

# Simple differential latencies modulate, but do not cause the flash-lag effect

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When a brief static flash is presented in physical alignment with a moving target, the position of the flash can seem to lag behind that of the moving target. Various explanations exist. One of the most popular is the differential latency hypothesis. This assumes that neural latencies for moving stimuli are shorter than those for static stimuli. Accordingly, the flash lag would occur because perception is temporally fragmented, with moving stimuli seen before static. To test this, observers were asked to make different judgments concerning the same stimulus. Observers either judged if color changes in moving and static stimulus sections were synchronous, or whether the different stimulus sections were aligned at the time of a color change. If the flash-lag were driven by a simple differential latency, we would expect both judgments to be marked by a temporal advantage for moving stimuli. Our results suggest the contrary, as only the later judgment was marked by a flash-lag effect. The apparent timing of moving and static color changes was veridical. However, when we introduced a systematic differential latency, by modulating image contrast, both judgments were affected. Our data therefore suggest that a simple differential can modulate flash-lag type effects, but they do not cause the phenomenon.

Keywords: flash lag, visual latency, image contrast

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## Introduction

The visual flash-lag effect is typically assessed by comparing the apparent relative positions of a brief static flash and a continuously moving target. When both stimuli are physically aligned in space and time, the flash appears to lag behind the position of the moving target, hence the term flash-lag (Mackay, 1958; Nijhawan, 1994).

One of the most popular accounts of the flash-lag is the differential latency hypothesis. The underlying assumption is that different stimuli have different perceptual latencies. Specifically, the theory proposes that the visual system responds with a shorter latency to moving than it does to static stimuli (Baldo & Klein, 1995; Kregelberg & Lappe, 2000; Murakami, 2001; Patel, Ogmen, Bedell, & Sampath, 2000; Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000). Accordingly, the apparent offset of flashed and moving stimuli would occur because of a perceptual delay for flashed relative to moving stimuli.

There is scant physiological evidence for a moving stimulus advantage of sufficient magnitude to explain the flash-lag. In fact, it has been shown that neurons in Macaque MT respond more rapidly to transient, as opposed to moving,

stimuli (Raiguel, Lagae, Gulyas, & Orban, 1989). This would appear to preclude activity in this region, and presumably its human homologue, from serving as the neural basis for the flash-lag. In contrast, small temporal advantages for moving, over static (or transient), stimuli have been observed in Macaque LGN (Orban, Hoffmann, & Duysens, 1985) and Cat primary visual cortex (Jancke, Erlhagen, Schöner, & Dinse, 2004). However, the extent of these advantages (~15 ms) is too small to provide a credible explanation for the flash-lag, which has variously been estimated as ~45–80 ms (Eagleman & Sejnowski, 2000a; Purushothaman et al., 1998; Whitney & Murakami, 1998).

While there is little physiological evidence for a sufficient temporal advantage for moving stimuli, there is some stronger behavioral support. For instance, manipulations of stimulus speed suggest that the flash-lag is consistent with a uniform temporal delay for static, relative to moving, stimuli (Brenner & Smeets, 2000; Kregelberg & Lappe, 2000; Nijhawan, 1994; but see Wojtach, Sung, Truong, & Purves, 2008). The differential latency hypothesis provides a simple explanation for this. It has also been shown that flash-lag magnitude can be modulated by stimulus-dependent variations in visual latency (Purushothaman et al., 1998). This too is consistent with the differential latency hypothesis. However, a

note of caution should be added to this last point. The fact that flash-lag magnitude can be modulated by latency changes does not dictate that a differential latency normally exists. Rather, the introduction of a latency difference might be an additional fact that modulates an effect that has a quite different underlying cause.

Perhaps the strongest prediction of the differential latency hypothesis is that moving stimuli should have a temporal advantage that results in them being seen before coincident static stimuli. Eagleman and Sejnowski (2000b) attempted to test this. They had observers judge the timing of a flash relative to the cessation of movement. They found no evidence for a temporal advantage for either stimulus event, which is seemingly inconsistent with the differential latency hypothesis. However, this challenge was somewhat undermined by the fact that there can be no flash-lag effect at the offset of a moving stimulus (Eagleman & Sejnowski, 2000a).

To test this central prediction of the differential latency hypothesis more directly, this study will use temporal judgments concerning continuously moving stimuli. Specifically, observers will judge the relative timings of color changes in continuously moving and static stimulus sections. In another condition, observers will judge the relative alignment of moving and static stimulus sections at the time of a color change.

We reason that if the flash-lag is driven by a simple differential latency, that causes moving stimuli to be seen *before* static stimuli, all perceptual decisions regarding moving stimuli should show a temporal advantage relative to static stimuli. In our experiments, this should include both our relative timing and alignment judgments. However, if the flash-lag is driven by processes that selectively impact spatial judgments, we would not expect a temporal advantage for moving stimuli when judging apparent timing.

## General methods

### Observers

Each of the experiments reported was completed by the authors and by three additional observers who were naïve as to the purpose of the study. All had normal, or corrected to normal, visual acuity.

### Procedure

Experiments were conducted in a darkened room. There were two experimental tasks, completed in different runs of trials. In the color synchrony judgment task, observers were required to judge whether color changes within rotating and static stimulus sections were synchronous or

asynchronous. In the spatial alignment task, the rotating and static stimulus sections changed color at the same times and observers were required to judge if they had been aligned or misaligned at the time of the color change.

## Apparatus

Visual stimuli were generated using Matlab software to drive a Cambridge Research Systems VisAge stimulus generator, and were displayed on a gamma corrected 21" Samsung SyncMaster 1100p+ monitor (1024 × 768 resolution; 120 Hz refresh rate). All stimuli were viewed from 57 cm, with the observer's head supported by a chinrest. Responses were recorded via a Cambridge Research Systems CB6 response box.

## Experiment 1

### Method

Stimuli consisted of sinusoidal luminance modulated gratings (see Figure 1) presented at 100 percent Michelson contrast. These surrounded a black central fixation point (diameter subtending 0.21 dva). The peak colors of the gratings alternated between red (CIE coordinates  $x = 0.63$ ,  $y = 0.33$ ,  $Y = 23.84$ ) and green (CIE coordinates  $x = 0.28$ ,  $y = 0.61$ ,  $Y = 23.84$ ). The outer rotating grating was contained within an annulus with an outer diameter subtending 4.3 dva and an inner diameter subtending 1.8 dva. The inner grating was contained within a circular window subtending 1.8 dva. The spatial frequencies of both gratings were 2 cycle/dva. The rate of rotation for the outer annulus was 0.5 cycles/second. On each trial the stimulus presentation persisted until the observer made a response, by pressing one of two response buttons.

During runs of trials for the color synchrony judgement task, color changes in the rotating stimulus section were manipulated relative to those within the inner static stimulus section according to the method of constant stimuli (ranging  $\pm 250$  ms from physical synchrony, sampled in 50 ms steps). To ensure that orientation did not provide a reliable cue on this task, the timing of the color changes were randomized in relation to the rotation cycle on a trial-by-trial basis.

During runs of trials for the spatial alignment task, the timing of synchronous color changes, in both stimulus sections, were manipulated relative to physical alignments of the two stimulus sections. This was also done via the method of constant stimuli across the same range of temporal offsets as the former task.

A run of trials consisted of 12 presentations of each of 11 timing relationships in a pseudo random order. Each

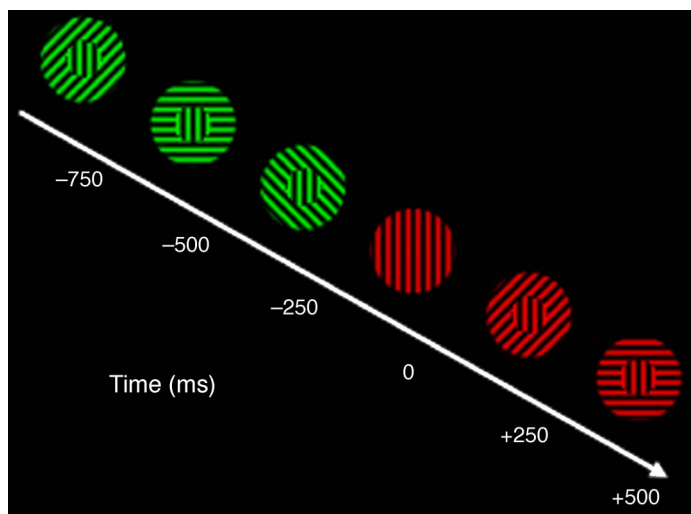


Figure 1. Depiction of the stimulus used in [Experiment 1](#). Epochs from a trial with a clockwise rotating annulus are depicted. In this case, the rotating and inner static sections of the stimulus change color when the two sections are physically aligned (0 ms).

observer completed 4 runs of 132 individual trials for each of the experimental tasks.

Data from each observer provided distributions of apparent color change synchrony, and of apparent static and moving stimulus section alignments, both as a function of relative timing. Gaussian functions were fitted to these distributions and the fitted peaks were taken as estimates of the observers' point of subjective synchrony (PSS) for the relevant experimental task.

## Results

[Figure 2](#) depicts PSSs for moving and static color changes for each observer, along with the average PSS and associated standard error of measurement. As can be

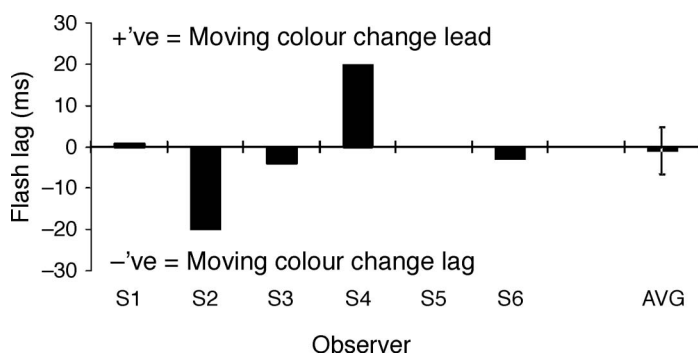


Figure 2. Bar plot depicting PSS estimates for moving and static color changes. Individual observer estimates are shown along with the average across observers. The error bar depicts  $\pm 1$  SEM.

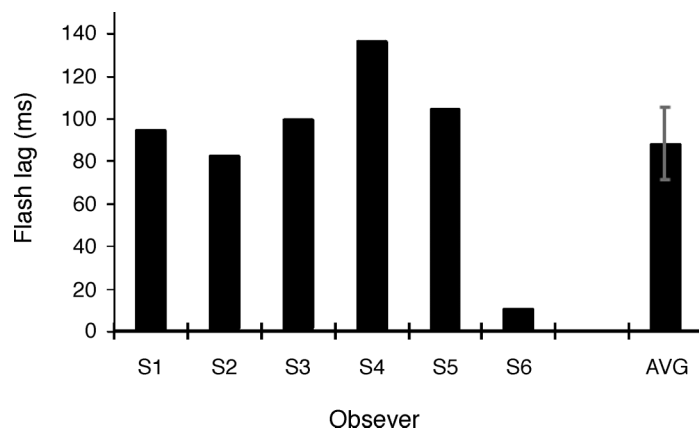


Figure 3. Bar plot depicting PSS estimates for color changes and alignments of the moving and static stimulus sections. Individual observer estimates are shown along with the average effect across observers. The error bar depicts  $\pm 1$  SEM.

seen, there was no evidence for a robust temporal advantage for moving, relative to static, color changes when observers judged if the two were synchronous or asynchronous (average offset  $-1 \pm 6$  ms;  $t_5 = -0.191$ ,  $p = 0.856$ ).

In contrast to color change synchrony judgements, a robust flash-lag effect was found for judgments of relative position at the time of a color change ( $t_5 = 5.15$ ,  $p < 0.01$ ; see [Figure 3](#)). If the two components of the stimulus were to seem aligned at the time of color changes, color changes had to occur *before* the rotating stimulus component became physically aligned with the static component ( $89 \pm 9$  ms). The magnitude of this effect was very similar to flash-lag magnitudes reported in previous studies (Eagleman & Sejnowski, 2000a; Nijhawan, 1994; Purushothaman et al., 1998; Whitney & Murakami, 1998).

## Discussion

[Experiment 1](#) is marked by a dissociation. A temporal advantage for moving relative to static stimulus sections was observed when making spatial alignment judgements, but not when making temporal synchrony judgments. These data are therefore inconsistent with a simple differential latency that causes observers to see moving stimulus sections before they see static stimulus sections.

What if, however, our hypothesis concerning the effects of a *simple* differential latency was erroneous? We have suggested that a simple differential latency should impact all types of perceptual decision, including both the temporal and spatial judgments of [Experiment 1](#). Is this characterization correct?

To assess this, we conducted a second experiment, wherein we manipulated image contrasts. It is generally

accepted that visual latencies are inversely related to image contrast (Burr & Corsale, 2001; Lennie, 1981; Roufs, 1963; Williams & Lit, 1983). It has also been shown that this type of manipulation can impact flash-lag magnitude (Purushothaman et al., 1998). But will a manipulation of image contrast also impact on the temporal synchrony judgements that we have used?

## Experiment 2

### Method

Details concerning [Experiment 2](#) are similar to those described for [Experiment 1](#), with the following exceptions.

In [Experiment 2](#) the rotating grating was contained within an annulus with an outer diameter subtending 4.3 dva and an inner diameter subtending 2 dva. The inner static grating had a diameter subtending 1.8 dva. There was therefore a 0.2 dva separation between the two stimulus components see [Figure 4](#).

Stimuli were set against a gray background (CIE coordinates:  $x = 0.28$ ,  $y = 0.29$ ,  $Y = 59.8$ ). This served as a white point for color space calculations. To induce reliable latency differences, color contrasts were manipulated. Gratings were modulated along the L-M and S-cone isolating axes of DKL color space (Derrington, Krauskopf, & Lennie, 1984). Prior to the experiment, these axes were determined for each observer using a minimum motion technique (Anstis & Cavanagh, 1983). Individual objective detection thresholds were then measured for each color axis. Moving and static stimulus sections in the subsequent experiment were then presented at multiples of each observer's detection thresholds.

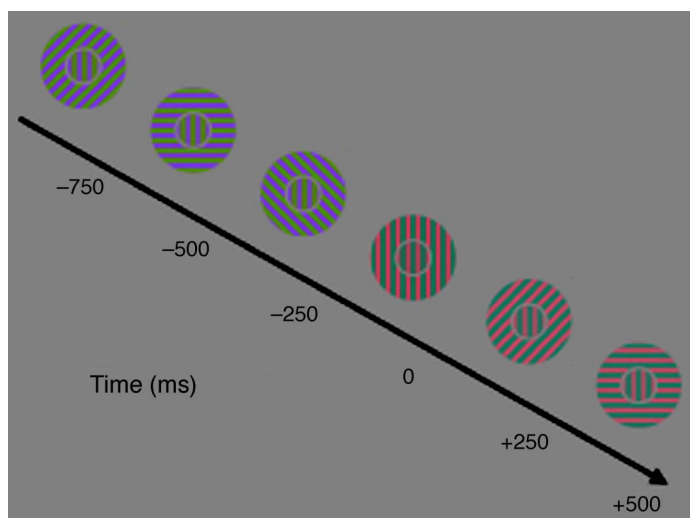


Figure 4. Depiction of stimulus used in [Experiment 2](#).

Apparent offset of moving relative to static colour changes as a function of moving colour contrast

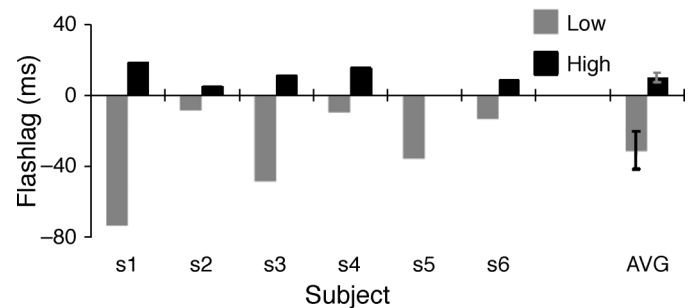


Figure 5. Bar plot depicting PSS for color changes in moving and static stimuli. Data are shown for each observer, along the average PSS across observers. Error bars show  $\pm 1$  SEM.

Modulating stimuli along cardinal axes of color space has two consequences. First, it allows us to easily manipulate image contrasts while alternating between different color states. Second, it might minimize the probability of different types of information projecting along the sub-cortical magno and parvo visual pathways at different rates of information transfer (Orban et al., 1985).

During experimental trials, inner static gratings were presented at twenty times the individual observers' chromatic contrast detection threshold. Surrounding annuli were presented at either 10 (low contrast condition) or at 30 (high contrast condition) times detection threshold.

As in [Experiment 2](#), both the static and rotating stimulus sections alternated between different color states, in this case between red-green and yellow-violet. Change timings were manipulated as described for [Experiment 1](#). Each observer was required to do 2 runs of trials, consisting of 12 presentations of each of the 11 timing relationships for each of the 2 moving stimulus contrast levels, all in a pseudo random order. Each run of trials therefore consisted of 264 individual presentations. Two runs of trials were completed for both the color synchrony and relative alignment tasks.

Gaussian functions were fitted to the derived individual distributions of apparent color change synchrony, and of apparent static and moving stimulus section alignments. The fitted peaks of these functions were taken as estimates of the observers' PSS for the relevant experimental task.

### Results

As can be seen in [Figure 5](#), observers showed opposite effects for the low and high contrast conditions. A flash-lag like effect was observed for color change synchrony judgments in the high contrast condition ( $10 \pm 3$  ms) whereas a flash-lead like effect was observed for color synchrony judgments in the low contrast condition ( $-31 \pm$



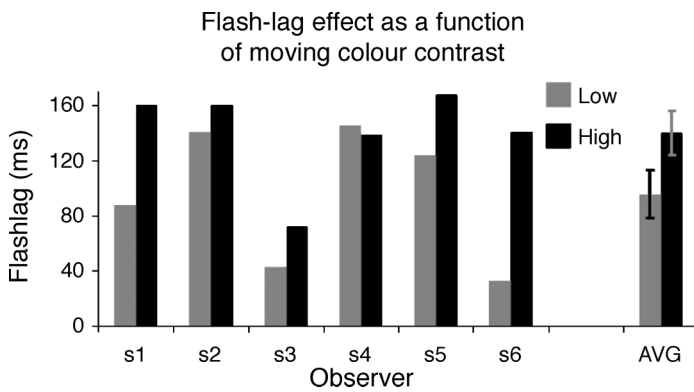


Figure 6. Bar plot depicting PSS for color changes and apparent alignments of the moving and static stimulus sections. Data are shown for each observer, along the average PSS across observers. Error bars show  $\pm 1$  SEM.

11 ms). A paired samples *t*-test showed that color synchrony judgments had been robustly modulated by image contrast ( $t_5 = -3.41$ ,  $p = 0.019$ ).

As can be seen in Figure 6, a flash-lag like effect was observed for relative position judgments concerning both high ( $131 \pm 16$  ms) and low ( $96 \pm 18$  ms) moving chromatic contrast conditions. A paired *t*-test revealed that, of the two conditions, a larger flash-lag effect had occurred in the high, as opposed to the low, contrast condition ( $t_5 = -2.65$ ,  $p = 0.045$ ).

## General discussion

Our data strongly suggest that a simple differential latency is not the underlying cause of the flash-lag effect. In two experiments we contrasted spatial and temporal judgements. In Experiment 1, a robust flash-lag effect occurred, but only when observers judged the relative positions of the moving and static stimulus sections. However, no temporal advantage for moving stimuli was observed when the timing of color changes was assessed. These data are therefore inconsistent with a simple latency difference that delays the perception of static relative to moving stimuli.

On the basis of Experiment 1, it was possible that our characterization of a simple differential latency was flawed. Rather than having a generic influence, the introduction of a simple differential latency might impact spatial judgments but have no consequence for temporal decisions (Eagleman & Sejnowski, 2000a; Nishida & Johnston, 2002; Rao, Eagleman, & Sejnowski, 2001). Experiment 2 suggests that this is untrue. We introduced a simple differential latency by modulating the color contrasts of moving stimulus sections. This manipulation impacted both spatial and temporal judgements.

The modulation of flash-lag magnitude with stimulus contrast echoes a previous study (Purushothaman et al., 1998). This has been taken as evidence that the flash-lag is usually driven by a differential latency for moving, relative to static, stimuli. Our data show that this does not necessarily follow. Our timing judgments were impacted by contrast. However, before this manipulation, the apparent timing of moving and static color changes was veridical. This shows that the introduction of a simple latency difference can introduce a temporal advantage where none had existed. Equally, the introduction of a latency difference could modulate a relationship that is shaped by other factors. Put simply, the fact that a relationship can be modulated via latency differences does not dictate that these are the only determinant.

Our data suggest that any simple differential latency between moving and static stimulus sections must usually be insufficient to explain flash-lag effects. However, we cannot exclude the possibility that a smaller advantage exists. Relevant evidence was provided by an examination of an orientation illusion (Arnold, Durant, & Johnston, 2003). This study made use of the tilt illusion (Gibson & Radner, 1937), which is characterized by an illusory tilt of a central stimulus when surrounded by a stimulus of a different orientation. It was found that when a central test grating was flashed when physically aligned with a rotating annulus, no tilt illusion was observed. This despite the fact that the two stimulus sections did not appear aligned due to the flash-lag (Arnold et al., 2003). These data are reminiscent of those here, in that neither data set is consistent with a differential latency of sufficient magnitude to account for flash-lag type effects. These earlier data, however, were consistent with a smaller,  $\sim 20$  ms, advantage for moving stimuli. This would be consistent with the magnitude of moving stimulus advantage suggested by some neurophysiology (Jancke et al., 2004; Orban et al., 1985; Raiguel et al., 1989).

While the current study was motivated by a desire to test the differential latency hypothesis, our data have implications for another explanation that was motivated by a consideration of visual latencies. The post-diction account proposes that the flash-lag arises as a consequence of a process that facilitates an accurate sense of timing, despite variations in visual latency (Eagleman & Sejnowski, 2000a; Rao et al., 2001). The proposal is that perceptions lag physical events by a considerable temporal margin. Hypothetically, this would allow the brain to consider a temporal extent of information before committing to a perceptual decision. The critical aspect of the proposal, however, is that the apparent timing of the perceptual content is post-dicted, such that we sense that a sensory event has occurred at an epoch preceding the perceptual decision. This could facilitate an accurate sense of timing despite different periods of time being required to reach different perceptual decisions.

As the hypothetical functional significance of post-diction is to facilitate an accurate sense of timing, despite

variations in visual latency (Eagleman & Sejnowski, 2000a; Rao et al., 2001), our data suggesting that timing judgments are shaped by visual latency, via manipulations of image contrast, are problematic. Our data suggest that this form of compensation either does not exist, or that it is incapable of achieving the functional outcomes that it is supposed to achieve. There are numerous similar data sets that pose the same conceptual dilemma (Adams & Mamassian, 2004; Arnold & Clifford, 2002; Arnold & Wilcock, 2007; Bedell, Chung, Ogmen, & Patel, 2003; Paul & Schyns, 2003; Roufs, 1963; Wilson & Anstis, 1969).

Throughout this manuscript, we have referred to a *simple* differential latency. By this, we imply a latency difference that arises at an early point of the visual hierarchy which therefore impacts all subsequent processing. Accordingly, we would expect it to shape all perceptual decisions concerning the impacted input and be a determinant of when stimuli can be seen. Our data suggest that image contrast can be used to instigate this kind of effect (Purushothaman et al., 1998), as it modulates both spatial and temporal judgments. We also believe that this scenario is implied by researchers who cite recordings from retina (Berry, Brivanlou, Jordan, & Meister, 1999) and LGN (Orban et al., 1985) as physiological support for latency difference explanations of the flash-lag. We would argue, however, that this cannot be the fundamental cause of the flash-lag. Our data clearly show that spatial judgments can reflect an apparent temporal advantage for moving stimuli in the absence of a matching advantage for timing judgments. The advantage for moving stimuli is therefore selective.

It is possible, however, that processes at higher echelons of the visual hierarchy might introduce their own differential latencies (Arnold, Clifford, & Wenderoth, 2001; Arnold & Wilcock, 2007; Bartels & Zeki, 1998; Bedell et al., 2003). As higher level activity can be functionally specialized (Zeki, 1978), such effects might only impact specific stimulus attributes (Arnold & Clifford, 2002; Moutoussis & Zeki, 1997) or types of perceptual decision (Bedell et al., 2003; Clifford, Arnold, & Pearson, 2003; Ogmen, Patel, Bedell, & Camuz, 2004). This type of scenario could be described as a *complex* differential latency due to the selectivity of the effects.

Flash-lag effects can occur when comparing the positions of moving and flashed stimuli (Mackay, 1958; Nijhawan, 1994). Our data suggest that such effects are not driven by a simple differential latency that causes moving stimuli to be seen before static, and thereby provides the former with a generic temporal advantage. Instead, it would seem that the effect is driven by more complex processes that selectively impact spatial judgments. Similar effects can be observed with stimuli that change position in auditory (Alais & Burr, 2003) or even color (Sheth, Nijhawan, & Shimojo, 2000) space. Accordingly, it would seem that the advantage is not tied to judgments concerning Cartesian space. Instead, it

may reflect the dynamics of the processes involved in determining and contrasting the instantaneous statuses of changing and non-changing stimulus attributes.

## Conclusions

Our data suggest that the flash-lag is not driven by a simple differential latency, which provides moving stimuli with a generic temporal processing advantage over static stimuli. However, our data also suggest that, when present, differential latencies will influence both spatial and timing perception. Thus, while a simple differential may not be a fundamental cause of the flash-lag, it can modulate the effect.

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## References

- Adams, W. J., & Mamassian, P. (2004). The effects of task and saliency on latencies for colour and motion processing. *Proceedings of the Royal Society of London B: Biological Sciences*, 271, 139–146. [[PubMed](#)] [[Article](#)]
- Alais, D., & Burr, D. (2003). The “Flash-Lag” occurs in audition and cross-modally. *Current Biology*, 13, 59–63. [[PubMed](#)] [[Article](#)]
- Anstis, S. M., & Cavanagh, P. (1983). A minimum motion technique for judging equiluminance. In J. Mollon & R. T. Sharpe (Eds.), *Color vision: Physiology and psychophysics* (pp. 156–166). London: Academic.
- Arnold, D. H., & Clifford, C. W. (2002). Determinants of asynchronous processing in vision. *Proceedings of the Royal Society of London B: Biological Sciences*, 269, 579–583. [[PubMed](#)] [[Article](#)]
- Arnold, D. H., Clifford, C. W., & Wenderoth, P. (2001). Asynchronous processing in vision: Color leads motion. *Current Biology*, 11, 596–600. [[PubMed](#)] [[Article](#)]

- Arnold, D. H., Durant, S., & Johnston, A. (2003). Latency differences and the flash-lag effect. *Vision Research*, *43*, 1829–1835. [[PubMed](#)]
- Arnold, D. H., & Wilcock, P. (2007). Cortical processing and perceived timing. *Proceedings of the Royal Society of London B: Biological Sciences*, *274*, 2331–2336. [[PubMed](#)]
- Baldo, M. V., & Klein, S. A. (1995). Extrapolation or attention shift? *Nature*, *378*, 565–566. [[PubMed](#)]
- Bartels, A., & Zeki, S. (1998). The theory of multistage integration in the visual brain. *Proceedings of the Royal Society of London B: Biological Sciences*, *265*, 2327–2332. [[PubMed](#)] [[Article](#)]
- Bedell, H. E., Chung, S. T., Ogmen, H., & Patel, S. S. (2003). Color and motion: Which is the tortoise and which is the hare? *Vision Research*, *43*, 2403–2412. [[PubMed](#)]
- Berry, M. J., II, Brivanlou, I. H., Jordan, T., & Meister, M. (1999). Anticipation of moving stimuli by the retina. *Nature*, *398*, 334–338. [[PubMed](#)]
- Brenner, E., & Smeets, J. B. (2000). Motion extrapolation is not responsible for the flash-lag effect. *Vision Research*, *40*, 1645–1648. [[PubMed](#)]
- Burr, D. C., & Corsale, B. (2001). Dependency of reaction times to motion onset on luminance and chromatic contrast. *Vision Research*, *41*, 1039–1048. [[PubMed](#)]
- Clifford, C. W., Arnold, D. H., & Pearson, J. (2003). A paradox of temporal perception revealed by a stimulus oscillating in colour and orientation. *Vision Research*, *43*, 2245–2253. [[PubMed](#)]
- Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *The Journal of Physiology*, *357*, 241–265. [[PubMed](#)] [[Article](#)]
- Eagleman, D. M., & Sejnowski, T. J. (2000a). Motion integration and postdiction in visual awareness. *Science*, *287*, 2036–2038. [[PubMed](#)]
- Eagleman, D. M., & Sejnowski, T. J. (2000b). The position of moving objects. *Science*, *289*, 1107a. [[PubMed](#)]
- Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect, and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology*, *20*, 453–467.
- Jancke, D., Erhlagen, W., Schöner, G., & Dinse, H. R. (2004). Shorter latencies for motion trajectories than for flashes in population responses of cat primary visual cortex. *The Journal of Physiology*, *556*, 971–982. [[PubMed](#)] [[Article](#)]
- Krekelberg, B., & Lappe, M. (2000). The position of moving objects. *Science*, *289*, 1107. [[PubMed](#)]
- Lennie, P. (1981). The physiological basis of variations in visual latency. *Vision Research*, *21*, 815–824. [[PubMed](#)]
- Mackay, D. M. (1958). Perceptual stability of a stroboscopically lit visual field containing self-luminous objects. *Nature*, *181*, 507–508. [[PubMed](#)]
- Moutoussis, K., & Zeki, S. (1997). A direct demonstration of perceptual asynchrony in vision. *Proceedings of the Royal Society of London B: Biological Sciences*, *264*, 393–399. [[PubMed](#)] [[Article](#)]
- Murakami, I. (2001). A flash-lag effect in random motion. *Vision Research*, *41*, 3101–3119. [[PubMed](#)]
- Nijhawan, R. (1994). Motion extrapolation in catching. *Nature*, *370*, 256–257. [[PubMed](#)]
- Nishida, S., & Johnston, A. (2002). Marker correspondence, not processing latency, determines temporal binding of visual attributes. *Current Biology*, *12*, 359–368. [[PubMed](#)] [[Article](#)]
- Ogmen, 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. *Vision Research*, *44*, 2109–2128. [[PubMed](#)]
- Orban, G. A., Hoffmann, K. P., & Duysens, J. (1985). Velocity selectivity in the cat visual system. I. Response of LGN cells to moving bar stimuli: A comparison with cortical areas 17 and 18. *Journal of Neurophysiology*, *54*, 1026–1049. [[PubMed](#)]
- Patel, S. S., Ogmen, H., Bedell, H. E., & Sampath, V. (2000). Flash-lag effect: Differential latency, not postdiction. *Science*, *290*, 1051. [[PubMed](#)]
- Paul, L., & Schyns, P. G. (2003). Attention enhances feature integration. *Vision Research*, *43*, 1793–1798. [[PubMed](#)]
- Purushothaman, G., Patel, S. S., Bedell, H. E., & Ogmen, H. (1998). Moving ahead through differential latency. *Nature*, *396*, 424. [[PubMed](#)]
- Raiguel, S. E., Lagae, L., Gulyas, B., & Orban, G. A. (1989). Response latencies of visual cells in macaque area V1, V2 and V5. *Brain Research*, *493*, 155–159. [[PubMed](#)]
- Rao, R. P., Eagleman, D. M., & Sejnowski, T. J. (2001). Optimal smoothing in visual motion perception. *Neural Computation*, *13*, 1243–1253. [[PubMed](#)]
- Roufs, J. A. (1963). Perception lag as a function of stimulus luminance. *Vision Research*, *3*, 81–91.
- Sheth, B. R., Nijhawan, R., & Shimojo, S. (2000). Changing objects lead briefly flashed ones. *Nature Neuroscience*, *3*, 489–495. [[PubMed](#)]

- Whitney, D., & Murakami, I. (1998). Latency difference, not spatial extrapolation. *Nature Neuroscience*, *1*, 656–657. [[PubMed](#)]
- 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. [[PubMed](#)]
- Williams, J. M., & Lit, A. (1983). Luminance-dependent visual latency for the Hess effect, the Pulfrich effect, and simple reaction time. *Vision Research*, *23*, 171–179. [[PubMed](#)]
- Wilson, J. A., & Anstis, S. M. (1969). Visual delay as a function of luminance. *American Journal of Psychology*, *82*, 350–358. [[PubMed](#)]
- Wojtach, W. T., Sung, K., Truong, S., & Purves, D. (2008). An empirical explanation of the flash-lag effect. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 16338–16343. [[PubMed](#)] [[Article](#)]
- Zeki, S. (1978). Functional specialization in the visual cortex of the monkey. *Nature*, *274*, 423–428. [[PubMed](#)]