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

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
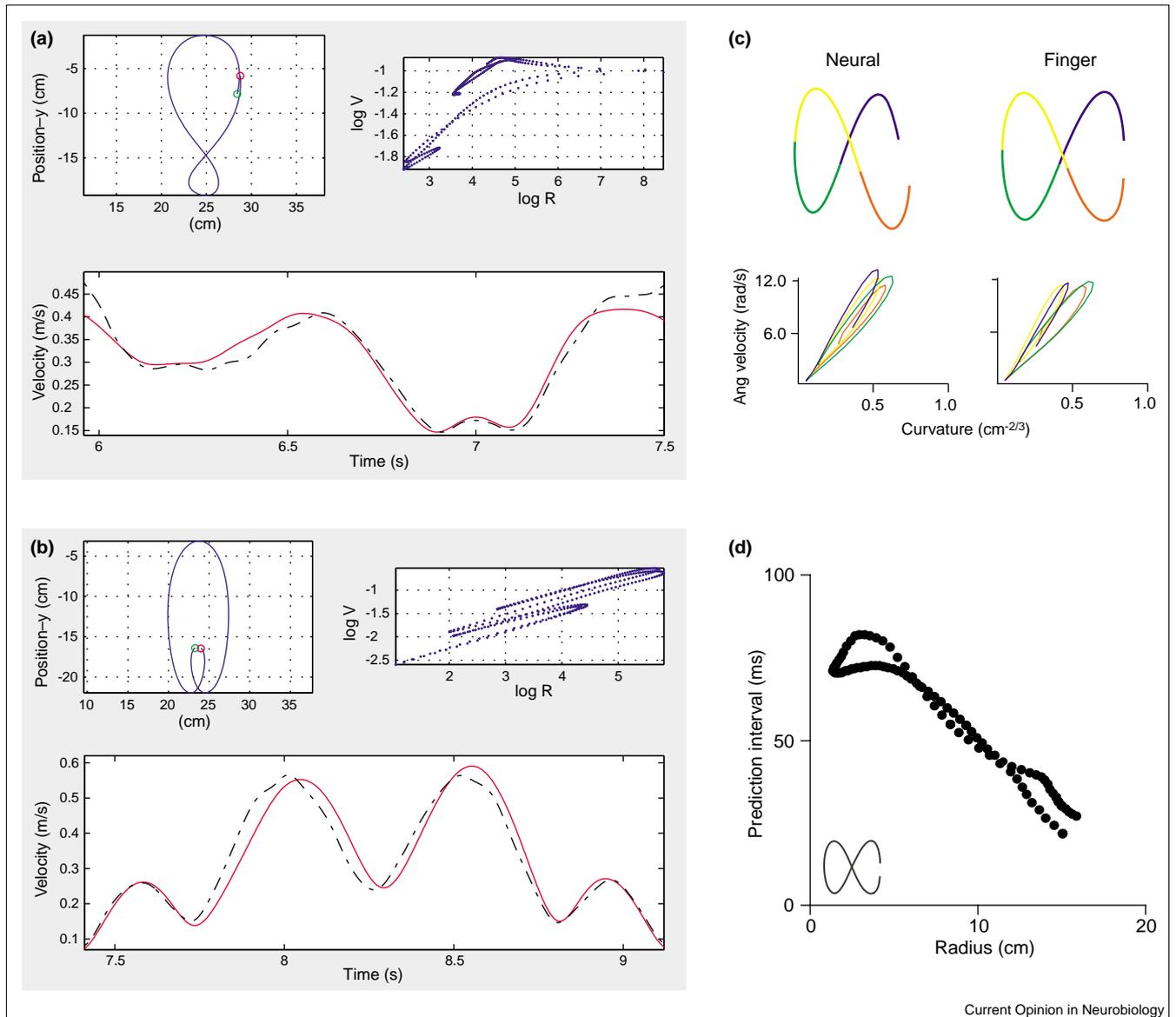
Hand trajectories and predictions of neural models during figure drawing tasks. **(a,b)** The hand paths and velocity profiles predicted by the minimum jerk model [30]. This model suggests that among all possible hand trajectories, the selected movements maximize motion smoothness, defined here as the 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 non-linear 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
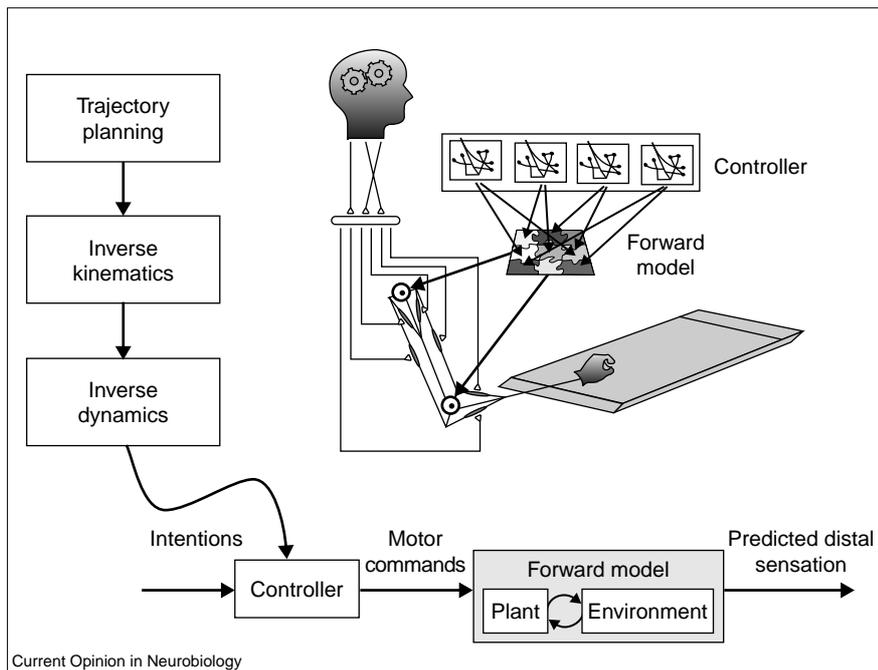
Schematic diagram that illustrates three hierarchical levels for planning multi-joint arm movements. First, a trajectory is planned in hand coordinates; second, the hand trajectory is transformed into joint trajectories by solving the inverse kinematics problem; finally, the joint torques are found by 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 mini-mization 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 calcula-tion 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 move-ment 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 pro-posed 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, microstimu-lation 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 move-ment 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 sensori-motor 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•].

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

1. Sabes PN: **The planning and control of reaching movements.** *Curr*
• *Opin Neurobiol* 2000, **10**:740-746.
The author discusses internal models and their importance for the study of visually guided reaching, including behavioral studies of on-line trajectory correction and of how the brain integrates feedforward control signals, sensory feedback, and predictions based on forward models.

2. Marder E, Abbott LF: **Theory in motion.** *Curr Opin Neurobiol* 1995, **5**:832-840.

3. Jordan MI, Rumelhart DE: **Forward models – supervised learning with a distal teacher.** *Cogn Sci* 1992, **6**:307-354.

4. Kawato M: **Internal models for motor control and trajectory planning.** *Curr Opin Neurobiol* 1999, **9**:718-727.

5. Georgopoulos AP, Schwartz AB, Kettner RE: **Neuronal population coding of movement direction.** *Science* 1986, **233**:1416-1419.

6. Hollerbach JM: **Computers, brains and the control of movement.** *Trends Neurosci* 1982, **5**:189-192.

7. Feldman AG: **Functional turning of nervous system with control of movement or maintenance of a steady posture. Controllable parameters of the muscle.** *Biophysics* 1966, **11**:565-578.

8. Bizzi E, Hogan N, Mussa-Ivaldi FA, Giszter S: **Does the nervous system use equilibrium-point control to guide single and multiple joint movements.** *Behav Brain Sci* 1992, **15**:603-613.

9. Pouget A, Zemel RS, Dayan P: **Information processing with population codes.** *Nat Rev Neurosci* 2000, **1**:125-132.

10. Amirikian B, Georgopoulos AP: **Directional tuning profiles of motor cortical cells.** *Neurosci* 2000, **36**:73-79.

11. Scott SH: **Population vectors and motor cortex: neural coding or epiphenomenon?** *Nat Neurosci* 2000, **3**:307-308.

12. Todorov E: **Cosine tuning minimizes motor errors.** *Neural Computation* 2002, in press.

13. Zhang K, Sejnowski TJ: **A theory of geometric constraints on neural activity for natural three-dimensional movements.** *J Neurosci* 1999, **19**:3122-3145.

14. Todorov E: **Direct cortical control of muscle activation in voluntary**
•   **arm movements: a model.** *Nat Neurosci* 2000, **3**:391-398.
This model assumes that the motor cortical neurons code for the overall force level generated by a group of muscles. It is argued that the seeming contradictions between such lower level control and the view that motor cortical populations code for hand kinematics can be settled by assuming that the motor cortex compensates for the dependence of muscle force on its length and velocity of shortening.

15. Schwartz AB, Moran DW: **Motor cortical activity during drawing movements: population representation during leminiscate tracing.** *J Neurophys* 1999, **82**:2705-2718.

16. Moran DW, Schwartz AB: **One motor cortex, two different views.**
•   *Nat Neurosci* 2000, **3**:963.
The authors argue against the claim that the model described in [14•] provides an adequate explanation for the variations of the time lag with path curvature. They claim that the model developed in [14•] is not consistent with known facts about motor physiology.

17. Georgopoulos AP, Ashe J: **One motor cortex, two different views.**
•   *Nat Neurosci* 2000, **3**:963.
The authors refute the claims in [11] and [14•] that the importance of target direction as an explanatory factor for cortical activity is an 'artifact'. The authors re-analyzed their neural discharge data and showed that the relationship between cell discharge and movement direction holds independently of the specific transformation or smoothness procedures used in the analysis.

18. Scott SH: **Reply to 'one motor cortex, two different views'.** *Nat*
•   *Neurosci* 2000, **3**:964-965.
The author argues that the controversy regarding the function of the motor cortex during arm movements is partially generated by differences in experimental protocols.

19. Snyder LH: **Coordinate transformations for eye and arm movements in the brain.** *Curr Opin Neurobiol* 2000, **10**:747-754.

20. Snyder LH, Batista AP, Andersen RA: **Intention-related activity in the posterior parietal cortex: a review.** *Vision Res* 2000, **40**:1433-1441.

21. Batista AP, Bueno CA, Snyder LH, Andersen RA: **Reach plans in eye centered coordinates.** *Science* 1999, **285**:257-260.

22. Batista AP, Andersen RA: **The parietal reach region codes the next**
••   **planned movement in a sequential reach task.** *J Neurophysiol* 2001, 85:539-544.
Neural recordings from the posterior PRR reveal neurons that are active during the delay period of a memory-guided reaching task, but are not active during a memory-guided saccade task. In another task, the monkey was required to reach for two targets in sequence. Before each movement was executed, PRR neurons predominantly represented the reach about to be performed and only rarely represented the remembered target for the second reach. Thus, the PRR primarily specifies the target for the impending reach and not the memory of subsequent targets.

23. Vetter P, Goodbody SJ, Wolpert DM: **Evidence for an eye-centered spherical representation of the visuomotor map.** *J Neurophysiol* 1999, **81**:935-939.

24. Carrozzo M, McIntyre J, Zago M, Lacquaniti FTI: **Viewer-centered and body-centered frames of reference in direct visuomotor transformations.** *Exp Brain Res* 1999, **129**:201-210.

25. McIntyre J, Stratta F, Droulez J, Lacquaniti F: **Analysis of pointing**
•   **errors reveals properties of data representations and coordinate transformations within the central nervous system.** *Neural Comput* 2000, **12**:2823-2855.
The authors of this paper use different types of errors to identify the coordinate frames subserving sensorimotor transformations. They review a series of experiments, in which subjects pointed to remembered three-dimensional visual targets under two lighting conditions and after two different memory delays. Simulations reproduced the patterns of errors observed in these tasks.

26. Gordon J, Ghilardi MF, Ghez C: **Accuracy of planar reaching movements. 1. Independence of direction and extent variability.** *Exp Brain Res* 1994, **99**:97-111.

27. Cohen YE, Andersen RA: **Reaches to sounds encoded in an**
•   **eye-centered reference frame.** *Neuron* 2000, **27**:647-652.
Recordings from neurons in the PRR were more strongly affected by eye position than initial hand position during a reaching task, consistent with coding in eye coordinates. A significant population of PRR neurons encoded reaches to auditory stimuli in an eye-centered reference frame. These results extend the hypothesis that, regardless of the modality of the sensory input or the eventual action, PRR neurons represent movement plans in a common, eye-centered representation. Neurons in the lateral intraparietal area are activated during eye movements and are also in an eye-centered representation.

28. Pouget A, Snyder LH: **Computational approaches to sensorimotor transformations.** *Nat Neurosci* 2000, **3**:1192-1198.

29. Pouget A, Sejnowski TJ: **Simulating a lesion in a basis function**
•   **model of spatial representations: comparison with hemineglect.** *Psychol Rev* 2001, **108**:653-673.
Contralateral neglect is shown to arise in a basis function model of the parietal cortex because lesions of the parietal cortex produce imbalances in the salience of stimuli that are modulated by the orientation of the body in space. Computer simulations reproduce the behavior of patients with hemineglect, including the following: neglect in line cancellation and line bisection experiments; neglect in multiple frames of reference simultaneously; relative neglect, a form of what is sometimes called object-centered neglect; and neglect without optic ataxia.

30. Flash T, Hogan N: **The coordination of arm movements: an experimentally confirmed mathematical model.** *J Neurosci* 1985, **5**:103-168.

31. Morasso P: **Spatial control of arm movements.** *Exp Brain Res* 1981, **4**:223-227.

32. Lacquaniti F: **Central representations of human limb movement as revealed by studies of drawing and handwriting.** *Trends Neurosci* 1989, **12**:287-291.

33. Kakei S, Hoffman DS, Strick PL: **Muscle and movement representations in the primary motor cortex.** *Science* 1999, **285**:2136-2139.

34. Bosco G, Poppele RE: **Proprioception from a spinocerebellar**
••   **perspective.** *Physiol Rev* 2001, **81**:539-568.
This review explores how proprioceptive sensory information is organized in the spinal cord. An analysis of the dorsal spinocerebellar tract system suggests that there is a global representation of hindlimb parameters rather than a muscle-by-muscle or a joint-by-joint representation.

35. Uno Y, Kawato M, Suzuki R: **Formation and control of optimal trajectories in human multijoint arm movements: minimum torque-change model.** *Biol Cybern* 1989, **61**:89-101.

36. Nakano E, Imamizu H, Osu R, Uno Y, Gomi H, Yoshioka T, Kawato M: **Quantitative examinations of internal representations for arm trajectory planning; minimum command torque change model.** *J Neurophysiol* 1999, **81**:2140-2155.

37. Smeets JBJ, Brenner E: **A new view on grasping.** *Motor Control* 1999, **3**:237-271.

38. Novak KE, Miller LE, Houk JC: **Kinematic properties of rapid hand movements in a knob turning task.** *Exp Brain Res* 2000, **132**:419-433.

39. Krebs HI, Aisen ML, Volpe BT, Hogan N: **Quantization of continuous arm movements in humans with brain injury.** *Proc Natl Acad Sci USA* 1999, **96**:4645-4649.

40. Lacquaniti F, Terzuolo C, Viviani P: **The law relating the kinematics and figural aspects of drawing movements.** *Acta Psychologica* 1983, **54**:115-130.

41. Harris CM: **On the optimal control of behaviour: a stochastic perspective.** *J Neurosci Methods* 1998, **83**:73-88.

42. Richardson MJE, Flash T: **The relation between kinematics and**
•   **geometry as predicted by the planning of globally smooth human hand trajectories.** *Soc Neurosci Abs* 2000, **26**:1719.
Smoothness maximization models are based on minimizing the integrated n^{th} order time derivative of hand position. These models predict the behavior for reaching and drawing tasks. Assuming a power–law relation between velocity and curvature, power laws for any order of smoothness and for different figural forms, were derived and shown to closely match experimental observations. Global smoothness criteria were also shown to give apparent segmentation in velocity versus curvature plots, challenging the notion that such features imply segmented planning by the motor system.

43. Viviani P, Flash T: **Minimum-jerk, two-thirds power law, and isochrony: converging approaches to movement planning.** *J Exp Psychol* 1995, **21**:32-53.

44. Handzel AA, Flash T: **Geometric methods in the study of human motor control.** *Cognitive Studies* 1999, **6**:309-321.

45. Pollick FE, Sapiro G: **Constant affine velocity predicts the 1/3 power law of planar motion perception and generation.** *Vision Res* 1997, **37**:347-353.

46. Harris CM, Wolpert DM: **Signal-dependent noise determines motor planning.** *Nature* 1998, **394**:780-784.

47. Todorov E: **Studies of goal-directed movements [PhD Thesis].** Cambridge, MA: Massachusetts Institute of Technology; 1998.

48. Scholz J, Schoner G: **The uncontrolled manifold concept: Identifying control variables for a functional task.** *Exp Brain Res* 1999, **126**:289-306.

49. Schaal S, Sternad D: **Origins and violations of the 2/3 power law in rhythmic three-dimensional arm movements.** *Exp Brain Res* 2001, **136**:60-72.

50. Sternad D, Schaal S: **Segmentation of endpoint trajectories does not imply segmented control.** *Exp Brain Res* 1999, **124**:118-136

51. Gielen C, Vrijenhoek EJ, Flash T, Neggers S: **Arm position constraints during pointing and reaching in 3-D space.** *J Neurophysiol* 1997, **78**:660-673.

52. Soechting J, Buneo C, Hermann U, Flanders M: **Moving effortlessly in three dimensions: does Donders' law apply to arm movement?** *J Neurosci* 1995,**15**:6271-6280.

53. Grea H, Desmurget M: Prablanc C: **Postural invariance in three-dimensional reaching and grasping movements.** *Exp Brain Res* 2000, **134**:155-162.

54. Medendorp WP, Crawford JD, Henriques DYP, Van Gisbergen JAM,
• Gielen CCAM: **Kinematic strategies for upper arm-forearm coordination in three dimensions.** *J Neurophysiol* 2000, **84**:2302-2316.
The authors show that the different forms of Donder's law obeyed by the upper arm depend on the coordination between the upper arm and forearm. Just as the head serves as a platform for the eyes [55•], the upper arm is a platform for the forearm. Adopting the approach suggested in [55•], the authors suggest that, in arm movements, the motor system may adopt different coordination strategies by applying kinematic non-holonomic rules that depend on velocity rather than on position.

55. Ceylan M, Henriques DYP, Tweed DB, Crawford JD: **Task dependent**
• **constraints in motor control: pinhole goggles make the head move like an eye.** *J Neurosci* 2000, **20**:2719-2730.
Human subjects performed head-free gaze shifts between visual targets while wearing pinhole goggles. On the basis of the type of Donder's strategies used in the different tasks, the authors conclude that the observed behaviors cannot be modeled using 'Donder's operators' but are readily simulated by modulating head velocity commands, as a function of position and task. It is concluded that the gaze control system uses such rules for motor optimization.

56. Gomi H, Kawato M: **Equilibrium-point control hypothesis examined by measured arm stiffness during multijoint movement.** *Science* 1996, **272**:117-120.

57. Gribble PL, Ostry DJ, Sanguineti V, Laboissiere R: **Are complex control signals required for human arm movement?** *J Neurophys* 1998, **79**:1409-1424.

58. Mah CD: **Spatial and temporal modulation of joint stiffness during multijoint movement.** *Exp Brain Res* 2001, **136**:492-506.

59. Stroeve S: **Impedance characteristics of a neuromusculoskeletal model of the human arm. II. Movement control.** *Biol Cybern* 1999, **81**:475-494.

60. Frolov AA, Dufosse M, Rizek S, Kaladjian A: **On the possibility of linear modelling the human arm neuromuscular apparatus.** *Biol Cybern* 2000, **82**:499-515.

61. Hodgson AJ, Hogan N: **A model-independent definition of attractor**
• **behavior applicable to interactive tasks.** *IEEE Trans Syst Man Cybern* 2000, **30**:105-118.
The authors define an attractor trajectory for repeated movements. They demonstrate how most previous attempts to test the EP hypothesis were based on inadequate models of the neuromuscular system and propose a model-independent way to test its validity.

62. Ghafouri M, Feldman AG: **The timing of control signals underlying**
• **fast point-to-point arm movements.** *Exp Brain Res* 2001, **137**:411-423.
The static component of a joint torque–position relationship is called 'invariant characteristic'. According to one version of the EP hypothesis, movements are produced by shifting the invariant characteristics of the muscles in joint space. Earlier studies have suggested that gradual, rather than step-like, EP shifts underlie fast point-to-point movements. In this study, the durations of EP shifts were evaluated by applying force perturbations to the hand during human reaching movements. The analysis of movement corrections suggests that in unobstructed movements the EP shifts end approximately at peak velocity.

63. Taylor CSR, Graziano MSA, Moore T: **Complex movements evoked**
• **by electrical stimulation of motor cortex in monkeys.** *Soc Neurosci Abs* 2001, **27**.
A train of electrical stimuli in motor cortex in monkeys evoked multi-joint movements that converged on a fixed posture; the postures are arranged to form a topographic map of hand position around the body. This map encompasses both primary motor and premotor cortex, suggesting that these areas are different parts of a single larger area.

64. Gribble PL, Ostry DJ: **Compensation for loads during arm movements using equilibrium-point control.** *Exp Brain Res* 2000, **135**:474-482.

65. Flash T, Gurevich I: **Arm trajectory generation and stiffness control during motor adaptation to external loads.** In *Self-Organization, Computational Maps and Motor Control.* Edited by Morasso PG, Sanguinetti V. Amsterdam: Elsevier Science Ltd.; 1997:423-482.

66. Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G: **Cortical mechanisms of human imitation.** *Science* 1999, **286**:2526-2528.

67. Doya K: **What are the computations of the cerebellum, the basal ganglia and the cerebral cortex?** *Neural Networks* 1999, **12**:961-974.

68. Hikosaka O, Rand MK, Sakai K, Lu XF, Nakamura K, Miyachi S, Doya K: **Parallel neural networks for learning sequential procedures.** *Trends Neurosci* 1999, **22**:464-471.

69. Spoelstra J, Schweighofer N, Arbib MA: **Cerebellar learning of accurate predictive control for fast-reaching movements.** *Biol Cybern* 2000, **82**:321-333.

70. Mussa-Ivaldi FA, Bizzi E: **Motor learning through the combination of**
•• **primitives.** *Phil Trans Roy Soc London* 2000, **355**:1755-1769.
The authors discuss how internal representations of movement dynamics are likely to be built, by combining the modular primitives observed in the spinal cord as well as other building blocks found in higher brain structures. Such force field primitives can be used by the nervous system for both generation and learning of a rich repertoire of motor behaviors.

71. Bizzi E, Tresch MC, Saltiel P, d'Avella A: **New perspectives on spinal**
• **motor systems.** *Nat Rev Neurosci* 2000, **1**:101-108.
In traditional schemes of motor control, the spinal cord plays a predominantly passive role by relaying the commands dictated to it by supraspinal systems. This review challenges this idea and presents evidence that the spinal motor system is an active participant in the production of movement.

72. Slotine JJE, Lohmiller W: **Modularity, evolution and the binding problem: a view from stability theory.** *Neural Networks* 2001, **14**:137-145.

73. Sanner RM, Kosha N: **A mathematical model of the adaptive control of human arm motions.** *Biol Cybern* 1999, **80**:369-382.

74. Shadmehr R, Mussa-Ivaldi FA: **Adaptive representation of dynamics during learning of a motor task.** *J Neurosci* 1994, **14**:3208-3224.

75. Thoroughman KA, Shadmehr R: **Learning of action through adaptive combination of motor primitives.** *Nature* 2000, **407**:742-747.

76. Krakauer JW, Ghilardi MF, Ghez C: **Independent learning of internal models for kinematic and dynamic control of reaching.** *Nat Neurosci* 1999, **2**:1026-1031.

77. Flanagan JR: **Composition and decomposition of internal models in motor learning under altered kinematic and dynamic environments.** *J Neurosci* 1999, **19**:B1-B5.

78. Mataric MJ: **Getting humanoids to move and imitate.** *IEEE Intell Syst*
• *Appl* 2000, **15**:18-24.
The author discusses observational learning and imitation and reviews studies in which humanoid robots learn by imitation using biological-like modular architectures and motion primitives.

79. Arbib MA, Billard A, Iacoboni M, Oztop E: **Synthetic brain imaging**; **grasping, mirror neurons and imitation.** *Neural Networks* 2000, **13**:975-997.

80. Wolpert DM, Ghahramani Z: **Computational principles of movement**
•• **neuroscience.** *Nature Neurosci* Suppl 2000, **3**:1212-1217.
The authors review several unifying principles of motor control and show how they apply to motor planning, control, estimation, prediction and learning.

81. Beer RD, Chiel HJ, Quinn RD, Ritzmann RE: **Biorobotic approaches to the study of motor systems.** *Curr Opin Neurobiol* 1998, **8**:777-782.

82. Schaal S: **Is imitation learning the route to humanoid robots?** *Trends Cogn Sci* 1999, **3**:233-242.

83. Kakei S, Hoffman DS, Strick PL: **Direction of action is**
• **represented in the ventral premotor cortex.** *Nat Neurosci* 2001, **4**:1020-1025.
The authors show that neurons in the ventral premotor area, which is a major source of input to the primary motor cortex were tuned to the direction of movement in space independent of forearm posture, unlike neurons in primary motor cortex that are tuned to intrinsic coordinate frames.

84. Scott SH, Gribble PL, Graham KM, Cabel DW: **Dissociation**
• **between hand motion and population vectors from neural activity in motor cortex.** *Nature* 2001, **413**:161-165.
The authors recorded from monkey primary motor cortex and found systematic biases between the population vector and the direction of hand movement. These errors were attributed to a non-uniform distribution of preferred directions of neurons. Other methods for decoding population vectors do not suffer from this bias.