

David J. Ostry · Anatol G. Feldman

A critical evaluation of the force control hypothesis in motor control

Received: 11 June 2003 / Accepted: 7 July 2003 / Published online: 13 September 2003
© Springer-Verlag 2003

Abstract The ability to formulate explicit mathematical models of motor systems has played a central role in recent progress in motor control research. As a result of these modeling efforts and in particular the incorporation of concepts drawn from control systems theory, ideas about motor control have changed substantially. There is growing emphasis on motor learning and particularly on predictive or anticipatory aspects of control that are related to the neural representation of dynamics. Two ideas have become increasingly prominent in mathematical modeling of motor function—forward internal models and inverse dynamics. The notion of forward internal models which has drawn from work in adaptive control arises from the recognition that the nervous system takes account of dynamics in motion planning. Inverse dynamics, a complementary way of adjusting control signals to deal with dynamics, has proved a simple means to establish the joint torques necessary to produce desired movements. In this paper, we review the force control formulation in which inverse dynamics and forward internal models play a central role. We present evidence in its favor and describe its limitations. We note that inverse dynamics and forward models are potential solutions to general problems in motor control—how the nervous system establishes a mapping between desired movements and associated control signals, and how control signals are adjusted in the context of motor learning, dynamics and loads. However, we find little empirical evidence that specifically

supports the inverse dynamics or forward internal model proposals per se. We further conclude that the central idea of the force control hypothesis—that control levels operate through the central specification of forces—is flawed. This is specifically evident in the context of attempts to incorporate physiologically realistic muscle and reflex mechanisms into the force control model. In particular, the formulation offers no means to shift between postures without triggering resistance due to postural stabilizing mechanisms.

Keywords Internal models · Inverse dynamics · Posture-movement problem · Stability · Predictive mechanisms

Introduction

The hypothesis that inverse dynamics computations and the specification of forces are inherent in neuromuscular control was formulated about 20 years ago (Hollerbach 1982). Predictive elements of force control have been documented more recently and have become central to the force control formulation. In essence, however, the formulation consists of three separate proposals: the notion of the central specification of forces; the derivation of their values using an internal model of inverse dynamics; and predictive control mechanisms based on forward and inverse internal models.

The force control hypothesis, the term which we will give to the notion as a whole, may have escaped evaluation because its sufficiency was demonstrated in work on robotics. This may have suggested that these principles were broadly applicable and included biological systems. Notions of force control are readily understandable in a mechanical framework. Thus physiological processes, in particular the generation of electromyographic (EMG) activity, may be considered in relation to mechanical variables such as position, velocity, acceleration, torques, stiffness, and viscosity. The use of mechanical terms is integral to the description of movement production. The question remains whether the language of

D. J. Ostry (✉)
Department of Psychology, McGill University,
1205 Dr. Penfield Avenue,
Montreal, QC, H3A 1B1, Canada
e-mail: ostry@motion.psych.mcgill.ca
Tel.: +1-514-3986111
Fax: +1-514-3984896

D. J. Ostry
Haskins Laboratories,
New Haven, Connecticut, USA

A. G. Feldman
University of Montreal,
Montreal, Canada

mechanics is sufficient for the understanding of control in neuromuscular systems (Von Holst and Mittelstaedt 1950/1973; Bernstein 1967).

In the present paper we have undertaken a critical review of the central notions in the force control formulation. The focus is on the strengths and weaknesses of this formulation that stem from its own theoretical framework. We are concerned specifically with the capacity of the force control model to explain existing physiological phenomena. We will first review the basic concepts of the force control formulation and present experimental data consistent with this view. We will then proceed with an evaluation of the models abilities and with an examination of evidence offered in its support.

Force control hypothesis

It is widely accepted that, in movement production, the nervous system relies substantially on motor memory, takes advantage of previous experiences, learning, implicit or explicit knowledge of physical properties of the body and the environment (Bernstein 1967; Lashley 1951). In the force control formulation, this capacity has become associated with internal models—hypothetical neural mechanisms that can mimic the input/output characteristics, or their inverses, of the motor apparatus (Kawato 1999).

In the force control formulation, desired movement trajectories are planned first in terms of spatial coordinates and their derivatives and then transformed into required forces and torques. In order to compute torques, the system uses an internal representation of dynamical equations of motion of the body interacting with the environment. The hypothetical computational process, which may be realized by a neuronal network, is called inverse-dynamics because it generates values of torques based on kinematics and thus inverts the input/output relationships inherent in actual (direct) dynamical laws—in which torques cause changes in kinematics rather than the other way around (Hogan 1990).

Feed-forward internal models are used to generate values of variables in a predictive manner. For example, they can be used to predict in advance the values of kinematic variables based upon estimates of the forces required for movement production. Such models can be used to compare the predicted and desired trajectories to generate appropriate movement corrections. Movement error information can also be used to update inverse and forward internal models (Jordan and Rumelhart 1992) and hence enable motor learning. It has been suggested that feedforward control yields stability by minimizing the effect of delays due to proprioceptive feedback (Kawato 1999). Forward internal models have also been justified by assuming that, in order to achieve desired movements, control signals must be adjusted based on anticipated sensory consequences using internal loops rather than comparatively long-loop sensory feedback. Yet another suggestion is that feedforward control helps to reduce the

effects of inevitable imprecision in inverse dynamics representations and associated computations of torques.

Variants of the internal model concept have differed in emphasis. Some have focused on motor planning and control based on feedforward or predictive mechanisms (Wolpert et al. 1995), while others have concentrated on inverse-dynamics (Katayama and Kawato 1993; Kawato and Gomi 1992; Shidara et al. 1993). A number of recent articles have presented evidence in support of the idea that control is based on paired inverse and forward internal models (Bhushan and Shadmehr 1999; Wolpert and Kawato 1998; Kawato 1999; Wolpert and Ghahramani 2000). It has also been suggested that a computational, model-based nature is characteristic of practically all aspects of motor control (Jordan and Rumelhart 1992; Wolpert and Ghahramani 2000). It has been proposed that there exist multiple internal models that mimic not only motor but also sensory and cognitive processes. In this framework, it has been suggested that multiple internal models can provide for the capacity to rapidly switch between environments with different dynamical properties.

Central specification of forces

The main idea of the force control model is that the control level of the nervous system directly deals with or calculates forces required for the production of voluntary movements. This notion is supported by an extensive literature demonstrating systematic relationships between force, EMG activity and movement parameters. The basic results are thus consistent with the idea of central specification of force. As an example, Gottlieb et al. (1989, 1990) and Corcos et al. (1989) have shown that in single joint elbow movements, joint torque, kinematic variables and EMGs were correlated with the task variables, distance and inertial load. Gottlieb and colleagues (1996), Koshland et al. (2000) and Gribble and Ostry (1999) have also shown that there is a systematic relationship between torque at the shoulder and torque at the elbow, over a wide range of conditions. Subjects are likewise capable of judging force output magnitude over a substantial range. Jones has shown that force estimation varies systematically with applied force over a range of magnitudes from 15 to 85% of maximum voluntary contraction (Jones 1989).

Electrophysiological data indicate that force is an important variable in voluntary movement production. Studies in which force and kinematic parameters are varied independently are particularly relevant. In these studies, the activity of neurons in cortical area 4 has been shown to vary with the direction of required force output rather than the direction of required movement (Evarts 1968; Georgopoulos et al. 1992; Kalaska 1989). Patients with cerebellar lesions show deficits consistent with a failure to control multi-joint interaction torques (Bastian et al. 1996). In other areas, such as cortical area 5 the activity of neurons is correlated primarily with movement

direction (Kalaska et al. 1990). However, taken together these data remain consistent with the possibility that forces are coded in central control signals.

Inverse models

From a mechanical point of view a full description of movement relies on information about kinematic variables, forces and torques. Kinematic variables can be measured directly using one of numerous recording techniques whereas inverse-dynamics computation remains practically the only method of deriving muscle torques especially in studies of multi-joint movement. Inverse-dynamics was used initially to characterize the forces associated with different patterns of locomotion (see Winter 1984 for review). Hollerbach (1982) hypothesized that movement production by the nervous system may involve similar computations, consisting of a transformation from endpoint to joint coordinates and then an inverse computation of joint torques based on the equations of motion of the arm. Since then, mathematical formulations of the force control scheme have focused extensively on the notion of inverse-dynamics, the idea that trajectory planning in kinematic coordinates is transformed to the joint torques necessary to realize the desired movements. The inverse model provides a predictive mechanism that is based on a model of expected dynamics.

The simplest formulations of the inverse-dynamics approach circumvent the need for a separate muscle mechanical model in which the values of many parameters are unknown—inverse-dynamics calculations provide time-varying measures of joint torques that, in conjunction with the systems equations of motion result directly in desired movements. However, variants of the inverse-dynamics formulation that explicitly include muscle properties have also been reported (Schweighofer et al. 1998; Bhushan and Shadmehr 1999).

Physiological evidence of inverse dynamics calculations has been offered in the context of patterns of cerebellar Purkinje cell activity (Gomi et al. 1998; Shidara et al. 1993). In particular, it has been shown that the simple spike firing patterns of Purkinje cells during reflex eye movements can be reconstructed from a linear combination of eye position, velocity and acceleration in a manner which is consistent with the relationship between these variables given by the equations of motion of the eye. It is suggested that this finding provides direct evidence of an inverse dynamics model in the activity of neurons in cerebellar cortex. This result together with the results of imaging studies (Tamada et al. 1999), and the demonstration of adaptation and learning in the cerebellum (Thach 1998), is offered as evidence that the cerebellum is a major site of internal models (Kawato 1999).

Forward models

Recent formulations of the force control notion have become linked to work on motor learning and to the idea that in order to achieve adaptation to mechanical load, the nervous system incorporates information about limb dynamics and external loads into control signals. Forward internal models of the motor system have been suggested as a way to achieve predictive adaptation (Jordan and Rumelhart 1992).

The predictive internal model formulation finds its origin in work on adaptive control and robotics. One of the earliest examples is the work of Ziebolz and Paynter (1954). These researchers proposed the use of a fast-time simulator that could predict the consequences of control actions and thus enable their adjustment to achieve desired outcomes. In Ziebolz and Paynter, prediction and control occur on two different time scales. In more recent work on control theory, predictive controllers appropriate to both linear and non-linear systems have been described (see Bhushan and Shadmehr 1999 for a summary). These suggestions have in turn been applied to work on human motor control, where they have been implemented as artificial neural networks (see Jordan and Rumelhart 1992; Kawato 1999 for reviews). It has been proposed that an internal model analogous to a Smith predictor is localized in the cerebellum (Miall et al. 1993; Miall and Wolpert 1996).

Recent formulations have distinguished between internal models dealing with sensory prediction (state estimation) and those involved in predicting movement. The Kalman filter has been the focus of work on sensory prediction. The Kalman filter is a mathematical autoregressive procedure that applied to motor systems predicts future sensory inputs from a combination of the current state of the motor system and a copy of the current motor command (Mehta and Shaal 2002; Wolpert et al. 1995). It is presumed to contribute to the ability to overcome problems associated with feedback delays.

The term internal model is now also widely used in studies of motor control in a more general, metaphorical sense to imply adjustments to the neural activity that are carried out as a result of previous learning or adaptation, rather than in the specific sense implied in the force control formulation in which learning and adaptation are based on internal reproductions of systems input/output relationships. There are now numerous behavioral and physiological examples of such adjustments. Evidence that the nervous system accounts for dynamics in movement planning provides support for feed-forward mechanisms that is consistent with the notion of predictive internal models.

Some of the most compelling evidence that the nervous system accounts for the dynamics of the limb and loads comes from studies of anticipatory postural adjustment and grip force modulation. Anticipatory postural adjustments have been shown to prevent the undesirable effects of perturbations. For example changes to body posture and activation of leg muscles precede the rapid elevation of the

arm (Belenkii et al. 1967). In studies of grip force during naturally occurring movements, subjects have been shown to make anticipatory adjustments to force output that are precise in magnitude and timing such that they vary in a predictive manner in conjunction with the reactive forces arising due to self-generated movement (Flanagan and Wing 1997). The ability of subjects to modify the control of arm movements in a predictive or feed-forward manner has been demonstrated more generally in the context of motion dependent loads. With practice subjects produce smooth straight line movements in the context of various loads. This ability has been demonstrated both for external loads (force fields) that vary with limb velocity (Lackner and DiZio 1994; Conditt et al. 1997; Gandolfo et al. 1996; Goodbody and Wolpert 1998; Shadmehr and Mussa-Ivaldi 1994) and intrinsic loads such as joint interaction torques in multi-joint movements (Almeida et al. 1995; Sainburg et al. 1995, 1999; Cooke and Virji-Babul 1995; Virji-Babul and Cooke 1995; Gribble and Ostry 1999). In order to achieve these adaptations, the nervous system must presumably incorporate information about limb dynamics and external loads into control signals so as to carry out the adjustments that match the load.

There has also been recent physiological evidence of adjustments to neural signals related to limb dynamics during motor learning in artificial mechanical environments. Gandolfo et al. (2000), Gribble and Scott (2002) and Li et al. (2001) recorded from single neurons in cortical area 4 while monkeys were trained to make reaching movements in motion dependent force fields. With training, many neurons changed their tuning properties in a manner consistent with changes in the load to the limb.

Recent studies have presented evidence in support of the idea that internal models involve sensory processing related to state estimation as well as predictive control of dynamics (Wolpert et al. 1995; Mehta and Shal 2002). Evidence for a sensory basis for internal model formation is reported by Wolpert et al. (1995) who asked subjects to estimate hand position during slow lateral movements. Subjects tended to overestimate movement extent when the movement was made with an assisting load but overestimated less when an opposing load was used. By comparing these observations with a theoretical scheme for state estimation based on a Kalman filter, Wolpert et al. concluded that their analysis supports the existence of an internal model. Mehta and Schaal (2002) distinguish between a sensory pre-processing stage and a control stage in movement production. These authors empirically analyzed the task of stabilizing a dynamic system that is unstable by itself—a pole on a finger—and concluded that at the stage of sensory pre-processing in this task, a forward internal model is used.

Mussa-Ivaldi, Shadmehr and colleagues have proposed possible neural underpinnings of internal model formation. The basic idea, originally proposed in the context of spinal mechanisms of movement production, is that planning and control are achieved by a vector summation of neural force field primitives (Giszter et al. 1993; Mussa-Ivaldi et al.

1994; Mussa-Ivaldi and Bizzi 2000). Thoroughman and Shadmehr (2000) describe a variant of this proposal in the context of studies of adaptation in arm movement to motion dependent force fields. Based on an analysis of trial-to-trial error magnitudes during force field learning, these authors propose that adaptation to altered limb dynamics is achieved by combining motor primitives that map muscle forces to desired hand velocity. The authors tentatively attribute the shape of the mathematically derived primitives to characteristics of tuning curves of cerebellar Purkinje cells and accordingly suggest that adaptation observed at the level of cortical neurons during force field learning may be due to cerebellar projections.

Evaluation of the force control model

In the preceding sections, we outlined experimental findings favoring the idea that the nervous system has the capacity to directly program forces and specify EMG activity. We also reviewed evidence that points to the extensive predictive capabilities of the nervous system in movement production. There can be little doubt that the nervous system integrates the knowledge of physical properties of the body and environment in this process. Moreover, it should be emphasized that regardless of whether specific explanatory constructs such as neural inverse dynamics calculations or predictive internal models (central simulation of dynamics) are correct or not, these constructs are applied to empirical findings which require appropriate explanation. However, it is important to recognize that internal models are theoretical constructs and should not be identified with the phenomena they attempt to explain. Other theories, not relying on these constructs may explain some of the same phenomena (Flash and Gurevich 1997; Gribble and Ostry 2000; Mehta and Schaal 2002).

In the following sections we will raise concerns about the general notion of force control and programming as a physiologically feasible process for movement production. We will also address the degree to which findings on force regulation can be taken as evidence for inverse dynamics and forward internal model computations. The validity of force control models is evaluated by comparison of predictions with empirical observations.

Characteristics of point-to-point movements

One of the central ideas in a number of versions of the force control formulation is the proposal that forces are neurally coded as EMG signals. In this regard, it is helpful to review the basic kinematic and electromyographic properties of point-to-point movements. Such movements are exemplified in Fig. 1B by a fast elbow flexion in a horizontal plane. Movement is initiated by EMG bursts in flexor muscles. Extensor muscles become active somewhat later and, after additional transient EMG bursts in flexor and extensor muscles, a new elbow angle is

established. Muscles remain active for a period of time at the end of movement but this co-activation gradually disappears as the final position is maintained (Suzuki et al. 2001).

Note that tonic EMG activity at the initial position was essentially zero and that EMG activity returned to zero after the movement of the arm to the new position. Other studies show the same phenomenon (e.g., Gottlieb et al. 1989). This implies that variables other than EMG signals are responsible for the specification of arm position. Figure 1B thus illustrates that postures *cannot be encoded* by EMG signals.

The same conclusion about the specification of position based on EMG can be reached from an analysis of the empirical EMG-force relation: regardless of position (muscle length), muscle activation and motor unit recruitment start when the external force can no longer be balanced by passive muscle resistance. Muscle activation increases in proportion to the force (Henneman et al. 1965; Desmedt and Godeaux 1977). In intact systems, proprioceptive feedback plays a fundamental role in scaling muscle activity and motor unit recruitment in relation to changes in force. This is evident from the absence of such scaling in deafferented patients: deprived of proprioceptive feedback, these patients maintain the same muscle activity when a load stretching the muscle is added or removed (Levin et al. 1995). In healthy individuals, depending on the change in load, the transition from one steady state posture to another can be associated with an increase, decrease or, as in Fig. 1B, no change in the tonic level of muscle activation. This suggests once again that different postures cannot be encoded by EMG signals. The fact that

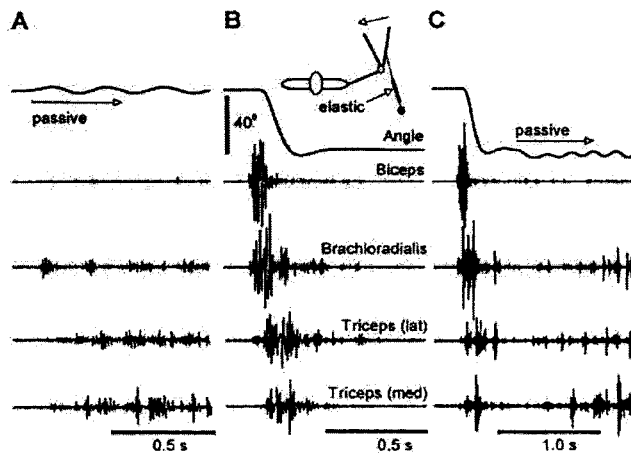


Fig. 1 Rapid elbow flexion movement (B) and reactions of muscles to passive oscillations at the initial (A) and final (C) positions (from unpublished work). Note that the activity of elbow muscles (*four lower traces in B*) at the initial elbow position is practically zero (background noise level) and, after transient EMG bursts, returns to zero at the final position. Muscles are activated in response to passive oscillations of the arm at the initial (A) and final (C) positions. An elastic connector was used to compensate for the small passive torque of non-active flexor muscles at the initial position of about 140°. The compensation was unnecessary for the final position (about 90°) since it is known that at this position the torque of passive elbow muscles is zero

force control strategies do manage to code for different postures by using EMG signals or forces points to possible inconsistencies of these formulations with empirical data. The following section considers this problem in more detail.

Von Holsts paradox and the central specification of force

Von Holst and Mittelstaedt (1950/1973) described a fundamental problem in motor control—the relation between posture and movement and in particular the problem of producing an intentional movement from one position to another. This task is not in fact as simple as it may seem although our everyday experiences show that we have no problem in moving the body or its segments from an initial posture and stabilizing it again in different postures.

The posture-movement problem as Von Holst characterized it is that there are powerful neuromuscular mechanisms (postural reflexes or posture-stabilizing structures) that generate EMG activity and forces in order to resist perturbations that might otherwise deflect the position of the body from an initial posture. At the same time it is clear that the organism can intentionally adopt different postures. How then is an intentional movement from the initial posture and the achievement of a new posture possible without triggering resistance? We will refer to this problem as Von Holsts posture-movement paradox.

Von Holst was aware, in part from his own experiments on animals, that some movements can be produced in the absence of proprioceptive signals (de-afferentation) and suggested that the intact central nervous system is an actively operative structure. He was especially critical of the classical reflex theory in which reflexes were considered as rigid, stereotypic responses to external stimuli. His views reflect our current understanding in which reflexes are broadly tunable, parameterized structures. Von Holst specifically focused on the question of how central signals (efferences in his terminology) can influence the transmission of afferent (vestibular and proprioceptive) signals to motoneurons in order to make a voluntary movement towards a new posture of the body. In his own words, Von Holst formulated the posture-movement problem in the following way (Von Holst and Mittelstaedt 1950/1973, p. 143; the italics are his).

In the terminology of the reflex theory, the organism is maintained exactly in its normal position through its postural reflexes. However, one can often observe with all animals and in human beings that they can adopt a posture *different* from the normal position for varying periods of time. ... In view of the continuously evocable postural reflexes, how are these deviant postures possible? As before, the reflex theory would state—through complete or partial inhibition of the equilibrium reflexes. Yet it can easily be shown that this interpretation is *not* valid. These requisite postures, which deviate from the norm, are

actually restored through the *same* corrective movements, when disturbed by some external impulse, as those which are seen in the restoration of the normal posture!

The quote shows that Von Holst considered the possibility that the paradox might be resolved if the resistive reactions to the deviation from the initial posture were completely or partially suppressed by the nervous system when the transition to a new posture was made. However, he rejected the suggestion that resistive reactions are suppressed during movement as conflicting with experimental observations. Specifically, any posture of the body is maintained by resisting reactions similar to those seen in the restoration of the initial posture in response to perturbation.

Another potential solution to Von Holst's paradox is the possibility that resistive postural reactions are weak and might be tolerated, rather than inhibited, during a movement. In support to this suggestion, one could refer to Fig. 1B and argue that since the initial and the final muscle activity was zero, only very small forces of inactive muscles resisted the active arm movement. Such a situation, when muscles are not activated in response to even rapid stretch, can actually be observed if subjects are instructed to completely relax (Wachholder and Altenburger 1927). Figure 1A and C show however that muscles are considerably activated in response to externally imposed cyclical perturbations at either the initial or the final positions. Other studies have also shown that when subjects maintain an arm posture, muscles resist perturbations with forces that progressively increase with the deviation from the initial position. The coefficient determining this increase (stiffness) depends on the arm geometry at the initial position but is generally in the range of 1–6 N/cm when measured at the level of the hand (Mussa-Ivaldi et al. 1985). In the absence of a postural resetting mechanism, a 30 cm displacement of the arm resulting from an active movement would generate a resistance of not less than 30 N. Such a resistive force would rapidly drive the arm back to the initial position as soon as the movement has been completed. In the case of single joint movement, we have estimated that the resistive forces tending to return the arm to the initial position for the movement illustrated in Fig. 1B would reach about 60 N (Asatryan and Feldman 1965). Postural-stabilizing forces are thus far from being negligible. The posture-movement problem must be dealt with by the nervous system.

The force control model and in particular elaborated versions of this formulation that incorporate muscle properties and feedback mechanisms are unable to resolve the Von Holst posture-movement problem. The details are provided below but basically the problem is that the model cannot account for how the body or its segments can voluntarily change position without triggering resistance. The generation of muscle torques would result in the movement of body segments from an initial position. In response, mechanisms of postural stabilization would generate resistance that would tend to return the segments to their initial position. Control levels might attempt to

reinforce the programmed action by generating additional torque that counteracts this resistance. However, this strategy would be non-optimal in terms of energy output, since it would require high forces not only for motion but for the maintenance of final posture (see above). The problem is that the force control model has no means to reset the postural state and therefore the transition between postures remains an unresolved issue in this model. This is not an inconsequential failing of the force control formulation. The unopposed shift between postural states is a fundamental characteristic of everyday motor activity. The inability of the force control strategy to re-establish posture at a new location without self-generated resistance is a basic failing of the formulation.

This failure of the force control formulation is revealed in an examination of the equations in versions of the model that incorporate muscle properties and reflexes. As an example, Schweighofer et al. (1998) describe a force control model in which in the absence of any external forces muscles generate zero tonic activity at an initial arm position but at the final position they generate activity that is proportional to movement distance or to the difference between the initial (l_0) and final (l) muscle lengths (see their Eqs. 6 and 8):

$$u = s(l_0 - l)$$

where u is the magnitude of activation of a muscle and s is a constant coefficient depending on muscle stiffness and moment arm. Note that l_0 is constant and thus tonic muscle activation is proportional to movement distance.

According to this formulation, the transition of the arm from one position to another is always associated with an increase in the tonic activity of agonist muscles (the muscles that shorten with the transition to the final arm position) even if the net joint torques are zero at both positions. Agonist and antagonist muscles in this model are coactive at the final arm position. Contrary to experimental observations (Fig. 1B), the coactivation and corresponding agonist and antagonist torques cannot be reduced without bringing the arm back to the initial position, since in this model these torques and activation are minimal only at this position. Indeed, some level of agonist-antagonist co-activation may be necessary for rapid movements and experiments show that such movements end with substantial co-activation of agonist-antagonist muscles that is rapidly reduced after the end of the movement (Fig. 1B; Gribble and Ostry 1998; Suzuki et al. 2001). The problem is that the force control strategy necessitates such co-activation even for slow movements and at any steady state posture different from the initial one. These predictions are incorrect: slow movements typically involve only reciprocal activation of agonist and antagonist muscles and steady state positions of the arm may be maintained without coactivation (Wachholder and Altenburger 1926; Wallace 1981). Moreover, after fast movements, coactivation gradually

decreases without motion of the arm (Lestienne 1979; Gottlieb et al. 1989; Fig. 1B).

It should also be noted that coactivation and postural controls cannot be dissociated in formulations such as that of Schweighofer et al. (1998). This prediction obviously conflicts with experimental observations showing that coactivation and postural controls are in principle separate. One can easily co-activate and de-activate agonist and antagonist muscles at any arm configuration without changing the configuration. Indeed, the model could be improved by introducing appropriate independent mechanisms for coactivation and deactivation of agonist and antagonist muscles. However, even with this improvement, the failure of the force control model related to the prediction of position-dependent changes in the tonic muscle activity with transitions from one posture to another, even in the cases when external forces are zero, will remain. This prediction not only conflicts with empirical observations (e.g., Fig. 1) but also with the known physiological rule that muscle activation and recruitment of motor units are graded according to muscle force rather than position (e.g., Desmedt and Godaux 1977).

Our analysis of the posture-movement problem shows that different steady state postures are not necessarily associated with different EMG levels. This means that, physiologically, the posture resetting mechanism is independent of muscle activation. Resetting in intact organisms is thus presumably associated with pre-motor changes in the state of the neuromuscular system elicited by descending pathways that modify the synaptic inflow to motoneurons. These inputs affect the membrane potentials of motoneurons whether the latter are activated or not (see section Threshold control). Sub-threshold changes in membrane potentials of motoneurons preceding EMG bursts have been observed experimentally. Tested with the H reflex, a sub-threshold facilitation of motoneurons starts 40–50 ms before EMG bursts during rapid voluntary movements in the ankle joint in humans (Kots 1975; Morin et al. 1982). Depolarization of flexor motoneurons starts about 100 ms before the onset of EMG activity producing hind limb motion towards the ear in scratching movements of decerebrated cats (Berkinblit et al. 1979).

One might reasonably ask whether Von Holsts problem could be resolved simply by combining notions of force control with the idea of voluntary change in limb position based on postural resetting. This has indeed been suggested in recent studies that focus on the predicted behavior of paired inverse and forward models (Bhushan and Shadmehr 1999). These formulations are of interest because they include both the central specification of forces and a mechanism for reflex based postural stabilization in which the set-point muscle length may be shifted by changing the muscle activation. The proposed re-setting mechanism may provide a means to shift between postures and at the same time to specify the additional forces that are needed to achieve the desired movements. At first glance, this would appear to resolve Von Holsts paradox while preserving the notions of force

control. However, the proposed re-setting mechanism is based on change in muscle activation and thus has problems that are similar to those in the Schweighofer et al. (1998) formulation.

The postulated central specification of force outputs is also incompatible with empirical evidence, even when combined with a mechanism for postural change. In the force control formulation by Bhushan and Shadmehr (1999), EMG activity consists of two additive components—one that depends on excitatory and inhibitory position- and velocity-dependent signals from proprioceptive afferents (reflex component) and the other that is specified by the controller regardless of proprioceptive feedback (central component). It is well known that unexpected unloading of the limb produces, at a very short latency (about 30 ms), a transient silent period in muscle activity (Hansen and Hoffman 1922; Merton 1951; Angel et al. 1965). Physiologically, the silent period results from a sudden decrease in the facilitation of motoneurons following a decrease in the activity of muscle spindle afferents elicited by muscle shortening with possible involvement of pre- and post-synaptic inhibition of motoneurons mediated by spinal interneurons on which proprioceptive afferents terminate. If some part of muscle activation was directly specified by central commands, as force control formulations suggest, then any reduction in EMG activity that accompanies the unloading of the limb would of necessity be incomplete, eliminating afferent or reflex based activity in motor neurons but not their central drive. The quiescent period in muscle activity in response to unloading during postural control shows that when proprioceptive inputs to motor neurons are temporarily decreased, there is no significant residual muscle activity and hence presumably no central specification of muscle activation that is independent of afferent input. Moreover, when unloading is produced during rapid point-to-point movement, a complete silent period in the first agonist burst can be observed (Adamovich et al. 1997). These results argue against the idea of a reflex-independent component of muscle activation. Thus even when notions of direct control of force and muscle activation are coupled with a mechanism that might provide postural resetting, the predicted behavior of the system is at odds with empirical data. This conclusion is also supported by neurophysiological data which show that, as a rule, descending systems mediate their influence on motoneurons via interneurons of proprioceptive loops. The existence of direct, monosynaptic inputs of descending pathways to motoneurons does not conflict with this rule since motoneurons themselves are obviously a part of such loops.

It is worth noting that this particular problem—the inability to achieve adequate postural resetting using force control—only arises with the addition of muscle properties and proprioceptive reflexes to the force control formulation. Simpler force control models in which only torques and kinematics are represented (e.g., Hollerbach 1982) are not subject to this criticism. They are fully capable of moving from initial to final postures, albeit with no

assurance of stability. It is rather revealing that the attempt to incorporate realistic biological properties such as muscle mechanics and reflexes actually worsens the performance of the model. Paradoxically, control levels in this model must counteract muscle and reflex dynamics rather than utilizing them as implied by the reafference principle of Von Holst and Mittelstaedt (1950/1973). In the absence of postural resetting, the system must overcome elastic, position-dependent resistance to movement from the initial position and also velocity-dependent resistance, potentially endangering the systems stability and energetically optimal performance.

Problems with inverse dynamics

Inverse dynamics is a potential solution to the problem of establishing a mapping between values for control variables and desired actions. Evidence consistent with this formulation has been offered in the context of firing patterns of Purkinje neurons in the cerebellar cortex during reflex eye movements (Gomi et al. 1998; Shidara et al. 1993). There is however otherwise no direct evidence of which we are aware in support of the idea that the nervous system establishes required muscle forces on the basis of inverse dynamics.

The firing frequency of Purkinje cells during reflex eye movement is shown to be linearly related to eye position, velocity and acceleration and to occur at an average time lead of less than 10 ms. The correlation does not however constitute evidence that Purkinje cells generate activity as a function of kinematics, that is, that Purkinje cells perform inverse dynamics calculations. Correlations of neuronal activity with mechanical variables may emerge following direct dynamical laws inter-relating the behavior of mechanical, afferent and neural components of the system. The same correlation would be observed if the kinematics were a function of Purkinje cell activity and not vice versa.

The estimated time-difference of less than 10 ms between Purkinje cell activity and kinematic measures (Gomi et al. 1998; Shidara et al. 1993) renders difficult the interpretation of the relationship between the measures. Many cells in the brainstem underlying the initiation of saccadic movements are active before or within this interval. In particular, de-recruitment of antagonist motor neurons starts 30–40 ms before the saccade, thus preventing resistance of antagonist muscles to the movement. Omni-pause neurons are deactivated 10–12 ms before movement and ocular motor neurons are activated 5–7 ms before the saccade (Fuchs and Kaneko 1985). At latency differences such as these, at which saccadic movement generators appear to be active prior to Purkinje cells, one cannot feel confident in attributing a role to Purkinje cells in either inverse or forward-dynamics calculations.

The finding that the discharge patterns of Purkinje neurons have a positional coefficient of negligible magnitude (Gomi et al. 1998; Shidara et al. 1993) is also

relevant. This means that Purkinje cells do not carry a step signal to keep the eye at the final position as required by the pulse-step model of saccadic eye movement (Robinson 1970).

We wish to note that the preceding critique of the hypothesis that cerebellar Purkinje cells carry out inverse-dynamic computations is not intended to argue against the role of these neurons in eye movement. In particular, the role of cerebellum and Purkinje neurons may be substantial in fast movements including saccades as evidenced by the observation of movement dysmetria in patients with cerebellar deficits (Selhorst et al. 1976; Hallet and Marsden 1981).

Let us consider next the logic of inverse dynamics computations for arm movement. It is assumed that the process starts from selection of a desired hand movement trajectory and velocity profile. It is known that a hand trajectory with a definite velocity profile does not define a unique pattern of joint rotations. For example, hand kinematics remain invariant whereas arm joint rotations change depending on whether or not pointing movements are combined with trunk motion (Adamovich et al. 2001). Inverse dynamics computations of joint torques cannot proceed unless the joint redundancy problem is solved. Moreover, a net joint torque does not define a unique force for each muscle crossing the joint, meaning that the inverse computation runs into an additional redundancy problem. Similarly, a muscle force does not determine a unique pattern of motor unit recruitment. Existing inverse dynamics formulations do not go beyond computations of EMG signals although, to complete the scheme, it would be necessary to resolve the manner in which input signals to individual motoneurons (post-synaptic potentials) are computed to produce the desirable EMG output. Fundamental non-linearities in the properties of motoneurons (the threshold and plateau-potentials) cannot be reversed without substantial simplifications of the dynamical input/output relationships in the system, which would reduce the reliability of model-based computations.

Zajac et al. (2002) analyzed the inverse dynamical computational strategy with regards to the redundancy problem arising in the computations of individual muscle torques. They considered different optimization criteria for its solution and concluded that due to pattern of torques produced by bi-articular muscles, the inverse computations may fail to find the contributions of individual muscles. They also noted that the decomposition of net joint torques into individual muscle torques can be made by assuming that all torques are static, but they raised concerns about the possible results given doubts about the appropriateness of the static optimization criterion and about the inability to estimate co-contraction.

Problems with forward internal models

The motivation for postulating predictive internal models is the systems demonstrated ability to compensate for inertial and interactive torques, to adapt to novel senso-

rimotor environments and to reduce or prevent movement errors. Nevertheless, observations of anticipatory motor processes or learning do not justify the claim that the nervous system uses internal models in the sense defined in the force control hypothesis, as predictive simulations. The point that must be emphasized is that whereas the nervous system may take account of dynamics in motion planning, there is no evidence that related adjustments to control signals involve a neural system that mimics the behavior of the sensorimotor system and objects in the external environment (Kawato and Wolpert 1998).

Variants of the internal model formulation distinguish a number of aspects of the predictive process — state estimation and output prediction (Karniel 2002). For output prediction, Mehta and Schaal (2002) showed that, theoretically, every model-based controller can be replaced by a direct controller that has exactly the same input/output function. They concluded that none of the studies suggesting the existence of a model-based control strategy could rule out the use of a non-model-based control strategy. Mehta and Schaal (2002) further showed that forward model-based control using a Smith predictor (Miall et al. 1993; Miall and Wolpert 1996) can be rejected on the basis of a formal mathematical analysis. The predictor relies on error in estimation of the current state variables by an internal model of the systems dynamics. It is unable to improve stability even if delays in the sensory-motor loops are small. Indeed, the Smith predictor may worsen the problem of stabilizing mechanically unstable systems such as a balancing a pole on a finger.

Postural stability in force control is a known problem identified in work on robotics. The basic problem is that the motion of a multi-joint arm obeys laws of mechanics that, in themselves, do not assure equilibrium or stability. Both position and velocity dependent feedback are needed to resist deflections and oscillation. Feedback introduces transmission delays that may, depending on their timing, actually reinforce oscillations and introduce instability. Avoidance of instability is indeed a primary motivation for postulating feedforward internal models. In the force control formulation, it is assumed that by making adjustments to control signals on the basis of differences between predicted and desired sensory consequences rather than by using actual afferent inputs from movements, effects of feedback delays are eliminated and the likelihood of instability is reduced.

Concerns regarding the potentially destabilizing effects of delays in position and velocity feedback are not wholly justified. The contractile apparatus associated with active motor units generates forces practically instantaneously following changes in position and velocity. These intrinsic muscle properties, termed reflexes by Brown and Loeb (2000), oppose the effects of delays in reflex pathways to motor neurons. Active muscle properties may thus subserve at least part of the role for which feedforward internal models have been postulated. Moreover, it is known (Elsgolts and Norkin 1971) that instability of dynamical systems can be minimized when position and velocity signals, even delayed, are combined in feedback

pathways, which is obviously the case for signals carried by muscle spindle afferents to motoneurons (Matthews 1972). Indeed, reflexes combined with proprioceptive position- and velocity-dependent feedback have been shown to be sufficient for stability of posture and movements if reflex delays are within the range of empirical values (St-Onge et al. 1997).

The idea that feedforward models can reduce the destabilizing effects of delays is not itself without problems. To the extent that feedforward control might act to minimize errors, it necessarily depends in a sensitive way on the accuracy of the model from which its predictions are derived. It has been well established over several decades of control systems research that model-based control strategies, especially those relying on the Smith predictor, are not robust—short-term performance comes at the cost of *instability* in the presence of model uncertainties (Otten et al. 1997; Mehta and Schaal 2002).

With the addition of muscle and reflex properties, the force control model leads to conflicting accounts of how the control level might manage system stability. On the one hand, it is assumed that feedforward models should ensure system stability by reducing the effects of feedback delays. On the other hand, the same or other internal models must be able to neutralize the position and velocity-dependent resistance of the muscle-reflex system to motion from the initial position and thus reduce stability (see above). It is rather paradoxical that muscle and reflex properties interfere with force programming and need to be counteracted in the force control model.

A number of recent papers have presented data to suggest the existence of a predictive internal model for sensory processing. Wolpert et al. (1995) used an internal model with a linear Kalman filter to explain the patterns of errors in the estimation of final positions in slow arm movements. The authors report a non-monotonic pattern of overestimation whose magnitude is increased for assistive loads and decreased for resistive loads. The pattern of error in the absence of load is given as the primary evidence for the use of internal models in state estimation. However the evidence for a non-monotonic error pattern is less than convincing. Different numbers of data points are used in calculation of bias errors for different stopping times and thus, it is not clear whether bias is reliably different for movements of different duration. Moreover, the patterns of error in the presence of load can be explained by an alternative hypothesis in which position sense comprises two components none of which involves an internal model (Feldman and Latash 1982). One component is the control signal associated with the postural resetting mechanism that establishes the spatial location of the effector in the absence of load. This central component is generated by the controller independent of proprioceptive feedback and can be retained in motor memory. The other component represents the deviation from this location elicited by the load. This deviation is derived from proprioceptive signals, for example, from the activity of muscle spindle afferents after the end of movement. The sign of the deviation

depends on the load direction. The afferent component is subtracted from the central component in the case of a resisting load and added when the load assists the movement. If subjects tend to exaggerate the contribution of afferent input into position sense, movement extent will be underestimated for an opposing load (relative to estimates in the absence of load) and overestimated for an assisting load as was reported by Wolpert et al. (1995). The point here is simple. The existence of an alternative account indicates that the Wolpert et al. demonstration should be considered as a possibility rather than as evidence of a forward model for state estimation. The Wolpert et al. findings indicate that subjects can make judgments about the current state of the system. Whether or not this process involves an internal model (representation of the structure of the system) remains an open question.

Mehta and Schaal (2002) considered a number of model-based and non-model based schemes for the task of balancing a pole on a finger. They concluded that an internal model analogous to a Kalman filter is used by the nervous system at the stage of sensory pre-processing in this task. In these schemes, however, it is taken for granted that the behavioral goal of subjects is to stabilize an otherwise unstable pole, in other words, to keep the pole in an upright position at a particular location in the workspace. A different interpretation of behavior in this task is that the nervous system exploits the dynamics of the pole to drive it in the desired direction without actually stabilizing it at any particular position. This interpretation is consistent with the remarkable ease with which we are able to move the pole in any desired direction. Recently, we made a short test and found that 85% of time the tip of the pole moves in the same direction as the finger, which accords with our assumption about taking advantage of pendulum dynamics to drive the pole in a desired direction. The point here is that, again, an alternative account of controlling the pole is possible. It is unclear whether the internal models invoked for the purpose of achieving stability would apply in this alternate conceptualization of the task. Note that we are not questioning the necessity of state estimation. Rather we are questioning the claims of evidence that this process involves internal models.

Schemes for learning and adaptation have been described that are not reliant on internal models of limb dynamics or inverse-dynamics calculations. Gribble and Ostry (2000) demonstrate that a number of phenomena often associated with predictive internal models, namely compensation for interaction torques during multi-joint movement and adaptation to motion dependent force fields could in principle be accomplished using a simple scheme in which non-force based control signals are incrementally updated on the basis of positional error related to equilibrium and actual trajectories (also see Flash and Gurevich 1997). The point of this demonstration is that viable schemes for adaptation may involve neither an explicit representation of forces nor inverse-dynamics

calculations, nor a predictive simulation of the motor apparatus.

Threshold control

A central point of our criticism of the force control formulation is that it fails to explain how movements occur without producing resistance due to posture-stabilizing mechanisms. The explanation requires the identification of a neurophysiological variable(s) the value of which is different for different voluntarily specified positions even though forces and tonic muscle activity may be the same at these positions (see Fig. 1B). Such a variable can be identified from Fig. 1 or similar figures published in literature.

It may be seen that the EMG activity at the initial position in Fig. 1B is zero but muscles actively reacted to passive oscillations of the arm at this position (Fig. 1A). This means that motoneurons of arm muscles before movement onset are in a *just sub-threshold state*. The fact that zero activity and reactions to passive oscillations are also observed at the final position (Fig. 1C) implies that the activation thresholds of motoneurons were reset to this position. The position at which muscles reach their activation thresholds is thus not constant. In other words, the threshold position was reset so that zero muscle activity could be restored but at another point in the workspace. This phenomenon is referred to as threshold control. The existence of threshold control follows not only from the simple analysis of the elbow flexion in Fig. 1 but also from many experimental studies in animals and humans, starting from work by Matthews (1959), and Asatryan and Feldman (1965). The feasibility of threshold control has been demonstrated in computer simulations of single- and double-joint arm movements (Gribble et al. 1998).

Threshold control not only provides a potential solution to the posture-movement problem but may underlie the production of movement. With each resetting of the activation thresholds, the systems previous position appears as a deviation from the newly specified threshold posture. The same neuromuscular mechanisms that produce EMG signals and forces in response to deviations from the previous position will produce EMG signals and forces that oppose deviations from a newly specified position.

Theoretically, threshold systems are non-linear and cannot be considered linear even locally, for small changes in variables. Since activation thresholds are controlled, the position of moving segments at which local linearity is broken may occur anywhere in the biomechanical range, making the neuromuscular system fundamentally non-linear. In contrast, the force control formulation relies on predictive properties of the Kalman filter or Smith predictor that assume the systems linearity. An extended Kalman filter can work for non-linear systems but only if they locally behave linearly (Nørgaard et al. 2000). Thus the predictive constructs developed in control systems

theory to meet the needs of technology do not fit to the neuromuscular system that is strongly non-linear.

Discussion

Force control theories have been successfully applied to robotics and are likewise successful in accounting for aspects of movement production in humans. This includes the relationship between kinematics and force and the adaptation of movement to motion dependent force fields. A major component of the force control hypothesis, that there are neuronal structures, internal models, specialized in inverse and forward computations of forces and kinematics, has been shown to be consistent with experimental findings. The term internal model is widely used in contemporary motor control studies.

Problems arise in attempts to integrate force control models with basic physiological properties of the neuromuscular system. In such cases, our analysis indicates that these models generate predictions that are in conflict with basic, well-established principles of movement production. We identified the following problems in the force control formulation: It lacks a physiologically feasible mechanism for postural resetting, conflicts with the empirical EMG-force relationship and disregards empirical evidence that threshold control underlies postural resetting and possibly movement production.

The empirical findings offered in support of inverse or forward internal models are either unconvincing (those based on the analysis of correlations of activity of Purkinje and cortical cells with mechanical variables), or not sufficiently specific since the same findings can be explained in terms of alternative formulations not relying on the notion of internal models. Such findings are related to force field learning, compensation of effects of interactive torques, balancing a pole on a finger, and perceiving hand position in arm movements. Many claims of support of internal models are unsubstantiated since they are based on a metaphorical use of the term internal model to denote any phenomena related to learning, adaptation, and anticipation.

There are theoretical problems inherent in the force control approach: Uncertainties in the solution of multiple redundancy problems associated with inverse computations, even if they rely on optimality criteria; the incompleteness of the logical structure (there is no resolution to the question of how the system computes synaptic inputs to motoneurons to produce the required EMG activity and forces); the necessity to oversimplify the actual input/output relationships in the system to make inverse computations possible, leading to low confidence in the results of inverse dynamics computations as well as to potential problems of stability; the reliance on internal models that assume the systems linearity, which is not the case for the neuromuscular system as a result of threshold non-linearities.

The destabilizing effects of delays in sensory-motor pathways are possibly overestimated in the context of

force control models. Comparatively small delays in proprioceptive feedback to motoneurons do not in themselves lead to instability (see above). Moreover, the effects of these delays are minimized due to non-delayed length- and velocity-dependent generation of forces by the contractile apparatus.

We described as an example force control models that incorporate muscle mechanical properties. An examination of the equations indicates that in order to produce a point to point movement, the system must generate not only the forces necessary to make the movement but also additional forces that are needed to overcome the resistance of posture-stabilizing mechanisms when the system moves away from the initial position. After a final position has been achieved, the tonic EMG activity and the forces that counteract the resistance cannot be reduced without bringing the system back to its initial position. The human motor system is not so deficient: When producing voluntary movements, no one experiences resistive forces that tend to return the body to its initial position unless biomechanical boundaries of motion of segments are approached.

Force control strategies not only produce unnecessary resistance to position change but could actually prevent the achievement of a motor goal. This point is illustrated by Tolstoy's short story about how peasants in Russia hunted a bear. The peasants put a container of honey on a branch of a tall tree. A heavy log was suspended by a rope from the same branch, immediately below the honey. In order to get the honey, the bear climbed the tree and pushed the log away. The harder the bear pushed, the more forcefully the log returned until eventually it struck the bear and threw it to the ground. The bear was a victim of the force control strategy applied to a system that has a tendency to return to its initial position.

Internal models for motor control

Internal models now go hand in hand with force control strategies: Computations of joint torques can only be produced by structures that, at least approximately, imitate the input-output relationships of central, reflex and mechanical components of the neuromuscular system. An often neglected consideration in the context of force control schemes is that they have little to offer in terms of accounting for the broader range of processes involved in control of movement. It is only reasonable to expect a model of motor control to account not only for joint torques but also for EMG patterns and control processes that are reflected in sub-threshold changes in membrane potentials of motoneurons, which are presumably independent of EMG, kinematics or force.

We would like to emphasize that while questioning the existence of force based mechanisms and inverse and forward dynamics calculations as ways to achieve desired motor output, we are not questioning the capacity of the nervous system to involve predictive or forward processes to improve motor performance. Equally, we are not

questioning the idea that movement production can involve state estimation as well as control. However we find no direct support for the idea that internal simulations underlie these abilities.

In modeling studies not relying on the idea of internal feedforward models, we have shown that control levels may take advantage of existing mechanisms to provide feedforward adaptation to force fields and compensation for interaction torques acting between limb segments (Gribble et al. 1998; Gribble and Ostry 1998, 1999, 2000).

Alternatives to force control

There are some positive lessons resulting from this analysis of force control models. For example, to be physiologically feasible, a postural resetting mechanism, possibly threshold control, must be an integral part of a motor control theory. Moreover, as described above, threshold control might also be an integral part of position sense and hence of state estimation.

The recognition of threshold control introduces the possibility of a set of theories of which the λ model (Asatryan and Feldman 1965) is a particular instance. Latash (1993) and Barto et al. (1999) have proposed models of motor function that are also based on threshold control but that differ in a number of ways from the λ model, especially with respect to the timing of control signals. Theoretical ideas related to threshold control have developed slowly in part due to the absence of a general mathematical theory related to threshold systems.

In our own work using the λ model, we have considered that postural resetting produced by shifts in muscle activation thresholds is a primary tool of movement production (Gribble et al. 1998). This mechanism is very powerful as evidenced by the large and rapid increase in joint torque that is observed when a fast movement is unexpectedly blocked at the initial position (Ghafouri and Feldman 2001). The mechanism of postural resetting, shifts in the muscle activation thresholds, offers an empirically based model of voluntary movement production and one that is supported empirically. The model has been developed beyond the posture-movement problem and now offers a potential solution to the problems of multi-muscle and multi-degree-of-freedom redundancy (Lestienne et al. 2000; Balasubramaniam and Feldman 2003).

One can consider the possibility of adding threshold control to the force control formulation. Threshold control implies that neural control levels specify spatial coordinates at which muscles become silent. Clearly, this control process does not deliver instructions on the motor output in terms of EMG signals, forces and movement trajectories. Threshold control thus conflicts with the main idea of the force control model that neural control levels directly deal with or calculate EMG activity and forces required for the production of movements. To avoid this problem, one can suggest that only activation thresholds are computed from the desired kinematics by a set of

inverse transformations. This would also be problematic: EMG signals and forces must be computed anyway since threshold values in the inverse dynamics approach can only be derived from these signals. In addition, such a derivation has its own problem: for threshold elements such as motoneurons, the input/output relationships cannot be inverted (see above). The force control formulation is thus incompatible with threshold control.

The neuromuscular system is a particular dynamic system in which forces are position-dependent. Such systems obey a physical rule that is related to the posture-movement problem but formulated in more general terms. Specifically, in order to bring such a system from one point of equilibrium (a combination of steady state values of position and forces) to another equilibrium point, the controller must change parameters that are *independent of state* (output) variables (Glansdorf and Prigogine 1971). Applied to the neuromuscular system, this physical rule is known as equilibrium point control. Proponents of the force control approach have rejected equilibrium point control (Lackner and Dizio 1994; Gomi and Kawato 1996; cf. Feldman et al. 1998). On the other hand, in mathematical models of movement production in the framework of force control, shifts in equilibrium are introduced *of physical necessity* (Schweighofer et al. 1998; Bhushan and Shadmehr 1999; Gomi and Kawato 1996). Contrary to the above rule, however, these shifts are achieved by changes in EMG activity that, due to its relation to muscle force, cannot be considered as independent of state variables. Thus, the primary failing of the force control approach is not in its inability to produce shifts in equilibrium points. Rather, the failure of the force control approach is in the manner in which it achieves equilibrium shifts.

Acknowledgements This research was supported by NIH grants DC-00594 and DC-04669 from the National Institute on Deafness and Other Communication Disorders, CIHR Canada, NSERC Canada, and FQRNT Québec. The authors thank Philippe Archambault and Paul L. Gribble for suggestions.

References

- Adamovich SV, Levin MF, Feldman AG (1997) Central modifications of reflex parameters may underlie the fastest arm movements. *J Neurophysiol* 77:1460-1469
- Adamovich SV, Archambault PS, Ghafouri M, Levin MF, Poizner H, Feldman AG (2001) Hand trajectory invariance in reaching movements involving the trunk. *Exp Brain Res* 138:288-303
- Almeida GL, Hong DA, Corcos D, Gottlieb GL (1995) Organizing principles for voluntary movement: extending single-joint rules. *J Neurophysiol* 74:1374-1381
- Angel RW, Eppler W, Iannone A (1965) Silent period produced by unloading of muscle during voluntary contraction. *J Physiol* 180:864-870
- Asatryan DG, Feldman AG (1965) Functional tuning of the nervous system with control of movements or maintenance of a steady posture: I. Mechanographic analysis of the work of the joint on execution of a postural tasks. *Biophys USSR* 10:925-935

- Balasubramaniam R, Feldman AG (2003) Guiding movements without redundancy problems. In: Kelso S, Jirsa V (eds) *Coordination dynamics*.
- Barto AG, Fagg AH, Sitkoff N, Houk JC (1999) A cerebellar model of timing and prediction in the control of reaching. *Neural Comput* 11:565–594
- Bastian AJ, Martin TA, Keating JG, Thach WT (1996) Cerebellar ataxia: abnormal control of interaction torques across multiple joints. *J Neurophysiol* 76:492–509
- Belenkii VY, Gurfinkel VS, Paltsev Y (1967) Elements of control of voluntary movements. *Biofizika* 10:135–141
- Berkinblit MB, Deliagina TG, Orlovsky GN, Feldman AG (1978) Oscillations of the membrane potential of motoneurons during generation of scratching. *Neurofiziologia* 10:92–94
- Bernstein NA (1967) *The coordination and regulation of movements*. Pergamon, Oxford
- Bhushan N, Shadmehr R (1999) Computational nature of human adaptive control during learning of reaching movements in force fields. *Biol Cybern* 81:39–60
- Brown IE, Loeb GE (2000) A reductionist approach to creating and using neuromuscular models. In: Winters JM, Crago PE (eds) *Biomechanics and neural control of posture and movement*. Springer, New York
- Conditt MA, Gandolfo F, Mussa-Ivaldi FA (1997) The motor system does not learn the dynamics of the arm by rote memorization of past experience. *J Neurophysiol* 78:554–560
- Cooke JD, Viji-Babul N (1995) Reprogramming of muscle activation patterns at the wrist in compensation for elbow reaction torques during planar two-joint arm movements. *Exp Brain Res* 106:177–180
- Corcos DM, Gottlieb GL, Agarwal GC (1989) Organizing principles for single joint movements. II. A speed-sensitive strategy. *J Neurophysiol* 62:358–368
- Desmedt JE, Godaux E (1977) Ballistic contractions in man: characteristic recruitment pattern of single motor units of the tibialis anterior muscle in man. *J Physiol* 264:673–693
- Elsgolts LE, Norkin SB (1971) *Introduction to theory of differential equations with delayed variables*. Science Publishing House, Moscow
- Evarts EV (1968) Relation of pyramidal tract activity to force exerted during voluntary movement. *J Neurophysiol* 31:14–27
- Feldman AG, Latash ML (1982) Interaction of afferent and efferent signals underlying joint position sense: empirical and theoretical approaches. *J Mot Behav* 14:174–193
- Feldman AG, Ostry DJ, Levin MF, Gribble PL, Mitnitski AB (1998) Recent tests of the equilibrium-point hypothesis (λ model). *Mot Control* 2:189–205
- Flanagan JR, Wing AM (1997) The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads. *J Neurosci* 17:1519–1528
- Flanagan JR, Ostry DJ, Feldman AG (1993) Control of trajectory modifications in target-directed reaching. *J Mot Behav* 25:140–152
- Flash T, Gurevich I (1997) Models of motor adaptation and impedance control in human arm movements. In: Morasso P, Sanguineti V (eds) *Self-organization, computational maps and motor control*. Elsevier North-Holland, Amsterdam, pp 423–481
- Fuchs AF, Kaneko CRS (1985) A brain stem generator for saccadic eye movements. In: Evarts EV, Wise SP, Bousfield D (eds) *The motor systems in neurobiology*. Elsevier Biomedical, Amsterdam, pp 126–132
- Gandolfo F, Mussa-Ivaldi FA, Bizzi E (1996) Motor learning by field approximation. *Proc Natl Acad Sci U S A* 93:3843–3846
- Gandolfo F, Li C, Benda BJ, Schioppa CP, Bizzi E (2000) Cortical correlates of learning in monkeys adapting to a new dynamical environment. *Proc Natl Acad Sci U S A* 97:2259–2263
- Georgopoulos AP, Ashe J, Smyrnis N, Taira M (1992) The motor cortex and the coding of force. *Science* 233:1416–1419
- Ghafouri M, Feldman AG (2001) The timing of control signals underlying fast point-to-point movements. *Exp Brain Res* 137:411–423
- Giszter SF, Mussa-Ivaldi FA, Bizzi E (1993) Convergent force fields organized in the frogs spinal cord. *J Neurosci* 13:467–491
- Glansdorf P, Prigogine I (1971) *Thermodynamic theory of structures, stability and fluctuations*. Wiley, Chichester
- Gomi H, Kawato M (1996) Equilibrium point control hypothesis examined by measured arm stiffness during multi joint movement. *Science* 272:117–120
- Gomi H, Shidara M, Takemura A, Inoue Y, Kawano K, Kawato M (1998) Temporal firing patterns of Purkinje cells in the cerebellar ventral paraflocculus during ocular following responses in monkeys I. Simple spikes. *J Neurophysiol* 80:818–831
- Goodbody SJ, Wolpert DM (1998) Temporal and amplitude generalization in motor learning. *J Neurophysiol* 79:1825–1838
- Gottlieb GL, Corcos DM, Agarwal GC (1989) Organizing principles for single-joint movements. I. Speed-insensitive strategy. *J Neurophysiol* 62:343–357
- Gottlieb GL, Corcos DM, Agarwal GC, Latash ML (1990) Organizing principles for single-joint movements. III. Speed-insensitive strategy as a default. *J Neurophysiol* 63:625–636
- Gottlieb GL, Song Q, Hong DA, Almeida GL, Corcos D (1996) Coordinating movement at two joints: a principle of linear covariance. *J Neurophysiol* 75:1760–1764
- Gribble PL, Ostry DJ (1998) Independent coactivation of shoulder and elbow muscles. *Exp Brain Res* 123:355–360
- Gribble PL, Ostry DJ (1999) Compensation for interaction torques during single- and multijoint limb movement. *J Neurophysiol* 82:2310–2326
- Gribble PL, Ostry DJ (2000) Compensation for loads during arm movements using equilibrium-point control. *Exp Brain Res* 135:474–482
- Gribble PL, Scott SH (2002) Overlap of internal models for mechanical loads during reaching in motor cortex. *Nature* 417:938–941
- Gribble PL, Ostry DJ, Sanguineti V, Laboisière R (1998) Are complex control signals required for human arm movement? *J Neurophysiol* 79:1409–1424
- Hallet M, Marsden CD (1981) Physiology and pathophysiology of the ballistic movement pattern. *Prog Clin Neurophysiol* 9:331–336
- Hansen K, Hoffman P (1922) Weitere Untersuchungen über die Bedeutung der Eigenreflexe für unsere Bewegungen. I. Anspannungs- und Entspannungsreflexe. *Z Biol* 75:293–304
- Henneman E, Somjen G, Carpenter DO (1965) Functional significance of cell size in spinal motoneurons. *J Neurophysiol* 28:560–580
- Hogan N (1990) Mechanical impedance of single- and multi-articular systems. In: Winters JM, Woo SL-Y (eds) *Multiple muscle systems. Biomechanics and movement organization*. Springer, New York, pp 149–164
- Hollerbach JM (1982) Computers, brains and the control of movement. *Trends Neurosci* 6:189–192
- Jones LA (1989) Matching forces: constant errors and differential thresholds. *Perception* 18:681–687
- Jordan MI, Rumelhart DE (1992) Forward models: supervised learning with a distal teacher. *Cogn Sci* 16:307–354
- Kalaska JF, Cohen DA, Hyde ML, Prudhomme M (1989) A comparison of movement direction related versus load direction related activity in primate motor cortex, using a two-dimensional reaching task. *J Neurosci* 9:2080–2102
- Kalaska JF, Cohen DA, Prudhomme M, Hyde ML (1990) Parietal area 5 neuronal activity encodes movement kinematics, not movement dynamics. *Exp Brain Res* 80:351–364
- Katayama M, Kawato M (1993) Virtual trajectory and stiffness ellipse during multijoint arm movement predicted by neural inverse models. *Biol Cybern* 69:353–362
- Kawato M (1999) Internal models for motor control and trajectory planning. *Curr Opin Neurobiol* 9:718–727

- Kawato M, Gomi H (1992) A computational model of four regions of the cerebellum based on feedback-error learning. *Biol Cybern* 68:95–103
- Kawato M, Wolpert D (1998) Internal models for motor control. In: *Sensory guidance of movement* (Novartis Foundation Symposium 218). Wiley, Chichester, pp 291–307
- Koshland GF, Galloway JC, Nevoret-Bell CJ (2000) Control of the wrist in three-joint arm movements to multiple directions in the horizontal plane. *J Neurophysiol* 83:3188–3195
- Kots ML (1975) *Organisation of voluntary movement*. Nauka, Moscow, p 247
- Lackner JR, Dizio P (1994) Rapid adaptation to Coriolis force perturbations of arm trajectory. *J Neurophysiol* 72:1–15
- Lashley KS (1951) The problem of serial order in behavior. In: *Jeffress LA (ed) Cerebral mechanisms in behavior*. Wiley, New York
- Latash ML (1993) *Control of human movement*. Human Kinetics, Champaign
- Lestienne F (1979) Effects of inertial load and velocity on the braking process of voluntary limb movements. *Exp Brain Res* 35:407–418
- Lestienne FG, Thullier F, Archambault P, Levin MF, Feldman AG (2000) Multi-muscle control of head movements in monkeys: the referent configuration hypothesis. *Neurosci Lett* 283:65–68
- Levin MF, Lamarre Y, Feldman AG (1995) Control variables and proprioceptive feedback in fast single-joint movements. *Can J Physiol Pharmacol* 73:316–330
- Li CS, Padoa-Schioppa C, Bizzi E (2001) Neuronal correlates of motor performance and motor learning in the primary motor cortex of monkeys adapting to an external force field. *Neuron* 30:593–607
- Matthews PBC (1959) The dependence of tension upon extension in the stretch reflex of the soleus of the decerebrate cat. *J Physiol (London)* 47:521–546
- Matthews PBC (1972) *Mammalian muscle receptors and their central actions*. Edward Arnold, London
- Mehta B, Schaal S (2002) Forward models in visuomotor control. *J Neurophysiol* 88:942–953
- Merton PA (1951) The silent period in a muscle of the human hand. *J Physiol* 114:183–198
- Miall RC, Wolpert DM (1996) Forward models for physiological motor control. *Neural Netw* 9:1265–1285
- Miall RC, Weir DJ, Wolpert DM, Stein JF (1993) Is the cerebellum a Smith predictor? *J Mot Behav* 25:203–216
- Morin C, Katz R, Mazieres L, Pierrot-Deseilligny E (1982) Comparison of soleus H reflex facilitation at the onset of soleus contractions produced voluntarily and during the stance phase of human gait. *Neurosci Lett* 33:47–53
- Mussa-Ivaldi FA, Bizzi E (2000) Motor learning through the combination of primitives. *Philos Trans R Soc Lond B Biol Sci* 355:1755–1769
- Mussa-Ivaldi FA, Hogan N, Bizzi E (1985) Neural, mechanical and geometric factors subserving arm posture in humans. *J Neurosci* 5:2732–2743
- Mussa-Ivaldi FA, Giszter SF, Bizzi E (1994) Linear combinations of primitives in vertebrate motor control. *Proc Natl Acad Sci U S A* 91:7534–7538
- Nørgaard M, Poulsen NK, Ravn O (2000) New developments in state estimation for nonlinear systems. *Automatica* 36:1627–1638
- Otten G, de Vries TJA, van Amerongen J, Rankers AM, Gaal EW (1997) Linear motor motion control using a learning feedforward controller. *IEEE/ASME Trans Mechanotron* 2:179–188
- Robinson DA (1970) Oculomotor unit behavior in the monkey. *J Neurophysiol* 33:393–404
- Sainburg RL, Ghilardi MF, Poizner H, Ghez C (1995) Control of limb dynamics in normal subjects and patients without proprioception. *J Neurophysiol* 73:820–835
- Sainburg RL, Ghez C, Kalakanis D (1999) Intersegmental dynamics are controlled by sequential anticipatory, error correction, and postural mechanisms. *J Neurophysiol* 81:1045–1056
- Schweighofer N, Arbib MA, Kawato M (1998) Role of cerebellum in reaching movements in humans. I. Distributed inverse dynamic control. *Eur J Neurosci* 10:86–94
- Selhorst JB, Stark L, Ochs AL, Hoyt WF (1976) Disorders in cerebellar ocular motor control. *Brain* 99:497–508
- Shadmehr R, Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14:3208–3224
- Shidara M, Kawano K, Gomi H, Kawato M (1993) Inverse dynamic model eye movement control by Purkinje cells in the cerebellum. *Nature* 365:50–52
- St-Onge N, Adamovich SV, Feldman AG (1997) Control processes underlying elbow flexion movements may be independent of kinematic and electromyographic patterns: experimental study and modeling. *Neuroscience* 79:295–316
- Suzuki M, Shiller DM, Gribble PL, Ostry DJ (2001) Relationship between cocontraction, movement kinematics and phasic muscle activity in single-joint arm movement. *Exp Brain Res* 140:171–181
- Tamada T, Miyauchi S, Imamizu H, Yoshioka T, Kawato M (1999) Activation of the cerebellum in grip force and load force coordination: an fMRI study. *Neuroimage* 6:S492
- Thach WT (1998) A role for the cerebellum in learning movement coordination. *Neurobiol Learn Mem* 70:177–188
- Thoroughman KA, Shadmehr R (2000) Learning of action through adaptive combination of motor primitives. *Nature* 407:742–747
- Virji-Babul N, Cooke JD (1995) Influence of joint interactional effects on the coordination of planar two-joint arm movements. *Exp Brain Res* 103:451–459
- Von Holst E, Mittelstaedt H (1950/1973) *Das Reafferenzprinzip. Wechselwirkungen zwischen Zentralnervensystem und Peripherie*. *Naturwissenschaften* 37:467–476, 1950. The reafference principle. In: *The behavioral physiology of animals and man*. The collected papers of Erich von Holst. Martin R (translator) University of Miami Press, Coral Gables, Florida, pp 139–173
- Wachholder K, Altenburger H (1926) Beiträge zur Physiologie der Willkürlichen Bewegung. X. Einzelbewegungen. *Pflügers Arch Ges Physiol* 214:642–661
- Wachholder K, Altenburger H (1927/2002) Do our limbs have only one rest length? A contribution to the measurement of elastic forces in passive and active movements. *Pflügers Archiv Ges Physiol* 215:627–640. Translated by D. Sternad. *Motor Control* 6:302–318
- Wallace SA (1981) An impulse-timing theory for reciprocal control of muscular activity in rapid, discrete movements. *J Mot Behav* 13:144–160
- Winter DA (1984) Biomechanics of human movement with applications to the study of human locomotion. *Crit Rev Biomed Eng* 9:287–314
- Wolpert DM, Ghahramani Z (2000) Computational principles of movement neuroscience. *Nat Neurosci Suppl*: 1212–1217
- Wolpert DM, Kawato M (1998) Multiple paired forward and inverse models for motor control. *Neural Netw* 11:1317–1329
- Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. *Science* 269:1179–1182
- Zajac FE, Neptune RR, Kautz SA (2002) Biomechanics and muscle coordination of human walking, part I: Introduction to concepts, power transfer, dynamics and simulations. *Gait Posture* 16:215–232
- Ziebolz H, Paynter HM (1954) Possibilities of a two-time scale computing system for control and simulation of dynamic systems. *Proc Natl Electronics Conf* 9:215–223