

The planning and control of reaching movements

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The notion of internal models has become central to the study of visually guided reaching. Armed with this theoretical framework, researchers are gleaning insights into long-standing problems in the field, such as the ability to respond rapidly to changes in the location of a reach target and the fine control of the multi-joint dynamics of the arm. A key factor in these advances is our increased understanding of how the brain integrates feedforward control signals, sensory feedback, and predictions based on internal models of the arm.

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Abbreviations

EMG electromyograph
PPC posterior parietal cortex
TMS transcranial magnetic stimulation

Introduction

The study of volitional movement has undergone rapid progress over the past several years. A major factor in this success has been the application of new theoretical ideas to the design and analysis of psychophysical investigations. Chief among these is the notion of internal models, hypothetical computations in the brain that either predict the outcome of some motor event (forward models) or calculate the motor command required to achieve some desired state (inverse models or feedforward controllers) [1]. Another key factor is the increased availability of functional imaging and transcranial magnetic stimulation (TMS), techniques that allow researchers to identify the neural substrates underlying complex behavioral phenomena. As a result, it has become easier to interpret psychophysical and computational findings in terms of our growing understanding of the neurophysiology of the sensorimotor pathways [2].

In the past year, significant achievements have been made in characterizing specific feedforward and feedback control structures involved in reaching. In particular, new results have clarified our understanding of the role of visual feedback in the early stages of reach planning and the ability to precisely control the complex dynamics of multijoint movements. Other major themes have been the role of learning in the maintenance of internal models and the manner in which intrinsic (e.g. joint, muscle) information

and extrinsic (e.g. perceptual, task-specific) information are combined to form a motor plan. In this review, I will discuss current trends in the study of goal-directed reaching, focusing on these recent results.

Feedback control: on-line trajectory control in the parietal cortex

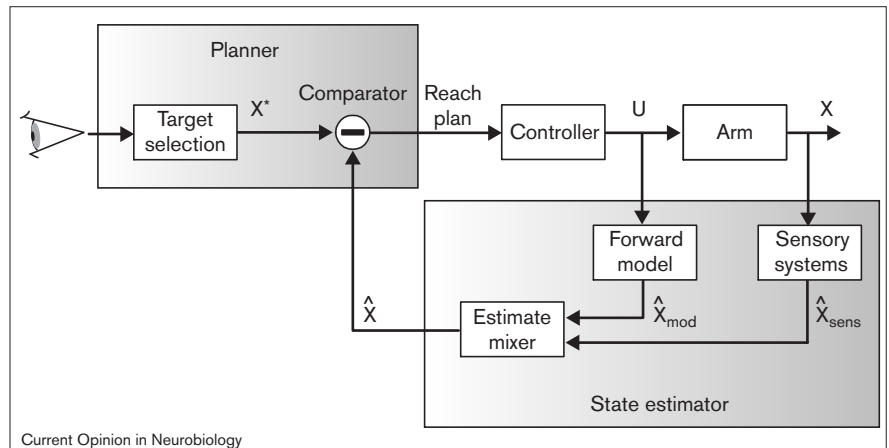
Visually guided reaching begins with the selection of a target from the visual scene and the formation of a movement plan. Recent studies of the posterior parietal cortex (PPC) and superior parietal lobe (SPL) in monkey have demonstrated that these areas contain the required combination of visual, somatosensory, and motor signals to be able to coordinate this first step [3–7]. New findings show that these early planning areas are not only responsible for the initial target selection and plan, but also play an ongoing role throughout the movement.

A shift in target location occurring near the onset time of a reaching movement can result in an on-line correction, independent of whether subjects can see their hand or whether the target jump was consciously perceived [8–12]. Desmurget and colleagues employed TMS to study the role of the PPC in this behavior [13••]. Subjects were instructed to reach and to make a saccade to a visual target that was sometimes surreptitiously shifted during the saccade. When TMS was applied to the contralateral PPC, corrective responses to a target jump were eliminated, whereas movement paths were unchanged for trials in which the target was kept stationary. This suggests that the completion of a feedforward plan does not require parietal control, but that parietal feedback mechanisms can override a plan in progress. In addition, movements to the same location with the ipsilateral hand were unaffected by the TMS pulse, contrary to what would be expected if the PPC were playing a purely visual role [3]. Other authors argue that on-line reach corrections could be performed by two separate systems: a fast, automatic feedback loop driven by the visual shift of the target, and a second, slower mechanism that is under cognitive control [14•,15•]. Comparison of normal subjects and a patient with bilateral lesions of the PPC suggests that only the fast mechanism is dependent upon the PPC [15•].

Figure 1 shows a schematic of how this on-line correction could occur. A comparator gauges the difference between the current estimated hand location and the desired location, and this information is sent downstream to a controller responsible for generating the correct motor commands (more will be said about the controller in the next section). A key element of this schematic is the state estimation based on mixing sensory feedback and internally generated predictions of hand location. There is ample evidence for the importance of sensory feedback in the

Figure 1

Schematic diagram of the internal models used in the target-shift task. X^* is the desired location of the arm, U is the command signal generated by the controller, and X is the current state of the arm. X is estimated both from sensory information and from the output of a forward (predictive) model [19], and these values (\hat{X}_{sens} and \hat{X}_{mod} , respectively) are then combined into a single state estimate, \hat{X} . The comparator is responsible for determining the correct movement, effectively subtracting the current state estimate from the desired state.



early stages of reach planning, including the strong influence that visual estimates of hand location have on a pending movement [16,17]. On the other hand, deafferented patients perform as accurately as normal subjects in a visually 'open loop' version of the target-shift task [18], suggesting that forward models [1,19–23,24] must also play a significant role (see also [25]). Indeed, it has also been shown that hand-position estimates from sensory feedback and from forward model predictions are combined in a statistically optimal way [21].

Desmurget and colleagues argue that the PPC contains both the state estimator for current arm position and the comparator [13]. This idea is supported by evidence that PPC and SPL contribute to the maintenance of internal representations of the arm and hand [26–28]. On the other hand, the PPC may only be responsible for updating the motor plan, and other structures might contain the state estimator and/or comparator. The cerebellum is a likely candidate [20,29,30]. Patients with cerebellar ataxia are less likely to make a corrected reach after a target shift, and they react more slowly when they do [31]. A positron emission tomography (PET) study of prism adaptation is also consistent with this theory [32]. Clower *et al.* reported that adaptation to prismatic displacement of the visual feedback led to increased activity in the PPC but not in the cerebellum. This result may seem at odds with the fact that cerebellar damage interferes with prism adaptation [33,34]. However, Clower *et al.* were specifically concerned with the locus of adaptation, and so they chose as their baseline condition a shifted-target paradigm similar to that discussed here. In this latter task, the direction of the target displacement was chosen randomly across trials in order to prevent adaptation. The role of the comparator, for example, is the same in the two tasks, and the lack of additional cerebellar activity in the adaptation case is probably due to cerebellar activation whenever movements result in a visual error signal [32].

Finally, it has recently been shown that the superior colliculus (SC) contains two populations of neurons that

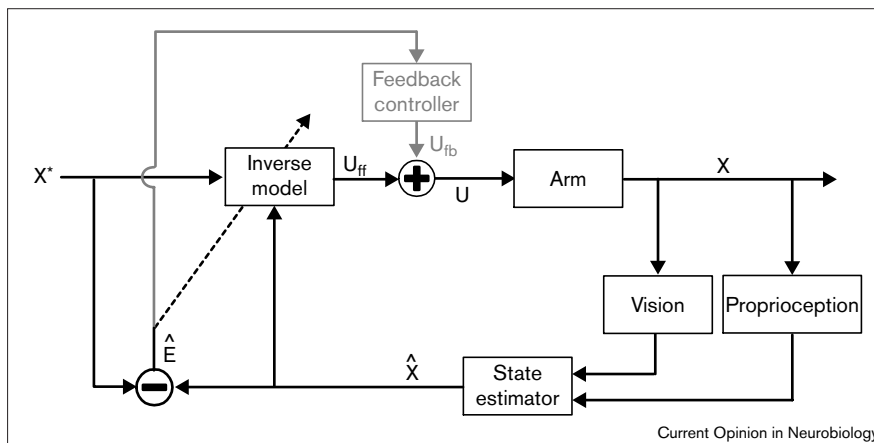
respond to arm movements, one using a gaze-centered reference frame and one employing an intrinsic representation, perhaps in a muscle or joint-based frame [35,36]. These cells project to the spinal cord and are thus ideally situated to play the role of the controller in Figure 1. The PPC projects to the SC, both directly and through frontal premotor areas [37], and these pathways could form a system similar to that responsible for generating saccades for fast, visually driven control of the arm.

Feedforward control: interaction torques and internal models

Whereas the early stages of visually guided movement are seen to be under the control of feedback loops, evidence is mounting that aspects of the later stages of motor control rely less on feedback than many researchers previously thought. Precise control of multijoint movements requires control of the interaction torques that arise when the motion of one joint causes acceleration at another [38]. The seminal work of Sainburg and Ghez [39,40] showed that patients who lack proprioception were unable to coordinate multijoint movements as a result of their inability to account for interaction torques. The long delay times required for proprioceptive feedback, as well as other observations [41], led the authors to conclude that compensation for interaction torques could be accounted for primarily by a feedforward controller that requires either proprioceptive or visual feedback for its maintenance (see Figure 2).

Three new studies paint a clearer picture of this feedforward mechanism. These papers all combined electromyograph (EMG) recording with inverse dynamics modeling, in which the various components of the joint torques, including the interaction torques, are estimated from the measured trajectory of the arm. Gribble and Ostry [42] investigated two-joint planar movements requiring only either rotation of the shoulder or of the elbow. They found that the onset of EMG activity at the stationary joint consistently preceded movement onset, providing conclusive evidence that at least some aspect of the compensation is feedforward. Two other

Figure 2



Schematic diagram of the internal models used in controlling multijoint arm movements. The desired motion of the arm X^* is fed into an inverse model of the arm, which acts as a feedforward controller, producing a command signal, U_{ff} . There is also evidence for late influence from a feedback control signal, U_{fb} [48]. The two commands are combined, through simple addition perhaps, to yield the final control signal U . The feedback pathway is illustrated in grey to reflect the fact that it plays a subordinate role as a result of feedback delays. The true state of the arm, X , is estimated with a combination of the visual and proprioceptive feedback. The state estimate, \hat{X} , serves as input to the inverse model, and is also compared to the desired state to yield an estimate of the current motor error (\hat{E}). The latter signal is used both in feedback control and to drive adaptation of the inverse model (dashed arrow) [75].

groups compared single-joint movements in a constrained and an unconstrained condition. Koshland *et al.* [43] studied a planar 'center-out' reaching task in which subjects typically exhibit little wrist motion, and Scheidt and Rymer [44] studied subjects making a planar arm movement that required only elbow rotation. In both cases, substantial interaction torques were seen at the stationary joint, requiring active compensation in the unconstrained movements, as verified by EMG. Remarkably, fixing of the unused joint had no effect on the timing or directional tuning [43] of these EMG patterns, confirming that interaction torques are accounted for by a feedforward mechanism.

As with deafferented patients, the multijoint movements of patients with cerebellar ataxia show an inability of these patients to account for interaction torques [45–47]. However, in the case of cerebellar subjects, visual feedback of the arm does not improve coordination, suggesting an impairment of the inverse model itself. A recent imaging study also supports the theory that the cerebellum computes feedforward control signals [29].

Sainburg *et al.* [48] studied adaptation to a novel inertia imposed upon the arm and saw evidence that the feedforward controller itself had adapted. It has also been reported that subjects with hemiparesis are unable to control interaction torques in their paretic arm [49], and normal subjects exhibit poorer anticipation of interaction torques in their non-dominant limb [50]. In both of these cases, the relatively impaired limb is used less often in everyday volitional movements, suggesting that learning is a continual process driven by motor experience. It is likely that this same internal model, or models closely allied with it, is responsible for learning to reach in environments in which novel forces are encountered [51–54]. In recent studies of this kind, researchers have been able to demonstrate that

physiological changes correlate temporally with behavioral measures of motor learning [55,56].

Finally, the existence of well-tuned feedforward controllers has important theoretical implications. The equilibrium point hypothesis [57] suggests that the spring-like neuromuscular properties of the arm could be exploited to simplify the task of the controller. Specification of a trajectory of intermediate postures, or equilibrium points, could be sufficient to execute an arm movement without having to invert the dynamics of the arm. Although the physical properties of the arm are surely exploited in order to simplify control [58,59,60], they are insufficient to account for the observations of this section. In fact, interaction torques are an example of how the mechanics of the arm can add complexity to the control problem. Yet even in simple point-to-point reaching they are compensated for with accurate predictive control.

Learning and multiple internal models

In the examples of the previous section, the inverse model is adapted in the face of motor error. It is plausible, however, that other components of the system could also adapt. A possible example comes from a case in which visual feedback plays an important role in computing the inverse dynamics of the arm. When reaching while rotating the torso, the arm is subjected to Coriolis forces, yet movement of the torso does not disrupt accurate reaching. This situation is formally similar to the control of multijoint interaction torques, suggesting that a feedforward model of the trunk–arm dynamics is used to solve the problem. Cohn *et al.* [61] have shown that visual input plays a large role. While sitting in a stationary seat, subjects viewed an image of a room rotating about them. Reaching movements displayed errors consistent with the expectation of Coriolis forces in the direction opposite to that of the visual rotation.

This result is compatible with the feedforward model of Figure 2, in which the state estimator is fooled by the visual input. Over time, proprioceptive and vestibular feedback were sufficient to adaptively correct the response. The fact that no after-effects were observed when the visual rotation ceased suggests that the inverse dynamics model was not altered, but rather that an adaptive state estimator learned to discount visual feedback when assessing trunk rotation. This interpretation could be tested by checking the extent to which vision aids reaching in a real rotating environment [53] before and after the visual adaptation.

Evidence for the existence of internal models is typically found through careful behavioral manipulations that isolate one aspect of the planning or control of movement. How then can the relationship between these models be understood? An important advance has been the development of an interference paradigm for addressing this issue. Modifying techniques from earlier studies of the learning of novel force fields [62], two laboratories have examined the interactions between the learning of kinematic perturbations, where the mapping from joint angles to visually perceived hand location is altered, and dynamic perturbations, in which the forces required to make a particular movement are changed. Krakauer *et al.* [63**] allowed subjects to adapt to reaching with a rotated visual map, with altered arm inertia, or both. They found no interference between the two tasks when learned sequentially or in parallel. Flanagan *et al.* reported similar results employing the visual rotation task and the learning of compensation for a viscous force field [64**]. These data imply a computational separation of the two internal models, a theoretically interesting finding in its own right, and a validation of the standard procedure of studying the systems in isolation.

Task-dependent optimal control

The task of the feedforward controllers discussed above is to allow for accurate control of the arm, which implies the existence of a motor plan. Recent thinking on the planning of reaching movements has been deeply influenced by the ‘minimum variance’ model of Harris and Wolpert [65,66*]. They posit a signal-dependent variability in movement control, in which variability scales with the magnitude of the command signal. Movement trajectories are then chosen to minimize the resulting end-point variability. In general, models that select movements by optimizing some quantity related to the trajectory are called optimal control models. The most successful prior theories were also optimal control models, but they maximized general, *ad hoc* criteria such as smoothness or efficiency, either intrinsically [67,68] or extrinsically [69] defined. Those models do not capture the task-specific planning effects that have been observed in experimental data (e.g. [70,71]). Although extrinsic models could be adapted to include task-specific constraints in a natural way, they cannot account for the physics of the arm and its controllers. The opposite is true for intrinsic models. What is required is a hybrid approach that utilizes the right combination of

criteria for any given task [70,72,73]. The minimum variance model provides a general framework for incorporating intrinsic and extrinsic information [65]. The quantity being optimised — the variance of the movement end-point — is entirely task-dependent, and in the case of simple point-to-point reaching, it is an extrinsic quantity. However, by accounting for the signal-dependent noise in movement production, the variance becomes a function of intrinsic variables. From this perspective, the key is not the choice of the optimization criterion nor even the model relating control signal to noise. Rather, it is in the ability to combine task-dependent criteria with a viable model of movement production.

An example of the generality of the minimum variance model can be seen in its application to obstacle-avoidance trajectories. Sabes and colleagues [70,74] showed that when subjects make reaching movements around obstacles, movement paths vary in a predictable manner depending on the spatial relationship between the obstacle and the arm. We suggested a model in which the inertia of the arm is taken into account to reduce the probability of colliding with the obstacle. However, there is no *a priori* reason why inertia should be favored over any other dynamic or kinematic factor that contributes to motor error. Hamilton and Wolpert have modeled the data from [70] using the same signal-dependent noise model: variability of a neural command signal scales with the magnitude of the signal. This assumption, combined with a biomechanical model of the arm, allows them to compute the expected end-point variability for a particular target trajectory. They were then able to find the trajectories that minimize the probability of collision with the obstacle and found good matches with the experimental results (A Hamilton, D Wolpert, personal communication).

Conclusions

Over the past year, researchers studying goal-directed reaching have made significant progress, capitalizing on recently developed theoretical and experimental tools. We have a better understanding of high-level visual feedback loops and of low-level feedforward mechanisms for controlling multijoint movements. The notion of internal models has been central in these advances. In most of this work, evidence of predictive control or adaptive state estimation is used to identify internal models. The next step is to elucidate the structure of these models — in particular, to identify what information they use and how that information is transformed for use by the motor system. The minimum variance model has also been influential in recent work, and the near future will undoubtedly see more applications of this model, as well as the development of new models that adopt a similar approach. Finally, steady progress is being made in illuminating the neurophysiology of the sensorimotor pathways involved in reaching. Continued effort will be required in order to merge this information with the behavioral and computational viewpoints discussed here.

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