

Servo Hypotheses for the Biological Control of Movement

Joseph McIntyre
Emilio Bizzi

Department of Brain and Cognitive Sciences
Massachusetts Institute of Technology

ABSTRACT. An analysis is made of equilibrium-point models for motor control, describing these models in the context of servo control mechanisms. We considered issues of speed and stiffness scaling that are incompatible with current formulations of the equilibrium-point models. A modification of the equilibrium-point models is proposed in which the central nervous system controls velocity as well as positions during the course of fast limb movements. Numerical simulations are presented that verify that such a servo control mechanism could successfully produce fast limb movements, as observed in human subjects.

Key words: elbow movements, equilibrium-point hypothesis, human arm movements, motor control

A number of researchers have proposed *servo control models* to describe the neural control of movement, based on the elastic properties of biological motor systems. Merton (1953) originally proposed a servo control model based on the stretch reflex, for generating movements. The reflex acts to control posture by increasing the activation of the muscles in proportion to the amount of muscle stretch. It was proposed that movements are generated by altering the set-point of the posture control servo through the gamma motor neuron drive. Thus the tasks of controlling movement and posture were unified under a single control scheme. Merton's servo hypothesis first brought forth the idea of *movement from posture*: The same neuromuscular system that acts to control the stationary position of the limb (i.e., the stretch reflex) could be used, with appropriate modulation of the set-point, to control movements as well.

Merton's (1953) hypothesis is inconsistent, however, with experimental observations of alpha-gamma coactivation as well as with analysis of stability in the face of significant feedback delays (to be discussed further). Although this theory has since been proven wrong for biological systems, the underlying concept of movement from posture remains. Feldman (1966a, 1966b, 1986) has proposed the *equilibrium-point model* for motor control, also based

on the feedback properties of reflexes. Bizzi, Hogan, and colleagues (Bizzi, Accornero, Chapple, & Hogan, 1984; Bizzi, Dev, Morasso, & Polit, 1978; Bizzi, Polit, & Morasso, 1976; Polit & Bizzi, 1979) have emphasized the elastic properties of the muscles themselves. They have demonstrated that goal-directed movements can be performed in the absence of sensory feedback. The spring-like mechanical behavior of the muscles acts without the problematic delays of the reflex circuitry. Common to both of these models, central motor commands act to select a desired equilibrium position. Under these models, movements are executed by a gradual shift in the equilibrium position from the initial to the final position (Bizzi & Abend, 1985; Hogan, 1984a). Evidence suggests that the equilibrium-point model for motor control is adequate for describing certain classes of multijoint movements (Bizzi & Abend, 1985; Flash, 1987).

An on-going discussion in the field of human motor control concerns feedforward versus feedback models of movement control. Does the central nervous system (CNS) represent movements in dynamic terms, with explicit representations of the forces and torques required for a movement? Or does the motor system rely on feedback only to generate the appropriate muscle forces from a central representation of the desired movement, thus creating a servomechanism for the control of movement? This article addresses the question by examining quantitatively the performance of several feedback-based control hypotheses.

Servo Models for Biological Motor Control

To focus the ensuing discussion on the issue of feedforward versus feedback control, we have adopted the follow-

Correspondence addresses: J. McIntyre, Laboratoire de Physiologie Neurosensorielle, 15 Rue de l'École de Médecine, 75270 Paris Cedex 06, France. E. Bizzi, Department of Brain and Cognitive Sciences, E25-526, M.I.T., Cambridge, MA 02139.

ing strict working definition of a servo: A *servomechanism* is an automatic control system for which the input to the system is simply a representation of the desired system output. Figure 1 illustrates this point. The system in Figure 1a fits the definition of a servo; the system in Figure 1b does not. Appropriate control via Circuit 1b requires knowledge of the system characteristics, thus requiring an element of feedforward control to achieve satisfactory performance. Circuit 1a, on the other hand, utilizes feedback alone to produce a movement close to the desired input.

Can the human motor system be described as a servomechanism? There is no question that the human motor system employs feedback to control movements. The neuromuscular system effectively corrects for external perturbations applied to movements and postures (McKeon, Hogan, & Bizzi, 1985). We wish to determine to what extent the peripheral motor system forms a position servo for the generation of limb movement. Can feedback alone account for the movements, or must the CNS provide a feedforward component based on the dynamics of the limb and the desired motion?

Review of Servo Hypotheses: Merton (1953)

The reflex servo loop proposed by Merton (1953) was an interesting hypothesis for movement control based on feedback alone. The theory was based on the gamma motor drives to muscles in the human motor system. Under this scheme, the gamma motor neurons would drive the muscle spindles through the desired trajectory of the limb. The error between the spindle movement and the actual muscle movement would generate the neural activity in the alpha motor neurons (via the spinal reflex) that actually drive the limb. This method is attractive from a computational point of view because it produces the desired movement without an explicit solution of the *inverse dynamics problem*.¹ To produce a limb movement, the CNS commands a time series of positions for the muscle spindles via the gamma motor neurons. The muscle forces and resulting joint torques are generated implicitly by reflex feedback onto the alpha motor neurons. Figure 2 shows a block diagram representation of the Merton reflex servo model of motor control.

Experimental and analytical evidence do not support Merton's (1953) theory, however. Feedback-loop delays may limit the speed of stable operation for such a system (Rack, 1981). In addition, alpha and gamma motor units are known to become active simultaneously (alpha-gamma

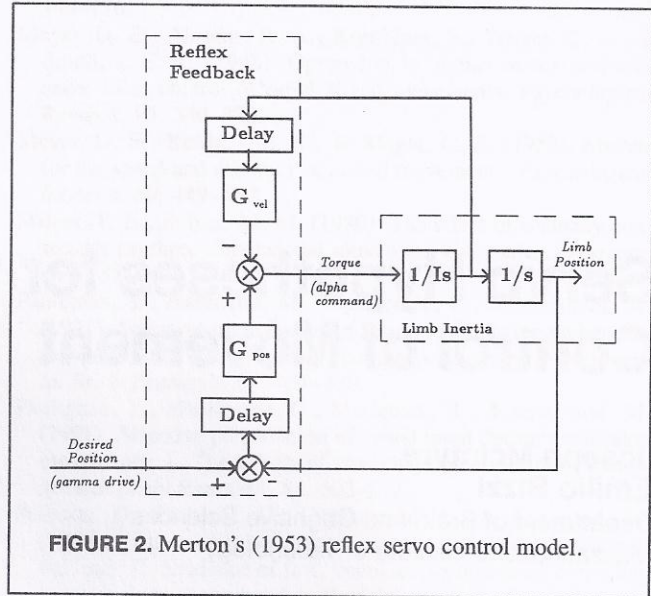


FIGURE 2. Merton's (1953) reflex servo control model.

coactivation) at the initiation of movement (Vallbo, 1970). The reflex servo hypothesis would predict a slight lead in the activation of the gamma motor neurons. Alpha motor neurons would fire only after the stretch reflex signal had reached the spinal cord, a delay of approximately 20 ms for the human arm. Finally, deafferented monkeys are known to be capable of directed movement of their limbs in the absence of reflex feedback (Bizzi et al., 1978; Bizzi et al., 1976). This would not be possible if reflex feedback were the sole source of alpha motor activation.

Equilibrium-Point Models

Alternatives to Merton's (1953) hypothesis that fall into the class of servomechanisms are described by the equilibrium-point models for motor control. Under these models, the mechanical properties of muscles and the myotactic reflexes generate equilibrium positions for the limb, at which the net force and torque acting on the limb is zero. Movements are generated as shifts in the equilibrium posture of the limb. The equilibrium-point hypotheses are in better agreement with the experimental data, yet they maintain the computational simplicity of Merton's reflex servo hypothesis.

Currently there are two formulations of the equilibrium-point hypothesis under consideration. The α model, as proposed by Bizzi, Hogan, and colleagues (Bizzi & Abend, 1985; Bizzi et al., 1976; Hogan, 1984a, 1985) relies on the spring-like properties of muscles to generate the forces required to cause movement. Feldman's (1966a, 1986) λ model, on the other hand, emphasizes the role of stretch reflexes for producing movements of the limb. In the following sections, we present these two models in a common block-diagram form to show how these two models are related and how they can be characterized as servo models for the control of movement. We consider here only models of free limb movements, in the absence of external forces or

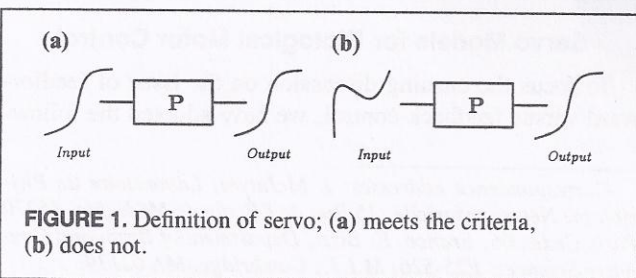


FIGURE 1. Definition of servo; (a) meets the criteria, (b) does not.

constraints. Note also that we leave out certain additional features of the lambda model that don't fit within the framework of a servo control mechanism, namely, the inclusion of direct descending influence on alpha and gamma motor neurons. We leave the consideration of these features to the Discussion.

α Model

The α equilibrium-point model is based on the mechanical properties of muscles. As a muscle is stretched, the tension in the muscle increases (Hoffer & Andreassen, 1981; Rack & Westbury, 1969). The muscle acts like a spring for passive displacements. For two or more muscles acting in opposition around a joint, there exists an equilibrium position at which the net torque acting on the joint is zero. The location of the equilibrium point is determined by the rest lengths and relative stiffness of the muscles, which are in turn determined by their activation levels (Bizzi, Chapple, & Hogan, 1982; Hogan, 1984a). If the limb is displaced from this position, the spring-like properties of the muscles generate the appropriate restoring torques to return the limb to equilibrium.

Figure 3 is a simplified model of the musculoskeletal system of a single joint. The position feedback gain, K , corresponds to the net stiffness of all the muscles acting around the joint, whereas B is the net viscosity. The inputs to this model system consist of a reference trajectory that specifies the equilibrium position of the joint as a function of time and a stiffness level determined by the level of agonist/antagonist coactivation. (We have assumed, for simplicity, that the viscosity, B , is dependent on K so as to produce a constant damping ratio with no load.) Limb movements can

be generated by adjusting the muscle activations to smoothly vary the equilibrium point along the desired path. As in Merton's (1953) reflex servo model, no explicit computation of inverse dynamics is performed. In contrast to the reflex-based model, however, stability is not an issue. Because the servo action that generates the movement is based on the mechanical properties of the muscles, there is no problem with feedback delays.

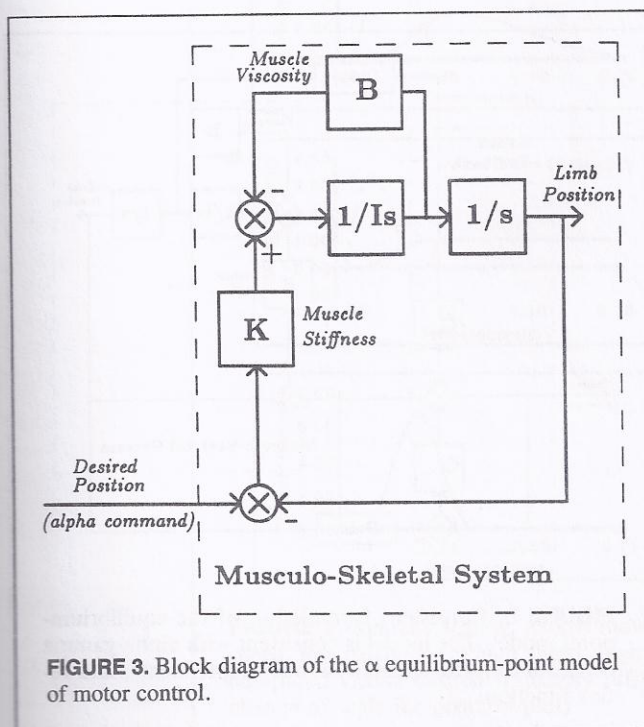
The experimental evidence for the α equilibrium-point model is quite strong. Deafferented monkeys can make pointing movements to visually selected targets in the absence of any sensory feedback about the location of the limb (Bizzi et al., 1984; Bizzi et al., 1982; Bizzi et al., 1976; Hogan, 1984a). Furthermore, the production of such movements is robust with respect to perturbations imposed by the experimenters (Bizzi & Abend, 1985; Bizzi, et al., 1984; Hogan 1982; Hogan, 1984a).

The α formulation of the equilibrium-point hypothesis is not completely satisfactory, however. Experiments with deafferented monkeys and humans have shown that motor performance in the absence of sensory feedback is seriously degraded. Although the limb may reach the desired final position, the trajectory of the arm is much more erratic than in normal subjects (Ghez, Gordon, Ghilardi, Christakos, & Cooper, 1990). Clearly, reflexes play an important role in the production of movements and should be included in any model of motor control.

λ Model

Under the λ equilibrium-point model for motor control, movements are also generated by shifts in the equilibrium posture of the limb. The λ model differs from the α model in the way that the equilibrium position is defined. Under the λ model, changes in equilibrium position are generated by adjustments to the threshold of the stretch reflex (Berkinblitt, Feldman, & Fukson, 1986; Feldman, 1986). The simplest possible interpretation of this formulation is shown in the block diagram of Figure 4a. Relating this block diagram to Feldman's terminology (Levin, Feldman, Milner, & Lamarre, 1992), the input of desired positions corresponds to the reciprocal command (r); the reflex gain G_{pos} , which could also be modulated during movement, corresponds to the coactivative command (c); whereas the gain G_{vel} corresponds to the damping factor μ (Feldman, 1986). Feldman has pointed out that due to the limited stiffness of the feedback system, the central command defining a given equilibrium position is dependent on the force acting on the limb, and as such, the model does not represent a servomechanism with regard to limb position. We consider here, however, only free limb movements with no external force load. It is probably true, based on measurements of limb stiffness (Bennet, Hollerbach, Yu, & Hunter, 1992), that static forces such as gravity must also be represented in the central motor command.

At first glance, this model appears to be identical to the Merton (1953) hypothesis. The model in Figure 4a differs



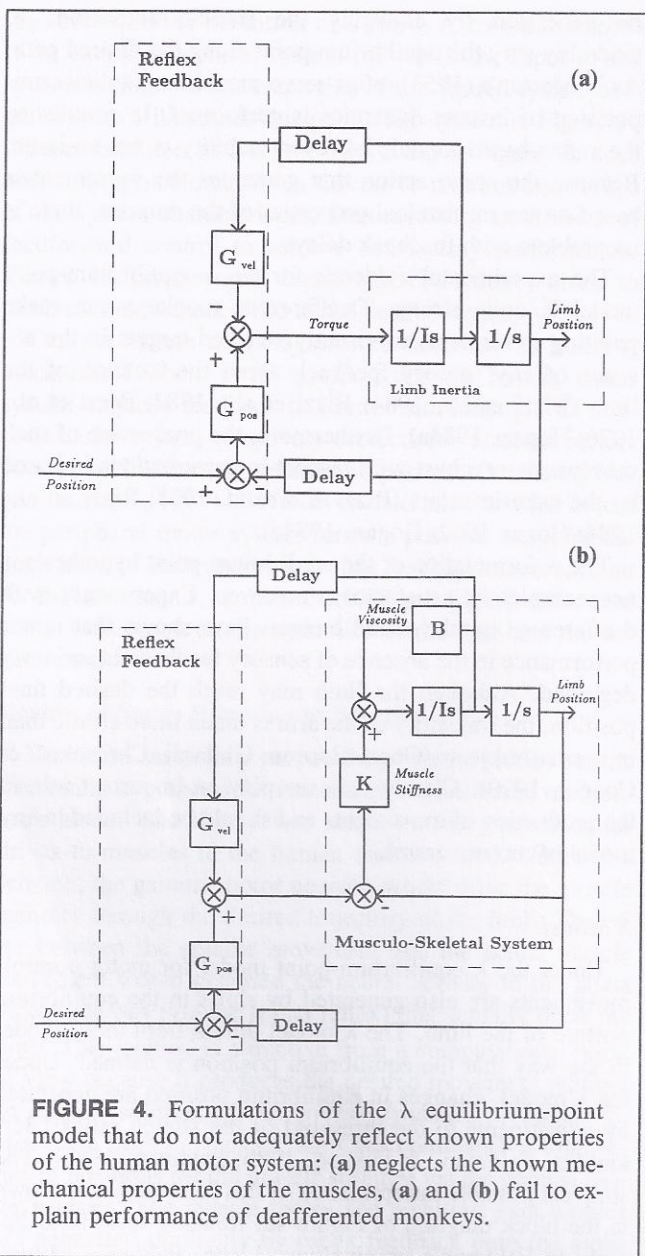


FIGURE 4. Formulations of the λ equilibrium-point model that do not adequately reflect known properties of the human motor system: (a) neglects the known mechanical properties of the muscles, (a) and (b) fail to explain performance of deafferented monkeys.

from the Merton circuit of Figure 2 in one subtle way. Because the subtraction of the CNS-generated reference signal and the spindle-generated position signal occurs in the spinal cord, there is no delay between the initiation of the central motor program and the alpha motor signal. This model is consistent with the experimentally observed alpha-gamma coactivation.

The model in Figure 4a represents the muscles as pure force generators and thus neglects the known mechanical properties of the muscles themselves (Hoffer & Andersen, 1981; Rack & Westbury, 1969). Model 4a also has the same inherent feedback delays as the Merton model and may therefore suffer from problems of stability. The equilibrium-point model is dependent on the mechanical properties of the muscles to provide stability to the system.

Figure 4b shows a second interpretation of the λ hypothesis, including muscle elastic and viscous behavior. The reflex circuit computes an equilibrium position for the musculoskeletal system, based on the sensory feedback from the limb. This equilibrium point is fed to the muscles via an appropriate combination of agonist and antagonist alpha motor commands. This model is, however, inconsistent with the experiments in deafferented monkeys. If the reflex pathways were cut, the muscles would no longer receive an alpha motor command that is consistent with the desired posture or movement.

The interpretation of deafferentation studies is subject to considerable debate, the main objection being that the deafferentation process radically changes the control system. The subject may be obliged to change the control strategy to accommodate the new system, and thus the behavior may have little connection with normal control of movement (Feldman, 1986; Houk & Rymer, 1981). On the other hand, there is evidence that intact human subjects can exploit the elastic properties of muscles through cocontraction to define a stable equilibrium position when loop delays limit the effectiveness of reflex feedback (Hogan, 1984b). Explanations for the production of movement in deafferented situations depend also on descending influences on the alpha motor neurons (Feldman, 1986). The model to be presented in Figure 5 reflects this influence and explicitly identifies the ability of the motor system to define an equilibrium position through this pathway. Other forms of descending control would be possible, but these would constitute a form of feedforward control, and thus would violate our definition of servo control. Of course, this in itself does not rule out such descending signals, but the beauty of the movement from posture hypothesis is lost (see Discussion).

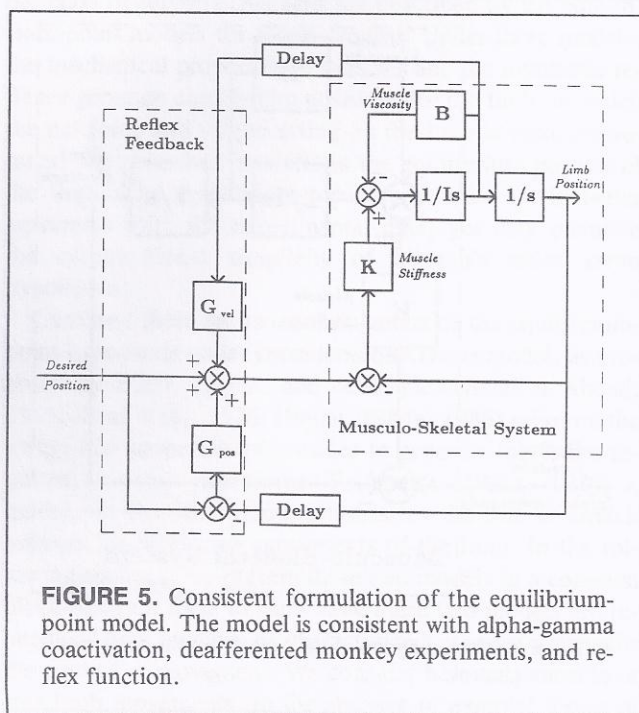


FIGURE 5. Consistent formulation of the equilibrium-point model. The model is consistent with alpha-gamma coactivation, deafferented monkey experiments, and reflex function.

Unified Equilibrium-Point Model

Figure 5 is the simplest interpretation of the equilibrium-point hypothesis that satisfies both the theoretical stability constraints and the experimental observations. In this model, the centrally generated equilibrium point is fed di-

rectly to the musculoskeletal system, via the alpha motor neurons. This signal is modified during the course of the movement by sensory feedback. The equilibrium position of the limb is defined by both the threshold of the stretch reflex and the mechanical properties of the muscles.

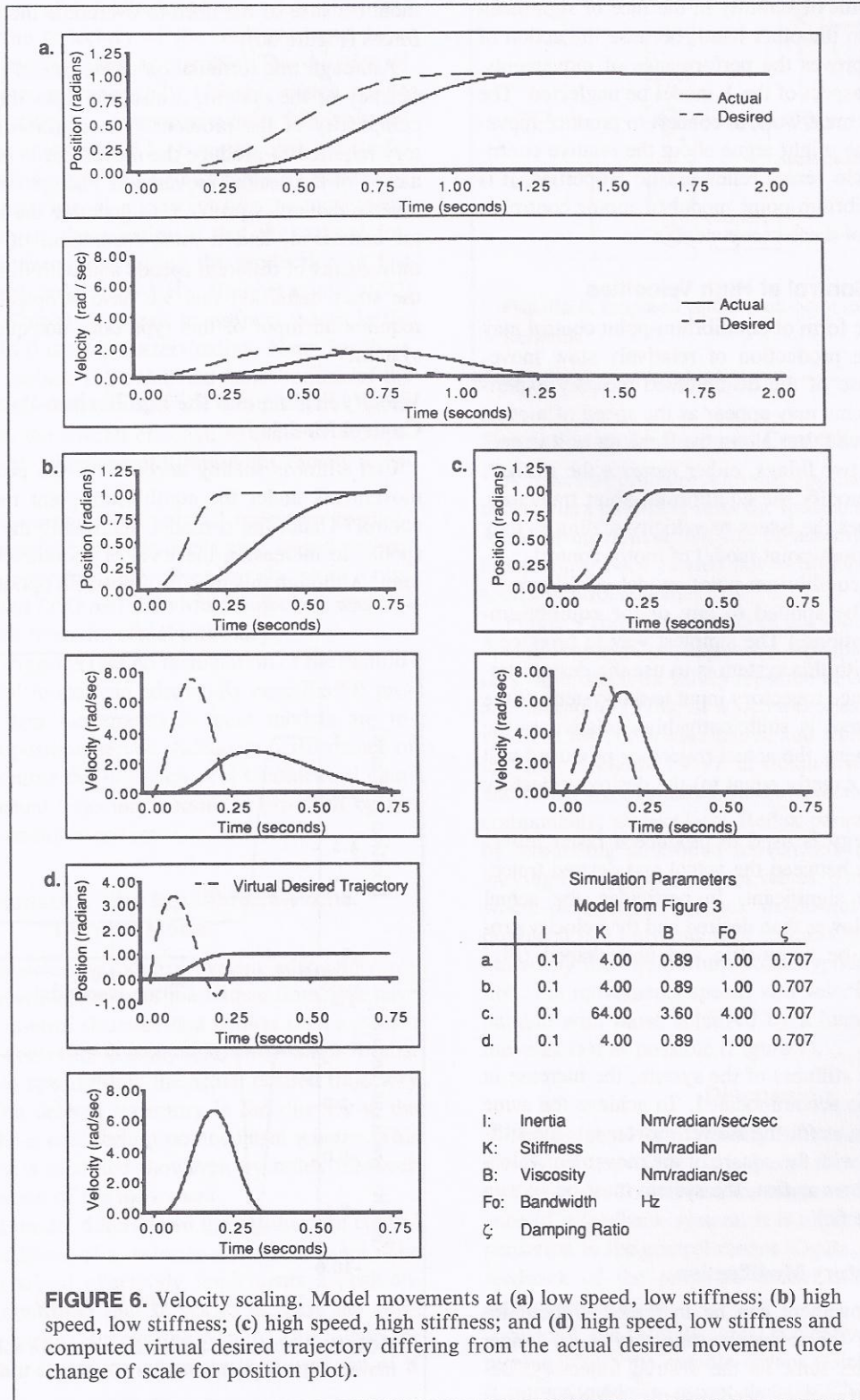


FIGURE 6. Velocity scaling. Model movements at (a) low speed, low stiffness; (b) high speed, low stiffness; (c) high speed, high stiffness; and (d) high speed, low stiffness and computed virtual desired trajectory differing from the actual desired movement (note change of scale for position plot).

The point of the foregoing discussion is that Figure 5 represents the only viable formulation of the equilibrium-point model. At the heart of this formulation is the α model shown in Figure 3. One cannot accept the equilibrium-point hypothesis without accepting the α model as an important component because the muscle elastic properties themselves define an equilibrium position, and these properties can alleviate problems of stability in the face of significant feedback delays. On the other hand, because the action of reflexes clearly improves the performance of movements, neither should this aspect of the λ model be neglected. The two control circuits must work in concert to produce movements. Although one might argue about the relative contributions of the muscle versus reflex elastic properties, it is clear that the equilibrium-point model of motor control is dependent on both of these components.

Servo Control at High Velocities

Whereas the basic form of equilibrium-point control may be adequate for the production of relatively slow movements (as in the case of the deafferented monkey experiments), some problems may appear as the speed of motion is increased. To move faster along the same path, it is necessary to do one of two things, either increase the stiffness of the muscles or modify the equilibrium-point trajectory. This section examines the issues of velocity scaling as they relate to the equilibrium-point model of motor control.

Consider the α equilibrium-point model of Figure 3. (This analysis can be applied to any of the equilibrium-point model formulations.) The simplest way to produce a desired trajectory with this system is to use the desired trajectory as the reference trajectory input to the system. If the stiffness of the system is sufficiently high relative to the speed of the movement, the actual trajectory produced will be close to (but not exactly equal to) the desired trajectory (Figure 6a).

If the same strategy is used to produce a faster movement, the difference between the actual and desired trajectories may become significant. In particular, the actual movement may be slower than desired and the velocity profile will no longer be symmetric and bell shaped (Figure 6b).

Stiffness Scaling

By increasing the stiffness of the system, the increase in desired speed can be accommodated. To achieve the same level of performance as for the slower movement, the stiffness must be scaled with the square of the movement velocity. To move four times as fast, the system must be sixteen times as stiff (Figure 6c).

Equilibrium Trajectory Modification

The speed of movement can be increased without increasing stiffness if the reference trajectory is no longer constrained to be the same as the desired trajectory. Because the reference trajectory need never be achieved, it has

been called a *virtual trajectory* (Hogan, 1984a; Latash & Gottlieb, 1991). Using this approach, the reference trajectory will initially lead, then lag the actual desired position during the course of the movement. The virtual equilibrium position, that is, the equilibrium position that would be achieved in static or quasi-static conditions, may in fact overshoot the final desired position during the fast movement because of the need to overcome inertial and viscous forces (Figure 6d).

Although this formulation of the model increases the efficiency of the system, it also increases the computational complexity of the problem. The equilibrium-point trajectory required to produce the movement is no longer simply a copy of the desired movement. The system must solve the inverse dynamics problem to generate the appropriate motor command, and it must recompute this command for movements of different speeds and with different loads. By the strict definition that we have adopted, a system that requires an input of this type does not qualify as a servo system.

Velocity Scaling and the Equilibrium-Point Control Models

Can stiffness scaling account for the production of fast movements under the equilibrium-point models of motor control? Under the α model, increasing the stiffness corresponds to increasing the level of cocontraction around the joint. Although this may be a possible option for increasing

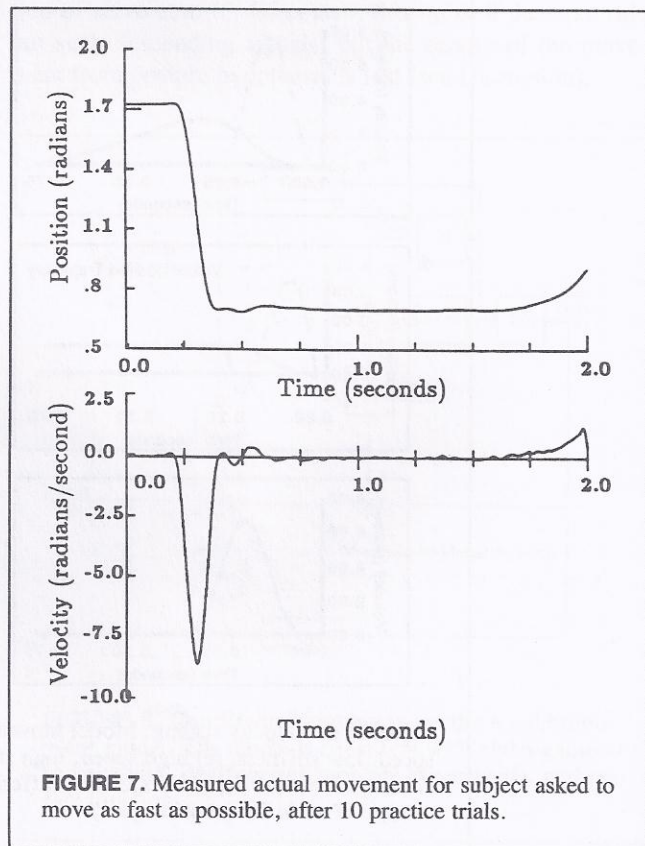


FIGURE 7. Measured actual movement for subject asked to move as fast as possible, after 10 practice trials.

speed, it is not necessarily the most efficient. Cocontraction requires an increase in the consumption of metabolic energy (Hogan 1984b). Under the λ model, an increase in stiffness could be achieved by either an increase in muscle stiffness or an increase in the reflex feedback gain. The latter, however, may be limited by the feedback delays of the system. In either case, the level of stiffness that would be required for fast movements of the human arm is relatively high. Figure 7 shows the trajectory of the limb produced by a subject asked to move as fast as possible. The duration of this movement was approximately 125 ms, which would require a servo stiffness of approximately 252 newton-meters/radian (for an estimated limb inertia of 0.1 Kg-m²).

The stiffness of the arm can be estimated by measuring the response to disturbances applied during the movement. Experiments such as these estimate that the natural frequency of the elbow is low during the production of fast movements, on the order of 1–3 Hz. (Bennet et al., 1992; Lanman, 1980). This corresponds to stiffness values in the range of 4.0 to 36.0 newton-meters/radian. Note that these estimates would include the combined contributions of the muscle mechanical stiffness and the stretch reflex gain. Thus, they reflect the overall effective stiffness of the system, regardless of which equilibrium-point model is assumed.

Hogan (1984a) computed the virtual trajectory required to produce a movement of a monkey's arm, based on estimates of stiffness for the limb. Even for the slow movements he described (700 ms) the virtual trajectory was significantly different from the actual trajectory.

The evidence suggests that no formulation of the equilibrium-point control model can adequately describe the production of fast arm movements if these models are restricted to act as position servos. Adequate performance of these models requires the inclusion of a feedforward component in the virtual trajectory command provided by the CNS to the sensorimotor system.

Enhancement of the Equilibrium-Point Control Model

Can any feedback-only control system adequately account for the known behavior of the human limb? We have proposed a new control structure that defines such a system (Figure 8). The controller is computationally simple in that the CNS needs to specify only the actual desired trajectory for the limb. The desired trajectory is fed directly to the muscles, as in the α equilibrium-point control scheme. This virtual trajectory is modified, however, by reflex feedback during the execution of the movement.

The proposed model differs from the equilibrium control model by the addition of a *velocity reference* signal. The addition of this signal effectively implements a position-plus-derivative controller that serves to increase the command following performance of the system. This allows the system to produce faster movements at a given level of K and G_{pos} .

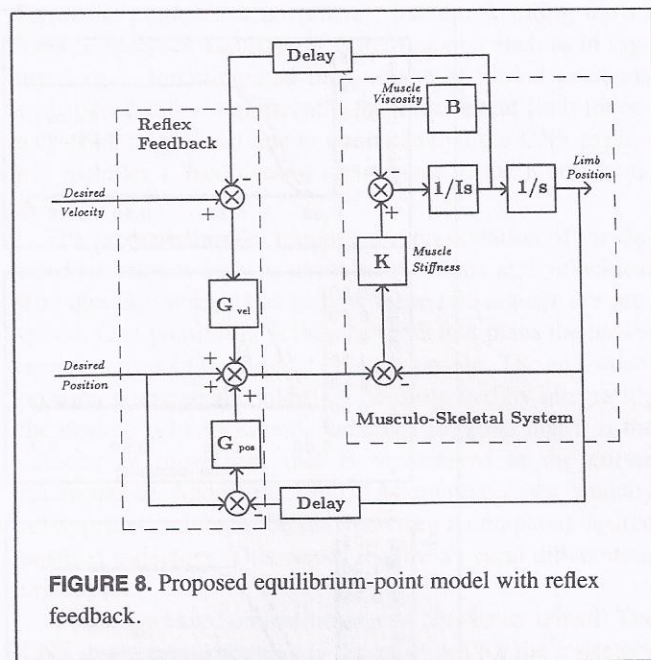


FIGURE 8. Proposed equilibrium-point model with reflex feedback.

Simulation of the Proposed Controller

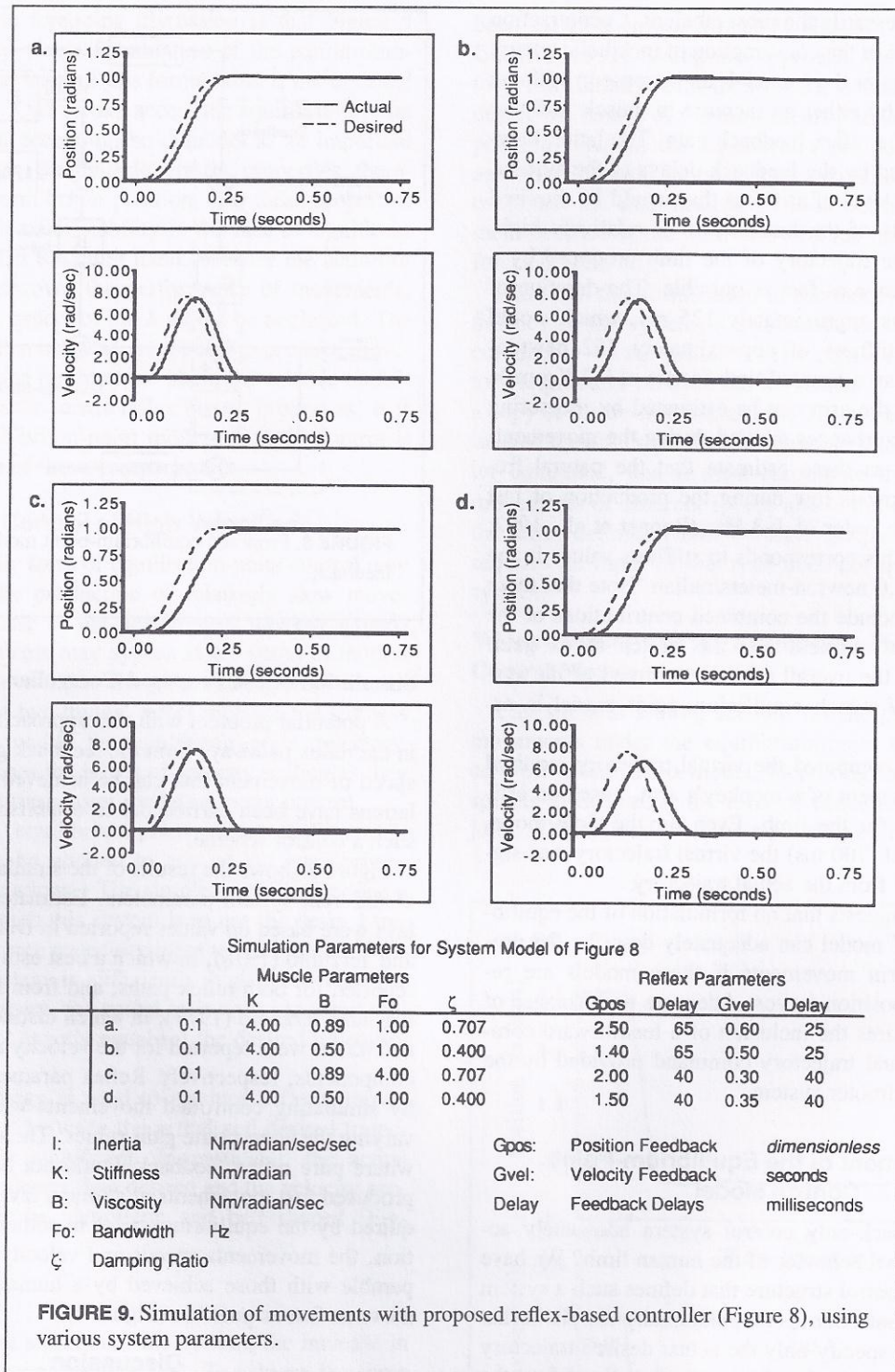
A potential problem with this approach is that the delays in the reflex pathways limit the feedback gains, and thus the speed of movement that can be achieved. Computer simulations have been carried out to establish the feasibility of such a control scheme.

Figure 9 shows the results of the simulations for a variety of different system parameters. Estimates of feedback delays were based on values reported in Dufresne, Soechting, and Terzuolo (1978), in which a best estimate of 47 ms was reported for both reflex paths; and from Dufresne, Soechting, and Terzuolo (1979), in which distinct values of 25 ms and 65 ms were reported for the velocity and position reflex components, respectively. Reflex parameters were selected by simulating controlled movements while systematically varying the appropriate gain values. The system was stable, where pure reflex feedback would not be, and the system produced fast movements at stiffness levels below those required by the equilibrium-point hypothesis alone. In addition, the movements speeds and velocity profiles are comparable with those achieved by a human subject asked to move as fast as possible (Figure 7).

Discussion

The proposal of a velocity reference signal is not completely ad hoc. First, it is based on sound control theory and practice. To increase the command following performance of a feedback system, it is common to add lead compensation to the control circuit (Ogata, 1970). The velocity feedback of the proposed model effectively implements such compensation.

Second, the velocity signal is clearly present in the signal received from the spindle organs (Gielen & Houk, 1987). It is reasonable to expect that the CNS makes use of this



information during the production of movement, because it is available.

Figure 5 and subsequent figures indicate two separate pathways for the specification of the desired position. Strictly speaking, this bifurcation of the command signal is not necessary; by superposition these signals could be combined into a single influence on the alpha motor neurons. However, proper combination of the two signals requires the knowledge of the reflex gain factor G_{pos} :

$$X_d^* = (1 + G_{pos}) X_d,$$

where X_d is the actual desired movement, and X_d^* represents the necessary descending command. The separation indicated in the figure is a simpler procedure, and one might even imagine that these two signals represent the independent descending control onto alpha and gamma motor neurons. In any case, the exact configuration is irrelevant to the ensuing discussion.

Feldman (1986) has indicated that the λ equilibrium-point model should include phasic control of movement through gamma dynamic motor neurons. However, he attributed this influence to the damping factor μ (G_{vel}), which affects the control variable λ based only on actual movement velocity, with no reference to a descending specification of movement velocity (see Equation 22 of Feldman, 1986). Such a formulation cannot serve to increase the bandwidth of the motor servo. The model proposed here in Figure 8 specifies explicitly a form for the descending command based on desired movement velocity.

More recently Feldman and colleagues have returned to a model of movement that does meet our definition of a servo controller (Levin et al., 1992). In these stimulation studies, it has been shown that a monotonic r command (equilibrium position) coupled with a monotonically increasing c command (coactivity, i.e., an increase in K or G_{pos}) can produce reasonable limb trajectories at high speeds of movement. This increase in feedback gain through the c command should be, and is not, reflected in the measured stiffness of the limb during movement (Bennett et al., 1992; Latash & Gottlieb, 1991).

The combination of feedforward and feedback control strategies, as in having a virtual equilibrium trajectory differing from the actual desired trajectory, remains a viable option for the control of movement that has not been eliminated by the foregoing analysis. Such strategies suggest a central program for the execution of the nominal movement, with feedback control to compensate for unexpected disturbances or errors in the feedforward model. These proposals have been variously described as *servo-assistance* (Rack, 1981) or *conditional feedback* (Houk & Rymer, 1981) systems. The addition of descending drive directly to alpha motor neurons, as has been suggested within the framework of the lambda equilibrium-point model, would also result in such a system. Experimental studies are in agreement with such an interpretation (Bennett et al., 1992; Hogan, 1984; Latash & Gottlieb, 1991).

The model proposed here is also consistent with a virtual trajectory or feedforward interpretation. The velocity reference signal can be characterized as a feedforward control signal based on the velocity of the intended movement and the viscosity of the motor system. A different interpretation, however, which is more evident from Figure 8, describes the system as two feedback control systems, one for position and one for velocity. Thus, we return to a servo control system, in accordance with our definition. The descending motor command specifies the kinematics of the desired motion, that is, the positions and velocities, without need for explicit knowledge of system dynamics. The proposed model is consistent with the above-mentioned experimental observations (Bennett et al., 1992; Hogan, 1984; Latash & Gottlieb, 1991). If only a position reference signal is assumed, the virtual trajectory computed based on stiffness measurements during movement would differ significantly from the actual trajectory. That is to say, if a system including a velocity reference signal, such as that of

Figure 8, produces a movement, but the resulting movement is analyzed assuming a system model, such as in Figure 5 or 3, the computed time course of virtual positions will indeed differ significantly from the actual limb trajectory. This might lead one to conclude that the CNS explicitly includes a feedforward component in the motor command.

The proposed model requires a representation of the desired movement both in terms of positions and velocities. The question remains as to how these two signals are produced. One possibility is that the CNS first plans the movement in terms of the desired velocity profile. The equivalent position commands could then be computed by integrating the desired velocity signal. Evidence suggests that it is the velocity of movement that is represented in the cortex (Schwartz & Anderson, 1990). Alternatively, the velocity reference signal could be derived from a computed desired position trajectory. This would require a neural differentiating circuit.

A strategy based on learning could also be imagined. The CNS might precompute only the positions for the trajectory of a novel movement. The movement then could be executed via one of the classical equilibrium-point models, using a relatively highly level of stiffness to ensure the fidelity of the movement. The CNS could then "remember" the signals generated by the velocity signals during these learning trials. For subsequent trials at low stiffness, the CNS would utilize this memory as the required velocity reference signal. A difficulty with any memory-based control scheme is that of initializing the memory for novel movements. The learning scheme based on our control model explicitly addresses this problem. By performing novel movements initially at high stiffness, the sensory organs themselves produce the exact pattern of activation required as a velocity reference signal for subsequent low-gain movements.

One could test for such a learning strategy if the ability to accurately measure the stiffness of a limb during novel movements were available. Unfortunately, current methods for estimating limb stiffness require averaging across multiple trials, thus masking any training effects (Bennett et al., 1992; Lanman, 1980).

Conclusions

Recent criticism of the equilibrium-point hypotheses for motor control have centered on the inability of these models to predict the characteristics of high-speed movements. The feedback gains (stiffnesses) that would be required for the servo-like production of fast movements have not been experimentally observed. Under these models, the command input cannot be a simple representation of the desired output. The command must contain a feedforward component based on the dynamics of the system, and thus the computational simplicity of a servomechanism is lost.

In this article, a modification of the equilibrium-point control structure has been proposed that fits a strict definition of a servomechanism. Under this model, the CNS

needs to specify only the parameters of the desired trajectory. The model requires a representation of the desired velocity as well as the desired positions to improve the command following performance of the system. Using realistic values for the feedback gains and delays, we have shown that the proposed controller can produce high-speed single-joint movements by using a pure feedback approach.

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NOTE

1. The problem of inverse dynamics is that of computing the forces or torques required to move the system through a desired trajectory.

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