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Forward modeling allows feedback control for fast reaching movements

Michel Desmurget and Scott Grafton

Delays in sensorimotor loops have led to the proposal that reaching movements are primarily under pre-programmed control and that sensory feedback loops exert an influence only at the very end of a trajectory. The present review challenges this view. Although behavioral data suggest that a motor plan is assembled prior to the onset of movement, more recent studies have indicated that this initial plan does not unfold unaltered, but is updated continuously by 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 a limb, such as the arm. In such a model, the probable position and velocity of an 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 appear to play a crucial role in this process. The ability of the motor system to estimate the future state of the limb might be an evolutionary substrate for mental operations that require an estimate of sequelae in the immediate future.

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Since the early contribution of Woodworth[1], the degree to which visually-directed movements are planned in advance or controlled online during their actual execution has been an issue of considerable debate[2–6]. After almost a century of controversy, the relative importance of three different models, namely the feedforward, feedback and hybrid, continues to be argued. Feedforward models propose that a motor command is defined in advance of the onset of

Box 1. Different types of feedback

The term 'feedback' has multiple meanings in the literature. In this review, it refers to processes that mediate hand path corrections by comparing the target position and an estimation of the hand location. This is the primary feedback mechanism that allows modulation of the initial motor command when it is inaccurate. From a theoretical point of view, we can segregate feedback loops into three categories: (1) sensory feedback, in which the location of the hand is estimated on the basis of sensory information; (2) non-sensory feedback, in which the location of the hand is estimated on the basis of efferent information; and (3) internal feedback, in which the location of the hand is estimated on the basis of both efferent and afferent signals. The term feedback alone refers to any of these loops.

movement. Within this context, the role of feedback loops is, at most, marginal and circumscribed to the very end of the trajectory[3,4,7–9] when hand velocity is low. Feedback models (Box 1), when regarded as the conceptual opposite of feedforward models, propose that the pattern of muscle activation that is required to point to the target is not defined prior to the onset of movement, but rather during the course of arm displacement. Thus, there is no *a priori* motor plan and the muscle command is generated in real time through an error signal that continuously compares the relative locations of the hand and target[10,11].

Hybrid models represent a trade-off between the feedforward and feedback hypotheses. In a hybrid model, a crude motor plan is assembled prior to the onset of movement (feedforward component). This initial plan does not unfold unattended, because it is imprecise[12–15]. Rather, it remains under the constant 'supervision' of powerful internal feedback loops that adjust and refine it in real time (feedback component). In this paper, we examine the validity of these three models for reaching movements of the hand in light of recent psychophysical, lesion-based and functional imaging studies. We show that both the feedforward and feedback hypotheses, when considered in isolation, are overly reductionistic. Consequently, we propose an integrative hybrid model of motor control in which preplanning and feedback control are both used by the nervous system. We first review the evidence that is generally believed to have established a dominant role for feedforward movement control, namely that sensory feedback loops are too slow to allow efficient trajectory control. Second, we show that feedback mechanisms can rely on much more than sensory inflow than has been thought traditionally. Feedback control strategies become viable if the instantaneous location of the hand can be inferred by the nervous system through a forward model that integrates efferent and afferent signals to infer, with no delay, the current state of the motor system (Box 2). Third, we argue against the plausibility that purely feedforward strategies generate rapid reaching movements. To this end, we show that online control by visual and non-visual information occurs early in a hand movement. We also provide evidence that the motor command is not generated exclusively in real time, which is contrary to the suggestion of purely feedback models. Finally, we discuss briefly the functional anatomy of internal feedback loops with emphasis on the potential contribution of the posterior parietal cortex (PPC) and the cerebellum.

Box 2. From robots to humans

Many of the concepts that are used to describe the planning and execution of human arm movements have been borrowed from robotic manipulators. Among these concepts, three are especially relevant for the present review, namely feedforward and feedback control and internal models.

In a feedforward control system, the set of muscle activations that drives a reach towards a target is defined prior to arm displacement. After the onset of movement, the motor command unfolds unaltered until the movement is completed. Computer programs that specify a series of commands to be performed in advance are a good analogy of feedforward control mechanisms.
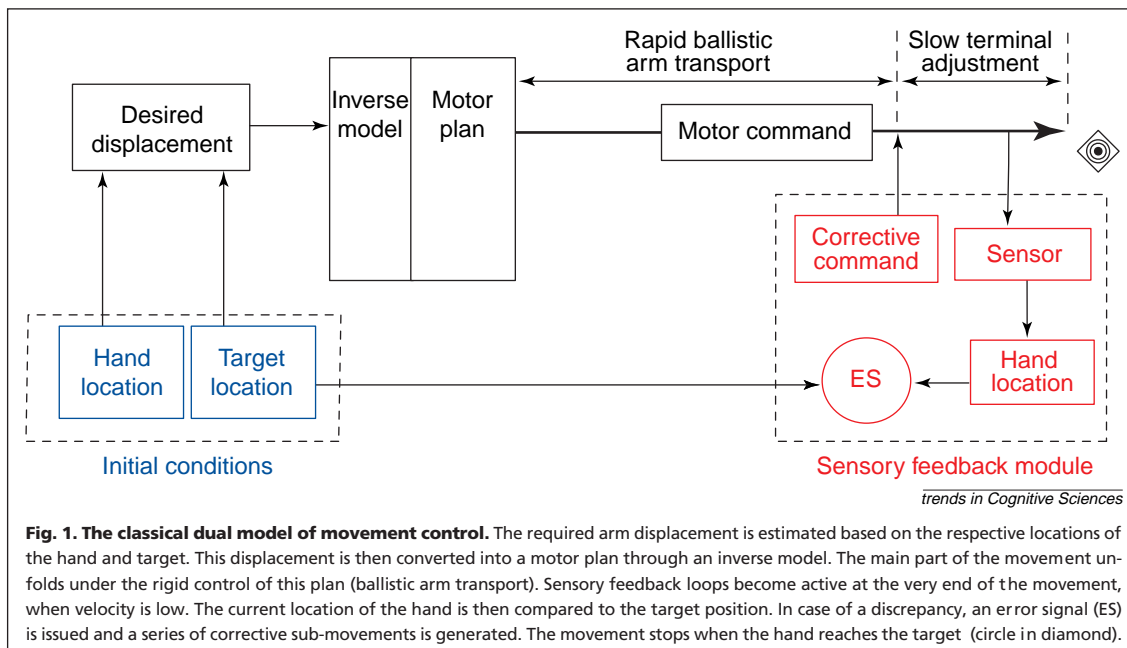
In a feedback control system, the current state of the system is compared to reference values. In the case of a discrepancy between these two parameters, an error signal is generated and used to modulate the behavior of the controlled system. The most common example of a feedback system is the thermostat, which compares the current temperature to a reference value and then modulates the response of the radiator. For reaching movements, the controlled system could be the arm, the reference state the target position and the current state the location of the hand. As long as the hand has not reached the target, a motor command is generated in real time (Refs a,b). Thus, muscle activations do not have to be specified in advance.

Internal models can be segregated into two categories, namely forward models and inverse models (Refs c,d). A forward model predicts the behavior of the motor system in response to a command and allows the CNS to estimate the current and future state of the effector immediately and without peripheral information. Forward models are particularly interesting in the context of feedback control systems. For instance, a forward model can produce an estimate of the movement end-point location as output, which can be compared to the target lo-cation. In the case of a discrepancy, a corrective command can be generated. An inverse model takes into account the inertial and viscous properties of the arm to estimate the motor command that will produce the desired displacement. Inverse models are therefore critical for feedforward control systems (Refs e,f).

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Fig. 1. The classical dual model of movement control. The required arm displacement is estimated based on the respective locations of the hand and target. This displacement is then converted into a motor plan through an inverse model. The main part of the movement unfolds under the rigid control of this plan (ballistic arm transport). Sensory feedback loops become active at the very end of the movement, when velocity is low. The current location of the hand is then compared to the target position. In case of a discrepancy, an error signal (ES) is issued and a series of corrective sub-movements is generated. The movement stops when the hand reaches the target (circle in diamond).

Sensory information and feedback control

During the last three decades, feedforward models of movement control have indisputably been the most influential. This dominance was based on the theoretical alternative that feedback loops should rely exclusively on sensory information, an assumption that was explicitly formulated in Keele's pioneering monograph, as follows. 'The concept of motor program might be viewed as a set of muscle commands that are structured before a movement sequence begins, and that allows the entire sequence to be carried out uninfluenced by peripheral feedback'[16]. Following this definition, the contribution of sensory information to movement control was widely investigated. Three types of results led to the conclusion that sensory feedback played a marginal role in movement accuracy. First, somatic deafferentation did not prevent subjects from executing relatively accurate movements in the dark. Second, some movements of short duration could be completed before the minimum delay required to process sensory information. Third, online corrections that were based on sensory feedback could produce unstable trajectories for pointing that was performed at a high or medium velocity. Among these arguments, the first is probably the least convincing, because deafferentation experiments have produced inconsistent results. Specifically, while some studies have indicated that humans or animals deprived of proprioception are able to perform relatively accurate movements[5,17,18], other experiments have shown that deafferented subjects exhibit dramatic motor impairments[5,19,20].
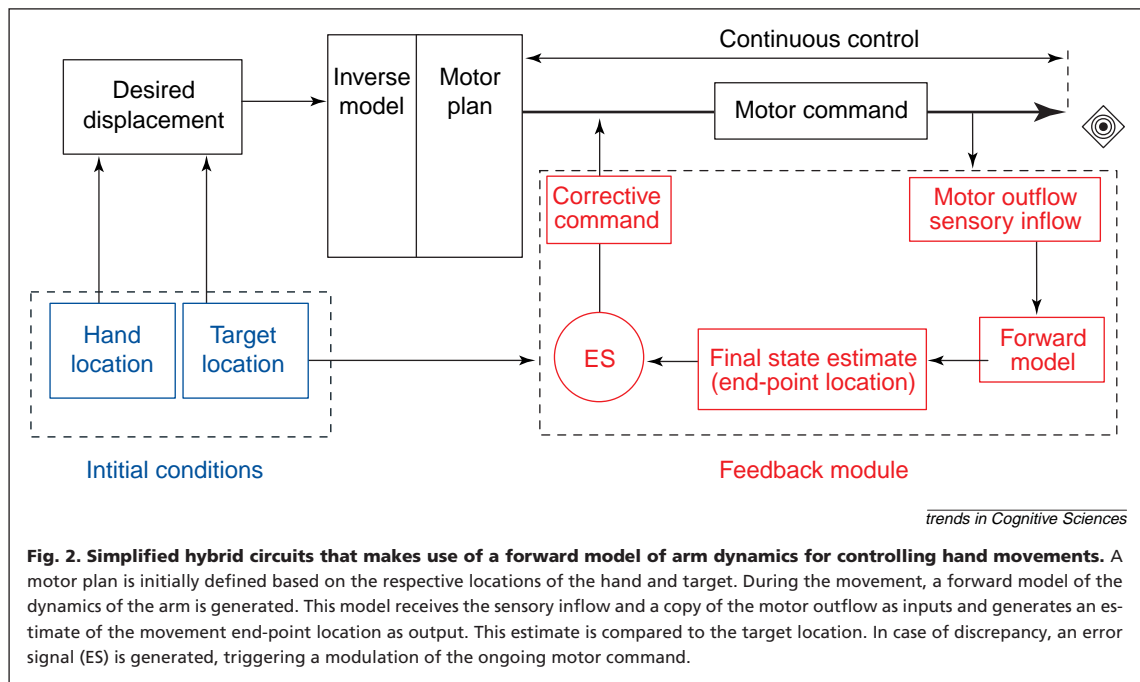
The strongest evidence against the use of sensory feedback to control movement trajectory is based on the physiological delay that is inherent in sensorimotor loops. If the processing of sensory information is long with respect to the duration of movement, the position of the hand will change dramatically by the time the feedback signal starts to influence the ongoing motor command, thus rendering the implemented correction inappropriate[21,22]. Behavioural experiments have shown that the minimum delay needed for a visual or proprioceptive signal to influence an ongoing movement is 80–100 ms (Refs 5,6), while that for the duration of visually-directed

reaching movements is typically 300–700 ms. On the basis of these results, it was concluded that sensory feedback loops could not be used to control hand trajectory[21,22].

To reconcile the abovementioned results with the fact that goal-directed movements are more accurate when proprioceptive or visual information is present, a dual model of motor control was proposed[3,4,7–9]. According to this model (Fig. 1), reaching movements are segmented into two components. The first is driven entirely by a motor plan and ensures rapid transport of the hand to the vicinity of the target. The second depends on sensory feedback loops and allows corrections at the very end of the trajectory, when the movement velocity becomes low. Classically, these corrections are viewed as a series of one or more sub-movements that are generated at discrete time intervals on the basis of a retinal error signal[5–8,23]. The dual model found strong support in the demonstration that viewing the hand during the first half of the trajectory did not improve movement accuracy more than when the hand was never visible[24,25]. In addition, tendon vibration experiments showed that altering proprioceptive feedback affected movement accuracy only when the vibration was applied at the end of the trajectory[26]. We shall examine alternative interpretations of these observations after developing the idea of forward models.

Feedback and the need for forward modeling

A displacement of the body with respect to the environment and *vice versa* generates the same retinal stimulation. To account for the ability of the nervous system to discriminate between these two situations, von Holst and Mittelstaedt[27] 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 the forward model[14,22,28–31]. The idea behind this concept is that the nervous system can progressively 'learn' to estimate the behavior of the motor plan in response to a given command. By integrating information that is related to initial movement conditions, motor outflow and sensory inflow, the probable position and velocity of the

Fig. 2. Simplified hybrid circuits that makes use of a forward model of arm dynamics for controlling hand movements. A motor plan is initially defined based on the respective locations of the hand and target. During the movement, a forward model of the dynamics of the arm is generated. This model receives the sensory inflow and a copy of the motor outflow as inputs and generates an estimate of the movement end-point location as output. 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.

effector can be determined (and even predicted). When a forward model is used to feed an internal feedback loop, control performance is improved significantly inasmuch as large delays that are associated with sensory feedback loops can be avoided. The advantage of forward modeling for movement control is illustrated schematically in Fig. 2. When required to reach a target, a subject first elaborates a motor plan, based on the initial movement conditions (i.e. the respective locations of the hand and target). During the realization of the movement, a forward model of the dynamics of the arm is generated. In its simplest version, this model receives as input a copy of the motor outflow. Based on this information, the end-point of the movement can be predicted and continuously compared to the target location. Discrepancies cause an error signal to be generated, which triggers a modulation of the motor command. More complex approaches have suggested that forward models do not only use motor outflow, but also use sensory inflow[29,30]. This view is supported by behavioral observations (see below) and has been modeled by Miall *et al.*[28] with reference to an engineering control scheme that is known as the Smith predictor. In this scheme, forward prediction is delayed by a period that is comparable to the sensory delay, thus making it possible to compare directly the predicted and sensory-based estimates. Any error that results from this comparison can then be used to update the current forward model of the dynamics of the arm.

One line of evidence that shows that non-sensory feedback loops can be used to guide biological actuators is found with eye movements. There is now considerable 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 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[32] and head-free gaze shifts[33]). Strikingly, such compensation does not require visual or proprioceptive feedback, because it can occur in complete darkness and after surgical

deafferentation of extraocular proprioception in monkeys[34]. These results have, thus, revealed the existence of a non-sensory feedback loop that can account for the remarkable accuracy of the saccadic system under normal conditions[35,36].

For arm movements, the existence of non-sensory feedback loops that make use of motor outflow was initially suggested by behavioral studies that showed that hand trajectory could be amended with a shorter latency than the minimal latency required to process peripheral information. For instance, Higgins and Angel[37] observed that the reaction time to an unexpected modification of the target trajectory in a manual tracking task was shorter than the proprioceptive reaction time. A similar result was reported by Jaeger *et al.*[38], who found that altering the proprioceptive signal through vibration did not modify the reaction time to a visual perturbation. Using a pointing task, Cook and Diggles[39] observed corrections to the hand path within 45 ms when the initial direction of movement was incorrect. This value was close to that reported by van Sonderen *et al.*[40] (30 ms) in a double-step task in which the initial target location was changed during or after the initiation of movement.

Convincing arguments were reported in an elegant study by Wolpert *et al.*[29], which suggested that a reliable estimation of the location of the hand could be obtained by combining efferent and afferent signals in a forward model. These authors required subjects to move their hand along a line while holding a manipulator. The hand was allowed to be viewed for 2 s prior to the onset of movement. 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 motor outflow and sensory inflow to estimate the location of the hand. By contrast, models based exclusively on either sensory inflow or motor

outflow were unable to predict the observed pattern of error. Hoff and Arbib[14] reached a compatible conclusion. They showed, for reaching movements, that control models that combine efferent signals and afferent information to estimate the current location of the hand and adjust the planned pattern of muscle activation successfully captured the kinematic characteristics of visually directed reaching. In particular, this model, which used a look-ahead predictor to compensate for delays, was able to account for the trajectory revision that is observed in behavioral experiments in which the target location is modified at the beginning of the hand movement or during the saccadic response.

Further arguments in favor of the conclusion that efferent and afferent signals are combined to generate a reliable forward estimation have been provided by recent studies on interjoint coordination. Gribble and Ostry[41] showed that electromyographic (EMG) activity in the shoulder and elbow joints varies in a predictive manner during reaching movements to compensate for interaction torque that arises from multijoint dynamics. This anticipatory response indicates that the nervous system can use a forward model to predict and offset the kinematic consequences of intersegmental dynamics. Interestingly, recent results indicate that sensory information is critical to set parameters for and update such a forward model. For example, Sainburg et al.[20] required two patients that presented with large-fiber sensory neuropathy to make a gesture similar to slicing a loaf of bread. Without being able to see their limb moving, these patients could not compensate for interaction torque, which led to severe impairments in interjoint coordination.

The best evidence for the presence of a forward model during reaching was provided recently by Bard et al.[18] A deafferented patient was instructed to look at and point to visual targets that were displayed in the peripheral field of vision, but was not allowed to look at the moving limb. In some trials, the target location was changed slightly during the course of the ocular saccade. Saccadic suppression prevented the patient from consciously detecting this manipulation, who was convinced that she pointed to a stationary target. The patient was able to correct her movement online to reach the new target location despite the absence of peripheral information. It is important to note that her corrections were not as accurate as those of control subjects, which suggests that motor outflow had to be combined with at least some sensory inflow to generate an optimal estimate of location of the hand.

Several studies have attempted to relate the pattern of end-point errors with key variables that are used to plan reaching movements[2,42,43]. For instance, Vindras et al.[44] showed that final errors in visually-directed movements that were performed without being able to view the moving limb reflected systematic biases in the estimation of the initial state of the motor apparatus. This kind of result might appear to contradict the idea that movement trajectory is controlled by internal feedback loops. However, this is not the case, because the estimation of the current location of the hand by a forward model will be affected in a systematic manner if either the estimation of the initial state of the motor apparatus or the inverse model that transforms the desired displacement into a motor command, is biased.
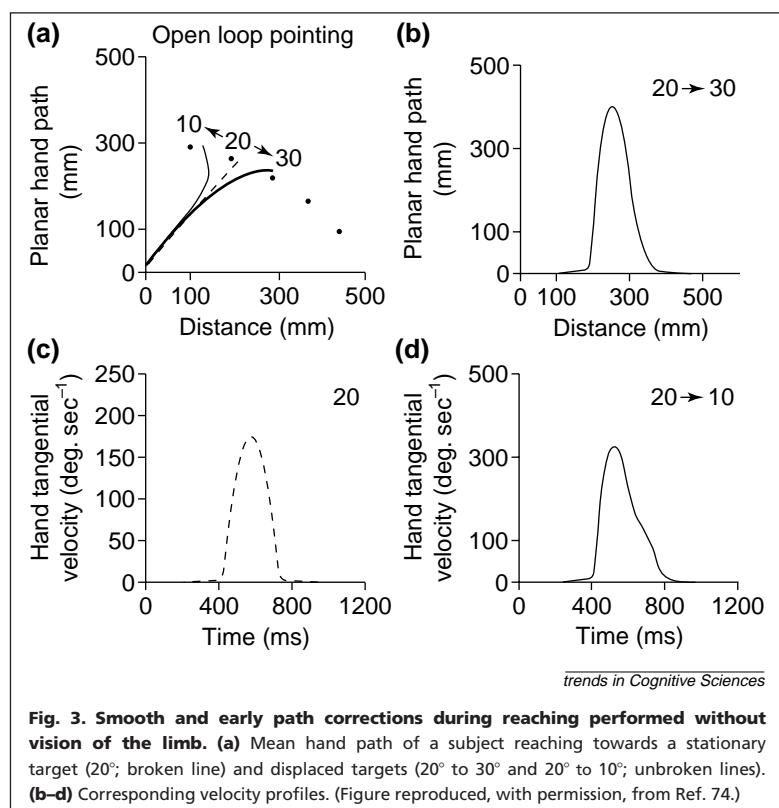
Arguments that support this claim can be found in studies showing that vision of the hand at rest, prior to movement, improves movement accuracy through an optimization of online feedback loops[45].

The studies reviewed in the foregoing section have established that forward models can combine motor outflow and sensory inflow to estimate the current and future states of the motor apparatus with negligible delays. These findings, therefore, obliterate the key argument against the use of feedback mechanisms for fast reaching movements.

Non-sequential, non-ballistic control of reaching

Two concepts, 'sequential control' and 'ballistic reaching', have strongly influenced our thinking of how motor plans are generated over time. For an external examiner, the relative coordination of the eyes, head and hand during goal-directed reaching appears to be sequential. When a subject points to a visual target in peripheral space, the eyes move first, followed by the head and finally the hand. The gaze arrives at the target before or at about the same time as the onset of the hand movement, because the duration of eye movement is brief[13,46]. Several researchers hypothesized that this sequential organization has a functional foundation[23,46] and consequently suggested that the nervous system had to achieve target foveation before building a reliable motor plan for the arm, because the extra-foveal visual signal did not allow for an accurate estimation of the target location[46,47]. This hypothesis was challenged by studies that showed that the serial organization of the eye, head and arm at the behavioral level results primarily from inertial factors. As shown by Biguer et al.[5,48], the EMG discharge for the eye, head and arm during fast reaching movements is nearly synchronous, indicating that the motor command is sent to these different effectors in parallel (the arm moves last simply because it has the greatest inertia). If one considers that the onset of an agonistic muscle contraction occurs 50–100 ms before the actual motion in a reaching movement[49], this observation concurs with psychophysical studies that have demonstrated that the arm movement generally follows the saccadic response with a lag of 60 to 100 ms (Refs 13,46).

The abovementioned observations indicate that the initial motor command can be issued on the basis of an imperfect estimation of the target location. At the end of the ocular saccade, after commands for arm movements have been initiated, the initial estimation of the target position is updated on the basis of foveal information. This updating is clearly demonstrated by the finding that arm movements are less accurate when the eyes are not free to move to the target[46,47]. We replicated and extended this finding recently (unpublished), using a protocol and apparatus similar to the one described in Prablanc et al.[46] Focusing on hand kinematics, we observed the following. First, the initial acceleration vector was not affected by the ability to move the eyes, which concurs with the idea that the initial motor plan is assembled on the basis of peripheral visual information. Second, the maximal velocity vector had a smaller magnitude in the eye-free condition than in the eye-fixed condition, which is in agreement with the observation that distances are usually overestimated in the peripheral visual field[46,47]. These observations suggest that an inaccurate

(a) Open loop pointing

Fig. 3. Smooth and early path corrections during reaching performed without vision of the limb. (a) Mean hand path of a subject reaching towards a stationary target (20°; broken line) and displaced targets (20° to 30° and 20° to 10°; unbroken lines). **(b–d)** Corresponding velocity profiles. (Figure reproduced, with permission, from Ref. 74.)

motor plan assembled on the basis of an imperfect estimate of the target location is corrected early in the course of the movement, specifically during the acceleration phase. This conclusion clearly challenges the idea that visually directed movements are ballistic during their early stage.

To investigate directly whether an intended action is a result of a preset pattern of non-modifiable commands, Prablanc and colleagues designed a set of behavioral experiments in which the initial inaccurate estimation of the target location during movement planning was artificially increased[12,13]. To achieve this, the authors used a double-step pointing paradigm in which the target location was modified slightly (target 'jump' paradigm) during the course of the ocular saccade. This procedure has the following three major advantages: (1) the target jump is not perceived consciously by the subject, because of saccadic suppression; (2) the target jump does not alter the organization of the oculomotor system, because saccadic responses to stationary targets involve an initial saccade that undershoots the target position and a single corrective saccade[35] to achieve accurate target acquisition; and (3) the target jump does not alter the organization of the manual response, because pointing movements to stationary targets involve an update of the target location at the end of the saccadic displacement, which is taken into account to amend the ongoing arm movement (see above). These points can be summarized by saying that unconscious double- and single-step situations are identical from a functional point of view. The intrasaccadic modification of the target location simply increases an error that is already present in the system, which supports the hypothesis that the same corrective processes are engaged in the 'jump' and 'stationary' trials. Using the target jump paradigm, Prablanc and colleagues observed that the hand path, which was initially directed to the first target, diverged progressively toward the

second target[12,13,15] (Fig. 3). Trajectory amendments were smooth, as indicated by the absence of discontinuities in wrist velocity curves, which exhibited the same bell-shaped profile for both the perturbed and control movements. Interestingly, corrections were detectable up to 110 ms after the onset of hand movement, which was roughly synchronized with the end of the ocular saccade, suggesting that hand trajectory was amended very early in the movement. The pattern of correction and the reaction time to the perturbation were similar, irrespective of whether the moving limb could be viewed[13]. This suggests that trajectory modifications that were observed in the double-step trials mainly depended on non-visual feedback loops, which is compatible with observations mentioned earlier that showed that vision of the limb during the first half of the trajectory has no effect on movement final accuracy[24,25]. However, the generality of this conclusion was challenged by Bard and colleagues, who designed a series of experiments based on the idea that peripheral vision might be particularly sensitive to the direction of the movement[6,23]. In their first experiment, the authors showed that the directional component of very fast aiming movements (<130 ms) could be corrected under the control of peripheral vision even when vision was only available during the first half of the trajectory[50]. In light of these and other data[6], the preservation of end-point accuracy that is observed when visual information is removed at the beginning of a movement might be explained by the fact that the motor command can still be optimized by potent terminal feedback loops.

Feedforward specification of the motor command

Given the powerful ability of forward models to adjust movement online, one might wonder whether any of the movement needs to be planned in advance[10,11]. For example, it has been shown that a control scheme that involves a progressive definition of the arm motor command, without any preplanning adequately predicts trajectories that capture the kinematic characteristics of visually-directed reaching[11]. This computational result, however, is not echoed by other experimental findings. Two main lines of evidence suggest that a representation of the upcoming motor command exists prior to the onset of reaching movements.

The first line of evidence comes from the study of fine predictive compensatory adjustments in single muscles. Gribble and Ostry[41] recently reported that EMG activity in the shoulder and elbow joints varied in a predictive manner to compensate for interaction torque that arises from multijoint dynamics. Similar results were reported for the adjustment of grip force during arm movements performed with a hand-held load[51] and for postural compensations that stabilize rapid arm movements[52]. Such adjustments can only be explained if the kinematic consequences of the upcoming motor command can be predicted precisely, i.e. if this motor command is, to some extent, 'known' in advance.

The second line of evidence that reveals the preplanning process comes from a recent transcranial magnetic stimulation (TMS)-reaching study that was carried out by our group[15] (Fig. 4). Subjects pointed to visual targets with their right hand, but vision of the arm was not allowed during this movement. In some trials, the target location was

displaced during the saccadic response, whereas in other trials, it remained stationary. As observed in earlier studies[12,13], the target jump elicited a smooth and progressive adjustment of the hand path. Strikingly, when a single TMS was applied over the left intraparietal sulcus (IPS) at the onset of hand movement, these smooth path corrections were disrupted and the subject pointed to the first target location. However, the hand trajectory to stationary targets did not become erratic, suggesting that relatively accurate movements can be performed in the absence of online feedback loops. If continuous control loops, in which the relative locations of the hand and target are compared, were used to generate the motor command in real time, disrupting these loops should have resulted in either errant or dramatically inaccurate trajectories to stationary targets. However, a control session that involved the same stimulation site but the other hand (left hand, ipsilateral to the stimulated site) failed to reveal any disruption of hand path corrections. This indicates that the feedback disruption observed for the right hand was not related to oculomotor deficits or to the inability of the subject to update the target location.

Unfortunately, the accuracy and the degree of detail of the initial motor plan cannot be established from the above-mentioned data. The fact that the motor deficits observed in some deafferented patients cannot be explained solely by their incapacity to define the initial state of the motor system[2,20,53] suggests that the initial motor plan is only crudely defined prior to the onset of movement and subsequently updated through internal feedback loops as the movement progresses. The loss of accuracy that is observed when online feedback loops are disrupted supports this view[15] (Fig. 4).

Functional anatomy of internal error corrections

Movements such as reaching are controlled by widely distributed cortical and subcortical sensorimotor areas. It is generally thought that parietal and pre-motor systems are essential for the selection, preparation and execution of a movement. Although the functional anatomy of internal feedback loops is not fully known, two areas within the distributed sensorimotor system are hypothesized to be critical for updating hand trajectory, namely the PPC in the region of the IPS and the anterior parasagittal cortex of the cerebellum[54,55]. In this section, we examine the potential contribution of these two structures to internal feedback.

Indirect evidence to suggest that internal feedback loops rely on the PPC comes from the observation that the reach responsiveness of neurons in area 7a of non-human primates changes as the unseen hand approaches a visual target[56]. A more convincing argument is provided by the TMS study described in the previous section. When the normal functioning of the PPC in the region of the IPS is perturbed after the onset of hand movement, feedback loops that allow correction of the ongoing movement are disrupted[15] (Fig. 4). This focal deficit was recently replicated in clinical studies that involved a patient that presented with bilateral ischemic lesions of the PPC (Ref. 57). This patient was asked to look at and point to visual targets presented on a computer screen in front of her. In some trials, the target remained stationary, whereas in other trials it 'jumped' to a new location at the onset of arm movement.
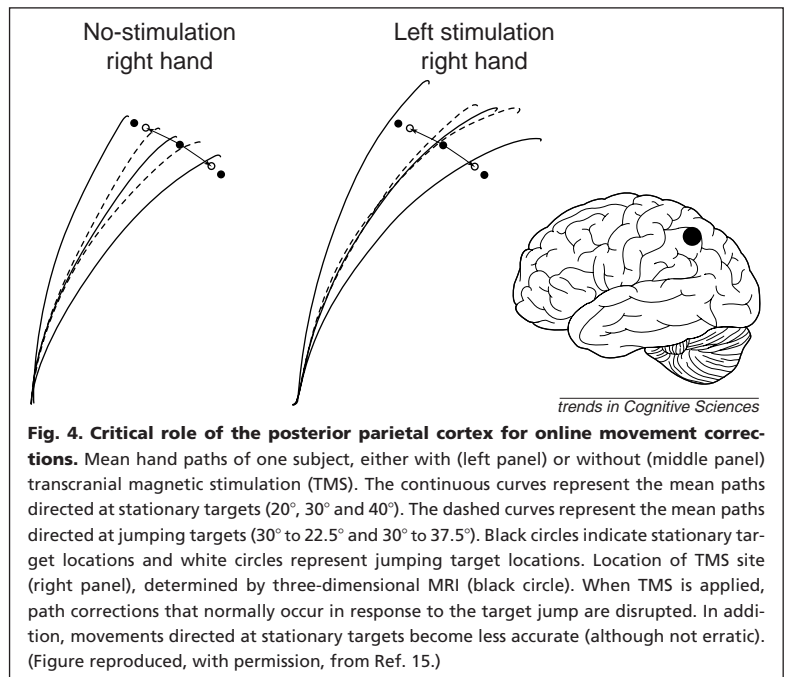

No-stimulation right hand   Left stimulation right hand

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Fig. 4. Critical role of the posterior parietal cortex for online movement corrections. Mean hand paths of one subject, either with (left panel) or without (middle panel) transcranial magnetic stimulation (TMS). The continuous curves represent the mean paths directed at stationary targets (20°, 30° and 40°). The dashed curves represent the mean paths directed at jumping targets (30° to 22.5° and 30° to 37.5°). Black circles indicate stationary target locations and white circles represent jumping target locations. Location of TMS 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). (Figure reproduced, with permission, from Ref. 15.)

The results indicated that the patient was able to reach the target properly in the stationary condition, but she presented a dramatic inability to correct her ongoing movements in the perturbed condition. In the latter case, the patient pointed generally to the initial target location before initiating a second movement to the final target position. Control subjects exhibited early modifications of the hand path, as expected from earlier studies[12,13,15].

Recent studies in the monkey and human have shown that the parietal cortex is highly differentiated with many functional subdivisions[58–60]. Unfortunately, the function of many of these subdivisions is not entirely understood and it is not clear which specific areas might be associated with internal feedback loops. In addition, progress in this area is hampered by the marked differences between the parietal lobe cytoarchitectonic organization of human and non-human primates[59]. Despite these obstacles, two potential roles for the PPC have been evoked in the literature, particularly in areas that involve the IPS. It was first suggested that the PPC might be involved in computing motor errors by comparing the actual target location with the location of the hand[15]. This view is supported mainly by the demonstration that the PPC is crucial for establishing stable relationships between heterogeneous information[58], i.e. for merging the arm- and target-related signals into a common frame of reference, which constitutes a crucial step in defining a motor error. An alternative (but not exclusive) hypothesis proposes that the PPC generates a forward model of the location of the hand. Indirect support for this view comes from the observation that several parietal structures are concerned with various types of predictive mechanisms[61–63]. Stronger support emerged with the finding that sensory signals from many modalities (e.g. visual, proprioceptive, auditory and vestibular), as well as efferent copy signals from motor structures, are integrated in the PPC (Ref. 64). This concurs with the idea that sensori-motor integration is a crucial feature of forward models.

Despite the abovementioned findings that implicate the PPC in feedforward models, several lines of evidence support

the idea that forwards models might rely on the cerebellum more than the PPC. Unlike the PPC, the cerebellum has long been associated with feedback control[28,65]. The original idea, proposed by Holmes[66], was that this structure is particularly important in the visual guidance of movement. This hypothesis was recently incorporated into a more general scheme in which it is assumed that the cerebellum plays a crucial role in elaborating forward and inverse internal models. Based on this idea (which has been reviewed elsewhere[30,31]), one could assign two functions to the cerebellum for movement guidance. First, this structure might contribute to the conversion of the error signal generated by the PPC into a motor command (inverse trans-formation). In support of with this view, it has been shown that inverse models are enclosed within the cerebellum[30,67,68] and that patients with cerebellar lesions are unable to compensate for multijoint interaction torques during movement planning[69]. A second potential function of the cer-ebellum is involvement in estimating the probable position and velocity of the effector (forward model). Of the supportive evidence, reviewed elsewhere[28,30,70], the following three ideas are especially convincing. First, in patients with cerebellar lesions, path corrections that are based on visual sensory information are characterized by excessive deviations and abnormal oscillations, as would be expected if feedback loops relied exclusively on delayed sensory information[71]. Second, an erroneous (or absent) forward model leads to tracking deficits that are similar to those observed in cerebellar ataxia[28]. Finally, cerebellar pathology leads to major deficits in motor tasks that rely on the generation of a forward model. For example, when normal subjects lift an object, the load on the hand increases with movement acceleration and variations in grip force anticipate this increase of load force[51,72]. This can only be explained if the kinematic consequences of an upcoming motor command can be predicted precisely through a forward model. Interestingly, the close coupling between grip and load forces is absent from patients with cerebellar lesions[73].

The abovementioned data suggest that internal feedback loops rely on both the cerebellum and the PPC. The exact functional role of these two structures, as well as the nature of their reciprocal interactions and their potential connections with other areas, remain to be investigated.

Concluding remarks

The present review indicates that no single computational algorithm can adequately describe the control processes that are used to perform goal-directed movements. Rather, reaching towards a target requires an integrative control scheme in which feedforward specification of the motor command, forward modeling of the dynamics of the arm and online updating of the initial pattern of muscle activation are synthesized in reliable feedback loops, which are thought to involve the cerebellum and PPC.

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Outstanding questions

• Classical models of motor control divide reaching movements into two components, namely a pre-programmed (or ballistic) component, which ensures rapid transport of the hand to the vicinity of the target, and a controlled component, which allows fine spatial adjustments at the end of the trajectory. Is this view still tenable?

• Does a delay in sensorimotor loops prevent the use of feedback to control the trajectory of the hand during reaching movements?

• Forward models allow prediction of the behavior of a controlled system (e.g. arm) in response to a given command in advance. What is the evidence that the nervous system uses this type of forward model to control reaching movements?

• What is the evidence that a motor plan is effectively assembled prior to the onset of movement? Is it plausible that the motor command is not planned in advance, but rather generated in real time via internal feedback loops?

• What are the anatomical structures that are associated with internal feedback loops that control ongoing movements?

• Are forward models used in other cognitive domains?

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