Understanding Sensorimotor Feedback through Optimal Control

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The general problem of "control" may be divided into two main categories, often designated open-loop and closed-loop (see Fig. 1). We adopt here the convention of using "controller" to designate a device that formulates a set of commands intended to change the state of a system, which commands are executed open-loop, i.e., without modification during the task. (We emphasize that this is a shorthand terminology, not to be confused with the standard usage in control theory denoting both open- and closed-loop components.) We use the term "regulator" to designate a device that attempts to stabilize the state of a system, generating only closed-loop commands, i.e., responses to deviations from the state detected by sensors in the system (Bryson and Ho 1975). Obviously, most complex systems require a mixture of the two types of control.

In sensorimotor neurophysiology, it is common to depict these kinds of controls schematically as if they were separate, even though the anatomical and physiological features of the structures in which they reside suggest a close interrelatedness. For example, the control of locomotion in quadrupeds has been seen as divided between a spinal central pattern generator (CPG), which generates an open-loop program of muscle activation, and various reflexes, also largely spinal, which adjust the activation in response to internal errors and external perturbations. Liddell and Sherrington (1925) first proposed the concept of the motoneuron as the "final common path" whereby the various sources of control signals would be summed to result in the net command to a motor unit. There is now little doubt that the motoneuron, like most central neurons, serves to integrate many disparate sources of input into a single-dimensional output. However, the later notion that these motoneuronal inputs are distinguishable into open-loop and closed-loop types deserves reexamination.

Ironically, Sherrington (1910) himself felt that locomotion was produced primarily through reflex pathways, i.e., from the sequential combination of sensory signals arising from the musculoskeletal mechanics of the limb. The need for an open-loop controller of locomotion was firmly established later by the surprisingly natural temporal patterns of motoneuronal output reported during fictive locomotion in paralyzed, de-
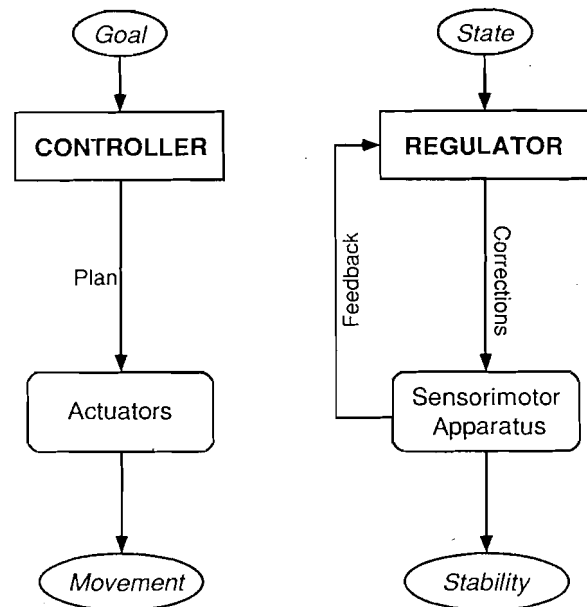
Figure 1. Two basic forms of control: open-loop (left) and closed-loop (right).

cerebrate cats (Stein 1978; Perret 1983). The identities of the neurons comprising this CPG remain unknown, but they appear to be at least partially coextensive with interneurons receiving primary afferent input. Although the CPG can function without modulated sensory input, such input can modify and reset its output to the motoneurons (Lennard 1985; Conway et al. 1987). Furthermore, the CPG can deeply modulate the gain of most, if not all, of the reflex pathways (see, e.g., Feldman and Orlovsky 1975). Given such relationships, can the theoretically useful concepts of open- and closed-loop control be applied at all to sensorimotor connectivity?

This question assumes even greater significance when applied to control of voluntary behaviors whose basic commands originate in "higher" centers such as motor cortex. As shown in the left panel of Figure 2, the usual schematic assumes that these descending commands (thick arrows) are integrated with the segmental reflexes (dashed arrows) at the final common pathways, the motoneuronal pools controlling each muscle. There are two things wrong with this simple view: (1) The proprioceptive signals from each muscle project largely to

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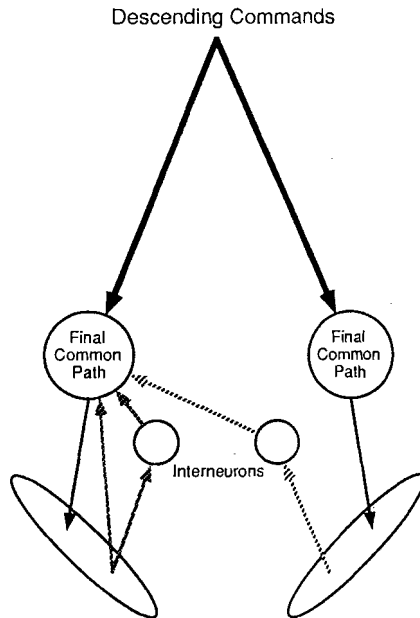
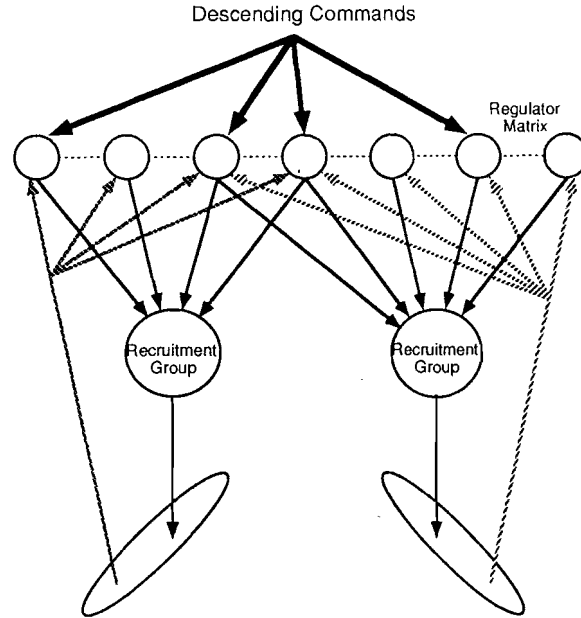## at motoneurons: ## at interneurons:

Figure 2. Historical view of spinal cord function (*left*) contrasted with a more contemporary view of the known circuitry (*right*). Dashed lines indicate proprioceptive feedback from muscles (*ovals*).

interneurons in which the signals from many different modalities and loci are combined and then routed to widely separated motor nuclei subserving the entire limb. (2) Most of the descending pathways terminate on these and other interneurons rather than directly onto motoneurons. For example, even in the primate there appears to be no direct corticospinal influence on any motoneurons except those of the digital muscles of the hand (Fetz and Cheney 1980).

The right panel of Figure 2 shows a more realistic schematic, in which both the proprioceptive feedback and the descending commands converge on a matrix of interneurons. We know that among these interneurons, there are at least some distinct subtypes with fairly predictable patterns of input (e.g., Renshaw cells, propriospinal cells, Ib-inhibitory interneurons, reciprocal inhibitory interneurons), but even these permit complex admixtures of widely distributed input signals (for review, see McCrea 1986). We also know of monosynaptic connections that convey signals directly from primary afferents to motoneurons without intercalated interneurons (spindle afferents to homonymous motoneurons), but even this form of connectivity appears to be deeply modulated by presynaptic inhibition from sources as diverse as cutaneous afferents (Jankowska et al. 1981) and the CPG itself (Duenas and Rudomin 1988).

For the above reasons, it seems useful for researchers to consider the possible matrix of connections between sensors and actuators as a blank slate, to be explored

without preconceived notions based on either known reflex pathways or analogies to simple servocontrol of individual torque motors. From the perspective of creating a complex and well-controlled movement despite being limited to such indirect control of motoneurons (Fig. 3), the problem is to find the set of interneurons that, when appropriately enabled and disabled, results in a controller-regulator combination that produces the desired motor output. Note that the behavior of such a hierarchical system is not described completely by the observable trajectory of motion of the limb. Rather, it necessarily includes a complex mechanical impedance to all possible perturbations of position, velocity, and acceleration that might be encountered (as defined by Hogan 1985).

We here describe the use of an engineering technique called "optimal control," which can be combined with models of musculoskeletal systems to generate matrices of such sensorimotor connectivity. For a given system in a given behavioral state, this matrix provides the best set of responses to the set of all possible small perturbations. Best is judged according to performance criteria that assign a weight to factors related to cost (expended effort) and benefit (various measures of stability). By noting the changes in these matrices and their simulated output that are produced by different assumptions about the model components, the external constraints and the performance criteria, one can gain considerable insight into the roles and relative importance of the various components and connections that have been
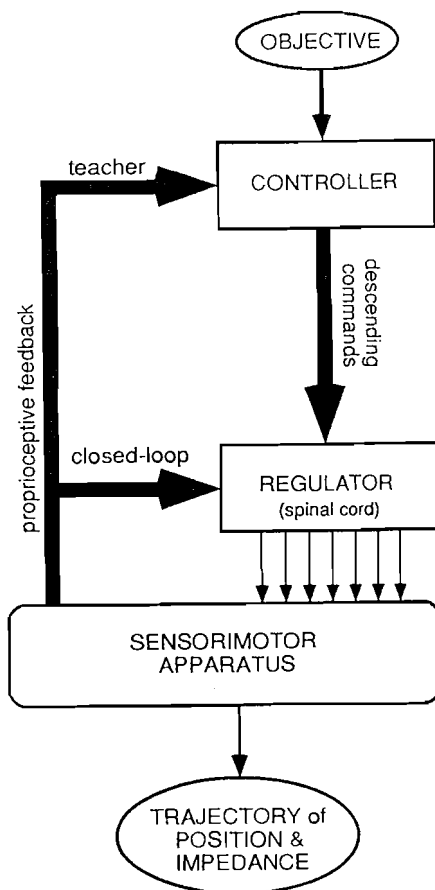
Figure 3. Proposed hierarchical relationship between open-loop controller and closed-loop regulator aspects of motor control.

described by anatomists and physiologists. From this new perspective, we have speculated rather broadly on the computational problems that must be solved by those higher centers that aspire to control such a spinal cord.

METHODS

A description of our model of the musculoskeletal system and techniques for kinesiological data collection and analysis have been published together with a review of other approaches to such modeling (Loeb et al. 1989). Mathematical implementations of models for sensory and motor components and for our application of linear quadratic (LQ) regulator design are described elsewhere (He et al. 1991). A review of technical considerations in the selection of model relationships and our approach to their empirical validation may be found in Loeb et al. (1990). Detailed methods for electrophysiological and neurokinesiological experiments in intact, naturally behaving cats have been published previously (Loeb et al. 1977; Loeb and Gans 1986; Hoffer et al. 1987; Pratt et al. 1990).

Briefly, the application of LQ control requires three types of input:

1. A complete mathematical model of the sensorimotor apparatus, including its mechanical interactions, the response of the actuators (functional groups of motor units) to command and feedback signals, and the sensitivity of sensors for all state variables (or estimators for those state variables built up from available sensors).
2. A target trajectory for the state variables, which we have taken to be their typical values during unperturbed locomotion in intact (albeit chronically instrumented) animals. This includes the trajectories of limb segments and the relative recruitment of individual muscles.
3. Performance criteria, which are the variously weighted ratios of two matrices, a cost matrix R derived from the degree of activation of the muscles, and a benefit matrix Q derived from the deviation of all other state variables from their nominal target trajectory. We have simulated the effects of other, simpler control schemes (e.g., muscle stiffness regulation; Houk 1979) by setting the appropriate terms in the Q matrix to zero.

The LQ method (Stein and Athans 1987) involves two assumptions: (1) that for small enough perturbations, the system is locally linear, and (2) that the appropriate measure of error to be minimized is quadratic, i.e., the sum of the squares of the deviations from the nominal trajectory in all of the state variables. The combination of a linear plant plus quadratic criterion implies linear state feedback control (Athans and Falb 1969); see Discussion.

For the purposes of LQ design, we have simplified the skeletal system into four segments (foot, shank, thigh, and pelvis) linked by three pin joints (ankle, knee, and hip) that permit movement only in the parasagittal plane. There are approximately 45 separately recruitable muscles with significant actions in this plane; these have been collected into 10 groups that have fundamentally different topology with respect to the degrees of freedom of the skeleton (see Fig. 4).

The K matrix contains the predicted gains between all sensors and all actuators at a given phase of the target trajectory and for a given set of performance criteria. In the models described here, each of the three joints had a sensor for joint angle (ϕ) and joint velocity ($\dot{\phi}$) and each of the ten muscle groups had a sensor for combined length and velocity (muscle spindle primary ending, designated Ia), force (Golgi tendon organ, designated Ib), and activation (derived from efference copy via Renshaw cells, designated RC). Thus, the complete K matrix consisted of 36 rows by 10 columns. Individual gains are presented here as signed logarithmic values ranging from ±0.001 (absolute values smaller than this were eliminated) to ±100 (see bar graph in Fig. 4).

The physiological relevance of a particular K matrix was assessed by observing the time course of the response of a simulated hindlimb under the control of this matrix when subjected to various small perturbations in
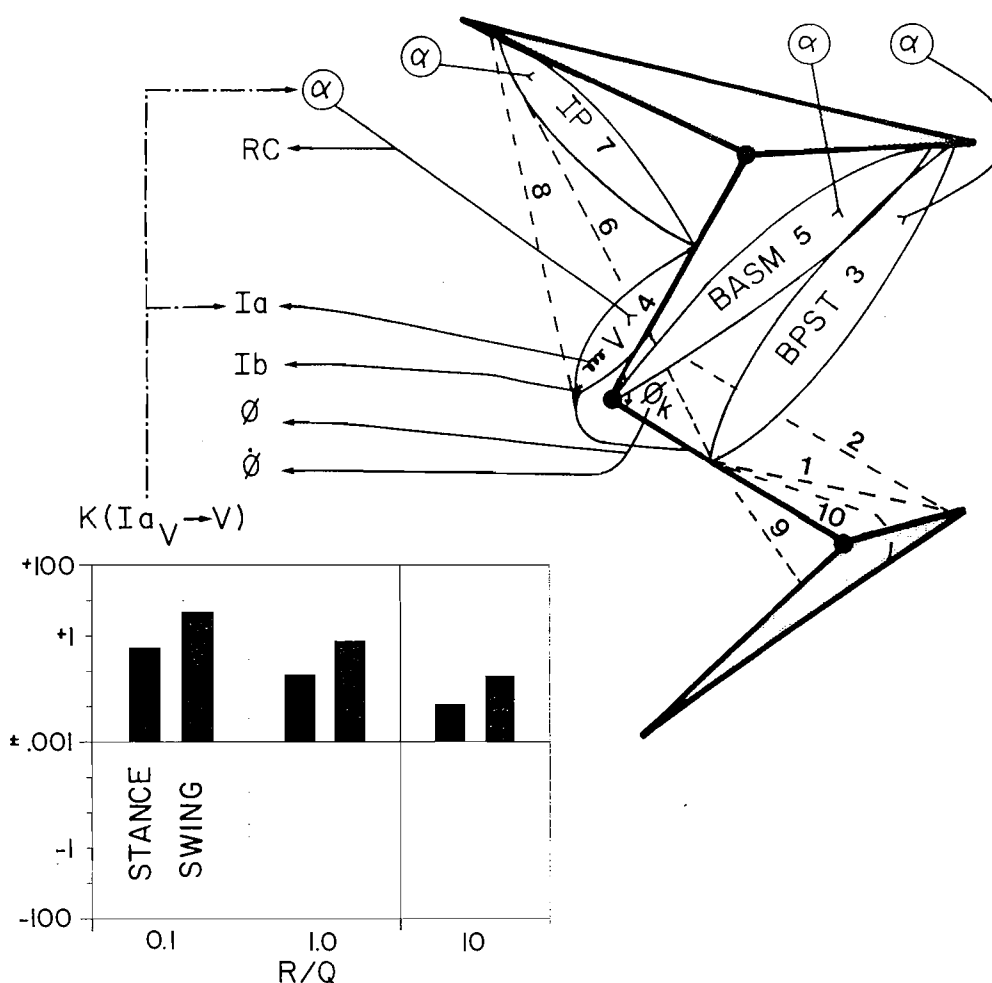
Figure 4. Basic musculoskeletal architecture of the cat hindlimb model, with ten muscle groups: six indicated by dashed lines and four (discussed in Fig. 6) by name ([V] vastus, knee extensor; [IP] iliopsoas, hip flexor; [BASM] biceps anterior and semimembranosus, hip extensor; [BPST] biceps posterior and semitendinosus, knee flexor plus hip extensor). Inset diagram shows typical gains for one element of the feedback matrix K (spindle Ia afferent from vastus muscle to homonymous α motoneurons) for six conditions: three performance criteria (R/Q) ranging from stiff (0.1) to loose (10) and two mechanical states, mid-stance (solid bars) and mid-swing (shaded bars) of walking. Other sources of feedback available include Golgi tendon organs (Ib), Renshaw feedback of motoneuron activity (RC), joint angles (ϕ) and joint velocity ($\dot{\phi}$).

posture. In particular, we compared the responses of the model system to those measured in intact cats following small horizontal displacements of the foot during quiet standing (Rushmer et al. 1983; Macpherson 1988).

RESULTS

As reported previously (Loeb et al. 1989; He et al. 1991), a relatively natural-appearing response to perturbations during standing could be achieved only by including in the performance criterion the feedback information from all available modalities of sensors and for intermediate R/Q ratios of about 1. Figure 5 depicts the complete K matrix for this condition. Features of note include the generally high positive feedback from homonymous Ia sensors (diagonal line of upward bars in the appropriate region of the matrix) and negative

feedback from homonymous Ib and RC sensors (diagonal lines of downward bars). Heteronymous (off-diagonal) connections are generally weaker, but in toto make up a significant part of the feedback control, particularly for the Ib and RC feedback. All of these are generally consistent with known patterns of reflex connectivity in the lumbosacral spinal cord of the cat (McCrea 1986); it is worth noting that these patterns emerged from a design process that starts out tabula rasa.

One problem with the matrix in Figure 5 is the relatively large gains for the joint angle and angular velocity sensors. There is considerable evidence suggesting that most of the sense of joint position and motion is derived from muscle spindles (Ferrell et al. 1987), probably from both primary and secondary endings. The LQ method requires a sensor or an estimator for all state variables; joint angle and angular velocity
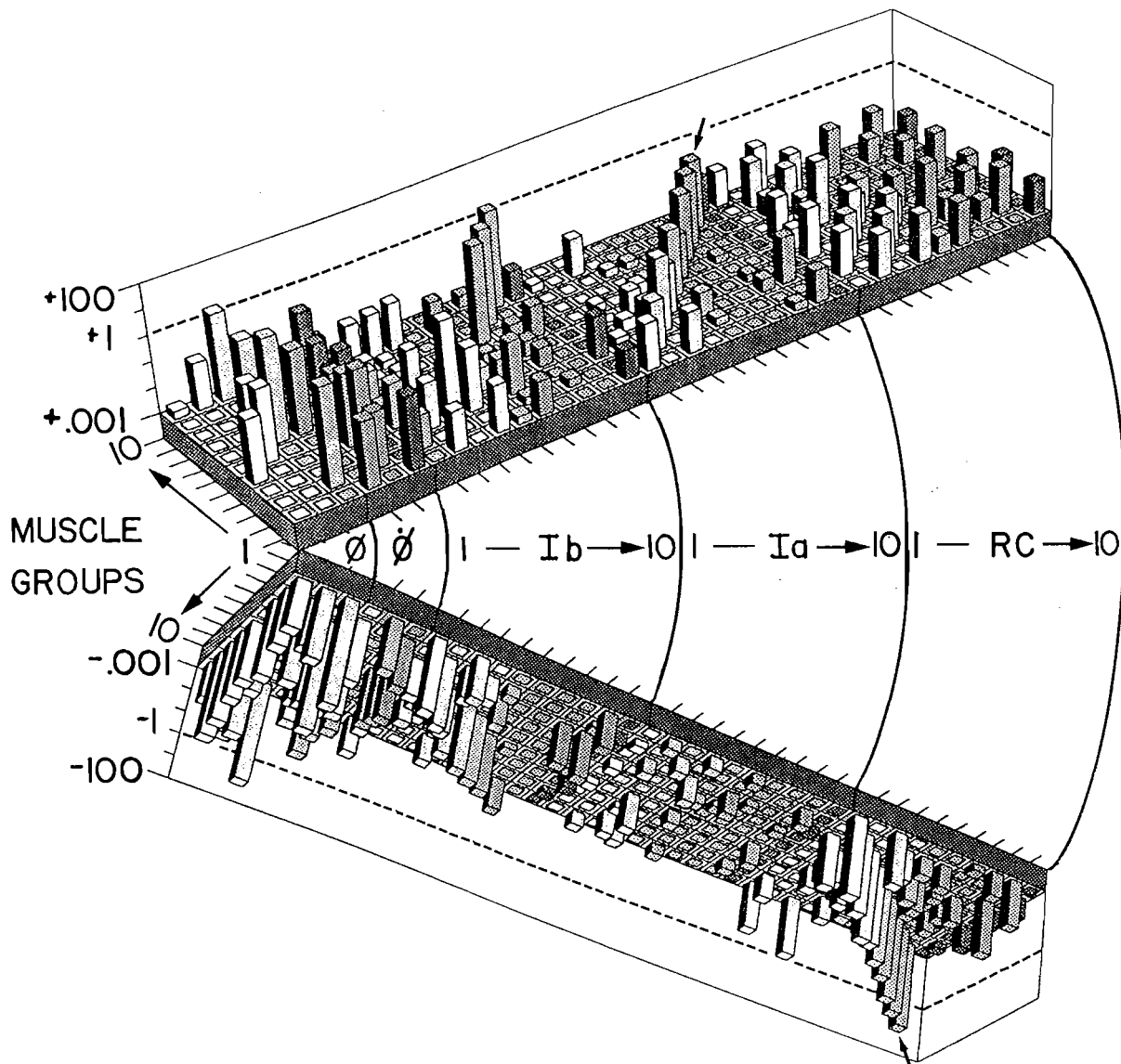
Figure 5. Full K-matrix for mid-stance, $R/Q = 1$, with positive gains above and negative gains below mirror-line. Afferent sources, identified along horizontal axis, connect at intersections with all muscle groups identified along vertical axis; receptor types and muscle numbers keyed to Fig. 4. Joint afferents $(\phi,\dot\phi)$ ordered from left to right as hip, knee, and ankle. Small arrows denote tendency for homonymous feedback to be positive from spindle (Ia) afferents and negative from Renshaw cells (RC).

are typically (but not necessarily) used as state variables in equations of motion. In principle, an "optimal estimator" for the joint variables could be determined by appropriately weighting the contribution of all of the muscle spindle afferents (probably requiring a model of the spindle secondary ending as a pure muscle length sensor, which we have not implemented here). However, the prevalence of multiarticular muscles in the cat hindlimb makes this a nontrivial task. An alternative is to rewrite the state equations in coordinates of the actual sensors believed to be present, a task currently under way. Meanwhile, it would be unwise to over-interpret the predicted distribution of the Ia projections (particularly the heteronymous projections) because they probably should include large contributions now buried in the joint sensor projections.

Figure 6 reflects a first attempt to examine the effects of different behavioral tasks and mechanical constraints on regulator design, focusing on just a few selected row-and-column intersections in the full K matrix. The predicted values are shown for mid-stance and mid-swing trajectory and boundary conditions, at three different R/Q values. An R/Q criterion of 1 produces a quite physiological response to perturbations during standing, whereas values of 0.1 and 10 produce behaviors that may be characterized as "too stiff" and "too loose," respectively. Unfortunately, there are no corresponding behavioral data during swing. The swing-phase feedback shows some startling reversals of sign from stance, particularly regarding the relative effects of joint position versus joint velocity and homonymous Ib feedback. Presumably, these reflect
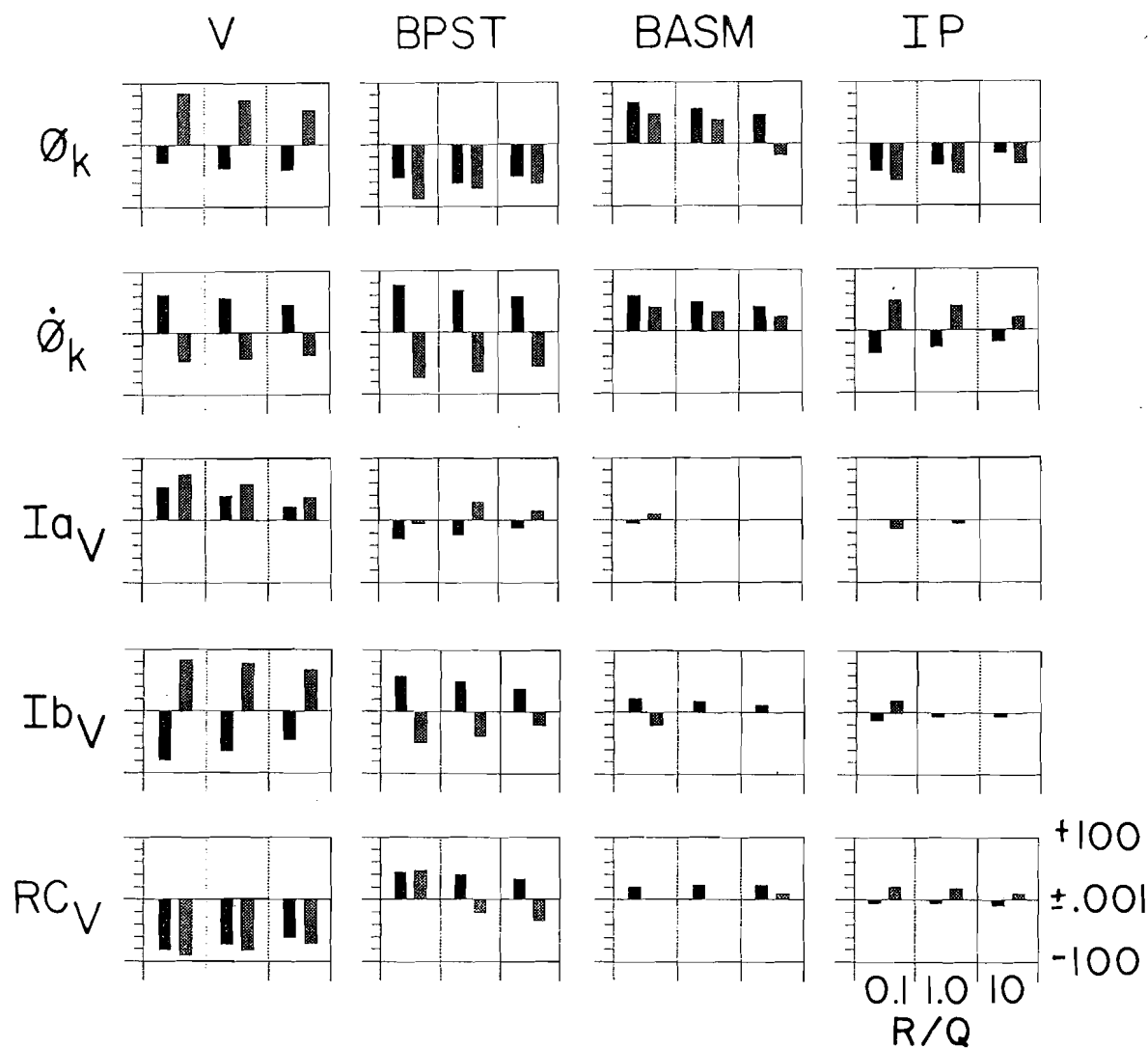
Figure 6. K-matrix values for connections between selected sensors (rows labeled ϕ_k, knee angle; $\dot{\phi}_k$, knee angular velocity; Ia$_v$, vastus spindle primary; Ib$_v$, vastus Golgi tendon organ; RC$_v$, vastus Renshaw cell) and selected muscle groups (columns at top, identified in Fig. 4). Each set of bar graphs indicates gains for different phases (stance, solid bars; swing, shaded bars) and performance criteria R/Q (see inset key in Fig. 4).

DISCUSSION

Experimental Testing of Feedback Predictions

We have used comparisons between real and simulated responses to perturbations to gauge the relevance of different performance criteria (He et al. 1991). There are at least three feasible methods to obtain more specific data regarding reflex connectivity and its gating during locomotion:

1. Stimulation of primary afferents while recording electromyographic reflexes in various muscles in walking cats. This method is hampered by the fact that the thresholds for electrical activation of Ia, Ib, and α motoneurons (projecting to RC) are generally not distinguishable. However, for particular combinations of sensors and actuators, the predicted effects may be robust enough to glean useful information from such mixed inputs.

2. Postsynaptic potential analysis of identified pathways in fictively cycling preparations (see, e.g., Pratt and Jordan 1987). Because of the extremely fine-grain approach and low yield of single-unit recording, it will again be necessary to select for robust predictions. However, information to guide the design of these tedious but critical experiments is one of the main benefits of LQ modeling.

3. Reflex plasticity following changes in musculoskeletal mechanics. Interestingly, the overall locomotor pattern of muscle recruitment appears to be relative-

ly unaffected by surgical changes such as tendon transfers (Sperry 1945; Forssberg and Svartengren 1983), but there is some evidence of changes in reflexes (Yumiya et al. 1979; McMahon and Wall 1989). Again, LQ modeling may be useful in directing the design of relatively long-term experiments that may require chronic instrumentation of young animals.

Limitations of Linear Regulators

The computational methods of linear quadratic regulator design are based on the assumption that even inherently nonlinear systems such as biological limbs can be adequately described by linear approximations when considering their behavior over small enough regions of their state space. From a biological perspective, this translates into four concerns:

1. How large does a perturbation have to be before it requires a response that lies outside the effective range of the regulator? Consider the maintenance of standing posture in bipeds. Small internal or external perturbations give rise to small swaying movements that require a carefully orchestrated distribution of small changes in muscle activation to maintain stability. However, once the center of gravity passes beyond the horizontal extent of the feet, the only viable strategy is the execution of a stepping movement to widen the base of support by relocating one foot (Nashner et al. 1979). A linear regulator would be an excellent choice for controlling sway, but it would have to be supplemented with a triggerable pattern generator to handle the stepping response. Presumably, this generator would reprogram the spinal regulator in the process of executing its response, much as we postulate that the CPG for locomotion prescribes its desired regulator.

2. How frequently during a large movement does the regulator matrix have to be updated? We have generated feedback matrices in which each gain term is not a single value but rather a continuous parameter (actually calculated in small time increments) that changes over the phases of the step cycle. However, it may be that the feedback matrix changes in only a small number of discrete phases during the step cycle. The question of whether locomotion or any other phasic behavior is controlled discretely or continuously is complex and contentious. There is evidence that such behaviors may be driven by oscillators composed of reciprocating "half-centers" (Lundberg 1980), but it is also clear that their elaboration into the detailed recruitment patterns of individual muscles (Abraham and Loeb 1985) and reflex gains (Abraham et al. 1985) introduces a more continuous form of control.

Figure 7 presents one alternative that seems consistent with recent findings about the temporal and spatial distribution of neural activity during fictive locomotion (Jordan 1990) and the effects of sensory
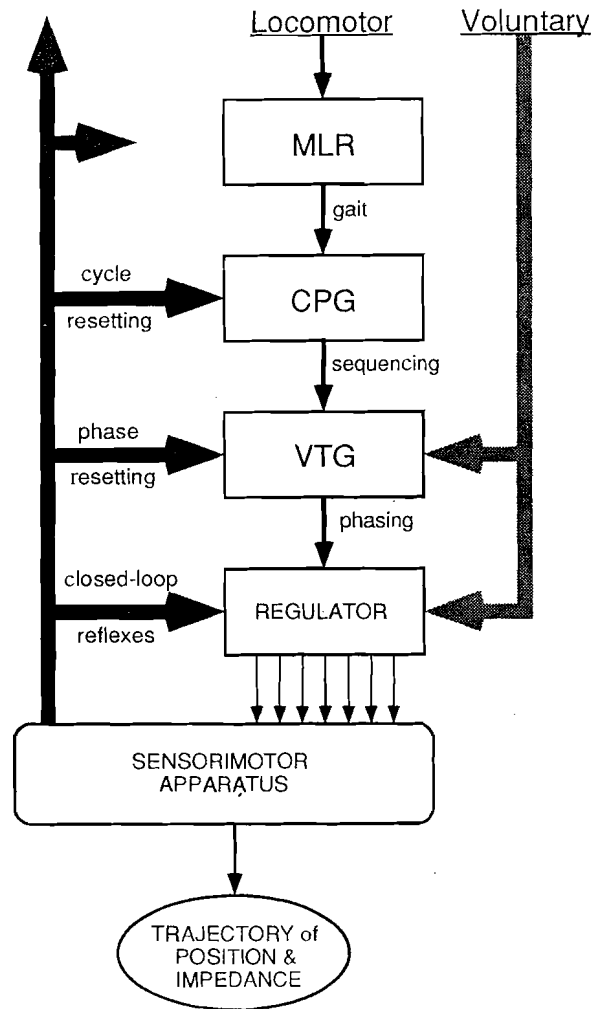

Figure 7. Schematic control system for locomotion, starting with mesencephalic locomotor region (MLR), central pattern generator (CPG), virtual trajectory generator (VTG), and interneuronal regulator matrix controlling the activation of multiple muscle groups (small arrows) in the limb.

perturbations. In the cat hindlimb, locomotion at different speeds can be produced by graded, nonphasic stimulation of the mesencephalic locomotion region (MLR; Severin et al. 1967). MLR neurons project to a group of interneurons beneath the dorsal horn in the lumbar spinal cord that seem likely to be the CPG producing the basic reciprocating drive required for alternating flexion and extension of each limb. However, much of their output does not go directly to the motoneurons in the ventral horn, but rather through interneurons in the intermediate laminae, here designated VTG for virtual trajectory generator. We speculate that these interneurons shape the bistable oscillation of the CPG into the more continuously modulated recruitment of motoneurons and gating of reflexes. Interestingly, different types of somatosensory stimuli introduced during locomotion result in distinctive effects on these putative functions (Lennard 1985). Small or

brief proprioceptive inputs give rise to classic short-latency reflexes (e.g., tendon-jerk), whereas large, long-lasting proprioceptive inputs appear to interrupt the CPG, which then restarts its oscillator when the stimulus is removed. Cutaneous stimuli give rise to reflexes that may shorten or lengthen the particular locomotor phase in which they are delivered, but do not reset the basic rhythm.

The relationship between the neurons comprising the VTG and the regulator is not clear. Although they are conceptually distinct processes in control theory and they seem to give rise to different behavioral reflexes (see above), they may actually reflect different emergent properties of the same group of interneurons. This is because the interneurons are connected among themselves as well as receiving inputs from primary afferents and controllers and generating outputs to motoneurons. Such lateral connections probably generate temporal properties such as those responsible for the widespread and consistent patterns of short- and long-latency excitatory reflexes (Forssberg 1979; Abraham et al. 1985).

3. Can the regulator be used to generate point-to-point (e.g. reaching) movements? This question is really a combination of the previous two, viewed from the perspective of a control scheme in which the controller simply provides a target state and then relies on an appropriately programmed regulator. It impacts critically on the potential role of the VTG described above. In principle, the regulator could be directly programmed to achieve stability for the desired final position of the limb, and the movement would be driven solely by the magnitude of the sensory error signal. (This would be akin to equilibrium point control as proposed by Feldman [1966] and Bizzi et al. [1982], but with a distributed regulator to replace the servocontrol of individual muscles.) However, the large initial deviation would be outside the range for which linear regulator design is normally appropriate.

There are three possibilities for generating large movements: (a) The controller could generate a continuous string of nominal positions and associated regulators in small increments (akin to virtual equilibrium point trajectory; Bizzi et al. 1984). However, this would be computationally intensive and vitiates most of the advantages of hierarchical control (see below). (b) Musculotendinous systems have a number of intrinsically stabilizing mechanical properties (Zajac 1990) that may make it feasible for a single regulator to achieve a satisfactory compromise between the dynamics of movement and the statics of posture maintenance. The mathematics for including such compromise criteria in regulator design have yet to be developed; however, intuitively this approach seems likely to lead to at least some unacceptable limitations (e.g., moving quickly but compliantly). (c) The controller could take advantage of the temporal properties of the VTG to introduce phasing into the expression of abruptly shifting

regulator designs. This has the attraction of making use of circuitry that seems likely to exist already in the spinal cord and which is under the continuous and local control of resetting reflexes that could handle unforeseen perturbations during the execution of the movement. Furthermore, it seems more consistent with the patterns of activity that have been recorded from motor cortex, which seems more concerned with initiating and terminating movements than with the detailed phasing of muscle recruitment during movements (Fetz et al. 1989; Kalaska et al. 1989).

4. Is linearity a likely or necessary property of neural information processing? There is no question that neural transmission in primary afferents, interneurons, and motoneurons displays a variety of highly nonlinear effects, ranging from the inevitable threshold properties (and associated temporal and spatial summation) to time-dependent effects such as potentiation, depression (Collins et al. 1984), and even bistable switching (Hounsgaard et al. 1988). However, the LQ method does not predict the details of neuronal transmission that must underlie the K matrices. LQ design in this context shares some of the features of linear regression analysis; it can be applied and evaluated in the manner that one would consider a linear curve fit to a noisy data set arising from a complex and poorly understood process. The utility of the analysis depends only on the strength of the correlation, not on any inference of causal relationships. If no reasonable correlation is discovered, then it is up to the researcher's intuition to select a candidate nonlinear regression technique. (Unfortunately, there are no practical methods currently available for nonlinear regulator design, although there is a nonquadratic method called H-infinity that tends to minimize the worst error rather than the mean square error, and hence may be biologically relevant; Francis 1987; Doyle et al. 1989.)

Advantages of Regulator-based Control

Redundancy. Because of the distributed nature of the feedback matrix, no individual sensor or feedback pathway assumes a disproportionate responsibility for responding to any particular perturbation. However, the sudden loss of certain terms could give rise to instability; furthermore, the absence of whole modalities of sensors produces clear and general degradations of performance even when the matrix is recomputed for the optimal control of the reduced system.

Speed. It is axiomatic in servocontrol that delays produce instability and require reductions in permissible gain and, hence, speed of response. It is axiomatic in biological systems that speed often means survival. Thus, one obvious advantage of the controller-regulator hierarchy proposed here is that it permits highly goal-specific reflexes to be programmed into the shortest available neural loops, the spinal-segmental reflexes.

Evidence for such goal-specific spinal reflexes comes from fingertip grasp studied by Cole and Abbs (1987) in humans (ironically, this is virtually the only muscular system in which the neuroanatomy would even permit strictly central control). When the position of the thumb was perturbed, the response was a short-latency (50–60 msec) adjustment of the position of the index finger that was attempting to meet it, even though the muscles controlling the index finger were not perturbed. After allowing for peripheral conduction time, the central delay for this rather clever reflex is 10–15 msec or less, strongly suggesting a spinal pathway. Even faster, goal-specific reflexes have been noted in orofacial muscles perturbed during vocalizations (Gracco and Abbs 1985).

It should be noted that we have not incorporated any neural delay into our models of the regulator for the cat hindlimb. This seems justified in the cat, where most of the total delay for segmental reflexes occurs in the electromechanical activation delay of the muscles (which is included in our component models for muscle dynamics). The inclusion of explicit delay terms in the regulator itself poses a severe computational burden for the regulator design process, which may need to be addressed for other systems.

Growth and functional adaptation. As the musculoskeletal system grows and adapts to different patterns of usage, there will certainly arise the need to adjust the gain of the reflexes. This suggests the need for some local growth rules to adjust the strength of synapses to and from individual interneurons and motoneurons. Although some degree of plasticity has been noted in the spinal cord (Wolpaw and Lee 1989), no general growth rules have been proposed. However, any such changes must interact in an orderly manner with the various sources of descending commands. If higher centers such as motor cortex bypassed these circuits, they would face the double problem of having to make their own detailed adjustments and identifying the changes in the segmental reflex circuits that might affect execution of the descending commands.

Phylogenetic development. It is useful to keep in mind that telencephalons with the capability of programming detailed limb movements are a relatively recent phylogenetic development, whereas spinal cords (and even invertebrate limb ganglia) have been generating and controlling very sophisticated limb movements for a very long time. The higher centers must have evolved incrementally in their needs and capabilities. Thus, it seems likely that their motor planning was based on using as much as possible of the segmental circuitry, even if this led to a proliferation of ad hoc pathways and coordinate frames that would offend a robotic systems designer.

Implications for the Organization of Descending Systems

We might still apply the analogy of a programmable industrial robot to the spinal cord. Its local computer might be expected to contain certain preset motor sequences (e.g., locomotor gaits) that are so frequently needed that it is efficient to encode them into a read-only-memory (e.g., CPG). It would also be capable of producing a virtually unlimited set of motor behaviors, but in this role, it would be largely dependent on programs down-loaded into it by a central controller (where the real "intelligence" would reside). This organization raises two difficult problems for the scientist who must "reverse engineer" such a system (as opposed to designing it from scratch): Namely, how are these programs written and how are they encoded?

If the spinal cord contains essentially all possible regulator and controller designs in its ensemble of interneurons, then the task of the movement designer is to find an acceptable set of interneurons whose net effects result in a controller and regulator combination that is appropriate to the task at hand. If all motor output must be mediated through such a combination (rather than specified directly to the actuators), then there is no way mathematically to invert the desired trajectory to calculate even one of the infinitely many patterns of descending signals that might suffice to perform the task. The method of linear quadratic regulator design that we have used here produces a prediction for the net reflex connectivity between sensors and actuators, but provides no information about how this might be distributed at the single interneuronal level. Furthermore, it is an algebraically intensive approach that is not at all suited to the computational properties of neurons.

Previous approaches to the problem of control system design have interpreted the spinal cord circuitry as a highly constrained and fixed regulator that simplifies the problem of invertability. For example, it has been assumed that the proprioceptive reflexes might "linearize" the complex dynamics of force output by individual muscles (e.g., stiffness regulation; Houk 1979) and that reciprocal neural connections and musculoskeletal mechanics between antagonist muscle pairs forming myotatic units (Lloyd 1946) might provide predictable "equilibrium points" for joint angles (Bizzi et al. 1982). If these regulatory properties are themselves highly dependent on the specifics of each descending program to the spinal interneurons, then such simplifications are not permissible, even if they are sometimes valid descriptors of emergent properties of the system.

This forces us to postulate that descending systems such as cerebral cortex must "learn" to generate each new output program by successive approximation rather than by inversion of the desired trajectory. Of course, this notion is not new (see, e.g., Loeb 1983), but the nature of the spinal cord system that must receive and implement such programs may shed some light on the arrangement and properties of the higher systems that must generate them. In particular, let us consider three preoccupations of cortical neurophysiology: (1) the existence of topical maps; (2) the relationship between the coordinates of these maps and the feature-extracting capabilities of neural networks; and (3) the flow of information that underlies the functional

adaptation of these networks. If the cortex uses a singular computational algorithm and the emergent properties of each specific area depend on its particular inputs and outputs (see, e.g., Diamond 1979), then how can such a machine be implemented to accomplish the apparently different tasks of cognition and motor control?

To implement a neural network as the motor controller shown in Figure 3, the input layer would be driven from some premotor region that would specify the objective to be reached, perhaps in coordinates of extrapersonal space, and the output layer would project to the interneurons forming the VTG and regulatory networks of the spinal cord, whose coordinates have no simple physical representation. Sensory feedback would be necessary for at least three functions, all of which are temporally removed from the immediate execution of each motor program: (1) to provide a "teacher" to reinforce network connections when the objective is successfully attained; (2) to signal the suc-

cessful or unsuccessful completion of a program and thereby to signal readiness for another program; (3) to provide haptic information to characterize objects by the manner in which their loads affect the execution of motor programs. Figure 8 shows such a "motor" network configuration. In contrast, it is usually assumed that the input layer of a cognitive neural network is derived from the representation of the sensory signal, that the output layer goes to other cortical areas, and that any teaching is mediated by "higher" centers. Certainly, there are ample data to suggest that the topicalities of many sensory cortical areas are derived from their sensory input, but such ascending information may not be the only or even the main inputs to a cognitive neural network.

Implications for the General Functions of Cerebral Cortex

The view of sensory cortex as the passive interpreter of sensory data is derived largely from the circumstances of most neurophysiological experiments to date. However, there is growing recognition of the powerful effects of "attention" on the receptive field properties of cortical neurons and on the importance of descending, corticofugal pathways (from sensory as well as motor areas) for shaping the transduction and transmission of information destined for the cerebral cortex (Fetz 1984; Harth et al. 1987; Desimone et al., this volume). This "active" view of perception may be more reconcilable with the operations of motor control. In fact, the scheme shown in Figure 8 can be interpreted as subserving the acquisition of sensory information as well as the attainment of physical goals.

Consider the visual system, in which the representation of the features of a scene must be assembled piecewise by the successive focusing of a high-resolution foveal region on individual regions of interest. The task of decomposing a complex scene is really the development of a series of efficient strategies for the active oculomotor exploration of that scene; the visual feedback from each successive eye movement must inform the interpretation of the last percept and direct the strategy to acquire the next (Ballard 1989). If one were to examine such a process in media res, one would expect to find a neural network that was looking actively for a particular feature that it expected to find and then reporting back whether such an object was found, where it was, and how it deviated from what it was expected to look like. Like motor cortex, sensory (and association) cortex would learn strategies to find and acquire particular objectives; it would report on what it has looked for, not what it is passively looking at. (Note that in many sensory systems, the efferent signals effecting this search may not cause overt movement but rather cause changes in receptor tuning and low-order signal processing, such as in cochlear, retinal, and fusimotor efferents.)

A brain composed of many modules identical to that shown in Figure 8 might be expected to have many
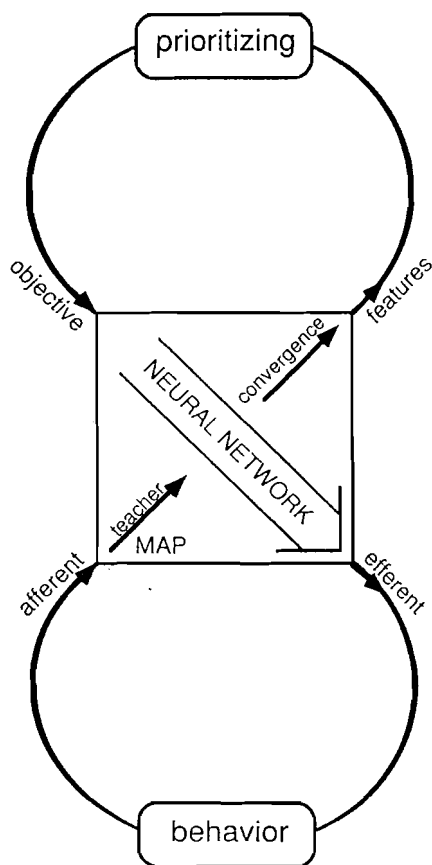

Figure 8. General module for acquisition and perception. Functional schematic of proposed model of a single cerebral cortical area that uses a neural network to translate an input specification of an objective into an efferent search and acquire strategy. Successful completion of the search is signified by afferent information that reinforces the connections defining the search strategy and passes on salient features regarding the acquired objective. It is hypothesized that the coordinate frame of this afferent information defines the topical map of the cortical area.

desirable emergent properties that are difficult to achieve with the usual configuration of input and output layers in neural networks: (1) It permits (in fact, requires) recursive computation in which the features realized in one cycle would inform the choice of objectives for another cycle. (2) It could thereby generate temporal sequences of motor output such as required for tool-using and other important forms of nondeclarative memory (Squire et al., this volume). (3) It preserves relative location of entities in space and time as intrinsic properties of those entities, which properties are recalled automatically in the process of interpreting a complex situation (e.g., finding sources of food; Allman and Zucker, this volume). (4) It provides a quasi-hierarchical architecture in which information passes freely and in parallel among many areas whose relative position in the chain depends on the nature of the ongoing activity. (5) Its requirement for constant prioritizing of conflicting suggestions about where to direct its receptors leads to the appearance of a single stream of goal-directed, "conscious" behavior.

The establishment of coordinates for the afferent-based map could be driven by an unsupervised neural network, that is, a self-organizing Hebbian network whose representation comes to reflect the inherent frequencies and coherences of patterns that tend to occur in the input data, without regard to any externally imposed goals. The learning task of a higher-order system projecting to such an area would be to discover this coordinate system, much as the motor cortex must discover the organization of the spinal interneurons. The signal specifying the objective to a cortical area would activate those neurons whose aggregate output effects should result in the desired behavior. Points of agreement between the sources of this efferent activity and the resultant afferent activity would then identify the connections to be strengthened, i.e., between those efferent neurons and their cortical inputs specifying the objective. Thus, each module would contain two neural network configurations arranged orthogonally: (1) an unsupervised network to establish the sensory representation and (2) a supervised network employing a knowledge of results that is physiologically plausible (in fact, inevitable) and appropriately configured topically. This arrangement would permit the gradual reassignment of cortical columns to deal with the changing frequency of particular cognitive and motor tasks required over the life of the animal (Merzenich, this volume).

In the specific case of motor cortex, the above analysis tells us more about what not to look for experimentally than about what we might find. It suggests that the topographical coordinates will be neither of the two alternatives that have been the traditional focus of experiments, i.e., neither muscles nor movements. Techniques such as microstimulation (Stoney et al. 1968) and spike-triggered averaging (Fetz and Cheney 1980) have confirmed the broad musculoskeletal topography that is apparent from clinical and experimental lesions, but the divergence of the descending effects of even a single corticospinal neuron belie any attempt to draw such muscle maps more finely. The population vector approach clearly demonstrates the presence of an input signal corresponding to the sort of extrapersonal space coordinates that appear to underlie the topography of some parietal and frontal areas that project to motor cortex (Georgopoulos et al. 1983), but the topographical arrangement of these motor cortical neurons appears not to be strongly related to their contribution to such vectors (A.P. Georgopoulos, pers. comm.). The scheme proposed in Figure 8 suggests that the map should be derived from the afferent information used to reinforce the neural network, but this begs the question of what coordinate scheme has been imposed on this information by its preprocessing in spinal cord, thalamus, and somatosensory cortex. Psychophysical experiments on kinesthesia suggest that we start by considering the orientation of body segments in extrapersonal space (Soechting and Ross 1984), a frame that seems attractive as a compromise between limb-end-point coordinates for the motor-cortical input and the spinal-regulator coordinates of its output. This is at least consistent with the types of information that are conveyed through those regions of the thalamus and sensory cortex that have been demonstrated to produce long-term potentiation in motor cortex (Iriki et al. 1989) and to facilitate learning of motor skills (Sakamoto et al. 1989).

CONCLUSIONS

Optimal controller design has been used to study human and animal jumping (Zajac et al. 1981; Hatze 1981; Pandy et al. 1990) and bipedal walking (Chow and Jacobsen 1971; Yamaguchi 1990), but not in combination with closed-loop regulation. In principle, it should be possible to apply engineering control theory to address questions such as the relative merits of different coordinate schemes for hierarchical systems such as those considered here. However, systems such as outlined in Figure 7 are near or beyond the limits of both current control theory and neurokinesiological methodologies for their exploration. Rather than expecting formal predictions from such modeling, it seems more realistic to use it as a tool to extend and to test our intuition about the workable relationships that might exist between musculoskeletal systems and the neural networks that must control them.

The current resurgence of interest in neural networks stems from several circumstances: (1) They offer a general mechanism that might handle many information-processing problems; (2) they are now sufficiently developed theoretically to anticipate their limitations; and (3) it is feasible to simulate them in computers to observe their interesting and often unpredictable emergent behaviors. We believe that optimal control offers the same three attractions to students of mechanical systems.

Neuroscientists who study sensorimotor control must understand simultaneously the properties of the neural

and the mechanical systems. If normal cognition is predominantly an active rather than a passive behavior, then the bidirectional interface between computation and control will turn out to be central to our understanding of much of animal behavior.

REFERENCES

Abraham, L.D. and G.E. Loeb. 1985. The distal hindlimb musculature of the cat: Patterns of normal use. *Exp. Brain Res.* **58**: 580.

Abraham, L.D., W.B. Marks, and G.E. Loeb. 1985. The distal hindlimb musculature of the cat. II. Cutaneous reflexes during locomotion. *Exp. Brain Res.* **58**: 594.

Athans, M. and P.L. Falb. 1969. *Optimal control.* McGraw Hill, New York.

Ballard, D. 1989. Behavioral constraints on computer vision. *Image Vision Comput.* **7**: 1.

Bizzi, E., W. Chapple, and N. Hogan. 1982. Mechanical properties of muscles: Implication for motor control. *Trends Neurosci.* **5**: 395.

Bizzi, E., N. Accornero, W. Chapple, and N. Hogan. 1984. Posture control and trajectory formation during arm movement. *J. Neurosci.* **4**: 2738.

Bryson, A.E. and Y. Ho. 1975. *Applied optimal control.* Blaisdell Publishing, Waltham, Massachusetts.

Chow, C.K. and D.H. Jacobsen. 1971. Studies of human locomotion via optimal programming. *Math. Biosci.* **10**: 239.

Cole, K.J. and J.H. Abbs. 1987. Kinematic and electromyographic responses to perturbation of a rapid grasp. *J. Neurophysiol.* **57**: 1498.

Collins, W.F., III., M.G. Honig, and L.M. Mendell. 1984. Heterogeneity of group Ia synapses on homonymous a-motoneurons as revealed by high-frequency stimulation of Ia afferent fibers. *J. Neurophysiol.* **52**: 980.

Conway, B.A., H. Hultborn, and O. Kiehn. 1987. Proprioceptive input resets central locomotor rhythm in the spinal cat. *Exp. Brain Res.* **68**: 643.

Diamond, I.T. 1979. The subdivisions of neocortex: A proposal to revise the traditional view of sensory, motor, and association areas. *Prog. Psychobiol. Physiol. Psychol.* **8**: 1.

Doyle, J.C., K. Glover, S.P. Khargonekar, and B.A. Francis. 1989. State space solutions to standard H^2 and $H^\times$ control problems. *IEEE Trans. Automatic Control* **31**: 831.

Duenas, S.H. and P. Rudomin. 1988. Excitability changes of ankle extensor group Ia and Ib fibers during spontaneous fictive locomotion. *Exp. Brain Res.* **70**: 15.

Feldman, A.G. 1966. Functional tuning of the nervous system with control of movement or maintenance of a steady posture. II. Controllable parameters of the muscle. *Biophysics* **11**: 565.

Feldman, A.G. and G.N. Orlovsky. 1975. Activity of interneurons mediating reciprocal Ia inhibition during locomotion. *Brain Res.* **84**: 181.

Ferrell, W.R., S.C. Gandevia, and D.I. McCloskey. 1987. The role of joint receptors in human kinaesthesia when intramuscular receptors cannot contribute. *J. Physiol.* **386**: 63.

Fetz, E.E. 1984. Functional organization of motor and sensory cortex: Symmetries and parallels. In *Dynamic aspects of neocortical function* (ed. G.H. Edelman et al.), p. 453. Wiley, New York.

Fetz, E.E. and P.D. Cheney. 1980. Postspike facilitation of forelimb muscle activity by primate corticomotoneuronal cells. *J. Neurophysiol.* **44**: 751.

Fetz, E.E., P.D. Cheney, K. Mewes, and S. Palmer. 1989. Control of forelimb muscle activity by populations of corticomotoneuronal and rubromotoneuronal cells. *Prog. Brain Res.* **80**: 437.

Forssberg, H. 1979. Stumbling corrective reaction: A phase-dependent compensatory reaction during locomotion. *J. Neurophysiol.* **42**: 936.

Forssberg, H. and G. Svartengren. 1983. Hardwired locomotor network in cat revealed by a retained motor pattern to gastrocnemius after muscle transposition. *Neurosci. Lett.* **41**: 283.

Francis, B.A. 1987. A course in $H^\times$ control theory. Springer-Verlag, Berlin.

Georgopoulos, A.P., R. Caminiti, J.F. Kalaska, and J.T. Massey. 1983. Spatial coding of movement: A hypothesis concerning the coding of movement direction by motor cortical populations. *Exp. Brain Res. (suppl.)* **7**: 327.

Gracco, V.L. and J.H. Abbs. 1985. Dynamic control of the perioral system during speech: Kinematic analyses of autogenic and nonautogenic sensorimotor processes. *J. Neurophysiol.* **54**: 418.

Harth, E., K.P. Unnikrishnan, and A.S. Pandya. 1987. The inversion of sensory processing by feedback pathways: A model of visual cognitive functions. *Science* **237**: 184.

Hatze, H. 1981. A comprehensive model for human motion simulation and its application to the take-off phase of the long jump. *J. Biomech.* **14**: 135.

He, J., W.S. Levine, and G.E. Loeb. 1991. Feedback gains for correcting small perturbations to standing posture. *IEEE Trans. Automatic Control* **518**. (in press.)

Hoffer, J.A., G.E. Loeb, W.B. Marks, M.J. O'Donovan, C.A. Pratt, and N. Sugano. 1987. Cat hindlimb motoneurons during locomotion: I. Destination, axonal conduction velocity and recruitment threshold. *J. Neurophysiol.* **57**: 510.

Hogan, N. 1985. The mechanics of multi-joint posture and movement control. *Biol. Cybern.* **52**: 315.

Houk, J.C. 1979. Regulation of stiffness by skeletomotor reflexes. *Annu. Rev. Physiol.* **41**: 99.

Hounsgaard, J., H. Hultborn, B. Jespersen, and O. Kiehn. 1988. Bistability of a-motoneurones in the decerebrate cat and in the acute spinal cat after intravenous 5-hydroxytryptophan. *J. Physiol.* **405**: 345.

Iriki, A., C. Pavlides, A. Keller, and H. Asanuma. 1989. Long-term potentiation in the motor cortex. *Science* **245**: 1385.

Jankowska, E., D.A. McCrea, P. Rudomin, and E. Sykova. 1981. Observations on neuronal pathways subserving primary afferent depolarization. *J. Neurophysiol.* **46**: 506.

Jordan, L.M. 1990. Brainstem and spinal cord mechanisms for the initiation of locomotion. In *Neurobiological basis of human locomotion* (ed. M. Shimamura et al.). Japan Scientific Societies Press/Springer-Verlag, Tokyo. (In press.)

Kalaska, J.F., D.A.D. Cohen, M.L. Hyde, and M. Prud'homme. 1989. A comparison of movement direction-related versus load direction-related activity in primate motor cortex, using a two-dimensional reaching task. *J. Neurosci.* **9**: 2080.

Lennard, P.R. 1985. Afferent perturbations during "monopodal" swimming movements in the turtle: Phase dependent cutaneous modulation and proprioceptive resetting of the locomotor rhythm. *J. Neurosci.* **5**: 1434.

Liddell, E.G.T. and C.S. Sherrington. 1925. Recruitment and some other factors of reflex inhibition. *Proc. R. Soc. Lond. B.* **97**: 488.

Lloyd, D.P.C. 1946. Integrative pattern of excitation and inhibition in two-neuron reflex arc. *J. Neurophysiol.* **9**: 439.

Loeb, G.E. 1983. Finding common ground between robotics and physiology. *Trends Neurosci.* **6**: 203.

Loeb, G.E. and C. Gans. 1986. *Electromyography for experimentalists.* University of Chicago Press, Chicago.

Loeb, G.E., M.J. Bak, and J. Duysens. 1977. Long-term unit recording from somatosensory neurons in the spinal ganglia of the freely walking cat. *Science* **197**: 1192.

Loeb, G.E., J. He, and W.S. Levine. 1989. Spinal cord circuits: Are they mirrors of musculoskeletal mechanics? *J. Motor Behav.* **21**: 473.

————. 1990. The use of musculoskeletal models to infer principles of sensorimotor control. In *Multiple muscle systems: Biomechanics and movement organization* (ed. J. M. Winters and S.L. Woo), p. 165. First World Congress of Biomechanics. Springer-Verlag, New York.

Lundberg, A. 1980. Half-centres revisited. *Adv. Physiol. Sci.* **1**: 155.

Macpherson, J. 1988. Strategies that simplify the control of quadrupedal stance. I. Forces at the ground. *J. Neurophysiol.* **60**: 204.

McCrea, D.A. 1986. Spinal cord circuitry and motor reflexes. *Exercise Sport Sci. Rev.* **14**: 105.

McMahon, S.B. and P.D. Wall. 1989. Changes in spinal cord reflexes after cross-anastomosis of cutaneous and muscle nerves in the adult rat. *Nature* **342**: 272.

Nashner, L.M., M. Woollacott, and G. Tuma. 1979. Organization of rapid responses to postural and locomotor-like perturbations of standing man. *Exp. Brain Res.* **36**: 463.

Pandy, M.G., F.E. Zajac, E. Sim, and W.S. Levine. 1990. An optimal control model for maximum-height human jumping. *J. Biomech.* (in press).

Perret, C. 1983. Centrally generated pattern of motoneuron activity during locomotion in the cat. In *Neural origin of rhythmic movements: Symposia of the society for experimental biology* (ed. A. Roberts and B. Roberts), p. 405. Cambridge University Press, Cambridge, United Kingdom.

Pratt, C.A. and L.M. Jordan. 1987. Ia inhibitory interneurons and Renshaw cells as contributors to the spinal mechanisms of fictive locomotion. *J. Neurophysiol.* **57**: 56.

Pratt, C.A., C.M. Chanaud, and G.E. Loeb. 1990. Complex muscles of the cat hindlimb. IV. Cutaneous reflex responses in the posterior thigh. *Exp. Brain Res.* (in press).

Rushmer, D.S., C.J. Russell, J.M. Macpherson, J.O. Phillips, and D.C. Dunbar. 1983. Automatic postural responses in the cat: Responses to headward and tailward translation. *Exp. Brain Res.* **50**: 45.

Sakamoto, T., K. Arissian, and H. Asanuma. 1989. Functional role of the sensory cortex in learning motor skills in cats. *Brain Res.* **503**: 258.

Severin, F.V., M.L. Shik, and G.N. Orlovski. 1967. Work of the muscles and single motor neurones during controlled locomotion. *Biofizika* **12**: 660.

Sherrington, C.S. 1910. Flexion-reflex of the limb, crossed extension reflex and reflex stepping and standing. *J. Physiol.* **40**: 28.

Soechting, J.F. and B. Ross. 1984. Psychophysical determination of coordinate representation of human arm orientation. *Neuroscience* **13**: 595.

Sperry, R.W. 1945. The problem of central nervous reorganization after nerve regeneration and muscle transposition. *Q. Rev. Biol.* **20**: 311.

Stein, G. and M. Athans. 1987. The LQG/LTR procedure for multivariable feedback control design. *IEEE Trans. Automatic Control* **32**: 105.

Stein, P.S.G. 1978. Motor systems, with specific reference to the control of locomotion. *Annu. Rev. Neurosci.* **1**: 61.

Stoney, S.D., Jr., W.D. Thompson, and H. Asanuma. 1968. Excitation of pyramidal tract cells by intracortical microstimulation: Effective extent of stimulation current. *J. Neurophysiol.* **31**: 659.

Wolpaw, J.R. and C.L. Lee. 1989. Memory traces in primate spinal cord produced by operant conditioning of H-reflex. *J. Neurophysiol.* **61**: 563.

Yamaguchi, G.T. 1990. Performing whole-body simulations of gait with 3-D, dynamic musculoskeletal models. In *Multiple muscle systems: Biomechanics and movement organization* (ed. J.M. Winters and S.L. Woo), p. 663. Springer-Verlag, New York.

Yumiya, H., K.D. Larsen, and H. Asanuma. 1979. Motor readjustment and input-output relationship of motor cortex following cross-connection of forearm muscles in cats. *Brain Res.* **177**: 566.

Zajac, F.E. 1990. Muscle and tendon: Properties, models, scaling and application to biomechanics and motor control. *CRC Crit. Rev. Biomed. Eng.* **17**: 359.

Zajac, F.E., M.R. Zomlefer, and W.S. Levine. 1981. Hindlimb muscular activity kinetics and kinematics of cats jumping to their maximum achievable heights. *J. Exp. Biol.* **91**: 73.