RESEARCH ARTICLE

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Compensation for loads during arm movements using equilibrium-point control

Abstract A significant problem in motor control is how information about movement error is used to modify control signals to achieve desired performance. A potential source of movement error and one that is readily controllable experimentally relates to limb dynamics and associated movement-dependent loads. In this paper, we have used a position control model to examine changes to control signals for arm movements in the context of movement-dependent loads. In the model, based on the equilibrium-point hypothesis, equilibrium shifts are adjusted directly in proportion to the positional error between desired and actual movements. The model is used to simulate multi-joint movements in the presence of both "internal" loads due to joint interaction torques, and externally applied loads resulting from velocity-dependent force fields. In both cases it is shown that the model can achieve close correspondence to empirical data using a simple linear adaptation procedure. An important feature of the model is that it achieves compensation for loads during movement without the need for either coordinate transformations between positional error and associated corrective forces, or inverse dynamics calculations.

Keywords Human · Arm movement · Motor learning · Equilibrium point · Mathematical model

Introduction

Several recent studies have explored the ability of subjects to modify the control of reaching so as to produce normal movements in the presence of motion-dependent loads. This ability has been demonstrated both for external loads

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such as artificial force fields (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994; Conditt et al 1997) and "internal" loads such as joint interaction torques in multi-joint movements (Koshland et al. 1991; Sainburg et al. 1993; Almeida et al. 1995; Cooke and Virji-Babul 1995; Ghez and Sainburg 1995; Sainburg et al. 1995; Virji-Babul and Cooke 1995; Gribble and Ostry 1999). In order to achieve this adaptation, the nervous system must presumably specify appropriate time-varying motor commands that specifically counteract loads. To date many of the models that have been proposed to account for this kind of motor adaptation have postulated that neural control signals directly specify the forces required for movement. In the present paper we explore how a position control model based on the equilibrium-point hypothesis may achieve similar compensation for loads during multi-joint arm movement (also see Flash and Gurevich 1997).

In direct force programming formulations – termed "force control" in the present paper – movement production typically involves the explicit specification of the time-varying forces and torques required to produce movement of the limb. In the context of these models it has been proposed that the signals for force control are derived by inverse dynamics calculations (Kawato et al. 1987; Uno et al. 1989; Kawato et al. 1990; Schweighofer et al. 1998). Alternate formulations suggest that control signals are positional in nature and movements arise as a consequence of shifts in a neurally specified equilibrium position of the limb [Feldman 1986; Feldman et al. 1990; Flanagan et al. 1993; Gribble et al. 1998; see McIntyre and Bizzi (1993); Bizzi et al. (1982) for other approaches to equilibrium-point control]. In equilibrium-point control schemes, muscle forces and joint torques are not explicitly computed but rather arise as a consequence of the moving equilibrium position and the mechanical properties of muscles and reflexes. This direct dynamics approach has seemed attractive; however, opponents of this formulation have argued for the need to explicitly specify forces in order to compensate for loads.

Experimental evidence in favor of positional control has been provided by empirical studies in which pertur-

bations are delivered to the limb both in postural tasks and during movement. Mussa-Ivaldi et al. (1985) report that after applying perturbations in statics, forces are generated which act to return the limb to the original posture (also see Flash and Mussa-Ivaldi 1990). Similarly, Won and Hogan (1995) have shown that when the limb is perturbed during reaching movements, restoring forces act to return the limb to the unperturbed trajectory. This positional stability during movement is consistent with the idea that shifts in a centrally specified equilibrium position underlie voluntary arm movement. Evidence for positional control is also provided by unloading experiments which suggest that control signals specify a threshold length or joint angle for force development, and that changes to this threshold may underlie voluntary changes in limb position (Feldman 1966; also see Feldman and Orlovsky 1972).

In the present paper we show that a model based on the equilibrium-point hypothesis may compensate for movement-dependent loads by modifying the form of time-varying equilibrium shifts using a simple iterative procedure. Examples of this formulation are presented in the context of both external loads imposed by artificial force fields, and changes in joint interaction torques associated with multi-joint reaching movements. Using a procedure in which positional control signals are adjusted in direct proportion to positional movement error, we demonstrate that equilibrium-point models can achieve adaptation comparable to that previously attributed to direct force control models, without the need for inverse dynamics calculations.

Materials and methods

Arm model

A model of two-joint planar arm motion is used to simulate shoulder and elbow rotation in a horizontal plane [see Gribble et al. (1998) for a full description]. Six muscles are modeled – single-joint elbow and shoulder flexors and extensors, and a double-joint flexor and extensor spanning both joints. Musculo-skeletal geometry is estimated from anatomical sources (An et al. 1981, 1989; Winters and Woo 1990). Muscle force generating ability varies with estimates of physiological cross-sectional area (Winters and Woo 1990). Equations of motion relating accelerations to joint torques were obtained using Lagrangian methods.

The muscle model used in the simulations is a variant of the Zajac (1989) formulation and includes excitation and contraction dynamics and passive muscle stiffness (Fig. 1C). Control signals are based on the λ version of the equilibrium-point hypothesis. In the model, muscle force depends on the difference between a muscle's actual length and a centrally specified threshold length for motoneurone activation, λ, as well as on length- and velocity-dependent afferent feedback and reflex delays. Simulated movements are produced by continuous, time-varying shifts in joint equilibrium angles. These joint-level equilibrium shifts, analogous to the R command in previous versions of the model (Feldman et al. 1990; Flanagan et al. 1990) involve coordinated changes in the values of individual muscle λs. In addition a co-contraction command analogous to the C command can independently change impedance at a given position or during movement. A full description of the procedure relating equilibrium shifts to individual muscle λs, and other aspects of the model may be found in Gribble et al. (1998).

Muscle model parameters related to limb stiffness and damping have been set in order to match empirical estimates of limb impedance in statics (Bennett 1993; Tsuji et al. 1995; Gomi and Kawato 1996). Muscle model parameters have been scaled so that stiffness at the shoulder and elbow have values of 12 Nm/rad and 6 Nm/rad in statics, and maximum values of 40 Nm/rad and 20 Nm/rad during movement. Viscosity in statics is 0.7 Nms/rad at the shoulder and 0.4 Nms/rad at the elbow, and the numerical values of viscosity during movement are 5–7% of maximum joint stiffness [see Gribble et al. (1998) for further details].

Simulations

A model is described for adjusting the time-varying form of equilibrium control signals in order to compensate for loads. In this formulation adjustments to control signals are based on a direct measure of movement error – the difference between desired and actual joint angles. Movement error is in the same coordinate space and shares the same units as simulated control signals (equilibrium joint angles). An advantage of this approach over inverse dynamics formulations is that it eliminates the need for inverse dynamics calculations to specify the compensatory forces (see Discussion). This model is also consistent with the idea that the equilibrium shift is gradual (Bizzi et al. 1984), and is similar in form to the actual movement (Won and Hogan 1995).

In the present formulation, control signals necessary to produce a desired movement are adjusted in the following way. Figure 1A shows an example using single-joint movement. An initial estimate of the control signal (*dashed line, first row*) corresponds to the time-varying joint angle associated with the desired movement (*alternating dots and dashes*), time-advanced by *d* ms, which corresponds approximately to transmission delays and muscle activation dynamics [see Zajac (1989) and Partridge and Benton (1981) for examples]. In the present simulations, a value of 120 ms for *d* was used (see below for sensitivity analyses). This initial command results in a simulated movement (*solid line*) that is different than the desired movement. It should be noted that the initial control signal is based entirely on the desired kinematics – no calculation of the required joint torques is involved.
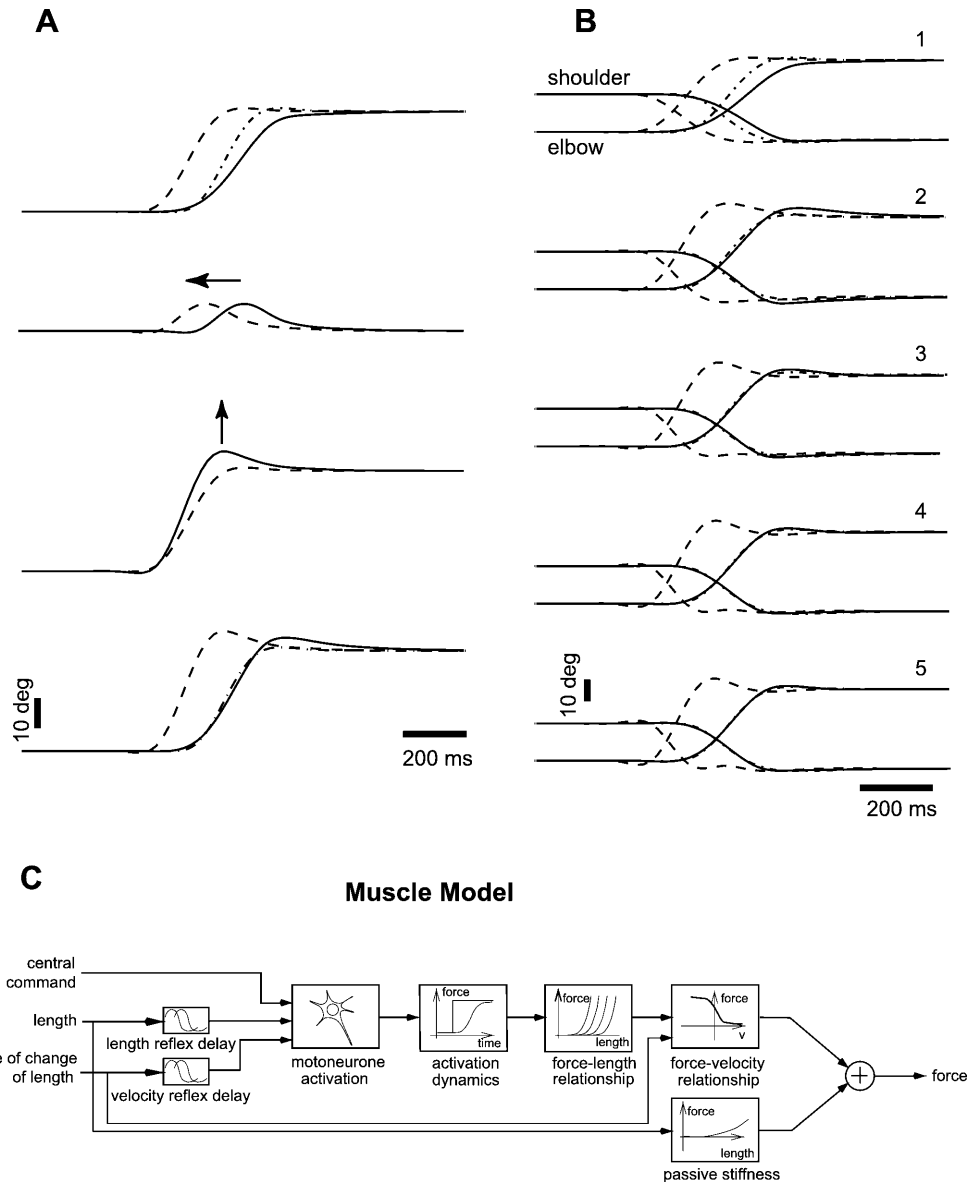
The difference between the desired and actual movement (*solid line, second row*) is likewise time-advanced by *d* ms (*dashed line*) and then added to the previous control signal. In this way information about movement error is directly incorporated into a new command. The *solid line* shown in the third row gives the new control signal and the *dashed line* shows the original command. The simulation is repeated using the new control signal (*fourth row, dashed line*) and results in a predicted movement (*solid line*) that is closer to the desired trajectory (*dots and dashes*).

This may be summarized as follows:

1. An initial time-varying joint equilibrium angle $R(t)$ takes the form of the desired movement M_{des}. This initial command is time-advanced by *d* ms (see below): $R(t)=M_{des}(t+d)$.
2. A simulated movement $M_{obs}(t)$ is produced using control signal $R(t)$.
3. The values of the time-varying joint angles associated with $M_{obs}(t)$ are subtracted from those associated with $M_{des}(t)$ to obtain time-varying movement error $M_{err}(t)$: $M_{err}(t)=M_{des}(t)-M_{obs}(t)$.
4. M_{err} is advanced in time and added to the control signal $R(t)$ to get a new control signal: $R'(t)=R(t)+M_{err}(t+d)$. Movement is then simulated using the new control signal, and the algorithm is repeated.

Figure 1B shows the effects of carrying out several iterations of this procedure. The simulated movement is a two-joint reaching motion involving shoulder flexion and elbow extension. *Panel 1* shows performance of the model before any adjustments are carried out. As above, an initial estimate of the control signals (*dashed lines*) corresponds to the desired joint angles (*dots and dashes*) time-advanced by *d* ms. The resulting simulated movements are shown with *solid lines*. After a single iteration using the model described above (*panel 2*), predicted movement more close-

Fig. 1A–C Procedure for modifying equilibrium shifts in the presence of loads. **A** The steps involved in adjusting the form of the neurally specified equilibrium shift (*dashed line*) to match simulated movement (*solid line*) to a desired motion of the limb (*dots and dashes*). The positional error between desired and actual movements (*second row*) is time-advanced (*dashed line*) and then added to the previous control signal (*third row, dashed line*) to give a new control signal (*third row, solid line*). This new signal results in a movement which better approximates the desired movement (*bottom row*). See text for details. **B** The effect of repeating the procedure 5 times. **C** The muscle mechanical model used to generate the simulated movements [see Gribble et al. (1998) for details]

A

B

10 deg

200 ms

10 deg

200 ms

C

Muscle Model

central command

length

rate of change of length

length reflex delay

velocity reflex delay

motoneurone activation

activation dynamics

force-length relationship

force-velocity relationship

passive stiffness

force

ly matches the desired movement. With successive iterations (*panels 3–5*) movement error is further reduced.

The model described above was used to assess the form of control signals needed to compensate for two classes of movement-dependent loads. First, reaching movements performed in a velocity-dependent force field are simulated. Second, two-joint reaching movements are simulated in which the direction of joint interaction torques at the shoulder and elbow are varied.

Results

Figure 2 gives simulations of planar reaching movements performed in a velocity-dependent force field comparable to that described by Bhushan and Shadmehr (1999). Figure 2A shows simulated movements in the absence of external forces. Eight movements, 10 cm in length, are simulated from a single central position. *Dashed lines* indicate simulated control signals and *solid lines* give predicted movements of the hand. The desired movement in each case is a

straight line minimum-jerk trajectory in Cartesian space (*dots and dashes*) (Flash and Hogan 1985). Movement duration is 500 ms which is comparable to that reported in Bhushan and Shadmehr (1999). Two iterations of the model described above were used to generate the control signals. Note that in the absence of loads, the simulated control signals are in all cases relatively straight and similar in form to the desired movement. The co-contraction command was constant throughout the simulated movements. The magnitude of the co-contraction command was associated with maximum joint stiffness of 38 Nm/rad at the shoulder and 19 Nm/rad at the elbow during movement [see Gribble et al. (1998) and text below].

Figure 2B shows predicted movements performed in a velocity-dependent force field using the same control signals as in Fig. 2A. The simulated force field was such that at any point in time forces at the hand were orthogonal to the instantaneous direction of hand motion and
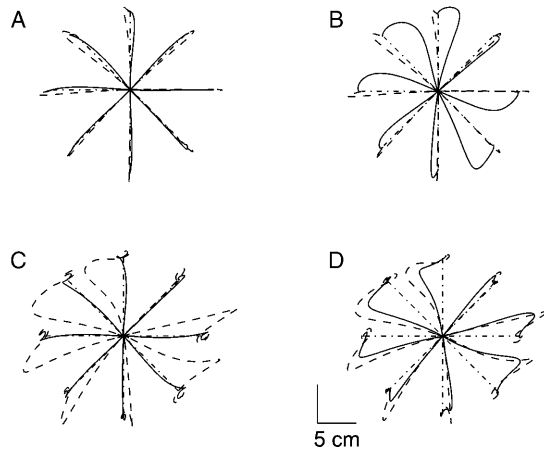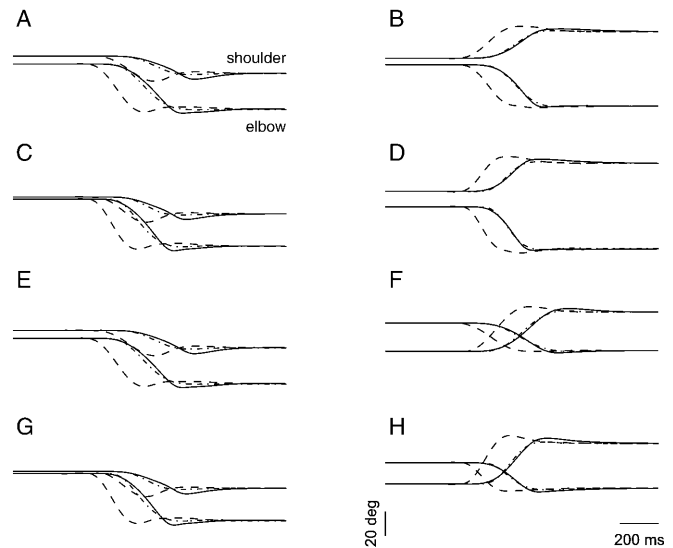
Fig. 2A–D Simulated reaching movements in a velocity-dependent force field. A Simulated hand trajectories (*solid lines*), desired trajectory (*dots and dashes*) and simulated equilibrium shifts (*dashed lines*) in a null field. B The effect of using the control signals given in A for simulated movements in a velocity-dependent force field (see text). C The results of using the adaptation procedure described in the text to modify the equilibrium shifts so as to produce straight hand movements in the force field. The modified equilibrium shifts are again shown with *dashed lines*. D The aftereffect associated with using the (adapted) control signals shown in C after sudden removal of the force field

Fig. 3A–H Modeled control signals for multi-joint pointing movements. In order to explore the control of interaction torques, the velocity and direction of joint motion are varied. All panels show shoulder angle as the upper trace at the beginning of movement. A–D Movements in which elbow motion is held constant but the direction of shoulder motion (and hence the direction of the interaction torque at the elbow) is reversed. E, F Movements in which shoulder motion is constant and the direction of elbow movement (and the direction of the interaction torque at the shoulder) is varied. Two movement speeds are shown: slower (A, B, E, F) and faster movements (C, D, G, H). Simulated co-contraction levels vary directly with peak movement velocity (see Gribble et al. 1998). Two iterations of the adaptation procedure were used for all movements shown here

varied in magnitude with movement velocity (Bhushan and Shadmehr 1999). It can be seen that large deviations in predicted movement (*solid lines*) occur relative to the desired movement (*dots and dashes*). Performance of the model under these conditions is similar to that observed by Bhushan and Shadmehr (1999) when subjects were first exposed to the force field prior to learning.

Figure 2C gives predicted movements after the procedure described above is used to modify control signals to bring the predicted movement into correspondence with the desired movement. Four to five iterations per condition were required to achieve this level of correspondence. It may be noted that the adjusted control signals (*dashed lines*) are almost mirror images of the unadapted trajectories (*solid lines*) in Fig. 2B. This reflects the changes in control signals required to offset the effects of the force field on the limb.

Finally, Fig. 2D shows the predicted after-effect associated with suddenly removing the force field. In empirical studies the rationale for examining the form of movement after removal of the force field is to understand the way in which control signals have been modified during learning. It has been proposed that the form of the movement following removal of the field reflects the form of the control signal needed to generate movements in the presence of the velocity-dependent load (Shadmehr and Mussa-Ivaldi 1994). In Fig. 2D it can be seen that the simulated movements (*solid lines*) following removal of the force field are indeed similar to the form of the equilibrium trajectory (*dashed lines*) needed to produce straight movements in the presence of the load.

It may be noted, particularly in Fig. 2C, that oscillation occurs at the end of the simulated movement. This

may arise due to factors such as underdamping, or alternatively it may reflect instability in the learning algorithm. In order to rule out the possibility that instability may result after further iterations, we repeated these simulations using 100 iterations of the adaptation procedure. It was found that the system remains entirely stable even after 100 iterations – the predicted movements are virtually identical to the desired movements, and the simulated equilibrium shifts are smooth, continuous functions. It may also be noted that while the simulations presented here provide a qualitative approximation to the experimental data, no attempt has been made to precisely match the many features of arm movement described in the Bhushan and Shadmehr (1999) formulation.

Figure 3 shows simulations of multi-joint reaching movements taken from Gribble and Ostry (1999). In that study, by varying the magnitude and direction of joint rotations, we manipulated naturally occurring loads that either assist or oppose movement. We showed that predictive changes in electromyographic activity are observed in shoulder and elbow muscles that vary with the torques at each joint which arise due to motion of the other joint ("interaction torques"). The aim of the simulations shown in Fig. 3 is to explore the extent to which the positional control scheme presented here can account for these predictive adjustments for loads due to multi-joint dynamics, and more generally, whether equilibrium-

point control can produce rapid, multi-joint movements using relatively simple and monotonic equilibrium shifts.

The movements shown in Fig. 3 were chosen to systematically vary the direction of joint interaction torques at the shoulder and elbow (torque at one joint due to motion at the other joint, including both velocity- and acceleration-dependent terms). Two kinds of movements are presented – movements in which elbow kinematics are held constant and the direction of shoulder motion is varied (Fig. 3A–D), and movements in which shoulder kinematics are constant and elbow direction is varied (Fig. 3E–H). Thus in Fig. 3A–D, the torque at the elbow due to shoulder motion is varied, whereas in Fig. 3E–H, the torque at the shoulder due to elbow motion is varied. The simulations are repeated for slower movements (Fig. 3A, B, E, F) and more rapid movements (Fig. 3C, D, G, H). As movement speed increases, the magnitudes of interaction torques likewise increase. Empirical data from one subject are shown with *dots and dashes*, simulated movements are shown with *solid lines* and control signals derived using the model described above are given with *dashed lines*. The flexion direction is downward. Two iterations using the model described above were used to generate the simulated control signals. Note that unlike in Fig. 2, in which we present both the control signals in the absence and presence of external load, in Fig. 3 we show only simulations after control signals have been adjusted to compensate for loads.

In all cases it can be seen that the simulated movements match the empirical data closely. The control signals are basically monotonic with some overshoot at the end of the simulated equilibrium shifts. Gomi and Kawato (1996) have claimed that in order to offset forces due to dynamics the form of equilibrium control signals for multi-joint movement must have a "complex" non-monotonic time-varying form. In contrast the present simulations suggest that appropriate changes to relatively simple equilibrium shifts are sufficient to predict empirical movement patterns for both slow and fast multi-joint movement involving interaction torques. The ability to predict movements using relatively simple equilibrium shifts is due to a number of muscle mechanical and reflex properties which are included in the model presented here, but are absent from the Gomi and Kawato (1996) formulation [see Gribble et al. (1998) for further details]. Some small differences can be seen in the form of simulated control signals for movements in which the joints rotate in the same direction compared to those in which the joints rotate in opposite directions (Fig. 3A versus B, C versus D, E versus F, and G versus H). Presumably these differences reflect the changes in control needed to offset inertial and dynamical effects such as interaction torques (Gribble and Ostry 1999).

In these simulations, the modeled co-contraction command was constant throughout the simulated movement. The magnitude of the command varied directly with movement velocity. This scaling of the co-contraction command in proportion to movement speed was based on

findings reported by Gribble et al. (1998) relating co-contraction to empirical measures of joint stiffness during movement (Bennett 1993). Specifically, it was found that when simulated co-contraction varied in proportion to movement speed, simulated joint stiffness matched values observed empirically for single-joint movement. It should be noted that the magnitude of the co-contraction command was scaled in proportion to movement velocity alone. Co-contraction values were not adjusted to compensate for the interaction torques involved in the simulated movements. Co-contraction values used in these simulations correspond to maximum shoulder joint stiffness levels in the range of 20 Nm/rad in statics and 60 Nm/rad during rapid movements (Gribble et al. 1998).

Elsewhere it has been suggested that high stiffness values are required in order to produce multi-joint movement using equilibrium control models (Gomi and Kawato 1996). The modeled stiffness of the limb in the present simulations matches that observed empirically for both single- and multi-joint movement (Bennett 1993; Gomi and Kawato 1996). High stiffness is not required to use equilibrium control in this formulation.

In the present study co-contraction levels were matched to values obtained in Gribble et al. (1998). When co-contraction levels were lower than those needed to match stiffness in empirical studies (Bennett 1993; Gomi and Kawato 1996; Gribble et al. 1998) the derived control signal tended to overshoot the target and displayed terminal oscillation about the final position. When co-contraction levels were higher than those inferred from empirical studies, the equilibrium shift came closer to replicating the form of the desired trajectory. See sensitivity analyses below for further details.

Sensitivity analyses were carried out to assess the dependence of model performance on the number of iterations in the adaptation procedure, the simulated co-contraction level and the time parameter, *d*. Simulations of the empirical data shown in Fig. 3 were used for these analyses. Figure 4A shows the effects of increasing the number of iterations (the number of times the control signal is adjusted in the model described above). As the number of iterations increases, the root mean square difference between the empirical and simulated movements decreases. Larger numbers of iterations result in smaller and smaller decreases in fitting error. Figure 4B shows the relationship between the number of iterations and the complexity of the simulated equilibrium shifts (assessed by the root mean squared jerk). As the number of iterations increases, the complexity of the control signal likewise increases in a monotonic fashion. Root mean squared jerk was chosen as a measure of complexity – in particular, of the non-monotonicity of the equilibrium shift – since jerk is inversely related to the smoothness of a time-varying function (Flash and Hogan 1985).

Figure 4C, D gives the dependence of model performance on the simulated co-contraction level. Figure 4C shows that the root mean squared difference between simulated and empirical movements decreases with high-
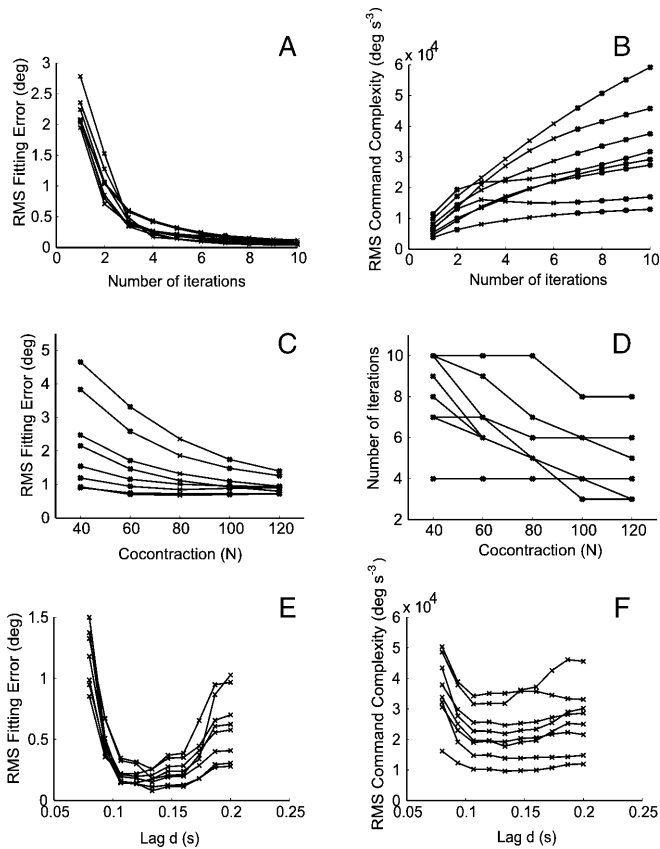
Fig. 4A–F Sensitivity analyses. Analyses were based on all movements shown in Fig. 3. The relationship between the number of iterations in the adaptation procedure and the fitting error (**A**) and the complexity of the resulting equilibrium shift (**B**) is shown. **C** The dependence of the fitting error on the level of simulated co-contraction. **D** The dependence of the number of iterations required to reach a fixed level of movement accuracy on the level of simulated co-contraction. The dependence of the fitting error (**E**) and the complexity of the equilibrium shift (**F**) on the value of *d*, the amount by which the error signal is time-advanced prior to summation with the control signal (see text)

er levels of simulated co-contraction. Two iterations of the model were used for the simulations shown in Fig. 4C. Figure 4D gives the relationship between co-contraction level and the number of iterations required to reach a fixed level of accuracy. As the co-contraction level increases, a tendency towards fewer iterations is observed. It may be noted, however, that the dependence of the number of iterations on the co-contraction level is relatively weak.

Figure 4E, F shows the relationship between model performance and *d*, the amount by which the error signal is time-advanced prior to summation with the control signal. The relation between the root mean squared fitting error (Fig. 4E) and *d* is a u-shaped function – as *d* increases, the error decreases to a minimum in the range of 120 ms, and then increases with larger values of *d*. The complexity of the simulated equilibrium shift (root mean squared jerk) shows a weaker dependence on *d* (Fig. 4F), however, the general form of the relationship is similar to that seen in Fig. 4E above.

Discussion

Models of motor control can be generally classified as either force or position controllers. Force control models may require coordinate transformations and inversions to derive control signals appropriate to desired movements, but as a result they can readily reproduce a wide variety of motor behaviors including movements in complex load environments. In contrast, equilibrium-point position controllers avoid the need for inverse dynamics calculations and simplify movement planning; however, reports of their applicability to more complex force environments have been limited (Flash and Gurevich 1997). In the present paper we have shown that an equilibrium-point model can produce arm movements in the presence of external and self-generated loads. We have shown that using a simple iterative model, equilibrium control signals may be adjusted based on position error to produce arm movements in the presence of loads.

An implication of the present results is that some information about limb dynamics and external loads is incorporated into control signals in order to carry out the adjustments that offset these loads. It has been suggested that this sort of predictive compensation may be based on "internal models" of the motor system. It has been proposed that the internal model is used both to compute the motor commands needed to produce specific movements (the "inverse model", e.g., Uno et al. 1989; Atkeson 1989; Kawato et al. 1990) and to anticipate the consequences of particular control signals (the "forward model", e.g., Jordan and Rumelhart 1992; Wolpert et al. 1995). The present model focuses on the determination of commands to produce specific movements, but avoids the explicit inversions proposed in other formulations. However, this is not incompatible with the more general notion of internal models, and in particular, with the notion that the nervous system learns to adjust control signals in a predictive manner to compensate for movement-dependent loads.

In this paper we propose a model of how sensory information is used to correct for movement errors. This may be distinguished from the related yet separate issue of generalization in motor learning. There is substantial evidence showing that subjects use information gained in learning to perform individual movements to generalize to novel situations (Shadmehr and Mussa-Ivaldi 1994; Lackner and Dizio 1994; Gandolfo et al. 1996; Conditt et al. 1997; Goodbody and Wolpert 1998; Conditt and Mussa-Ivaldi 1999). The model presented here is not a model of generalization but comprises one of its essential components. Generalization is presumably based on the kinds of information obtained in the acquisition of individual movements. The model proposed here may be incorporated in any model of generalization that involves a learned mapping between control signals and desired states (Jordan and Wolpert 2000).

There are a number of advantages of the present model. First, as noted above, there is no need for inverse dynamics calculations in order to specify the control sig-

nals required for a given movement. In the model, time-varying muscle forces and joint torques arise as a consequence of the shifting equilibrium, muscle properties and reflexes, and are not explicitly computed. In contrast, in force controllers, errors in position must be transformed into appropriate changes in force. Moreover, an advantage of equilibrium-point models such as the one used in the present paper is that, consistent with empirical findings both in statics and during movement, mechanical stability is generally preserved. Force control models do not necessarily provide similar assurances of stability. Some recent force-based models have included additional servo-control mechanisms to provide stability (e.g., Shadmehr and Mussa-Ivaldi 1994; Bhushan and Shadmehr 1999), however, elements of these models are linear, whereas the muscle mechanical properties and reflexes that contribute to stability in the human arm are known to be nonlinear in form (e.g., Houk and Rymer 1981; Zajac 1989).

A further characteristic of the present model is that the proposed error signal may be directly available to the nervous system. For example, information from muscle spindle afferents may be combined at a cortical level with signals related to desired movement to make adjustments to control signals. The present model assumes that by means of this proprioceptive afferent mechanism, the nervous system develops a representation of the changes to control signals needed to offset movement-dependent loads. However the present model differs from other related proposals in that a fast-time simulation (a "forward model") is not used to adjust central commands (Jordan and Rumelhart 1992; Wolpert et al. 1995; Bhushan and Shadmehr 1999).

The algorithm presented here may be compared to and contrasted with recent models based on feedback error learning and reinforcement learning. Feedback error learning uses a feedback controller (such as a linear servo controller) to guide the learning of a concomitant feedforward controller (an inverse model) (Kawato et al. 1987, 1990; Kawato and Gomi 1992). Specifically, a feedback motor command which is proportional to observed movement error is used during ongoing movement control as an error signal to train an inverse model of limb dynamics. In contrast, in models of reinforcement learning, force control laws are formed using simple learning mechanisms based on a scalar reward signal rather than a complete trajectory [see Sutton and Barto (1998) for review]. However, no "internal model" is required. A disadvantage of reinforcement learning algorithms is that they take a long time to converge. In feedback error learning and reinforcement learning, information about movement error is used, albeit in a more indirect manner than in the algorithm presented here, to modify control signals for movement. Moreover, in contrast to the present model, force-based algorithms for feedback error learning and reinforcement learning typically assume that descending neural control signals explicitly specify time-varying muscle forces or joint torques.

An equilibrium-point control model that provides compensation for loads has also been described by Flash and Gurevich (1997). In their formulation, adaptation to loads involves the modification of both limb stiffness and the time-varying form of the equilibrium trajectory. Their model assumes that in order to compensate for a given load, the form of the equilibrium shift is modified in proportion to the ratio of the load force to the stiffness of the limb. As in the model described in the present paper, no coordinate transformations between movement error and muscle forces are required to generate changes in the control signal since the ratio of load force to limb stiffness has units of position, as does the equilibrium control signal itself. Their model differs from the one presented here to the extent that a representation of external joint torques and joint stiffness is required in order to make changes to control signals. In the present model positional error alone is used to adjust control signals.

The issue of force versus position control has been recently linked to the issue of the complexity of the time-varying control signal. For example, Gomi and Kawato (1996) reject the equilibrium-point hypothesis on the basis of a postulated "complex" non-monotonic equilibrium shift (but see Gribble et al. 1998). One of the aspects of the original formulation of the λ version of the equilibrium point hypothesis was indeed that movements may be produced by using simple constant rate equilibrium shifts and that muscle mechanical properties and reflexes tend to dominate forces arising from dynamics. While this may be generally true for slow movements, recent data has pointed to the need for more complex control signals to compensate for and anticipate dynamic loads (Flanagan and Wing 1997; Gribble and Ostry 1999). Although this may be inconsistent with the notion of simple equilibrium shifts, it is incorrect to assume that this is evidence for force control and cause for the rejection of position control models in general (Gomi and Kawato 1996). Indeed the present results show that equilibrium models can readily achieve compensation for dynamic loads using a simple procedure for modifying the form of equilibrium shifts.

Isometric force adjustment tasks may also be implemented using the present model (Feldman et al. 1990). In order to produce a given set of forces, for example to generate an isometric force against an object, the control signal must specify a virtual position within or beyond the object such that the difference between the actual limb position at the point of object contact and the virtual position leads to the desired force. Force adjustment tasks using the model thus require the adjustment of a positional control signal to produce a desired force. In this context information concerning the relation between positions and forces is needed.

A potential concern with permitting increased complexity of positional control signals in the context of an equilibrium point model is the extent to which the resulting formulation can be falsified. The version of the equilibrium-point model presented here and elsewhere (Feldman 1986; Feldman et al. 1990; Gribble et al. 1998)

makes testable predictions about several aspects of the mechanism underlying movement control. For example, it proposes that agonist and antagonist activation are linked through "reciprocal" central commands. The model also makes specific predictions about the relative levels of central and afferent contributions to muscle activation during movement. Moreover, the present formulation can provide explicit predictions about the time-varying form of muscle activity associated with adapted control signals.

The model presented here relies on the assumption that information about the control signal, the desired trajectory and the actual trajectory is available to the nervous system following a movement in order that adjustments may be carried out on the basis of positional error. Whereas the specific mechanisms underlying the retention of information needed for adaptation are unknown, there is evidence from psychophysical and imaging studies of force-field learning that mechanisms exist for representing and storing this kind of information (Brashers-Krug and Shadmehr 1996; Shadmehr and Brashers-Krug 1997; Shadmehr and Holcomb 1997). Control signals associated with force-field learning are initially stored in a labile form that has a time course in the range of 4–6 h. Following consolidation, a more permanent representation may be maintained for several months.

In the present formulation it has been possible to reproduce empirically observed movement patterns on the assumption that the magnitude of the co-contraction command is held constant over the course of a given movement. However, consistent with empirical data, we have assumed that the magnitude of the co-contraction command is scaled in proportion to movement speed (Bennett 1993). Likewise, in modeling studies in order to reproduce empirically observed patterns of limb stiffness the magnitude of the co-contraction command must be scaled in proportion to movement speed (Gribble et al. 1998).

In the simulations presented here, the adaptation procedure was halted after a fixed number of iterations. Other stopping rules may be used as well. For example, if simulations are based on empirically recorded movements, the procedure may be halted once movement accuracy falls within a range associated with the empirically measured variability. We have repeated the simulations shown in Fig. 3 using a stopping rule based on ±3 SDs about the average trajectory. In all cases, two or three iterations were required to generate simulated movements that fell within this range.

In principle one may continue to iterate the procedure to achieve any desired level of movement accuracy. However, as illustrated in Figs. 1B and 4, as the number of iterations increases, smaller and smaller reductions in fitting error are associated with increases in the complexity of the modeled control signal. To guard against over-fitting, empirically based criteria such as described above may be used to limit the number of iterations. More generally, information about movement errors may be provided by sensory feedback and used in conjunction with the accuracy requirements of the task in order determine the need for further adaptation.

As a first approximation, we have assumed that in the process of modifying control signals, the positional error signal may be directly added to the previous control signal using a gain of 1.0. As a consequence the model achieves compensation for loads using a small number of iterations. However, as is true of other models of adaptation, the gain of the error signal remains a free parameter that may be estimated on the basis of empirical data. The time course of compensation in the model may thus be increased by using smaller multiples of the error signal.

Although we have demonstrated that the algorithm presented here successfully adapts for loads in the context of the present human arm model, presumably the stability of the algorithm in systems with other dynamics, or when coupled to other loads, may vary. The generalizability of the algorithm to other mechanical environments thus remains to be established.

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