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Automatic online control of motor adjustments in reaching and grasping

Valérie Gaveau[a,b], Laure Pisella[a,b], Anne-Emmanuelle Priot[a,c], Takao Fukui[a], Yves Rossetti[a,b], Denis Pélisson[a,b], Claude Prablanc[a,b,*]

[a] INSERM, U1028, CNRS, UMR5292, Lyon Neurosciences Research Center, ImpAct, 16 avenue du doyen Lépine, 69676 Bron cedex, France
[b] Université Lyon 1, Villeurbanne, France
[c] Institut de recherche biomédicale des armées (IRBA), BP 73, 91223 Brétigny-sur-Orge cedex, France

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ABSTRACT

Following the princeps investigations of Marc Jeannerod on action–perception, specifically, goal-directed movement, this review article addresses visual and non-visual processes involved in guiding the hand in reaching or grasping tasks. The contributions of different sources of correction of ongoing movements are considered; these include visual feedback of the hand, as well as the often-neglected but important spatial updating and sharpening of goal localization following gaze-saccade orientation. The existence of an automatic online process guiding limb trajectory toward its goal is highlighted by a series of princeps experiments of goal-directed pointing movements. We then review psychophysical, electrophysiological, neuroimaging and clinical studies that have explored the properties of these automatic corrective mechanisms and their neural bases, and established their generality. Finally, the functional significance of automatic corrective mechanisms–referred to as motor flexibility–and their potential use in rehabilitation are discussed.

1. Introduction

When performing a simple reaching movement such as looking and pointing at a button at a moderate speed under normal viewing conditions, different sources of noise at either the sensory level (visual, proprioceptive) or the motor planning stage may result in an inaccurate response. In such situations, continuous control–which occurs mostly outside the scope of awareness–and a final voluntary correction during the homing phase are usually called for.

Understanding such an apparently simple action requires some knowledge of the basic operation of the oculomotor system, of the head motor control system, and of their coordination through the vestibulo-ocular reflex during a natural gaze orientation toward the object (Bizzi, Kalil, & Tagliasco, 1971; Laurutis & Robinson, 1986; Pélisson & Prablanc, 1986; Pélisson, Prablanc, & Urquizar, 1988). It also requires some knowledge of the way the object and the hand are represented in the body (or other) reference frame (Bernier & Grafton, 2010; Beurze, Toni, Pisella, & Medendorp, 2010), and of how these representations are transformed into motor commands (Rossetti, Desmurget, & Prablanc, 1995; Sober & Sabes, 2005). In addition, the role of the different visual and kinesthetic feedback loops must also be taken into account for understanding the mechanisms of movement execution (Filimon, Nelson, Huang, & Sereno, 2009). Lastly, updating of object location when gaze is anchored on its goal involves a representation of all sensory, oculomotor, cephalic, and multisegmental motor-related signals within a distributed network centered on the posterior parietal cortex (PPC) (for a review, see Andersen, Snyder, Bradley, & Xing, 1997; Snyder, Batista, & Andersen, 2000).

The work that has been carried out on this topic during the last three decades is a tribute to the major contribution of Marc Jeannerod's thoughts concerning the links between action and perception. Many of his fellow researchers are still pursuing this line of research, using new methodological tools. From the 60s, Marc Jeannerod started on a long scientific path as a neurophysiologist and a neuropsychologist, to understand how the brain implements visually-guided behavior in natural gaze orientation, reaching and grasping. His first investigation of rapid eye movements during sleep, in collaboration with Michel Jouvet and Jacques Mouret (Jeannerod, Mouret, & Jouvet, 1965), provided him with a strong hint of the projective–as opposed to reactive–nature of behavior, and its implications. The main idea that guided his scientific approach is that action is initiated on the basis of internal representations (Jeannerod, 1990) and involves feedback,

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* Corresponding author at: INSERM, U1028, CNRS, UMR5292, Lyon Neurosciences Research Center, ImpAct, 16 avenue du doyen Lépine, 69676 Bron cedex, France. Tel.: +33 4 72 91 34 11; fax: +33 4 72 91 34 03.
E-mail address: claude.prablanc@inserm.fr (C. Prablanc).

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which validates and strengthens sensory and motor representations. He extended this idea into the cognitive sciences, from the observation of actions to the preparing of execution, motor imagery, shared representations, and the ability to attribute mental states, intentions, or actions to others (Jeannerod, 2006). As head of INSERM Unit 94, he began in the early seventies to study simple sensorimotor systems such as the oculomotor system (Prablanc & Jeannerod, 1974, 1975) and its interaction with the vestibular system (Clément, Courjon, Jeannerod, & Schmid, 1981; Schmid & Jeannerod, 1979). Using a similar approach, he extended this research to the study of the coordination between the oculomotor and upper-limb sensorimotor systems. He addressed the sensorimotor coordination problem through various complementary approaches, mainly, related to brain activity and visuomotor neonatal development (Flandrin, Courjon, & Jeannerod, 1979; Vital-Durand & Jeannerod, 1974), motor psychophysics (Prablanc, Echallier, Jeannerod, & Komilis, 1979; Prablanc, Echallier, Komilis, & Jeannerod, 1979), and anatomical structures with selective cortical lesions (Jeannerod, 1985, 1986a, 1986b, 1988; Jeannerod, Michel, & Prablanc, 1984).

Marc Jeannerod made key contributions to the exploration of brain mechanisms for the optimization of final movement accuracy in the following two domains: planning and online corrective processes, which ensure movement guidance toward the target once the movement has been initiated (Pélisson, Prablanc, Goodale, & Jeannerod, 1986); visuomotor adaptation processes, which resolve a conflict induced by lateral prism displacement of the visual field (Prablanc, Tzavaras, & Jeannerod, 1975b) or by rotation of the visual feedback of the moving hand (Prablanc, Tzavaras, & Jeannerod, 1975a). Another major contribution from Marc Jeannerod is the understanding of the coordination between the reach and grasp components of an action (Jeannerod, 1984, 1994; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Jeannerod, Decety, & Michel, 1994; Paulignan, Jeannerod, MacKenzie, & Marteniuk, 1991; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991). He initiated a fruitful collaboration with Giacomo Rizzolatti, Michael A. Arbib and Hideo Sakata (Jeannerod, et al., 1995) based on a combination of complementary electrophysiological, anatomical, neuropsychological and modeling approaches of visuomotor transformations.

Marc Jeannerod's interest in the control of movement led him to explore the relationship between automatic corrective control and intention. Following the original observation that performing an automatic correction can be dissociated from both the awareness of target jump and the awareness of performing a correction (Pélisson, et al., 1986), he further explored the timing of these events. An important finding was that the latency of visual awareness of goal modification was longer than the sensorimotor response (Castiello, Paulignan, & Jeannerod, 1991). Using a method based on experiments performed by Prablanc, Echallier, Jeannerod, et al. (1979), Prablanc, Echallier, Komilis, et al. (1979b) and Pélisson, et al. (1986), he showed that the conscious estimation of hand position can be dissociated from the real position of the hand, and relies predominantly on visual rather than proprioceptive feedback (Farrer, Franck, Paillard, & Jeannerod, 2003; Fourneret & Jeannerod, 1998). A logical extension of this line of research addressed the issue of self-recognition (Jeannerod, 2003) and the sense of agency in healthy individuals (Farrer, Bouchereau, Jeannerod, & Franck, 2008; Jeannerod, 2009) and patients (Daprati, et al. 1997). The innovative nature and power of this paradigm are substantiated by its extensive use in the motor-control and motor-cognition fields (for reviews, see Farrer, same issue; Frith, same issue).

Movement execution has long been considered as composed of two phases: a major pre-planned phase followed by a final corrective phase during the very end of the movement. However, many studies of goal-directed movement have neglected to address the sensory sources of motor planning error (visual, kinesthetic), which is primarily concerned with precise knowledge of the initial state of effectors and goal specification. For instance, in the traditional speed-accuracy tradeoff approach (Fitts, 1954; for a review, see Jeannerod, 1988; Keele & Posner, 1968; Meyer, Abrams, Kornblum, Wright, & Smith, 1988; for a review, see Paillard, 1996; Zelaznik, Hawkins, & Kisselburgh, 1983), or in the more recent formalization of the motor minimum-variance theory (Harris & Wolpert, 1998), these factors are not completely taken into account. In particular, the dynamic contribution of the oculomotor system to goal specification and online movement correction is usually ignored.

When a close target appears within the peripheral visual field and a subject is required to look and point at it as accurately as possible, the natural sequence which is typically observed is an eye saccade with an average latency of 200 ms, followed 50–100 ms latter by a limb movement (Biguer, Jeannerod, & Prablanc, 1982; Megaw & Armstrong, 1973; Prablanc, Echallier, Jeannerod, et al., 1979; Prablanc, Echallier, Komilis, et al., 1979; Rossetti, Stelmach, Desmurget, Prablanc, & Jeannerod, 1994; Sarlegna, et al., 2003; Vercher, Magenes, Prablanc, & Gauthier, 1994). However, the onset of EMG deltoid activity is nearly synchronous with saccade onset (Biguer, et al., 1982). As a result, the apparent sequence of activations of the different effectors depends mostly on their inertia, while the orienting and reaching responses are likely initiated in parallel.

During the orienting saccade, the central nervous system (CNS) needs to partly inhibit the fast retinal slip–the so-called 'saccadic suppression'–(Bridgeman, 1995; Li & Matin, 1997; Matin, 1974) in order to reduce or cancel the noisy transient retinal signals. In a perceptual task of target detection, Bridgeman, Lewis, Heit, and Nagle (1979), taking advantage of the 'saccadic suppression', observed that when a target was slightly displaced at the onset of the orienting saccade, subjects were unable to report the displacement but were still able to point at the displaced target. The authors concluded that some information, which is unavailable to the cognitive visual system, is available to a motor-oriented visual system under conditions simulating normal perception. This observation fitted nicely with the identification of two visual streams (for a review, see Jeannerod & Rossetti, 1993; Schneider, 1969; Ungerleider & Mishkin, 1982): a ventral stream for perception, and a dorsal stream for action—an idea that was later developed in the context of clinical observations of patients with lesions of the occipito-temporal or occipito-parietal pathways (Caminiti, 1999; Goodale & Haffenden, 1998; Goodale & Milner, 1992; Gréa, et al., 2002; Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003). The idea that the dorsal stream does not require visual awareness has recently been supported by empirical evidence (Milner, 2012). It appears that the main role of the dorsal stream is to provide real-time 'bottom-up' visual guidance of movements. Further dissociations have been demonstrated within the dorsal stream using neuroimaging, neuropsychology and neurostimulation methods. Using fMRI in healthy subjects, Beurze et al. (2010) have shown that planning reaches into the visual periphery is metabolically more costly than planning reaches toward foveally viewed targets, both in the PPC and in the dorsal premotor cortex (PMd). Consistent with this finding, Prado et al. (2005) found that reaching an object in foveal vision involved the medial intraparietal sulcus (mIPS) and the caudal part of the PMd, whereas reaching an object in peripheral vision involved a more extensive network including the parieto-occipital junction (POJ). Lesions of the latter structure cause the visual-field effect of optic ataxia (Karnath & Perenin, 2005), i.e., a misreaching biased toward the line of gaze in the visual field controlateral to the lesion (Blangero, et al., 2010), while more anterior lesions of the superior parietal lobule and intraparietal