Spinal Cord Circuits: Are They Mirrors of Musculoskeletal Mechanics?

Gerald E. Loeb
Bio-Medical Engineering Unit
Queen's University, Kingston, Ontario

Jiping He
William S. Levine
Department of Electrical Engineering
University of Maryland, College Park

ABSTRACT. Over the past decade, research at three different levels of sensori-motor control has revealed a degree of complexity that challenges traditional hypotheses regarding servocontrol of individual muscles: (a) The connectivity of spinal circuits is much more divergent and convergent than expected. (b) The normal and reflex-induced recruitment of individual muscles and compartments of muscles is more finely controlled than was noted previously. (c) The mechanical interactions among linked skeletal segments and their often multiarticular muscles are neither simple nor intuitively obvious. We have developed a mathematical model of the cat hind limb that permits us to examine the influence of individual muscles on posture and gait. We have used linear quadratic control theory to predict the optimal distribution of feedback from a hypothetical set of proprioceptors, given different assumptions about the behavioral goals of the animal. The changes in these predictions that result from changes in the structure and control objectives of the model may provide insights into the functions actually performed by the various circuits in the spinal cord.

THE SPINAL CORD was long thought to be primarily a relay for descending commands to individual motor nuclei. Its local interneuronal circuits were assigned the relatively simple functions of generating rapid, preprogrammed reflexes and regulating and linearizing the properties of each muscle, thus simplifying the control problem for the higher centers (e.g., Houk, 1979). We now know that both the descending and the segmental circuits are highly divergent (recently reviewed by McCrea, 1986) and appear to control the mechanics of the limb as a whole rather than individual muscles. Furthermore, the intrinsic mechanical properties of each muscle are nonlinear (e.g., Joyce, Rack, & Westbury, 1969) in ways that cannot be linearized by the relatively slow and rather diffuse reflex loops. Instead, the neural control systems must anticipate substantial mechanical effects from these intrinsic properties of the musculoskeletal system, effects that may tend to stabilize or destabilize the limb, depending on the ongoing task (Rindos, 1988; Zheng, Hemami, & Stokes, 1984).

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Unfortunately, the simple mechanical-output and servocontrol models developed for single muscles are not readily expanded to deal with the mechanics of multiarticulated limbs and their variously designed muscles. More realistic models of musculoskeletal mechanics are required so that reasonable hypotheses regarding motor control can be developed and tested. It is our belief that the complexities of the neurological control system reflect complementary complexities in the musculoskeletal system. The latter mechanical system is amenable to systematic analysis by traditional engineering techniques such as inverse dynamic analysis. The form of the resultant equations, however, makes it most unlikely that CNS control is based on such a formal approach to Newtonian mechanics. Therefore, we have been examining other approaches to control, such as linear quadratic (LQ) regulator design (Athans, 1971). In the LQ design process, the Newtonian model is used only as a temporary formalism to describe the mechanical properties of the system and to calculate an optimal configuration of feedback from the sensors (proprioceptors) onto the actuators (motoneuronal pools). The Newtonian model can then be run as a simulation to observe the responses of the musculoskeletal system to applied perturbations while the responses of the sensory feedback matrix are probed, much as one would probe a functioning nervous system. Because the experimenter can systematically vary the mechanical properties and behavioral goals of the model, the various patterns of feedback can be tested for their functional roles rather than guessed at from the much more fragmentary data that are available from experimental animals.

History of Musculoskeletal Modeling

Students of muscles and movement have often resorted to models to summarize the salient observations of experiments and to make inferences about variables that are not directly measurable. These models, however, have usually been confined to particular levels of analysis, such as the regulation of force output of a single muscle or the net

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forces resulting in the motion of the whole organism. This paper presents an interim report of a collaborative project to develop a complete set of quantitative and orderly relationships that characterizes the biomechanics of the cat hind limb from the level of fundamental properties of muscle sarcomeres to the level of coordinated behavior, such as locomotion. The project differs from previous attempts at "global" modeling (e.g., Hatze, 1977) in that we require that each relationship in the model and the parameters for those relationships satisfy the following criteria:

1. The individual terms of the relationship must be related to physical entities rather than just mathematical coefficients for curve fitting. For example, we model the passive elasticity of muscles as a combination of tendons and aponeurotic sheets with one set of properties and a muscle belly whose mechanical properties depend on the fundamental properties of individual sarcomeres combined into a series and parallel arrangement that is specified by the muscle-fiber architecture.

2. An anatomical or physiological property will be modeled only if it can be shown to be significant for the behavior of the system and only for those ranges of behavior that occur normally. For example, previous studies of the active force-output of tetanically stimulated muscles have described large "yielding" transients that occur in the sudden transition from isometric to lengthening (Joyce et al., 1969), whereas muscle behavior is much simpler for physiological rates of stimulation and acceleration (Rindos, 1988).

3. Each parameter of a relationship must be quantifiable by direct anatomical or physiological measurement, using a method that provides enough resolution so that the behavior of the relationship is stable over the range of uncertainty for that parameter.

4. Each relationship must be cross-checkable; that is, it must be possible to make two independent predictions regarding two independent measurements that can be obtained in the laboratory or inferred from separate relationships of the model.

Thus, the global model is actually composed of several layers of modeled processes, each of which draws on substantial experience elsewhere in modeling and measuring such processes. A list of models follows:

• The force generating capabilities of active sarcomeres (e.g., Huxley & Simmons, 1971; Pollack, 1983; White & Thorson, 1973; Wood & Mann, 1981)

• Whole muscles as equivalent series and parallel elastic elements (e.g., Bahler, 1968; Baildon & Chapman, 1983; Zajac, in press)

• The time-course of the active state (e.g., Edman, 1970; Julian & Sollins, 1973; Podolsky & Nolan, 1973; Taylor, 1969) and its relationship to EMG (e.g., Crosby, 1978; Hof & Van den Berg, 1981a, 1981b, 1981c, 1981d; Moritani & DeVries, 1978; Patla, Hudgins, Parker, & Scott, 1982)

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• The geometrical and biomechanical properties of various muscle fiber architectural arrangements (e.g., Gans, 1982; Goldspink, 1981; Huber, 1916; Otten, 1988, Sacks & Roy, 1982; Wottiez, Huijing, & Rosendal, 1983)

• The effects of tendon pathways and insertions on joint torque (e.g., Brand et al., 1982; Elftman, 1966)

• The degrees of freedom of individual joints (e.g., Crowninshield, Johnston, Andrews, & Brand, 1978; Wongchaisuwatt, Hemami, & Buchner, 1984).

• The observed limb motion during natural behavior (e.g., Arshavsky, 1965; Goslow, Reinking, & Stuart, 1973; Halbertsma, 1983; Manter, 1938; Tokuriki, 1973), and the inverse dynamics of that motion (Hoy & Zernicke, 1985; Mena, Mansour, & Simon, 1980; Patriarco, Mann, Simon, & Mansour, 1981; Zajac, Zomlefer, & Levine, 1981).

There have been, however, only a few experimentally backed attempts to cross boundaries between these modeled processes, that is, to predict muscle force-output from EMG under dynamic conditions (Hof & Van den Berg, 1981d; Olney & Winter, 1985) or to resolve net joint torques, determined by inverse dynamic analysis, into the work of individual muscles (Crowninshield & Brand, 1981; Davy & Audu, 1987; Pierrynowski & Morrison, 1985a, 1985b). The latter problem is particularly important because theories of motor control are now oriented toward servocontrol of single muscles (e.g. Berkinblit, Feldman, & Fukson, 1986; Houk, 1979; Merton, 1953), whereas the spinal cord circuitry underlying such control is characterized by widespread divergence and convergence between sensory and motor pools (for review, see McCrea, 1986). Such circuits may relate better to joint or limb control schemes (e.g. Ghez & Martin, 1982; Hogan, 1984, 1985). Attempts to infer muscle work in humans from inverse dynamics have had to rely on optimization strategies (e.g., minimal force or recruitment level), which are often arbitrary, cannot be confirmed experimentally, and require assumptions that conflict with the experimental testing of hypotheses about motor control.

The locomotor behavior of the cat hind limb has been selected for several reasons:

1. Since Sherrington, this has been the most widely studied preparation in which to study reflex control and sensorimotor integration in mammals.

2. The neural and musculoskeletal elements appear to be highly evolved for the efficient production of agile locomotion, the predominant activity of the hind limb.

3. There is sufficient diversity in the architectural and physiological properties of the musculature to permit sampling of a range of motor control and coordination problems without the model becoming intractable.

4. The motion and muscle actions are largely in the parasagittal plane of the limb segments and their hinge-like joints, making a two-

dimensional model a reasonable approximation of the complete behavior.

5. Step cycle patterns at various gait speeds are complex enough to include many kinematic variations but reproducible enough to compile and compare data from multiple individual cats having similar physiognomy.

6. It is possible to obtain accurate, quantitative, and reproducible measurements of EMG from all significant muscles, and even substituent compartments of muscles, using chronically implanted electrodes that do not interfere with normal behavior (in contrast to the situation in humans).

7. Sufficient homologies are present between the sensorimotor apparatus of cats and other mammals so that the approach to modeling developed in this project should be applicable with modest alterations to other behaviors, limbs, and species (including humans). Changes, however, such as plantigrade versus digitigrade locomotion (in humans versus cats, respectively) introduce important changes in the roles of anatomically homologous structures. Thus, the modeling methods are likely to be valid, but specific conclusions and predictions of a particular model are likely to be highly species specific.

Methods

Musculoskeletal Model

For the studies described here, we used a simplified version of our model of one hind limb that has three skeletal segments (foot, shank, and thigh), which are constrained by pin-joints to move in the parasagittal plane and which terminate in a pelvis. We grouped the 30 muscle compartments that act on these joints in this plane into 10 groups based on their patterns of gross mechanical action on the joints (Figure 1 and Table 1). Morphometry, muscle architecture, skeletal lever arms, and mechanical properties, such as center of mass and rotational inertia, were measured in cadavers. The values were converted to dimensionless numbers so that data from multiple, similarly built specimens could be pooled (for details, see He, 1984; Levine, 1986; see also Zajac, in press). The following is a subjective description of the structure and properties of the components of the model; formal mathematical descriptions have been published by He, Levine, and Loeb (1988).

Muscle Activation Model

For each muscle group, we determined total physiological cross-sectional area (PCA) and mean points of origin and insertion on the skeleton. The group was then modeled as a single actuator consisting of parallel generators of active and passive force in series with an elastic tendon. The spring-functions for both the passive muscle and the tendon included an exponential term that dominated the low-strain
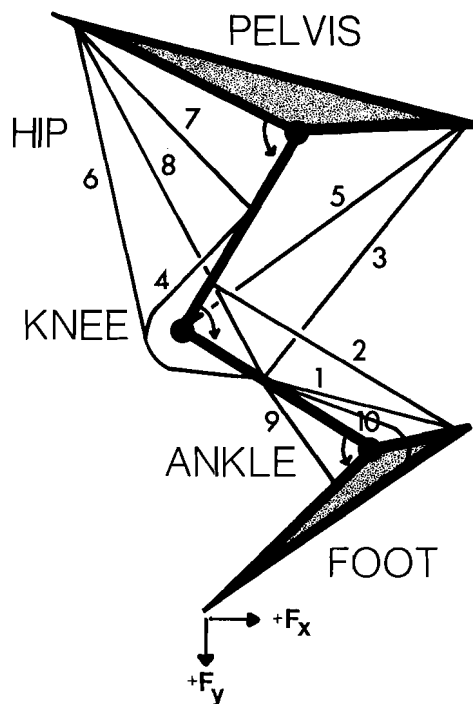
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Figure 1. General form of the musculoskeletal model; see table for description of the 10 muscle groups indicated. Joint angles increase in extension (arrows); ground force shown as applied by tip of foot, positive for support (Fy) and propulsion (Fx).

part of the curve and a linear term at higher strain (Abrahams, 1967; Ker, 1981). The active muscle generated tension that was dependent on its level of activation multiplied by a force/length term and a force/velocity term. The activation term included separate time-constants for rate of rise and fall in response to motor unit recruitment. Both time-constants became shorter at higher levels of recruitment to simulate the different properties of slow and fast twitch units. The force/length and force/velocity functions were continuously differentiable versions of the classical relationships of Gordon, Huxley, and Julian (1966), Hill (1938), and Joyce et al. (1969); see Zajac, Chapelier, Levine, and Zomlefer (1983) for specific mathematical implementation.

Proprioceptor Models

One of the requirements of optimal control theory is that there must be either a direct measurement of, or an internal estimator for, each state variable of the system. The system of equations that we used for our models requires inputs of joint angle, joint velocity, muscle length, muscle velocity, muscle force, muscle recruitment, and muscle activation. The first five of these state variables have obvious counterparts

TABLE 1
Definition of Muscle Groups Used in LQ Model

Group #	Joint Action			Constituent Muscles	PCA cm²	Recruitment[a] % max. EMG
	A	K	H			
1	E	–	–	soleus (SOL)	0.91	90
				plantaris (PLA)	3.4	43
2	E	F	–	medial gastrocnemius (MG)	4.0	25
				lateral gastrocnemius (LG)	4.6	18
3	–	F	E	biceps femoris posterior (BFP)	7.6	12
				semitendinosus (ST)	2.3	40
				gracilis anterior (GRA)	0.44	15
				gracilis medial (GRM)	0.44	15
				gracilis posterior (GRP)	0.45	15
4	–	E	–	vastus medialis (VM)	3.0	30
				vastus intermedius (VI)	3.0	60
				vastus lateralis (VL)	5.0	15
5	–	–	E	biceps femoris anterior (BFA)	2.1	40
				semimembranosus anterior (SMA)	1.7	10
				semimembranosus posterior (SMP)	3.4	10
				caudofemoralis (CF)	0.6	40
				adductor femoris (AF)	4.5	80
				tensor fascia latae posterior (TFP)	0.66	20
6	–	E	F	rectus femoris (RF)	5.4	50
				tensor fascia latae anterior (TFA)	0.86	15
				sartorius anterior (SAA)	1.3	50
7	–	–	F	iliopsoas (IP)	1.0	40
8	–	F	F	sartorius medial (SAM)	0.3	50
9	F	–	–	tibialis anterior (TA)	1.16	20
				extensor digitorum longus (EDL)	0.95	33
				peroneus longus (PL)	0.72	43
10	E	–	–	tibialis posterior (TP)	1.8	15
				peroneus brevis (PB)	1.0	40
				flexor hallucis longus (FHL)	4.8	30
				flexor digitorum longus (FDL)	0.9	30

[a]Smoothed EMG activity during walking expressed as percentage of maximal amplitude recorded from each muscle during various activities (including vigorous paw shaking, which is presumed to cause nearly complete recruitment of most muscles).

Abbreviations: A–ankle, K–knee, H–hip, E–extension, F–flexion, PCA–physiological cross-sectional area

in the naturally occurring proprioceptors described below. The initial level of muscle recruitment is specified by the initial conditions of the model, but recruitment, of course, changes in response to perturbations. The model requires feedback of these recruitment changes to estimate changes in muscle fiber activation. Such feedback occurs naturally in the form of recurrent collaterals from motoneurons to Renshaw cells. Thus, in our model, recurrent feedback among the various

motoneuron pools is handled in the same manner as the feedback from traditional proprioceptors.

Each muscle was assumed to have a population of tension-sensing receptors, with properties similar to Golgi tendon organs (GTO), and stretch-sensing receptors, with properties similar to spindle primary endings (Ia). The Ia receptors responded to an additive function of absolute length and rate of length change. To simulate the biasing effects of the fusimotor system, each term of the Ia function was multiplied by a coefficient to make that term produce an output covering half of the available dynamic range for the maximal range of that input encountered during the stance phase of walking. This keeps the output of the Ia within a dynamic range of 0 to 1, with approximately equal weighting for length and velocity. This constitutes a local linearization of the optimized fusimotor control scheme suggested by Loeb and Marks (1985) based on activity recorded from muscle spindle afferents from the cat hind limb during normal walking.

Each joint was equipped with sensors for absolute joint angle and angular velocity. There is considerable doubt that physiological joint receptors provide the major share of kinesthetic information (Ferrell, Gandevia, & McCloskey, 1987). The present model is designed to determine the importance of such state feedback, with the intention of eventually using the individual muscle proprioceptors to calculate the joint state variables.

Kinesiological Data Collection and Analysis

Figure 2 shows the general flow of data in the modeling system. The kinesiological data consisted of observed motion (from a stroboscopic video system and computer-assisted stick-figure generation), ground reaction forces (from a multiaxis force plate), and multichannel EMG recordings (using chronically implanted, epimysial-patch electrodes, percutaneous connectors, and signal processing methods described in Loeb and Gans, 1986).

Ground forces and stick-figure motion were combined with cadaver data on the mechanical properties of the skeletal segments to calculate net joint torques using a conventional Newtonian mechanical solution for the inverse dynamics (He, 1986). EMG data were combined with stick-figure data and cadaver data on musculoskeletal architecture to determine the length and velocity of the sarcomeres and their level of activation (Muscle Kinematics in Figure 2). Changes in motor pool recruitment generated tensions according to the model of muscle properties described above. For the work reported here, we chose the midstance phase of slow walking as the initial steady state to which perturbations would be applied, because the mechanical constraints are then similar to that of standing, for which behavioral responses to perturbations are available from intact cats (Macpherson, 1988a, 1988b).
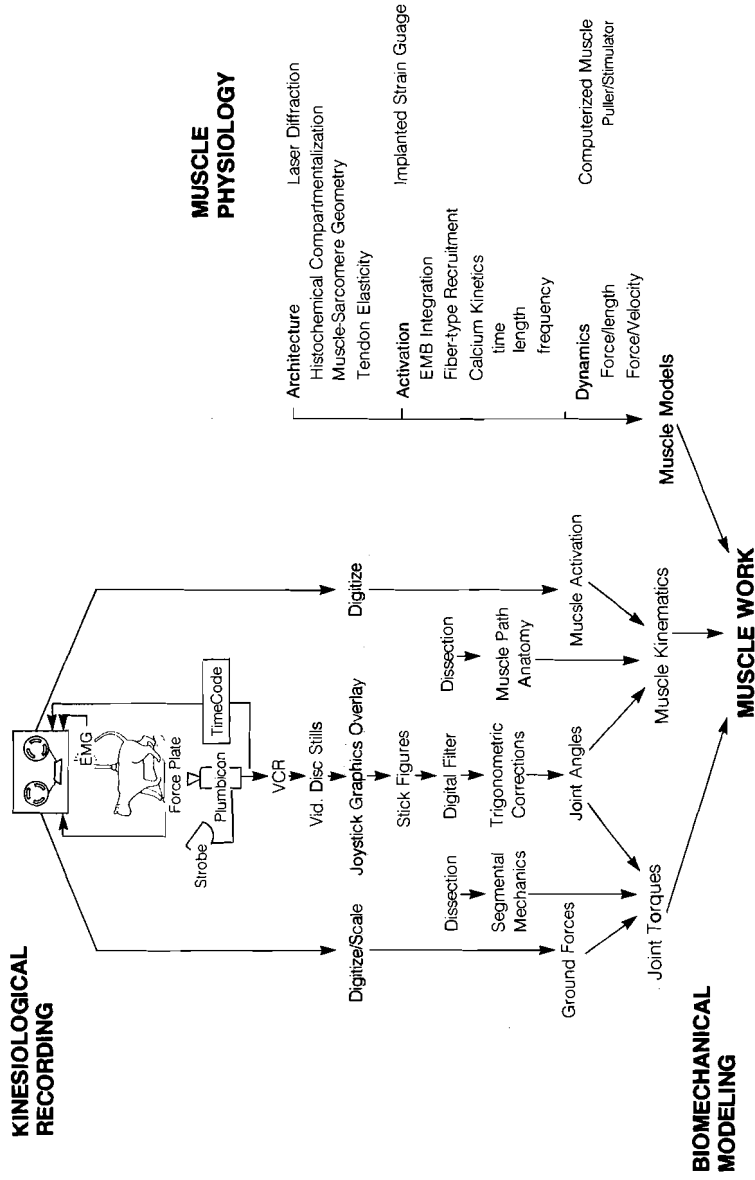
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Figure 2. The data management scheme for the modeling project has been divided into three separate tasks: (a) kinesiological recording to obtain state variables for normal behavior, (b) biomechanical modeling whereby kinesiological data is transformed into the muscle kinematics and joint torques, and (c) muscle physiology models whereby the EMG recordings are transformed into estimates of the time course of force generation.

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Linear Quadratic (LQ)-Controller Design

Given a sufficient number of sensors for the mechanical states of a system, it is possible to calculate a matrix of feedback from those sensors onto all of the available actuators (in this case, the 10 motor pools), so that the response of the system to small perturbations is optimized for certain performance criteria (Athans & Falb, 1966; Bryson & Ho, 1969). LQ theory is one of several approaches to computing such optimal controllers; it has been applied to many complex control problems (Athans, 1971). We have assumed that, in a living organism, there are generally two competing criteria: minimizing both the deviation from the desired state and the expenditure of effort involved in returning to and holding that state. (Similar performance trade-offs have been examined extensively in robotic systems; Stein & Athans, 1987.) In our model, these criteria were grouped into two matrices, whose individual elements could be adjusted to change the importance of minimizing various state variables; the larger the value of the element, the more the model sought to minimize perturbations of the corresponding state. The weighting matrix for effort (R) had diagonal terms corresponding to the recruitment levels of all 10 muscle groups. The weighting matrix for deviation (Q) had terms corresponding to the 26 proprioceptive sensors for the state variables (Ia and GTO for each muscle, and joint angle and velocity for each joint). By setting certain of the terms in the Q matrix to zero, we could simulate a controller for only certain measures of perturbation, that is, those corresponding to the nonzero terms in Q. To date, we have examined four such perturbation-control schemes: (a) individual muscle-stiffness control, in which only deviations in muscle length and force are minimized; (b) joint-angle-only control; (c) muscle-length-only control; and (d) global control (no zero terms on the diagonal elements of Q, as described below). Our implementation of the LQ modeling techniques is described in detail by He (1988).

For each type of deviation matrix, Q, we examined a full range of weighted linear combinations with the effort matrix, with the relative weighting expressed as the R/Q ratio. A large R/Q ratio signifies strong emphasis on minimizing effort at the expense of tolerating larger and longer lasting deviations following a perturbation from the initial mechanical state. Conversely, a small R/Q ratio signifies relatively stiff control of the desired state, even if that requires high levels of motor pool recruitment in response to a small perturbation. More graphically, a freshly deceased cat would have an R/Q ratio of infinity, and a cat in rigor mortis would have an R/Q ratio of zero.

The predicted feedback matrices for the above optimization criteria were plotted on a specialized logarithmic scale that captures the wide range of values that tend to occur as the R/Q ratio is changed, including reversals in sign. The model also permitted simulations of responses to perturbations, producing plots, with respect to time, of limb position, ground forces, proprioceptive (state variable) activity, and

"reflexive" recruitment of motor pools. As our test perturbation, we chose a small (5 cm) horizontal displacement of the foot during quiet standing, a paradigm that has been studied extensively in cats (Macpherson, 1988a, 1988b; Rushmer, Russell, Macpherson, Phillips, & Dunbar, 1983). In the simulation, as in the real cat, the perturbation initially was absorbed primarily by hip motion. The foot was on the ground, and the limb supported an inertial mass equal to one third of the body weight. This mass was selected as a compromise between the quadrupedal stance paradigm of Macpherson (1988a), in which the body weight is distributed approximately evenly among the four legs, and the stance phase of diagonal walking, in which the weight is distributed between the two limbs that are on the ground. It has been our experience that the LQ models are quite robust. Relatively large quantitative changes in Newtonian model parameters produce smoothly distributed changes in the predicted feedback matrices. Qualitative changes in the structure of the feedback matrices require qualitative changes in the structure of the Newtonian model or the behavioral goals for which the LQ-controller was optimized.

Some Predictions Regarding Proprioceptive Feedback

For all four types of control examined, the optimized feedback matrix called for widespread divergence from individual sensors onto motor pools, including those pools whose mechanical output did not directly influence the sensor in question. Figure 3 shows a small portion of the feedback matrix among the proprioceptors and motor pools for the uniarticular extensor muscles operating at the ankle (soleus), knee (vasti), and hip (biceps femoris anterior). The entire matrix from which it is drawn consists of feedback from each of the 3 muscle sensor groups (Renshaw, spindles, and GTOs) from each of the 10 muscle groups plus joint receptors from the 3 joints (a total of 33 inputs), onto each of the 10 motor pools. The individual graphs shown in the figure represent the way in which the gain of a particular feedback element (1 sensor onto 1 motor pool) would vary as the desired "stiffness" of control (R/Q ratio) is varied.

The tendency for sensory feedback to be directed to muscles that were widely divergent from the source was greater for larger R/Q ratios; for example, models that emphasized conservation of effort by producing less "stiff" responses relied more on feedback between different muscle groups (heteronymous) than within a single muscle group (homonymous). The first three control strategies, however, which tried to maintain equilibrium for only a subset of the state variables, produced responses to perturbations that tended to be unphysiological for any R/Q ratio. For example, regulation of joint angle or muscle length only resulted in feedback patterns that produced unrealistically large and abrupt changes in muscle activation. More physiological responses were seen for the global control strategy (Figures 3 and 4) in which the feedback matrix was designed to maintain the

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initial state, as measured by all of the state variables (and weighted according to the range of each state variable for the normal walking cycle). Figure 4 presents the results of the simulation, in which the Newtonian model, which was used to calculate the feedback matrix, was subjected to a mechanical perturbation while the feedback matrix controlled the response of the 10 muscle groups. The model returned to the desired equilibrium with a time course of joint angles, ground forces, and changes in muscle activation (excitatory, inhibitory, or even multiphasic in some muscle groups) that was generally similar to that seen in normal cats subjected to a similar perturbation (Macpherson, 1988a, 1988b).

We are still in the process of an exhaustive determination of the minimal set of regulated state variables needed to achieve physiological responses in this musculoskeletal system. The results to date, however, constitute the first direct tests of the adequacy of currently popular theories of servocontrol, when extended to multiarticular systems. They suggest that previous theories of servocontrol may be too narrowly drawn in two different ways: First, they emphasize minimizing perturbations of only particular variables (e.g., muscle length or joint angle, analogous to having many zero terms in our Q matrix). Second, they emphasize homonymous rather than heteronymous feedback (analogous to having many zero terms in our feedback matrix).

In examining our feedback matrices for the global control strategy (Figure 3), we did note many broad similarities to traditionally defined spinal cord circuits. Homonymous feedback from Ia receptors was always excitatory, and from GTOs and Renshaw cells was always inhibitory, regardless of R/Q ratio. Homonymous feedback was generally much stronger than heteronymous feedback, but this was strongly dependent on R/Q ratio, because the amplitude of the homonymous feedback decreased greatly at high R/Q ratio (loose control). The amplitudes of the heteronymous terms showed no consistent trend as R/Q ratio increased, with examples of decreases, increases, and even sign reversals of feedback. Although any single heteronymous feedback term was usually smaller in amplitude than the corresponding homonymous terms, there were a larger number of heteronymous terms whose cumulative effect dominated the responses, even for the midrange values of R/Q that produced the most physiological responses to the test perturbation.

One interesting pattern that emerged consistently for all control strategies and R/Q ratios is diagrammed in Figure 5. In general, any feedback projection to the monoarticular extensors of one joint (bar ending circling back onto itself) tended to have the reverse sign in its effect on the extensors of the adjacent joint (ball ending projecting to extensor muscles at adjacent joint). For example, the GTOs of the vasti group (monoarticular knee extensors) inhibited the homonymous muscle group but excited the hip and ankle extensors. Reciprocally, the GTOs in the ankle and hip extensors excited the knee extensor muscles. Similar sign reversals in adjacent joints were seen for spindle
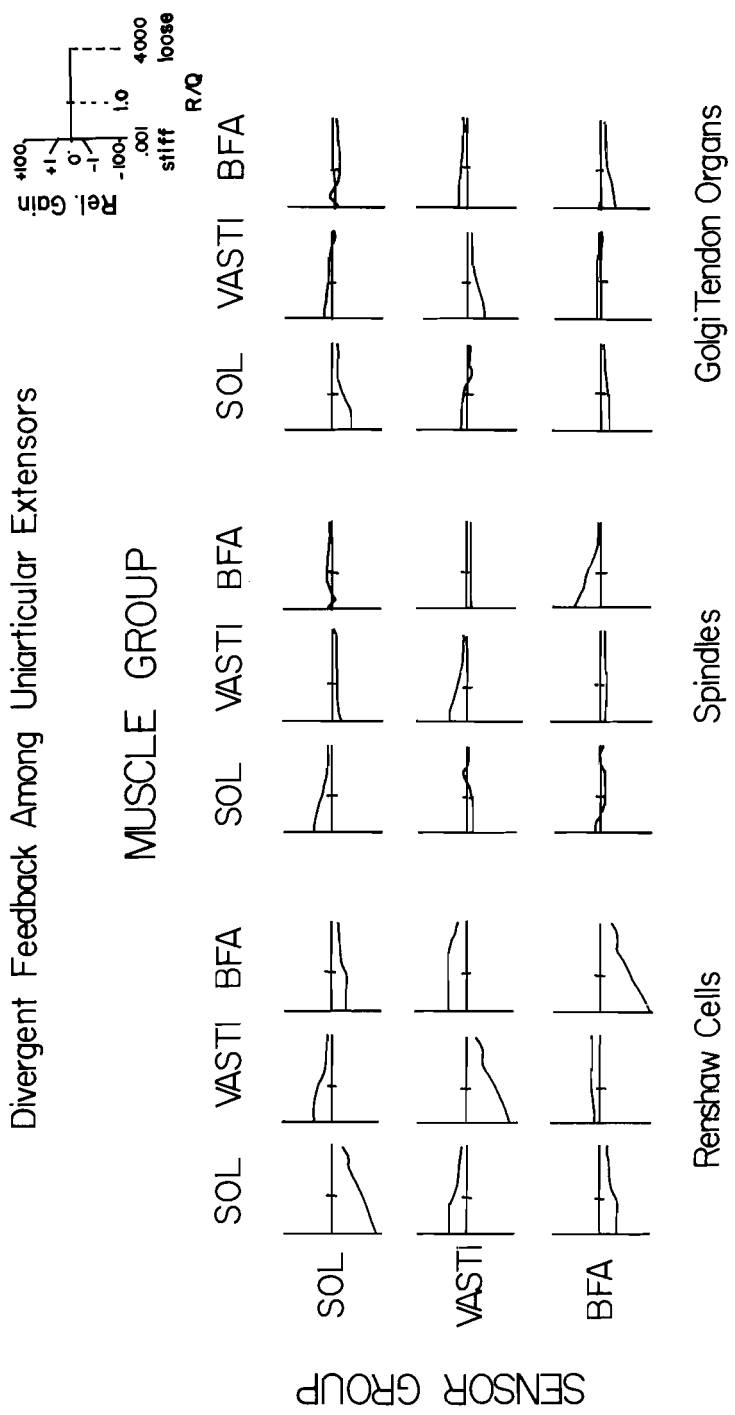
Figure 3. A portion of an LQ feedback matrix for a global control strategy. Each graph in the array shows the feedback from a proprioceptor (row) onto a motor pool (column) in a logarithmically compressed scale that ranges from +100 to −100 with a small linear range of ±1 around zero (key at the upper right). The abscissa ranges from an R/Q ratio of .001 (stiff control) to 4,000 (loose control), with the tick mark indicating a value of 1.0 which produced a physiologically realistic response to the test perturbation (see Figure 4).
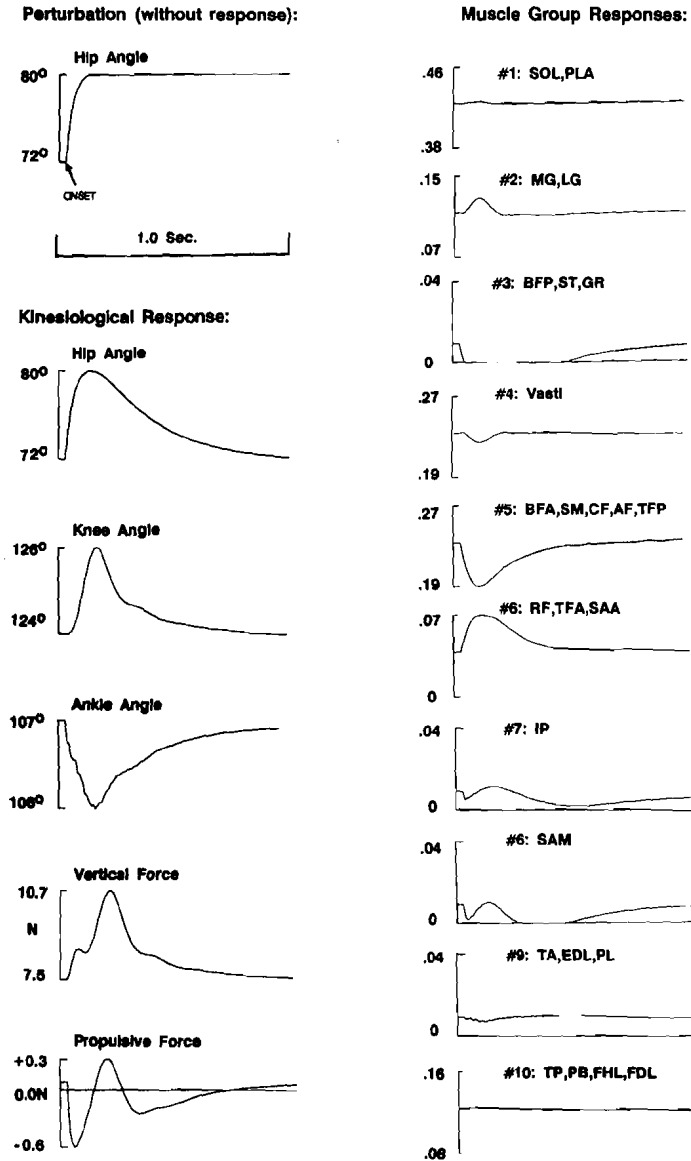
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Perturbation (without response):

Hip Angle

80°

72°

ONSET

| 1.0 Sec. |

Kinesiological Response:

Hip Angle

80°

72°

Knee Angle

126°

124°

Ankle Angle

107°

106°

Vertical Force

10.7

N

7.5

Propulsive Force

+0.3

0.0N

-0.6

Muscle Group Responses:

.46   #1: SOL,PLA

.38

.15   #2: MG,LG

.07

.04   #3: BFP,ST,GR

0

.27   #4: Vasti

.19

.27   #5: BFA,SM,CF,AF,TFP

.19

.07   #6: RF,TFA,SAA

0

.04   #7: IP

0

.04   #6: SAM

0

.04   #9: TA,EDL,PL

0

.16   #10: TP,PB,FHL,FDL

.06

Figure 4. Response of model as controlled by the feedback matrix shown in Figure 3 (L/ Q ratio of 1.0) to a backward horizontal displacement of the foot from an initial steady state. The top left trace shows the time course of the perturbation (which affects mainly the hip angle) in the absence of any response; other traces show kinesiological responses (in real physical units for a typical adult cat) and reflex changes in muscle recruitment (normalized to a range of 0–1, representing zero to maximal recruitment of each muscle group).

and joint afferent and Renshaw cell projections. (It is not clear whether there is a corresponding pattern among flexor muscles because the cat has no muscles with pure knee flexor action.) We believe that this projection pattern is a direct consequence of the scissoring action of the skeleton, in which support is provided by extensors on opposite sides of the limb as one proceeds from ankle extensors (on the posterior side of the shank) to knee extensors (on the anterior side of the thigh) to hip extensors (on the posterior side of the thigh).

There is, of course, an extensive literature on the distribution of such heteronymous projections as determined in acute electrophysiological experiments (for review, see McCrea, 1986). Trends, such as that suggested above, are not readily discernible in these papers, probably for several reasons. First, our model predicts that different control circuits will be needed for different mechanical situations, such as standing and walking, and the "state" of the spinal cord was not known in most acute experiments (this can be overcome by using pharmacological activation of the neural oscillator for walking). Second, several parallel interneuronal systems are known, whose contributions must be summed to determine net projection strengths; conversely, our model separates certain types of feedback (e.g., muscle length and joint angle information) that may be derived from the same receptors (muscle spindles). Third, to date these experiments have focused on very short latency pathways.

So far, we have concentrated on discerning general patterns and trends in the feedback matrices of LQ-controllers for this model musculoskeletal system. Such general patterns provide an instructive and
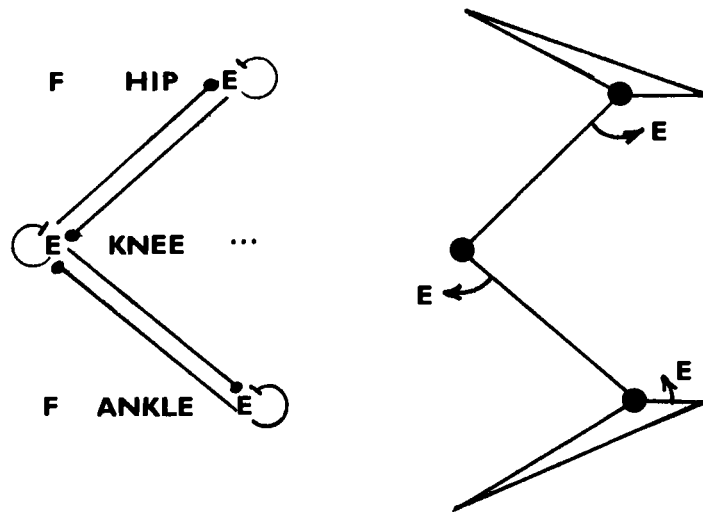
Figure 5. General pattern of inverted feedback noted between extensors of adjacent joints; see text for discussion. E denotes extensor motion and muscle groups; F denotes flexor muscle groups at corresponding joints.

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robust overview of the control problems posed by such a system because they are relatively insensitive to changes in the specifications of the sensory and motor components and the optimization criteria over physiologically plausible ranges. It should be noted that we are not proposing that the spinal cord functions as an LQ-controller per se, any more than we would propose that it produces the neural program for walking by inverse dynamic analysis. Rather we are simply using LQ theory as a convenient tool to predict the kinds of feedback that should occur in the spinal cord if it were attempting to cope in a general way with the mechanical properties of the limb.

In a sense, the model and a particular controller design constitute a metaphor for one possible relationship between the cat hind limb and the spinal cord. It remains to be seen whether the organization of specific spinal cord circuits is accurately predicted by any particular feedback matrix produced by the model. At the very least, such models will be useful in pointing out unpredicted relationships between sensors and actuators that should be particularly interesting items for experimental investigation. Such information should be useful in the design of acute studies of interneuronal projections and chronic studies of reflex responses to electrical stimuli, because such studies require technically difficult experiments that are limited in their capacity to survey even a small number of potential projections.

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