

## Untangling spatial from temporal illusions

The flash-lag effect (FLE) is a phenomenon in which a flash aligned with a moving object appears to spatially lag behind the stimulus. In their recent review of the FLE, Krekelberg and Lappe conclude that 'the influence of differential latencies on the perception of position of moving objects... is undeniable' [1]. They refer to the hypothesis that differences in physiological latencies might translate directly into perceptual time differences. This idea has enjoyed recent popularity as a proposed explanation for the flash-lag illusion [2–4]. However, this is inconsistent with evidence that timing judgements between flashes and moving objects are very accurate [5]. Recent research suggests that the FLE, as opposed to being a temporal illusion, is a consequence of spatial interpolation [5–7].

The appeal to differences in physiological latency to explain the FLE runs the risk of oversimplification, given the many shortcomings that hypothesis must contend with. First, the differential latency (DL) model predicts that the outcome of a 'race' between *de novo* movement and a flash can be changed, by giving the flash a head start; however, this hypothesis has been tested and disproved [6]. Second, the DL model predicts that the onset time of a flashed and moving object will be misperceived; this hypothesis has also been tested and disproved [8]. Third, the DL model runs into difficulties in the 'flash-initiated' paradigm, in which the flash and moving object appear simultaneously: the DL model predicts that the moving object will suffer the same delay as the flash, as it suddenly appears from nowhere. However, the continuous and flash-initiated conditions yield the same psychophysical result [6]. Fourth, skepticism about the DL explanation of the FLE is warranted by the conspicuous absence of physiological support. In fact, as Krekelberg and Lappe acknowledge, the available physiology in the medial temporal area (MT) speaks against the DL model. Thus, the differential latency

hypothesis lacks a sufficient base of support, and any direct connection between the timing of neural signals and the timing of perception is cast into doubt by a critical analysis of the extant data.

Much of the confusion in the stormy world of flash-lag literature can be attributed to a single assumption that has not been critically assessed: the assumption that a measured *spatial* difference can be directly translated into a *temporal* difference. Having assumed such translation, almost all reports on the FLE measure a perceived spatial offset (e.g. 1° of visual angle), but report a putatively corresponding time difference (e.g. 70 ms).

Our alternative view, if correct, is fatal to this assumption: even while a moving object has a real-world time corresponding to each position, it could be that the pairing is no longer veridical, or even retained, in the representation of the stimulus in the nervous system. Given the distributed processing in the visual system, a logical possibility is that position information is not persistently represented, but instead is only computed when needed. In other words, when an observer is asked where a moving object was at a particular moment, a special (and possibly rare) computation is then performed. A smear of spatial positions must be evaluated (deblurred) into a single, unambiguous answer. The result of this computation can be non-veridical – that is, a smear of spatial activity across cortex can be evaluated at some intermediate position. In this view, time can be stamped with high fidelity, but the position associated with that time is the result of a deblurring process that interpolates over a smear of recent positions [5–7]. The observer is only able to report a perceived position after this computation is complete [9]. This framework naturally explains other illusions, such as the Fröhlich effect, in which a moving object that appears suddenly is not seen in its true starting position, but instead some distance into the trajectory [10]. This suggests that the FLE is another incarnation of the Fröhlich effect, one in which the spatial landmark takes on a temporal stamp as a result of being flashed instead of being static [6].

Spatial interpolation over occupied positions of the moving object offers an explanation for the FLE that has many advantages. First, it is consistent with other illusions (e.g. the Fröhlich effect). Second, it is consistent with subjects' ability to accurately judge temporal relationships between flashed and moving objects [5]. Third, it does not embed the assumption that a measured spatial judgement translates directly into a temporal illusion. Fourth, it accounts naturally for the rounding of the curve seen in Whitney and Murakami's reversal of the moving object, for which they were forced to appeal to an additional mechanism (neural delay variability or a separate spatiotemporal averaging filter) [3]. Thus, in contrast to Krekelberg and Lappe's statement that latency differences 'undeniably' influence perception, a spatial explanation could prove more parsimonious.

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## Response: Untangling spatial from temporal illusions

Eagleman and Sejnowski take issue with our claim that latencies undeniably influence the perception of position. The Hess [1] and Pulfrich [2] phenomena, however, elegantly demonstrate just this. In these illusions, a decrease in brightness and the concomitant increase in latency cause a moving object to appear to lag behind an otherwise identical object. Burr and Ross [3] made this even more explicit by presenting stimuli with a slight temporal offset to different eyes. The visual system interprets this temporal offset as a spatial disparity. Of course, this does not imply that differential latencies (DL) are all there is to the flash-lag effect [4]. Nevertheless, we believe that Eagleman and Sejnowski's arguments against DL are far from conclusive.

First, they point out that '...timing judgements between flashes and moving objects are very accurate'. However, their published data [5] show only accurate timing judgements between flashes and motion-offset. Flash-lag at motion-offset is quite different from standard flash-lag [6]. In fact, Eagleman and Sejnowski's own data [7] show that there is no flash-lag at motion-offset. Hence, these timing judgements give us no information whatsoever on what causes the flash-lag effect. Timing judgments at motion-onset, or during ongoing motion, could address this issue. To date, however, no verifiable data have been published on this topic.

Second, Eagleman and Sejnowski state that, in the DL model, giving the flash a head start should reduce its delay and reduce the flash-lag effect. We agree this should be the case. However, their experiment [7] does not test this prediction. As Whitney and Cavanagh [8] and Patel *et al.* [9] have pointed out, the subjects were instructed to report the perceived beginning of the trajectory of the moving object, rather than the offset between the moving and flashed object (the usual report in flash-lag experiments). The perceived onset of a trajectory is beyond the physical onset of the trajectory (the Fröhlich effect). In their experiment, Eagleman and Sejnowski varied the time of appearance of a pointer that subjects used to indicate the onset. There is no reason to assume that

this time of appearance should affect the perceived onset. This is, indeed, what the authors found, but it has no bearing on the flash-lag effect.

Third, Eagleman and Sejnowski argue that the DL model cannot explain flash-lag at motion-onset because '...the moving object will suffer the same delay as the flash, as it suddenly appears from nowhere'. We believe this oversimplifies what latency is: it is not just determined by the retinal input in some infinitesimal window at stimulus onset, but by a multitude of factors, including general arousal, contextual effects, and crucially also the stimulation immediately following the stimulus. In the time between the photons first hitting the retina and observer first becoming aware of the stimulus, there is ample opportunity for neural interactions to speed up or slow down the response [10].

Finally, the fact that the available physiology in the medial temporal area (MT) speaks against the DL model can, at best, be used to argue that differential latencies in MT are not the neural correlate of the flash-lag effect. Generalizing to the whole brain is quite a stretch, especially given that there is evidence for small latency differences of the right sign in the lateral geniculate nucleus, and that only very few electrophysiological studies have even addressed this issue.

Having argued in favour of the DL model for a few paragraphs now, it is about time to re-state that we do not actually believe that this model explains all aspects of the flash-lag effect [4]. On the contrary, we too believe that it is essential that 'a smear of spatial positions must be evaluated. ...into a single, unambiguous answer'. In our terminology this is temporal averaging; the system evaluates the positional difference between (the representation of) a flashed and a moving object over a period of time and reports the average. Because, on average, the flashed object is behind the moving object, a flash-lag will be reported [11,12]. Eagleman and Sejnowski have extended this view to a more complicated process of spatiotemporal integration that they call postdiction. Postdiction extends averaging to a more general view of internal model building, adds a mechanism to weigh the sources of information the visual system uses and, importantly, it makes explicit why the system would want to do this [13]. These are provocative ideas and well worth pursuing, but they undeniably need more published data to support them.

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