The influence of visual target information on the online control of movements

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A B S T R A C T

The continuously changing properties of our environment require constant monitoring of our actions and updating of our motor commands based on the task goals. Such updating relies upon our predictions about the sensory consequences of our movement commands, as well as sensory feedback received during movement execution. Here we focus on how visual information about target location is used to update and guide ongoing actions so that the task goal is successfully achieved. We review several studies that have manipulated vision of the target in a variety of ways, ranging from complete removal of visual target information to changes in visual target properties after movement onset to examine how such changes are accounted for during motor execution. We also examined the specific role of a critical neural structure, the parietal cortex, and argue that a fundamental challenge for the future is to understand how visual information about target location is integrated with other streams of information, during movement execution, to estimate the state of the body and the environment in order to ensure optimal motor performance.

1. Introduction

A hallmark of human behavior is the wide variety of movements that we can perform. We can successfully complete a range of tasks with varying spatial and temporal characteristics, in diverse environments and under different constraints. Despite the tremendous heterogeneity in task conditions, voluntary actions such as eating, drinking, dressing and so on generally appear to be accomplished with relative ease. However, the complex and interacting nature of the underlying control processes becomes readily evident in cases of disease, for instance when patients suffer neurological damage and make movements that are poorly coordinated and inaccurate. Here we focus on *one* aspect of this control – the ability to rapidly update and modify ongoing actions to successfully achieve the task goal. Such online motor control relies on information provided by sensory systems such as vision (Franklin & Wolpert, 2008; Gomi, 2008; Goodale, Pélisson, & Prablanc, 1986; Hansen, Tremblay, & Elliott, 2008; Saunders & Knill, 2004), proprioception (Sainburg et al., 1995; Scott, 2012), audition (Boyer et al.,

2013) and the vestibular system (Bresciani et al., 2002), as well as fast internal loops (Desmurget & Grafton, 2000) which presumably predict the sensory consequences of movement commands. A large body of research has been dedicated towards the understanding of how each of these systems contributes to the online control of actions. Here we review a set of studies that have examined how vision of the target is used to update motor commands and thereby modify the ongoing action. We focus on paradigms that have primarily employed arm movements since these movements are likely to be influenced by low-level movement control mechanisms (Prablanc & Martin, 1992) as well as higher-order cognitive processes (Cameron et al., 2009; Striemer, Yukovsky, & Goodale, 2010).

In healthy individuals, the easiest and most popular method for studying the role of visual information in online motor control has been to examine how task performance is affected when vision is occluded. As early as 1899, Woodworth asked healthy adult participants to perform a manual aiming task under two conditions: with eyes open and with eyes closed. Woodworth suggested that this manipulation would "open" the visual feedback loop, and comparison of the aiming accuracy in vision and no vision conditions would provide some information about the role of vision in precise aiming. Woodworth (1899) found that when hand movements were performed at moderate speed, removing vision impaired final movement accuracy. However, the comparison of

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vision and no-vision conditions is ambiguous: when participants are asked to close their eyes, they are deprived of all visual signals – of the target position, of the environmental background and of the hand position. Thus, even if removing visual information is found to be detrimental to motor performance, it is unclear whether the deficit arises from suppression of information about the target, the environment, the hand or a combination of these. More recent studies have sought to answer these questions by examining the effects of selective changes in visual information on online movement control. For instance, visual feedback of hand position has been shown to be important for rapidly adjusting movement trajectory (Franklin & Wolpert, 2008; Hansen, Tremblay, & Elliott, 2008; Sarlegna et al., 2004; Saunders & Knill, 2004), and Gomi (2008) has reviewed the rapid corrective processes that take into account visual information about the environmental background. Here we review how visual information about the target of the movement is used for online movement control while focusing primarily on two main methods used in the literature: occluding vision of the target or perturbing it.

2. Eliminating visual information of the target

Most studies that have temporarily eliminated visual information of target location have examined its effect on final movement accuracy (Berkinblit et al., 1995; Elliott, 1988; Prablanc, Pelisson, & Goodale, 1986; Prablanc et al., 1979). An early study by Thomson (1983) that investigated "locomotor pointing" showed that when participants had to walk toward a *memorized* target location, they could do so quite accurately. Thomson (1983) suggested that continuous visual information about the intended target location may not be necessary, and that humans may be able to adequately guide their movements based on an internal representation of the target location. These findings however were challenged by Elliott (1986), who showed that the accuracy of movements to a target location was greater with continuous visual information of the target. This was shown to be the case in the locomotor pointing task similar to that of Thomson (1983) as well as during targeted reaching (Elliott, 1988).

Prablanc, Pelisson, and Goodale (1986) also reported that unseen arm movements were more accurate when they were performed toward a target visible throughout the trial compared to when visual target information was eliminated upon movement onset. These results were consistent with Elliott's reports (1986, 1988) and further supported the idea that goal-directed movements can be adjusted during movement execution. Importantly, from a theoretical standpoint, Prablanc, Pelisson, and Goodale (1986) noted that because continuous visual information of target position could be used in guiding the *unseen* hand, online adjustments were not necessarily based on a visual comparison (or a "visuo-visual" comparison) of the target position with the current hand position. Instead adjustments could occur through a comparison of the visually-defined target position and the hand position determined with non-visual, somatosensory and/or efferent signals. Berkinblit et al. (1995) later confirmed and extended the findings of Prablanc, Pelisson, and Goodale (1986) to three-dimensional reaching arm movements.

Desmurget et al. (1995) used a slightly different suppression method to study the importance of continuous visual target information. To specifically investigate whether vision of the target could be used for online adjustments during the deceleration phase of the movement (i.e., from peak velocity to movement completion), these authors extinguished the target at the time of peak movement velocity. Desmurget et al. (1995) observed a greater final movement accuracy when the target was visible throughout movement execution compared to when it was turned off at peak velocity. This indicated that visual information about the target could be used to adjust movement kinematics even in the deceleration phase of movement, providing further support to earlier suggestions of continuous use of this visual information for online control.

In 2005, Desmurget and colleagues asked whether the greater final accuracy observed with a visible compared to a non-visible target was related to the accuracy of the ocular saccade to the target (because of eye–hand coupling, reviewed in Bekkering & Sailer, 2002; Gaveau et al., 2014). By demonstrating that ocular saccades had the same final accuracy regardless of whether the visual target was shown continuously or switched off at saccade onset, they argued against the hypothesis that the greater final accuracy of arm movements when the target was visible was related to the accuracy of the ocular saccade to the target. Importantly, Desmurget et al. (2005) also showed that while the initial motor plan appeared to be similar when the target was continuously visible or switched off rapidly, movements toward visible targets were more accurate because continuous availability of target information allowed motor commands to be adjusted and refined during movement execution. These online adjustments were considered to be "smooth" as the movement trajectory and the velocity profile did not drastically differ between visible and extinguished target conditions. Further, movement duration was not significantly affected by the experimental manipulation, suggesting that this corrective process may not be time-consuming. Lastly, Desmurget et al. (2005) showed that such functionally-relevant adjustments could be observed shortly after peak acceleration, thus suggesting that visual target information could be rapidly used to adjust the ongoing movement.

It is worth noting that a number of other studies failed to reveal significant differences between vision-of-the-target and no-vision-of-the-target conditions when considering final movement accuracy measures (e.g., Carlton, 1981; Elliott, 1992). While these findings are in contrast with those discussed above, they certainly do not provide conclusive evidence that visual target information is not used for the guidance of reaching movements. Instead, such results often point to the flexibility available within the nervous system, where movements may be reliably guided based on an internal representation of the target (Graziano, Hu, & Gross, 1997; Heath & Westwood, 2003). Importantly however, because the accuracy of the internal representation of the target may decay over time (Elliott, 1992; Heath & Binsted, 2007), motor performance has been shown to benefit from continuous visual information of the target in most conditions.

Instead of the typical target-visible versus not-visible task conditions, Izawa and Shadmehr (2008) used a different approach as they assessed the effects of manipulating the reliability of target information on manual aiming. These authors asked subjects to reach to targets that could be presented with different levels of "blur". On occasional trials, after movement onset, the level of blur could be changed so that the center of the target was more, or less, accurately displayed. Izawa and Shadmehr (2008) showed that as the uncertainty about the center of the target increased, the variability of the endpoint of subjects' reaches also increased. These results thus elegantly showed that information about the target is not simply used in a binary manner (present or absent) but rather, the reliability of the information about the target is also taken into account to evoke an online adjustment of the motor commands that is as efficient as possible. In line with this, Izawa and Shadmehr (2008) showed that the rate of change of motor output in response to changes in the properties of the target depended on the visual properties of the target. These results highlight the degree of sophistication within the nervous system to use different visual features of the target for generating the online response (Veerman, Brenner, & Smeets, 2008).

3. Visual illusions

While the studies reviewed above demonstrate that the intended target and its properties are continuously monitored to adjust our movements, studies employing visual illusions (Aglioti, DeSouza, & Goodale, 1995; Glover, 2002) suggest that it is the *perceived* rather than the actual properties of the target that modulate online responses. The widely-used Ebbinghaus illusion results in the perception that, if an annulus of small circles surrounds a central circle, the central circle appears to be larger than it actually is (size-contrast illusion). Conversely, a central circle surrounded by larger circles appears to be smaller than it actually is. While the effects of the Ebbinghaus illusion have mainly been investigated in the context of grasping actions (Goodale, 2011; Smeets, Brenner, & Martin, 2009), such illusions have also been shown to affect the online control of simple reaching movements. For instance, Handlovsky et al. (2004) showed that when a target was suddenly surrounded by an annulus of small circles after movement onset, reaching movements were executed faster. This could be explained by the illusion of the target appearing larger, thereby resulting in a reduction in the accuracy constraints of the reach and consequently, an increase in movement speed (Fitts, 1954).

In another commonly studied pictorial illusion, the Müller-Lyer illusion, the orientation of the ends of an arrow influences our perception of the length of the line between the ends (Bruno, Bernardis, & Gentilucci, 2008). If the length of the segment is the same in both cases, it appears to be shorter when flanked by outward-pointing arrows (wings in: < >) or longer when flanked by inward-pointing ones (wings out: > <). Such illusions have been shown to influence the amplitude of pointing movements (de Grave, Brenner, & Smeets, 2009; Grierson & Elliott, 2009). Mendoza et al. (2006) presented a certain configuration (no wings, wings in or wings out) until participants started their movement toward the vertex of the picture, and then occasionally switched the configuration. They found that the switched configuration had a clear effect on several kinematic markers. For instance, when a wings-in configuration was presented initially but was then switched to a wings-out configuration upon movement onset, there was a significant increase in movement duration as well as in constant and variable movement errors. The effect of the illusion was observed on kinematic measures late in the movement, with or without visual feedback of the moving limb (see also Heath, Neely, & Binsted, 2007). These findings thus provide support to the idea that the perceived properties of the target strongly influence movement execution.

4. Perturbing target information: the double-step paradigm

Studies that have utilized methods such as removal of target information or modification of its properties have been useful in demonstrating that these parameters influence the online control of goal-directed movements. However, another method, the so-called "double-step" paradigm, has been instrumental to identify key features of the online response adjustment process as well as more generally, the visuomotor feedback system. In this paradigm, subjects are typically instructed to reach as fast and accurately as possible to the visually displayed target. On a few trials, at some time during the movement planning or execution phase, a second target is shown while the first one is extinguished, resulting in the perception that the target has been "displaced". Megaw (1974) was among the first to demonstrate that once a target displacement is perceived, online motor responses are rapidly observed, thus demonstrating that it is possible to modify an action during its execution (for a review, Gaveau et al., 2014; Prablanc, Desmurget, & Gréa, 2003).

Georgopoulos, Kalaska, and Massey (1981) investigated whether the latency of the online corrections would be affected if the target was displaced at different times during the movement. In their experiment on non-human primates, the target could be displaced during movement preparation or during movement execution, 50–400 ms after the presentation of the initial target. These authors showed that regardless of when the target jumped, movement trajectories were adjusted at latencies similar to a normal reaction time (~250 ms). Soechting and Lacquaniti (1983) replicated these findings with three-dimensional movements performed by human subjects, and noted that corrective muscle activations (in the biceps and deltoid muscles) were observed ~100 ms after the target displacement. Since then, researchers have mostly used conditions in which the target displacement was triggered at the time of movement onset toward the initial target position (e.g., Brenner & Smeets, 1997; Danion & Sarlegna, 2007; Desmurget et al., 2004; Fautrelle et al., 2010; Gritsenko, Yakovenko, & Kalaska, 2009; Izawa & Shadmehr, 2008; Pisella et al., 2000; Reichenbach et al., 2009) or slightly after movement onset (25 ms after movement onset in Johnson, Van Beers, & Haggard, 2002; approximately at peak acceleration in Mutha, Boulinguez, & Sainburg, 2008; 100 ms or 200 ms after movement onset in Liu & Todorov, 2007). Again under such conditions, movement corrections toward the displaced target can be clearly observed, providing further support to the idea that motor commands are updated in a continuous fashion. Crucially, these studies have also shown that online modifications in humans could be initiated substantially faster than initially thought (Keele & Posner, 1968). We will examine the latency of the corrective response in a later section in much more detail.

4.1. Factors influencing the online corrective responses

Barrett and Glencross (1989) investigated whether temporal constraints imposed onto movement execution could affect the quality of the online response to a target jump. They studied the effect of systematically varying the time of the target displacement on the ability to make corrective responses during rapid movements. In their study, target displacements were triggered at movement onset or 50, 100, 150, 200, 250 or 300 ms later. They observed complete corrections when the target was displaced at movement onset. However, because movements had to be completed in ~350 ms, the amount of correction decreased as the time of target displacement after movement onset increased, demonstrating that the quality of online corrections could be affected by the temporal constraints imposed during the task. In other words, the corrections usually observed after a sudden target displacement could be incomplete because of a lack of time to execute the corrective response.

The notion that temporal requirements could constrain online movement control is supported by several other studies (Brenner & Smeets, 1997; Ma-Wyatt & McKee, 2007). Blouin et al. (1995b) showed that online corrections were not possible for fast movements (~200 ms movement duration) when both movement amplitude and direction had to be controlled. However, when Blouin et al. (1995a) asked subjects to control only movement direction, corrective responses to target displacements could be observed for these fast movements. These results were confirmed by Turrell et al. (1998), and suggest differences in the online control of movement amplitude and direction. Saunders and Knill (2005) suggested that such differences could arise due to differences in sensory uncertainty for direction and amplitude control. Since noise that corrupts position estimates would be higher in the primary movement direction (amplitude control) versus perpendicular to the direction of movement (direction control), the central nervous system would be more sensitive, and thus would correct more efficiently, for perturbations in movement direction compared to movement amplitude. However, Oostwoud Wijdenes, Brenner, and Smeets (2013) have recently demonstrated equally efficient (in terms of latency)

corrections for both amplitude and direction perturbations. In their study, when the target was displaced at movement onset so that it required an online modification of the planned movement direction or amplitude, the measured latency was ~120 ms in each condition.

Komilis, Pélisson, and Prablanc (1993) also tested the effects of temporal limits on online control mechanisms. They triggered the target displacement at the time of peak movement velocity and showed that amplitude adjustments were present but incomplete as the hand could not reach the new, displaced target, presumably because of insufficient time. More recently, Liu and Todorov (2007) offered an alternative explanation for why corrections may be incomplete when the target displacement occurs late in the movement. These authors observed only partial compensation for target displacements that occurred 300 ms after movement onset, despite allowing substantially greater time for correcting the movement than would be required to make the same movement in isolation. Using an optimal feedback control model (Todorov & Jordan, 2002), Liu and Todorov (2007) suggested that as the movement progressed, the nervous system became less sensitive to positional errors, and stopping the movement in a stable manner was prioritized. Liu and Todorov (2007) reasoned that if positional gains (i.e., sensitivity to positional errors) remained high toward the end of the movement, terminal oscillations would occur, conflicting with the requirement to stop. By down regulating the sensitivity to positional errors, it appears that the nervous system achieves endpoint stability while compromising the efficiency of the corrective response. These results suggest that when responding to changes in target location during movement, the visuomotor system takes into account not only the time available to make the correction, but also the cost involved in making the correction in terms of stability. Overall, the flexible nature of the online adjustments in response to target displacements fits well with the idea that visual signals about target position are processed differently depending on task constraints.

In the pioneering work of Megaw (1974), the latency of the corrective response appeared to be smaller when the correction required a continuation of the ongoing movement rather than a reversal (see also Sarlegna et al., 2003). In a variant of the double-step paradigm, Carlton and Carlton (1987) tested the idea that these differences in response latency might be related to the state of the muscle at the time of response initiation. The authors examined responses to visual stimuli presented during movement execution which instructed subjects to "Continue" or "Reverse" their movement. Carlton and Carlton (1987) showed that the latency of amplitude correction (assessed with surface electromyography) in a "Continue" condition was shortest when the second visual stimulus was presented early during the movement, i.e., when the agonist muscle for the primary action was active. However, the response in the "Continue" condition was delayed when the second target appeared late, i.e., when the antagonist was active. Opposite trends were observed for the "Reverse" condition, suggesting that the state of the motor system influences the online correction which appears to be flexibly modulated according to the context of the task.

Higher-level, 'cognitive' factors have also been shown to modulate corrective responses to target displacements. For instance, Cameron et al. (2009) and Striemer, Yukovsky, and Goodale (2010) observed that when subjects were instructed to ignore target displacements, corrective responses toward the target were substantially smaller, although not completely inhibited, than in the control condition. There is also evidence that the online control of movement depends on the statistical properties of the stimuli i.e., its uncertainty, as cues about the frequency of the target displacements have been shown to affect the online response. For instance, Boulinguez and Nougier (1999) informed subjects that the target could jump rightward, rather than leftward, on 25%, 50% or 75% of the trials. These authors noted that prior knowledge of the probability of the target displacement improved the efficiency of online movement control.

Sarlegna et al. (2003) asked whether the availability of visual information about hand location could influence the online response and found that online responses were observed after ~320 ms when hand visual feedback was available, while they were observed after ~390 ms without such visual information. While these findings contrasted with previous findings of Prablanc and Martin (1992), who observed that (the latency of) movement adjustment was not affected by the presence of hand visual feedback, Reichenbach et al. (2009) also found faster corrections to target displacements when visual feedback of the hand was available. The authors suggested that this advantage could arise because the relative positions of the hand and target could be rapidly computed in a single, visual coordinate system, thereby minimizing the need for coordinate transformations. Importantly, Reichenbach et al. (2009) showed that the facilitation effect of hand visual feedback was specific to online responses to target perturbations, as no such effect was observed in a reaction time control experiment or when the unseen hand was perturbed by a force pulse. Collectively, these findings indicate that the availability of hand visual feedback facilitates online adjustments made in response to changes in visual information of the target location.

Bard et al. (1999) addressed whether online corrections were possible without vision and proprioception. In other words, they tested the possibility that comparison of the location of a visual target and the hand as required for initiating movement corrections could occur solely based on predictive internal feedback mechanisms. These authors studied the ability of a patient deprived of proprioception to correct the trajectory of rapid reaching movements without vision of the hand. Bard and colleagues used a task in which a small target jump was initiated during the ocular saccade to the target, thereby ensuring that the deafferented patient (GL) was unaware of the jump. They noted that the patient could adjust her movement towards the displaced target despite the lack of any sensory feedback about hand position, a finding that has since been corroborated (Medina et al., 2010; Sarlegna et al., 2006). Sarlegna et al. (2006) also tested the ability of patient GL to correct reaching movements in response to large, consciously perceived, target displacements and noted that even when the target was not visible during movement execution (the second target was only briefly illuminated), the patient could correct her movement trajectories. Moreover, the latency of her corrections was similar to that of age-matched healthy control subjects, but her movements were less smooth than controls, likely because of deficits in motor coordination in the absence of proprioception (Sainburg et al., 1995). These studies thus showed that proprioceptive signals substantially contribute to the coordination and accuracy of our arm movement corrections but may not be essential to make the online adjustment itself. Indeed, online corrections can occur based on a central monitoring of movement commands that are adjusted using rapid internal feedback loops (Desmurget & Grafton, 2000).

In summary, the online response to a change in target location appears to be influenced by a myriad of factors ranging from task instructions to temporal constraints to availability of peripheral information of hand position. Importantly, these factors appear to be well accounted for during the formulation of the optimal response.

4.2. Online corrections without awareness of the target displacement

There has been great interest in identifying whether online responses require that the error (induced by target displacement) is consciously perceived. The well-known phenomenon of saccadic suppression of displacement perception – the increased threshold

of visual perception during saccadic eye movements (Bridgeman et al., 1979; Wurtz, 2008) – has been exploited to address this question. Under conditions in which the target is displaced during the ocular saccade to its original location, subjects verbally report being unaware of the displacement when it is small (Blouin et al., 1995a; Chua & Enns, 2005; Goodale, Pélisson, & Prablanc, 1986; Gritsenko, Yakovenko, & Kalaska, 2009), yet show corrective movements to reach the displaced target location.

The pioneering study of Goodale, Pélisson, and Prablanc (1986) clearly demonstrated that substantial online adjustments of arm movement amplitude could be made in the absence of conscious perception of the target jump (see also Pelisson et al., 1986). Goodale, Pélisson, and Prablanc (1986) altered the target location during the ocular saccade toward the target, near arm movement onset. To do so, they recorded eye and hand movements in an experimental set-up where visual targets were shown on a mirror. These targets were reflected below the mirror, which also served to block direct view of the hand. A trial started by having subjects foveate on a fixation point. A target was then illuminated in peripheral vision and subjects had to look and point toward this target. A small target displacement (10% of the movement amplitude) could be triggered during the ocular saccade. In response to this shift in target location, clear and complete modifications of movement amplitude were observed, even though subjects were unaware of the target displacement and their corrective adjustments. The authors emphasized that the presence of such corrections, despite the absence of vision of the moving hand, indicated that online guidance of movement did not depend on a visuo-visual comparison of hand and target positions. Moreover, there was no noticeable modification of the velocity or acceleration profiles compared to movements when the target was not displaced. Thus, while movements were corrected to reach the new target location, movement duration was comparable to that in the unperturbed condition, suggesting that online corrections, did not require additional processing time. Goodale, Pélisson, and Prablanc (1986) proposed that these subtle modifications reflected the normal process of updating the internal representation of target location at the end of the saccade, similar to what occurs when the target is not displaced. This update results in the fine-tuning of movement commands to bring the hand toward the desired target location. Because the authors reported that subjects did not consciously perceive the target displacements, their study provided strong support to the idea that online control mechanisms do not necessarily depend on conscious awareness of an error (see also Castiello, Paulignan, & Jeannerod, 1991; Gritsenko, Yakovenko, & Kalaska, 2009).

To test the generality of this idea, Prablanc and Martin (1992) examined corrective responses to directional rather than amplitude displacements as in the experiments of Goodale, Pélisson, and Prablanc (1986) and Pelisson et al. (1986). Following detailed kinematic analyses, Prablanc and Martin (1992) found that rapid corrections could occur well before peak velocity, ~150 ms after the target displacement. These findings, which have been replicated in several studies (Desmurget et al., 1999, 2001, 2004; Gritsenko, Yakovenko, & Kalaska, 2009), thus extended earlier results by showing that rapid adjustments to movement *direction* could also be initiated without conscious awareness of the error. These studies not only suggest that errors that do not reach conscious awareness can be effectively corrected, but they also provide strong support to the idea that perception and action might be mediated by independent neural mechanisms (Chua & Enns, 2005; Milner & Goodale, 1995).

4.3. Automaticity of online trajectory corrections

As briefly mentioned earlier, the requirement to ignore a target displacement often results in a small but clear response toward the displaced target (Cameron et al., 2009; Striemer, Yukovsky, &

Goodale, 2010). These and other previous findings indicate some level of "automaticity" or "hard-wiring" for these rapid visuomotor responses. Pisella et al. (2000) investigated this possibility by asking subjects to stop their ongoing movement in response to actual target displacements or to a change in target color. The hypothesis was that if corrections to target displacements are automatic to some degree, they would not be completely inhibited compared to when a color switch was used. Pisella et al. (2000) found that this was indeed the case, with subjects making a large number of unintentional corrections towards the displaced target location when it was actually shifted, but not when there was a color shift. They suggested that the reaction to a change in target location might represent a low-level, "automatic" response, which might occur independent from higher-order aspects of cognitive processing (see also Cressman et al., 2006). In another double-step study, Sarlegna et al. (2006) asked subjects to remember the positions of targets and initiate movement corrections toward the remembered positions upon hearing a sound played close to movement onset. Movement corrections were clearly present but their latency was longer compared to corrections toward visible targets. This supports the idea that online responses to other arbitrary signals are slower, possibly less automatic, than online responses to visual target displacements.

The idea that online corrections in response to changes in target location are largely "low-level" in nature was also supported by a study of Diedrichsen et al. (2004) who asked subjects to simultaneously point to two separate targets, one with each hand. In some trials, both targets could be displaced either in the same direction or in opposite directions. Diedrichsen et al. (2004) observed that the trajectory of both hands could be efficiently controlled even when the hands were being moved at the same time. In fact, they found similar adjustments of hand trajectory in response to a target displacement, regardless of whether the other hand reached to a stationary target or a displaced target location. Overall, this near-independent control of the two hands suggested that the attentional cost for such online corrections is low. This was recently confirmed by McIntosh, Mulroue, and Brockmole (2010), who showed that a cognitively-demanding task performed in parallel to a pointing task did not impair the ability to correct movement trajectories in response to target displacements.

The idea of automaticity of online corrections is also supported by studies that used an "anti-point" paradigm (Day & Lyon, 2000; Johnson, Van Beers, & Haggard, 2002). During the task, subjects were required to respond in a direction opposite to the direction of the target displacement. Day and Lyon (2000) showed that trajectory adjustments in the required direction (opposite to that of the target displacement, latency >160 ms) were often preceded by adjustments *in* the direction of the target displacement. These adjustments were labeled as "automatic", and it was proposed that "voluntary" corrections are triggered later during movement execution. Cressman et al. (2010) extended this view by showing that the automatic corrective responses were also engaged during very slow movements. Indeed, they found no significant differences in the latency of the automatic component for movements of similar amplitude but that lasted either 500 ms or 1200 ms. Thus, even when the temporal constraints are small, the automatic system is still engaged, perhaps as a « default » to enable fast feedback-mediated corrections.

Recently, Gritsenko and Kalaska (2010) showed however that the fast, automatic adjustments could be selectively suppressed with learning. In their study, a mirror transformation was introduced such that when subjects moved their hand rightward, the cursor moved leftward. Subjects' behavior in response to perceived target displacements was tested before and after they were exposed for ~200 trials to this visuo-motor transformation. In the first block under mirrored feedback conditions, Gritsenko and

Kalaska (2010) showed that the first observed adjustments were non-functional: for instance, when the target was displaced rightward at movement, the hand response was 'automatically' oriented rightward, resulting in the cursor moving leftward, away from the target. These adjustments were very rapid, occurring ~100 ms after the perturbation. After adaptation to the mirrored vision conditions however, Gritsenko and Kalaska (2010) observed suppression of these automatic, non-functional adjustments, while the functional adjustments continued to occur at a latency similar to that observed during control trials. It still remains unclear whether with extensive learning, the functional component itself could emerge at a latency similar to that of the early "automatic" component, and whether training in other visuomotor conditions could transfer to the mirrored perturbation conditions. Nevertheless, the current consensus appears to be that a target displacement elicits two clearly distinguishable components, an early "automatic" response and a delayed "voluntary" response.

4.4. The posterior parietal cortex as a critical neural substrate for online responses to changes in target location

Day and Lyon (2000) suggested that the early corrective components may be mediated by subcortical brain structures, while later corrections might be mediated by cortical regions (see also Day & Brown, 2001; Fautrelle & Bonnetblanc, 2012). To our knowledge, the suggestion by Day and Lyon (2000) for distinct neural substrates has not been investigated in detail. In fact, most neurophysiological research has been focused on identifying cortical correlates of target jump responses. In particular, a large effort has been dedicated towards understanding the role of posterior parietal regions in this process given the understanding that posterior parietal cortex is critical for updating of target location relative to the current location of the hand (see Gaveau et al., 2014; Prablanc, Desmurget, & Gréa, 2003 for a review). Mountcastle et al. (1975) were among the first to show that a number of neurons in the posterior parietal cortex fire exclusively during active targeted movements. The firing pattern of these neurons was such that they did not respond to target presentation or to non-targeted arm movements, but fired only during the execution of the arm movement toward the visual target, and stopped firing once the arm reached the target. This suggested that some posterior parietal neurons could be involved in the computation or correction of an error signal between the hand and the target. More recently, Archambault, Caminiti, and Battaglia-Mayer (2009) recorded from parietal neurons in non-human primates while they performed unconstrained reaching movements. The authors observed that neuronal activity in parietal cortex was modulated starting ~150 ms after a target jump. Careful analysis of neuronal firing rates showed that after the target displacement, the activity of the neurons was substituted with the activity observed when the monkey reached directly to that target from the initial position (in single-step trials). The control of double-step trials thus appeared as if two single-step trials were superimposed with a delay of approximately 150 ms (see also Archambault, Ferrari-Toniolo, & Battaglia-Mayer, 2011; Georgopoulos et al., 1983). Importantly, parietal cells activity preceded (by ~20 ms), and strongly correlated with, changes in hand kinematics suggesting a critical role for parietal cortex cells in the online control of arm movements.

A clear demonstration of the role of the posterior parietal cortex in human online motor control came from Desmurget et al. (1999). The authors used a double-step paradigm in which subjects had to reach for visual targets with their unseen right hand. Smooth adjustments of the fast reaching movements toward the second target were observed in response to the target displacement that occurred during the ocular saccade to the initial target. However, when a magnetic pulse was applied transcranially over the left

posterior parietal cortex just after arm movement onset, trajectory corrections were largely inhibited, and movements continued toward the initial target. Desmurget et al. (1999) proposed that the absence of trajectory corrections was due to disrupted estimation of hand position. Desmurget et al. (2001) later studied similar experimental conditions with functional neuroimaging and found that the contralateral intraparietal sulcus showed larger activation in double-step trials than during simple reaching trials. This reinforced the idea that the posterior parietal cortex plays an important role in the online regulation of goal-directed movements, a result supported by subsequent studies (Diedrichsen, Hashambhoy, Rane, & Shadmehr, 2005; Reichenbach et al., 2011; Tunik, Frey, & Grafton, 2005). Interestingly, Glover, Miall, and Rushworth (2005) have proposed that the role of the posterior parietal cortex might specifically be to initiate, rather than to fully execute, the corrective adjustments.

Pisella et al. (2000) had the opportunity to test a stroke patient with an ischemic lesion restricted to the left and right parietal cortices. This patient with optic ataxia was able to accurately point to stationary targets but her ability to correct the ongoing movement was dramatically impaired when the target was displaced at movement onset. This study (see also Gréa et al., 2002; Rossit et al., 2012; Schaefer, Mutha, Haaland, & Sainburg, 2012) thus provided converging clinical evidence that the parietal cortex plays a critical role for the rapid regulation of reaching movements in response to changes in target location. Mutha et al. (2014) tested patients with unilateral lesions to parietal or frontal cortex who had to perform a double-step task with their ipsilesional arm and noted that left parietal lesions clearly impaired the accuracy of the corrective response. A few studies have indicated a role for other neural structures, including the cerebellum (Bonnefoi-Kyriacou et al., 1998), basal ganglia (Desmurget et al., 2004; Diedrichsen et al., 2005) and frontal cortical regions (particularly of the right hemisphere, see Mutha et al., 2014) in such online corrections. However, the specific role of these structures during online motor control remains unclear.

How might the parietal cortex mediate online corrections to target displacements? Recent studies suggest that the role of the parietal cortex in movement modification may be shared with its role in motor learning. Several lines of work have repeatedly demonstrated that the parietal cortex is a key node in developing and storing internal representations of well-learned actions. Patients with parietal lesions fail to adapt to novel visuomotor conditions (Mutha, Sainburg, & Haaland, 2011a, 2011b), and studies in apraxic patients with parietal damage reveal that such patients often fail to recall previously well-learned actions (Goldenberg, 2003; Pearce, 2009). It is possible that such parietal-mediated learning processes and movement modification processes are related. In fact, neural networks (at the cortical level) including left parietal regions that are activated during action modification in response to target displacements (Desmurget et al., 2001) are strikingly similar to those thought to represent learned actions (Shadmehr & Holcomb, 1997). As stated in the previous section, it appears that responses to target jumps may contain an early, well-learned, «automatic» component that is difficult to modify or inhibit (Day & Lyon,2000; Pisella et al., 2000), is driven by spatial goals and could be developed through prior real-world experience, as well as perhaps a later component tuned to the more specific details of the target such as its exact location. It is plausible that parietal regions represent the well-learned, automatic component of the response just like they represent other well-learned actions, and this component is "released" whenever a target displacement is detected (Mutha et al., 2014). This suggestion is consistent with that of Glover, Miall, and Rushworth (2005), who proposed that the parietal cortex may be the neural substrate for the rapid initiation of an online corrective response, while a more detailed execution of the response

may recruit additional cortical regions (e.g., the dorsal premotor cortex and primary motor cortex, see Archambault, Ferrari-Toniolo, & Battaglia-Mayer, 2011 and Mutha et al., 2014). Certainly, whether distinct sub-regions within the parietal cortex mediate the representations of well-learned actions versus automatic online responses needs to be investigated in detail. Additionally, alternative possibilities about the role of parietal regions cannot be discounted. One possibility is that parietal regions mediate proprioception-based estimation of hand position required to plan the new response, as suggested by Desmurget et al. (1999). Another possibility is that parietal regions are involved in the computation of an error signal between the estimated hand position and the displaced target location, or simply relay the computed error to motor cortical regions. These possibilities remain to be investigated.

4.5. Latency of the visuomotor feedback loop

While the posterior parietal cortex is clearly identified as a critical neural substrate for the initiation of corrective responses to target jumps, there is a large variety of findings concerning the minimum latency required to initiate the correction. Several studies, notably Soechting and Lacquaniti (1983) and Prablanc and Martin (1992), showed that human subjects could correct their hand path during movement execution within ~150 ms (see also Brenner & Smeets, 2003; Cressman et al., 2006; Day & Lyon, 2000; Diedrichsen et al., 2004, 2005; Gritsenko, Yakovenko, & Kalaska, 2009; Izawa & Shadmehr, 2008; Paulignan et al., 1991). Consistent with this rapid visuomotor processing loop, several studies reported that movement kinematics could be modulated by a target displacement even before peak velocity (Desmurget et al., 2001; Prablanc & Martin, 1992; Turrell et al., 1998). However, several other studies have reported longer response latencies (~300 ms) to target displacements (d'Avella, Portone & Lacquaniti, 2011; Danion & Sarlegna, 2007; Flash & Henis, 1991; Johnson, Van Beers, & Haggard, 2002; Mutha, Boulinguez, & Sainburg, 2008; Sarlegna et al., 2003, 2006). Differences between task conditions, analytical methods, choice of thresholds to identify response onset (Oostwoud Wijdenes, Brenner, & Smeets, 2014a; Prablanc & Martin, 1992; Reichenbach et al., 2009) and differences in the time of target displacement across studies could explain some of the latency differences (Liu & Todorov, 2007; Mutha & Shabbott, 2008).

An intriguing possibility is, again, that the response to a target jump consists of (at least) two components (an early "automatic" component and a later "voluntary" response), and different studies, depending on their experimental conditions, differentially tap into one of these. For example, conditions where a response is required to be initiated as soon as possible could result in the release of the early automatic component while conditions in which no spatiotemporal restrictions are placed, the early component could be suppressed in favor of the more detailed response that occurs later. Support for this idea comes from the study by Mutha, Boulinguez, and Sainburg (2008), in which a target displacement led to a late corrective response, ~230 ms after the displacement when no temporal constraint was placed on the initiation of the response. However, when a mechanical perturbation was applied 100 ms after the displacement of the target, the corresponding proprioceptive reflex response was strongly modulated by the preceding target jump. This indicated that a target jump generally results in a short-latency response which can either be gated or released depending on task conditions.

4.6. Manual tracking and interception of a moving target

In studies using the double-step paradigm, the initially displayed target is often extinguished and another target is illuminated elsewhere. This is quite similar to a target disappearing and reappearing at a different position, and this sequence of events can lead to the perception that the target « jumps » from the first location to the second. Such apparent target motion clearly influences corrective responses to a target displacement (Oostwoud Wijdenes, Brenner, & Smeets, 2014b). Multiple studies however (Brenner & Smeets, 1997; Day & Lyon, 2000; Gréa et al., 2002; Nijhof, 2003), utilized tasks in which the target was actually continuously moved from one position to the other, requiring subjects to continuously track the target with their hand. In a manual tracking task, when target motion is unpredictable, tracking errors are quite small, highlighting the efficiency of online control mechanisms (Miall, 1996; Sarlegna, Baud-Bovy, & Danion, 2010). Indeed Sarlegna, Baud-Bovy, and Danion (2010) found that when the target motion was most unpredictable, the latency between the target motion and the hand tracking motion was as low as ~130 ms. The tracking task has also been instrumental in identifying some other aspects of the visuomotor processing loop. For instance, Miall (1996) showed that visual processing time decreased as the speed of target motion increased. Miall (1996) estimated that for a doubling of target speed, the time to initiate a response decreased from ~340 ms to ~260 ms. However, it remains unclear whether testing greater target speeds may result in a visuomotor processing time which would be consistent with the currently proposed ~100 ms visuomotor latency (for target jumps), or, in other words, whether, as temporal constraints increase, the automatic corrective component identified for target jump responses can be engaged during tracking tasks.

Other studies have employed tasks in which subjects are required not to track, but to intercept moving targets (Whiting, Gill, & Stephenson, 1970; Zago et al., 2009). These studies have shown that the direction of target motion can be rapidly estimated with minimal visual cues (Mrotek, Flanders, & Soechting, 2004). Moreover, this estimate appears to be continuously updated during target motion such that interceptive actions can be adjusted within 150 ms in response to sudden changes in target direction (Brenner & Smeets, 2009). Thus, these studies have led to conclusions similar to those drawn from studies using other paradigms: visual information of target position is continuously monitored during movement, in order to make rapid corrective responses that ensure task success.

5. Online control based on visual information of the environment

A relatively new body of research suggests that not only information about the intended target, but also information from the entire visual environment is exploited for the online control of movement (Gomi, 2008; Whitney, Westwood, & Goodale, 2003). Several studies have demonstrated that the addition of a structured visual environment to a dark environment improves the accuracy of targeted reaching movements (Blouin et al., 1993; Conti & Beaubaton, 1980; Krigolson & Heath, 2004; Magne & Coello, 2002). However, in several of these studies, information about the environment was available prior to movement onset and it is unclear whether the improvement in performance was due to more accurate planning or more efficient online control. Other studies have attempted to distinguish these possibilities by perturbing the visual environment and examining the effects on motor performance. Gomi (2008) has excellently reviewed the state of the research in this area. Briefly, shifts in the visual environment during the movement induce substantial modifications of movement kinematics (Abekawa & Gomi, 2010; Brenner & Smeets, 1997; Hansen, Tremblay, & Elliott, 2008; Proteau & Masson, 1997; Scotto Di Cesare et al., 2011, 2014; Whitney,

Westwood, & Goodale, 2003). For instance, if the visual environment shifts leftward during a reaching movement, the hand trajectory is also deviated leftward after the shift in ~120 ms (Saijo et al., 2005; Whitney, Westwood, & Goodale, 2003). The online response is affected by the velocity of the visual change, but what exactly gives rise to the response remains unclear. While some studies have suggested that the response is caused by a shift in the perceived target location (Brenner & Smeets, 1997; Whitney, Westwood, & Goodale, 2003), others have suggested that this response is observed even without any perceptual shift in the location of the target (Saijo et al., 2005). In fact, Saijo et al. (2005) demonstrated the existence of these quick responses in the absence of any target, during the "follow-through" phase of a hitting motion. These authors suggested that such responses are reflexive in nature, similar to a reflex eye movement that stabilizes a retinal image. More research is now needed to firmly establish the neural mechanisms underlying such responses.

The ability to use information from the environment during movement is also critical for avoiding any obstacles present between the hand and the target. Two recent studies have investigated whether visual information of obstacle location is used during the execution of reaching movements. Aivar, Brenner, and Smeets (2008) tested whether the sudden change in the location of a virtual obstacle during movement execution can be rapidly taken into account to adjust the hand trajectory. They observed fast responses to the visual shift in obstacle location, but correction latencies were slightly longer compared to those observed when the target was displaced; the cause of this increased latency remains unclear. Chapman and Goodale (2010) used a slightly different methodological approach: in their study, the obstacle was not displaced, but the target was. The target displacement was such that the obstacle, which was initially beyond the first target, was now located between the current location of the hand and the displaced target. Trajectory corrections were rapidly observed, both, to avoid a collision with the obstacle and to reach the displaced target. These results suggested that objects in the environment are monitored during movement execution as well as the intended target is.

Grierson and Elliott (2009) specifically tested the interaction between the processes of responding to changes in the environment versus the target. In one experiment, they used a Müller-Lyer illusion to induce perceptual shifts in the location of the intended movement endpoint. This perturbation affected endpoint accuracy through movement adjustments that were observed late in the movement. In a second experiment, Grierson and Elliott (2009) then observed that shifting the environmental background affected endpoint accuracy through changes in movement kinematics during the early phases of movement. Interestingly, when both perturbations were triggered during the same movement, there was no interaction between the two adjustment processes. This suggested that two visual feedback loops mediating corrective responses to changes in target location and shifts in the visual environment might operate independently. Overall, these findings support the idea that online motor control takes into account information not only of the target but also the entire visual environment signals when adjusting limb trajectory to achieve the desired task goal.

6. Summary and future challenges

The purpose of this review was to highlight converging lines of evidence that suggest that efficient online motor control takes into account visual information about the target during point-to-point reaching movements. We first considered studies in which binary information about the presence or absence of a visual target provided an understanding of how availability of target information

influences online motor control. We then considered whether changes in the properties of the target are accounted for during the formulation of the online response. The bulk of the review focused on the double-step paradigm, which has been instrumental for understanding several aspects of the online motor response system such as the latency of the visuomotor feedback loop and its underlying neural substrates. We reviewed a wealth of studies that have identified the posterior parietal cortex as a key substrate for online visuomotor control and offered a novel perspective on how a parietal specialization for representing and planning learned actions could also explain its role in online control. Finally, we briefly touched upon studies that proposed that it is not just information about the target, but the entire visual environment that appears to be accounted for when movements should be adjusted online. While we are at a point now where we understand, from several lines of work, that changes in visual information about the target and the environment are used for online motor control, we see three major challenges for the future.

The first challenge is to understand exactly *how* these changes in visual information are converted into the corrective motor commands. Newer computational models have begun providing some clues about how such movement commands might be generated. Prominent among these has been the optimal feedback control model proposed by Todorov and Jordan (2002). In this control scheme, feedback gains are adjusted based on estimates of limb and environmental state to generate a motor command that is optimal for achieving the task goal. The gains thus represent sensorimotor transformations, which convert the sensory estimates into commands for movement. In such controllers, errors are corrected only if they interfere with achievement of the task goal but are ignored otherwise, following a "minimum intervention" principle. Another interesting feature of optimal feedback control is that no desired hand trajectory is specified prior to movement onset, as it flexibly emerges based on continuous adjustments of the motor commands. This control scheme has been valuable in explaining several features of voluntary movements (Scott, 2004). However, challenges remain in terms of explaining behavior that may not always be optimal. For instance, Day and Lyon (2000) observed early corrections in the direction of a target displacement when they were asked to correct in the opposite direction. If optimal motor commands are continuously updated, why would (non-optimal) early corrections in the direction of the jump be observed when they interfere with goal achievement (correcting in the opposite direction)? Which factors constrain changes in the control policy? Are automatic adjustments of movement trajectory always sub-optimal?

The optimal feedback control scheme relies on a stable estimate of limb state. Understanding how visual information about the target is integrated with all other sensory information provided not just by the visual system but also the proprioceptive, auditory and vestibular systems to generate an estimate of limb state is another challenge that remains to be addressed. While early studies suggested that people might treat vision as the most reliable source of information and ignore other sources such as somatosensory feedback (Rock & Harris, 1967), current theories posit that the nervous system uses all the information possible from the multiple feedback channels in order to generate a state estimate (Ernst & Banks, 2002; van Beers, Sittig, & Denier van der Gon, 1996; van Beers, Sittig, & Denier van der Gon, 1999). Further, it appears that the estimate of limb state is derived not just based on sensory feedback, but is also crucially dependent on the prediction of the sensory consequences of movement commands (Danion & Sarlegna, 2007; Desmurget & Grafton, 2000; Shadmehr, Smith, & Krakauer, 2010; Wolpert & Flanagan, 2001). It is possible that peripheral feedback information is combined with the predicted sensory consequences in a Bayesian manner, i.e. each modality is weighted

based on the reliability of the information it provides so that the variance of the resultant state estimate is minimized. Some support for this idea has come from the work of Kording and Wolpert (2004), who showed that subjects' corrective responses to a cursor displacement while reaching to a target was a function of both subjects' prediction of its location and its actual location relayed by visual feedback. The more uncertain subjects were about the location of the cursor (because of the presence of experimenter induced noise), the more they relied on their predictions about where the cursor would be to make the corrective response. Other studies have provided support for such statistically-optimal integration of predictions and sensory feedback for state estimation in a variety of contexts (Dokka et al., 2010; Gritsenko, Yakovenko, & Kalaska, 2009; Stevenson et al., 2009), but clearly, more work needs to be done to answer how the brain integrates the multiple feedback sources for the generation of an estimate of limb state? Focus has been on vision, proprioception and efference copy but do the other sensory systems such as the vestibular, tactile or auditory systems contribute substantially? Can this complex issue be studied by experimental and/or computational approaches?

Finally, the neural substrates mediating these different processes remain to be clearly elucidated. Scott (2012) recently reviewed the possible, numerous brain structures which underlie sensorimotor control. However, which cortical and sub-cortical neural networks underlie sensory prediction, and its integration with sensory feedback for state estimation? Which neural structures convert the state estimates into motor commands? To us, these are key questions that will hopefully be addressed in the near future.

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