

organism simultaneously maintain sensory information at five different time-scales: the current sensory input, the anticipated now and future, and previous predictions of the now and the future. By combining information at the different time-scales in an appropriate way, it is possible both to change the currently anticipated now and to make future predictions more accurate. The most appropriate way to model the combination of time-scales is presumably to use feed-forward models from control theory (Grush 2004; Kawato 1999). The predictions can be generated with different Kalman filters. The Kalman gains of the scales can be weighted in different ways, depending on the experience of the organism.

Assuming the gaze system is correctly tuned, via some feed-forward mechanism, the temporal unfolding of the ongoing interaction with the visual target contains the information needed to predict the location of the ball in the future; but the task for the hand is not to move to any arbitrary point along the predicted trajectory of the ball. Instead, the sensory-motor system must direct the hand to the location where the ball will be once the motor command to reach that location has been executed. This introduces an additional type of complexity, since the time in the future when the hand will catch the ball depends on properties of the arm and hand as well as on the ball. Although this is strictly also true for eye movements, the physical lag of the system becomes more critical for arm movements.

The properties of the flash-lag effect become perfectly sensible within this framework. Because unexpected events cannot become part of the anticipated now until after a processing delay, they will be perceived as lagging any predictable event. Moreover, since point events are perfect predictors of themselves, an adaptive system will learn to let them replace any prediction based on prior information.

In the flash-terminated condition, the flash becomes part of the anticipated now at the same time as the detection of the disappearance of the target. The flash and the disappearance of the target should therefore be perceived as simultaneous and occurring at the physical location where these two events actually take place. Once this information is received, the best prediction is that the moving object disappeared where it was at the time of the flash. This does not mean that the movement of the object is not extrapolated; it only suggests that that extrapolation is replaced by better information when it is available. Although it is possible that biased competition plays a role in this process, it may be sufficient to assume that a system that adapts its predictions to actual information will learn to behave in this way.

It is clear that the number of different time-scales that are necessary in the brain is much larger than the few described here. Given that substantial delays influence all processing in the brain, it appears necessary to compensate for these by predictive mechanisms at all levels. This suggests that predictive abilities should be necessary at the level of individual neurons – or at least local circuits. The ongoing dynamical interaction among different parts of the brain is not too different from the brain's interaction with the external world.

ACKNOWLEDGMENT

This work was funded in part by the European Union project MindRaces, FP6-511931.

Visuomotor delay in interceptive actions

doi: 10.1017/S0140525X0800383X

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Abstract: Neural delays, which are generally defined as visuomotor delays in interceptive actions, must be compensated to enable accurate timing in movement. Visuomotor delays can depend on the kind of task, the use of information, and the skill of the performer. The compensation for such delays does not necessarily require prediction or representation but can be made by an attunement of some parameters in what is called a *law of control*.

In this target article, Nijhawan proposes that neural delays in perception must be compensated by visual predictions and internal models. He emphasizes that this compensation is particularly important in interceptive actions and that this issue remains to be addressed. We agree, but would like to point out that there are empirical data and an alternative hypothesis which do not depend on the use of internal models.

In interceptive actions, researchers generally refer to a *visuomotor delay* (VMD) to define the time period between the pick-up of information and its use in producing an adjustment in movement (e.g., Tresilian 1993). It has been shown that VMD duration depends on the task (Benguigui et al. 2003). Lee et al. (1983) calculated VMDs that ranged from 50 to 135 msec in a ball striking task. Whiting et al. (1970) showed, in a ball-catching experiment, that performance did not degrade when the occlusion of the final part of the trajectory was equal or inferior to 100 msec. This period of time was interpreted as a VMD during which no information was used for catching. Bootsma and van Wieringen (1990), in a table-tennis task, observed that the variability was minimal at about 100 msec before contact. This phase of minimal variability was described as the end of the control of the action, reflecting the duration of VMD.

Some researchers have shown that VMD could be longer than 100 msec. McLeod (1987) reported that expert cricket batsmen, confronted with unexpected changes in the ball trajectory at the bounce, needed at least 190 msec to adapt their swing to the new trajectory. Benguigui et al. (2003) demonstrated in a task consisting of intercepting a moving stimulus with a thrown projectile, that movements were initiated around 200 msec after a specific source of information had reached a critical value. This delay was interpreted as a VMD between the pick-up of the information and the initiation of movement.

The duration of VMD appears to depend on the use of information. It can be as short as 100 msec when information is used in a continuous mode, but can reach values near 200 msec when information is used in a discrete mode, such as the beginning of the movement or some important correction of that movement.

One can assume that (1) a short VMD and (2) an accurate compensation of it are essential for accurate timing. First, because information is continuously changing during the approach of a moving object, a reduction in VMD allows later pick-up of increasingly accurate information as contact draws near. The later the information pick-up, the more accurate the interceptive action will be (Lobjois et al. 2006). Le Runigo et al. (2005) showed that the time required to produce an adaptation in an interceptive movement after an unexpected change in the moving object's velocity was shorter in expert tennis players (162 msec) than in novices (221 msec). They also showed that the reduction of VMD was highly correlated to timing accuracy, suggesting that a reduced VMD provides the opportunity to improve on-line regulations and to adapt these regulations at later stages before contact.

Second, the movement itself must compensate for VMD under the constraint of an incompressible delay. Moreover, the difficulty in compensating for VMD would increase as VMD increases, as is the case in older adults (Bennett & Castiello

1995). Lobjois et al. (2006) showed that this increase in VMD explained the lateness of elderly people in a coincidence-timing task. Interestingly, elderly people who had a regular sport activity (e.g., tennis) and who had an increase in VMD that was similar to that of sedentary elderly people were not late in their responses. These results suggest that sport practice also allows a better compensation for the age-related VMD increase.

Although the problem of compensation for VMD has not yet been extensively addressed, some suggestions deserve consideration. When an interceptive movement is very short and controlled in a ballistic mode (movement time: $MT \leq 150$ msec; Tresilian et al. 2004), the actors have to estimate temporally the ensemble of the visuomotor sequence, including VMD and the MT, and detect the instant at which time-to-collision (TTC) becomes equal to the duration of this sequence (Benguigui et al. 2003).

Analogous mechanisms could be also involved when action must be controlled with continuous regulation. In contrast to Nijhawan's claim (sect. 7.2.1.1), the visual system is not an accurate predictor of moving objects when the last part of the trajectory is occluded beyond a duration of 200 msec (or of a VMD). Numerous studies using prediction motion tasks consisting of estimating the TTC of a moving object after the occlusion of the final part of the trajectory have shown that accuracy and variability in timing responses are dramatically affected by occlusions longer than 200 msec (e.g., Benguigui et al., in press). This means that for MTs above 200 msec, on-line regulation of movement is indispensable for dealing with both unpredictable and predictable changes in the object trajectory.

Once again, however, on-line regulations require compensation for VMD. This compensation process can be understood according to the calibration principle laid out by ecological psychologists (Jacobs & Michaels 2006). As motor control is based on laws corresponding to functional relationships between information and movement (Warren 1988), the calibration process consists in attuning some parameters of the law of control in order to adapt the movement to the constraints of a specific task. Regarding VMD compensation, laws of control include some parameters that do not correspond to a representation of VMD as is suggested by Nijhawan. Instead, these parameters have to be set according to the task-dependent effect of VMD in the interceptive timing. This process could explain why athletes who master a specific set of skills (exploiting a specific law of control) generally need a few trials of preparation to optimize their efficiency when beginning a new session of practice. This process could also correspond to an issue of learning that remains to be explored.

ACKNOWLEDGMENTS

We thank Michael P. Broderick and Isabelle A. Siegler for feedback on earlier draft of this commentary.

NOTE

1. For instance, even if the acceleration of a moving object is detectable by the visual system and theoretically predictable, results have shown that the perceptuo-motor system is unable to make predictions in extrapolating time-to-collision (TTC) that take into account the variation of velocity (Benguigui et al. 2003).

Flash-lag: Prediction or emergent property of directional selectivity mechanisms?

doi: 10.1017/S0140525X08003841

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Abstract: 3D FORMOTION, a unified cortical model of motion integration and segmentation, explains how brain mechanisms of form and motion processing interact to generate coherent percepts of object motion from spatially distributed and ambiguous visual information. The same cortical circuits reproduce motion-induced distortion of position maps, including both flash-lag and flash-drag effects.

Perceived position of objects is often distorted in the presence of motion. In addition to the flash-lag effect discussed in the target article, other examples include flash-drag effects (Whitney & Cavanagh 2000) and illusory boundary distortion by motion (Anderson & Barth 1999; De Valois & De Valois 1991; Ramachandran & Anstis 1990; Weiss & Adelson 2000). The same neural circuits that carry out directional selectivity, motion integration and segmentation computations are suggested to underlie phenomena of distortion of positional maps (Berzhanskaya et al. 2004).

The model 3D FORMOTION (Berzhanskaya et al. 2007) is based on formotion (Grossberg et al. 2001) and employs feedforward and feedback circuits involving areas V1, V2, medial temporal (MT), and medial superior temporal (MST) to solve both the motion aperture and correspondence problems (as well as motion capture, barber-pole illusion, plaid motion, and integration of object motion across apertures). It incorporates depth-selective input from V2 (FACADE) to MT (Formotion) to simulate the separation of ambiguous boundaries in depth (chopsticks illusion) and motion transparency.

1. Description of 3D FORMOTION features relevant to the distortion of positional maps. The formotion model consists of a few stages (see Fig. 1). The first stage in the motion system consists of directionally insensitive transient cells that respond briefly to a change in the image luminance, irrespective of the direction of movement. The second stage is the directionally sensitive layer. Directional selectivity results from a combination of gradient processing (Reichardt 1961; van Santen & Sperling 1985) and an asymmetric inhibition mechanism (Jagadeesh et al. 1997; Livingstone 1998). Further, short-range filters accumulate motion signals in a certain direction. Finally, spatial competition weakens ambiguous signals from line interiors and also amplifies feature-tracking signals. The spatial competition kernel has an asymmetric shape with its excitation offset from inhibition in the direction of motion. On the basis of anatomical connections and directional opponency, these spatial/directional competition units are allocated to the layer 4B of V1. As will be demonstrated later, asymmetric inhibition at this motion processing stage may contribute to the flash-lag effect.

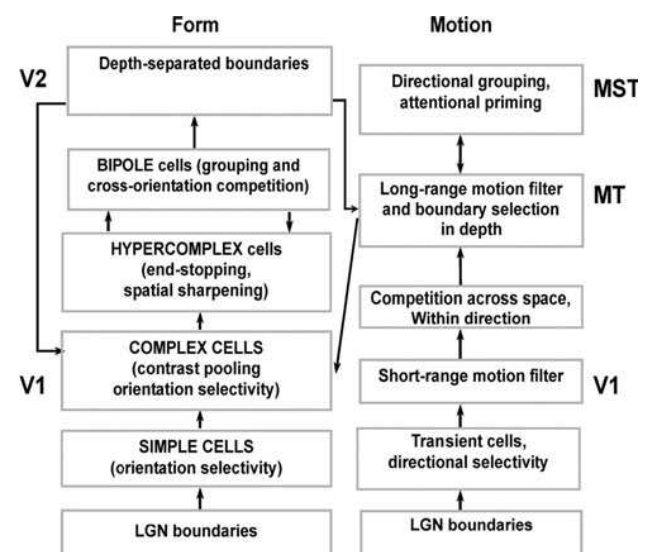


Figure 1 (Berzhanskaya). Schematic view of 3D FORMOTION.