

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; Kerkelberg & 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

caused by a visual prediction based on the preceding object motion.

Several experiments have been performed in which a target moves both before and after the flash, but changes its speed or direction of motion at an unpredictable moment around the time of the flash. According to Nijhawan's account of visual prediction, the target's motion after the flash should be irrelevant for its perceived position at the time of the flash. However, the perceived position has been shown to depend on the target's motion up to 80 msec after the flash (Brenner & Smeets 2000; Eagleman & Sejnowski 2000; Whitney & Murakami 1998). This result is inconsistent with any kind of motion extrapolation. It is also unlikely that it is primarily caused by neuronal signals pertaining to the flashed target taking longer to reach the brain than ones pertaining to the moving target (Whitney & Murakami 1998), because the flash-lag effect can be demonstrated with a very bright flash and a dimly lit moving object.

The dependence of the flash-lag effect on what happens after the flash can readily be explained if one regards perception as an active process (O'Regan & Noe 2001). If so, the location of the moving object is not evaluated continuously. It is only evaluated when one needs to know it. The flash indicates that this is the case. As determining the position in response to the flash takes time, the result is a judged position that the object only reaches some time after the flash. The fact that the moving object is perceived ahead of its location at the time of the flash is therefore not due to extrapolation, but to sampling its position too late. This implies that the flash-lag effect should decrease if one can convince subjects to start evaluating the location of the moving object before the flash is registered. A way to achieve this earlier sampling is by making the moment of interest more predictable. Indeed, the flash-lag effect is reduced (and even absent in some subjects) under such conditions (Brenner & Smeets 2000).

Besides the doubts about the role of visual prediction in the flash-lag phenomenon, there is also a more fundamental problem with the main claim of the target article. Nijhawan's interesting claim is that visual prediction provides the prediction needed to compensate for neuronal delays when interacting with moving objects. However, when trying to intercept a moving target, subjects tend to pursue the target with their eyes. This is so not only in laboratory conditions (Mrotek & Soechting 2007) but also, for instance, during the final approach phase when hitting a ball in cricket (Land & McLeod 2000). Moreover, subjects are better at an interception task when they pursue the target with their eyes than when they fixate somewhere near the point of interception (Brenner & Smeets 2007). One reason for pursuing the target is that pursuit eliminates the blur caused by retinal motion, leading to more precise vision. However, the lack of retinal motion means that the predictive mechanism proposed in the target article will not be working. Therefore, in the situations in which prediction is needed most in daily life, the proposed mechanism cannot contribute to such prediction.

The way in which subjects pursue moving targets can give us insight into how prediction works. It is known that pseudo-random smooth target motion is pursued with delays of more than 200 msec (Collewijn & Tamminga 1984; Koken & Erkelens 1992). Targets moving at a constant – and therefore predictable – speed are pursued with a negligible delay (Barnes & Asselman 1991). If this reduction in visuomotor delay were caused by the kind of visual prediction proposed in the target article, it would only work when the target motion is constant. This is not the case: Negligible delays are also found when the target motion is predictable, but not on the basis of the directly preceding visual information (Thier & Ilg 2005). For instance, humans can pursue sinusoidal motion with minimal delays. It only takes about half a cycle of the sinusoidal target motion to achieve the minimal tracking delay. If the target disappears, or changes its motion, the sinusoidal eye movement continues for about half a cycle (van den Berg 1988). Additional evidence against the

proposed visual prediction is that the prediction in pursuit is task-specific.

When following a target with their eyes, subjects make errors in the smooth pursuit that are corrected by catch-up saccades that are predictive: They compensate for the errors that develop during their programming and execution. These catch-up saccades could be based on a visual prediction, or on a motor prediction specific to the pursuit. In the former case, the errors in pursuing a smoothly moving target should also be compensated for when making a saccade in response to a sudden jump of the target. However, in such an experiment, the saccade amplitude is matched to the target jump (Smeets & Bekkering 2000). So the prediction that subjects make in order to be able to track the moving target is specific to pursuit.

Our conclusion is that if the low-level predictive mechanisms proposed by Nijhawan exist, they are responsible neither for the flash lag effect nor for the motion extrapolation in our interaction with moving objects.

Anticipating synchronization as an alternative to the internal model

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Abstract: The fundamental assumption of compensation for visual delays states that, since delays are dealt with, there must be compensatory mechanisms. These mechanisms are taken to be internal models. Alternatives for delay compensation exist, suggesting that this assumption may not be fundamental, and nor should the existence of internal models be assumed. Delays may even be employed in their own compensation.

A case is made for the ubiquity of anticipatory behavior by the sensory-motor system, including visual perception. There is no question that anticipation is ubiquitous; however, that ubiquity tends to prompt assumptions about the world which may not be warranted. For instance, “the fundamental assumption of compensation for visual delays, [...] which states: ‘In the absence of mechanisms compensating for visual delays, many behaviors in otherwise healthy animals would be disrupted.’” (target article, sect. 6.1, para. 2; italics in original).

The nature of these compensating mechanisms is of particular importance. If a tacit assumption which goes along with “the fundamental assumption” is that those compensation mechanisms are forward models, then the assumption may not be fundamental. The existence of alternative explanations for anticipatory behavior strongly suggests that the assumption should not be regarded as axiomatic. Moreover, the term *compensation* connotes both the presence of error and active correction. The term *anticipation* will be used to avoid these implications.

Here, we present an alternative paradigm for anticipatory systems, which may be useful when considering the anticipation for visual delays. This alternative comes in the form of anticipating synchronization (Ciszak et al. 2004; Voss 2000). In one of its simplest manifestations, anticipating synchronization is a coupling of two dynamical systems such that the slave system is able to synchronize with the future of the master system. The general form of this coupling is shown in the following system of equations:

$$\begin{aligned}\dot{x} &= f(x(t)) \\ \dot{y} &= f(y(t)) + kx(t) - y(t - \tau)\end{aligned}$$