Computational approaches to motor control

Tamar Flash* and Terrence J Sejnowski†

New concepts and computational models that integrate behavioral and neurophysiological observations have addressed several of the most fundamental long-standing problems in motor control. These problems include the selection of particular trajectories among the large number of possibilities, the solution of inverse kinematics and dynamics problems, motor adaptation and the learning of sequential behaviors.

Addresses
*Department of Computer Science and Applied Mathematics,
The Weizmann Institute of Science, Rehovot, Israel 76100;
e-mail: tamar@wisdom.weizmann.ac.il
†The Salk Institute, Howard Hughes Medical Institute, 10010 North
Torrey Pines Road, La Jolla, CA 92037, USA; e-mail: terry@salk.edu

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Abbreviations

EP	equilibrium point
PRR	parietal reach region

Introduction

The focus of our review is limited to recent models of multi-joint movements aimed at unraveling the computational principles and associated neural representations subserving motor planning and execution. This includes recent investigations into spatial representations and coordinate frames for movement generation and sensorimotor transformations. We also review recent models of hand and joint trajectory planning and the type of constraints and strategies used to resolve kinematic redundancies. In this review, we complement and update a previous *Current Opinion in Neurobiology* review [1•].

In motor control, online sensory information must be integrated with knowledge acquired through experience and learning. Thus, the associated neural machinery must be highly adaptive and versatile but at the same time be capable of performing highly complex sensory information processing, sensorimotor transformations and motor planning.

Computational models allow quantitative descriptions of both the mechanical actions of muscles and the neural commands activating them. They can be used to simulate and explore the implications of different control hypotheses, which can then be compared with experimental observations. Models of the motor system need to be developed with a range of abstraction from schematic to detailed, each providing a different perspective [2]. The degree of abstraction should match the level in the motor hierarchy. This is of more than theoretical interest as the motor system may itself contain models of the environment and its own actions [1•,3,4]. The integration between sensory information and efferent copies of motor commands are linked by inverse and forward models.

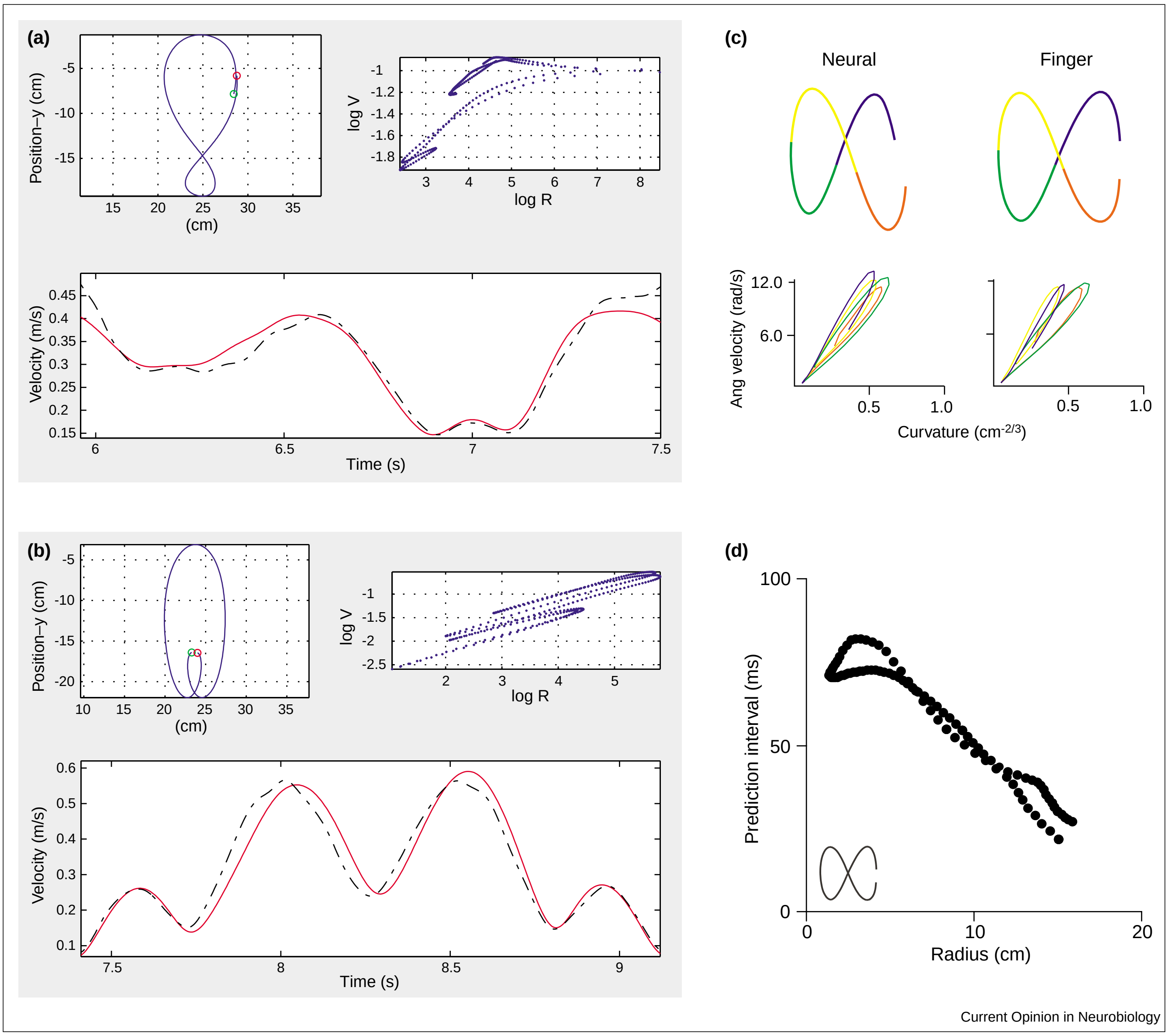
Research in motor control is plagued (or perhaps blessed) with controversies, some of which involve quite fundamental questions. Recent progress in resolving several of these controversies will be addressed here. One example concerns the question of the motor variables that are coded by neural populations [5]. Another issue is the tension between inverse dynamics [6] and the equilibrium point (EP) hypotheses [7,8] for motor execution.

Neural population coding

In a population code, information about a variable is represented by the pattern of activity in a large number of cells [9]. The direction of arm movement during reaching is coded by neurons whose firing rate varies as the cosine of the angle between a cell's preferred direction — where it is maximally active and the actual movement direction. Cosine tuning curves for the direction of hand movement expressed in external spatial coordinates (a high-level variable) are ubiquitous in the brain, although curves with more sharply peaked shapes have been reported recently [10]. Alternatively, many have argued that the cortex represents low-level parameters, such as muscle force [11]. Assuming that motor cortical neurons do indeed code for muscle force, the cosine tuning is optimal, in the sense that it minimizes the net effect of neuromotor noise, resulting in minimal motor errors [12]. In that model, the amount of neuromotor noise, which may originate from both central and peripheral sources, was assumed to scale with the magnitude of the motor command. Cosine tuning can also result from geometric constraints [13].

Another interpretation of cosine tuning is that cortical neurons code for the force level generated by groups of muscles [14•]. This is consistent with the coding of hand direction and speed by the population vector, in which each cell contributes a vector in the direction of its preferred direction in proportion to its firing rate. This may also account for the discrepancy in direction between the population vector and movement direction in the presence of external loads. The time lag between the neural activity as expressed by the population vector, and the movement it codes for (denoted as the population interval), has been found to increase with increases in path curvature [15] (see Figure 1d). An explanation for the latter observation has been suggested by the model described in [14•]. The implications of the model for the issue of whether the motor cortex explicitly codes for higher task-level parameters, such as hand movement direction in external coordinates, or for intrinsic parameters, such as joint rotations or muscle forces, are under active debate [16•–18•].

Figure 1



Current Opinion in Neurobiology

Hand trajectories and predictions of neural models during figure drawing tasks. **(a,b)** The hand paths and velocity profiles predicted by the minimum jerk model [30]. This model suggests that among all possible hand trajectories, the selected movements maximize motion smoothness, defined here as the trajectory that minimizes the rate of change of hand acceleration (jerk). The hand paths are shown for two patterns: a figure of eight – upper left in (a) – and a double limaçon – upper left in (b). The predicted velocity profiles for these two figural forms (red solid curves, bottom panels) closely matched those of the recorded movements (dashed black curves, bottom panels). Also illustrated (upper right panels) is the piecewise constant relationship between hand velocity (V) and radius of curvature (R), when plotted in logarithmic scales. **(c)** Neural and finger trajectories during a figure of eight drawing task. A time series of population vectors calculated during the task was temporally integrated to yield the neural trajectory. Individual movement segments are marked by different colors. Segment boundaries correspond to maxima of tangential velocity. Also shown is the two-thirds power law representation in the actual hand kinematics (finger) and those predicted by population vectors (neural). **(d)** Magnitude of the prediction interval increases as the path becomes more curved (the radius of curvature decreases). Panels (c) and (d) reproduced with permission from [15].

Coordinate systems and sensorimotor transformations

The execution of a simple reaching movement requires a series of computational processes that include visual acquisition of the target, coordination of multi-modal proprioceptive signals, and ultimately the generation of motor commands to drive the arm towards the target. These processes involve internal representations of the target and limb positions and coordinate transformations between different internal reference frames [19]. In the early stages of visual processing, visual inputs are encoded in a retinal (eye-centered) reference frame modulated by eye position, called a ‘gain field representation’ [20]. Eye-centered spatial representations are also used for working memory of eye movements [19] and for ongoing or intended arm movements [21,22••]. These findings suggest that response selection may precede sensory to motor coordinate transformations.

An eye-centered coordinate system during reaching is also supported by several behavioral studies. Vetter *et al.* [23] have investigated how a target location, initially coded in a visual coordinate system, can be transformed into motor coordinates during visually guided movement. They show that, when a discrepancy between the actual finger position and the visual feedback of finger position was limited to one location within the workspace, a remapping induced a change in pointing. This remapping extended over the entire workspace and was best captured by a spherical coordinate system centered near the eyes. McIntyre *et al.* and others [24,25•] have recently used the errors observed during a pointing task to identify the internal coordinate systems and transformations that occur during reaching. They find that the coordinate systems used depend on the amount of visual feedback available and the memory delays introduced between target presentation and motor initiation.

Several psychophysical studies suggest that reaching movements may be internally represented as a motor vector error, pointing from the initial hand location towards the target [26]. Recently, neural recordings from the parietal reach region (PRR) and area 5 have revealed the coding of target position in eye-centered coordinates when reaching for an auditory stimulus, and that these can be modulated by initial hand position [27•].

Sensorimotor transformations can be organized in a general context of basis functions [28], which are flexible intermediate representations for generating arbitrary nonlinear coordinate transformations as well as for learning and working memory. The variety of reference frames affected by neglect after parietal lesions can be explained if the basis functions in the two hemispheres have contralateral gradients [29•], so that lesions lead to imbalances in the salience of stimuli.

Hand trajectory planning

The invariances and kinematic features of hand trajectories provide insights into general strategies for motor planning [30]. For example, it has been proposed that multi-joint arm movements are planned in either hand coordinates [30,31], joint coordinates [32] or in both coordinate systems, as supported recently by evidence from the analysis of cortical and afferent signals [33,34••].

What rules govern the selection of particular limb motions among the infinite number of possible ones [30]? Figure 1 shows some results from several recent studies concerned with this general issue. Optimization models assume that the brain selects trajectories that maximize the smoothness by optimizing a movement cost function [30,35–39] (e.g. Figure 1a,b). The trajectory shape of horizontal planar drawing and curved movements follows the so-called ‘two-thirds power law’: the angular velocity varies with the two-thirds power of the curvature [40] (Figure 1a–c). By minimizing the mean square of high-order derivatives of the hand’s position [41], it has been possible to analytically account for the power laws observed for different motor tasks involving reaching and periodic drawing motions [42•], without including velocity information at ‘via points’ along the curves, as in previous models [43]. A general mathematical framework for the coupling between velocity and curvature based on differential geometry has been proposed [44,45].

The minimum variance model of motor planning assumes that humans plan movements that minimize the transmission of error, caused by biological noise, as reflected in the variance of the end-point position [46]. This hypothesis accounts for the kinematic features of saccadic eye movements, reaching arm movements and the two-thirds power law. Within the framework of linear control theory with intrinsic activity-dependent noise, as found in neural recordings, a cost that combines both minimum variance and effort predicts trajectories for a wide range of pointing tasks and matches those observed in humans [47]. Redundant degrees of freedom, discussed below, are used in the model to reduce the motor error, and might be divided into controlled and uncontrolled variables [48].

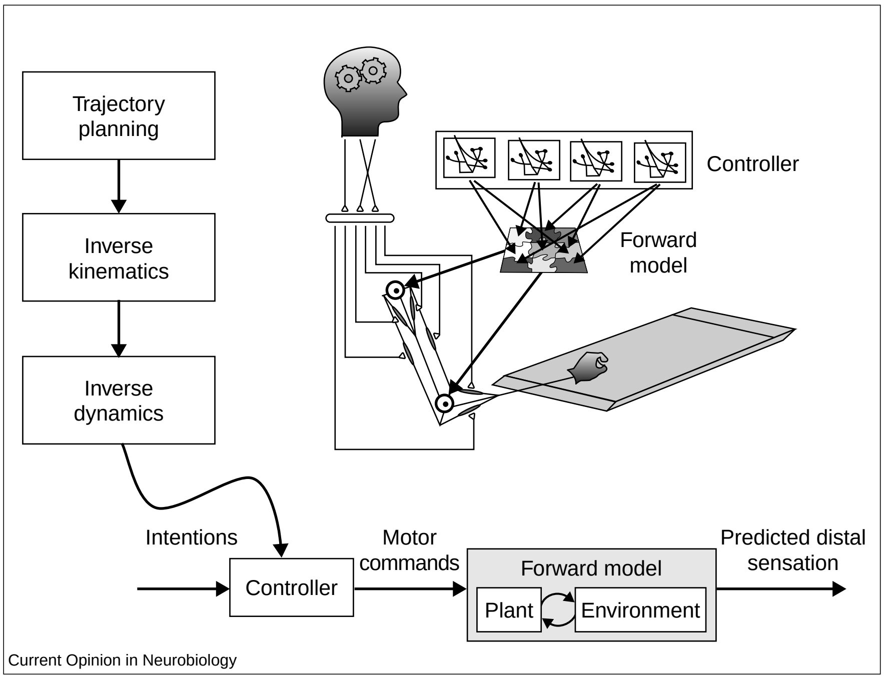
Although segmentation of apparently continuous movements has been reported, the existence of primitive sub-movements has not been clearly demonstrated and movement segmentation as inferred from the two-thirds power law (Figure 1) might be an epiphenomenon [42•,49,50]. However, other approaches have found sub-movements in a knob-turning task [38] and in arm movements in patients recovering from stroke [39].

Kinematic constraints and computations

Figure 2 shows a general scheme of the computational problems underlying the generation of multi-joint arm movements. Any planned trajectory must be transformed into joint coordinates before it can be executed. The solution to this inverse kinematics problem is particularly complex when there are excess degrees of freedom. Even the order of joint rotation will affect the final position of a limb. A solution to this problem is suggested by Donder’s law of the eye, which states that for any gaze direction, the eye always assumes the same unique orientation in three dimensions and that the amount of ocular torsion is a unique function of the direction of gaze. A similar behavior is also obeyed by the orientation of both the head and shoulder during three-dimensional movements.

Several recent studies have examined the validity of Donder’s law for reaching movements. Although a fully extended arm obeys this law [51], there are some minor violations for arm-pointing movements, involving both shoulder and forearm rotations [52]. For unexpected target

Figure 2



Schematic diagram that illustrates three hierarchical levels for planning multi-joint arm movements. First, a trajectory is planned in hand coordinates; second, the hand trajectory is transformed into joint trajectories by solving the inverse kinematics problem; finally, the joint torques are found by computing the inverse dynamics [6]. An alternative to inverse dynamics is based on equilibrium point control. After the trajectory is planned, the controller, shown on the bottom, maps intentions to motor commands. A forward model (possibly of both the controlled limb and of the environment) maps the motor commands to predicted sensations. Both the controller and the forward model might be composed of neural systems with modular architectures. The schematic hand controller in the upper right panel illustrates the forward model as a map that predicts joint proprioception and movement from the controller output.

shifts, the final arm posture is neither more variable nor different from the one in the absence of such a shift [53], and can be accounted for by a model involving the minimization of kinetic energy [52]. Different forms of Donder's law apply to the upper and lower arm during pointing [54•]; a control model for arm pointing similar to that suggested for head–eye coordination has been developed [55•].

Inverse dynamics and equilibrium point models

The transformation of a planned limb movement into an appropriate set of motor commands requires the calculation of joint torques, which is called the inverse dynamics problem (Figure 2). This is a difficult computational problem and two competing solutions have been proposed. According to one hypothesis, sometimes referred to as the direct inverse modeling approach, the brain creates and adaptively updates internal models of the limb dynamics [1•,4,6]. The brain does not explicitly compute the necessary joint torques. Instead, it controls both posture and movement by relying on the spring-like properties of muscles and reflex loops. According to this equilibrium point (EP) hypothesis, posture is controlled by defining a stable equilibrium position for the limb, whereas movement is achieved by gradually shifting the equilibrium position along a desired trajectory [7,8].

Two arguments against the EP control scheme are that unrealistically high degrees of stiffness are needed and that the internally represented EPs must be highly complex [56]. However, the apparent complexities arise from the use of simplified models of force generation [57]. When more accurate models of the neuromuscular system are used to characterize the limb impedance [58,59] and time delays are included in force generation, the EP trajectories needed to realize reaching movements become less complex [60]. Hodgson and Hogan [61•] have proposed a model-independent means for testing the validity of the EP hypothesis. In fast, unobstructed movements, the EP shifts end approximately at peak velocity [62•], suggesting that fast movements do not need continuous control. If the EP were being computed in the cortex then one might expect that cortical stimulation would produce changes in posture. In previous experiments, microstimulation of motor cortex produced weak muscle activation, but when a sufficiently large number of neurons are microstimulated, the body assumes a fixed posture independent of the starting position [63•].

In a model of EP learning, externally applied velocity-dependent loads and intersegmental interactions were compensated for by adapting the EP shifts [64]. Similarly, compensation for external loads was calculated on the basis of adaptive modifications of both the limb stiffness and time-dependent EP trajectory [65].

Motor learning and adaptation

During learning, the brain acquires an inverse dynamics model of the controlled limb. However, the learning of an inverse model is problematic because the motor command error, which could provide a training signal, is not directly available to the brain [3] (Figure 2). Hence, distal movement errors derived from sensory information must be first converted into motor errors before they can be used to train an inverse model. A summary of learning schemes founded on the use of internal models are available in [1•]. Mirror neurons in the premotor cortex, which are activated both during a goal-directed motor act and by observing the same motor act, could provide a means for learning motor skills by mimicry [66].

Many brain systems are involved in motor learning. A recent model of motor learning [67] assumes that the cerebellum is specialized for supervised learning, the basal ganglia subserves reinforcement learning, and the cerebral cortex implements unsupervised learning. In the model, sequential procedures are acquired independently by two cortical systems, one using spatial coordinates and another using motor coordinates in the early and late stages of learning, respectively [68]. Loop circuits between the basal ganglia and the cerebellum support both cortical systems. Another cerebellar model suggests how fast arm movements can be executed in spite of the long conduction delays in the nervous system and temporal mismatch [69].

Learning and control are simplified when there is a relatively small number of motor primitives, which are simpler building blocks or units of action that can be assembled into a richer repertoire of more complex movements or behaviors [70••]. Such modular architectures (Figure 2) may exist within the spinal cord as well as in higher brain structures [71]. However, even if all modules are stable, not every combination of modules is guaranteed to be stable [72]. A load adaptation scheme designed on the basis of this approach, involving a flexible combination of simple computational elements [73], produced behavior that was qualitatively similar to human performance [74]. A recent model suggests that humans learn the dynamics of reaching movements through a flexible combination of primitives that have Gaussian-like tuning functions of hand velocity, as observed in the brain [75].

Finally, subjects have been studied performing reaching movements under novel environments while the kinematic and dynamic properties were altered [76,77]. The subjects were able to learn multiple internal kinematic and dynamic models that compensated for each transformation and, remarkably, were able to combine and decompose these models.

Conclusions and future directions

Considerable progress has been made in the past few years in modeling several levels of movement generation, including hand and joint trajectory planning, motor learning and execution. In this article, we have reviewed several of these models, as well as recent attempts to uncover the neural representations subserving sensorimotor transformations and response selection during reaching and drawing movements. In particular, we examined new approaches that used modular architectures and constructed complex, as well as sequential behaviors from action units. Some important topics that are not reviewed here for lack of space are learning from imitation [66,78•,79] and internal estimation, prediction and self-awareness [80]. Biologically inspired robotic systems can test our understanding of motor control. These approaches include the development of systems that mimic insect locomotion [81], and humanoid robots [82]. As these robots become more sophisticated, cognitive capabilities can be integrated into the sensorimotor control systems.

Update

Two studies published while this review has been in press have recorded activity from neurons in monkey primary motor cortex and ventral premotor area. Kakei *et al.* [83•] show that neurons in the ventral premotor area are tuned to the direction of movement in space, unlike neurons in the primary motor cortex that are tuned to intrinsic coordinate frames. These have been found to show biases between the direction of the population vector and the direction of hand movement [84•].

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