

Single mechanism, divergent effects; multiple mechanisms, convergent effect

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Abstract: It is commonplace for a single physiological mechanism to seed multiple phenomena, and for multiple mechanisms to contribute to a single phenomenon. We propose that the flash-lag effect should not be considered a phenomenon with a single cause. Instead, its various aspects arise from the convergence of a number of different mechanisms proposed in the literature. We further give an example of how a neuron's generic spatio-temporal response profile can form a physiological basis not only of "prediction," but also of many of the other proposed flash-lag mechanisms, thus recapitulating a spectrum of flash-lag phenomena. Finally, in agreeing that such basic predictive mechanisms are present throughout the brain, we argue that motor prediction contributes more to biological fitness than visual prediction.

It is likely that multiple mechanisms combine to create the flash-lag phenomenon: persistence, priming, backward masking, temporal dilation, and even attention have all been demonstrated in one study or another (Bachmann & Pöder 2001; Baldo & Namba 2002; Kanai et al. 2004; Kregelberg & Lappe 2001; Namba & Baldo 2004; Sheth et al. 2000). It seems that cleverly designed experiments can prove the importance of one's favored model, but in vanishingly small parameter regimes. For example, experiments on the flash-terminated condition support extrapolation, but the results are limited to degraded, uncertain stimuli (Fu et al. 2004; Kanai et al. 2004). Other experiments support differential latency, but these use stimuli of much lower luminance (Patel et al. 2000; Purushothaman et al. 1998).

We have previously argued that a very basic consideration of neuronal response profiles can recapitulate a wide array of flash-lag related mechanisms and effects (Kanai et al. 2004). As a stimulus moves in physical space, it maps out a topographically corresponding path in cortical space. At a given time instant, there are the following components: (A) cells at the "current" location of the stimulus are the most active; (B) cells in the immediate past path of the motion contain residual activity; (C) cells in the distant past path contain below-baseline activity caused by adaptation and intracortical inhibition; and (D) cells in the family of future motion paths have above-baseline sub-threshold activity through intracortical excitation. This pattern of activity arises from the basic temporal response profile of a single neuron to input, and from the fact that lateral connections between neighboring neurons tend to cause net excitation to weakly firing neurons and net inhibition to strongly firing neurons (Henry et al. 1978; Levitt & Lund 1997; Somers et al. 1998; Stemmler et al. 1995). These four components of the spatiotemporal response profile have strengths that depend not only on factors intrinsic to the neuronal network, but also on stimulus parameters such as luminance, speed, and so on.

These components can implement various mechanisms related to flash lag and motion processing. Component D could be descriptively labeled as priming, and if the activity in D is high enough to shift the centroid of the activity distribution forward, it could partially underlie a motion extrapolation mechanism. C could be a critical part of the neural basis for motion deblurring. When component B is prominent, differential latency for motion and flash arises: The spatiotemporal integral of the activity of A+B will reach perceptual threshold faster than a temporal integral of a stationary flash. Finally, stimulus conditions such as uncertainty will determine whether the activity in A alone suffices for awareness, or whether B needs to be added; this is a plausible neural basis for two different Bayesian

estimators – conditional mean and maximum likelihood. Thus, the tuning of a simple neural mechanism can give rise to myriad psychophysical phenomena and high-level models.

When distilled down to the idea of lateral propagation of cortical activity, we agree that prediction is intuitive and should be neurally omnipresent. The above properties of neurons are generic and found in almost all networks – sensory and motor. One question that arises then is: What is the relative contribution of sensory and motor prediction to successful behavior?

We argue that prediction in the motor realm seems to be more effective and useful. First, visual prediction is applicable if a target moves with uniform velocity, but motion is hardly ever uniform in real life – physical (friction) and internal (attention, interest) factors often disrupt the smooth flow of motion. Second, motor prediction does not need to be as accurate as visual prediction. The agent can often over-compensate for the movements of the target, thus arriving at a common intersection point some time before the target. This allows the agent some slop, and with it, the flexibility to compensate for change in target speed, and for relatively small synaptic delays within its own nervous system. All delays – visual, synaptic, and of the muscle or tool-based effector – are available in a lump sum and are undifferentiated to the motor system as motor error. Motor systems routinely compensate for delays of the order of seconds, which arise from slow effectors. Such a system should be well-equipped to accommodate 100 msec of visual synaptic delay. Thus, the motor system seems to be the workhorse. Although this is but an isolated example, we note that prism adaptation begins in the motor system; one's motor system compensates for errors weeks before one begins to correctly perceive the world.

Visual prediction at the neural level is then just one of many important mechanisms in two senses: it is only one of the mechanisms which contribute to the flash-lag effect, and it is only one of the types of "neural prediction" which contribute to our biological fitness. In the case of flash-lag, variations in stimulus conditions can dictate the relative importance of visual prediction. In the case of biological fitness, it seems that visual prediction is just a small jumpstart – a small, subthreshold benefit to the organism in comparison to other predictive brain mechanisms.

The mechanisms responsible for the flash-lag effect cannot provide the motor prediction that we need in daily life

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Abstract: The visual prediction that Nijhawan proposes cannot explain why the flash-lag effect depends on what happens after the flash. Moreover, using a visual prediction based on retinal image motion to compensate for neuronal time delays will seldom be of any use for motor control, because one normally pursues objects with which one intends to interact with one's eyes.

In his target article, Nijhawan proposes that early visual processing provides the prediction that is needed to deal with sensory-motor delays when we interact with moving objects, rather than such prediction arising from complex motor strategies as is generally assumed. He argues that the flash-lag effect and related phenomena illustrate the visual basis of such prediction. In his discussion of the extensive literature on this topic, he ignores several findings that show that the flash-lag effect cannot be