FEEBACK OR FEEDFORWARD CONTROL: END OF A DICHOTOMY.

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Since the pioneering monograph of Woodworth (Woodworth 1899), the respective contribution of feedforward and feedback processes to movement generation has been an issue of considerable debate. The last century has seen the pendulum swing back and forth constantly between these two extreme conceptions. The feedforward view dominated the field early. It was argued that a pattern of muscle activation had to be defined in advance of a movement since the dexterity of the motor system was not dramatically altered when vision was absent and unable to guide an ongoing movement toward a target (Bowditch and Southard 1880) (Woodworth 1899). Supporters of a feedback control model responded quickly to this claim by stressing that vision was not the only source of sensory information and that movement could be guided though proprioceptive feedback. In order to support this assertion, evidence was provided confirming that monkeys with a deafferented limb were only able to produce erratic movements (Mott and Sherrington 1895) (Lassek 1953). This result was promptly challenged by two observations showing, first, that monkeys were able to recover relatively normal motor functions within a couple of weeks provided they were forced to rely exclusively on their deafferented limb (Knapp et al. 1963) (Taub and Berman 1968) (Taub 1976), and second, that delays in sensorimotor loops were too prolonged to allow useful sensory feedback control for fast reaching movements (Hollerbach 1982). Supporters of the feedback concept fought back claiming that the ability to generate accurate movements in the absence of any sensory input did, in no way, imply that the motor command was assembled in advance. This rebuttal originated in the so-called "equilibrium point model", which had provided evidence that the pattern of muscle activation could be generated gradually during an on-going movement, in the form of a progressive shift of the equilibrium arm configuration toward the target (Bizzi et al. 1984) (Bizzi et al. 1992) (Flanagan et al. 1993) (Feldman and Levin 1995). Far from concluding the debate, this result provoked a vigorous counter-offensive by supporters of feedforward models who pointed out that the equilibrium point hypothesis lacked consistent support, at least for multi-joint movements (for a review Desmurget et al. 1998). In other words, although a progressive shift of the equilibrium arm configuration could provide a purely feedback basis for motor control, experimental observations of unrestrained reaching or pointing movements clearly contradicted this idea. This was a strong blow to feedback models. After almost a century of controversy, the feedforward conception of motor control dominated. It provided theoretical underpinnings for most of the studies aimed at understanding how visually-directed movements were generated. This hegemonic domination was further reinforced by the observation that computational models ignoring totally the potential contribution of feedback loops were remarkably successful at capturing the main characteristics of reaching movements, including Fitt's law (Plamondon and Alimi 1997), the pattern of end point errors (Flanders et al. 1992) (Vindras et al. 1998) (Desmurget et al. 1999a), the typically bell-shaped aspect of velocity profiles (Flash and Hogan 1985) (Uno et al. 1989) (Plamondon and Alimi 1997) (Harris and Wolpert 1998), and the curvature of movement paths (Flash 1987) (Uno et al. 1989) (Harris and Wolpert 1998).

Like the mythological Phoenix who perpetually rose up from his ashes, the feedback-feedforward controversy recently returned. After two decades of unchallenged stability, the pendulum has slowly started to swing back. This time however, it did not return to its original point but stopped in a new area somewhere between the feedforward and feedback views. The main aim of this chapter is to delineate this area. To this end, we will proceed in five steps. First, we will review evidence generally presented as establishing the dominant role of feedforward movement control, namely that accurate movements can be generated in the absence of sensory information and that sensory feedback loops are too slow to allow efficient feedback control during the entire trajectory. Second, we will show that despite this "evidence", on-line control by visual and non-visual information occurs early and smoothly in movement. Third, we will provide a framework within which the nature of these early corrections can be understood. In particular, we will show that feedback mechanisms can rely on much more than sensory inflow, as traditionally thought. Feedback control strategies become viable if the nervous system can infer the instantaneous and future hand location through a "forward model" that integrates efferent and afferent signals to infer, with no delay, the current and upcoming state of the motor system. Fourth, we will show that the motor command is not generated gradually during the course of the movement on the basis of feedback loops comparing in real time the respective locations of the hand and target. To this end, we will provide converging arguments showing that a crude motor plan, subject to subsequent optimization, is assembled before movement onset. Finally, in a fifth section, we will discuss the functional anatomy of movement feedback loops with emphasis on the potential contribution of the posterior parietal cortex and the cerebellum.

Ballistic reaching movements: original evidence.

In computer science, a program describes "*a fragment of code that is stored on a disk and that specifies a series of actions that are carried out sequentially*". By analogy, in neuroscience, a motor program defines "*a series of neural commands that are structured in advance and that unfold sequentially until the completion of the movement*" (Keele 1968) (Arbib 1981). Identifying the existence and the content of a program is quite easy in computer science. All you need to do is examine the source code and launch an executable file. Completion of the executable without further input demonstrates the existance of the program. However, inferring the structure of the source code based on the behavior of an executable file can be difficult. This disconnection between source code and behavior is even more arduous in neuroscience. In this case, the only way to demonstrate the existence of a motor program is to show that all the instructions necessary to bring the hand to the target are available in the system before movement onset. A translation of this premise into a working hypothesis was initially proposed by Keele in a now famous monograph (Keele 1968). According to this author, a movement could be considered as resulting from a motor program if it could be carried out uninfluenced by peripheral feedback. In other words, all that is necessary to prove the existence of a motor program is to show that accurate and structured movements can be performed in the absence of any peripheral information. To support this still widely held belief four experimental observations are put forward. These observations are detailed below.

Reaching without proprioception.

Although one might expect the motor behavior of deafferented patients to be consistent, the literature abounds with conflicting observations in both humans and monkeys. The controversy started with the pioneering paper of Mott and Sherrington (Mott and Sherrington 1895) who reported that monkeys only produced erratic movements with their numb limb after a unilateral deafferentation. As noted by the authors "*from the time of performance of the section onwards, the movements of the hand and foot are practically abolished*". While confirmed by subsequent studies (Lassek and Moyer 1953) (Lassek 1955) (Twitchell 1954), these results were severely challenged by behavioral observations showing that deafferented animals were able to recover virtually normal motor functions (Munk 1909) (Knapp et al. 1963) (Taub and Berman 1968) (Bossom 1972) (Bossom 1974) (Taub 1976). In an attempt to reconcile these contradictory results, Knapp et al. (Knapp et al. 1963) showed that motor performance improved, in fact, only when the animals were forced to use their deafferented limb. As shown by the authors, deafferented monkeys exhibited fewer motor impairments after a bilateral than after unilateral rhizotomy.

The main evidence supporting the idea that proprioceptive signals were not critical for movement execution was provided Polit and Bizzi (Polit and Bizzi 1979) in a now famous experiment. These authors trained 3 monkeys to perform single joint pointing toward visual targets presented in a dark room. These targets were selected among a set of 17 LEDs distributed every 5 deg in front of the monkey. They were randomly presented and the animal had to point towards the selected target with an accuracy of about 15 deg. Following a period of training, intrathecal deafferentation of the arm territory at the dorsal root level (C2-T3) was performed and controlled by a stretch-reflex recording. After recovery from surgery, deafferented monkeys were still able to reach to the targets with sufficient accuracy. When the elbow angle position was unexpectedly modified by transiently loading the arm about 150-200 ms prior to movement onset, neither normal nor deafferented monkeys displayed a significant decrease in movement accuracy. The same was also true when the load was applied during the ongoing elbow movement. From these findings, Polit and Bizzi (Polit and Bizzi 1979) concluded that joint movements depended mainly on neural patterns specified before movement onset. They also suggested that, through the selection of a muscular equilibrium point, these preprogrammed patterns defined a mechanical attractor which could be reached without knowledge of the initial configuration of the motor apparatus. We will return to these assertions latter in the discussion.

Generalization of the Polit and Bizzi (Polit and Bizzi 1979) experimental results to humans was obtained by Kelso and Holt (Kelso and Holt 1980). These authors required human subjects to reach to a previously learned position with their thumb. A load could be unexpectedly applied during the displacement of the thumb. Results showed that subjects were easily able to perform this task, even when the moving finger was deafferented by applying an inflated strap around the wrist joint. Even if this particular result could not be reproduced by Day and Marsden (Day and Marsden 1982), several observations have since confirmed that deafferented subjects are able to realize a wide range of finger movements with remarkable accuracy (Rothwell et al. 1982) (Sanes et al. 1985). This however should not be considered a reliable proof that proprioception is not critical for movement control. Indeed, the ability of deafferented subjects to perform successfully simple laboratory tasks frequently obscures their inability to use their hand in more ecological conditions, where single-joint movements are the exception. With respect to this, Rothwell et al.

(Rothwell et al. 1982) described, for instance, a deafferented patient whose "hands were relatively useless to him in daily life […] despite his success with these laboratory tasks". Likewise, Munk (Munk 1909) emphasized, in monkeys, that even if deafferented animals were able to recover some impressive level of dexterity, they still performed very awkward and unskilled movements when compared to their normal congeners.

If one admits, as suggested by Polit and Bizzi (Polit and Bizzi 1979), that it is not necessary to know the state of the motor apparatus to plan accurate movements, then the propensity of deafferented subjects to generate clumsy and ataxic multijoint movements challenges the feedforward view of motor control. However, Polit and Bizzi's results were never successfully replicated and a vast majority of studies carried out during the last 20 years have shown that estimating the initial state of the motor apparatus has a major influence on the accuracy of movement planning (for a review (Desmurget et al. 1998)). Evidence supporting this view is even found in Polit and Bizzi's original work. Although the monkeys trained by these authors were able to compensate for undetected modifications of the arm location in the main experimental condition, they were totally unable to adjust for positional shifts affecting the starting posture of their upper-arm: when the center of rotation of the elbow joint was shifted forward, the monkeys were no longer able to reach accurately to the targets. Another line of evidence supporting the idea that defining the initial state of the effector is a necessary step of movement planning was provided by behavioral experiments showing that systematic pointing errors reflect biases in the estimation of the initial hand location. This point was initially identified by Prablanc et al. (Prablanc et al. 1979a) who compared the accuracy of visually directed movements performed under two different conditions. In the first condition, vision of the hand was never allowed (FOL: full open loop). In the second condition, vision of the hand was allowed only in a static position prior to movement onset (DOL: dynamic open loop). Results showed that movement accuracy was significantly better in the DOL than in the FOL condition. These data were subsequently reproduced and generalized in several studies (Rossetti et al. 1995) (Desmurget et al. 1997) (Vindras et al. 1998). An important contribution of these latter studies was to establish that the hand needed to be seen in foveal or peri-foveal vision to obtain a significant reduction of the systematic errors. When the arm was seen in the peripheral visual field the only effect observed was a reduction of variable errors without modification of the mean movement accuracy (Rossetti et al. 1994) (Desmurget et al. 1995). This observation fits well with the idea that foveal vision of the limb at rest optimizes the hand localization process. Peripheral vision does not allow such an improvement because spatial estimations are not accurate in the peripheral visual field (Prablanc et al. 1979b) (Bock 1993). Additional evidence supporting this conclusion can be found in the demonstration that the representation of the hand location is significantly biased in the dark (Vindras et al. 1998) (van Beers et al. 1998) (Desmurget et al. 2000). Recent data have shown that this bias cannot be related to a tendency of the proprioceptive signal to "drift" in the dark (Desmurget et al. 2000), as had been suggested in the past (Paillard and Brouchon 1968) (Wann and Ibrahim 1992). Seeing the hand at rest allows the nervous system to reset a systematic bias of the proprioceptive signal with respect to the visual world (Desmurget et al. 1995) (Desmurget et al. 2000).

In light of the previous comments we can suggest that the inability of deafferented subjects to perform multijoint movements reflects a trajectory planning impairment rather than a feedback deficit. Evidence supporting this view is provided by tendon vibration experiments. In these experiments, vibrating the biceps tendon prior to movement onset significantly affects movement accuracy (Larish et al. 1984), while applying the vibration during the initial two-third of the movement has no effect on end-point errors (Redon et al. 1991). Another more indirect line of evidence comes from reaching studies showing that EMG activity varies in a predictive manner to offset the influence of interaction-torque arising from multijoint dynamics (Sainburg et al. 1995) (Flanagan and Wing 1997) (Gribble and Ostry 1999). Because feedforward compensatory mechanisms require a precise estimation of both the limb geometry and the limb inertial properties, the motor system has to rely on proprioception during movement planning. This point was clearly demonstrated by Sainburg et al. (Sainburg et al. 1995) in a recent experiment during which two patients presenting with large-fiber sensory neuropathy were required to make a gesture similar to slicing a loaf of bread. Without vision of the moving limb, the patients were unable to compensate for interaction-torque, leading to severe impairments in interjoint coordination. In contrast, when allowed to see their arm at rest, prior to movement, they were able to generate virtually normal movements. As shown by Ghez et al. (Ghez et al. 1995) when these two patients were required to point to visual target with prior vision of the limb (DOL) the movement end point error, the final end point variability, the path curvature as well as the number of late secondary movements were optimized.

In summary, the previous results, when considered together, suggest that accurate movements can be performed in the absence of dynamic proprioceptive feedback (i.e. while proprioception is critical for movement planning its absence during the movement itself only produces limited effects). This conclusion is in agreement with the hypothesis that visually directed movements are under the control of a motor program that is modifiable by feedback loops.

Reaching in the dark.

The first experimental contribution to the problem of visual control of movement was provided by Woodworth in a long monograph published in Psychological review more than 100 years ago (Woodworth 1899). Woodworth asked human subjects to perform repetitive movements with a hand-held pencil. He reported three main results: (1) movement accuracy degraded significantly with hand velocity when vision of the movement was allowed; (2) movements executed with visual feedback involved small corrective movements at the end of the trajectory; (3) movement accuracy was not affected by hand velocity when vision of the movement was not allowed, i.e. when subjects were required to point with their eyes closed. From these results, it was concluded that the speed-accuracy interaction observed in the presence of visual feedback could be explained by the inability of the subjects to control their movement visually when hand velocity went above a critical threshold. According to Woodworth "the bad effect of speed consists in rendering impossible a delicate current control in preventing those later and finer adjustments by means of which a movement is enabled to approximate more and more closely to its goal". When prevented from exerting this "current control" the subject has to rely on a "first impulse", which may be considered as the direct ancestor of Keele's motor program. In an interesting development, Woodworth even suggested that motor virtuosity was achieved by progressively eliminating final adjustments to rely exclusively on the "first impulse".

During the last century, many studies have confirmed and generalized Woodworth's conclusions. It was established that vision exerted its influence only at the very end of the movement, when velocity is slow. This was done by Cartlton (Carlton 1981) who required subjects to place circular rods in small holes positioned at various distances. Results showed that viewing the hand during the first half of the trajectory did not improve movement accuracy with respect to a condition where the hand was never visible. Cartlton concluded that the initial part of the movement was under the control of a pre-planned set of motor commands and that fine movement accuracy was achieved through final intermittent repositioning impulses whose direction and amplitude was given by a retinal error signal. A similar conclusion was reached by Beaubaton and Hay (Beaubaton and Hay 1986) in a classical reaching task in which subjects were required to point to visual targets under absent, total, or partial visual control. We will examine alternative interpretations of the data presented by Carlton (Carlton 1981) and Beaubaton and Hay (Beaubaton and Hay 1986) later in this chapter.

Before bringing this section to an end, a last point is worth mentioning. As noted above, seeing the hand at rest prior to movement onset improves the accuracy of visually directed movements. This might suggest that the usual comparison between total open loop (hand never visible) and total closed loop (hand always visible) overestimates the ability of visual feedback loops to correct erroneous trajectories. Indeed, part of the accuracy deficit observed in the total closed loop situation might not be related to a feedback deficit, but to a planning bias. In agreement with this view Prablanc et al. (Prablanc et al. 1979a) showed that fast reaching movements contained substantial end-point errors even when vision was available during the movement only. These errors were significantly larger than those observed in a total closed loop condition. A consitent result was reported by Gentillucci et al. (Gentilucci et al. 1996). These authors required subjects to point to the more distant vertex of closed and open configurations of the Muller-Lyer illusion, as well as to the vertex of control lines. Two main conditions were investigated. In the first condition (full-vision condition) subjects saw both stimulus and their hand before and during movement. In the second condition (non-visual feedback condition) they saw the stimulus, but not their hand during movement. The Muller-Lyer illusion dramatically affected pointing kinematics with respect to the control lines. Subjects undershot and overshot the vertex location, respectively, in the closed and open configuration showing that hand trajectory could not be fully corrected in response to the initial illusion, even when vision was present during the entire trajectory.

Reaching too fast for the peripheral system.

The strongest evidence rejecting the use of sensory feedback to control movement trajectory is based on the existence of incompressible physiological delay in sensorimotor loops. Indeed, when the processing of sensory information is long with respect to the movement duration, the position of the hand changes dramatically by the time the feedback signal starts to influence the ongoing motor command, and the implemented correction becomes inappropriate (Hollerbach 1982) (Gerdes and Happee 1994).

The time necessary for visual information to influence the ongoing movement was first investigated with repetitive movements by Woodworth (Woodworth 1899) and Vince (Vince 1948) who reported delays higher than 400 ms. These values seemed a little bit high with respect to visuo-motor reaction times which are usually well below 400 ms. This led Keele and Posner (Keele and Posner 1968) to perform a new experiment in which discrete pointing movements were investigated. Two conditions were tested by the authors: open loop (only the target was visible) and closed loops (both the hand and the target could be seen). The shortest movement duration for which movements were more accurate in the closed loop condition was 260 ms. No difference was observed for 190 ms movements. Keele and Posner concluded that the minimal delay for visual information to influence the movement was within the range of 190-260 ms. Further data confirmed the validity of this initial estimation (Beggs and Howarth 1970, 290 ms) (Wallace and Newell 1983, 200 ms) (Cordo 1987, 200ms). However, other studies provided evidence that 200 ms might still represent an overestimation of the delay inherent to visual feedback loops. Carlton (Carlton 1981) suggested, for instance, that vision was only used at the end of the trajectory when velocity becomes low. As a consequence, he argued that measuring the entire movement biases the results as an overestimation. To test this hypothesis he required subjects to point with a stylus to visual targets displayed in the sagittal plane. In a first experience, five conditions were considered: 0%, 25%, 50%, 75% or 93% of the trajectory occluded by a physical shield. Result showed that movement accuracy was not different in the 0% and 50% visual condition. In a second experiment, Carlton re-investigated the 75% and 93% occlusion condition in more detail and measured the time elapsed between the appearance of the hand in the visual space and the occurrence of corrective submovements. He found a value of 135 ms. Using a similar protocol Beaubaton and Hay (Beaubaton and Hay 1986) showed that movements of 130 ms (total duration) were more accurate when the subjects were allowed to see the second half of the trajectory with respect to a condition where vision was occluded during the entire movement. This latter observation suggests that visual control of movement can be significantly faster than 100 ms in some circumstances. A compatible observation was reported by Zelaznik at al. (Zelaznik et al. 1983, 100 ms) in an experiments using a protocol similar to the one initially developed by Keele and Posner. An important contribution of Zelaznick at al. was, however, to demonstrate that vision was used more quickly in blocked experimental sessions that in randomized designs. This indicates that the nervous system is more efficient at processing visual signals when it knows, in advance, that vision will be available.

The time necessary for proprioceptive information to influence the ongoing movement was first evaluated by Vince (Vince 1948). This author trained human subjects to make accurate movements while pulling a handle attached to a spring. He observed that the subjects needed 160 ms to adjust their movement and compensate for an unexpected modification of the stiffness of the spring. A slightly shorter delay (120 ms) was subsequently reported by Chernikoff and Taylor (Chernikoff and Taylor 1952) who used a paradigm requiring the subjects to react as fast as possible when their arm was suddenly dropped from a passively maintained position. Dewhurst (Dewhurst 1967) obtained an even shorter delay (100 ms) using an active maintenance task in which the subjects had to react as fast as possible when the weight of the load they were holding was unexpectedly increased. Although the range of [100 ms -150 ms] was subsequently validated in many studies (Higgins and Angel 1970, 136 ms) (Cordo 1990, 120 ms) (Flanders and Cordo 1989, 150 ms), a few experiments have identified much shorter proprioceptive reaction times. For instance, Crago et al. (Crago et al. 1976) asked human subjects to hold a handle attached to a motor in a reference position. They observed active corrections after a delay of only 70 ms when the force exerted by the motor was suddenly modified.

When considered together, the previous data indicate that the minimal delay for a proprioceptive signal to influence movement kinematics is within the range [70 ms-150 ms]. This large range may be explained by different factors such as the characteristics of the task (arm actively maintained or passively sustained) or the nature of the parameters studied (acceleration, velocity or position signal). The predictability of the motor perturbation may also be a critical factor, as was the ability to predict the availability of the visual signal (see above). This was demonstrated by Newell and Houk (Newell and Houk 1983). As reported by these authors, when the direction of the perturbation was consistent from trial to trial the mean reaction time was significantly smaller (135 ms to 181 ms depending on the subject) than when the direction of the perturbation was randomized (158 ms to 234 ms depending on the subject).

In order to obtain a better estimation of the proprioceptive reaction time, some authors have proposed to consider EMG activity instead of the overt modifications of the arm kinematics. They argued that this might be a fairer approach considering the existence of a delay between the application of the muscle contraction and the actual displacement of the limb. Rather than settling the issue, these electrophysiological studies triggered a series of unexpected questions. Indeed, they did not replicate behavioural observations, but ended up identifying three levels of proprioceptive regulation usually designated M1, M2 and M3 (Lee and Tatton 1975) (Evarts and Vaughn 1978) (Marsden et al. 1978) (Agarwal and Gottlieb 1980). M1 appears after only 15-25 ms. It is thought to represents the spinal functional stretch reflex. M2 appears after 40 to 60 ms. It has been described classically as a long latency supraspinal stretch reflex (Godaux and Cheron 1989 for a discussion). It may be worth noting here that neither M1 nor M2 are of sufficient magnitude to counteract the force generated when the arm is dropped from a passively maintained position or when the weight of an actively sustained object is suddenly increased. This explains why these short latency reflex responses failed to be identified in the behavioral paradigms described in the previous paragraph. M3 appears after 70-80 ms. Agarwal and Gottlieb (Agarwal and Gottlieb 1980) have proposed to designate this response "postmyotatique " to emphasize its non reflex origin.

Numerous studies were carried out to examine the validity of the reflex versus non-reflex classification proposed to account for the existence of M1, M2 and M3. For instance, Marsden et al. (Marsden et al. 1978) required human subjects to produce a constant isometric contraction of the thumb flexors in response to an external force. When the amplitude of this force was suddenly increased, the subjects were required to: (H1) let go; (H2) flex the thumb as fast as possible; (H3) maintain their position. Results showed that EMG activity recorded in the flexor pollicis longus always presented a double burst (M1, M2) irrespective of the experimental instruction. A supplementary burst (M3) was observed only when the subject was explicitly instructed to react to the perturbation (H2, H3). This indicated that M1 and M2 had a reflex origin while M3 resulted from a voluntary response. Although confirmed by Agarwal and Gottlieb (Agarwal and Gottlieb 1980), these observations could not be replicated in several subsequent studies (Hagbarth 1967) (Evarts and Tanji 1974) (Lee and Tatton 1975) (Rack 1981) leaving the problem largely unresolved. The issue was finally settled by Evarts and Vaughn (Evarts and Vaughn 1978) in a very elegant study in which biceps activity was recorded during a movement requiring a contraction of this muscle (in this case no reflex activity is present). The subjects held a handle mobile around a horizontal axis. When this handle was rotated clockwise the subjects were instructed to accentuate its movement by performing a quick clockwise rotation of the forearm (suppination). Results revealed a large EMG burst in the biceps muscle 70 ms after the perturbation (M3). No earlier response, potentially related to M1 or M2 was observed.

In summary, the data presented in this section indicate that sensory signals can be processed fairly quickly by the central motor system. However, even the smallest values reported in this section (70 ms) remain large in regard to movement duration (400 to 600 ms typically). In 70 ms the hand can travel a few centimeters making it impossible to efficiently use sensory feedback during the fastest part of the trajectory.

Reaching in two steps: the dual model of movement control.

The main results presented until now can be summarized as follows: (1) accurate movements can be performed in the absence of a dynamic sensory signal (i.e., vision or proprioception during the movement); (2) removing vision during the first half of the movement trajectory or biasing the proprioceptive signal through tendon vibration during the first two-thirds of the movement has no effect on end-point accuracy; (3) end-points errors are reduced when a sensory signal is present; (4) the processing of visual and proprioiceptive information is too slow to allow sensory feedback control when the hand location is changing rapidly. When considered together these observations suggest that sensory feedback loops improve movement final accuracy by allowing fine control of the hand displacement at the very end of the trajectory, when velocity is low. Presented in a more formal way, this conclusion states that reaching movements are segmented into two components: *an initial ballistic component*, entirely driven by a motor plan and insuring a fast transport of the hand into the vicinity of the target; Second, *a final homing component*, dependent on sensory feedback loops and allowing fine corrections at the very end of the trajectory. Classically these final corrections are viewed as a series of one or more submovements generated at discrete time intervals (Meyer et al. 1988) (Milner 1992) (for a review Jeannerod 1988). In agreement with this view, it was shown that reaching movements can be represented as a composite of several submovements each of which represents a scaled version of a prototypic ballistic entity (Milner 1992). Also, it was found that the first portion of this entity usually covered 80% or more of the total movement distance (Meyer et al. 1988) (Milner 1992). This dual model of movement control is illustrated in figure 1. It has long been the prism through which subsequent studies of motor control have been interpreted.

Continuous feedback loops for fast reaching movements: recent evidence.

Before going further, some semantical clarifications are relevant to avoid ambiguity. In the present chapter, we will segregate feedback loops into two categories designated non-sensory, and internal. The epithet *non-sensory* will qualify feedback loops for which only the efferent information can be used to determine the hand location. The epithet *internal* will qualify feedback loops for which both the sensory (vision or proprioception) and efferent information can be used to determine the hand location. These internal loops will be designated visual when the subjects can see their hand moving and non-visual when they cannot. The term feedback alone refers to any feedback loop without distinction.

To further distinguish between two different types of feedback we will also discriminate between three different types of errors designated extrinsic, intrinsic and motor. The epithet *extrinsic* will designate errors related to an erroneous localization of the goal of the movement (e.g. overestimation of the target distance with respect to the body). The epithet *intrinsic* will designate errors related to an erroneous estimation of the state of the motor apparatus prior to movement onset (e.g. estimating that the hand is closer to the body than it actually is). Finally, the epithet *motor* will designate errors related to an erroneous estimation of the motor command required to bring the hand from its starting location to the target location.

We will now review behavioral evidence showing that movement errors can be corrected early, even for fast reaching movements.

Non-sensory feedback loops.

A displacement of the body with respect to the environment or a displacement of the environment with respect to the body generates the same retinal stimulation. To account for the ability of the nervous system to discriminate between these two situations, von Holst and Mittelstaedt (Von Holst and Mittelstaedt 1950) proposed that a copy of the motor command was stored somewhere in the brain and used to interpret the perceptual input. This conclusion was extended and generalized leading to the concept of non-sensory feedback loop. According to this view, a copy of the efferent signal sent to the muscle can be used to estimate the current state of the motor apparatus with no delay and thus to prompt efficient path corrections in response to extrinsic errors.

A first line of evidence showing that non-sensory feedback loops can be used to guide biological actuators is found with eye movements. There is now extensive evidence that the oculomotor system uses an efferent signal to control saccadic eye movements. Perturbation experiments indicate that if gaze is shifted during the preparation or the execution of a saccade toward a flashed target, then a compensatory saccade which accurately brings gaze onto the remembered target location is generated (head-fixed saccade, (Keller et al. 1996) head-free gaze shifts, (Pélisson et al. 1995)). Strikingly, such compensation does not require visual or proprioceptive feedback, since it occurs in full darkness and after surgical deafferentation of extraocular proprioception in monkeys (Guthrie et al. 1983).

For arm movements, the existence of non-sensory feedback loops was initially suggested in behavioural studies showing that hand trajectory could be amended with a shorter latency than the minimal latency required to process peripheral information. Early evidence supporting this idea was provided by Higgins and Angel (Higgins and Angel 1970). These authors instructed eleven subjects to hold a manipulandum which could be displaced to the right or to the left. In the first experimental condition, the subjects were trained to use the manipulandum to displace a line presented, in front of them, on a cathode ray tube. A rightward movement of the manipulandum generated an upward displacement of the line while a leftward movement generated a downward displacement. The subjects were instructed to bring this line in coincidence with a target line stepping from one position to another. In the second experimental condition, the subjects were simply required to hold the manipulandum in a median position and to react as fast as possible to any force that may be generated to move the manipulandum away from its central position. Results showed, for the first condition, that subjects sometimes initiated their movement in the wrong direction. In this case they needed between 83 ms (fastest subject) and 122 ms (slowest subject) to initiate a motor correction. These delays were significantly higher than the ones observed in the propioceptive reaction time task (between 108 and 169 ms). For each subject, the reaction time observed in the first condition was shorter than the reaction time observed in the second condition, supporting the idea that errors in movement initiation can be amended by a central mechanism which operates more rapidly than sensory feedback. A similar conclusion was reached by Jaeger et al. (Jaeger et al. 1979) who showed that altering the proprioceptive signal through tendon vibration did not modify the reaction time to a visual perturbation. These data are in agreement with other studies showing the existence of very rapid movement corrections during pointing movements directed at an erroneous target. Cook and Diggles (Cooke and Diggles 1984) observed, for instance, successful hand path corrections 45 ms after movement onset, when the initial direction of the motor response was erroneous. This value was close to the one reported by van Sonderen et al. (Van Sonderen et al. 1989, 30 ms) in a double-step task where the initial target location was changed during or after movement initiation. These values of 45 ms and 30 ms are much too fast to be of sensory origin (see above).

The best evidence showing that non-sensory feedback loops can be used to guide the hand toward the target, in response to an initial extrinsic error was provided recently by Bard et al. (Bard et al. 1999). These authors required a deafferented patient to look and point to visual targets displayed in the peripheral visual field. Vision of the moving limb was not allowed. In some trials the target location changed slightly during the course of the ocular saccade. Because of saccadic suppression this manipulation was not consciously detected by the patient, who was convinced that she pointed to a stationary target (see next section for details). The patient was able to correct her movement on-line and to reach to the new target location despite the absence of peripheral feedback. It is however important to note that her corrections were not as accurate as the corrections observed for control subjects, suggesting that under normal conditions the motor outflow is combined with at least some sensory inflow to generate an optimal estimate of hand location. This point will be addressed in more detail in a following section.

Internal non-visual feedback loops.

For an external examiner, the relative coordination of eye, head and hand during goal-directed reaching appears sequential. When a subject points to a visual target in peripheral space the eyes move first, followed by the head and ultimately the hand. Because eye movement duration is brief, the gaze arrives at the target before or around hand movement onset (Prablanc et al. 1979b) (Prablanc et al. 1986) (Prablanc and Martin 1992) (Desmurget et al. 2001Prablanc and Martin 1992). Based on the observation that the extra-foveal visual signal (peripheral vision) does not allow an accurate estimation of the target location (Prablanc et al. 1979b) (Bock 1993) it was suggested that the delayed hand movement reflected an obligatory requirement to foveate a target before a reliable motor plan for the arm could be constructed (Paillard 1982). This appealing hypothesis was however disproved by further studies showing that the serial organization observed, at the behavioral level, for the eye, the head and the arm resulted in fact primarily from inertial factors. When EMG activity is considered in spite of the usual external kinematics markers, it appears that the neural command reaches the eye, the head and the arm at nearly the same time. The arm reaction time is last simply because it has the greatest inertia. If one consider that the onset of the agonist muscle contraction occurs 50 ms to 100 ms before the actual arm motion for reaching movements (Biguer et al. 1982) (Turner et al. 1995), this result agrees with psychophysical studies showing that the overt arm movement follows generally the saccadic response with a lag of 60 to 100 ms (Prablanc et al. 1979b) (Prablanc et al. 1986) (Prablanc and Martin 1992) (Desmurget et al. 2001).

The above observations indicate that the initial motor command is issued on the basis of an imperfect estimation of the target location. At the end of the saccadic displacement, when the hand starts moving, the target location is re-estimated on the basis of accurate peri-foveal information. This updated information can then be used by the nervous system to adjust the ongoing trajectory, as initially demonstrated by Prablanc et al. (Prablanc et al. 1986). These authors required subjects to point without vision of the moving limb "as quickly and accurately as possible" to visual targets presented in their peripheral visual field. Four conditions were considered: (1) The target was turned off just before the end of the ocular saccade preventing the subject from re-estimating the target location at the end of the saccadic response. (2) The target was turned off 120 ms after the end of the ocular saccade allowing re-estimation of the target location by foveal vision. (3) The target remained illuminated throughout the entire pointing movement. (4) The subject was asked to look at the target first before initiating a reaching movement with the arm. The target was off turned at hand movement onset. In this fourth condition the subject had the opportunity to program arm movement on the basis of a perfectly accurate estimation of the target location. Results showed that movement error was minimal in condition 3, maximal in condition 1, and intermediate in conditions 2 and 4. This confirms that the initial motor program is partially inaccurate because of the existence of an erroneous estimation of the target location (1 versus 4). This also shows that movements initiated on the basis of accurate foveal information are not necessarily perfectly accurate and that further corrections occur during movement execution (3 versus 4). Finally, this data clearly demonstrates that the motor system can amend the ongoing movement when it has the opportunity to update target location (1 versus 2).

In order to investigate in greater detail whether fast reaching movements are the result of a preset pattern of un-modifiable commands, Prablanc and colleagues designed a new experimental paradigm in which the initial inaccurate estimation of the target location during movement planning was artificially increased, unbeknownst to the subject (Goodale et al. 1986) (Pélisson et al. 1986) (Prablanc and Martin 1992). To achieve their goal, the authors slightly modified the target location during the course of the ocular saccade. This procedure has three major advantages: (1) because of saccadic suppression, the target jump is not perceived consciously by the subject; (2) because saccadic responses to stationary targets involve an initial saccade undershooting the target position and a secondary corrective saccade achieving accurate target acquisition (Becker and Fuchs 1969) (Prablanc and Jeannerod 1975) (Harris 1995), the target jump does not alter the organization of the oculomotor system; (3) because pointing movements to stationary targets involve an update of the target location at the end of the saccadic displacement, and because this update is taken into account to amend the on-going arm trajectory (see above), the target jump does not alter the organisation of the manual response. In fact, one may summarize the previous points by saying that pointing directed at stationary or unconsciously displaced targets are identical from a functional point of view. The intra-saccadic modification of target location simply increases an error that is already present in the system.

In a first series of experiments Prablanc and colleagues required subjects to point "as quickly and accurately as possible" to visual targets presented, at different distances, along a fronto-parallel line (Pélisson et al. 1986) (Goodale et al. 1986). Vision of the moving limb was not allowed. In half of the trials the target remained stationary while in the other half it was slightly displaced during the ocular saccade either to the right or to the left. The magnitude of the target jump represented between 6.6% and 10% of the initial movement amplitude (e.g. 2 cm for a 30 cm movement; 4 cm for a 40 cm movement). Results showed that the subjects were fully able to correct the ongoing trajectory in response to the target jump. The observed corrections were surprisingly smooth as shown by the absence of discontinuities on the wrist velocity curves, which exhibited the same bell-shaped profile for both the perturbed and control movements (figure 2, upper panel). This important observation disproves the proposal that a lack of discontinuity in the velocity curve implies an absence of path correction. Finally, the results also indicated that path amendments did not involve any increase in movement duration, supporting the idea that the perturbed trials were corrected by adjustments to an existing program rather than the generation of a new motor program. These observations were further replicated and generalized by Prablanc and Martin (Prablanc and Martin 1992). In this study, the targets were initially presented at 20, 30 and 40 deg on a circle centered on the hand starting point (radius 30 cm). As a consequence, the target jump (10 deg to the right or to the left) did not simply imply a modulation of the movement amplitude as was the case when targets were presented along a line (Pélisson et al. 1986) (Goodale et al. 1986), but a complete reorganization of the current motor pattern. Results showed that hand trajectory smoothly diverged from their initial control path (first target) to reach the new target location (figure 2, lower panel). Corrections were detectable 110 ms after hand movement onset showing that hand trajectory was amended very early. Interestingly, Prablanc and Martin also observed that the pattern of path correction, and the reaction time to the perturbation, were similar whether or not vision of the moving limb was available. This suggests that non-visual feedback loops represent the main process through which extrinsic errors are corrected (see also, Komilis et al. 1993).

In contrast to their efficiency at correcting extrinsic errors, non-visual feedback loops seem quite poor at rectifying intrinsic errors. As shown by several studies, final errors in visually-directed movements performed without vision of the moving limb reflect in large part, systematic biases in the estimation of the initial state of the motor apparatus. This was initially demonstrated by Rossetti et al. (Rossetti et al. 1995) in a behavioral experiment where subjects were asked to point toward visual targets without visual reafference from their moving hand. Two conditions were considered. In the first condition, the pointing fingertip was viewed through prisms that created a visual displacement, while the target was presented outside the shifted field and thus was normally seen (no shift). Presence of the proprioceptive-visual mismatch was not detected by the subjects. In the second condition, both the index fingertip and the target were seen normally, i.e. the relationship between the hand and the target was not altered. Comparison between these two conditions showed that the visual shift of the fingertip position prior to movement induced a systematic bias of the movement end-point, in a direction opposite to the visual shift. Interestingly, this shift was already present on the initial movement direction (which was rotated to the left) and on-line feedback loops did not reduce it significantly. The same apparent inability of on-line feedback loops to successfully correct extrinsic errors was also reported by Vindras et al. (Vindras et al. 1998) in a recent study. These authors tested the performance of human subjects in three sensorimotor tasks. In the first task subjects aimed at 48 targets spaced regularly around two starting positions. Results revealed the existence of a systematic pattern of errors across targets, i.e., a parallel shift of the end points that accounted, on average, for 49% of the total error. The systematic errors were found to decrease dramatically in the second condition where subjects were allowed to see their hand before movement onset. The third task was to use a joystick held by the left hand to estimate the location of their (unseen) right hand. The systematic perceptual errors in this condition were found to be highly correlated with the motor errors recorded in the first condition, supporting the idea that systematic pointing errors reflect to a significant extent the erroneous estimation of initial hand position. This result was interpreted as showing the primacy of feedforward control over feedback control. Another interpretation will be proposed below.

Internal visual feedback loops.

Based on physiological and psychophysical studies, Paillard (Paillard 1980) (Paillard 1996) proposed the existence of two visual feedback channels for movement control: *a static channel* that operates in central vision, provides accurate position cues, and is essential for the discrete path corrections observed at the end of the movement (see dual model of motor control); *a kinetic channel* that operates in peripheral vision, provides motion cues, and is essential for controlling movement initial direction. In order to test the validity of this hypothesis, Bard et al. (Bard et al. 1985) designed a first study in which a purely directional aiming task was investigated. Subjects were seated on a chair. They held the tip of a pointer that could be rotated on a ball-joint fixed to the floor. A strip of Plexiglas containing the visual targets was placed in front of the subjects, at eye level. Four targets were used: one in front of the subject, and the others at 10, 20, and 30 deg in the right hemifield. The subjects were instructed to fixate the median target and to move the pointer toward the illuminated target without stopping under it. Directional errors were defined as the angular deviation between the pointer and the target position when the arm crossed the target line. Results showed that directional accuracy was greater when vision was allowed. This was also true for rapid movements as brief as 110 ms. Strikingly, the authors reported that this positive effect of vision was still present when the second half of the movement was occluded by a physical board, suggesting that visual error could be processed in much less than 110 ms. The potential role of peripheral vision for controlling movement direction was further documented in subsequent studies carried out by the same group. Blouin et al. (Blouin et al. 1993a) (Blouin et al. 1993b) established that early visual control of movement direction was present even when the subjects were not able to see their hand at rest (light was turned on at movement onset). This critical point was not perfectly clear in the method section of the seminal paper published by Bard et al. (Bard et al. 1985). In addition to this clarification, another major contribution of Blouin et al. (Blouin et al. 1993a, see also Teasdale et al. 1991) was to show that the directional component of aiming movements could be significantly improved when the experimental instruction required the subjects to stop below the target, i.e. to control both movement direction and movement amplitude, as is the case in classical reaching tasks.

Based on these observation several hypothesis can be put forward to account for the inability of previous studies to identify a positive effect of early visual corrections on the accuracy of fast reaching movements (Paillard 1996, for a detailed discussion). A first possibility is that the early studies investigated sagittal (Carlton 1981) or para-sagittal movements (Beaubaton and Hay 1986), which did not favor the occurrence of directional errors. Bard et al. (Bard et al. 1990) failed, for instance, to observe any positive effect of peripheral vision for sagittal movements. Another factor may be that the error parameters studied in earlier studies were not very "sensitive". Carlton measured, for instance, the number of "hits" (a miss or touch score) while Beaubaton and Hay considered the distance between the hand and the target. As emphasized by Paillard (Paillard 1996), this latter parameter is probably the worst you can choose to detect a potential effect of peripheral vision on early path corrections. Indeed, distance error does not vary with directional errors: if you point to a target presented on a vertical screen, distance error will be the same whether you reach 1 cm to the right or 1 cm to the left. Finally, the absence of a difference between a condition where vision is always visible and a condition where it is only present during the second half of the trajectory does not imply that early visual control is ineffective. It could also occur if the visual feedback process that takes place during the second half of the movement is powerful enough to correct any errors that could not be amended by initial loops.

Progressive recruitment of the primary arm movers.

The idea that limb transport is ballistic and under pre-programmed control was originally supported by behavioral studies on the organization of muscle activity during goal-directed movements. Rapid reaching movements generally exhibit a typical triphasic pattern of activation in which the initial agonist burst is followed by an antagonist activation, then a small agonist burst at the end of the hand displacement (Jeannerod 1988). Since this pattern is still observed when proprioceptive information is absent (Rothwell et al. 1982) (Jeannerod 1988), it was concluded that the triphasic EMG activation has a central origin. Although this idea was never directly challenged, a series of experiments recently carried out by Flanders and colleagues suggest that a pre-programmed triphasic pattern of EMG activity may evolve within a larger motor repertoire. These authors recorded EMG activity from nine superficial elbow and shoulder muscles, while human subjects made rapid arm movements. They showed that the different muscles were recruited gradually and that the pattern of activation varied as a function of movement direction (Flanders et al. 1996). They proposed that this gradual involvement may represent a neuromuscular control strategy in which burst timing contributes to the specification of movement direction. On this basis, it may be tempting to speculate that the ongoing trajectory might be controlled, to a certain extend, by adjusting the temporal pattern of muscle activation. This hypothesis fits well with a second study, carried out by the same group, and aimed at determining the pattern of activation of single motor units recruited in the biceps and deltoid during the production of an isometric force (Herrmann and Flanders 1998). The best directions of the single motor units, determined by measuring their firing rate and threshold force, were found to change gradually with their position in the muscle (best directions vary gradually with location in the muscle rather than clustering into separate groups). Based on this organization, Hermann and Flanders proposed that various units could be recruited, at different points in the movements, according to their mechanical action. They suggested that a large flexibility of the hand trajectory could be achieved through a gradual recruitment and derecruitment of the units ideally suited for the production of the required force vector at any given time. This remarkable result offers a potential neuromuscular substrate allowing us to understand how the muscle pattern of activation may be smoothly adjusted during the ongoing movement.

Forward modeling allows feedback control for fast reaching movements.

In the previous sections we have shown that: (1) purely sensory loops cannot be used to control fast reaching movements (Hollerbach 1982) (Gerdes and Happee 1994); (2) hand trajectory can be updated early and smoothly in response to extrinsic errors (Pélisson et al. 1986) (Prablanc and Martin 1992); (3) early and smooth corrections of the hand trajectory can occur in the absence of any sensory information (Bard et al. 1999). In this latter case, however, corrections are not as accurate as in control subjects. When considered together these elements suggest that the motor system is able to combine both efference and afferent signals to control fast reaching movements during their time course. The nature of this combination has been formalized under the concept of a "forward model". The idea behind this concept is that the motor system can progressively learn to estimate its own behavior in response to a given command (efferent signal). During the movement, this prediction can be used to estimate the current state of the motor apparatus and to predict what the final state will be. In parallel to this predictive activity, the system can also "store" its successive predictions in a "delayed buffer". If the delay is equivalent to the time necessary to process sensory information then the predicted and sensory estimated states can be compared directly. This comparison can be used to update the current estimation (Miall et al. 1993). To make this "predictive scheme" clear, let us take a very simple example (the reader must bear in mind that this example only has an illustrative purpose). Imagine that a motor command is produced at the time $t_0 = 0$ ms.

After 100 ms (t_1) the motor system can estimate the distance already traveled by the hand, based on the command that was generated. This information can be used to correct the current hand path when an extrinsic error is detected (e.g. when the target location has been updated at the end of the ocular saccade). 100 ms after t_1 (t_2 = 200 ms) a sensory signal has finally been processed. This sensory signal is however not related to the current hand position (t_2 = 200 ms) but to the position that the hand had 100 ms earlier (t_1 = 100 ms). If the stored predicted position (for t_1 = 100 ms) and the actually observed sensory position (delivered at t_2 = 200 ms but related to t_1 = 100 ms) matches then everything is fine and the current prediction (t_2 = 200 ms) is validated (note that this mechanism of comparison can of course involve other parameters such as the predicted and actual proprioceptive reafferences). In contrast, if a discrepancy is detected, the motor system can use the mismatch information to update its current estimation. With such a model, the probable position and velocity of the effector can be estimated with negligible delays, and even predicted in advance, thus making feedback strategies possible for fast reaching movements.

A possible way that forward modeling might allow on-line motor control is illustrated in figure 3. When required to reach a target, the subject first elaborates a motor plan based on the initial movement conditions (respective locations of the hand and target). During the realization of the movement, a forward model of the arm's dynamics is generated. In its simplest version, this model receives as input a copy of the motor outflow (figure 3, upper panel). In a more general form, this model receives as input a copy of the motor outflow and an error signal defined by comparing a stored estimate of the motor state with the delayed sensory estimate (figure 3, lower panel for details). The output of this forward model is a prediction of the movement end-point. This prediction can be compared continuously with the target location. In case of discrepancy an error signal is generated triggering a modulation of the motor command.

Convincing evidence suggesting that a reliable estimation of the current state of the motor apparatus can only be obtained by combining efferent and afferent signals was reported by Wolpert et al. (Wolpert et al. 1995). These authors required subjects to move their hand along a line while holding a manipulator. Vision of the hand was allowed for 2 s prior to movement onset. The manipulator was connected to a torque motor that induced resistive or assistive force to the movement. At the end of the trial the subjects estimated the location of their hand using a visual spot controlled by the other hand. The temporal propagation of measured errors exhibited by the subjects could be fully accounted for by assuming that the motor control system integrates both the motor outflow and the sensory inflow to estimate the hand location. Models based exclusively on either the sensory inflow or the motor outflow were unable to predict the observed pattern of error. A compatible conclusion was reached by Hoff and Arbib (Hoff and Arbib 1993) in a simulation study. These authors showed, for reaching movements, that control models combining efferent signals and afferent information to estimate the current hand location and adjust the planned pattern of muscle activation captured successfully the kinematic characteristics of visually directed reaching. In particular, this model, which used a look-ahead predictor to compensate for delays in sensorimotor loops, was able to account for the trajectory corrections observed in double step trials (Pélisson et al. 1986) (Goodale et al. 1986).

Further indirect arguments supporting the conclusion that efferent and afferent signals are combined to generate a reliable forward estimation of the arm dynamics were provided by recent studies on interjoint coordination. To understand the nature of these arguments it is necessary to remember that movement torques arise not only from the muscles acting on the joints but also from interactions among all the moving segments. As initially demonstrated by Hollerbach and Flash (Hollerbach and Flash 1982), these torque interactions are significant for multijoint arm movements and they have to be compensated one way or another. It was first suggested that the compensation was achieved "mechanically" through muscle springlike properties and reflex activity (Flash 1987) (Bizzi et al. 1992). This initial view was however questioned by Kawato and colleagues who provided computational evidence that a failure to integrate explicit compensations for limb dynamics in the initial motor command would lead to erratic and maladapted trajectories (Katayama and Kawato 1993) (Gomi and Kawato 1996). In order to investigate the controversy in more detail Gribble and Ostry (Gribble and Ostry 1999) studied a reaching task in which muscle activity was directly measured. Human subjects were required to perform single- and multijoint pointing involving shoulder and elbow motion. Movement parameters related to the magnitude and direction of interaction torques were manipulated in a systematic way. The results showed that the central control signal sent to the elbow and shoulder muscles were adjusted, in a predictive manner, to compensate for interaction torques arising from multijoint dynamics. Such anticipatory adjustments suggest that the nervous system is able to use a forward model to predict and offset the kinematic consequences of intersegmental dynamics. Interestingly, recent results have indicated that sensory information is critical to parameterize and update this forward model. Sainburg et al. (Sainburg et al. 1995) required, for instance, two patients presenting with large-fiber sensory neuropathy to make a gesture similar to slicing a loaf of bread. It was shown that without vision of the moving limb, these patients were unable to compensate for interaction-torque leading to severe impairments in interjoint coordination.

In a previous section we mentioned that internal non-visual feedback loops were apparently quite poor at rectifying intrinsic errors. To support this idea, we provided evidence that final errors in visually-directed movements performed without vision of the moving limb reflected systematic biases in the estimation of the initial state of the motor apparatus. At first sight, this observation may appear in contradiction with the idea that movement trajectory is controlled on-line by powerful feedback loops. A close look at the data shows however that this conclusion is misleading. Indeed, the previous considerations on forward modeling have shown that the estimation of the current hand location will be affected in a systematic manner if either the proprioceptive signal (Rossetti et al. 1995) (Vindras et al. 1998) or the inverse model that transforms the desired displacement into a motor command (Vindras and Viviani 1998), are biased. A study performed by Desmurget et al. (Desmurget et al. 1995) illustrates this point. These authors instructed a to visual target without vision of their moving limb. Pointing accuracy was measured in two conditions where the hand was either never visible ('Never'), or only visible in static position prior to movement onset ('Static'). It was shown that viewing the hand prior to movement greatly decreased endpoint variability ('Static') as compared to the control condition ('Never'). This effect was associated with a significant modification of the movement kinematics: the 'Static' condition induced a shortened acceleration phase with a corresponding lengthened deceleration phase, when compared to the 'Never' condition. These results were compatible with the idea that viewing the hand prior to movement onset allowed a decrease of pointing variability through a feedback process. To address this hypothesis Desmurget et al. performed an additional experiment identical to the first one except that the target was turned off during the deceleration phase of the movement. It was shown that turning the target off had no effect upon the 'Never' condition but induced a significant increase of pointing variability in the 'Static' condition. This result shows that vision of the static hand decreases movement end-point variability, not only by improving movement planning, but also by optimizing feedback control: when the noise attached to the estimation of the hand location is reduced, the noise contained in the forward model decreases, and movement variability declines.

Internal feedback loops are not used to generate the motor command in real time.

The "equilibrium point" (EP) model provides a very powerful conceptual reference frame from which it becomes possible to understand how visually directed movements might be generated in the absence of any *a priori* specification of the motor command. To make this point clear, let us present briefly the theoretical foundations of the EP model. Consider a mass (M) placed on a table and attached to two horizontal springs (S1 and S2). The magnitude of the two opposite forces (F1 and F2) exerted on M depends of both the stiffness (k) and the length (L) of S1 and S2 (F= kL). When F1 equals F2, M is in equilibrium. If one modifies suddenly the stiffness of one of the springs, M moves to reach a new equilibrium state. As a consequence, a simple way to control the position of the mass is to adjust the relative stiffness of the springs acting on it. By analogy, one may propose, based on the spring-like properties of biological actuators, that a simple way to move the hand to a given spatial position is to set the length-tension curves of all the muscles acting on the upper-limb in such a way that the torques exerted by agonist and antagonist muscles nullify each other when the hand is at the desired position (for a review (Feldman 1986) (Bizzi et al. 1992) (Desmurget et al. 1998)).

In its original formulation, the EP hypothesis suggested that visually directed movement were achieved, "in one step", by shifting suddenly the equilibrium configuration of the arm to its terminal state (Polit and Bizzi 1979) (Feldman 1986). This idea was however challenged by the observation that point-to-point movements followed roughly straight hand paths in the task space, irrespective of the experimental conditions (Morasso 1981) for a review (Desmurget et al. 1998). To account for this point, it was suggested that the equilibrium configuration of the arm was in fact not shifted in one step, but gradually displaced toward the target (Bizzi et al. 1992) (Feldman and Levin 1995). Evidence supporting this view was initially provided by Bizzi et al. (Bizzi et al. 1984) in the context of single-joint movements. These authors trained three monkeys to perform forearm movements toward a visual target presented in a dark room. The performance of the animals was tested prior to and after a bilateral dorsal rhizotomy. Two conditions were considered: arm held in the initial position, arm displaced toward the target at movement onset. As would have been expected if the nervous system had programmed a gradual shift of the arm equilibrium position, Bizzi et al. observed for both the intact and deafferented animals that (1) the hand initial acceleration increased gradually with the duration of the holding period in the Held condition; (2) the forearm moved back in the direction of movement starting point in the Displaced condition, before reversing its displacement to return to the target. Evidence supporting a generalization of the "continuous EP shift" hypothesis to multi-joint movements were further provided in modeling studies combining experimental observations and computer simulations (Flash 1987) (Hatsopoulos 1994) (Gribble and Ostry 1996). These modeling studies were undertaken under two different approaches. The first approach postulated that the series of EPs to be followed was determined in advance (Flash 1987) (Bizzi et al. 1992) (Hatsopoulos 1994). The second approach proposed a more general formulation in which the arm equilibrium configuration was shifted in real time based on a negative feedback loop aimed at nullifying the hand-target distance (Flanagan et al. 1993) (Feldman and Levin 1995). The latter hypothesis is very appealing for at least three reasons: First, it does not require the computation of a motor plan prior to movement onset which greatly simplifies the mechanism of movement generation by removing the need for complex non-linear inverse transforms; Second, it provides a unified framework within which movement generation and movement control do not need to be segregated; Third, it is very powerful at capturing the kinematic features of visually directed movements directed at stationary and jumping targets.

Unfortunately, the attractiveness and computational power of the "continuous EP shift" hypothesis are not echoed by recent experimental findings establishing clearly that the upcoming motor command is, at least partially, defined prior to movement onset. The first evidence sustaining this conclusion comes from the identification of fine predictive compensatory adjustments during reaching movements (the kinematic consequences of an upcoming motor command can only be anticipated and canceled if the motor command is know in advance). Several examples of such anticipated compensations can be found in the literature. Gribble and Ostry (Gribble and Ostry 1999) showed, for instance, that EMG activity in the shoulder and elbow joints varied in a predictive manner to offset interaction-torque arising from multijoint dynamics (see above). In the same vein, Flanagan and Wing (Flanagan and Wing 1997) reported the occurrence of fine predictive grip force adjustment during vertical arm movements performed with a hand-held load. Likewise, De Wolf et al. (De Wolf et al. 1998) described subtle anticipated postural compensations in the case of rapid arm movements.

The second evidence revealing the existence of a preplanning process comes from a recent transcranial magnetic stimulation (TMS) study carried out by our group (Desmurget et al. 1999b). The experimental protocol was similar to the one used by Prablanc and Martin (Prablanc and Martin 1992) in their pioneering study. Subjects were instructed to point to visual targets. Vision of the arm was not allowed during the movement. In some trials the target location was displaced during the saccadic response whereas in other trials it remained stationary. Two conditions were tested for each hand. In the first condition, the TMS coil was placed over the left posterior parietal cortex of the subject but no pulse was delivered. In the second scondition, the coil was placed over the same location and a single TMS pulse was applied at hand movement onset. Three main results were observed (figure 4): (1) path corrections that normally occurred in response to the target jump were disrupted by the stimulation when the subjects were required to use the right hand (contralateral to the stimulation site); (2) movements directed at stationary targets remained fairly accurate despite feedback disruption (right hand session); (3) no feedback disruption was observed for movements performed with the left hand, invalidating the possibility that the effect observed for the right hand was related to a visual or oculomotor deficit. When considered together, these results show that disrupting the continuous control loops comparing the relative locations of the hand and target does not give rise to erratic and totally maladjusted trajectories, as would be expected if negative internal feedback loops were used to generate the motor command in real time.

Functional anatomy of Internal feedback loops.

The last two decades have been dominated by the hypothesis that reaching movements were primarily under pre-programmed control and that sensory feedback loops exerted only a limited influence at the very end of the trajectory. As a consequence, functional investigations have focused primarily on the cerebral structures participating in motor preparation and execution yielding few insights into the functional anatomy of on-line movement guidance. This latter issue was first investigated only recently by Inoue et al. (Inoue et al. 1998). Using Positron Emission Tomography, these authors examined the functional anatomy of internal visual feedback loops. A target board was placed in front of the subjects. Six red targets (light-emitting diodes, LEDs) were presented on this board. They were aligned around a circle centered on a green LED (visual fixation). The fixation point and one of the six targets were switched on and off alternatively during the scans. Three tasks were considered. In the control task (C), subjects were instructed to "look" at the lit LED. In the reaching with visual feedback task (V) and the reaching without visual feedback task (W), the subjects had to "look and point" to the lit red LED with their right index fingers. The (V) minus (C) and (V) minus (W) contrasts revealed common significant increase in regional Cerebral Blood Flow (rCBF) in a large set of areas including the supramarginal cortex, the premotor cortex and the posterior cingulate cortex of the left hemisphere (contralateral to the reaching hand), the caudate nucleus and the thalamus of the right hemisphere and the right cerebellar cortex and vermis. The (V) minus (W) contrast identified specific additional activations in the right prefrontal cortex, the right lateral occipital and occipito-temporal cortex, the right superior parietal cortex, the right insula, the left premotor cortex, the left posterior cerebellum and the brainstem. The existence of such an extended network for processing visual feedback of hand movements may appear surprising at first glance, specially if one consider that many of the areas identified by Inoue et al. have been linked to movement preparation in the past (Grafton et al. 1992) (Grafton et al. 1996) (Deiber et al. 1996) (Lacquaniti et al. 1997) (Turner et al. 1998) (Winstein et al. 1997). A close look at the experimental protocol adopted by Inoue et al. allows some clarification of this point. To present the targets, the authors used a head mounted display which only granted vision of the hand in "the later stages" of the movement. As already mentioned earlier in this chapter, initial and late visual corrections seem to rely on different neural networks and to involve different processes (Paillard 1980) (Paillard 1996). The terminal corrections investigated by Inoue et al. have been shown to engage a series of one or more submovements generated at discrete time intervals on the basis of a retinal error signal. This indicates that the large cerebral network identified by the authors is not only reflective of the areas integrating terminal visual feedback of the hand but also of the areas processing retinal errors, planning corrective submovements, and estimating final accuracy (this estimation was not possible in the W condition). This latter factor might explain, for instance, the unexpected medial prefrontal activation reported by the authors in the (V) minus (W) contrast.

A second functional study on movement guidance was recently carried out by our group (Desmurget et al. 2001). Unlike Inoue et al. (Inoue et al. 1998), we investigated reaching movement performed without vision of the moving limb. This choice was based on the observation that internal non-visual feedback loops represent the primary process allowing early corrections of extrinsic errors (see above). Seven subjects were required to "look at" (Eye) or "look and point to" (EyeArm) visual targets whose location either remained stationary or changed undetectably during the ocular saccade. Functional anatomy of non-visual feedback loops was identified by comparing the reaching condition involving large corrections (Jump) with the reaching condition involving small corrections (Stationary), after subtracting the activations associated with saccadic movements and hand movement planning [(EyeArm-Jumping minus Eye-Jumping) minus (EyeArm-Stationary minus Eye-Stationary)]. Statistically, this double difference amounted to an interaction inasmuch as the areas identified were the areas that increased their responsiveness when larger corrections had to be performed. Behavioral data showed, in agreement with earlier studies (Prablanc and Martin 1992) (Desmurget et al. 1999b), that the subjects were both accurate at reaching to the stationary targets and able to update their movement smoothly and early in response to the target jump. PET difference images showed that these corrections were mediated by a restricted network involving the parietal cortex, the frontal cortex, and the cerebellum (figure 5). The parietal activation was located in the left intraparietal sulcus, in a region that is generally considered the rostral part of the Posterior Parietal Cortex (PPC). The cerebellar activation was found in the right anterior parasagittal cerebellar cortex, in a region associated with the production of arm movements. The frontal activation was located in the arm-related area of the primary motor cortex. The potential role of these structures is discussed below.

In addition to the PET data reported above, other recent evidence now links the PPC to the process of movement guidance. Among this evidence, the TMS study described in the previous section is indisputably the most compelling. When the normal functioning of the PPC is perturbed after hand movement onset, internal non-visual feedback loops allowing correction of the on-going movement are disrupted (Desmurget et al. 1999b). This deficit was recently replicated in clinical studies involving a patient presenting with bilateral ischemic lesions of the PPC (Pisella et al. 2000). This patient was asked to "look and point" to visual targets presented in front of her, on a computer screen. In some trials, the target remained stationary, whereas in other trials it jumped, at movement onset, to a new location. Results indicated that the patient was able to reach the target properly in the stationary condition. By contrast, she presented a dramatic inability to correct her ongoing movements in the perturbed condition. In this latter case, the patient pointed generally to the initial target location before initiating a second movement to the final target position. The control subjects exhibited early modifications of the hand path, as expected from earlier studies (Pélisson et al. 1986) (Prablanc and Martin 1992) (Desmurget et al. 1999b).

Functionally, it has been suggested that a major role of PPC in movement guidance might be to determine whether and to what extent the current motor response is inadequate (Desmurget et al. 1999b) (Desmurget and Grafton 2000). This hypothesis is based on the observation that PPC displays three main properties that would be expected from an error detection module. First, it modulates its neural activity as the hand approaches the target, i.e. as the motor error varies (MacKay 1992). Second, it has access to a representation of the target and current hand location through afferent information coming from many sensory modalities (visual, proprioceptive, vestibular), and the main motor structures (Andersen et al. 1997) (Brodal and Bjaalie 1997). Third, it is critical for establishing stable relationships between heterogeneous information, i.e. for merging arm and target related signals into a common frame of reference (Clower et al. 1996) (Colby 1998) (Xing and Andersen 2000). To make this latter point clear it is necessary to emphasize that the DME is not an absolute parameter, as implicitly suggested for the sake of clarity in the initial sections of this paper. The DME can be computed in various reference frames for goal-directed movements. For instance, it may be defined in a retinal reference frame as the spatial vector joining the retinal projections of the hand and targets (Paillard 1980) (Paillard 1996). Also, it may be defined in an egocentric reference frame centered on either the head (McIntyre et al. 1997), the trunk (Yardley 1990), the hand (Gordon et al. 1994) (Vindras and Viviani 1998), or the shoulder (Flanders et al. 1992). In this case, the error may be defined in extrinsic (or Cartesian) coordinates (Prablanc and Martin 1992) (Hoff and Arbib 1993), or in intrinsic coordinates (e.g. difference between the current posture and the postural state to be reached, (Desmurget and Prablanc 1997) (Gréa et al. 2000). DME may also be represented in an allocentric frame of reference (moving a cursor on a screen using a mouse), or in an object centred reference frame (grasping a cup of coffee requires that you locate both the position of the cup in an egocentric frame of reference and the location of the handle in relation to the cup). As emphasized above, neurophysiological and clinical studies have demonstrated that the construction and maintenance of these multiple frame of references depended critically on the PPC. For instance, Carey et al. (Carey et al. 1997) reported the case of a patient with a so called "magnetic misreaching" who slavishly reached straight to the fixation point at which she was looking when required to reach to a target presented in her extrafoveal visual field. More recently, Binkofski et al. (Binkofski et al. 1999) defined two new clinical syndromes termed "mirror agnosia" and "mirror ataxia" in patients with lesions of the PPC. The patients were asked to reach and grasp a small ball attached to a stick held by the examiner. Under direct vision the patients could readily perform this task. However, when the ball was seen as a reflection in a mirror, the patients could not make accurate reaches. The "agnostic" patients with larger lesions always reached toward the mirror, rather than towards the object. The "ataxic" patents, with smaller lesions, could reach in the general direction of the target but had difficulty locating it using vision. A critical step necessary to perform these types of reaching movements is the coregistration of multiple frames of reference.

Computation of a DME error by the PPC might be achieved through forward modeling. According to this view, a forward model of the arm's dynamics would be maintained within the PPC. Based on this model the final state of the system (e.g. hand position, posture) would be predicted. This prediction would then be compared to the reference state to reach (e.g. target location, target posture). A discrepancy between these two values would give rise to an error signal, as detailed in an earlier section (figure 3). Although there is no direct evidence that PPC may generate a prediction of the final state to be reached by the motor system, several arguments suggest that this assumption is not totally unfounded. As expected from the structure allowing forward estimation of the arm dynamics, the PPC integrates sensory signals from many modalities (visual, proprioceptive, auditory, vestibular), as well as efferent copy signals from motor structures (Andersen et al. 1997). In addition, recent studies have provided evidence that the PPC is involved in motor tasks requiring state prediction. Eskandar and Assad (Eskandar and Assad 1999) trained monkeys to use a joystick to guide a visual spot to a target. Sensory and motor aspects of this task were experimentally dissociated by occluding the spot transiently and by varying the relationship between the direction of the joystick and spot movements. The authors observed that neurons in the lateral intraparietal area did not respond to either visual input or motor output, but rather encoded a predictive representation of the movement of the stimulus. In agreement with this result, Sirigu et al. (Sirigu et al. 1996) (Sirigu et al. 1999) showed that patients with PPC lesions were not able to predict, through mental imagery, the time necessary to perform visually guided pointing gestures. Also, during the execution of finger movements, these patients were unable to decide whether a hand shown on a screen placed in front of them was their own hand or an alien hand. From this it is possible to hypothesize that complex motor disorders such as ideomotor apraxia are due to an inability to create a stable internal model of a gesture or action rather than a disturbance of a motor memory or retrieval.

Once defined in task coordinates (e.g. spatial or joint vector), the DME needs to be converted into an actual corrective command. In the case of reaching movements, a primary candidate for this function is the cerebellum. This structure receives abundant input from PPC via the pontine nuclei (Brodal and Bjaalie 1997) (Middleton and Strick 1998). In addition, converging evidence have demonstrated that inverse models were represented within the cerebellum (Wolpert et al. 1998) (Kawato 1999) (Imamizu et al. 2000) and that patients with cerebellar lesions displayed a chronic inability to accurately define the pattern of muscle activation required to direct the hand along a specific path (Bastian et al. 1996) (Day et al. 1998). Although, on-line trajectory adjustments are not suppressed after extensive lesions of the cerebellum in human (Day et al. 1998), path corrections generated by cerebellar patients are characterized by excessive deviations and ill-tuned muscle activation patterns. Such inappropriate compensations are also observed in manual tracking tasks (Haggard et al. 1995).

The previous observations suggest that the cerebellar contribution to on-line movement guidance may be to convert the dynamic motor error signal computed by PPC into an appropriate corrective command. Ultimately, this corrective command needs to interfere with the ongoing motor command. In light of the PET study carried out by our group (Desmurget et al. 2001), and reported above, one may suggest that this interference is achieved by modulating the neural signal issued by the primary motor cortex. In agreement with this view, it has been shown that the M1 receives substantial input from the cerebellum via the ventrolateral thalamus (Asanuma et al. 1983) (Brodal and Bjaalie 1997) (Hoover and Strick 1999). Also, it has been suggested that the motor system is organized in a relative hierarchy such that the primary motor cortex is mainly involved in the low-level aspects of motor control. Consistent with this idea, it was shown that purely kinematic and dynamical aspects of the movement are more commonly represented in the motor cortex than, for instance, in the parietal or premotor areas which seem to encode more abstract variables (Alexander and Crutcher 1990) (Scott et al. 1997) (Shen and Alexander 1997) (Turner et al. 1998).

Given this hypothetical scheme for updating a motor command, is there data showing that the PPC cerebellum and motor cortex are working as a functionally connected network? One way to address this question is to test for functional connectivity of the PET imaging data reported above (Desmurget, 2001). We used the technique of partial least squares (PLS) to identify brain areas in which there was a strong correlation with activity measured within the intraparietal sulcus (PPC) that was specific to the eye-hand tasks (McIntosh, 1996). To do this, the PPC activity was cross-correlated with activity from every other voxel in the brain, for all four tasks (eye, eye-hand, eye-jump, eye-hand-jump). This large correlation matrix was evaluated with singular value decomposition and reliable latent variables were identified by permutation testing (methodologic details are described in McIntosh, 1999). Of particular interest was the second latent variable, which identified PPC-brain-task interactions where the eye-hand tasks scaled inversely to the eye only tasks. The results shown in figure 6, show strong, eye-hand related correlations of PPC activity with left superior parietal and motor cortex, left SMA, left putamen and right anterior cerebellum. Stated differently, during on-line control of eye-hand reaching, neural and synaptic activity in these areas scale with the PPC. This finding supports the basic model linking PPC cerebellum and motor cortex as a functional unit for on-line control. It also implicates the basal ganglia in this process as well.

In conclusion, the present section provides evidence in support of the hypothesis that parietal-cerebellar circuits are critical for hand movement guidance. Based on recent neurophysiological and clinical observations, we hypothesize that PPC computes a dynamic motor error by comparing, through forward modeling, the updated location of the visual target and the estimated movement end-point. This dynamic motor error is then sent to the cerebellum which converts it into a corrective motor command. The corrective signal influence finally the ongoing motor command by modulating the neural signal issued by the primary motor cortex. Of course, this model does not imply that others areas, such as the premotor cortex, the colliculus, or the basal ganglia cannot be involved in movement guidance. In agreement with this observation, recent evidence have for instance suggested that basal ganglia play a critical role in the regulation of movement force during the movement (Turner et al. 2000) (Grafton et al. 2001). This contribution may have been missed in the PET study described above (Desmurget et al. 2001) inasmuch as the correction was almost exclusively directional in this case. It is clear that further studies need to be performed to fully understand the functional anatomy of movement guidance.

Concluding remarks.

Because accurate movements can be achieved in absence of sensory information, it has been argued, in the past, that reaching movements were primarily under pre-programmed control and that sensory feedback loops exerted only a limited influence at the very end of a trajectory. The present chapter challenges this view. We demonstrated that the ongoing movement unfolds under the constant supervision of powerful internal feedback loops. These loops rely on a forward model that integrates the sensory inflow and motor outflow to evaluate the consequence of the motor commands sent to the arm. With such a model, the probable position and velocity of the effector can be estimated with negligible delays, and even predicted in advance, thus making feedback strategies possible for fast reaching movements. The parietal lobe and cerebellum play a critical role in this process.

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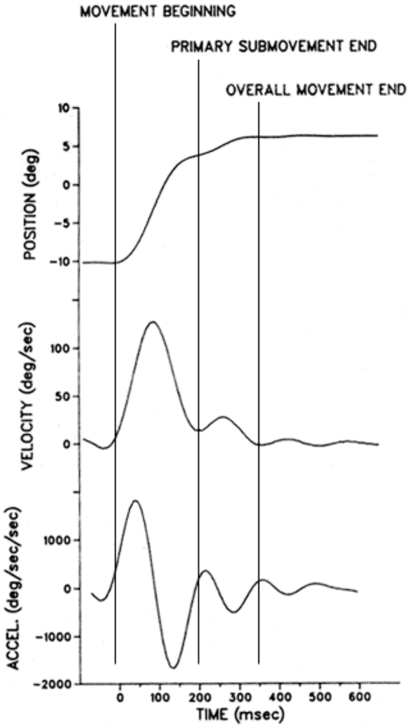

Figure 1: Individual position, velocity and acceleration signals for a single joint reaching movement performed with the elbow toward a visual target. As shown on the figure, the trajectory can be divided into two components (segmented by vertical lines): a main movement covering more than 80% of the required displacement (from movement beginning to the primary submovement end) and a submovement bringing the hand on the target (from the primary submovement end to the overall movement end). (Adapted from Meyer et al. 1988).

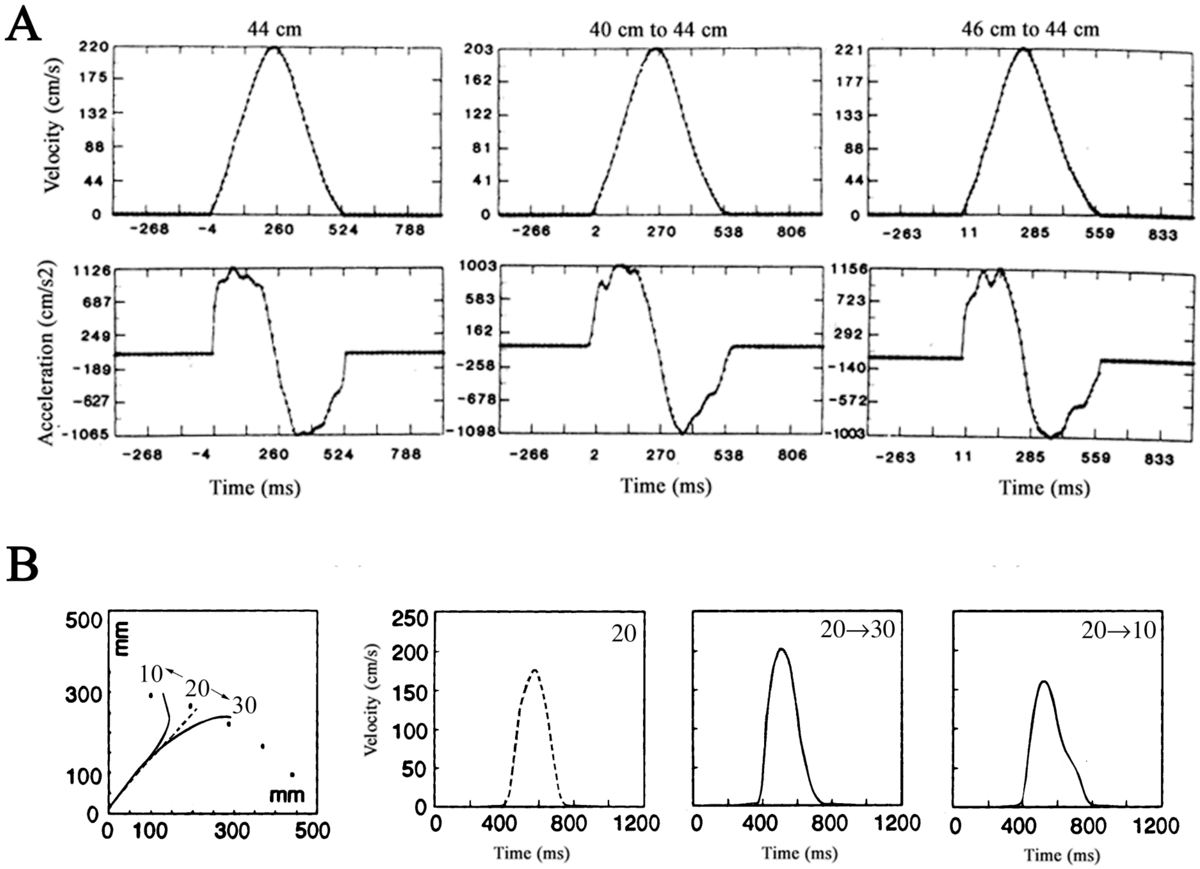

Figure 2: Ilustration of the smooth and early path corrections observed during reaching performed without vision of the limb. Upper Panel (A): Initial data by Pelisson et al. (Pélisson et al. 1986) showing that neither the hand velocity profiles nor the hand acceleration profiles were different for reaching movements performed to stationary targets (first column, 44 cm movement amplitude), or to targets that were displaced collinearly to the movement initial direction during the oculomotor response (second column: 40 to 44 cm; third column: 46 to 44 cm). Lower Panel (B): Mean hand path performed by one subject to a stationary target (20 deg; dashed line) and to targets that were displaced during the course of the ocular saccades (20→30, 20→10; continuous lines) (left column). Corresponding velocity profiles are presented (Adapted from Martin and Prablanc 1991).

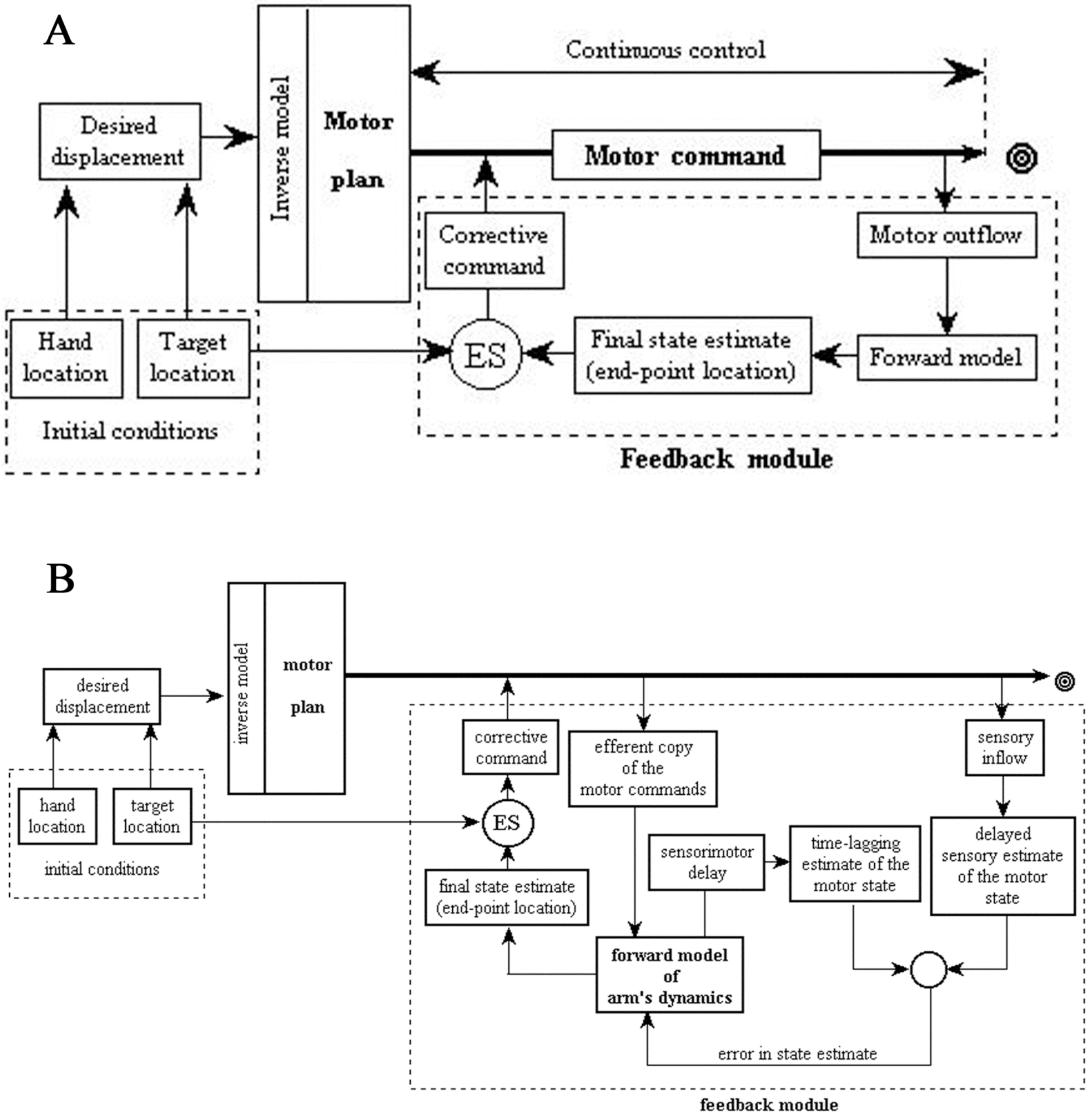

Figure 3: Potential motor circuits making use of a forward model of arm the dynamics for controlling hand movements. Upper panel represents a purely efferent model. In this case, a motor plan is initially defined based on the respective locations of the hand and target. During the movement a forward model of the arm's dynamics is generated. This model receives as inputs the motor outflow. It generates as output an estimate of the movement end-point location. This estimate is compared to the target location. In case of discrepancy an error signal (ES) is generated triggering a modulation of the ongoing motor command. The movement stops when the hand reaches the target estimated location (◎). Lower panel represents a model making use of both the efferent and afferent signals. A motor plan is initially defined. During the movement a forward model of the arm's dynamics is generated. This model receives as input the motor outflow and and error signal obtained by comparing the estimated and observed state estimate (Smith predictor, (Miall et al. 1993)). This comparison can involve parameters such as the predicted and proprioceptively infered hand location. It can also involve the predicted and observed proprioceptive reafferences. Because of delays peripheral loops, the current estimated state has to be delayed by a duration equal to the sensorimotor delay to be compared to the afferent signal. The forward model generates as output an estimate of the movement end-point location. This estimate is compared to the target location. In case of discrepancy an error signal (ES) is generated triggering a modulation of the ongoing motor command. The movement stops when the hand reaches the target estimated location (◎). (Adapted and extended from Desmurget and Grafton 2000).

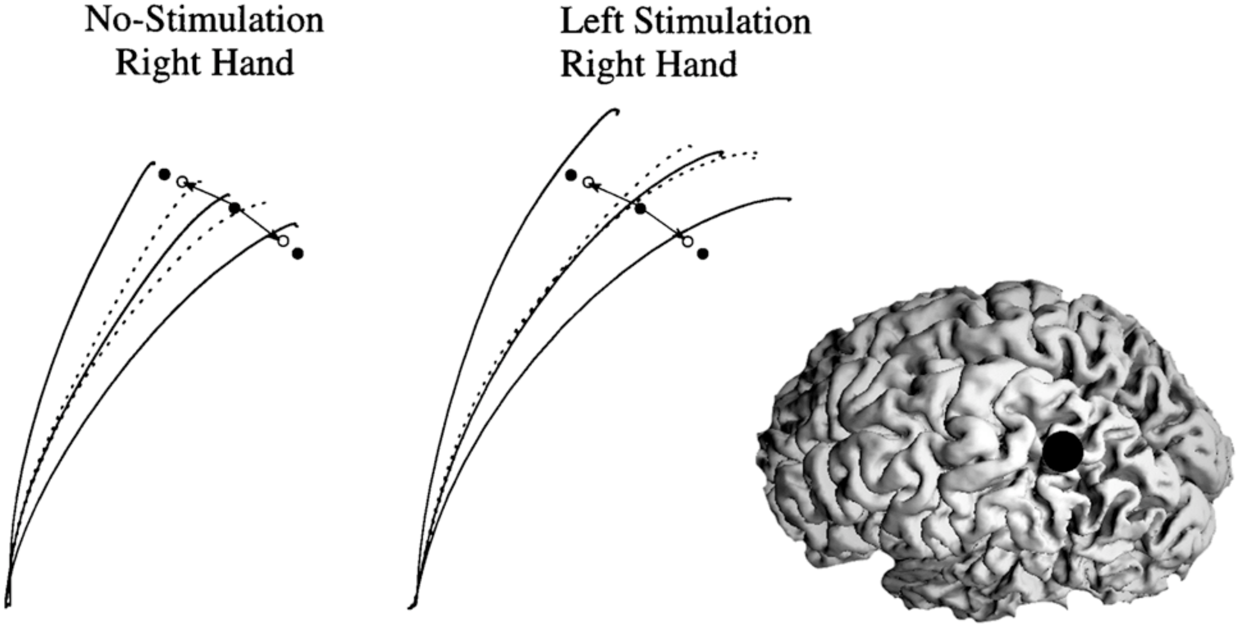

Figure 4: Illustration of the critical role of the PPC for on-line movement corrections. Mean hand paths performed by one subject, with (left panel), and without (middle panel) magnetic stimulation. The continuous curves represent the mean paths directed at stationary targets (20, 30, 40 deg). The dashed curves represent the mean paths directed at jumping targets (30→22.5, 30→37.5). Black circles indicate stationary target locations while white circles represent jumping target locations. TMS location site (right panel) determined by three-dimensional MRI (black circle). When TMS is applied, path corrections that normally occur in response to the target jump are disrupted. In addition, movements directed at stationary targets become less accurate although not erratic (Adapted and extended from Desmurget et al. 1999b).

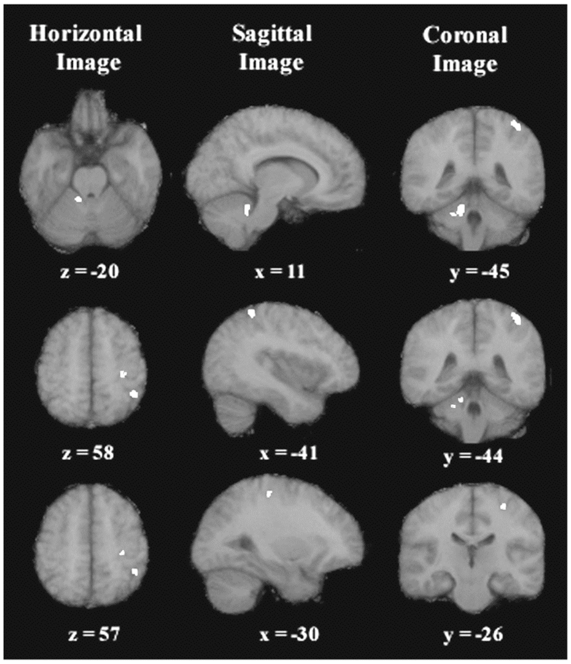

Figure 5: Functional anatomy of non-visual feedback loops, addressed by PET. Horizontal, sagittal and coronal difference images are presented. Activations are shown superimposed on a mean magnetic resonance image (MRI) in Talairach coordinates. On the horizontal and coronal images, the anatomic right side is shown on the left side. On the sagittal images, positive values of x designate the right hemisphere (ipsilateral to the reaching arm), negative values the left hemisphere (contralateral to the reaching arm). The upper row is centered on the cerebellar activation site. The middle row is centered on the posterior parietal activation site. The lower row is centered on the precentral activation site. (Adapted from Desmurget et al. 2001).

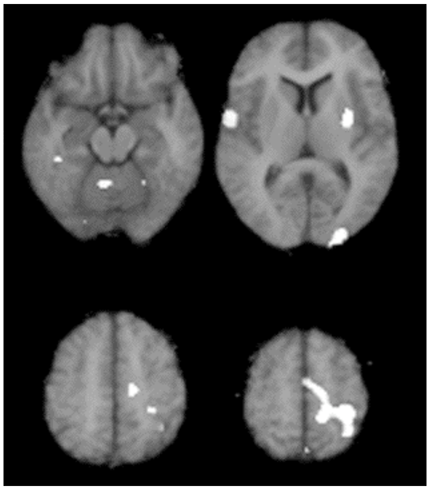

Figure 6: Functional connectivity of parietal cortex during on-line error correction. Brain areas showing strong, task specific (eye-hand movements) correlation with activity in intraparietal cortex (using data from Desmurget et al, 2001) are shown in white. For both stationary and jump conditions of the eye-hand task (and inversely the eye only tasks) activity of the left superior parietal and motor cortex, left SMA, left putamen and right anterior cerebellum correlated with that in the intra-parietal sulcus. Significance of the brain salience images was determined by boot-strap testing of latent images, with a standard error cutoff of 2 (see McIntosh, 1996 for method). Image left is the right brain.