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 longstanding 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 multi-joint 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
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
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 impairelimb 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 endpoint — 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.
Acknowledgements
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References and recommended reading
Papers of particular interest, published within the annual period of review, have been highlighted as:
• of special interest
**of outstanding interest


10. van Sonderen JF, Gielen CC, Denier van der Gon JJ: Motor programmes for goal-directed movements are continuously adjusted according to changes in target location. Exp Brain Res 1989, 78:139-146.


This is one of two papers claiming that fast responses to changes in visual target location are the result of an automatic system. Reach target locations were shifted after movement onset. Instructions varied with trial block: subjects were required either to reach to the new target or to a non-cued location offset from the original target by the same amount but in the direction opposite from the new target. Reaction time analysis shows a separation of short-latency movements toward the visual target displacement (even in the opposite-direction condition, i.e. when this was the incorrect response) and long-latency movements toward the non-cued location.


This paper uses a clever experimental design to study the on-line correction of reaching movements. The authors argue that on-line changes in plan are the result of two different systems: a fast, automatic system that is directly driven by movement of the target, and a slower system that appears to be under cognitive control. The results would be more compelling if perturbation reaction times were presented in addition to movement times. Analysis of a patient with optic ataxia suggests that the PPC is required for the automatic pathway only. However, the overall slower movement times for the patient make these data somewhat difficult to interpret.


This paper offers a novel explanation for the slight curvature typically observed in reach paths. The authors compared the path curvature of movements made with correct visual feedback and those with visual feedback displaced to the left or right. Curvature was shown to depend upon the relationship between the actual and the visual hand location. The data were consistent with a model in which feedback-dependent biases in the representation of hand location lead to errors in the planned direction of hand displacement.


This is a study of adaptation in predictive internal models. Subjects held the handles of two force-generating manipulanda, one with each hand. A predictable, transient increase in load force was generated at the right hand, and the resulting modulation of grip force was recorded. In the self-generated condition, an upward movement of the left hand triggered the upward pulse in load force at the right hand, as if the subject were grasping a single object with both hands. In the cued condition, the left hand remained stationary, and an acoustic tone signaled the increase in load force at the right hand. In the self-generated condition, subjects exhibited an increase in grip force that preceded the load force pulse. Furthermore, they were able to adapt the timing of their response to the introduction of a 250 ms delay between motion of the left hand and load force pulse at the right. In the cued condition, however, the grip-force response was largely contingent on feedback of the load force pulse, and the introduction of a delay between the tone and the force pulse had little effect. This suggests that internal models can more easily learn to predict variable consequences of one’s own actions than arbitrary stimulus response pairs.


42. A compelling argument in favor of the feedforward control of interaction torques. The authors report on three sets of planar arm movements: one requiring only shoulder rotation, one requiring only elbow rotation, and one set selected so that pairs of movements require either the same elbow or shoulder rotation and displacements of opposite sign at the other joint. In all cases, EMG activity at both joints precedes movement onset. Furthermore, as movement speed and direction are varied, the level of EMG activity scales with the magnitude of the interaction torques at the relevant joint.


61. This paper presents a clever and novel experimental paradigm: iterated practice. Subjects are asked to trace out the lines of a template, and the template for subsequent trials is the actual movement of the previous trial. Movements tend to converge to a set of smooth trajectories which can be described with a small number of parameters. This paradigm could help discover classes of ‘natural’ movements, or, in the language of optimal control movements that are nearly optimal according to some planning criterion.


63. This is a vivid demonstration that visual input can affect the feedforward control of movement in complex ways. The visual illusion of rotation is sufficient to cause errors in reaching that are consistent with the expectation of Coriolis forces in the opposite direction. Although subjects lose this response after repeated trials, there is no adaptation after-effect. This suggests a recalibration of an optimal state estimator rather than a retuning of the dynamics of the arm.


One of two important papers that use an interference paradigm to assess the interaction between kinematic and dynamic adaptation (see also [64••]). The paper explores adaptation to the rotation of the visual field (clockwise or counterclockwise) on the feedback displayed on a video monitor and an altered inertia of the arm (mass placed medial or lateral to the forearm). First, the authors demonstrate that for either the kinematic or dynamic tasks the consolidation of learning of one version (the counterclockwise visual rotation or the lateral mass) is disrupted by an intervening training session with the other (clockwise rotation or medial mass). The authors then show that learning the dynamic task does not interfere with the consolidation of the kinematic task and that the two tasks can be consolidated in parallel. These findings suggest a computational separation between the kinematic and dynamic internal models.


One of two important papers that use an interference paradigm to assess the interaction between kinematic and dynamic adaptation. Using a rotation of the visual field (kinematic) and a viscous force field (dynamic), the authors investigate whether learning each task separately leads to improvement in learning the two in parallel (composition effect), and whether learning them in parallel helps in learning them sequentially (decomposition effect). Evidence for the composition effect was clear, but only the kinematic task seemed to benefit from prior experience with two tasks in parallel. The authors note that improvement in the combined task may be mostly attributable to improvement in the more difficult kinematic task. This complicates the interpretation somewhat, as both the composition and the decomposition effects may be explained by a lack of interference from the dynamic task on the kinematic task (see also [63••]).

66. Harwood MR, Mezey LE, Harris CM: The spectral main sequence of human saccades. *J Neurosci* 1999, 19:9098-9106. The saccadic 'main sequence' is the linear relationship between duration and amplitude of saccades. This paper presents a novel frequency-domain analysis showing that a similar linear relationship holds between the location of well-defined troughs in the spectrum and the inverse of the duration. From the perspective of this review, the key element of the paper is the possibility of a new tool for distinguishing the predictions of various trajectory planning models. In this case, the minimum variance model makes a significantly better prediction of this linear relationship than several competing models, even though their predictions are quite similar when viewed in the time domain. Whether similar transformations can help to distinguish models of reaching movements is an open question.


