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Error Detection is Critical for Visual-Motor Corrections

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Abstract

The target article (Smeets, Oostwoud Wijdenes, & Brenner, 2016) proposes that short latency responses to changes in target location during reaching reflect an unconscious, continuous, and incremental minimization of the distance between the hand and the target, which does not require detection of the change in target location. We, instead, propose that short-latency visuomotor responses invoke reflex- or startle-like mechanisms, an idea supported by evidence that such responses are both automatic and resistant to cognitive influences. In addition, the target article fails to address the biological underpinnings for the range of response latencies reported across the literature, including the circuits that might underlie the proposed sensorimotor loops. When considering the range of latencies reported in the literature, we propose that mechanisms grounded in neurophysiology should be more informative than the simple information processing perspective adopted by the target article.

The success of goal-directed actions inherently depends on the ability to monitor errors in our movements and correct them. Such errors might arise from intrinsic variability or “noise” within the sensorimotor system, inadequacies in motor planning or unpredictable environmental perturbations. A number of paradigms have been employed to study the processes and neural mechanisms underlying error detection and correction. The classic “target jump” paradigm has undeniably been one of the most prominent among them (Gaveau et al., 2003; Prablanc, Desmurget, & Grea, 2003; Sarlegna & Mutha, 2014). In this paradigm, a target for reaching is shown, and at some point before or after onset of a movement, the target location is unpredictably shifted to a new location. Subjects are expected to modify their movement to account for this change and end the reach at the new location. Because of its apparent simplicity, this paradigm has been extensively employed to address several questions about visual-motor corrective mechanisms. However, despite extensive investigation, a fundamental characteristic of the corrective response has remained poorly understood and intensely debated—its latency (Mutha & Shabbott, 2008). Estimates of the latency of such corrections have ranged from as low as 105 ms to as high as 330 ms (Brenner & Smeets, 1997; Danion & Sarlegna, 2007; Day & Lyon, 2000; Diedrichsen, Nambisan, Kennerley, & Ivry, 2004; Gritsenko, Yakovenko, & Kalaska, 2009;

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Mutha, Boulinguez, & Sainburg, 2008; Paulignan, Jeannerod, MacKenzie, & Marteniuk, 1991; Prablanc & Martin, 1992; Sarlegna et al., 2003; Sarlegna, 2006; Soechting & Lacquaniti, 1983). While longer correction latencies may be explained based on the finding that voluntary reaction time to a visual stimulus is approximately 200 ms, an explanation of corrective latencies shorter than reaction time has been lacking.

Critique

In the target article, Smeets and colleagues (Smeets, Oostwoud Wijdenes, & Brenner, 2016) offer a new perspective on the short latency of the corrective response. Using Donders' simplistic model of information processing in which detection, identification, selection and execution are serially organized components of sensorimotor behavior (Donders, 1969), the authors argue that the short latency corrective responses to target displacements emerge because the "detection" stage is not necessary to identify a change in the location of the target. Instead, the target location, relative to hand, is continuously updated based on retinal signals, which results in an automatic and continuous adjustment of motor behavior. While an explanation of the underlying sensorimotor processes is difficult to discern from the article, the idea seems to be that the response is unconscious, continuous, and incremental. This process, according to the authors, eliminates the need to detect an error, presumably because there is no threshold, i.e., the signal driving the motor adjustment is simply the difference between current hand and target positions, regardless of any change in either one.

A fundamental aspect of any sensorimotor response is the underlying neural circuitry and the delays inherent in that circuit, including the afferent and efferent pathways, and axonal propagation and synaptic delays (Sherrington, 1906). Unfortunately, these details are completely lacking in the target article. The article also leaves out many other critical features of neural function such as activation thresholds and gains of sensorimotor circuits. For example, in well-characterized sensorimotor circuits such as the stretch reflex, the spinal and supraspinal circuits have different loop delays in response to the same stimulus (Matthews, 1991; Pruszynski et al., 2011). These delays are associated with the distance that a particular signal travels and the number of intervening synapses. In addition, activation thresholds and circuit gains, which can be modulated at many levels under different task conditions (Adamovich, Levin, & Feldman, 1997; Shapiro, Gottlieb, Moore, & Corcos, 2002), form important elements that define the sensitivity of the response to a given stimulus. Such modulation in itself can lead to responses with distinct characteristics including different apparent latencies and magnitudes. Simply describing a process as incremental and continuous does not eliminate the need to identify these important features of the sensorimotor loop. As an example, the equilibrium point hypothesis describes a well-elaborated motor control scheme, which employs the stretch reflex as a fundamental element of control in an incremental and continuous fashion (Feldman, 2009; Latash, 2008). Though this scheme proposes muscle activation based on the difference between the current configuration and a specified referent configuration for the body part(s) in question, it places great emphasis on the underlying mechanisms and circuitry including position detection and reflex thresholds and gains, fundamental elements in this motor control process.

Unfortunately, while Smeets et al. state that constant tracking of limb and target positions might drive motor adjustments in response to changes in target location, they do not outline the basic sensorimotor elements and characteristics of the underlying sensorimotor loops. Latencies to visuomotor perturbations such as target displacements have been well-studied and while it is clear that the shortest latency responses can approach nearly 100 ms, it is also apparent that different task conditions can lead to longer response times that can vary with modulation of thresholds and gains, as well as recruitment of circuits of progressively increasing complexity at different levels of the nervous system. Smeets et al.'s explanation for the short latency visuomotor responses comes at the expense of and failure to account for such longer latency corrections noted across a number of studies. They implicitly assume that the mechanisms that lead to longer latency corrections are the same as the mechanisms that drive movement *initiation* in response to a visual stimulus, and that these are separate from the mechanisms driving the short latency corrections. However, their proposed mechanism undermines this claim: an incremental and continuous process should apply to any target condition. Why would this process be aborted in favor of a qualitatively different process? If, in fact, such a “decision” has to do with the amplitude of the target position change, this implies a detection and evaluation process required to switch from one or the other type of ‘control’. How is such a decision to be made without detecting the stimulus?

Nonetheless, even if one agrees that the mechanisms underlying short and long latency responses are distinct, the claim that short latency corrections occur because a change in target location is not “detected” is highly suspect for various reasons. Smeets et al. equate “detection” to a declarative process by which subjects are able to report a change in the location of the target. There is no evidence that sensory detection requires declarative knowledge that something has been sensed or detected, even when a clear motor response occurs. For example the vestibuloocular reflex is a clear example of a sensory detection—motor response process that is nondeclarative in nature (Squire, 2009). In addition, visual saccades are often not declaratively recognized and are often difficult to suppress even when subjects focus their attention on inhibiting them. In the limb motor system, modulation of grip force with object friction and weight, and even hand choices made during reaching are not declarative processes, but nevertheless, require sensory detection (Danion & Sarlegna, 2007; Coelho et al., 2013). This idea is further supported by findings that motor actions can be modulated by visual illusions such as the size-weight illusion (Flanagan, Bittner, & Johansson, 2008; Gordon, Forssberg, Johansson, & Westling, 1991), which mandate detection and evaluation. Thus, Smeets et al.'s proposition that detection of a change in target location depends on declarative knowledge clearly lacks experimental support. In addition, the fact that subjects modify their ongoing actions, despite being unaware of a given target displacement does not indicate that the nervous system has not “detected” this change. The authors themselves state “there is no way to circumvent the time taken by retinal processes or conduction times in the optic nerves”. Clearly, these signals inform the sensorimotor system about the new location of the target, and are therefore an integral component of the process that “detects” that the location of the target has changed. The cognitive process of being able to report this change in location is not necessary for either detection or for motor response modification.

What mechanism then might underlie the short, ~100 ms latency associated with the change in target position? It is plausible that these short-latency responses are the output of reflex or “startle” like visuomotor circuits, with contributions from all the essential elements of a sensorimotor loop including detection, processing and loop delays. This proposition is supported by the finding that proximal muscles show a minimum response time of ~80 ms to visual target information (Pruszynski et al., 2010). In the incremental-continuous model proposed in the target article, there seems to be no explanation *why* such a delay might occur at all. Should not the continuous nature of retinal modulation result in continuous modulation of motor responses rather than occurring at a discrete latency?

The hypothesis that short-latency visuomotor responses occur from reflex or startle like mechanisms is further supported by studies that have argued that these responses are at least partially “automatic” and “hard-wired” (Day & Lyon, 2000; McIntosh, Mulroue, & Brockmole, 2010; Pisella et al., 2000). In other words, these responses are difficult to modify or inhibit, and appear to be resistant to cognitive influences, making them conceptually similar to the short-latency component of the stretch reflex. Day and Lyon (Day & Lyon, 2000) have suggested that this early component may be subcortically mediated, possibly via a pathway involving the superior colliculus, a target of rich visual information from retinal ganglion cells. Other studies have implicated the parietal cortex in this early, automatic response—disruption of parietal circuits either through TMS or lesions leads to a disruption of the early component of the response (Desmurget et al., 1999; Grea et al., 2002; Mutha, Stapp, Sainburg, & Haaland, 2014; Reichenbach, Bresciani, Peer, Bulthoff, & Thielscher, 2010; Schaefer, Mutha, Haaland, & Sainburg, 2011). In fact, neural circuits that are active when responding to a target displacement, including parietal regions (Desmurget et al., 2001), bear a striking resemblance to those involved in representing learned actions (Shadmehr & Holcomb, 1997). Regardless of the mechanism however, it is plausible that this learned response is rapidly “released” whenever a change in target location is detected and signaled. Thus, in contrast to the proposition of Smeets and colleagues that corrective responses occur at short latency because a target jump need not be “detected,” we suggest that a response is executed as soon as target displacement is detected.

The notion that a response is triggered at short latency whenever a target jump is detected suggests that this response may not be as sophisticated or tuned perfectly to task goals. This indeed appears to be the case. Mutha, Boulinguez and Sainburg (2008) investigated the modulation of spinal reflex circuits by changes in visual information implemented using target displacements. Reflex responses were elicited by means of a robot-induced stretch of the biceps muscle while subjects made single-joint elbow extension movements to a visual target. On some trials, the location of this target was shifted either further away from the existing target location such that greater elbow extension was required to reach it, or toward the start position so that the ongoing extensor action had to be inhibited and reversed. Critically, this target displacement was implemented 100 ms before the mechanical perturbation to stretch the muscle was applied. The effect of the preceding jump on the reflex response was clear—the reflex response was down-regulated when the jump was further away, while it was up-regulated when the target was displaced toward the start-position. Similar results have been reported by Franklin and colleagues for “visuomotor” reflexes (Franklin, Franklin, & Wolpert, 2014). This indicates that the target displacement,

within a short latency of 100 ms, induced direction-dependent modulation of spinal circuits suggesting that this is a somewhat ‘smart’ response, in that it is adapted to the direction of the visual perturbation, relative to the ongoing movement. However, the tuning of reflex circuits based on amplitude of the jump was completely absent—the magnitude of the change in the reflex response remained the same regardless of how far the target was jumped in a particular direction (Mutha et al., 2008). Amplitude-dependent modulation occurred at a latency that was close to voluntary reaction time. These results point to the limited sophistication of the early component of the target jump response, consistent with what would be expected if a set response was rapidly executed based on a visually detected change in target location.

Summary

The classic “target jump” paradigm has been one of the most prominent paradigms for studying visuomotor corrections. A large number of studies have indicated that the latency of such responses varies from some 100 ms to over 300 ms. In the target article, Smeets and colleagues attempt to explain the short latency response by suggesting a process that ‘skips’ the detection stage of sensorimotor responses. They instead suggest that detection of a change in the goal location is not required because the adjustment is based on continuous tracking and incremental updating of hand and target position. They also appear to, at least semantically, confuse the existence of a detection process with whether subjects have declarative knowledge of that process. Unfortunately, the neurophysiological basis for the different response times, including essential circuit elements such as loop delay, gain and threshold are skipped in the target article. Given the vast literature on a large variety of sensorimotor responses to unanticipated events, a more parsimonious explanation is that the short latency visuomotor responses, such as those seen in response to target jumps, recruit shorter loops that involve less processing than the longer latency responses. Studies supporting this interpretation have shown that short latency responses are only weakly tuned to the geometrical conditions of the target jump than longer latency responses. Thus, task conditions that do not require more sophisticated responses or that demand rapid reactions are likely to elicit shorter, more autonomous, but less sophisticated responses. By exploiting a simple information-processing model to explain such responses, the authors unfortunately bypass a necessary and perhaps more critical discussion of the biological underpinnings for shorter and longer visuomotor response latencies. When considering the range of latencies reported in the literature, a mechanistic model grounded in neurophysiology would perhaps be more fruitful and informative for guiding future research on visuomotor responses.

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