works for discrete events. The reason for this is simple: neural latencies differ drastically for different sensory modalities as well as within a modality for different stimuli (e.g., Bolz et al. 1982; Sestokas & Lehmkuhle 1986). The absence of a coordinating influence that can also compensate for brief, non-moving events would necessarily lead to a fragmentation of the phenomenally experienced world. For example, the brighter portions of a briefly seen object would seem to have occurred at different time than the darker portions. As multimodal, briefly presented, non-moving objects are not perceptually fragmented, and because many of the demonstrations of temporal adaptation have successfully used stationary, briefly presented, discrete stimuli, there must be some form of temporal compensation that does not involve spatial prediction.

Finally, in their experiments, Cunningham et al. (2001a; 2001b) noted that many participants complained about apparent perceptual changes during temporal adaptation. More specifically, as behavior in the delayed conditions approached normal levels, the participants began to indicate that the visual and proprioceptive events, which were separated by up to 400 msec, seemed to occur simultaneously. A number of studies have since empirically confirmed this perceptual shift in the point of subjective simultaneity (Fujisaki et al. 2004; Navarra et al. 2007; Vatakis et al. 2007; Vroomen et al. 2004). Several of these studies used brief, discrete, stationary stimuli. In general, these results suggest that adaptation to temporal delays is at least partially perceptual in nature. Nijhawan argues that prism adaptation, to the degree that it occurs in the visual system, is support for the theory that the visual system is engaged in prediction. Thus, the evidence that humans can both behaviorally and perceptually compensate for changes in delayed information would seem to be support for the claim of visual prediction in general, if not for spatial extrapolation in particular.

In sum, the human sensorimotor systems can compensate not only for their own internal characteristics, but also for external changes in both the spatial and temporal relationships between the senses. Moreover, at least for temporal adaptation, this compensation occurs partially in the perceptual systems, implying that they are engaging in some form of prediction. As temporal adaptation also works for discrete as well as continuous events and is not necessarily motion based, it cannot be fully explained by spatial extrapolation. Nijhawan states that, "The goal of visual prediction is to use priors contained in the unfolding visual stimulus to create a perceived state of the world that matches, as far as possible, the actual state of the world" (sect. 4, para. 2). Given what is known about how spatial and temporal compensation mechanisms adapt, this statement might be amended to make the strong involvement of previous experience more explicit: The goal of visual prediction is to use priors acquired from both previous experience and the currently unfolding visual stimulus to create a perceived state of the world that matches, as far as possible, the actual state of the world.

Asynchronous neural integration: Compensation or computational tolerance and skill acquisition?

James E. Cutting
Department of Psychology, Cornell University, Ithaca, NY 14853-7601.
jec7@cornell.edu
http://people.psych.cornell.edu/~jec7/index.htm

Abstract: Nijhawan argues that neural compensation is necessary to account for couplings of perception and action. Although perhaps true in some cases, computational tolerance for asynchronously arriving

continuous information is of more importance. Moreover, some of the everyday venues Nijhawan uses to argue for the relevance of prediction and compensation can be better ascribed to skill.

> *It is the mark of an educated man to look for precision in each class of things just so far as the as the nature of the subject admits . . . and not to look for precision in all things alike.*
> — Aristotle, *Nicomachean Ethics*, I, 1094b24 & 1098b5

Nijhawan reviews the need for theoretical consideration of delays brought about by differential neural transmission time. Such a need is unequivocal in some situations, and the flash-lag effect, which Nijhawan has championed for some time, seems reasonably accounted for in such terms.

However, not all neural delays need be compensated for. Instead, there is often wide tolerance for integrating diverse continuous signals. As an example, consider first the asynchronous presentation of auditory speech and its visual signal. What are the tolerances in the perceiver for detecting that anything is amiss? As it turns out, the window is fairly large and asymmetrical. The auditory delays referenced to the visual signal can be between -45 msec (an auditory lead) and $+200$ msec (an auditory lag; Grant et al. 2004). Rewritten, this is $\sim 80 \pm 120$ msec. The 80 msec value can be taken as a difference in the delay between the auditory and visual systems. It might need to be "compensated" for, and it is consistent with Nijhawan's report. However, the tolerance window of ± 120 msec from that mean value suggests that no compensation is necessary. Instead, information in both signals is temporally distributed and, arriving differentially from auditory and visual modalities, is seamlessly integrated within a fairly wide temporal window.

This first example, however, is not about perception and action, with which Nijhawan is most concerned. Therefore, consider a second case – the disfluency effects of delayed auditory feedback while speaking. Stuart et al. (2002) reported no performance differences among 0, 25, 50 msec delays, but there were many disfluencies at 200 msec delays. In other words, the coupling of auditory perception and vocal action is no more affected by a 50 msec delay than by listening to oneself normally. This too suggests tolerance, not compensation.

Of course, this second line of evidence concerns audition, which is not the modality of Nijhawan's focus. Therefore, let us consider, third, the results from the literature on delayed visual feedback. In a functional magnetic resonance imaging (fMRI) study, Farrer et al (2007) showed that subjects had no differential awareness of a 0 versus 100 msec visual delay in watching themselves pluck pegs from a board, and their performance did not suffer either. Moreover, the angular gyrus, which seems to register awareness of such asynchrony, was not substantially engaged until delays of 150 msec and longer. Again, this suggests tolerance for décalage in signals, this time visual and motor.

Nijhawan's primary interest concerns the prediction of the visual location of a moving object in space. The most critical everyday venues for such needs are in hunting and in ball games. Among the latter – whether baseball, cricket, tennis, or ping pong – one can rightly argue for a required accuracy of ~ 5 msec when hitting a ball with appropriate control (Bootsma & van Wieringen 1990; Land & McLeod 2000; Lobjois et al. 2006; Tresilian 1993; Watts & Bahill 1990). Nijhawan's point is that the visual system – retina to V1 and beyond – is slow by comparison.

Nonetheless, in all of these sports, the best participants are involved in highly stereotyped, highly practiced situations. Moreover, the relevant behavior of the opponent and the flight of the ball are distributed over as much as a second and often more. In baseball, those deemed excellent hitters – that is, they can accurately hit the ball 3 out of 10 times against the best pitchers – earn well more than US$1000 per swing of their bat.

Skill accrued over many years – and a background of appropriate genetics – is required to perform at this level. Moreover, there is ample evidence that hitters cannot follow the ball near

the critical time when they need to hit it (Land & McLeod 2000; Watts & Bahill 1990), and visual acuity in the periphery, where the ball arrives when it is hit, is extremely poor. Hitting skills are not due to higher cognition. Indeed, thinking often interferes with performance (e.g., Beilock et al. 2004). But such performance is also not due to the kind of neural compensation that Nijhawan addresses. Instead, it is the result of a skill-driven refinement of perception and action in the context of the information distributed in time.

A kind of compensation does occur in a number of situations. In archery, and in trap and skeet shooting, the sportsperson must aim to lead the target that is being shot at. Yet it seems unlikely that one should look for pure sensory or motor accounts in such feats. Instead, and again, it is the skill of the individual calibrated over repeated practice that allows targets to be hit.

None of this is to denigrate Nijhawan's attempt at laying out the needs for a coherent theory of dynamic neural organization. My purpose is simply to state that computational tolerance for the time-staggered arrival of integrable neural information, and skill acquired over many long bouts of practice, are likely to be more important than is compensation.

Prediction and postdiction: Two frameworks with the goal of delay compensation

David M. Eagleman
Department of Neuroscience, Baylor College of Medicine, Houston, TX 77030.
eagleman@bcm.edu
http://neuro.bcm.edu/eagleman

Abstract: Although prediction is one of the key tasks of intelligent brains, it often proves impossible in an unpredictably changing world. Hence, brains often decide what happened retrospectively. This framework of postdiction, the opposite of prediction, stands as an alternative or complimentary framework to prediction. I further show how motor-sensory recalibration demonstrates delay compensation at the perceptual level.

To construct an up-to-date, dynamic picture of the outside world, brains have to overcome a problem: different sensory signals are processed at different speeds in different parts of the brain. As Nijhawan emphasizes, all this processing takes time – time during which the outside world continues to change. One clever method by which nervous systems can reduce this problem is by predicting, whenever possible, the next state of the world (see Hawkins & Blakeslee 2004; Nijhawan 1994; Suddendorf & Corballis 2007; and the present target article). Nijhawan has long championed the idea that prediction happens at the level of the perceptual system (e.g., Nijhawan 1994), mitigating temporal delays at early, premotor stages. My comments here reinforce an emphasis on the brain's need to compensate for delays, but I offer some additional methods that the brain may use beyond prediction.

Prediction and postdiction: Two frameworks with the goal of compensation. In conjunction with any prediction it attempts, the brain also appears to implement a *postdictive* strategy (Eagleman & Sejnowski 2000). This term simply means that the brain continues to collect information after an event (such as a flash) while settling on its best estimate about events and their timing in the outside world. Postdiction is easily illustrated by apparent motion: When the first stimulus disappears, one cannot perceive the motion until after the second stimulus has appeared (in an unpredicted location). Nonetheless, one has the illusion of seeing it move on the fly. Obviously, this can only happen when perception is generated retrospectively (Eagleman 2001).

In the context of the flash-lag effect (FLE), three empirical findings seem to support postdiction: the flash-initiated (Khurana & Nijhawan 1995), flash terminated (Nijhawan

1992), and motion-reversing (Whitney & Murakami 1998) conditions – all of which illustrate that the motion information after the flash, not before it, drives the effect (Eagleman & Sejnowski 2000). Nijhawan suggests that these challenges might be accounted for by a rapidly arbitrated competition between rivaling neural representations. Although he avoids the term postdiction, a biased competition model nonetheless requires it. The competition between a predictive model and new incoming information cannot be tipped until the new information is collected after the flash. No matter how rapidly the arbitration occurs, it still is postdictive.

There are competing explanations for the FLE that do not require the predictive component at all. For example, one alternative draws on the fact that motion signals shift localization judgments (for a review, see Whitney 2002). We have shown that the motion signals collected after an event are the ones that bias perceived position (Eagleman & Sejnowski 2007). Our evidence supports the framework that incoming motion information updates localizations so that the data do not become stale (for details, see Eagleman & Sejnowski 2007). This is a purely postdictive explanatory framework for the FLE.

To understand why postdiction is necessary, one only has to examine the tasks and resources of the visual system. As one of its tasks, the visual cortex tries to get the timing of outside events correct; for its resources, it has to deal with the foibles of the populations that feed it. The retina and visual thalamus have circuitries that cause incoming signals to temporally spread from the first stages of the visual system based, for example, on their luminance (Gawne et al. 1996; Lee at al. 2007; Maunsell et al. 1999). For the visual brain to correctly align the timing of events in the world, it may have to wait $\sim$100 msec for the slowest information to arrive – thereby allowing the visual system to discount different delays imposed by the early stages.

The reason for the vigorous debate between prediction and postdiction is that both sides enjoy strong support: On the one hand, brains use every available opportunity to predict what is coming next, thus saving valuable processing time; on the other hand, experiments show that perceptions can be changed retrospectively, as may be necessitated by an unpredictably changing world.

The important thing to note is that both the predictive and postdictive frameworks have the same goal: to perceptually place the location of a moving object closer to its real-world position. Prediction does this by guessing ahead; postdiction does this by allowing incoming motion signals to advantageously adjust location judgments. Both techniques lead to the perception of a moving object closer to its real-world position. The advantage of postdiction is its ability to naturally account for sudden motion reversals such as bounces and ricochets; however, it is possible that both mechanisms are implemented in different contexts or in different areas of the nervous system. Future experiments are required to determine these details.

Perceptual compensation for temporal delays. Finally, I want to expand on part of Nijhawan's argument. He correctly points out that compensation can take place at the level of the motor output or the perceptual input (or anywhere in between). He argues on the side of perceptual compensation, a position that has traditionally received little attention, in part because of the paucity of direct experimental support. However, in his target article he leaves out a critical example that supports perceptual compensation: the recalibration of motor sensory systems when exposed to delayed feedback.

The recalibration story begins with a mystery: Given that multisensory signals arrive in the brain at different times, how can the brain decide which events were supposed to be simultaneous in the outside world? We have proposed that the brain perceptually recalibrates its expectations about the arrival times of signals by employing a simple assumption: when the motor system executes an act (such as knocking on a door), all the resulting feedback should be assumed to be simultaneous, and any delays should