1994, 2008) proposed that a spatial projection process might effectively move the perceived position of a moving stimulus forwards along its trajectory, partially compensating for the neural delays which would otherwise entail our perception being up to 100 ms "out of date." Khurana and Nijhawan (1995) and Nijhawan (2008) surmised that the M pathway might underlie this spatial projection process. Nijhawan (1994, 2008) maintains that the spatial projection process is based on the moving stimulus' trajectory before the flash is displayed, but this seems to be at odds with the findings reported above whereby the onset trajectory flash-lag illusion is found to be undiminished, or even larger, compared to that found with a continuous trajectory. Also, one might expect that Nijhawan's spatial projection process would lead to the perception of an overshoot with the reversal trajectory whereas the opposite—an undershoot—is found. This problem is avoided in Eagleman and Sejnowski's (2007) spatial projection theory, in which the projection is determined only by motion after the flash. Nijhawan (2008) (see also Maus, Khurana, & Nijhawan, 2010) has responded by claiming that spatial projection processes may be very fast and can initiate the spatial projection within as little as 2 ms, thus potentially providing a projected position for the moving stimulus quickly enough to account for the onset trajectory illusions.

A standard method for reducing or eliminating M pathway processing is to make the stimulus purely chromatic and equiluminant with its background (Lee et al., 1989; Livingstone & Hubel, 1987). Any risk of luminance artifacts in the stimulus may be further diminished by immersing the moving stimuli in luminance noise (Baker, Boulton, & Mullen, 1998; Chappell & Mullen, 2010; Mullen, Yoshizawa, & Baker, 2003). Figure 1 illustrates how the moving stimulus appeared in our experiments. Chappell and Mullen (2010) used only a continuous trajectory and compared localizations for moving stimuli defined by luminance contrast with those equiluminant-in-noise. When the flash was luminance defined, they found that the flash-lag illusion was on average eliminated for the equiluminant moving stimulus in luminance noise and, in fact, for 6 out of 11 subjects it became a significant flash-lead illusion. This finding is consistent with the spatial projection theories, especially if the projection is mediated by the M pathway (Khurana & Nijhawan, 1995; see also Nijhawan, 2008).

Nijhawan (2008) has claimed that the same mechanisms are responsible for the illusions perceived with continuous and onset trajectories, and Eagleman and Sejnowski (2007) take the equality of illusion magnitudes across these trajectories as an important result, suggesting the same process is responsible for both. If their single process theories are to account for our contrast manipulation, then they must predict that when contrast is reduced, illusion magnitudes will be reduced for the onset trajectory to the same extent as they are for the continuous trajectory. Likewise, if their theories account for the illusion with a reversal trajectory with the same process, they must also predict a reduction in its magnitude. To preview, we found this

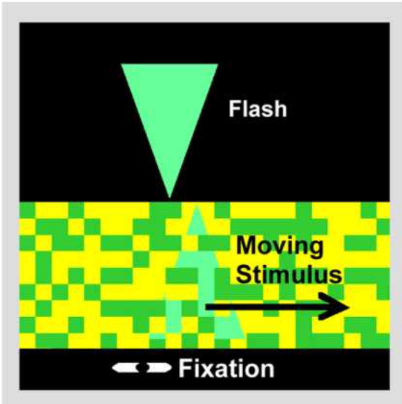

Figure 1. Stimuli for an equiluminance-in-luminance noise condition. The moving stimulus is the lighter green triangle in the lower half of the figure—with noise being displayed on frames alternate to those on which the triangle is displayed, it does appear somewhat as depicted. The flash appeared above it when the moving stimulus was close to the Fixation.

not to be the case when we reduced contrast by using equiluminant stimuli in noise. We wish to make it clear, though, that we are not questioning whether a spatial projection process may contribute to localization, but whether the onset and reversal trajectories are appropriate for revealing the most important processes contributing to localization of a smoothly moving stimulus.

No strong claims have been made that the temporal integration theory (Krekelberg & Lappe, 1999, 2000; Lappe & Krekelberg, 1998) can account for all trajectory results, although Krekelberg and Lappe (2001) seemed to suggest it might. Temporal integration models the flash-lag illusion by assuming that the perceived relative spatial offset between the flash and the moving stimulus is based on an integration of the difference of their spatial positions over a window of integration of some duration. Since a relative position computation cannot begin until the flash has appeared, any window must yield a perceived position for the moving stimulus ahead of that of the flash. Assuming that the computation begins with the flash's appearance for all three trajectories, the theory predicts illusions of the same size for the three trajectories without further assumptions.

The temporal integration model assumes the computation is terminated when information about the flash's position (which is kept activated after the flash has physically disappeared) becomes unavailable (Krekelberg, 2001). In Chappell and Mullen (2010), this termination time should be the same for moving stimulus conditions with the same flash parameters. However, for their moving equiluminant-in-noise stimulus, it is reasonable to assume that position information reaches the site where integration is occurring with a longer latency than it would for a luminance-defined stimulus (Barbur, Wolf, & Lennie, 1998; Beaudot & Mullen, 2001; Bowen, 1981). This latency difference means that when integration terminates, less "advanced" position information will be included in the integration for the equiluminant-in-noise moving stimulus than for the luminance-defined stimulus and a smaller illusion will be predicted. The same logic also predicts a smaller illusion for the onset and reversal trajectories when the moving stimulus is equiluminant-in-noise.

In summary, all of the theories described above, if used to predict the illusion magnitudes in our experiment based on a single process, must predict that any stimulus manipulation, including equiluminance-in-noise, would reduce the illusion magnitude equally for continuous, onset, and reversal trajectories. However, the claims for the spatial projection theories are based on studies using only luminance-modulated stimuli, and the theorists seem to have taken into account only studies that found similar magnitudes of illusions across these trajectories. As noted above, however, significant differences have frequently been reported. Following from these findings, it is reasonable to propose that additional processes may be involved for an onset trajectory (Chappell et al., 2006; Öğmen et al., 2004), and if so we would *not* expect similar effects of reducing the contrast across the three trajectories.

Our studies

In the current study, we sought to measure the effects with onset, reversal, and continuous trajectories, the latter replicating Chappell and Mullen's (2010) findings. In Experiment 1, we employed moving luminance-defined stimuli and moving equiluminant-in-noise stimuli and measured the subject's localization performance via the flash-lag illusion, using these three trajectories, in order to extend empirical findings on localization and test relevant theories. Slightly different effects of the contrast manipulation across the trajectories would allow an interpretation whereby one process dominated localization for all trajectories and contrasts, but was somewhat moderated by a secondary process. Dramatically different effects would argue for different processes dominating localization for the different conditions. The latter was the case, and we describe additional candidate processes in the General discussion to account for our results.

When the point of appearance of a suddenly appearing moving object is compared to that of a persisting stationary "landmark," the beginning part of the trajectory is often found to be invisible (see review in Experiment 2, Discussion), an effect known as the Fröhlich illusion (Kirschfeld & Kammer, 1999). We also measured this illusion in trials interleaved with onset trajectory flash-lag trials, in order to control for the possibility that, in the onset trajectory condition with equiluminant-in-noise stimuli in Experiment 1, we were actually measuring a Fröhlich illusion rather than a flash-lag illusion (see Experiment 1, Discussion). As well if the same process underlies the Fröhlich illusion as underlies the flash-lag illusion, as claimed by Eagleman and Sejnowski (2007), then it should also be reduced by the equiluminance-in-noise manipulation, following the same arguments as those above for the flash-lag illusion. Indeed the corresponding arguments for the other theories also predict a reduction. Thus in addition to being a control, Experiment 2 also provided further important constraints on theories of visual localization. We consider the implications of both experiments in the General discussion.

Experiment 1: Effect of equiluminance-in-noise on localization with various trajectories

Method

Subjects

Data for twelve naïve subjects with ages between 18 and 30 ($M = 22.75$, $SD = 3.17$) are reported. One additional subject was excluded due to an inability to perform the task reliably. All had normal or corrected acuity and color (Ishihara Test) vision. The project was approved by the Griffith University Human Research Ethics Committee and adhered to the tenets of the Helsinki Declaration.

Stimuli and procedure

Stimuli were displayed on a 21” color gamma corrected monitor (640 × 479 pixel at 160 Hz), positioned 103 cm from the subjects’ eyes. A green color, with a luminance that was functionally equiluminant to a neutral yellow background (~54 cd/m^2, Minolta CS-100A chromameter, 1° measurement angle), was found for each subject using the method of minimum motion (Anstis & Cavanagh, 1983). For the moving stimulus, a triangle (1.2° × 1.5°, top vertex 1.75° above fixation) of this green was presented on either a yellow or a black (~1 cd/m^2) background strip, on every second frame of presentation. The triangle remained at each position for three presentations (and thus over five frames), with the distance between positions yielding a speed of 16°/s, and the direction for the trial being randomly chosen, either leftwards or rightwards. For continuous and reversal trajectory trials there was sufficient time before the flash for the moving stimulus to emerge from the edge of the screen. A comparable time elapsed for onset trajectory trials before the flash and moving stimulus appeared.

For the equiluminant stimuli presented in luminance noise, the stimulus presentations alternated with frames on which a horizontal strip of small green (~31 cd/m^2) and yellow (~76 cd/m^2) squares (.13° × .13°) was displayed, with the color for each square being chosen randomly for each frame. The noise strip extended 0.25° beyond the vertical extremes of the moving stimulus. If P1 represents the moving stimulus being presented at its first position, P2 a presentation at the next position, etc., and N represents a display of just a noise strip, then this condition may be represented N-P1-N-P1-N-P1-N-P2-N-P2-N-P2-N, etc. When no noise was present, the intervening frame was uniformly black (B), so, B-P1-B-P1-B-P1-B-P2-B-P2-B-P2-B, etc.

The flash was always green on a black background, and it also appeared for three presentations, alternating with a uniform black frame (total ~ 31 ms). It was positioned in a 1° horizontal window centered above fixation, its horizontal position within this window being determined randomly from a uniform distribution on each trial. Vertically, the tips of the two stimuli were 0.5° apart (see Figure 1). Its dimensions were the same as those of the moving stimulus but the shape was inverted.

Trials were blocked by trajectory type, with the conditions described here interleaved with two other control contrast conditions not reported here. Subsequent to testing, these control conditions were found to be affected by a programming error and the data were discarded. There is no reason to believe the presence of these discarded control conditions in any way altered the results reported here. The horizontal offset between the moving stimulus and the flash was systematically varied, in order to construct a psychophysical function. The flash’s position was determined first, as above. For the onset and reversal trajectories, the offset was relative to the point of appearance or reversal of the moving stimulus. In all cases, the subject’s task was to indicate if the flash was to the left or right of the moving stimulus. An initial generic set of offsets were used for all subjects, but as testing proceeded, an adaptive method of constant stimuli tuned these offsets for each condition/subject so as to measure each illusion magnitude as efficiently as possible, the latter being computed via logistic regression.

Results

Figure 2 displays our average data. Overall, the interaction between trajectory and contrast was significant, $F(2, 22) = 59.91$, $p = 1.3 \times 10^{-9}$, $\eta_p{}^2 = .85$. Considering just the continuous and onset trajectories,

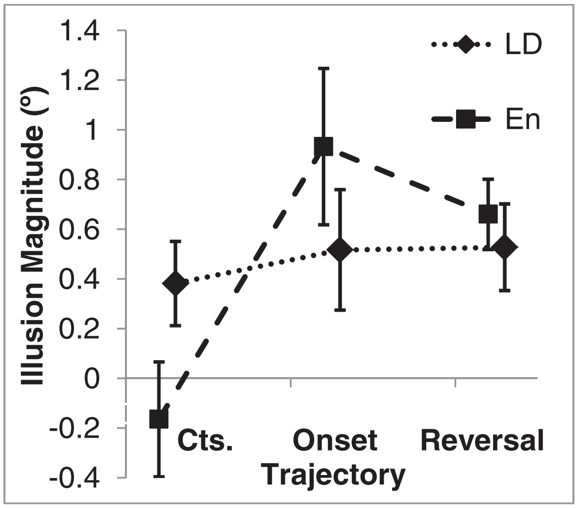

Figure 2. Flash lag illusion magnitude in degrees plotted for three different types of trajectory: Continuous (Cts.), onset, and reversal. Average data for 12 subjects. LD = stimuli were luminance-defined stimuli, En = equiluminant stimuli-in-noise. Error bars are 95% confidence intervals.

the cross-over interaction between trajectory and contrast was again highly significant, $F(2, 22) = 109.03$, $p = 4.8 \times 10^{-7}$, $\eta_p^2 = .91$, and the interaction was also significant for just the onset and reversal trajectories, $F(2, 22) = 11.12$, $p = 0.007$, $\eta_p^2 = .50$.

For the continuous trajectory, the decrease in illusion size changing from a luminance-defined moving stimulus to one equiluminant-in-luminance noise was significant, $t(11) = 9.36$, $p = 1.4 \times 10^{-6}$, $d = 2.70$; (all p values for t tests in this paper are 2-tailed) as were the corresponding increases in illusion size for the onset, $t(11) = 6.61$, $p = 3.8 \times 10^{-5}$, $d = 1.91$, and reversal trajectories, $t(11) = 3.10$, $p = 0.01$, $d = 0.90$. Comparing across trajectories, the only significant differences were between the continuous and onset trajectories, $t(11) = 9.52$, $p = 1.2 \times 10^{-6}$, $d = 2.75$, and between the continuous and the reversal trajectories, $t(11) = 8.15$, $p = 5.5 \times 10^{-6}$, $d = 2.35$, for the equiluminant-in-noise moving stimulus.

Discussion

The equiluminant-in-noise contrast for the moving stimulus eliminated the flash-lag illusion, but only for the continuous trajectory, replicating Chappell and Mullen (2010). The cross-over interaction, however, demonstrates that this contrast manipulation had the opposite effect with the other two trajectories, with the illusion significantly increased for both. Clearly, predominantly single process theories (for example, Eagleman & Sejnowski, 2007; Krekelberg, 2001; Nijhawan, 2008), cannot account for this cross-over interaction. With our equiluminant-in-noise moving stimulus, however, the flash-lag illusion magnitude difference between these trajectories was dramatic ($d = 2.75$), and the finding of a null illusion with continuous trajectory combined with a significant illusion for the onset trajectory replicates Patel et al.'s (2000) results with a low contrast moving stimulus and a bright flash.

There was a possibility that the illusion measured in our onset trajectory with equiluminant-in-noise moving stimulus might have been a Fröhlich illusion rather than a flash-lag illusion. That is, in this condition the moving stimulus might take longer to become visible than in the luminance condition, and so subjects might have been reporting just the position of appearance of the moving stimulus relative to perhaps a persisting representation of the flash position (Krekelberg, 2001). To address this concern we measured the Fröhlich illusion with other parameters similar to those used in Experiment 1, and did so in a block that also measured the flash-lag illusion, so that the illusion magnitudes could be directly compared. However, pilot experiments indicated that the Fröhlich illusion might not be reliably different from zero with the Experiment 1 settings. This could have been because the moving stimulus was displayed at its first position over five frames, making it more difficult for the beginning of its trajectory to be suppressed (see Other possible processes to account for onset trajectory illusions, below). So, all conditions were also run with the moving stimulus presentation at each position over three frames.

Experiment 2: Controlling for a Fröhlich illusion

Method

Subjects

Data for 11 naïve subjects with ages between 18 and 55 are reported, with two others were excluded due to inability to perform reliably on the motion minimization task used to obtain a subjective equiluminant point. Five had also performed Experiment 1.

Stimuli and procedure

Stimuli were identical to those used in Experiment 1, with the following exceptions. Only onset trajectories were tested. For measurements of the Fröhlich illusion, a triangle with the same spatial and color properties as the flash appeared 750 ms before the moving stimulus appeared, and remained on for the whole trial. Subjects were informed via an on-screen message whether the next trial would be a flash-lag or a Fröhlich condition.

In Experiment 1, the moving stimulus triangle remained at each position for three presentations (extending over five frames/position). As noted above, all conditions were also run with the moving stimulus presentation at each position extending over three frames (with a noise or other frame interleaving as before—approximately 12.5 ms shorter than the five frame presentation).

When the moving stimulus was displayed over five frames/position, in the luminance-defined conditions, it was displayed as follows using the same notation as in Experiment 1: B-P1-P1-P1-P1-P1-B-P2-P2-P2-P2-P2-B, etc. This sequence was different from Experiment 1, where the second and fourth frames were uniformly black: B-P1-B-P1-B-P1-B-P2-B-P2-B-P2-B, etc. These parameter settings were being piloted in other work, and were inadvertently used for Experiment 2. Similarly, when the moving stimulus was displayed for three frames/position in luminance-defined conditions, it appeared on three consecutive frames: B-P1-P1-P1-B-P2′-P2′-P2′-B, etc. The second position here (P2′) is different from before because the moving stimulus dwells at each position for a shorter time here (i.e., three frames instead of five), and therefore it moves a shorter distance to its new position, so as to maintain the same speed in all conditions. For equiluminance-in-noise conditions the moving stimulus was also displayed over either five or three frames, but every second frame contained noise "overlaid" on the stimulus, exactly as in Experiment 1, e.g., N-P1-N-P1-N-P1-N-P2-N-P2-N-P2-N, etc. There were thus eight conditions (frames/position × illusion type × contrast), and these were tested in a single block.

Results

Figure 3 displays our average data. Means for corresponding conditions in Experiment 1 were slightly smaller for both levels of presentations/position, but for the five subjects who did both experiments, not significantly so for either ($ps > 0.15$).

To check whether a Fröhlich illusion was being measured in the equiluminant-in-noise conditions in Experiment 1, we can compare with the five frames/position condition in Experiment 2 because the moving stimulus presentation was identical in the two experiments. The difference between flash-lag and Fröhlich illusions here was highly significant, $t(10) = 3.43$, $p = 0.006$, $d = 1.03$, as it was also for three frames/position, $t(10) = 3.59$, $p = 0.005$, $d = 1.08$. For completeness, the differences between illusions for luminance-defined moving stimuli were also significant for five frames/position, $t(10) = 4.03$, $p = 0.002$, $d = 1.21$, and for three frames/position, $t(10) = 4.16$, $p = 0.002$, $d = 1.25$.

Overall, the three-way interaction was not significant ($p = 0.16$, $\eta_p^2 = .19$) but the two-way interaction

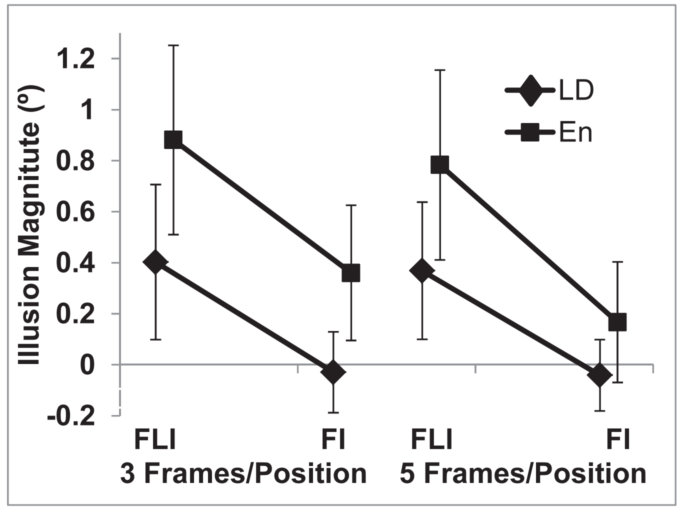

Figure 3. Flash-lag and Fröhlich illusions as a function of frames/position and contrast. Average data for 11 subjects. FLI = flash-lag illusion. FI = Fröhlich illusion. LD = luminance-defined conditions. En = equiluminant-in-luminance noise. Error bars are 95% confidence intervals.

between frames/position and contrast was, $F(1, 10) = 53.18$, $p = 2.6 \times 10^{-5}$, $\eta_p^2 = .84$. After collapsing across illusion type, for equiluminant-in-noise conditions the mean for three frames/position ($M = .62$) was significantly greater than that for five frames/position, $M = .48$, $t(10) = 5.46$, $p = 2.78 \times 10^{-4}$, $d = 1.65$. However, for luminance-defined conditions, the corresponding means ($M = .19$, $M = .16$) were not significantly different ($p = 0.2$, $d = .41$). The main effects of illusion type, $F(1, 10) = 16.81$, $p = 0.002$, $\eta_p^2 = .63$, frames/position, $F(1, 10) = 16.66$, $p = 0.002$, $\eta_p^2 = .63$, and contrast, $F(1, 10) = 37.65$, $p = 1.10 \times 10^{-4}$, $\eta_p^2 = .79$, were all significant.

As the confidence intervals indicate, with luminance-defined moving stimuli, neither Fröhlich illusion was significantly different from zero ($d = -0.12$ for three frames/position, $d = -0.19$ for five frames/position). Five subjects in fact exhibited significant onset repulsion, in which the moving stimulus was perceived to appear projected backwards in the direction from where it actually appeared (Thornton, 2002). Even if these subjects were excluded, the Fröhlich illusions were still very small: $M = 0.12°$ for three frames/position and 0.10°, and non-significant ($p = 0.24$ and $p = 0.21$). The contrast manipulation significantly increased the Fröhlich illusion for both five frames/position, $t(10) = 4.11$, $p = 0.002$, $d = 1.24$, and three frames/position, $t(10) = 5.90$, $p = 1.5 \times 10^{-4}$, $d = 1.78$.

Discussion

The flash-lag illusions in Experiment 2, compared to those in Experiment 1 were smaller, although not significantly so, and were both reliably different from zero. The corresponding illusions for equiluminant-in-noise stimuli were similar, although slightly smaller, suggesting any differences may also have been due to subject differences. In any case, for the purposes of control, the only condition where there was a suggestion we might have been inadvertently measuring a Fröhlich illusion in Experiment 1 was the equiluminance-in-noise onset trajectory flash-lag condition. Stimulus presentation for this condition was identical in the two experiments for the five-frames/position condition. The flash-lag illusion with the same moving stimulus settings was significantly larger than the corresponding Fröhlich illusion, as it was for each of the other moving stimulus conditions (cf. Chappell et al., 2006). We conclude we were not measuring a Fröhlich illusion with our equiluminance-in-noise onset trajectory condition in Experiment 1.

Neither of the two frames/position settings yielded a Fröhlich illusion with luminance-defined moving stimuli. Whereas there have been numerous reports of significant Fröhlich illusions (Chappell et al., 2006; Kerzel & Müsseler, 2002; Kirschfeld & Kammer, 1999; Müsseler & Aschersleben, 1998; Müsseler & Kerzel, 2004; Whitney & Cavanagh, 2002), in fact there have also been a number of reports of null Fröhlich illusions (Gauch & Kerzel, 2008; Kerzel, 2002; Kerzel & Müsseler, 2002; Kreegipuu & Allik, 2003; Müsseler et al., 2002). Also, significant and non-significant Fröhlich illusions have been reported often within the same papers, or even the same experiments with different stimuli (e.g., Experiment 1; Kerzel & Müsseler, 2002). Regarding the reasons for this variation, Kerzel (2002) found that the Fröhlich illusion occurred more reliably if the positions of simultaneously present stimuli were compared, as in our studies, and stimulus speeds were higher. If, on the other hand, a mouse was used to indicate where the moving stimulus had appeared, and lower speeds were used, then onset repulsion—the opposite of the Fröhlich illusion—was more likely. The switch-over speed appears to be in the range of 15-20°/s (see also Kerzel & Gegenfurtner, 2004). As noted, five of our subjects in Experiment 2 exhibited significant onset repulsion. Actis-Grosso and Stucchi (2003) have found onset repulsion, averaged across all subjects, when the appearance point was compared to a ruler 4.1° above the motion, with speeds of 4.1 and 16.1°/s.

We have previously reported different magnitudes for the Fröhlich illusion and flash-lag illusion with onset trajectory (Chappell et al., 2006), and the relative unreliability of the Fröhlich illusion—we are not aware of reports of null onset trajectory flash-lag illusions—provides another piece of converging evidence that they are based on different processes. As well, reducing contrast and adding luminance noise increased the Fröhlich illusion and replicated the increase in the flash-lag illusion found in Experiment 1. Cai (2009) previously reported that just adding noise to the moving stimuli also increased the Fröhlich illusion.

In conclusion, Experiment 2 was not only a control for the Fröhlich illusion, especially in the equiluminance-in-noise onset trajectory condition, but it also yielded important new data that constrain theories of localization. We believe it is the first to find a null Fröhlich illusion in a within-subjects comparison with a significant onset trajectory flash-lag illusion. It added to our earlier work showing a smaller Fröhlich than flash-lag illusion with onset trajectory (Chappell et al., 2006).

General discussion

The conditions of Experiment 2 are relatively simpler to interpret, so we begin our discussion with these, and the comparison with the onset trajectory flash-lag illusion. Table 1 shows a summary of our theory comparisons.

Theoretical implications of Experiment 2

Previously reviewed theories

To account for the data from Experiment 2, and other studies that found null Fröhlich illusions, a theory must first be able to predict a null Fröhlich illusion and also a non-null Fröhlich illusion, depending on circumstances, and generally produce a non-null onset trajectory flash-lag illusion. On the face of it, Nijhawan's (2008) spatial projection theory is best placed to predict a null Fröhlich illusion. It would predict a null illusion when there is no position information from times before the judgment of position. As noted above, to account for the non-null onset trajectory flash-lag illusion, however, it must posit an ultra-short latency projection process. The first challenge for this theory is to explain why these processes have apparently not influenced perception in the absence of a flash both in our experiment and others (Gauch & Kerzel, 2008; Kerzel, 2002; Kerzel & Müsseler, 2002; Kreegipuu & Allik, 2003; Müsseler et al., 2002), but have in other Fröhlich experiments (Chappell et al., 2006; Kerzel & Müsseler, 2002; Kirschfeld & Kammer, 1999; Müsseler & Aschersleben, 1998; Müsseler & Kerzel, 2004; Whitney & Cavanagh, 2002). Could stimulus differences between experiments have plausibly affected these processes to produce these differences?

Secondly, why has the impact of these spatial projection processes been increased when a flash was present (see Chappell et al. (2006) for the influence of an irrelevant flash)? The same motion information for the moving stimulus is available in both the Fröhlich and flash-lag conditions in Experiment 2. This was also true in the corresponding conditions reported by

	Nijhawan (2008)	Eagleman & Sejnowski (2007)	Krekelberg & Lappe (2000)	Kirschfeld & Kammer (1999)
Null Fröhlich	?	?	?	Y
Varying mag. Fröhlich—in general	?	?	Y	Y
Varying Fröhlich in Experiment 2 (contrast)	N	N	N	Y
Smaller Fröhlich than FLI	N	Y	N	Y
Experiment 1 cross-over interaction	N	N	N	Y

Table 1. Theories' performance (without additional processes) against key findings. *Notes*: All according to our analysis: 'Y' = can be accounted for, 'N' = in our view there are principled reasons implying it cannot be accounted for (without additional processes), '?' = possible arguments could be made that manipulations might affect theory processes to produce results.

Chappell et al. (2006), for which a significant Fröhlich illusion was reported, but about half of the size of the flash-lag illusion, in a within-subjects comparison. In general, one might expect that the presence of the flash as a spatial marker would entail more processing resources being allocated to it, thus detracting from other processes such as the spatial projection posited by Nijhawan (2008). Yet if his theory is to explain our results, those processes are more effective in the presence of the flash.

Currently we are not aware that the flash has any role in localizing the moving stimulus in Nijhawan's (2008) theory. We (Chappell et al., 2006; Sarich, Chappell, & Burgess, 2007) and others (e.g., Linares et al., 2007) have previously argued for such a role and Experiment 2 adds further compelling evidence in support. We turn now to the other two theories reviewed in our Introduction, which do assume such a role.

Eagleman and Sejnowski's (2007) theory maintains that localization is based on motion occurring after the point being localized. Again the challenge for them is to explain why different stimulus conditions vary the efficacy of their spatial projection process, in order to produce Fröhlich illusions of various sizes. They suggested that, while the flash is the cue for their spatial projection process in the flash-lag paradigm, the sudden onset of the moving stimulus is the cue in the Fröhlich paradigm. If for some reason the flash is a *less* effective cue so that the spatial projection process starts later and thus projects the location further along the trajectory, then their theory could predict a larger flash-lag than Fröhlich illusion.

A temporal integration model such as Krekelberg and Lappe's (1999) can also predict Fröhlich illusions of varying magnitudes just by varying the window size, although it is not so clear how it could plausibly predict a null illusion. As noted above, for Krekelberg (2001) the integration should terminate when the persisting flash signal extinguishes. Unfortunately, the landmark in our Fröhlich conditions was displayed for much longer than the flashes in our flash-lag conditions, which would seem to predict a larger Fröhlich than flash-lag illusion.

As specified in the Introduction, without further processes added all three theories reviewed should predict a smaller Fröhlich illusion in equiluminance-in-noise conditions than in luminance-defined conditions, the opposite of what was found.

Other possible processes to account for onset trajectory illusions

Kirschfeld and Kammer (1999) proposed an account specifically of the Fröhlich illusion in which they assumed that the first part of a suddenly appearing moving stimulus' trajectory may be backward masked by its later appearances. The operation of such a process is supported by reports that the contrast of a drifting grating is reduced at the trailing edge of the motion (Arnold, Thompson, & Johnston, 2007; Whitney et al., 2003), as well as Chappell's (2007) finding of suppression of a flash's perceived contrast behind a moving stimulus. Kirschfeld and Kammer (1999) proposed that a balance of excitatory and inhibitory processes supports perception of a stimulus that has been moving for some time (see their figure 6 and also Kanai, Sheth, & Shimojo, 2004), but at the beginning of a trajectory there is a latency in the responding of the excitatory processes (cf. Öğmen et al., 2004). The excitatory processes are thus dominated by the inhibitory ones leading to the Fröhlich illusion, which reveals those inhibitory processes.

In general, this theory could predict Fröhlich illusions of different magnitudes by positing a different balance of excitatory and inhibitory processes as a function of stimulus conditions. In particular, to account for our null Fröhlich illusion, excitatory processes related to the initial position of the moving stimulus would have to be sufficiently strong to resist the inhibitory processes due to the stimulus appearing later at adjacent positions. In fact, the possibility that our stimuli appearing at each position for five frames duration (see Experiment 2, Method) might lead to just such an outcome was a motivation for manipulating frames/position in Experiment 2. Consistent with this line of reasoning, in our equiluminance-in-noise conditions, the Fröhlich illusion was smaller in the five frames/position condition where there was more excitation at the position of first appearance, than in the three frames/position condition. This effect warrants further experimental investigation. If one assumes that equiluminance-in-noise affects the efficacy of the excitatory processes in this model, then the larger Fröhlich illusion under these conditions, compared to the luminance-defined conditions, would be explained.

Kirschfeld and Kammer's (1999) account maintains that focal attention to the moving stimulus speeds its processing, and particularly the excitatory processes. Among other things, this process reduces its latency to perception, thus providing a differential latency account of the flash-lag illusion (see also, Purushothaman, Patel, Bedell, & Öğmen, 1998; Whitney & Murakami, 1998) for a continuous trajectory (Kirschfeld, 2006). We have previously demonstrated that the flash-lag flash captures attention (Sarich et al., 2007). It would be reasonable to suppose, then, that this flash diminishes the attentional resources available for processing the moving stimulus. With an onset trajectory, then, the flash further increases the latency of the excitatory processes, so that by the time activation crosses a threshold for perception, a later position is being perceived than would have been in the absence of a flash. Hence an attention-based account here rather naturally explains the larger onset trajectory flash-lag illusion than Fröhlich illusion.

Theoretical implications of Experiment 1

A single process model cannot accommodate the cross-over interaction between trajectory and contrast that we found in Experiment 1. There would seem to be two main ways that an explanation can be developed. One is to maintain the assertion of the theories reviewed in the Introduction, that a single process accounts for at least most of the findings across the three trajectories with luminance-defined stimuli. One might then further assume that equiluminance-in-noise nulls that process, but also brings into play a process or processes which is/are otherwise "dormant," in order to explain the results with onset and reversal conditions. The second way is to posit processes that can account for our contrast manipulation, but which differ across trajectorie*s*, even for luminance-defined stimuli. We discuss both approaches below.

One process for luminance-defined conditions

For the sake of argument, suppose the process explaining all three illusions with contrast-defined stimuli is spatial projection mediated by the M pathway. Given that the flash-lag illusion with continuous trajectory is reliably nulled by our contrast manipulation, it is reasonable to assume that the effects of this process are also substantially reduced for the onset and reversal trajectories. All else being equal, one would expect the illusions with these trajectories to also be nulled.

Of course, the opposite has occurred, with the onset trajectory illusion in particular being increased in magnitude by approximately 80%. Hence, whatever new processes are assumed to be revealed by the equiluminance-in-noise manipulation have to be capable by themselves of producing much larger illusions than the baseline flash-lag illusion. What might these processes be?

The most obvious candidate is simply masking (Breitmeyer & Öğmen, 2006)—the combination of equiluminance and especially luminance noise inhibits processing of the moving stimulus so that it does not become visible until later after its onset or reversal, than it would in the absence of equiluminance-in-noise. This could account for the larger illusions with onset and reversal trajectories in Experiment 1, and the larger Fröhlich illusion in Experiment 2.

The main problem is that the empirical rationale for explaining results across trajectories with the same process is questionable, given the substantial number of studies with luminance-defined stimuli finding different illusion magnitudes, some of them dramatic, particularly between the continuous and onset trajectories (Chappell et al., 2006; Linares et al., 2007; Müsseler et al., 2002; Öğmen et al., 2004; Patel et al., 2000). We turn now to an account of our cross-over interaction which does not seek to maintain that the same process(es) can account for the flash-lag illusions measured with luminance-defined stimuli (or those equiluminant-in-noise, for that matter) for each of the continuous, onset and reversal trajectories.

Processes differ across luminance-defined trajectories

There is good reason to believe spatial projection does contribute to perception of position with a continuous trajectory. A flash's perceived position is biased by adjacent motion (flash-drag; Whitney & Cavanagh, 2002), and the perceived position of an envelope is biased by the motion of an internal drifting grating (De Valois & De Valois, 1991), or dots (Ramachandran & Anstis, 1990). Thus it is likely that a moving stimulus biases its own position forwards along its trajectory. As discussed by Chappell and Mullen (2010), the reduction in the flash-lag illusion when M pathway processing is reduced is consistent with the spatial projection being achieved via back-projections from V5/hMT to V1.

What other processes might be invoked to account for the differences across trajectories noted at the end of the last section, as well as the effect the flash has on perception? An obvious candidate again is the backward masking posited by Kirschfeld and Kammer (1999). This accounts by itself for the Fröhlich illusion with luminance-defined stimuli (when observed), as already discussed. The presence of a flash in a flash-lag paradigm or equiluminance-in-noise both interfere with the excitatory processes in this model, so that it takes longer for them to overcome the inhibitory processes, and larger illusions result.

If the onset and reversal trajectories do not reveal spatial projection at work, a corollary is that these trajectories do not have utility for discriminating between the spatial projection theories, and in particular whether it is motion *before* (Nijhawan, 2008) or *after* (Eagleman & Sejnowski, 2007) the flash which underlies the projection. We note, however, that Brenner and Smeets (2000) and Whitney, et al. (2000) measured the flash-lag illusion at a range of time points before and after a moving stimulus suddenly increased or decreased its speed. Localization with such a trajectory is likely to be less affected by the backward masking process. The flash-lag magnitude in these studies began changing to be commensurate with the final speed (its magnitude is roughly proportional to speed) 60 to 80 ms before the speed change occurred, suggesting that if spatial projection is operating, its output is based on motion after the flash.

Other theories

Following the same arguments as above, the temporal integration process alone (Krekelberg & Lappe, 2000), whichever brain region it is taking place in, could not account for our Experiment 1 data. It could be, however, that spatial projection processes in V5/hMT, contributing to localization with continuous trajectories, utilize such a process. As noted by Chappell and Mullen (2010), the fact that their contrast manipulation eliminated the flash-lag illusion was also consistent with the differential latency theory (Purushothaman et al., 1998; Whitney & Murakami, 1998). In the context of the flash-lag illusion, this theory posits that moving stimuli are simply perceived with a shorter latency than flashes. Proponents of this theory, however, explicitly state that additional processes are needed to model onset and reversal trajectories (Öğmen et al., 2004; Whitney & Murakami, 1998), and so their theory is not in conflict with our data.

Reversal trajectory conditions

Clearly, results obtained using the reversal trajectory with the moving equiluminant stimulus in luminance noise behaved more like the onset trajectory than the continuous trajectory, exhibiting a significant increase in illusion magnitude, although the effect size was smaller. Generally the same arguments with regard to theories would therefore also follow from our results with this trajectory. However, the interaction between trajectory type (onset vs. reversal) and contrast was also significant—the increase in magnitude with the equiluminance-in-noise stimulus was significantly less for the reversal trajectory. The simplest assumption would be that a new representation does not have to be established (Yantis, 1996) when an object reverses direction. What is not clear, however, is why such processes apparently did not affect luminance-defined moving stimuli (onset and reversal illusions had the same magnitude), and why such processes would not generally produce a Fröhlich illusion, for example in our Experiment 2. Further research is needed on this issue.

Conclusions

We have presented data revealing that making the moving stimulus equiluminant and immersing it in luminance noise has highly differential effects across three different motion trajectories. We have argued that any theory that posits that a single process can account for results across the six conditions in Experiment 1 must be inadequate. If these theories were supplemented with the assumption that the luminance noise has a powerful masking effect for onset and reversal conditions, then the cross-over interaction in Experiment 1 might be accounted for. However Experiment 2 provided an even greater challenge for these theories finding a significantly smaller Fröhlich (indeed null for luminance-defined stimuli) than flash-lag illusion with onset trajectory. We found that Kirschfeld and Kammer's (1999) model, which already includes multiple processes, performed best accommodating our data. We have argued that the reversal and onset trajectories are well suited for revealing the inhibitory process in their model. Because this process may obscure or override the effects of the processes that underlie perception of a continuous trajectory, however, onset and reversal trajectories may not be appropriate for revealing the continuous trajectory processes and testing theories of the perception of that trajectory.

Keywords: localization, visual, theories, magnocellular, flash-lag

Acknowledgments

We would like to thank two anonymous reviewers for their extensive and helpful feedback, for suggesting the "noise reveals processes" account of Experiment 1, and for suggesting the control Experiment 2. We would like to thank David Hardwick for assistance with data checking and graphics. We would like to acknowledge the support of the Applied Cognitive Neuroscience Research Unit, Behavioural Basis of Health, Griffith Health Institute, and of a NSERC grant (RGPIN 183625-05) to K. T. Mullen.

Commercial relationships: none
Corresponding author: Mark Chappell.
Email: m.chappell@griffith.edu.au.
Address: Applied Cognitive Neuroscience Research Unit, Griffith Health Institute, and School of Applied Psychology, Griffith University, Brisbane, Australia.

References

Actis-Grosso, R., & Stucchi, N. (2003). Shifting the start: Backward mislocalization of the initial position of a motion. *Journal of Experimental Psychology: Human Perception and Performance, 29,* 675–691.

Anstis, S., & Cavanagh, P. (1983). A minimum motion technique for judging equiluminance. In J. D. Mollon & L. T. Sharpe (Eds.), *Colour vision: Physiology and psychophysics* (pp. 155–166). London: Academic Press.

Arnold, D. H., Thompson, M., & Johnston, A. (2007). Motion and position coding. *Vision Research, 47,* 2403–2410.

Baker, C. L., Jr., Boulton, J. C., & Mullen, K. T. (1998). A nonlinear chromatic motion mechanism. *Vision Research, 38,* 291–302.

Barbur, J. L., Wolf, J., & Lennie, P. (1998). Visual processing levels revealed by response latencies to changes in different visual attributes. *Proceedings of the Royal Society London B, 265,* 2321–2325.

Beaudot, W. H. A., & Mullen, K. T. (2001). Processing time of contour integration: The role of color, contrast and curvature. *Perception, 30,* 833–853.

Bowen, R. W. (1981). Latencies for chromatic and achromatic mechanisms. *Vision Research, 21,* 1457–1466.

Breitmeyer, B. G., & Öğmen, H. (2006). *Visual masking: Time slices through conscious and unconscious vision*. Oxford: Oxford University Press.

Brenner, E., & Smeets, J. B. (2000). Motion extrapolation is not responsible for the flash-lag effect. *Vision Research, 40,* 1645–1648.

Cai, R. (2009). *Magnification of the Froehlich effect under noise*. Paper presented at the Vision Sciences Society conference, Naples, FL.

Chappell, M. (2007). Mapping a field of inhibition surrounding visual stimuli. *Journal of Vision, 7*(10): 8, 1–14, http://www.journalofvision.org/content/7/10/8, doi:10.1167/7.10.8. [PubMed] [Article]

Chappell, M., Hine, T. J., Acworth, C., & Hardwick, D. (2006). Attention "capture" by the flash-lag flash. *Vision Research, 46,* 3205–3213.

Chappell, M., & Mullen, K. T. (2010). The Magnocellular visual pathway and the flash-lag illusion. *Journal of Vision, 10*(11):24, 1–10, http://www.journalofvision.org/content/10/11/24, doi:10.1167/10.11.24. [PubMed] [Article]

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

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

Eagleman, D. M., & Sejnowski, T. J. (2007). Motion signals bias localization judgments: A unified explanation for the flash-lag, flash-drag, flash-jump, and Frohlich illusions. *Journal of Vision, 7*(4):3, 1–12, http://www.journalofvision.org/content/7/4/3, doi:10.1167/7.4.3. [PubMed] [Article]

Gauch, A., & Kerzel, D. (2008). Comparison of flashed and moving probes in the flash-lag effect: Evidence for misbinding of abrupt and continuous changes. *Vision Research, 48,* 1584–1591.

Kanai, R., Sheth, B. R., & Shimojo, S. (2004). Stopping the motion and sleuthing the flash-lag effect: Spatial uncertainty is the key to perceptual mislocalization. *Vision Research, 44,* 2605–2619.

Kerzel, D. (2002). Different localization of motion onset with pointing and relative judgments. *Experimental Brain Research, 145,* 340–350.

Kerzel, D., & Gegenfurtner, K. R. (2004). Spatial distortions and processing latencies in the onset repulsion and Fröhlich effects. *Vision Research, 44,* 577–590.

Kerzel, D., & Müsseler, J. (2002). Effects of stimulus material on the Fröhlich illusion. *Vision Research, 42,* 181–189.

Khurana, B., & Nijhawan, R. (1995). Reply to extrapolation or attention shift. *Nature, 378,* 566.

Kirschfeld, K. (2006). Stopping motion and the flash-lag effect. *Vision Research, 46,* 1547–1551.

Kirschfeld, K., & Kammer, T. (1999). The Fröhlich effect: A consequence of the interaction of visual focal attention and metacontrast. *Vision Research, 39,* 3702–3709.

Kreegipuu, K., & Allik, J. (2003). Perceived onset time and position of a moving stimulus. *Vision Research, 43,* 1625–1635.

Krekelberg, B. (2001). The persistence of position. *Vision Research, 41,* 529–539.

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 on a slow averaging process. *Vision Research, 40,* 201–215.

Krekelberg, B., & Lappe, M. (2001). Neuronal latencies and the position of moving objects. *Trends in the Neurosciences, 24,* 335–339.

Lappe, M., & Krekelberg, B. (1998). The position of moving objects. *Perception, 27,* 1437–1449.

Lee, B. B., Martin, P. R., & Valberg, A. (1989). Sensitivity of macaque retinal ganglion cells to chromatic and luminance flicker. *Journal of Physiology, 414,* 223–243.

Linares, D., Lopez-Moliner, J., & Johnston, A. (2007). Motion signal and the perceived positions of moving objects. *Journal of Vision, 7*(7):1, 1–7, http://www.journalofvision.org/content/7/7/1, doi: 10.1167/7.7.1. [PubMed] [Article]

Livingstone, M. S., & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *The Journal of Neuroscience, 7,* 3416–3468.

Maus, G. W., Khurana, B., & Nijhawan, R. (2010). History and theory of flash-lag: Past, present, and future. In R. Nijhawan & B. Khurana (Eds.), *Space and time in perception and action* (pp. 477–499). Cambridge: Cambridge University Press.

Mullen, K. T., Yoshizawa, T., & Baker, C. L. Jr. (2003). Luminance mechanisms mediate the motion of red-green isoluminant gratings: The role of "temporal chromatic aberration." *Vision Research, 43,* 1235–1247.

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., & Kerzel, D. (2004). The trial context determines adjusted localization of stimuli: Reconciling the Fröhlich and onset repulsion effects. *Vision Research, 44,* 2201–2206.

Müsseler, J., Stork, S., & Kerzel, D. (2002). Comparing mislocalizations with moving stimuli: The Fröhlich effect, the flash-lag effect, and representational momentum. *Visual Cognition, 9,* 120–138.

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

Nijhawan, R. (2008). Visual prediction: Psychophysics and neurophysiology of compensation for time delays. *Behavioral and Brain Sciences, 31,* 179–198.

Öğmen, H., Patel, S. S., Bedell, H. E., & Camuz, K. (2004). Differential latencies and the dynamics of the position computation process for moving targets, assessed with the flash-lag effect. *Vision Research, 44,* 2109–2128.

Patel, S. S., Öğmen, H., Bedell, H. E., & Sampath, V. (2000). Flash-lag effect: Differential latency, not postdiction. *Science, 290,* 1051a.

Purushothaman, G., Patel, S. S., Bedell, H. E., & Öğmen, H. (1998). Moving ahead through visual latency. *Nature, 396,* 424.

Ramachandran, V., & Anstis, S. M. (1990). Illusory displacement of equiluminous kinetic edges. *Perception, 19,* 611–616.

Sarich, D., Chappell, M., & Burgess, C. (2007). Dividing attention in the flash-lag illusion. *Vision Research, 47,* 544–547.

Shen, M., Zhou, J., Gao, T., Liang, J., & Shui, R. (2007). The perceived position of a moving object is not a result of position integration. *Vision Research, 47,* 3088–3095.

Thornton, I. M. (2002). The onset repulsion effect. *Spatial Visual, 15,* 219–243.

Whitney, D. (2002). The influence of visual motion on perceived position. *Trends in Cognitive Sciences, 6,* 211–216.

Whitney, D., & Cavanagh, P. (2002). Surrounding motion affects the perceived locations of moving stimuli. *Visual Cognition, 9,* 139–152.

Whitney, D., Goltz, H. C., Thomas, C. G., Gati, J. S., Menon, R. S., & Goodale, M. A. (2003). Flexible retinotopy: Motion-dependent position coding in the visual cortex. *Science, 302,* 878–881.

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

Yantis, S. (1996). Attentional capture in vision. In A. F. Kramer, M. G. H. Coles, & G. D. Logan (Eds.), *Converging operations in the study of visual selective attention* (pp. 45–76). Washington, DC: APA.