The detection continuum for motor control comprises preparation and adjustments

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Commentary to

Movement Adjustments have Short Latencies Because there is no Need to Detect Anything

by Jeroen B.J. Smeets, Leonie Oostwoud Wijdenes, and Eli Brenner

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Most studies investigating movement preparation report substantial longer reaction times than studies probing response times to adjust an ongoing movement. However, both behaviors constitute control processes that transform sensory information about the environment into motor commands. Smeets et al. (2015) base their review on the hypothesis of a qualitative difference between the two sensorimotor control processes. By ruling out that the three latter movement stages proposed by Donders (1969) - identification, selection, and execution – are responsible for the difference, they argue for a specific role of the detection stage. Specifically, they reason that the detection in (target) change is only necessary for movement initiation and thus constitutes the qualitative difference between the two behaviors. In contrast to this view, I will advocate that change detection is not a qualitatively discriminating feature between the two processes. Instead, the difference in response time might rather stem from different decision criteria (Wolpert and Landy, 2012) set on the detection threshold. This threshold is rather conservative for movement initiation and more relaxed for online adjustments. However, both are states on the same continuum. Thus, movement initiation and online adjustments might even not be qualitatively different at all.

Preamble on detection. The term detection is central to the review by Smeets et al (2015) and yet it was ill-defined in that paper. Here, detection is not used the way a cognitive psychologist would do: a conscious percept operationalized by the ability to report a stimulus. Rather, I am (partially!) using the term parallel to Smeets and colleagues, who refered to a study in which reporting the target detection was not necessary to initiate a movement (Schmidt, 2002). In this respect, detection means that sufficient sensory evidence is gathered to change the physiological state of the (motor) system. As such, detection constitutes a continuous process determined by a decision criterion: the detection threshold. However, despite their previous acknowledgement that detection of target change does not necessitate conscious report of the change, Smeets et al. cite studies with online adjustments to unperceived target displacements as evidence for their hypothesis that online motor control does not require change detection – but movement initiation does. This line of argumentation is, in my opinion, inconsistent.

Target (change) detection is not the bottleneck for movement initiation. Neural populations in primary motor cortex (M1) are tuned to the direction of arm reaches (Georgopoulos et al., 1986). These neurons increase their firing rate during the preparatory phase of the movement starting 60-80ms after target presentation when monkeys perform the task of reaching to one of several targets. However, even during speeded responses, muscle activity is usually not observed until 100ms later (Georgopoulos et al., 1982). Indeed, a recent study showed that the directional tuning of a larger proportion of M1 neurons was locked to the onset of target presentation than to movement onset, with a significant fraction driven by both events (Rao and Donoghue, 2014). Furthermore, this study demonstrated that the directional population code in M1 evolved over time, suggesting that some further processing took place before initiating the movement. Importantly, however, visual target information was already coded in motor structures much earlier.

Along this line, Perfiliev et al. (2010) demonstrated that movement initiation can actually be as fast as online adjustments. In their study, human participants were instructed to catch a ball as soon as it started moving. Even though they were free in catching strategy, movements were executed with the corresponding arm, i.e. the right hand when the ball moved to the right. Mean electromyographic latencies for the catching arm were on average 144ms (SD 20), with earliest occurrences ranging from 90 to 110ms. These latencies are the same duration as response latencies to visual target perturbations during movement execution (cf. the papers cited in Smeets et al., 2015). Notably, this experiment also comprised the selection stage for arm choice, i.e. the responses were not even the simplest form of speeded reaction times.

Online adjustments require change detection. Fifteen years ago, evidence from the preceding decade cumulated in the formulation of "hybrid models" (Desmurget and Grafton, 2000; Sabes, 2000) that continuously utilize sensory information and forward models of the movement (Wolpert et al., 1995) to estimate internal models of the current body state (Kawato, 1999). Based on these states, the motor command is then adjusted (if necessary!). The idea of a "reflexive" nature of these online control loops became popular. Early findings about processing adjustments without conscious visual awareness (Goodale et al., 1986; Prablanc and Martin, 1992) were complemented with studies proposing an "automatic pilot" (Pisella et al., 2000), or subcortical processing (Day and Brown, 2001). Along this line, it follows logical that online adjustments might not even necessitate change detection. The early feedback control models (Desmurget and Grafton, 2000; Sabes, 2000) contained a module comparing the desired state with its current estimate to issue a corrective command. If this model was true, this would be the part where change detection comes in – the correction would only be signaled if a change was detected. Admittedly, the comparator would be agnostic to whether e.g. the motor command was off, the hand position previously wrongly estimated, or the target truly changed position. But a change between previous and current state needed to be detected in order to implement an adjustment.

What would be the alternative to such a model? The one alternative that the motor command is calculated from scratch at each instant in time instead of adjusting the current plan, had already been discarded 15 years ago (Desmurget and Grafton, 2000). I am neither aware of a good reason nor new evidence to revive this idea. The other alternative would be that the "corrective" command is in fact an "adjustment" signal - which needs to have the opportunity for sending a "null" change. Such a mechanism might be what Smeets and colleagues had in mind with "every action potential that is somehow related to the position of the target […] the estimate of the target's position will shift a little". In a technical system, it would indeed be a reasonable implementation to send "zero" to maintain a stable communication pipeline. But the nervous system is no technical system and a zero - or null - signal would effectively be no signal at all. Hence, a decision to signal or not based on the detection of a change is necessary.

On a related note, the sunflower example seems simple enough to demonstrate that detection is not necessary to keep facing a moving target, the sun in this case. However, as plain as a plant might be compared to the complexity of a mammal brain, the process of phototropism follows the same mechanistic principles. Simplified, photoreceptors sense the sunlight and initiate a cascade involving growth hormones in an inverse relationship between light and the production of growth hormones (Goyal et al., 2013). As a consequence, the side receiving less light grows faster, effectively turning the flower towards the light-source. Hence, in order to move towards the sun, the plant needs to first detect the sunlight. Admittedly, the plant might not detect a change in sun position, but only when the light difference yields a difference in hormone levels strong enough to unequally grow the plant, then the flower "turns".

Decision criterion for detection. When we accept that movement initiation and online adjustments both require change detection – can the detection stage still be the cause for the different timings in response onset? Yes it can. As elaborated in the preamble, detection is here regarded as a continuous process and depending on the decision threshold, detection can occur earlier or later in time. Detection for online control seems a very "leaky" process: Clear responses can be observed to sudden movements of objects close to the actual target (Diedrichsen et al., 2004) and even to background motion (Gomi, 2008). These findings support the interpretation that decision thresholds for online control processes are rather low, signaling a detection of change as soon as there is motion attributable to the target. Detection for movement preparation seems to be much more conservative most of the time, and highly dependent on task constraints, e.g. the classical trade-off between speed and accuracy (Fitts, 1966). From the perspective of optimal control (Todorov, 2004), change detection for online adjustments might simply constitute the low-cost / high-gain end of the cost function spectrum (Shadmehr and Krakauer, 2008). Detection for movement initiation then seamlessly falls in into line with criteria ranging from relaxed ones close to online control (Perfiliev et al., 2010) to more and more strict ones typically observed for movement preparation.

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