

The Magnocellular visual pathway and the flash-lag illusion

Mark Chappell

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



Kathy T. Mullen

McGill Vision Research, Department of Ophthalmology,
McGill University, Canada



Determining how the visual system locates moving stimuli continues to be an experimental and theoretical challenge. By making a moving visual stimulus equiluminant with its background, and immersing it in luminance noise, the spatial lead it normally enjoys over a flashed stimulus (the flash-lag illusion) was completely eliminated (the illusion was actually reversed for 6 out of 11 participants). As this manipulation is typically used to reduce Magnocellular (M) visual pathway processing, this is strong evidence that processing in this pathway advances the moving stimulus' perceived position. However, when the flashed stimulus was also made equiluminant in luminance noise, the illusion reappeared, indicating that M pathway processing contributed to its perception too. The presence of the illusion when both stimuli were equiluminant in luminance noise indicates that the illusion can be generated in the absence of M cell activation. To explicate the result with moving stimuli, we displayed two adjacent moving stimuli, one luminance-modulated, and the other equiluminant in noise. The latter was perceived to significantly lag the former (an 'M-P-Hess' illusion), and 39% of the difference in flash-lag illusions, with comparable moving stimulus contrasts, could be accounted for by this illusion.

Keywords: motion, Magnocellular pathway, flash-lag, motion-biasing, position

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Introduction

In the *flash-lag illusion*, a moving stimulus presented in alignment with a flashed stimulus appears further along the path of its movement than it actually was when the flash was displayed. This illusion continues to be an important testing ground for theories of how we perceive the position of moving stimuli (Eagleman & Sejnowski, 2007; Nijhawan, 2008). Here we seek to further constrain such theories by investigating the neurophysiological basis of the illusion.

The projections of the Magnocellular (M) visual pathway underpin the processing of moving stimuli (Livingstone & Hubel, 1987). Thus, one might expect the M cell pathway to play a role in the flash-lag illusion, and indeed Khurana and Nijhawan (1995) and more recently Nijhawan (2008) speculated that it may give the moving stimulus a processing advantage, translating into the observed spatial lead of the moving stimulus over the flash. Cantor and Schor (2007) and Fu, Shen, and Dan (2001) found that a larger flash-lag illusion occurs for lower spatial frequency stimuli. Cantor and Schor (2007) noted that this is consistent with M pathway involvement, given that pathway's preference for such stimuli (Livingstone & Hubel, 1987). We sought a more direct demonstration.

The M pathway predominantly responds to luminance differences, and so its processing may be minimized by

presenting stimuli which differ from their background in color but not luminance (*equiluminance*) (Livingstone & Hubel, 1987). Individual differences in visual systems imply that the functional equiluminant point should be found separately for each participant, for example with the method of minimum motion (Anstis & Cavanagh, 1983). However, previous studies that so customized their stimuli (Arnold, Ong, & Roseboom, 2009), or used near-equiluminant stimuli (Chappell, Hine, & Hardwick, 2002), failed to find an effect on the magnitude of the flash-lag illusion of using equiluminant moving stimuli. This may have been because even genuinely equiluminant stimuli still elicit some motion processing via the M-pathway. The fact that masking chromatic stimuli with luminance noise selectively increases motion detection thresholds, but not stimulus detection thresholds, indicates that such noise removes intrinsic luminance responses to motion generated by equiluminant stimuli (Baker, Boulton, & Mullen, 1998; Mullen, Yoshizawa, & Baker, 2003). We thus used luminance noise masking of our equiluminant stimuli, which also had the additional benefit of eliminating any residual extrinsic luminance artifacts in those stimuli. We address further what processes luminance noise may be affecting in our [General discussion](#).

We report two experiments. In the first we used stimuli that were either luminance-modulated, equiluminant, or equiluminant in luminance noise. We varied this contrast independently for the flash and for the moving stimulus in

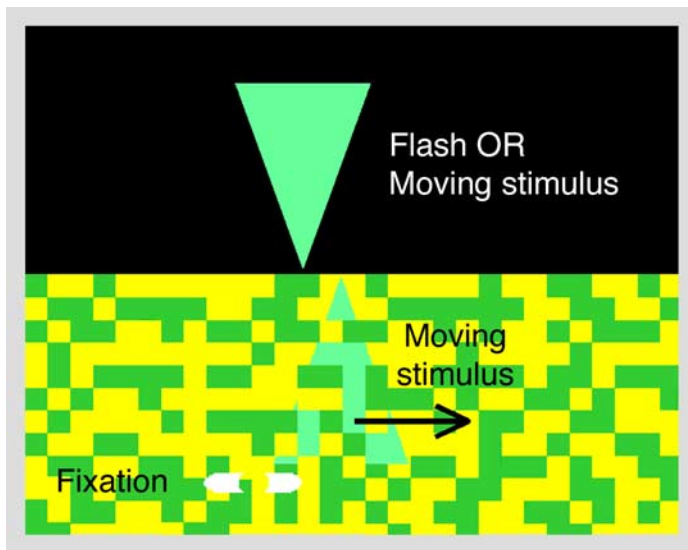


Figure 1. Stimuli for both experiments. The lower half illustrates a moving triangular stimulus immersed in luminance noise (E_n), whereas the upper half illustrates a luminance-modulated stimulus. For a flash-lag condition the upper stimulus appeared briefly in one location. In some conditions in [Experiment 2](#) both stimuli traversed the display with the same speed and direction of motion. Stimuli and luminance noise (if present) were presented on alternate frames.

the flash-lag paradigm, yielding nine main experimental conditions. When flashed and moving stimulus contrasts were different, a horizontal boundary divided the display into two equal halves, with one stimulus appearing in the top half, the other in the bottom half (see [Figure 1](#)). If M-pathway processing contributes to the perception of the moving stimulus spatially leading the flash, then we expected that at least making the moving stimulus equiluminant in noise should reduce the magnitude of the illusion, compared to when the moving stimulus was luminance-modulated (flash contrast being held constant). On the other hand, if making the flash equiluminant in luminance noise slowed its processing, then the flash-lag illusion should be larger with such a flash than with a luminance-modulated flash (moving stimulus contrast being held constant). The second experiment sought to elucidate the findings of the first, and is described after those findings have been reported.

Experiment 1

Method

Participants

Data for 11 naïve participants (after the exclusions detailed below), three female, with normal or correct to normal acuity and color (Ishihara Test) vision are

reported. Across both experiments nine participants were not able to respond consistently to the minimum motion task (see below), and so they were excluded. One participant experienced discomfort during testing, one developed an eye-ache, neither completed testing, and thus both were excluded from [Experiment 1](#). One participant could not meet the reliability criterion for all the flash-lag conditions (see [Procedure](#)) in a reasonable number of sessions, and so was excluded from [Experiment 1](#).

Apparatus and stimuli

Stimuli were presented with a VSG 2/3 graphics card on a 21-inch gamma-corrected color monitor (vertical refresh rate of 120 Hz and a 640×479 resolution) viewed at 102 cm using a chin rest. As shown in [Figure 1](#), the flashed and moving stimuli (speed of $16.4^\circ/\text{s}$, leftward or rightward) were isosceles triangles (1.6° in height and 1.2° in width), with the flashed triangle spatially inverted with respect to the moving triangle. The top vertex of the horizontally moving triangle was located 1.8° above the center of a white fixation line (see [Figure 1](#)), while the lower vertex of the flashed triangle was separated from the moving triangle by 0.5° (when present, the horizontal boundary between backgrounds was in the center of this interval). The moving stimulus emerged from the boundary of the display. Horizontally the flashed triangle appeared in a 1° wide uniform random window, symmetrically above fixation.

The fixation line subtended a total length of 1.1° , and had a missing central section of 0.4° .

Equiluminant stimuli had a neutral yellow ($\sim 50 \text{ cd/m}^2$) background, measured with a Minolta CS-100A chroma-meter with a 1° measurement angle. Anstis and Cavanagh's (1983) method of minimum motion was used to find the pure green which was equiluminant with this background. The grating parameters closely matched theirs, but gratings appeared on every second frame, with a uniform neutral yellow screen on interleaved frames, to match the flash-lag presentation. An adaptive method of constant stimuli was used, and testing stopped when both confidence interval segments were smaller than 100 levels (128 levels in [Experiment 2](#)) on the 32768 level DAC. This required between 35 and 90 trials with most participants—5–10 minutes of testing. Luminance-modulated stimuli had half the luminance of equiluminant stimuli, but appeared on a black background (upper half, [Figure 1](#)).

Stimulus frames were interleaved with mask frames that were either uniformly black, uniformly neutral yellow, or a checkerboard of luminance noise squares. When the mask was black ($\sim 2 \text{ cd/m}^2$) this reduced the luminance of the stimuli by 50%. The noise squares were 0.13° on each side. They were either a brighter yellow ($\sim 73 \text{ cd/m}^2$) or a darker green ($\sim 26 \text{ cd/m}^2$) than the neutral yellow, this color being chosen for each square independently and randomly on each frame. Ambient lighting was dim.

In order for the flashes to be sufficiently visible, it was found necessary to display them for three separate frames—there were thus two intervening frames of noise, neutral yellow, or black. Ideally the moving stimulus would have been displayed at each station it occupied for three frames also. However the resulting motion was judged to be insufficiently smooth, and so the moving stimulus occupied each position for two frames, with one intervening frame. Thus the moving stimulus occupied one position for the first presentation of the flash, and then a slightly advanced position for the second two presentations of the flash. All measurements of the separation of the stimuli were made from the latter moving stimulus position.

We wished to control for the possibility that the large black background for the luminance-modulated stimuli was affecting responding. There were thus also conditions where the neutral yellow background was used with bright yellow (BY) (moving or flashed) stimuli (~ 73 cd/m²).

Procedure

Observers indicated by pressing one of two keys on a keyboard whether the vertex of the flashed triangle was seen to the left or to the right of the vertex of the moving triangle.

The fourteen conditions were tested in blocks which contained two, three or four conditions. Conditions were fully randomized within a single block. Illusion magnitudes were computed with an adaptive method of constant stimuli.

Flashed and moving stimuli were displayed at a range of horizontal offsets and participants' dichotomous responses were used to compute points of subjective equality (PSE) via logistic regression. This was done online and the range of offsets being tested for each participant-condition was periodically adjusted so as to efficiently estimate the PSE. The reliability criterion adopted was that the total 95% confidence interval width in each of the conditions be no greater than 0.7°. Where this was not met in a single session the block was tested again in a subsequent session, and data from the two sessions was merged. A minimum of 84 trials per condition were tested in [Experiment 1](#) (60 in [Experiment 2](#)).

Results

The top-left graph in [Figure 2](#) shows data averaged across participants. Focusing on the main experimental conditions (closed symbols), moving from left to right on the graph represents effectively lessening the luminance contrast for the moving stimulus; luminance-modulated (L) to equiluminant (E) to equiluminant in noise (En).

Moving upward represents lessening luminance contrast for the flash. To control for effects of having a black background in luminance-modulated conditions, the moving stimulus could also be bright yellow on a neutral yellow background (BY, three left-most points in graphs), as could the flash (BY-Ctrl., remaining two open symbols).

As can be seen from the 95% confidence intervals, for main experimental conditions (closed symbols), all flash-lag illusions were significant, except those with luminance-modulated flash (L) and equiluminant (E) or equiluminant in luminance noise (En) moving stimulus. A 3×3 repeated measures ANOVA on the main experimental conditions revealed a significant effect of moving stimulus contrast, $F(2, 9) = 19.22$, $p = 0.001$, $\rho\eta^2 = 0.81$, of flash contrast, $F(2, 20) = 21.51$, $p = 0.00001$, $\rho\eta^2 = 0.68$, but no interaction ($p = 0.19$, $\rho\eta^2 = 0.54$, moving stimulus and interaction by multivariate test as sphericity violated).

After collapsing across flash contrast, the difference between luminance-modulated and equiluminant moving stimuli was not significant ($p_{2-tailed} = 0.06$, $d = 0.64$), but that between luminance-modulated and equiluminant in luminance noise moving stimuli was ($M_L = 0.60$, $M_{En} = 0.15$, $t(10) = 4.03$, $p_{2-tailed} = 0.002$, $d = 1.22$), as was that between equiluminant and equiluminant in luminance noise moving stimuli ($M_E = 0.43$, $M_{En} = 0.15$, $t(10) = 6.32$, $p_{2-tailed} = 0.00009$, $d = 1.90$). *In summary, using a luminance modulated moving stimulus as a starting point, making the moving stimulus equiluminant did not affect the flash-lag illusion, but making it equiluminant in noise did result in a significant reduction of the illusion magnitude.*

After collapsing across moving stimulus contrast, the difference between luminance-modulated and equiluminant flashes was significant ($M_L = 0.15$, $M_E = 0.53$, $t(10) = 5.70$, $p_{2-tailed} = 0.0002$, $d = 1.72$), as was that between luminance-modulated and equiluminant in luminance noise flashes ($M_L = 0.15$, $M_{En} = 0.50$, $t(10) = 4.85$, $p_{2-tailed} = 0.001$, $d = 1.46$), but that between equiluminant and equiluminant in luminance noise flashes was not ($p_{2-tailed} = 0.68$, $d = 0.13$). *Starting from a luminance-modulated flash, making the flash equiluminant significantly increased the illusion magnitude, but adding luminance noise had no additional effect.*

No comparison between a bright yellow stimulus on neutral yellow background control condition, and its corresponding experimental condition, approached significance ($ps > 0.27$, $ds < 0.23$).

When the flash was luminance-modulated, and the moving stimulus was equiluminant in luminance noise, six participants had a significant flash-lead effect. Generally the pattern of participant's data followed that of the overall means, but as [Figure 2](#) shows there was considerable variation in flash-lag magnitudes.

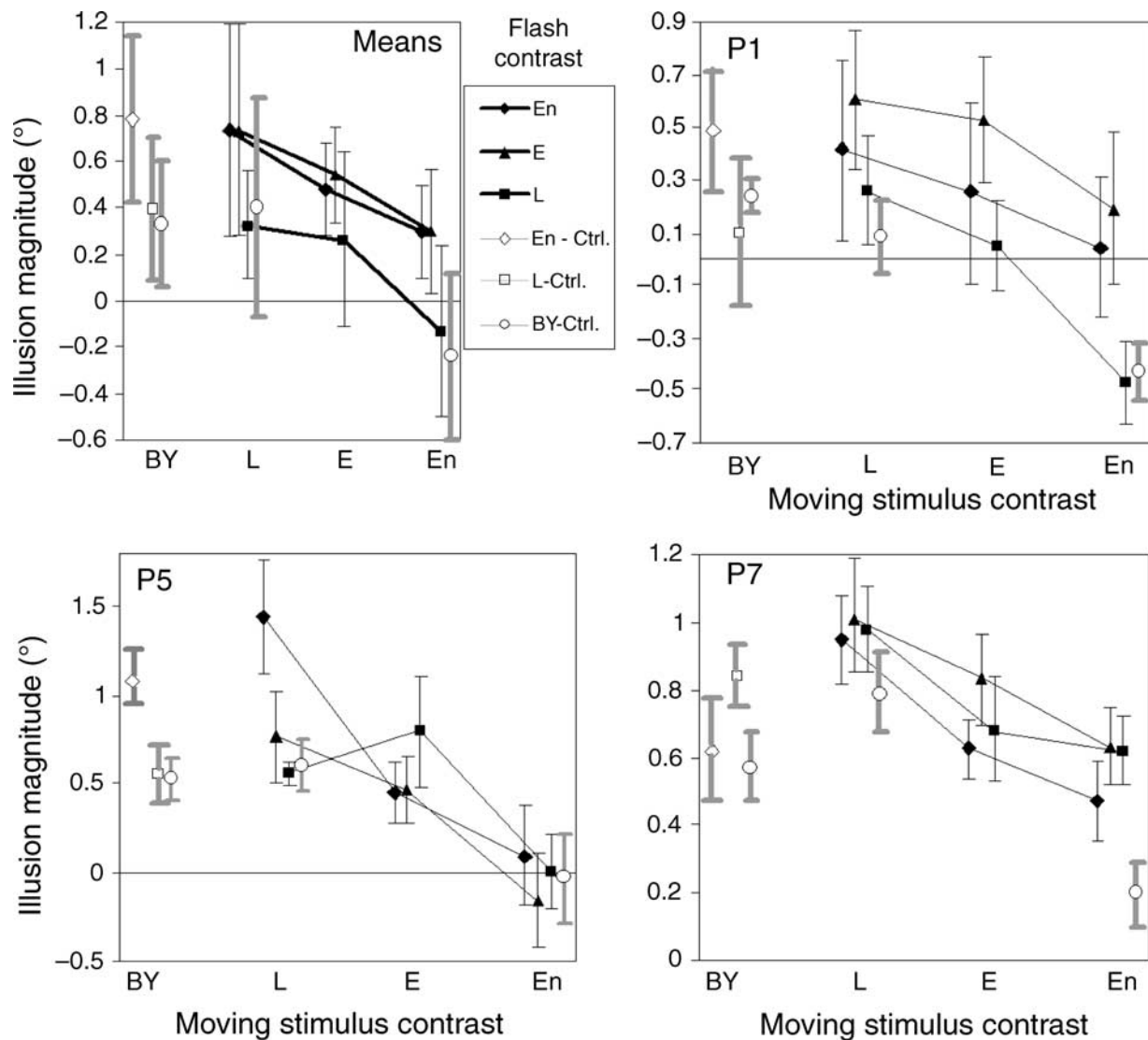


Figure 2. Results for [Experiment 1](#)—means and three representative participants. Conditions with filled symbols and black lines are main experimental ones, open symbols correspond to control conditions. ‘En’ = Equiluminant in luminance noise, ‘E’ = Equiluminant, ‘L’ = luminance-modulated, ‘BY’ = Bright Yellow on mid-yellow background, ‘En-Ctrl.’ = Equiluminant in noise flash, ‘L-Ctrl.’ = luminance-modulated flash, ‘BY-Ctrl.’ = Bright Yellow flash on mid-yellow background. Error bars are 95% confidence intervals.

Discussion

As had previously been found (Arnold et al., 2009; Chappell et al., 2002), making the moving stimulus equiluminant with its background did not result in a reliable reduction in the magnitude of the flash-lag illusion, compared to a condition where it was luminance-modulated (although note that Arnold et al., 2009 did not separately manipulate the contrast of moving stimulus and flash). However, the addition of luminance noise to the moving stimulus lead to a dramatic reduction, with the illusion being completely nulled, on average, and converted into a flash-lead illusion for half of the participants (when the flash was luminance-modulated). Hence, the use of luminance noise to eliminate the residual M cell processing of equiluminant stimuli (Baker et al., 1998; Mullen et al.,

2003) appears to be crucial to reducing the flash-lag illusion magnitude. Interestingly, Durant and Johnston (2004) were able to demonstrate a reduction in the *flash-drag illusion*, where a flash’s perceived position is modified by the presence of an adjacent stimulus containing motion, using luminance noise (they used white dots flickering on and off simultaneously on a gray background), with *non-equiluminant* stimuli.

Luminance noise may have facilitated our finding in part because the moving stimulus traverses the retina, and the equiluminance point varies across this (Livingstone & Hubel, 1987), creating a luminance artifact that is also eliminated by the luminance noise. Support for this idea comes from our findings manipulating flash contrast, as flashes all appeared in a limited region above fixation. Here making the flash equiluminant did significantly

increase the illusion, in agreement with Chappell et al.'s (2002) findings. However, their suggestion of an interaction between flash and moving stimulus contrast was not found here. Interestingly, the addition of noise to the flash had no further effect. See our [General discussion](#) for further comments on this point. Note that these findings with regard to the flash do not help to explain the spatial advantage of the moving stimulus over the flash under normal (luminance-modulated) conditions. They do suggest that the M-pathway facilitates processing of the flash—when it does not do so the illusion is even bigger. Note also that when both stimuli were equiluminant in noise we still found a significant flash-lag effect, not significantly different in magnitude from that when both were luminance-modulated ($p = 0.56$).

Nijhawan (1994, 2008) has proposed that a predictive process, based on motion earlier in the trajectory, allows us to perceive moving stimuli closer to their veridical position than processing delays (~ 100 ms, Nijhawan, 2008) should permit. Eagleman and Sejnowski (2007) similarly contend that a compensatory process biases forwards the perception of the position of moving stimuli, but based on motion later in the trajectory than the position being perceived. Our data do not discriminate between these *spatial projection* accounts, but they do beg the question; If two stimuli were to move alongside each other, one luminance-modulated, and one equiluminant in noise, would we perceive the luminance-modulated one to lead? Could we directly perceive the spatial projection predicted by these theories? Work by Nguyen-Tri and Faubert (2003) investigating the *fluttering heart illusion* (when a colored heart on a differently colored background is moved with that background, it appears to ‘drift’ on that background) suggests so. They displayed an equiluminant (with background) stimulus and a luminance-modulated stimulus oscillating back and forth on horizontal trajectories one above the other, and asked, “... whether the color target appeared ahead or behind the neutral target *in terms of phase* (2AFC).” [italics ours] (p. 630), while they varied the relative phase. They found the equiluminant stimulus to be lagging the luminance-modulated one by approximately 20 ms.

Our [Experiment 2](#) sought to probe more directly the spatial discrepancy by having the two stimuli make a single pass across the display, with participants comparing their relative positions as they passed fixation. Of particular interest was: Would the spatial discrepancy measured between the two moving stimuli account for the difference between the two flash-lag illusions with the two respective moving stimulus contrasts?

Experiment 2

In [Experiment 2](#) two critical conditions from [Experiment 1](#) were replicated—both had a luminance-modulated

flash and there was either a luminance-modulated or an equiluminant in noise moving stimulus (the latter condition appeared as shown in [Figure 1](#)). Additionally there were two conditions with the same two moving stimuli in the lower half of the display, but the flash was replaced with a luminance-modulated moving stimulus in the top half of the display in both cases.

Method

Participants

11 naïve participants, three female, with normal or correct to normal acuity and color (after one individual excluded) vision took part. Five had participated in [Experiment 1](#).

Apparatus and stimuli

These were as already described with the addition of conditions in which the flash in the upper half was replaced with a stimulus moving with the same velocity as the lower moving stimulus, but with various horizontal offsets from it. Stimuli in the top half of the display were always luminance-modulated.

Procedure

In trials with two moving stimuli participants indicated if the top one was to the left or right of the bottom one, as they passed above the fixation. Responses made before this time were not recorded, and participants were informed they had responded too early. Participants were timed out 2.5 s. after the flash had disappeared, or after the upper moving stimulus had passed fixation.

The four conditions described above were randomly interleaved within a single block. To control for the possibility that alternating with equiluminance in luminance noise conditions might cause carry-over habituation of the M pathway to the luminance-modulated conditions, and reduce the flash-lag illusion with luminance-modulated moving stimulus, an additional block was tested with just the two luminance-modulated conditions.

Results

The top-left graph in [Figure 3](#) shows data averaged across the eleven participants, with the closed symbols representing the main experimental conditions. The left flash-lag (FL) symbol represents a condition where both moving stimulus and flash were luminance-modulated (L), whereas for the right one the moving stimulus only was changed to be equiluminant in luminance noise (En). We thus replicated two [Experiment 1](#) conditions, and under ‘normal’ conditions for a flash-lag paradigm, we found a significant flash-lag illusion, which was nulled by making

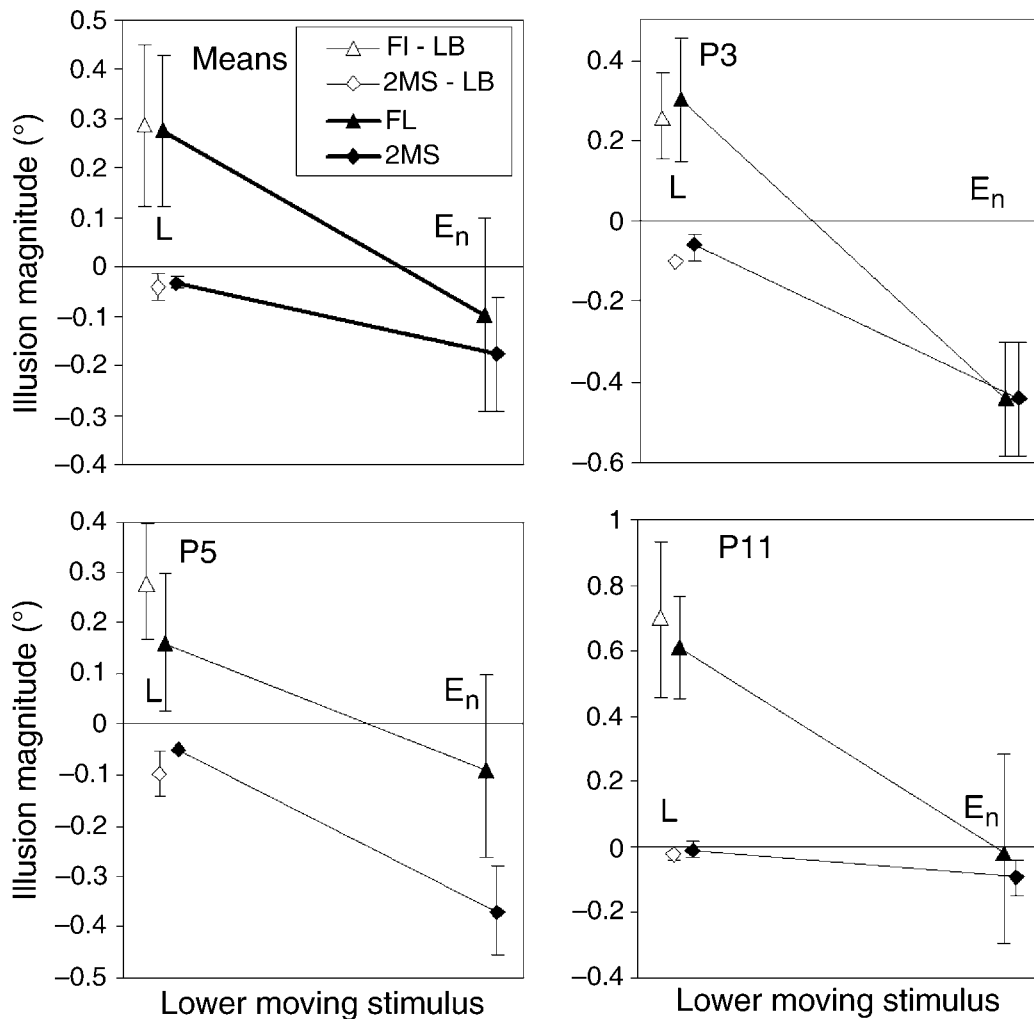


Figure 3. Means (degrees of visual angle) for 11 naïve participants and three representative participants. ‘FL’ = Flash-Lag conditions, ‘2MS’ = compare positions of 2 Moving Stimuli conditions. ‘FL-LB’ = Flash-Lag conditions, blocked with only a luminance-modulated condition, ‘2MS-LB’ = compare positions of 2 Moving luminance-modulated Stimuli, blocked with only a luminance-modulated condition. The four conditions represented by filled symbols were tested in a single block. Error bars are 95% confidence intervals.

the moving stimulus equiluminant in luminance noise ($t[10] = 5.8$, $p_{2-tailed} = 0.0002$, $d = 1.7$). Four participants had a significant flash-lead illusion in the latter condition, one of whom had not been in Experiment 1.

For the remaining two main conditions two stimuli traversed the display together (2MS), the upper one always being luminance-modulated. When the lower one was also luminance-modulated (L), there was a small but significant bias ($t[10] = 5.8$, $p_{2-tailed} = 0.0002$, $d = 1.7$). Of most interest, when the lower moving stimulus was equiluminant in luminance noise (E_n) it was indeed perceived to lag significantly behind the luminance-modulated moving stimulus ($t[10] = 3.5$, $p_{2-tailed} = 0.006$, $d = 1.1$).

The difference between these conditions was significant ($t[10] = 3.1$, $p_{2-tailed} = 0.012$, $d = 0.9$).

If the spatial advantage of a luminance-modulated moving stimulus over that of an equiluminant in luminance noise moving stimulus could account for the difference in flash-lag illusions with the moving stimuli of different contrast (L vs. E_n), the two sloping lines in Figure 3 should be parallel. This was not the case—the interaction was significant ($F[1, 10] = 13.7$, $p = 0.004$, $\eta^2 = 0.6$). The proportion of difference accounted for was 39%.

Control conditions were also tested where luminance-modulated lower moving stimulus conditions were run in a separate block, i.e. not interleaved with trials where the lower moving stimulus was immersed in luminance noise. The flash-lag ($t[10] = 0.3$, $p_{2-tailed} = 0.8$, $d = 0.09$) and the 2 moving stimuli ($t[10] = 1.0$, $p_{2-tailed} = 0.4$, $d = 0.3$) illusion magnitudes did not differ from their corresponding ones when interleaved.

Discussion

If both stimuli in [Figure 1](#) were moving together from left to right, and displayed as shown, they may well be perceived to be aligned. This illusion is arguably an extreme variant of the Hess illusion, in which a lower contrast moving stimulus is perceived to spatially lag a higher contrast moving stimulus (Whitney, 2002), as one of our stimuli had zero (luminance) contrast. However, our manipulation has the added benefit over the Hess illusion that it minimizes M pathway processing for one moving stimulus, and thus yields insight into the underlying neurophysiology of our illusion. We believe that this Magno-Parvo-Hess (M-P-Hess) illusion is a promising paradigm for the further study of the M pathway contribution to the perception of moving stimuli.

It is unsurprising that a single spatial bias process cannot account for the flash-lag illusion. Attentional contributions to the flash-lag illusion have been demonstrated (Baldo, Kihara, Namba, & Klein, 2002; Namba & Baldo, 2004; Sarich, Chappell, & Burgess, 2007) and attenuating M pathway processing will affect these (Laycock, Crewther, & Crewther, 2008; Steinman, Steinman, & Lehmkuhle, 1997). It may be that attention returns to the moving stimulus from the flash (Baldo & Klein, 1995) in the flash-lag task, and does not need to do this with two moving stimuli.

Of course, our results are entirely consistent with the M pathway simply conferring a temporal advantage (cf., Purushothaman, Patel, Bedell, & Ögmen, 1998; Whitney & Murakami, 1998), which for a moving stimulus is perceived as a spatial advantage. Our measured spatial advantage of the luminance-modulated moving stimulus over the equiluminant in noise moving stimulus translates to a temporal advantage of about 11 ms. with our stimulus speed. Interestingly, this is at the lower end of estimates based on physiology and VEP studies (Bullier, 2001; Laycock et al., 2008; Laycock, Crewther, & Crewther, 2007; Moutoussis & Zeki, 1997) for how much sooner information might reach V1 via the M pathway than via the P pathway—thought to be about 20 ms.

General discussion

Our results in both experiments are consistent with M pathway facilitation of processing of the moving stimulus, resulting in it being perceived further along its trajectory than it would be in the absence of such processing. Thus, the facilitation in the models proposed by Eagleman and Sejnowski (2007) and Nijhawan (1994, 2008) could be occurring via the M-pathway. Indeed, if our manipulation making the moving stimulus equiluminant in luminance noise is only affecting M pathway processing, then given that we have completely nulled

the flash-lag illusion (with a ‘normal’, i.e. luminance-modulated, flash), the whole spatial advantage of the moving stimulus over the flash, when both stimuli are luminance-modulated, could be attributed to processes occurring in this pathway, and areas to which it projects. On the other hand, it does not seem to be the case that the M pathway confers a *differential* processing advantage on the moving stimulus (Khurana & Nijhawan, 1995; Nijhawan, 2008). The flash also benefited from M pathway processing, with a very similar change in flash-lag illusion magnitude to that which resulted from manipulating moving stimulus contrast (with our stimulus parameters). Thus, when the flash was also equiluminant in luminance noise a flash-lag illusion was again observed, indistinguishable from that when both stimuli were luminance-modulated. The most parsimonious conclusion would seem to be that processes other than those specific to the M pathway underlie the flash-lag illusion with luminance-modulated stimuli. With different parameters, however, the M pathway benefits to moving stimulus and flash may not be equal, so that this pathway does contribute to the illusion.

The flash-lead measured with six participants in [Experiment 1](#), and four in [Experiment 2](#) means that if the flash and moving stimulus were displayed with the positions shown in [Figure 1](#), these participants may well have reported that they were aligned. Such a flash-lead effect has only previously been found by making the flash extremely bright, and the moving stimulus very dim (Ögmen, Patel, Bedell, & Camuz, 2004; Purushothaman et al., 1998). In our experiment the moving stimulus actually had half the luminance when it was luminance-modulated compared to when it was equiluminant (see [Experiment 1 Apparatus and stimuli](#)). Stimulus luminance per se was therefore a counter-confound, tending to reduce the effect of our moving stimulus contrast manipulation. The relatively low luminance of our moving stimulus—one-third to one-quarter of that used in most other studies—likely accounts, at least in part, for the modest size of our flash-lag illusion with luminance-modulated stimuli.

Our findings are consistent with other studies showing that attenuating processing in the M pathway reduces position biasing due to motion. Durant and Johnston’s (2004) study has already been described. Ashida, Yamagishi, and Anderson (2007) investigated whether making a drifting grating equiluminant within its stationary envelope reduced the position bias of the envelope (De Valois & De Valois, 1991), compared to when the grating was luminance-modulated. When the position had to be remembered and indicated by touching a screen, there was a reduction of the position biasing of the envelope (but not when position was compared with a co-existing marker).

What processes might our manipulation involving luminance noise be revealing? As discussed by Baker et al. (1998) and Mullen et al. (2003) a likely possibility is that

the delayed post-receptoral processing of long-wave cone signals compared to middle-wave cone signals within the luminance pathway generates dynamic artifacts within the luminance system in response to moving equiluminant stimuli, as has been demonstrated previously (Stromeyer, Kronauer, Ryu, Chaparro, & Eskew, 1995; Stromeyer et al., 2000). It is informative to examine this proposal in the light of our results. In [Experiment 1](#), we found that adding luminance noise to an equiluminant flash did not further increase the flash-lag illusion, whereas adding noise to an equiluminant moving stimulus significantly reduced the illusion (whose magnitude had not been affected as we went from luminance-defined to equiluminant stimuli). This indicates that the luminance artifacts masked by the luminance noise only substantially affected the processing of the moving stimulus. Processing of the moving stimulus depends critically on the precise integration of signals over space and time. It is therefore unsurprising that suppressing these M-pathway luminance artifacts with luminance noise has specifically removed a processing advantage the moving stimulus was deriving from them.

McGraw, Walsh, and Barrett (2004) found that TMS stimulation to V5/MT reduced illusory motion shift due to adaptation to drifting gratings, leading them to propose that it is focal for the influence of motion on position perception. Others have also suggested that feedback from V5 to V1 underlies various motion biasing phenomena (Durant & Johnston, 2004; Nishida & Johnston, 1999; Whitney & Cavanagh, 2000). Since V5 is predominantly fed by the M pathway (Laycock et al., 2008; Nassi & Callaway, 2009) TMS and luminance noise may be viewed as alternative techniques for ‘taking out’ this area.

A possible mechanism for the biasing would be the activation by V5 projections of position representations in V1 ‘ahead’ of those being activated by bottom-up processes (cf. Kirschfeld & Kammer, 1999). To resolve the conflict between the two positions (or a spread of positions) in favor of those activated via V5, it could be that projections from V5 also inhibit position representations ‘behind’ those activated by V5. Certainly this would be consistent with the finding that the contrast at the ‘tail’ of a grating, moving within a stationary envelope, is perceived to be less than that in other parts (Arnold, Thompson, & Johnston, 2007; Whitney et al., 2003), and Chappell’s (2007) finding that the contrast of a flash is suppressed around, and particularly behind, a moving stimulus. In the latter case the suppression extended out to 10.5° from the moving stimulus, strongly suggesting feedback from a higher area rather than horizontal projections within an area (Angelucci & Bullier, 2003).

Input to the primate dorsal processing stream is dominated by the M pathway (Laycock et al., 2007; Tootell, Reppas, Kwong, et al., 1995). Our results would then place the locus of the flash-lag illusion in the ventral stream. This would be consistent with the finding that often perception exhibits larger illusions than motor tasks.

For example, White, Linares, and Holcombe (2008) showed that the luminance levels of moving stimuli did not affect the ability to anticipate an interception with a button-press, whereas they did affect perception of the position of the moving stimuli. We anticipate, however, that if the interception experiment were done with our equiluminant in luminance noise moving stimuli, that interception performance would be affected, as the M-pathway and dorsal stream were attenuated.

By separately and independently rendering the flash-lag stimuli equiluminant and immersing them in luminance noise we have revealed M-pathway contributions to the processing of both. As these contributions were similar in magnitude under our stimulus parameters, taken together they could not account for our illusion with all luminance-modulated stimuli. A second experiment with two moving stimuli again revealed the facilitatory effect of M-pathway processing on the perceived position of a moving stimulus.

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Corresponding author: Mark Chappell.

Email: m.chappell@griffith.edu.au.

Address: School of Psychology MG, Griffith University, 176 Messines Ridge Rd., Mt Gravatt, 4122, QLD, Australia.

References

- Angelucci, A., & Bullier, J. (2003). Reaching beyond the classical receptive field of V1 neurons: Horizontal or feedback axons? *The Journal of Physiology*, 97, 141–154.
- 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., Ong, Y., & Roseboom, W. (2009). Simple differential latencies modulate, but do not cause the flash-lag effect. *Journal of Vision*, 9(5):4, 1–8, <http://>

- www.journalofvision.org/content/9/5/4, doi:10.1167/9.5.4. [PubMed] [Article]
- Arnold, D. H., Thompson, M., & Johnston, A. (2007). Motion and position coding. *Vision Research*, *47*, 2403–2410.
- Ashida, H., Yamagishi, N., & Anderson, S. J. (2007). The relative contributions of colour and luminance signals towards the visuomotor localisation of targets in human peripheral vision. *Experimental Brain Research*, *183*, 425–434.
- Baker, C. L., Jr., Boulton, J. C., & Mullen, K. T. (1998). A nonlinear chromatic motion mechanism. *Vision Research*, *38*, 291–302.
- Baldo, M. V. C., Kihara, A. H., Namba, J., & Klein, S. A. (2002). Evidence for an attentional component of the perceptual misalignment between moving and flashing stimuli. *Perception*, *31*, 17–30.
- Baldo, M. V. C., & Klein, S. A. (1995). Extrapolation or attention shift? *Nature*, *378*, 565–566.
- Bullier, J. (2001). Integrated model of visual processing. *Brain Research Reviews*, *36*, 96–107.
- Cantor, C. R. L., & Schor, C. M. (2007). Stimulus dependence of the flash-lag effect. *Vision Research*, *47*, 2841–2854.
- 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., & Hardwick, D. (2002). The flash-lag effect and equiluminance. *Clinical and Experimental Ophthalmology*, *30*, 213–216.
- De Valois, R. L., & De Valois, K. K. (1991). Vernier acuity with stationary moving gabors. *Vision Research*, *31*, 1619–1626.
- Durant, S., & Johnston, A. (2004). Temporal dependence of local motion induced shifts in perceived position. *Vision Research*, *44*, 357–366.
- Eagleman, D. M., & Sejnowski, T. J. (2007). Motion signals bias localization judgments: A unified explanation for the flash-lag, flash-drag, flash-jump, and Fröhlich 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]
- Fu, Y.-X., Shen, Y., & Dan, Y. (2001). Motion-induced perceptual extrapolation of blurred visual targets. *Journal of Neuroscience*, *21*, RC172.
- Khurana, B., & Nijhawan, R. (1995). Reply to Extrapolation or attention shift. *Nature*, *378*, 566.
- Kirschfeld, K., & Kammer, T. (1999). The Fröhlich effect: A consequence of the interaction of visual focal attention and metacontrast. *Vision Research*, *39*, 3702–3709.
- Laycock, R., Crewther, D. P., & Crewther, S. G. (2008). The advantage in being magnocellular: A few more remarks on attention and the magnocellular system. *Neuroscience and Biobehavioral Reviews*, *32*, 1409–1415.
- Laycock, R., Crewther, S. G., & Crewther, D. P. (2007). A role for the ‘magnocellular advantage’ in visual impairments in neurodevelopmental and psychiatric disorders. *Neuroscience and Biobehavioral Reviews*, *31*, 363–376.
- Livingstone, M. S., & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *Journal of Neuroscience*, *7*, 3416–3468.
- McGraw, P. V., Walsh, V., & Barrett, B. T. (2004). Motion-sensitive neurones in V5/MT modulate perceived spatial position. *Current Biology*, *14*, 1090–1093.
- Moutoussis, K., & Zeki, S. (1997). A direct demonstration of perceptual asynchrony in vision. *Proceedings of the Royal Society of London B*, *264*, 393–399.
- 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.
- Namba, J., & Baldo, M. V. C. (2004). The modulation of the flash-lag effect by voluntary attention. *Perception*, *33*, 621–631.
- Nassi, J. J., & Callaway, E. M. (2009). Parallel processing strategies of the primate visual system. *Nature Reviews Neuroscience*, *10*, 360–372.
- Nguyen-Tri, D., & Faubert, J. (2003). The fluttering-heart illusion: A new hypothesis. *Perception*, *32*, 627–634.
- 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*, 179–239.
- Nishida, S., & Johnston, A. (1999). Influence of motion signals on the perceived position of spatial pattern. *Nature*, *397*, 610–612.
- 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.
- Purushothaman, G., Patel, S. S., Bedell, H. E., & Öğmen, H. (1998). Moving ahead through visual latency. *Nature*, *396*, 424.
- Sarich, D., Chappell, M., & Burgess, C. (2007). Dividing attention in the flash-lag illusion. *Vision Research*, *47*, 544–547.

- Steinman, B. A., Steinman, S. B., & Lehmkuhle, S. (1997). Transient visual attention is dominated by the Magnocellular stream. *Vision Research*, *37*, 17–23.
- Stromeyer, C. F., III, Gowdy, P. D., Chaparro, A., Kladakis, S., Willen, J. D., & Kronauer, R. E. (2000). Colour adaptation modifies the temporal properties of the long- and middle-wave cone signals in the human luminance mechanism. *The Journal of Physiology*, *526*, 177–194.
- Stromeyer, C. F., III, Kronauer, R. E., Ryu, A., Chaparro, & Eskew, R. T., Jr. (1995). Contributions of human long-wave and middle-wave cones to motion detection. *The Journal of Physiology*, *485*, 221–243.
- Tootell, R. B., Reppas, J. B., Kwong, K. K., et al. (1995). Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *Journal of Neuroscience*, *15*, 3215–3230.
- White, A. L., Linares, D., & Holcombe, A. O. (2008). Visuomotor timing compensates for changes in perceptual latency. *Current Biology*, *18*, R951–R953.
- Whitney, D. (2002). The influence of visual motion on perceived position. *Trends in Cognitive Sciences*, *6*, 211–216.
- Whitney, D., & Cavanagh, P. (2000). Motion distorts visual space: Shifting the perceived position of remote stationary objects. *Nature Neuroscience*, *3*, 954–959.
- 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*, 656–657.