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Automatic online control of motor adjustments in reaching and grasping



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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.

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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 Jouvét and Jacques Mouret (Jeannerod, Mouret, & Jouvét, 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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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; Fournier & 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, & Kesselburgh, 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 later 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 contralateral to the lesion (Blangero, et al., 2010), while more anterior lesions of the superior parietal lobule and intraparietal

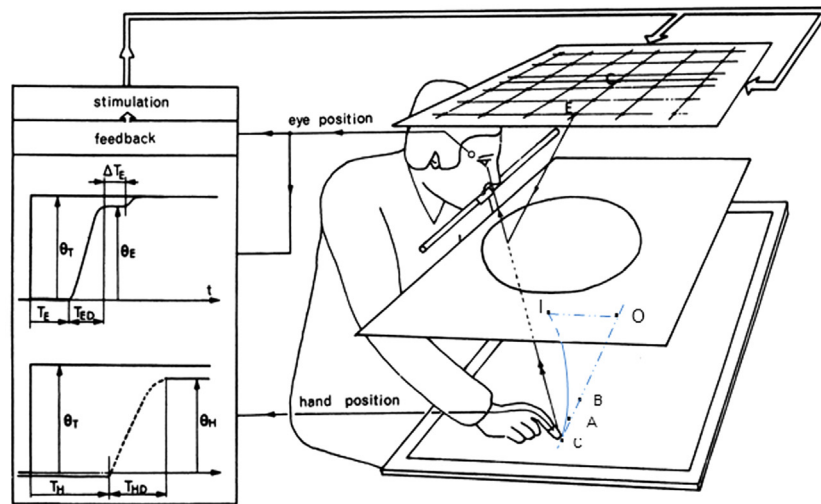


Fig. 1. Initial apparatus used to implement real-time investigation of the eye-hand coordination (modified from Prablanc, Echallier, Komilis, et al., 1979). It basically includes a target presentation plane, a pointing plane and midway in between a half reflecting mirror allowing seeing both the target (or an object) on the pointing plane and the whole limb. However, the vision of the hand can be instantaneously occluded, triggered online by an eye- or hand-movement velocity threshold. Similarly, the initial stimulus can be independently and instantaneously interrupted, or its location perturbed, triggered by an eye or hand movement velocity threshold. This apparatus makes it possible to disentangle visual feedback of the moving limb from retinal error signals resulting from the simultaneous vision of the target and limb. It also makes it possible to provide or remove vision of the limb, either prior to the movement or only during limb motion, allowing researchers to assess the role of limb vision in planning and controlling the movement.

sulcus cause the hand effect of optic ataxia (Blangero, et al., 2010; Karnath & Perenin, 2005; Perenin & Vighetto, 1988). Besides these distinct but complementary parietal modules for pointing to central and peripheral visual targets, Gréa et al. (2002), Pisella et al. (2000), and Desmurget et al. (1999) have identified a specific module for online motor control within the parietal cortex, which is not involved in pointing to foveated stationary visual targets. However, the link between the deficit of reaching in peripheral vision and the deficit of online correction is still a matter of debate. While the studies of Gréa et al. (2002), Pisella et al. (2000), and Desmurget, et al., (1999) have suggested a common module for these two types of deficit, a recent study from Buiatti, Skrap, and Shallice (2013) has provided evidence for distinct parietal modules involved in different aspects of motor control, with a possible dissociation between modules involved in planning a reach toward peripheral visual targets and modules involved in online motor control in response to moveable targets. Another type of modular organization of the parietal cortex relates to the type of movement feedback. Indeed, a recent fMRI study (Filimon, et al., 2009) has reported multiple parietal regions involved in the reaching network, with a functional gradient from more anterior regions involved in proprioceptive feedback processing to more posterior ones involved in visual feedback processing (see also Wenderoth, Toni, Bedeleem, Debaere, & Swinnen, 2006). In summary, these studies together suggest multiple, complementary, types of modular organization of the parietal cortex, in relation to movement feedback modality (visual versus proprioceptive), motor guidance relative to gaze (central versus peripheral), and the type of motor processes (planning versus automatic correction).

2. The unaware double-step pointing paradigm

In order to investigate how a planned movement is controlled naturally after its initiation, and to highlight how non-intentional fast corrective processes are operating, one has to introduce errors large enough to detect modifications of the trajectory of the movement, but small enough in order not to elicit some learning during an experimental paradigm. An adequate method consists in introducing

a planning error unknown to the subject while preventing visual feedback of the movement, which guarantees a minimum cognitive interference. The planning error may affect either the amplitude of the movement or its direction. Therefore, it is still an open question whether the same automatic corrective process operates in these two conditions, as it has been suggested that planning of amplitude and direction relies on distinct processes (Vindras, Desmurget, & Viviani, 2005). In addition, it is possible that the awareness of a change in the location of the goal of the action does not influence the nature of the automatic corrective process when the awareness of this change follows the movement correction (Castiello, et al., 1991). Finally, such planning errors must remain sufficiently scarce and unpredictable so as to prevent the confounding motor modifications related to sensorimotor adaptation processes. Indeed, as will be detailed in Section 2.1 below, such planning errors in the 'unaware double-step task' are elicited by a slight displacement of the visual target during the saccadic response. Thus, if the target perturbation was systematic and constant over trials, sensorimotor adaptation of both saccadic eye movements (Pélisson, Alahyane, Panouillères, & Tilikete, 2010) and limb movements (Magescas & Prablanc, 2006) would be expected. Given the tight relationship between oculomotor control and sensory representation of target in space illustrated by recent studies (e.g., Zimmermann & Lappe, 2010), adaptive modifications of saccades would represent a further confounding factor in the study of online corrections of goal-directed hand movements.

2.1. Amplitude double-step

Considering the inaccuracy of peripheral vision (Curcio & Allen, 1990; Curcio, Sloan, Kalina, & Hendrickson, 1990; Lewis, Garcia, & Zhaoping, 2003) and of the primary saccade toward a peripheral target (Becker & Fuchs, 1969; Deubel, Wolf, & Hauske, 1982), Goodale, Pelisson, and Prablanc (1986) and Pélisson et al. (1986) hypothesized that target updating at saccade end allows both a secondary saccade, which brings the fovea onto the target, and a locking of the unseen hand guidance to the target (Prablanc & Pélisson, 1990). The rationale for this hypothesis was that the introduction of a small artificial error at the end of the primary saccade would not be consciously detected, and that both natural

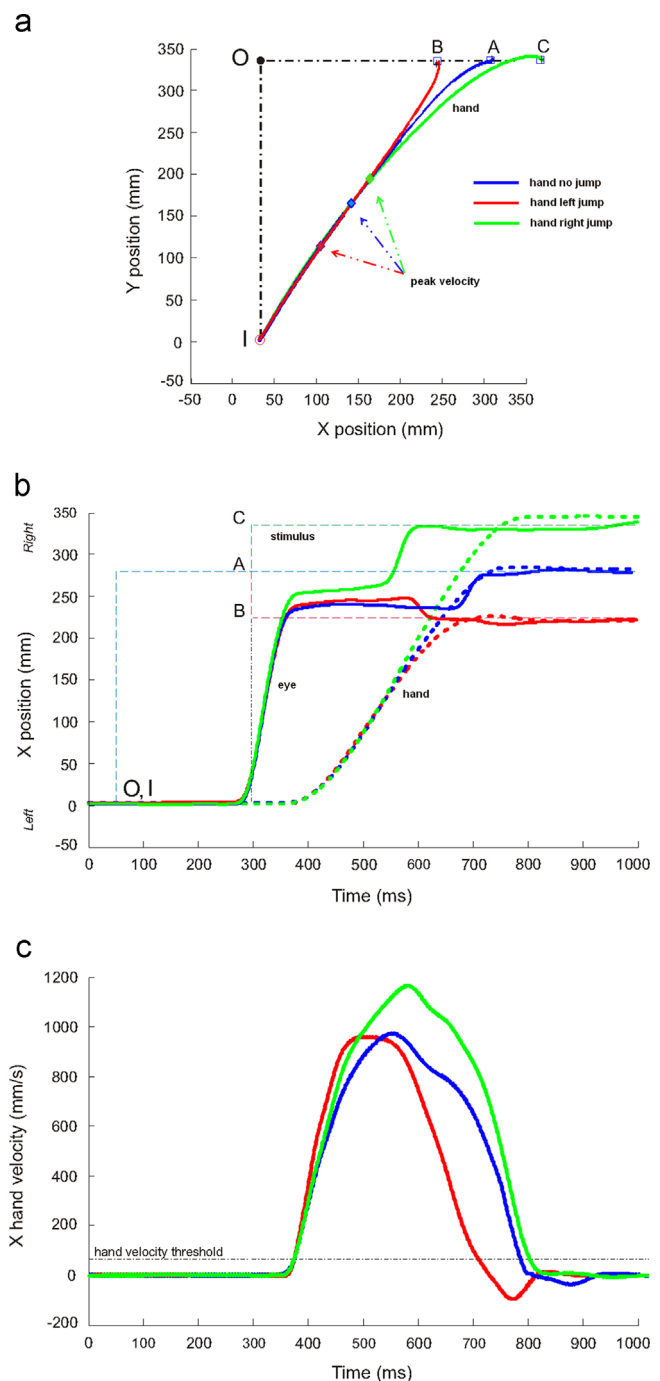
and artificial path errors would be equally corrected by comparing the updated target location at the end of the orienting saccade and the current knowledge of the unseen moving limb. They designed a real-time psychophysical paradigm (the “unaware double-step task”) in which target jumps (in or out) were randomly intermixed with no target jump, and limb vision was suppressed at the onset of hand movements (dynamic open loop). The perturbation resulting from the double-step stimulation influenced only the amplitude of the movement, its direction remaining unchanged. The experimental apparatus used in this series of studies is shown in Fig. 1. The major results were that: (1) no subject was able to report a target jump; (2) saccadic gain remained unchanged; (3) the hand endpoint was shifted in the direction of, and by the same amplitude as, the target displacement; (4) the duration of perturbed hand pointing movements was similar to that of unperturbed pointing; (5) velocity and acceleration profiles of perturbed movements were not substantially different from those of unperturbed movements. In each condition, velocity profiles were bell-shaped, with a deceleration phase slightly longer than the acceleration phase. These results clearly indicated a very early, automatic, and smooth correction of movements in response to the target perturbation. This behavior, observed with an inter-stimulus interval corresponding to the 200–250 ms saccadic latency, contrasted with most of the classical double-step studies, which elicited voluntary corrections characterized by the addition of sub-movements and an increased total movement duration as soon as the inter-stimulus interval exceeded 200 ms. With respect to the saccadic response, Gaveau et al. (2003) reported that displaced retinal feedback at saccade onset could slightly influence the amplitude of large saccades. Recently, Cameron, Enns, Franks, and Chua (2009) have confirmed this very fast dynamic updating, showing that part of the updating of the target jump may occur during the deceleration phase of the saccade.

Further properties of the unaware double-step task have been investigated in experiments requiring a saccadic orientation toward a target, with and without concurrent hand pointing (Blouin, Bridgeman, Teasdale, Bard, & Fleury, 1995; Blouin, Teasdale, Bard, & Fleury, 1995). The authors proposed that the CNS favors spatial perception constancy of a jumping stimulus when it is within the

extreme variability limits of the oculomotor response, whether the saccade is performed alone or is coordinated with a hand pointing. Indeed, as the average saccadic response is known to undershoot by about 10% the stimulus eccentricity, a post saccadic error of 10–20% remains undetected. Therefore, as long as the target jump is within these limits, the subject cannot know whether the saccadic error, which is detected at the end of the orienting saccade toward the target, is natural or artificial.

It is interesting to note that some analyses of pointing accuracy toward a target without any perturbation have similarly argued for the existence of a permanent modulation of the ongoing motor response. Using a real-time methodology, Prablanc, Pélisson, and Goodale (1986) investigated specifically how the duration of target presentation influenced the execution of a pointing response to stationary targets. Initial vision of the hand prior to movement

Fig. 2. A typical illustration of an “unaware double-step” experiment in which the target direction is unexpectedly perturbed at saccade onset while pointing, the subject being unaware of the perturbation (modified from Prablanc & Martin, 1992). Closed-loop condition, i.e., vision of the hand is available throughout the movement. Individual trials recordings. For clarity, all saccade onsets and hand-movement onsets have been aligned relative to the unperturbed onsets. FIR-filtered data at 40 Hz (eye) and 20 Hz (hand). (a) Trials are randomly non-perturbed (blue, point A), perturbed to the left (red, A,B), or perturbed to the right (green, A–C) at saccade onset. Subjects are instructed to look and point as quickly and accurately as possible to the peripheral target when it appears. Initial eye fixation is on point O, whereas initial hand position is on point I. IO is the sagittal line. The spatial paths of the hand for three types of individual trials are quite close up to mid-flight, and they smoothly diverge afterwards to end-up on the final target location. Left perturbation: red; no perturbation: blue; right perturbation: green; square: target location; open circle: hand position at end of saccade from O to A; diamond: hand location at peak hand velocity; cross: hand location at the end of hand movement (based on hand-velocity threshold). Notice that, at saccade end, the hand has not yet started its movement, and peak hand velocities occur at different times in the three conditions; at the hand velocity threshold (80 mm/s), the hand is almost on the final target. Observe the natural curvature of unconstrained pointing movements. (b) Spatio-temporal organization of the horizontal eye (horizontal gaze projection on the pointing surface) and hand components of the responses: all three primary saccades are hypometric, and are followed by corrective saccades which bring the fovea onto the target. The hand movements follow an initial common pattern and then smoothly diverge. Continuous curves: eye; dashed curves: hand; dashed line: stimulus; same color conventions as in (a); (c) horizontal hand velocity profiles: observe the early peak velocity changes corresponding to the right and left perturbations. The zero horizontal velocity intercept shows the reduced movement time for the left perturbation and the slightly increased movement time for the right perturbation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



was always available, and then removed at hand-movement onset. Subjects made free hand-pointing movements as quickly and accurately as possible in four conditions. For the first three conditions, the peripheral target was turned off at saccade onset, turned off just after saccade end, or remained permanently lit. In these three conditions, the hand movement started near saccade end. In the fourth condition, subjects were instructed to move the eyes first and then to point at the target. The results clearly indicated that increasing the duration of target presentation increased pointing accuracy in the first three conditions. Surprisingly, the fourth condition—in which the initial effector state and the target state were perfectly known prior to the movement—produced larger errors than the third condition, where the movement had been initiated on the basis of a poor retinal signal but updated by post-saccadic vision of the target, and then foveated. This result highlights the importance of the synergic response between the eye and the hand. [Desmurget et al. \(2005\)](#) further investigated the experiment of [Prablanc et al. \(1986\)](#) through a detailed analysis of the kinematics of unseen hand movements under different conditions of target vision. They confirmed that target updating allowed subjects to smoothly amend both constant and variable planning errors despite a lack of visual feedback of the movement. The most remarkable feature of this automatic corrective mechanism is that it operates within the time constraints of motor planning and requires little additional time. Online control of fast hand pointing to an unaware double-step target ([Magescas, Urquizar, & Prablanc, 2009](#)) has been studied under closed loop (with the hand always visible), without cognitive load, and without prior familiarization to double-step target stimulation. It has been found that at the very first trial, the automatic corrective mechanism compensated for most of the artificially induced error. Although the paradigm involved repeated pointing to an unaware double-step target over 60 trials, motor-response variability across trials varied very little and was similar to that observed during control trials involving a single step. In addition, movement duration for a double-step target did not increase by more than 40 ms relative to movement duration for a single-step target.

2.2. Directional double-step

In order to show that the unaware automatic drive of reaching was not limited to the control of movement amplitude, [Prablanc & Martin \(1992\)](#) applied the unaware double-step paradigm in a situation in which the target perturbation required mainly a directional change of hand pointing. The conditions were globally the same as in [Pélissou et al. \(1986\)](#) and [Goodale et al. \(1986\)](#), i.e. targets jumped at the onset of the orienting saccade (see [Fig. 1](#) and [Fig. 2a, b](#)), and included a session with the hand visible (closed loop) and a session without visual feedback of the hand (open loop). The overall results were very similar to those of the previous unaware double-step experiment. Subjects never detected any target jump. Perturbed movements exhibited early and smooth directional corrections with single-peak velocity profiles ([Fig. 2c](#)). The reaction time to the perturbation was evaluated at around 142–167 ms, near the time to peak velocity, irrespective of the test condition (closed loop or open loop). The mean duration of perturbed movements was only 65–80 ms longer than that of unperturbed ones (mean=420 ms). Approximately 90% of the constant error was corrected, constant and variable pointing errors being slightly higher for open-loop than for closed-loop conditions. The authors' conclusion was that this automatic process was driven by an internal feedback loop comparing updated target location and kinesthetic feedback and/or efference copy (rather than visual feedback) of the hand. Since subjects were always unaware of the perturbation, the authors suggested that the

observed corrections of path direction were as natural as were movement-extent corrections for the previous double-step experiment, with a change in amplitude only.

Corrections of ongoing movements in response to perturbations can be characterized (1) by their latency, i.e. the earliest point where the spatio-temporal parameters (such as time-to-peak velocity, peak velocity, or orientation of the velocity profile, i.e. the spatial path) begin to deviate from the unperturbed responses; (2) by the possible occurrence of a secondary peak on the velocity profile indicating the existence of a sub-movement; (3) by a possible lengthening of movement duration to compensate for the perturbation. While most double-step experiments entailed double-peak velocity profiles and lengthened movement durations, automatic movement corrections to (amplitude or directional) unaware double step were characterized by single-peak smooth velocity profiles, and movement durations similar to movement durations toward stationary targets corresponding to the same path length ([Goodale, et al., 1986](#); [Pélissou, et al., 1986](#); [Prablanc & Martin, 1992](#); [Wijdenes, Brenner, & Smeets, 2013](#)).

In addition to the unaware double-step pointing paradigm, other studies using a pointing task with a visual backward masking paradigm have also shown automatic motor correction for a stimulus which could not be consciously perceived ([Cressman, Franks, Enns, & Chua, 2007](#); [Fukui & Gomi, 2012](#); [Schmidt, 2002](#)).

2.3. Is non-awareness of the goal perturbation a pre-requisite for unintentional fast automatic online corrections?

Whether the unawareness of the jump was necessary for the occurrence of automatic corrections was further investigated by [Komilis, Pélissou, and Prablanc \(1993\)](#). They tried to identify the time constraints beyond which the movement was no longer modifiable online. The experimental apparatus and the instructions given to the subjects were the same as in [Pélissou et al. \(1986\)](#). Rather than jumping randomly at saccade onset, the target jumped randomly at the onset of the hand movement (12.5%) or at peak velocity (12.5%), or it remained stationary (in 75% of the trials). Note that during a synergic eye-hand pointing task, the orienting saccade ends a few tens ms before the hand movement onset when the instruction is to point as fast and accurately as possible to a target. Thus, when target locations were unexpectedly perturbed by an amount of 10–15% of the initial movement amplitude, they were clearly perceived. Subjects were not allowed to perform secondary hand movements if they felt (or saw) that their movement endpoint was inaccurate. Two experiments were carried out: the limb either disappeared at hand movement onset (dynamic open loop) or remained visible all throughout the movement (closed loop). Very similar results were obtained in these two experiments, which revealed only a marginal effect of visual feedback on automatic corrections. The acceleration phase remained unchanged irrespective of the single- or double-step stimulation. Single peaked-asymmetrical velocity profiles with a longer deceleration phase were observed for both types of stimulation (single or double step), irrespective of the condition (dynamic open-loop or closed-loop), with an average acceleration time of 185 ms and an average deceleration time of 265 ms.

When the target jump occurred at hand movement onset, subjects spontaneously modulated their deceleration to compensate for 88–100% of the amplitude jump, increasing the total movement duration by about 25 ms. No learning phase was necessary to obtain this automatic, flexible behavior. Conversely, when the target jump occurred at peak hand-movement velocity, subjects were unable to compensate for more than 20–40% of the amplitude jump. The authors' conclusion was that the motor error was dynamically evaluated during the acceleration phase and corrected during the

deceleration phase, and depended little upon the visual feedback of the moving limb for durations in the 400–500 ms range.

To determine whether, in response to a small aware target jump, the flexible automatic correction of the ongoing reaching is not only active—as in [Komilis et al. \(1993\)](#) experiment—but also overrides voluntary processes, [Pisella et al. \(2000\)](#) performed an experiment where subjects had to point to visual targets presented on a touch screen placed in the fronto-parallel plane. Arm responses were programmed and executed under free vision. In 20% of the trials, the target direction could be randomly displaced a few degrees apart (3.5°) at the onset of the hand movement. In separate sessions, subjects had to correct their movement to compensate for the target location change ('location-go') or instead immediately stop their response in-flight ('location-stop'). Subjects produced a large number of online corrections in the 'location-go' condition, but surprisingly, they produced a significant number of inappropriate online corrections in the 'location-stop' condition. This failure to completely suppress inappropriate responses indicated that flexibility can be generated in an automatic mode that escapes conscious and voluntary processes. These results are in line with other studies showing a temporal dissociation between motor responses and subjective awareness ([Castiello, et al., 1991](#); [Johnson, van Beers, & Haggard, 2002](#)).

A similar type of study was undertaken by [Day and Lyon \(2000\)](#) who addressed the question of the relationship between automatic behavior and intention. [Day and Lyon \(2000\)](#) studied subjects' behavior under double-step pointing triggered at movement onset. Subjects were required to either point to a target, which was stationary (in most of the trials) or randomly moving aside by a few cm (pro-pointing task), or to point at the opposite side (anti-pointing task). In the pro-pointing task, the reaction time to the displaced target was about 125 ms, whereas in the anti-pointing task, it was about 200 ms, preceded by an initial automatic wrong correction similar to the pro-pointing behavior.

Therefore, if non-awareness of the perturbation is a sufficient condition for fast automatic corrections of an ongoing movement, it does not appear to always be necessary; nonetheless, non-awareness of the perturbation ensures that no learning is involved as corrections occur even without visual feedback of the movement, i.e., without retinal error. In addition, most automatic fast corrections seem irrepressible, functional, and characterized by a movement duration which does not significantly increase—or, if it does, it increases by much less than the reaction time to the perturbation, as discussed below.

2.4. Differences between aware classical double-step experiments and double-step experiments inducing automatic corrections

Many studies have highlighted the continuous availability of the visual incoming signals to the motor system ([Diedrichsen, Hashambhoy, Rane, & Shadmehr, 2005](#); [Georgopoulos, Kalaska, & Massey, 1981](#); [Gielen, Van den Heuvel, & van Gisbergen, 1984](#); [Soechting & Lacquaniti, 1983](#)). However, a fast reaction time to a sudden change in stimulus location during an ongoing movement is not a specific marker of automatic unaware and involuntary corrections. Training may allow subjects to react faster despite a substantial increase in the total movement duration needed to reach the stimulus. Consistent with this hypothesis, in a double-step experiment [Soechting and Lacquaniti \(1983\)](#) found that EMG changes occurred as early as 110 ms, and were related to early intentional modifications of the trajectory; these latencies were similar to those obtained for a single-step trial. Other double-step reaching experiments have led to a similar conclusion ([Gielen, et al., 1984](#); [van Sonderen, Gielen, & Denier van der Gon, 1989](#)). However, none of these experiments assessed the total movement duration; the goal was to show the lack of a refractory period after

a movement was planned. In addition, in most of these experiments, large changes in movement amplitude or direction occurred as a result of the perturbation. Therefore, the relative amplitude or direction of the perturbation appears as an essential factor allowing both aware and unaware smooth corrections to an ongoing movement and, consequently, a flexible response.

[Paillard \(1975\)](#) defined the flexibility of the motor system as "the error it can tolerate without modifying its internal structure": even automatic corrections in unaware double-step are not unlimited and are time- and velocity-sensitive. For instance, [Blouin, Teasdale et al. \(1995\)](#) performed an "unaware double-step" experiment with small perturbations but very fast hand movements (210 ms); i.e. twice as fast as in [Prablanc and Martin \(1992\)](#), and they did not observe any corrections of the ongoing hand movement. By contrast, the same team ([Bard, et al., 1999](#)) showed fast corrections to an unaware double step when movement duration was longer (about 300 ms). [Diedrichsen et al. \(2005\)](#) performed a neuroimaging experiment involving an aware double-step stimulation with a 25-deg directional change triggered at movement onset. Despite a fast reaction time to the perturbation, the response clearly exhibited two velocity peaks, consistent with the superposition of two motor commands, the second one ending long after the first one. Thus by contrast with fast intentional corrections to an ongoing movement, which exhibit secondary peak velocity profiles and increased movement time, automatic online corrections are not only fast but also smooth, with a single velocity peak, and they introduce almost no additional time ([Desmurget, et al., 1999](#); [Desmurget, et al., 2001](#); [Prablanc & Martin, 1992](#)). Thus whether they are conscious or not, automatic corrections seem to rely specifically upon the intrinsic flexibility of the motor system. As discussed below, functional features such as initial planning and large corrective sub-movements or single movements slightly modulated by small error signals, are likely to correspond to distinct neural mechanisms ([Prablanc, Desmurget, & Gréa, 2003](#)).

Another study from [Gritsenko, Yakovenko, and Kalaska \(2009\)](#) analyzed the double-step paradigm under either awareness or not of the target displacement during the orienting saccade using a paradigm similar to [Prablanc and Martin \(1992\)](#). They similarly observed very early (120–150-ms latency range) and smooth corrections, which compensated for most of the displacement when the movement did not exceed 600 mm/s for a 150-mm extent. They carefully analyzed the motor corrections as a function of the direction of the jump from about 3° to 15° , and did not find any discontinuity in the error-vs.-direction function. They concluded that a single corrective process was responsible for the observed behavior, likely based on a forward internal model. They considered their results as incompatible with the dual-mode hypothesis, according to which the limit of flexibility makes it necessary to switch from a modulation of the synergies to a radical change calling for a reprogramming, with a corresponding increase in total movement duration, although it is likely that a larger jump (up to 30°) would have revealed a disruption of the initial motor program.

A more functional approach of the fast-corrective movements to an ongoing pointing movement—performed in an upright posture—to a jumping target has been carried out by [Fautrelle, Prablanc, Berret, Ballay, and Bonnetblanc \(2010\)](#). They recorded both kinematic and EMG of the whole axio-proximal posture from the shoulder to the tibia muscles. Rapid voluntary motor corrections in the upper and lower limbs—with latency responses shorter than 100 ms—were obtained by contrasting electromyographic activities in perturbed and unperturbed trials. However, the amplitude of the jump (which approximated one third of the initial movement) at movement onset was too large to allow a smooth online correction as evidenced by a clear double-peak

velocity profile and a corresponding substantial increase in movement duration. Conversely, a jump of the same amplitude occurring about 200 ms prior to the movement onset, led to a smooth correction without lengthening of the total movement duration, suggesting that the flexibility of the response depended upon a trade-off between the amplitude of the jump and its timing.

A recent study from [Wijdenes et al. \(2013\)](#) investigated fast corrections to a target jump in either direction or amplitude, about 25 ms after hand-pointing onset. The movement amplitude (950 mm) was large compared to that used by [Gritsenko et al. \(2009\)](#), and the target perturbation was applied ± 50 mm along the movement or orthogonally, i.e. with a 5% extent or directional perturbation. In line with [Pélisson et al. \(1986\)](#) findings, the perturbations did not result in any meaningful increase in movement duration (< 20 ms), even though most corrections were adequate.

3. Putative mechanisms of fast automatic pointing corrections to a change in target location

3.1. Error signal between target perception and visual feedback of the limb

For a goal-directed movement toward a stationary target, the estimated reaction time to a visually detected error varies from 110–120 ms to 190–270 ms, depending on test conditions—especially, the temporal and spatial uncertainty ([Carlton, 1981, 1992](#); [Conti & Beaubaton, 1980](#); [Hay & Beaubaton, 1986](#); [Jeannerod, 1988](#); [Keele & Posner, 1968](#); [Paillard, 1996](#); [Zelaznik, et al., 1983](#)). Thus the error signal provided by the simultaneous vision of target and hand could, in principle, be involved in error correction to target jumps. The roles of visual feedback of the limb, and of the dynamic error between target and hand, were assessed by [Prablanc and Martin \(1992\)](#) and [Komilis et al. \(1993\)](#). These authors compared differential pointing behavior between open loop and closed loop. Both studies found similar results for the constant errors, whether or not the hand was seen. Reaction times to the perturbation and constant end-point errors were not significantly different between the open and closed-loop conditions, indicating that the main source of correction was not visual. Although only pointing variability decreased under the closed-loop condition, this observation would seem to considerably reduce the role of visual feedback in automatic corrections.

However, different results have been obtained in other studies. To evaluate the role of visual feedback of the movement, and to estimate the visual reaction time to target-hand visual error signals, more recent studies have introduced small unexpected and unaware visual perturbations from the hand. For instance, in [Sarlegna et al. \(2003, 2004\)](#), visual feedback was provided via direct vision of a LED on the finger. During the orienting saccade to the target, the LED was switched to another position, a few degrees from the index fingertip.

In the same study they compared target perturbations of equivalent size. Due to saccadic suppression, either altered visual feedback of the fingertip or target jumps were unnoticed by subjects. The results clearly showed earlier and greater online modifications in arm movement amplitude for changes in target position than for changes in seen hand position, which suggests that updating the visual feedback of the movement is not functionally equivalent to updating the location of the target. Another experiment involving altered visual feedback of the hand was conducted by [Saunders and Knill \(2003\)](#). In their experiment, visual feedback of the fingertip was provided using a virtual luminous sphere, the location of which was locked to the fingertip. At hand-movement onset the sphere was slightly displaced (2 cm)

orthogonally to the movement. The displacement was unnoticed by the subject. Movement was corrected online with an average latency of approximately 160 ms. However, the frequency of perturbation was quite high, and the initial movement amplitude was unique. Therefore, despite the fact that trials were randomized, learning cannot be excluded. Also, it is interesting to note that, although fast reaction times for the (unaware) perturbations were observed, the total movement duration was increased in Saunders and Knill's experiment with respect to that of the non-perturbed movements. In a study similar to Saunders and Knill, and to [Sarlegna et al. \(2003, 2004\)](#), [Balslev, Miall, & Cole \(2007\)](#) showed that partial proprioceptive deafferentation through rTMS slowed down the reaction time for initiating a motor correction in response to a visual perturbation in hand position, but not to a target jump. They suggested that visual and proprioceptive channels facilitate each other, and that rapid detection of visual feedback errors depends on an intact proprioceptive signal.

3.2. Visual-to-proprioceptive error signal

When pointing at a visual target, vision of the target may be compared with dynamic proprioceptive signals from the limb to correct the movement, and proprioceptive reaction times are compatible with a visual-to-kinesthetic error signal ([Cordo, Carlton, Bevan, Carlton, & Kerr, 1994](#)). In addition, the vibration of antagonist muscles can induce biases in goal-directed movements ([Redon, Hay, & Velay, 1991](#)). Therefore, movement corrections based on these signals is plausible. However, a study of unaware double-step pointing in a patient suffering from total peripheral neuropathy without motor deficit has revealed that, for movement durations of about 300 ms, fast corrections can be performed without visual feedback and proprioception ([Bard, et al., 1999](#)). This study indicates that the motor system can modify unseen erroneous trajectories using central feedback loops comparing the goal and an efferent copy (i.e. a forward internal model of the upper limb response), or using a feedforward correction mode.

3.3. Influence of visual background motion

In most of the experiments cited above, there was no visual background. However, it is known that background visual information can influence arm motor control in a reflex manner, similar to what has been observed for postural and ocular motor control (for a review, see [Gomi, 2008](#)). [Saijo, Murakami, Nishida, and Gomi \(2005\)](#) have shown ultra-fast manual motor modulation induced directly by large-field visual motion during reaching toward a stationary target. The visual background was a random dot pattern which started to move at 0.7 m/s at hand movement onset, orthogonally to the pointing movement. The ongoing hand movement was involuntarily deviated in the direction of background motion, with a latency of about 125 ms, irrespective of target vision. Other studies have also shown that visual motion induces motor response biases, and it has been suggested that visual motion induces a drift in the body-reference representation of the target ([Brenner & Smeets, 1997](#); [Whitney, Westwood, & Goodale, 2003](#)). However, these studies have not yet teased apart the contributions of self-induced and passive visual background motion.

3.4. Feedforward mechanisms

Attempts to explain the double-step response as a simple mechanism have been made. First, [Flash and Henis \(1991\)](#) suggested that the observed response obeys a simple law of additivity of the control signals, compatible with combined planning of the main movement and of a sub-movement. [Flanagan, Ostry,](#)

and Feldman (1993) suggested another interpretation involving a linear shift between two successive equilibrium points of a reference trajectory. While both models were able to account for the experimentally-observed corrections, these corrections were voluntary and, for inter-stimulus intervals corresponding to a saccadic reaction time (200–250 ms), the velocity profiles of the end point effector usually exhibited two peaks. Moreover, the total movement durations were much larger than those involving automatic corrections in the unaware double-step paradigm.

3.5. Control through an internal forward model

The notion of an internal model based on efference copy (for a review, see Bridgeman, 1995; von Holst & Mittelstaedt, 1950) was proposed primarily to account for fast feedback processes that are incompatible with sensory conduction and processing delays, as demonstrated in very quick movements—such as a saccadic eye movements (Robinson, 1975)—or in quick limb movements (Hoff & Arbib, 1993; Kawato, 1999; Kawato & Wolpert, 1998; Miall, Weir, Wolpert, & Stein, 1993; Schweighofer, Arbib, & Kawato, 1998; Wolpert & Miall, 1996). The forward model enables the CNS to predict the consequences of motor commands. It allows canceling the deleterious effect of delays in feedback loops. Miall et al. (1993) were among the first to propose that the cerebellum could behave like a limb-state predictor. More recently, Torres and Zipser (2002) proposed a geometric model with seven-degrees of limb freedom, which directly addressed the ability to perform quick online corrections, i.e., flexible responses from current limb states. Desmurget and Grafton (2000) proposed a forward model allowing a comparison between the current limb state derived from the output of internal forward model with the updated location of the target to drive the fast flexible corrections observed in unaware double-step experiments.

The experiments on double-step stimulation mentioned above have provided convincing arguments for a key role of prediction, i.e., for a forward internal model of the instantaneous limb state. However, the latter experiments (Sarlegna, et al., 2003; Saunders & Knill, 2003), which stress the importance of visual feedback during the execution of a movement, suggest that the forward internal model is not totally insensitive to these dynamic signals. However, when the forward model becomes completely inadequate under force-field perturbations (Diedrichsen, et al., 2005; Lackner & Dizio, 1994; Scheidt, Conditt, Secco, & Mussa-Ivaldi, 2005; Shadmehr & Mussa-Ivaldi, 1994), even veridical feedback signals are insufficient for performing flexible corrections; they can only support late movement correction and involve a reprogramming, or the addition, of a delayed sub-movement.

The error signal may be derived either from delayed comparison between the expected sensory feedback (i.e. the output of the forward model) and the actual feedback (Diedrichsen, et al., 2005), or from the instantaneous comparison between the goal representation and the expected sensory feedback (Desmurget & Grafton, 2000). The former process is useful for adaptation to inter-sensory and visuomotor conflicts, such as prism adaptation or rotated visual feedback; the latter process is the driving error signal for fast online control (Magescas, et al., 2009).

Based on the results discussed above, it appears that the forward internal model of the limb is likely to play the major role in early corrections of ongoing movements, when the initial planning turns out to be erroneous. At later movement stages, multisensory visual and proprioceptive feedback supplies finer-grained information. Consistent with this view, neurophysiological and modeling approaches have emphasized the role of multi-sensory fusion for accurate spatial limb representations (Graziano, Cooke, & Taylor, 2000; Ladavas & Farne, 2004; van Beers, Sittig, & Denier van der Gon, 1996, 1999).

4. Generalization beyond pointing: reach-to-grasp

Attempts to generalize fast, smooth, and automatic corrections from reaching to grasping have been undertaken through perturbations of object location (Chieffi, Fogassi, Gallese, & Gentilucci, 1992; Paulignan, MacKenzie, et al., 1991) or orientation (Desmurget & Prablanc, 1997; Desmurget, et al., 1995) at movement onset. They have led to the hypothesis that a change in intended posture governs the fast online reorganization of behavioral responses, as for unperturbed responses (Desmurget & Prablanc, 1997; Flanders, Helms-Tillery, & Soechting, 1992; Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Engelbrecht, 1995; Soechting & Flanders, 1995). Gréa, Desmurget, and Prablanc (2000) extended previous work to totally unconstrained reaching and grasping movements, where objects (spheres) were randomly displaced at hand-movement onset. Most perturbed reach-to-grasp movements were characterized by a single, bell-shaped wrist-velocity profile. However, it is interesting to notice that in 25% of the trials the movement exhibited a double-peak velocity profile, indicating a sequence of two overlapping planned movements reminiscent of those classically described in the literature on double-step experiments. This particular behavior was generally related to too-fast initial movements, which resulted, paradoxically, in longer total movement durations than normal-paced movements. Buch, Mars, Boorman, and Rushworth (2010) also interpreted such movement updating as resulting from reprogramming.

In the reach-to-grasp experiments, when focusing upon the transport component of the movement, i.e. on the location and orientation of the wrist, the automatic correction of the reach-to-grasp process in response to a change in object orientation is similar to that of a pointing in response to a change in target location. It strongly suggests that the automatic online corrective process for small planning errors is not an epiphenomenon restricted to a reduced-cue environment, but is a general property of goal-directed movements, provided these errors are not too large. Automatic online corrections to an unaware small double step or to a small double step triggered at hand movement onset are under the control of fast processes that do not seem to involve an additional decision making and do not introduce substantial increase in movement time. By contrast, the corrections to a large double step involve a decision making and a new planning, which even with very fast reaction times lead to significantly increased movement times. However, it seems likely that there is a transition between these two extreme types of corrective processes. This transition may be dependent upon both movement velocity and the size of the required switches among the movement synergies, when the limits of flexibility of the ongoing response have been exceeded.

5. Neurophysiological substrates

5.1. Online control in animals

The observation that rapid processing of visuomotor signals is necessary to execute online corrections of limb movements has led to the suggestion that fast sub-cortical loops may be involved in their control. A contribution of the superior colliculus (SC) to the control of such movements was first suggested by the finding that, in the cat, the latency of “mid-flight” corrections of reaching movements in response to a target jump was prolonged after a lesion of the spinal cord at the level of C2, indicating an involvement of the tectospinal pathway (Alstermark, Gorska, Lundberg, & Pettersson, 1990). Although this conclusion has been recently challenged (Pettersson & Perfiliev, 2002), the contribution of the SC in online corrections of limb movement is additionally supported by an electrical stimulation study in the cat (Courjon,

Olivier, & Pélisson, 2004). When delivered just after the onset of a goal-directed reaching movement, electrical stimulation of the SC resulted in consistent trajectory perturbation of the forelimb extremity. This forelimb perturbation followed stimulation onset by 50–60 ms, and was often observed in the absence of concomitant gaze or head displacement. Thus, fast access to the SC network for limb motor output is compatible with the hypothesis of a collicular involvement in “mid-flight” corrections of reaching movements, which have a latency of about 100 ms in the cat (Alstermark, et al., 1990). In addition, it has been shown in monkeys that the responses of some collicular cells are related to visually-guided reaching movements of the forelimb (Stuphorn, Bauswein, & Hoffmann, 2000; Werner, Hoffmann, & Dannenberg, 1997).

In addition to being involved in adaptive mechanisms, the cerebellum has also been suggested to be responsible for online movement corrections (Prevosto, Graf, & Ugolini, 2010). This suggestion is based on considerations of the role of cerebellar cortical and nuclear pathways to mIPs in visual and proprioceptive guidance of movement, and of the cerebellar encoding of kinematic features of movements (Casabona, Bosco, Perciavalle, & Valle, 2010; Ebner, Hewitt, & Popa, 2011). The cerebellum has also been shown to be differentially involved in predictable and unpredictable load perturbations (Shimansky, Wang, Bauer, Bracha, & Bloedel, 2004). While cerebellar integrity was not critical for the capacity to acquire or modify and execute a previously acquired adaptive strategy based on an off-line modification of the motor plan for predictable perturbations, the adaptive mechanism governing the development and execution of the online modification of the motor program in response to sensory cues was cerebellar dependent for unpredictable perturbation. Interestingly this cat's study of paw reaching shows some similarities in the deficits after inactivation of the interposed and dentate cerebellar nuclei, with the deficits observed in a cerebellar patient with focal lesions around the right dentate nuclei and the brainstem (Liu, Ingram, Palace & Miall, 1999). More recently Popa, Hewitt & Ebner (2012) have investigated the activity of simple spike discharge of Purkinje cell during a manual tracking of a pseudorandom target. They found that cells encoded both prediction and feedback about the tracking error. They hypothesized that a dual error representation may provide the signals needed to generate sensory prediction errors used to update a forward internal model.

The involvement of cortical areas in online visuomotor guidance has been investigated in primates (Faugier-Grimaud, Frenois, & Stein, 1978; for reviews, see Buneo & Andersen, 2006; Galletti, Kutz, Gamberini, Breviglieri, & Fattori, 2003 for the parietal cortex; Georgopoulos, 1998 for the motor cortex). The medial parieto-occipital cortex is a key structure in the dorsomedial visual stream. Recent physiological studies in monkey have suggested that within the medial parieto-occipital cortex, area V6A is a bimodal visual/somatosensory area that processes visual information such as shape, motion, and space for the control of reaching and grasping movements (Fattori, et al., 2010). The transport phase of reaching and grasping is associated with V6A somatosensory and skeletomotor activities. Moreover selective V6A lesions in monkey produce misreaching and misgrasping in visually guided movements of the arm contralateral to the lesion. As V6A is reciprocally connected with PMd which controls arm movements (Gamberini, et al., 2009), the medial parieto-occipital cortex could be a candidate for online visuomotor guidance of prehension in both proximal and distal movements. The similarity of deficits in monkeys with clinical deficits observed in optic ataxia patients suggests a homology between human and monkey superior parietal lobules. The role of the superior parietal lobule in online visuo-manual guidance has been demonstrated by Archambault, Caminiti, and Battaglia-Mayer (2009). Recently Hwang, Hauschild, Wilke, and Andersen (2012) and Battaglia-Mayer, et al., (in

press) developed a monkey model of optic ataxia by parietal inactivation in monkeys through muscimol injection. After inactivation of the parietal reach region (PRR), Hwang et al. (2012) found a reaching impairment under peripheral vision but not under foveal vision, without oculomotor impairment, while Battaglia-Mayer et al. (2012) showed an impairment of both planning and online control of both hand and eye movements after inactivation of the superior parietal lobule (SPL). The latter tested online control using a double-step paradigm involving a large change in stimulus location. The increased correction time that they observed with respect to control trials was in line with the lengthened response time to double-step stimuli in optic ataxia patients (Gréa, et al., 2002; Pisella, et al., 2000).

Among the few experiments investigating the neural correlates of online motor control in unpredictable double-step experiments, Georgopoulos, Kalaska, Caminiti, and Massey (1983) was the first to carry out a detailed investigation of single cells firing in the motor cortex (M1) to elucidate the neural mechanisms by which this control is achieved. The second step corresponded to a target jump in the opposite direction to the first target location and thus involved an intentional visuomotor correction. The inter-stimulus interval varied from 50 to 400 ms, i.e. before and after the reaction time. They found that the motor cortical discharge that elicited the movement could be interrupted by the target shift, and was replaced with only a small additional delay by a new discharge pattern appropriate for the movement to the new target. This result highlighted a substitution of motor commands without any refractory period in a double-step response. Archambault et al. (2009) performed a similar study extended to free movements in a 3D space on monkey parietal area 5. They also found a substitution of the discharge pattern observed for the movement to the first target by a new one similar to that observed for a movement to the second target. As to the issue of optic ataxia (OA), corresponding to a lesion of the PPC, the authors considered that their results could not support the hypothesis of a deficient automatic corrective process in OA, because there was no mean to determine whether the discharge pattern they observed resulted from a computation of a new motor command or from an updating of the old one. In another study Archambault et al. (2011) extended the electrophysiological study of online control of hand trajectory to double-step targets by examining the temporal evolution of the population activity of hand-related cells in the frontoparietal system. The time of divergence of the population activity related to the presentation of the second target at movement onset obeyed a systematic activation order of PMd, followed by M1 and PPC. These results in addition to the comparison with the population activity associated with a single target led the authors to hypothesize that M1 plays a more direct and earlier role in providing precise control of hand kinematics on an ongoing basis, whereas PMd provides an earlier command signal to update the motor output when a second target is presented at a variable interval after a first one. The observed activity in the parieto-frontal network thus represents the change of motor intention during a not-yet-accomplished movement. Although this sophisticated study shed more light on the neural activity within the frontoparietal network corresponding to an intentional change in motor goal, it did not provide evidence that the corrections triggered for small changes in the motor goal could be carried out by the same neural process.

In a recent study Dickey, Amit, and Hatsopoulos (2013) investigated the neural coding of corrective movements in monkey motor and premotor cortices in response to a double-step stimulation. By contrast with other freely moving experiments where the second step imposed a movement in the opposite direction, the movement was restricted to a single joint and the forward or backward perturbations were small as compared to the initial movement. They tested two alternative hypotheses: summation vs. replacement. The summation hypothesis, proposed by Flash

and Henis (1991), posits that the observed motor response results from a linear summation of a neural command to the first target and of a second command from the first to the second target. The replacement hypothesis on the opposite posits that the cell discharge observed for the movement toward the first target is interrupted of, and is substituted with a new one, similar to that observed for the movement to the second target. While the majority of neurons had an activity consistent with the summation hypothesis and on the average were leading the hand velocity, one third of the neurons analyzed from M1 and premotor cortices exhibited a single-trial neural activity better explained with the replacement hypothesis and on the average were lagging the hand velocity. Their paradigm involving small forward or backward target jumps (close to double-step paradigms eliciting automatic corrections), as well as those imposing an intentional movement reversal (Archambault, et al., 2009) accounted for a short neural and behavioral reaction time. Interestingly, for either forward or backward target jumps, both reaction times and movement durations were not significantly different from those corresponding to a single target and exhibited results similar to those of the experiments eliciting automatic corrections.

5.2. Online control in humans

A psychophysical study in a split-brain patient has provided evidence for a contribution of sub-cortical structures in the generation of online corrections of limb movements (Day & Brown, 2001). No additional correction time was observed when the pointing target was displaced in the hemifield contralateral to the reaching arm, contrary to expectations based on the delayed inter-hemispheric transfer of visual information. It cannot be ruled out that the involvement of subcortical structures, which is suggested by the results of this study, developed progressively in the subject of the study in order to compensate for the complete agenesis of the corpus callosum. However, more recent studies have confirmed the presence of reach-related activity in the superior colliculus (Himmelbach, Linzenbold, & Ilg, 2013; Linzenbold & Himmelbach, 2012). Altogether, these data suggest the possibility of a recruitment of fast subcortical loops in the production of online corrections of limb movements, but they do not definitively establish whether this recruitment is necessary in healthy human subjects. The role of the cerebellum in online control has been highlighted by Liu et al. (1999) who observed, on a single clinical case with focal lesions around the dentate nuclei and the brainstem, a dissociation between 'on-line' and 'off-line' visuomotor control reminiscent of the Shimanski et al.'s study in the animal. More recently Fautrelle, Pichat, Ricolfi, Peyrin & Bonnetblanc (2011) have addressed the issue of prediction vs. non prediction in the differential involvement of the cerebellum in a task of catching a ball.

The contribution of the PPC, not only to the visuomotor transformation of goal-directed movements, but also to their online control has been also shown. Results indicate that the PPC plays a role in covert attention (e.g. Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000). In addition, a contribution of the PPC in online control of hand movements has been proposed in humans, based on complementary neuropsychological, transcranial magnetic stimulation (TMS) and imaging approaches (Desmurget, et al., 1999; Desmurget, et al., 2001; Gréa, et al., 2002; Pisella, et al., 2000; Reichenbach, Bresciani, Peer, Bulthoff, & Thielscher, 2011; Tunik, Frey, & Grafton, 2005).

First, a TMS study revealed that a transient interference of the PPC applied in healthy subjects at the start of an arm-pointing movement impaired the production of fast on-going corrections in response to a target jump (Desmurget, et al., 1999). This study further indicated that the performance of the arm ipsilateral to the TMS-stimulated PPC remained normal; so did movements toward

stationary targets. Thus, this study eliminated a global involvement of the PPC in the online control of motor responses. Note that a similar conclusion was reached in a TMS study focusing on the anterior part of the intraparietal sulcus for the online control of the distal component of a reach-to-grasp response (finger grip formation, Tunik, et al., 2005). In contrast, when grasping movements have to be reprogrammed (Paulignan, Jeannerod, et al., 1991), a related TMS approach showed that inhibition of a planned action was activated by the ventral premotor-primary motor (PMv-M1) connections (Buch, et al., 2010). Accordingly, a lesion of the frontal cortex should further boost the efficacy of online corrections by freeing the automatic pilot from inhibitory control (Rossetti & Pisella, 2003).

Second, three clinical studies of patients suffering from optic ataxia consecutive to a lesion of the superior part of the PPC have provided data in line with this conclusion. In the first study (Pisella, et al., 2000), an optic ataxia patient was tested in the same condition as in normal subjects (described above). In contrast to normal subjects, the patient exhibited a complete absence of automatic online corrections when instructed to correct a movement to compensate for a change in target location. This finding indicates a critical role of the PPC in the production of fast, automatic adjustments of on-going limb responses to a stepping target. In the second study, this conclusion was extended to reach-to-grasp movements (Gréa, et al., 2002). Here, the bilateral optic ataxia patient was asked to reach to grasp a circular object which could be displaced suddenly at the time of arm-movement onset (Fig. 3). Arm responses were again programmed and executed in central vision. Under these conditions, "control" movements toward stationary targets showed characteristics (trajectory and final accuracy of the hand-transport component, coupling with hand shaping component) similar to those of healthy subjects. In contrast, "perturbed" movements produced by the patients were executed toward the initial target location, and a secondary movement was generated to reach the displaced target. This behavior differed markedly from that of healthy subjects, who did not produce any secondary movement but instead amended their hand trajectory "in-flight" in order to reach the displaced target. A third recent study suggested that the deficit of reach correction to double-step stimulus in optic ataxia is not specific to goal updating and visuomotor transformation (McIntosh, Mulroue, Blangero, Pisella, & Rossetti, 2011). In their experiment, McIntosh et al. produced target jumps upon movement onset while subjects maintained their gaze on a fixation point. Target jumps could move the target toward or away from fixation. Results revealed that the numbers of sensorimotor and of perceptual detections were highly correlated across all conditions. This indicates that the basic deficit of optic ataxia patients is not purely sensorimotor. Rather, the authors hypothesized that the deficit results from impaired orienting of attention, as online motor corrections require both attentional and motor reorienting. Using rTMS, Ciavarro et al. (2013) have shown that attentional reorienting signals are used by area pV6A in humans to rapidly update the current motor plan, or the ongoing action, when the target unexpectedly changes location. More specifically, these authors proposed a direct involvement of the action-related dorso-medial visual stream in attentional reorienting and a more specific role of the posterior V6A area in the dynamic, online control of reaching actions (Ciavarro, et al., 2013). This is consistent with the interpretation according to which the deficits of optic ataxia patients in peripheral vision, and with automatic piloting, implicate that eye and hand targets are at least temporarily dissociated (Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006; Pisella, et al., 2009; Rossetti & Pisella, 2002). Taken together, these studies suggest that the normal function of the PPC is necessary for the production of online corrections of goal-directed hand responses. However,

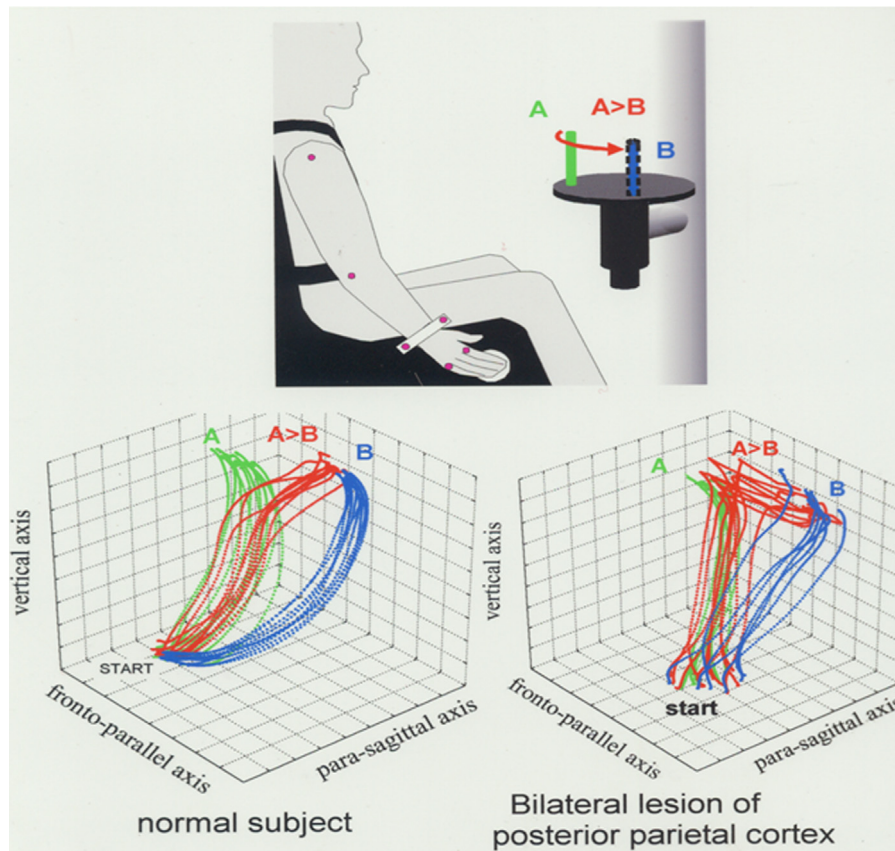


Fig. 3. Test of flexibility in reaching and grasping an object for normal subjects and for a bilateral optic ataxia patient (modified from Gréa et al., 2002). Upper part: subjects sat on a chair facing the cylinder for grasping, their trunk immobilized by a harness to prevent shoulder movement. The cylinder could suddenly jump at movement onset. Recordings of 3D position of the right wrist index finger and thumb were made. At the beginning of each trial, the right hand rested on the starting point. After the object was moved to a given location, a tone was used to indicate to the subjects that they had to grasp the object. Two types of trials were randomly interleaved. During unperturbed trials, the object remained at the same location until movement completion. In those cases, the object could be presented at position A or B. During the perturbed trials, the object suddenly and unexpectedly jumped at movement onset from A to B or B to A (in this example, it was A, B). Lower part: left-wrist hand path to A (green), B (blue), or jump from A to B (red). Left side: healthy subjects, wrist path of reach-to-grasp response was successfully amended online. Right side: bilateral optic ataxia patient. Although reaction time and movement time were normal, wrist path could not be corrected online, and fingers closed on an absent object. A second movement from A to B was necessary in order to reach and grasp the object. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the results do not provide information concerning the extent of the neural network involved in such automatic control; as suggested by results described in the previous paragraph, this network may involve other cortical, as well as non-cortical, structures.

This question was addressed in a neuroimaging study in healthy human subjects (Desmurget, et al., 2001). Using PET, these authors measured the metabolic change associated with neural activity (regional cerebral blood flow) when healthy subjects performed arm-pointing movements. The study involved four different sessions and a two-by-two factorial design: two different instructions (pointing with or without a simultaneous eye response) and two target types (stationary or displaced at eye- or hand-movement onset). The interaction term, revealing the metabolic changes related specifically to the online correction of arm movements to perturbed targets, revealed three areas of significant rCBF increase: the contralateral PPC, the ipsilateral anterior cerebellum, and the contralateral motor cortex. This network fits well with the larger network involved in the generation of externally (versus internally) guided movements (e.g. Debaere, Wenderoth, Sunaert, Van Hecke, & Swinnen, 2003). Notably, no activation of the basal ganglia was observed.

The lack of involvement of the basal ganglia is further supported by behavioral studies in Parkinson-disease (PD) patients. Indeed, it was found that PD patients had a normal capability to generate smooth and unaware adjustments of the on-going trajectory to a target jump (Desmurget, et al., 2004) or to a

stationary target (Negrotti, Secchi, & Gentilucci, 2005). Interestingly, Desmurget et al. (2004) also reported that PD patients were impaired at generating corrective reaching sub-movements to large and consciously detected target perturbations (Desmurget, et al., 2004). A similar deficit had previously been observed for Huntington patients (Smith, Brandt, & Shadmehr, 2000). The few instances where basal ganglia are involved in correction mechanisms, are when these corrections depend upon contextual decision processes (Tunik, Houk, & Grafton, 2009) or when there is a need for dynamic control of force within an ongoing movement (Grafton & Tunik, 2011). All in all, these studies indicate that the two extreme types of online corrections of a goal-directed limb response (automatic, fast and smooth corrections versus intentional, slow and large corrections) might rely on different neural substrates, and that the basal ganglia might be involved specifically in the second type.

In addition, the findings of Thaler and Goodale (2011a, 2011b) about a different role of visual feedback for the control of target-directed and allocentric movements is consistent with the idea that these two types of movements may be mediated by different networks, as they have distinct representations. The findings also suggest a similar conclusion to that reached by Desmurget et al. (1999), who showed that hand movements performed between two given points had quite distinct kinematic properties (path curvature, velocity profile) depending on whether subjects performed reaching or tracing movements.

5.3. Rehabilitation perspectives

Pisella et al. (2000) and Day and Lyon (2000) have identified two different pathways of visuo-manual guidance: a fast automatic pathway, and a slow intentional pathway. These two parallel pathways have different timings and different neural substrates (Pisella, et al., 2000), but both converge to the primary motor area (Rossetti & Pisella, 2002, 2003; Rossetti, Pisella, & Pélisson, 2000). The fast automatic online visuomotor pathway involves the superior parietal lobule (Pisella, et al., 2000), and it probably involves shortcuts from the mediadorsal parieto-occipital area toward PMd and M1; the intentional visuomotor pathways involve longer routes toward the primary motor area through the prefrontal cortex (Pisella, et al., 2000). Hemiparesis consecutive to various cortical and subcortical anterior lesions may correspond to the damage of intentional visuomotor routes. The automatic visuomotor pathway could be preserved, in which case its stimulation could maintain some muscular activity in hemiparetic patients (thus avoiding spasticity), or it could be less damaged, in which case it might provide an alternative, less effortful way to stimulate the recovery of hand movements following frontal damage. While classical motor neuro-rehabilitation methods are mainly based on the training of intentional and effortful movements (Rode, Rossetti, & Boisson, 1996), the potential for rehabilitation of hemiparetic patients through the use of automatic reaching movements has begun to be evaluated (Gaveau, et al., 2013). Gaveau and collaborators took advantage of the fact that automatic movement reactions are elicited when reach targets location are suddenly displaced during movement. They compared motor performance in a first group (Auto) of hemiparetic patients using this task to a second (Control) group, which was trained using static targets. The results showed an improvement in motor performance of the trained hemiparetic arm (as indicated by an increase in the Fugl-Meyer score) for the Auto group, but not for the Control group. These preliminary results indicate that the use of automatic motor reactions is effective in the rehabilitation of the paralyzed arm, and can complement current rehabilitation techniques.

6. Conclusion

The various experiments described above have led to the conclusion that reaching and grasping flexibility is an automatic physiological process allowing small modulations of the motor control signals when the ongoing response departs from its goal. Flexibility is embedded within the overall organization of goal-directed movements (for reviews, see Andersen, et al., 1997; Scott, 2004; Snyder, et al., 2000). It relies upon a neural process, which bypasses most of the fronto-striatal structures (Desmurget, et al., 2004; Desmurget, et al., 2001), but requires the integrity of several key structures: the PPC (Desmurget, et al., 1999; Galletti, et al., 2003; Gréa, et al., 2002; Pisella, et al., 2000) where hand and target locations are represented (for a review, see Battaglia-Mayer, Caminiti, Lacquaniti, & Zago, 2003; Filimon, et al., 2009) but also the anterior cerebellum (Desmurget, et al., 2001); both structures are necessary for building-up a motor error signal and a forward model of the limb response. Although the double-step paradigms that have been used to reveal fast flexible responses used artificial errors, flexibility is likely to occur in normal life as it can unfold either completely independently of awareness, or before awareness occurs. In addition, one of its characteristic features is to escape intentional control. However, not all double-step responses rely upon flexibility. Whereas corrections occurring under complete unawareness undoubtedly reflect flexible processes, corrective responses to consciously perceived small double-steps at movement onset have almost the same kinematic characteristics as responses with unaware corrections, provided they are within the

limits of modulation of the initial response synergies. Observed deficits in the ability to consciously correct perturbed movements in patients with PPC lesions, and the inability of normal subjects to prevent unintentional corrections to a small target jump, strongly suggest that both conscious and unaware corrections rely on similar automatic flexible processes. However, it is likely that when target perturbations become too large to be compensated by a modulation of the general motor pattern, or when the movement is too fast, flexible corrections can no longer be implemented. In this case, a new time-consuming decisional stage involving the fronto-striatal circuitry is required, as can be observed in normal subjects (Gréa, et al., 2000) and, more dramatically, in PD patients (Desmurget, et al., 2004).

Evaluating whether a movement is under flexible control or is composed of a main movement with added sub-movements may be difficult because of the filtering of the limb mechanical properties and because added sub-movements may become undetectable. However, the total duration of motor responses, including sub-movements, is generally lengthened. In addition, results of neuroimaging and clinical studies (Desmurget, et al., 2004; Desmurget, et al., 2001) suggest a marginal involvement of prefrontal stages in flexible responses. In contrast to this, if a corrective added sub-movement (as observed with double peaks in velocity profiles) strongly relies on prefrontal stages, it should clearly appear in brain activity through evoked response potentials. Such evoked potentials have been observed for aware error detection and correction, and the error-related negativity has been considered as a signal for monitoring a motor conflict (Carter, et al., 1998; Rodriguez-Fornells, Kurzbuch, & Munte, 2002).

From this review, it appears that intentional changes to an ongoing response to large perturbation of target location are always possible with a short reaction time, but do not allow a smooth correction and mostly cannot prevent a substantial increase in movement time. By contrast, unaware (necessarily small) or aware small perturbations of target location at movement onset, allow such rapid, automatic and smooth corrections without substantial additional time. It remains to determine the limits between a corrective movement which would involve a smooth modulation of the initial synergies only, and a corrective movement needing some form of replanning or additivity of the motor commands. These limits likely depend upon at least three factors: the extent of the perturbation in terms of synergies rather than in terms of cartesian errors, the movement velocity, and the time at which the perturbation is applied during the movement. For the perturbation time, these limits have been roughly assessed and seem to be limited to a visual processing during the acceleration phase of the movement (Komilis, et al., 1993). In parallel, the direct electrophysiological counterparts of those two apparently distinct processes will have to be explored using real-time EEG or MEG methods, or cell recording in primates. Despite the sophisticated statistical methods that have been developed, the difficulty of such investigations lies in the capability to isolate neuronal populations, if the unintentional corrective processes do really involve populations distinct from those highlighted in the intentional corrections to an ongoing movement,

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