



Visually-guided correction of hand reaching movements: The neurophysiological bases in the cerebral cortex



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ABSTRACT

The ability of human and non-human primates to make fast corrections to hand movement trajectories after a sudden shift in the target's location is a key feature of visuo-motor behavior. In healthy individuals, hand movements smoothly adapt to a change in target location without needing to complete the movement to the first target location, as typical of parietal patients. This finding indicates that the nervous system continuously monitors the visual scene and is able to integrate new information in order to produce an efficient motor response. In this paper, we review the kinematics, reaction times and muscle activity observed during the online correction of hand movements as well as the underlying neurophysiological processes studied through single-cell neural recordings in monkeys. Brain stimulation, lesion and imaging studies in humans are also discussed. We demonstrate that while online correction mechanisms strongly depend on the activity of a parieto-frontal network of which the posterior parietal cortex is a crucial node, these mechanisms proceed smoothly and are similar to what is observed during simple point-to-point movements. Online correction of hand movements would rely on feedforward and feedback mechanisms in the parietal cortex, as part of the activity within the fronto-parietal network for the planning and execution of visuo-motor tasks.

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1. Introduction

Reaching for objects and targets in the environment is an essential aspect of behavior in both human and non-human primates. This activity requires an adequate coordination and integration of sensory (vision, proprioception) and motor processes. Reaching for stationary objects requires constant feedforward and feedback activity within the Central Nervous System (CNS). At a first level, feedforward processes are necessary to plan out the reaching movement, while feedback is used to control for errors during movement execution and to monitor the outcome. Human and non-human primates are able to adapt their ongoing movement in response to a rapid change in the target's location. In such target shift conditions, the CNS does not complete the hand movement to the original target, but smoothly adjusts it in order to reach the second target location. This will be possible if there is enough time

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for the online correction, given the natural hand movement reaction time. The smooth, online correction of hand movement in response to a shift in target location constitutes evidence that visual information has a continuous access to the CNS and that brain centers continuously monitor ongoing movements, making the required adjustments due to changing task demands.

In humans, lesions to the posterior parietal cortex (PPC) can lead to optic ataxia (OA), a condition characterized by the inability to accurately guide the hand to visual targets in the absence of purely motor or visual deficits. Patients with OA are unable to correct their ongoing hand movements in a double-step target paradigm (Battaglia-Mayer et al., 2014; Gaveau et al., 2014; Grea et al., 2002; Pisella et al., 2000; Prablanc, Desmurget, & Grea, 2003). Instead, they complete their hand movement to the original target location, before redirecting their hand toward the second target. The parietal, dorsal premotor and motor cortical areas are thought to form a recurrent network that is crucial for the coordination of hand and eye movements, including planning, execution and control (for reviews see Battaglia-Mayer et al., 2003; Caminiti et al., 2010). The parietal areas are the sources of the visual input whereby this distributed network composes and controls hand movements to visual targets (Battaglia-Mayer et al., 2014;

Caminiti, Ferraina, & Johnson, 1996; Johnson et al., 1996). The role of these areas with respect to the online control of movement has been studied over the last 30 years in both human and non-human primates, using a variety of methodologies including psychophysical measurements, transcranial magnetic stimulation (TMS), lesion studies, imaging and neural activity recordings. The objective of this paper is to review and compare the evidence related to the cortical control of the online correction of hand movements.

2. Psychophysics of double-step hand movements

To study hand and eye behavior during sudden changes of motor plan, a “single-step/double-step” paradigm may be adopted. In these experiments, the subject starts with the hand or finger at an initial location, then is presented with a first target and is instructed to reach for it as fast as possible (single-step condition). However, in some random trials, the location of the reach target suddenly shifts in space (double-step condition), requiring a redirection of the hand movement toward this new location. The ratio of single- to double-step trials, as well as their order, is kept from the subjects in order to prevent any prediction, that could influence their behavior.

In single-step (direct) trials, there is an initial eye saccade to the target, followed by a hand movement. Note that the initial saccade may be followed by one or more corrective saccades. Thus we distinguish an eye reaction time (eRT1), a hand reaction time (hRT1) and a hand movement time (hMT). In double-step (corrected) reaches, the presentation of the second target leads to another eye saccade, followed by a change in the hand trajectory. Whereas eye saccades occur quickly and are not corrected mid-flight, the hand movement trajectory is adjusted online after the presentation of the second target. Thus we distinguish a first and second eye

reaction time (eRT1, eRT2), a first and second hand reaction time (hRT1, hRT2) and a hand movement time (hMT). Behavior during single- and double-steps reaches is summarized in Fig. 1.

For an online correction to be observed, there needs to be enough time for the subject to react; e.g., the interval between the movement time to the first target and the time of shift in target location should be larger than the visuo-motor reaction time. Conversely, if the shift in target occurs too early (e.g., at the start of the initial reaction time), then the subject will reach for the second target directly, without initiating a movement toward the first target. Conversely, if the shift occurs too late, then the movement to the first target may already have been completed. Thus, in general, the shift in target location ranges from the later part of the initial hand reaction time period, to some maximum time during hand movement, depending on extent and speed. Within these timing constraints, subjects are able to produce smooth, corrective hand movements in response to a shift in target (Oostwoud Wijdenes, Brenner, & Smeets, 2011).

Paradigms of double-step hand movements presented in the literature vary both in terms of location and timing of the target shift (for recent reviews see Battaglia-Mayer et al., 2014; Gaveau et al., 2014). In experiments, targets can be displaced either parallel to the initial movement direction, e.g. further and closer (Soechting & Lacquaniti, 1983) or, more frequently, perpendicular to the movement direction (Brenner & Smeets, 1997; Briere & Proteau, 2011; Desmurget et al., 1999; Goodale, Pelisson, & Prablanc, 1986; Gritsenko, Yakovenko, & Kalaska, 2009; Johnson, Van Beers, & Haggard, 2002; Oostwoud Wijdenes, Brenner, & Smeets, 2011; Prablanc & Martin, 1992; Proteau, Roujoula, & Messier, 2009; Reichenbach et al., 2009; Veerman, Brenner, & Smeets, 2008). Timing of the target shift can be set within 0–200 ms from the onset of hand movement (Brenner & Smeets, 1997; Briere & Proteau, 2011; Johnson, Van Beers, & Haggard, 2002; Oostwoud

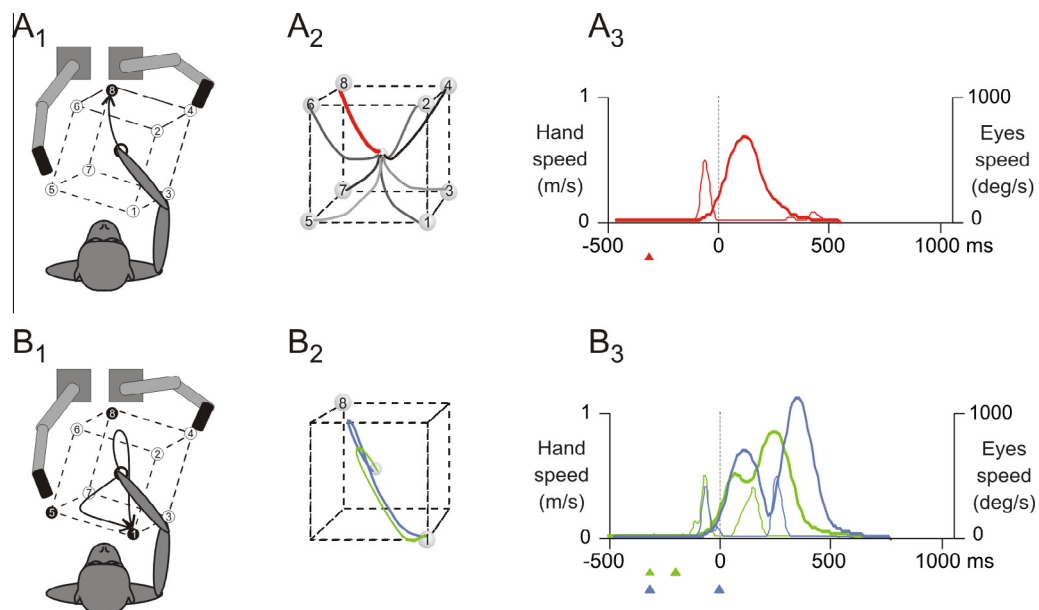


Fig. 1. Experimental apparatus, task, and behavioral performance. Monkeys performed single-step direct reaches (A_1 ; from the center to target 8) or made double-steps hand movement corrections (B_1) of 90° (from the center to target 5 and then to target 1), or 180° (from center to target 8 and then to target 1), within a reaction-time paradigm where target were presented at the vertices of an imaginary cube, in an intermingled randomized design. Therefore, animals could not predict which target would appear and which trial (single- or double-step) they had to perform. Lit targets were positioned by two robot-arms in total darkness. (A_2) Examples of hand movement trajectories in different directions of direct reach trials. (A_3) Examples of eye (thin curve) and hand (thick curve) speed profile during single-step, direct reaches, aligned to the onset of hand movement (0). The red triangle on the abscissa indicates the moment of target presentation. (B_2) Examples of corrected reaches when a change of target location occurred from 8 to 1. The hand path originally directed to target 8 reverses toward target 1, after presentation of the latter during hRT1 (green) or at the onset of hMT1 (blue). Notice that the path length toward the first target is a function of the time the target stays on, therefore it is shorter when the target jump occurs during hRT1 than at the onset of hand movement (hMT1). (B_3) Hand (thick curves) and eye (thin curves) velocity profiles during double-step reaches, when the target jumps during hRT1 (green curves) or at hMT1 (blue). Triangles refer to the time of first and second target presentation in different reaching conditions, i.e. target jump occurring during reaction-time (green) or at the onset of movement-time (blue). (Reproduced with modifications from Archambault, Ferrari-Toniolo, & Battaglia-Mayer, 2011.)

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