be perceptually adjusted until simultaneity is perceived (Stetson et al. 2006). Although this recalibration is normally adaptive, note a strange consequence: Imagine we repeatedly inject a tiny delay (e.g., 100 msec) between a subject's key-press and a subsequent flash for a dozen trials, and then we suddenly remove the delay. Because the perceptual systems have recalibrated to compensate for the delay, the subject now perceives that the flash occurred before the key-press: an illusory reversal of action and sensation (Cunningham et al. 2001a; Stetson et al. 2006). Note that this recalibration is no mere party trick – it is critical to solving the problem of causality, which requires, at bottom, temporal order judgments. The only way causality can be accurately determined in a multisensory brain is to keep the temporal delay of signals calibrated in the face of different sensory pathways operating at different speeds. This example serves to buttress Nijhawan's general argument that compensation for delays can take place at very early, perceptual levels.

Transient signals per se do not disrupt the flash-lag effect

doi: 10.1017/S0140525X08003890

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Abstract: Nijhawan's theory rests on the assumption that transient signals compete with predictive signals to generate the visual percept. We describe experiments that show that this assumption is incorrect. Our results are consistent with an alternative theory that proposes that vision is instead *postdictive*, in that the perception of an event is influenced by occurrences after the event.

Nijhawan has presented a predictive theory of visual motion perception. He notes that because of the delays inherent in visual processing, the visual system cannot detect events at the instant at which they occur. He argues that the visual system compensates by using the information it has to predict the current state of the world. In other words, he suggests that we do not see reality, but rather, the visual system's best guess at reality is based on slightly out-of-date information. To support this theory, Nijhawan relies heavily on a particular visual illusion – the flash-lag effect. Here, we briefly describe experiments that Nijhawan's account cannot handle. Although Nijhawan's predictive theory can readily account for the standard flash-lag paradigm, the flash-terminated version poses a problem. In this version of the paradigm, the moving object disappears at the time of the flash. As Nijhawan notes in the target article, "At the outset, spatial extrapolation should continue beyond the time of unpredictable disappearance of the object. Yet these displays produce no flash-lag effect" (sect. 5.2.2, para. 1). To explain why the flash-lag effect does not occur under these circumstances, Nijhawan makes an additional assumption. He proposes that the transient signal produced by the disappearance of the moving object generates a neural representation (perhaps thalamic) that competes with and eventually overwhelms the predictive representation (perhaps cortical) that would normally cause the flash-lag effect. We will refer to this as the transient signal assumption.

The support for this assumption comes from Maus and Nijhawan (2006, reviewed in section 5.2.2 of the target article). That study did not employ a flash-lag design. Instead, Maus and Nijhawan demonstrated that when a moving object disappears gradually by moving behind a variable neutral density filter, it remains visible past its standard luminance threshold. This finding could be caused by hysteresis (Palmer 1999). In any case, it does not address the issue of whether the presence of a transient signal eliminates the flag-lag effect (i.e., the transient signal assumption).

To test this assumption, we used a reversed-contrast version of the flash-lag paradigm in which the background was gray and the moving object changed from black to white at the moment of the flash. The resultant transient signal must be at least as large as in the flash-terminated version (probably larger, since the neurons in the thalamus are sensitive to contrast polarity; Hubel & Wiesel 1961). If Nijhawan's transient signal assumption is correct, this should abolish the flash-lag effect. Nevertheless, the magnitude of the effect was just as strong with our stimulus as in the standard flash-lag paradigm (i.e., with no transient).

Perhaps Nijhawan's proposed transient signals do not originate in the thalamus and are generated by cells that are not sensitive to contrast polarity (Hubel & Wiesel 1962). Such cells respond as strongly to a white dot as they do to a black dot and so may not generate a transient signal in the reversed-contrast version of the flash-lag effect. If it is assumed that it is these cells that need to generate the relevant transient signals, then this might explain why the flash-lag effect still occurs in our reversed-contrast version of the paradigm. We tested this hypothesis by comparing two versions of the flash-lag paradigm. In one case, the Michelson contrast of the moving object was reduced from 0.30 to 0.04 at the moment of the flash. In the other case, it was reduced from 0.04 to 0; that is, it disappeared. The first condition should produce a larger transient than the second, yet we found the flash-lag effect to be of normal strength in the first case but entirely absent in the second. It appears that, contrary to the transient signal assumption, the flash-lag effect is not disrupted by transients but only by the actual disappearance of the moving object.

Why, then, does the flash-lag effect vanish in the flash-terminated condition? Nijhawan proposes his transient signal assumption as the reason, but our data fail to support that account. Our data are more compatible with the *postdictive* theory of Eagleman and Sejnowski (2007). In brief, this theory postulates that the apparent position of the moving object at the time of the flash is influenced by the motion of the object after the flash. In other words, consistent with our observations, the flash-lag effect should occur in any situation in which the moving object does not disappear, irrespective of any transient signals that might be generated at the time of the flash. This theory can readily account for all our data without invoking any additional mechanisms.

Mental and sensorimotor extrapolation fare better than motion extrapolation in the offset condition

doi: 10.1017/S0140525X08003907

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Abstract: Evidence for motion extrapolation at motion offset is scarce. In contrast, there is abundant evidence that subjects mentally extrapolate the future trajectory of weak motion signals at motion offset. Further, pointing movements overshoot at motion offset. We believe that mental and sensorimotor extrapolation is sufficient to solve the problem of perceptual latencies. Both present the advantage of being much more flexible than motion extrapolation.

Nijhawan claims that the offset of a smoothly moving object masks the extrapolated trajectory of the moving object. Therefore, the flash-lag effect is suppressed in the flash-terminated condition. In an experiment using gradual variation of luminance across the trajectory, the final position was found to be misperceived in the direction of motion (Maus & Nijhawan 2006). The reason given in this study was that the gradual variation of luminance reduced the transient at stimulus offset. Contrary to Nijhawan's hypothesis, forward displacement of the final position of a moving target has been repeatedly observed with strong offsets. Jennifer Freyd (1987) was the first to observe displacement of the final position of an object undergoing implied motion (see overview in Hubbard 2005). She presented a stationary rectangle for 0.25 sec at three different orientations. The successive views implied the rotation of the object in a certain direction. Each view of the object was separated by a blank interval of 0.25 sec, and the remembered final position was probed after a retention interval of 0.25 sec. It is unlikely that low-level motion receptors were stimulated in this paradigm. The stimuli did not even reliably evoke an impression of apparent motion. Thus, the observed localization error has to be due to high-level, cognitive processes. In fact, when the motion type was systematically varied from implied to smooth motion by reducing the stimulus-onset-asynchrony (SOA) of consecutive presentations, the forward extrapolation was found to decrease: The worse the quality of the motion signals, the larger the error (Kerzel 2003). The interpretation was that observers who are confronted with intermittent motion signals, may engage in "mental extrapolation" where they try to predict the upcoming target positions. Mentally extrapolating the future trajectory induces errors in judging the last seen object position.

Nijhawan argues that a gradual reduction of luminance contrast reveals motion extrapolation because masking by the transient at target offset is reduced (Maus & Nijhawan 2006). However, it is just as likely that these conditions reveal mental extrapolation that is induced by the absence of a clearly visible offset. Under conditions of high uncertainty, observers are more likely to predict the stimulus position based on what they expect, rather on the basis of what they see. Thus, the gradual luminance variation may bring high-level and not low-level extrapolation mechanisms to the fore.

Further, one may wonder how much motion extrapolation contributes to accurate sensorimotor control. Let us consider the case of a subject placed in front of a touch-sensitive monitor. When prompted to rapidly hit a moving object with his index finger, the subject will take $\sim$0.3 sec to initiate the movement, and another $\sim$0.35 sec to transport the hand from a home-key 20 cm in front of the monitor to the screen surface. Thus, a total of $\sim$0.65 msec elapses from the moment the imperative signal is presented to the moment the screen is touched. It is clear that subjects who plan to hit the currently visible position will miss the target considerably (at the most: 0.65 sec $\times$ v, where v is target velocity). Hence, accurate interception of moving objects necessarily implies prediction of future positions. An intriguing hypothesis is that sensorimotor computations factor in visual delays. That is, interceptive actions are directed at the position the target will have reached in the time required to move the hand to that position plus visual delays (at the most: $[0.65 + 0.1 \text{ sec}] \times v$, with visual delays equaling 0.1 sec). Pointing to the offset position of a moving object should isolate sensorimotor compensation for visual delays, as the system does not need to take into account the future trajectory. In fact, pointing movements overshoot the final position by a distance that roughly corresponds to the flash-lag effect (Kerzel & Gegenfurtner 2003). In contrast, perceptual judgments were centered on the true offset position. Thus, we believe that visual delays are not treated differently from other types of delays (time to decide, time to move, etc.). The sensorimotor system aims at positions further ahead that correspond to the respective delays.

A characteristic of sensorimotor compensation is that it is flexible and task-dependent. In a set of experiments on the Fröhlich illusion (Fröhlich 1923), we observed that localization judgments (mouse pointing) were affected by rapidly changing visuomotor strategies. In the classical Fröhlich illusion, the perceived onset position of a moving object is displaced in the direction of motion. Possibly, the first part of the trajectory is missed because of attentional latencies and metacontrast. When the onset position is predictable because the target always appears in two narrow regions of space, this error is reproduced with pointing movements. However, when the onset position is highly unpredictable because the target appears randomly in a large region of space, the error is eliminated or even slightly reversed (Müsseler & Kerzel 2004). Our interpretation was that with high uncertainty, subjects try to correct for having missed the initial part of the trajectory by pointing to positions opposite to the direction of motion. Analysis of the time course showed that the effect of uncertainty emerged after only about 10 trials. That is, subjects changed their response strategy as soon as they noticed that the target position appeared in random places. Further, perceptual judgments, which were unaffected by predictability when run in a separate block of trials, showed the same effect of predictability when randomly intermingled with pointing movements (Müsseler et al., in press). Thus, visuomotor strategies may affect the way retinal stimulation is evaluated.

Given the capacity to rapidly adapt visuomotor translation to changing circumstances, one may wonder whether motion extrapolation is needed to deal with visual latencies. Although it cannot be ruled out that such a mechanism exists, assuming its existence does not seem parsimonious. Other, more flexible mechanisms may do the job. Our proposal is that mental extrapolation of target motion and sensorimotor predictions solve the problem of visual latencies.

ACKNOWLEDGMENTS

Dirk Kerzel was supported by the Swiss National Foundation 10011-107768/1 and PDFM1-114417.

What's in a name change? Visual prediction makes extrapolation real and functional

doi: 10.1017/S0140525X08003919

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Abstract: Nijhawan redraws our attention to the problem of accurately perceiving an ever-changing visual world via a sensory system that has finite and significant communication times. The quandary is compelling and stark, but the suggestion that the visual system can compensate for these transmission delays by *extrapolating the present* is not so unequivocal. However, in this current airing of contradictory issues, accounts, and findings, Nijhawan trades *spatial extrapolation* – a rather specific concept introduced earlier (in Nijhawan 1994) for *visual prediction* – a far more expansive notion that forces the issue of both the perceived reality and functional significance of compensation.

The discrepancy between visual information being delayed and behavior being accurate is unquestionable. It therefore might seem odd to take up the functionality of visual compensation. However, why should there be sensory compensation when later end effectors can compensate adequately? Of course, here one might ponder whether perceiving at all has functional significance, given that actions can be undertaken in the absence of accurate vision in terms of position information (Goodale et al. 1986). It is at this juncture in the present exposition that re-branding spatial extrapolation as visual prediction makes a tangible and productive difference.