

Spinal programs for locomotion

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Introduction

In comparing the current level of knowledge regarding the function and control of the oculomotor system with that for the skeletomotor system, one is immediately struck by a disparity. Oculomotor research is characterized by accurate quantitative methods, well-defined performance criteria, mathematical models of control and feedback regulation, and a highly evolved theoretical basis in engineering control systems. Skeletomotor research has been and continues to be plagued by phenomenological description, intractable, unstable and inappropriate models, and an allied field of robotic engineering whose greatest contribution continues to be proofs of the impossibility of trajectory planning in real time (Loeb, 1983).

Of course, it might be argued that the skeletomotor system is simply a more complicated embodiment of the principles underlying oculomotor control, and that the state of knowledge simply lags behind for that reason. However, I shall argue that the oculomotor system represents an almost singular exception to the more general function and control of striate muscles. Rather than offering a cleaner crucible in which to concoct and test general theories of motor control, it has provided a protected niche for the preservation of a seductive oversimplification inherited from the study of isolated muscles. Muscle physiology research continues to be artificially constrained by the undeniable observation that activated muscles contract. If the muscle

is attached to an initially stationary but movable object, then the object moves when the muscle contracts, providing a class of phenomena for measurement by the muscle physiologist. However, the primary process within the muscle that is modulated by changes in the neurally controlled state of activation is not length or even tendon strain. Rather, it is a complex, statistically distributed set of forces in the cross-bridges, which are highly dependent on the direction and magnitude of cross-bridge motion.

It is only in circumstances such as the eyeball and ear pinna that muscles find themselves controlling the unopposed motion of virtually massless, inelastic objects in a frictionless, low-viscosity medium. Under such circumstances, muscles are well described and easily replaced by simple actuator mechanisms of the sort commonly employed in conventional electromechanical engineering. However, in more typical skeletomotor configurations, the addition of large inertial effects, gravity and other external loads, and elastic storage represent not mere complexities, but rather compel the motor system to adapt entirely different modes of operation. In such systems, one frequently encounters muscles with highly specialized internal architectures to improve performance under such kinematically diverse conditions as active shortening, active lengthening, and isometric force generation. The torques and length changes of a given muscle acting across one joint may depend on the position of the joint and possibly of other joints spanned by mul-

tiarticular muscles. Such actuators are a far cry from the simple torque motors of robotic systems, so it is not surprising that mechanical engineering has had little to offer in the way of biologically relevant computational models or control theories.

In studying the function of any single muscle in such a dynamic system, the muscle should not be considered directly as a cause of the observed motion; rather, it is better considered as a generator of an "impulse" added to the system. Impulse is the kinetic contribution to momentum given by the product of force and time. The impulse is the resultant of the interaction of the activated cross-bridge sites (bearing calcium and ATP but not necessarily attached) with the motion that is largely imparted to the muscle by the inertia of limb segments and the action of other forces external to the muscle, including other muscles. As we shall see, there is evidence that both the anatomical architecture and the neurophysiological control circuitry for the muscles of locomotion are highly dependent on the particular kinematic conditions under which each muscle is called upon to provide this impulse. If there are any single, unifying principles of motor control, they must be expressed in terms that transcend the concerns local to any such specialized structure as the extraocular muscles, which deal with only one kinematic condition.

The locomotor program in the cat hindlimb

The phenomenology of terrestrial locomotion has been thoroughly studied in many species having two, four or six legs used in a variety of gait patterns. There has been special interest in the cat hindlimb during walking and trotting because of the ease with which these gaits are elicited in various intact and reduced preparations, and the wealth of data available on the anatomical and physiological properties of the myoskeletal and neural systems as they have been studied in this species in isolation over the past century (for reviews, see Grillner, 1975; Wetzel and Stuart, 1976). The cat hindlimb model is a fortuitous choice, because it appears to represent a highly evolved and thus presumably op-

timized structure for the efficient generation of sustained locomotion needed for predatory hunting. This is not to say that such locomotion is the sole activity of the hindlimb or that it has been entirely optimized with efficiency as the only goal. Rather this suggests the likelihood that the highly organized and largely invariant structures to be found in the cat hindlimb derive from real function rather than evolutionary accident and that this function is likely to be expressed during locomotion. While much of the general structure of the cat hindlimb is undoubtedly inherited from other, perhaps very different ancestors, the specifics have come to embody a great wealth of constructive and instructive improvements resulting from the interplay of random mutations with their consequences in situations with various probabilities of occurrence (for discussion, see Partridge, 1982).

A fairly complete phenomenology of cat locomotion has been available in the literature for some time (see Table I), but it has been only superficially analyzed biomechanically. Data collection methods external to the animal (cinematography and force plates) have permitted analysis of the stability of the quadrupedal patterns and extraction of joint angles and some muscle lengths. The availability of reasonably reliable EMG signals spurred the observation that at least some muscles tended to become active when operating near their optimal lengths, as determined during tetanic electrical stimulation of single muscles in acute preparations (Stephens, 1975). However, even more important than the length/tension properties of muscle are the velocity/tension properties (see Joyce et al., 1969). These have large, nonlinear effects on force output, energetic efficiency, and on the generation of proprioceptive signals from muscle spindles. Only a few muscles having suitable tendon structures have been monitored by surgically implanted force transducers (Walmsley et al., 1978; O'Donovan et al., 1982; Abraham and Loeb, 1985), and there has been no quantitative analysis of muscle velocity in any of the kinesiological studies. A further weakness is the absence of a thorough analysis of the free-body forces operating in this complex open-

TABLE I

Phenomenology of cat locomotion

Quadrupedal locomotion studies	Classical references
Myoskeletal anatomy	Crouch (1969)
Gait patterns and stride lengths	Hildebrand (1966) Arshavsky et al. (1965) Stuart et al. (1973)
Step cycle phase times	Goslow et al. (1973) Miller et al. (1975a,b)
Ground forces	Manter (1938)
Joint angles	Engberg and Lundberg (1969) Goslow et al. (1973)
Muscle lengths	Goslow et al. (1973)
EMG phasing	Engberg and Lundberg (1969) Tokuriki (1973a,b)
Length/tension correlate	Stephens et al. (1975) (incomplete)
Muscle forces	incomplete — see text
Muscle velocity	not available
Velocity/tension correlate	not available
Joint torques and segmental momentum	not available

linked segmental structure, a difficult but tractable problem of inverse dynamic analysis which has been addressed in humans.

Thus, for most hindlimb muscles, it is not possible to state the kinematic conditions under which they generate their output impulses, whether or not these kinematic conditions are homogeneous, or (for multiarticular muscles) how they arise from the complex motion of multiple limb segments. Conversely, it is thus not possible to state which muscles perform their roles by actively shortening, which serve as nearly isometric stiffeners, and which constitute highly elastic force conveyors. As we shall see (and as one might have guessed), these different functional roles are accompanied by substantial and specific specializations at a variety of levels ranging from muscle fiber architecture to the generation and reflexive use of proprioceptive feedback.

Fig. 1 shows a summary of the actions of the

major muscle groups in the cat hindlimb at various points in the walking step cycle (phases from Phillipson, 1905). It is derived from many different experimental sources and from biomechanical modeling techniques still under development in a collaborative project with Professor William Levine of the Electrical Engineering Department of the University of Maryland (Loeb et al., 1983; Marks et al., 1984). The stick figure sequence at the bottom represents every second field of a 60 field per second videotaped walking sequence, with joint positions determined by a combination of skin markers and trigonometric equations based on post-mortem measurement of limb segments. In each figure at the top, the location of each of eleven major muscle groups is shown by a fine line if the muscles are inactive (or nearly so) and by a spindle-shaped thickening if the muscles are generating substantial amounts of active force (relative to the peak for each muscle in the step cycle as measured by EMG and, in some cases, tendon strain gauges). Each active muscle is depicted with one or two arrows signifying the length changes imparted to the muscle by the motion at the one or two joints crossed by the muscle. Arrows pointing distally (from proximal origin to distal insertion) indicate lengthening motion while arrows pointing proximally indicate shortening motion. When there are two arrows, the more proximal indicates the sign of the motion imparted by the more proximal joint crossed. Arrows pointing towards or away from each other thus indicate that the active tension in the muscle is causing an acceleration of the motion at one joint with a deceleration of the motion at another joint. The net length change experienced by the muscle depends on the relative magnitude of the effects of motion at each joint, and is not shown here. Also not shown and still in progress is a quantitative reconciliation of the various active muscle torques acting across each joint with the net joint torques obtained from inverse dynamic analysis of the observed limb motion and measured ground forces.

One of the most striking general findings is the scarcity of muscles in which the active mechanical action is an unambiguous shortening (all arrows

Cat Hindlimb During Normal Treadmill Walking

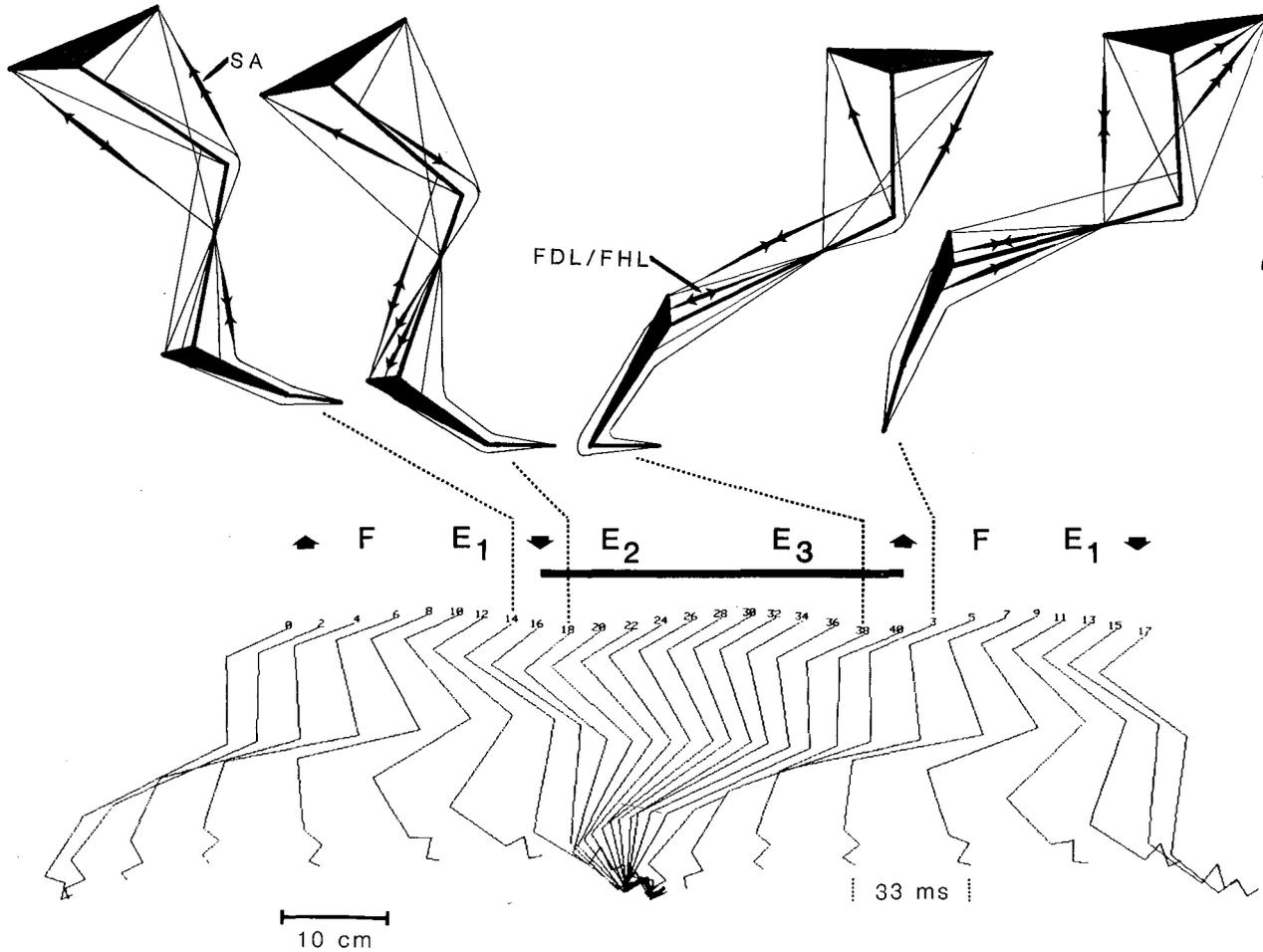


Fig. 1. Stick figure sequence at bottom taken from videotape stills of cat walking, showing corresponding phases from Phillipson (1905) step cycle (flexion, F; first extension during swing, E₁; yield during early stance, E₂; and push-off at late stance, E₃). Arrows indicate footlift (up) and footfall (down); heavy line indicates period of foot contact with treadmill surface. Four stick figures at top taken from the points indicated by the dotted lines, showing approximate anatomical course of eleven major muscle groups as fine lines (inactive) or spindle-shaped thickened lines (generating active force output) with arrows as described in text. SA, sartorius pars anterior muscle; FDL/FHL, anatomically synergistic pair of flexor digitorum and hallucis longus muscles.

pointing proximally). This simple, classical notion of a muscle at work arises only in some of the lightly loaded flexors during swing phase (far left and far right diagrams) and in the pure hip extensors during stance (E₂ and E₃, middle two diagrams). Some of the flexion motions at the knee and toes are generated by muscles that pass excessive flexion momentum at a proximal joint (hip and ankle, respec-

tively) to the more distal joint by becoming stiffly elastic. Most of the early stance phase muscle activity is concerned with limiting the yielding under the load of the body weight. At the end of the stance phase, the highly extended position of the joints places the monoarticular knee and ankle extensors at a disadvantageous length for tension generation, so much of the final push-off is generated by biar-

ticular muscles, with compensatory stretching at one of their joints. This provides the fringe benefit of decelerating the hyperextending angular momentum (particularly in the thigh and shank), making the ensuing flexion task less difficult.

From the foregoing description, it should be clear that the contribution of any single muscle to the locomotor behavior is not evident from a simple gross anatomical description of the actions of the muscle at the joint(s) it crosses. Even less obvious is the identity of the muscles which are in some way "synergistic" and the nature of the proprioceptive information which such muscles might need to exchange for their coordinated control. Such functional dilemmas may well underlie at least some of the dismaying complexity evident in the interneuronal projections among motor nuclei (Jankowska and McCrea, 1983; Harrison et al., 1983). However, some interesting patterns of muscle recruitment have emerged that begin to suggest that the central pattern generators may use kinematics as at least one organizing principle.

Existence of task groups of motoneurons in anterior sartorius

The anterior sartorius (SA) muscle originates on the anterior iliac crest (most rostral extreme of the pelvis) and inserts on the patella, permitting it to act as a flexor of the hip joint and an extensor of the knee. The diagrams indicate that it is active in the swing phase (E₁, first diagram) and again in the late stance phase (E₃, third diagram). The swing phase active tension assists in the motion of both hip and knee in ways that add constructively, resulting in high-speed shortening (1-3 muscle rest lengths per second, depending on gait speed). The stance phase activity occurs when the hip and knee motion are out of phase. In fact, the lengthening contributed by the extending hip outweighs the shortening occurring at the extending knee, causing a net active lengthening. Recordings during unrestrained walking from single alpha motoneurons projecting to this muscle (made using floating microelectrodes chronically implanted in the ventral roots) dem-

onstrate that two entirely independently recruited groups of motoneurons are responsible for these two periods of EMG recruitment (Hoffer et al., 1980, 1982). More detailed studies of the recruitment patterns within the muscle and of the microanatomical organization of the spinal motor nucleus suggest that the segregation is purely functional rather than spatial (Pratt et al., 1984; Loeb et al., 1984). We have just begun a search for selective interneuronal projections from the central pattern generator and from the various proprioceptors, which connectivity might be expected to underlie such a functional specialization.

"Reciprocal" use of the long digit flexors

The flexor hallucis longus (FHL) and the flexor digitorum longus (FDL) muscles in the cat both originate on the tibia, pass around pulleys on the extensor side of the ankle joint, and insert on a common tendon distributed to all four distal phalanges (claws) (Goslow et al., 1972). The second through fourth diagrams in Fig. 1 (top) indicate apparently continuous periods of activity for this pair of anatomical synergists, but in fact stance phase activity occurs predominantly in flexor hallucis longus, while a brief EMG burst at the beginning of flexion occurs only in flexor digitorum longus (O'Donovan et al., 1982). The multiarticular path of the tendons causes both muscles to be rapidly lengthened during stance phase. The active flexor hallucis longus, a pinnate muscle, is thus an efficient generator of propulsive forces throughout the stance phase (lengthening muscles generate higher forces with lower ATP turnover than isometric or shortening muscles). The recruitment of flexor digitorum longus coincides with the unloaded flexion of the toes in the early swing phase, suggesting that it might be actively shortening, much like the other flexors. However, it is also a pinnate muscle (Sacks and Roy, 1982), which would exacerbate the inherent inefficiency of active shortening. A close examination of the force and length data from implanted transducers indicates that the stretch applied via the dorsiflexing ankle effectively reverses the shortening

from the toe motion, resulting in more nearly isometric function (Abraham and Loeb, 1985; also seen in records of O'Donovan et al., 1982). Interestingly, the pulley radius for the two muscles at the ankle is substantially different (3 mm for flexor digitorum longus and 5 mm for flexor hallucis longus; Rindos and Loeb, unpublished data), presumably representing some optimization of the ratio of effective lever arms across the joints for each of the two kinematically different tasks.

Specialized fusimotor programming of the muscle spindles

As sensors of muscle length, muscle spindle afferents contribute kinesthetic information that almost certainly contributes to the coordinated regulation of muscle recruitment. However, the activity of these afferents is complexly and nonlinearly determined by length, velocity, and activity in intrafusal muscle fibers controlled by several kinds of gamma and beta motoneurons (Lennerstrand and Thoden, 1968; Hulliger et al., 1977). Theories suggesting that there are stereotyped rules for the use of the fusimotor system (e.g., alpha-gamma coactivation) have not taken into account these diverse effects on afferent sensitivity. In particular, the optimization of stretch sensitivity in a lengthening muscle (usually via gamma dynamic motoneurons) is incompatible with the generation of any activity at all in rapidly or even modestly shortening spindles. Conversely, the gamma static motoneuron influence needed to preserve afferent activity during shortening causes afferent discharge that is high and poorly sensitive to fluctuations in velocity in lengthening muscle. Thus, it should not be surprising that the patterns of recruitment of the various types of intrafusal regulatory motoneurons appear to be highly dependent on the normal kinematic function of the muscle (for review, see Loeb, 1984). However, this has resulted in some consternation among those who would hope to find single, unifying rules for the control of all muscles.

Conclusions

Skeletal muscles must contend with inertial loads and external forces, factors that do not exist in oculomotor control. These factors have resulted in complex, multiarticular specializations of muscles and tendons that allow them to operate in modes (e.g., spring-like) that do not occur in the extraocular muscles. These added factors represent not simply complications of underlying, uniform principles of muscle function and motor control, but rather force the neuromuscular systems into one or more modes of operation having no analogs in oculomotor control (see Loeb, 1985). It is likely that within single skeletal systems such as the cat hindlimb and even within some single muscles such as the anterior sartorius, the need arises for multiple, independent, and fundamentally different control schemes. It will be the task of the next few years to identify the number and roles of different control schemes arising in striate muscles throughout the body. Once such an understanding has been obtained, it may be fruitful to look again for underlying, unifying themes in motor control.

One analogy that seems to express the nature of this search is that of a novice computer programmer examining the codes of a large number of different compilers to figure out what they are. The structure evident in the code itself will depend almost entirely on the particular language being compiled and the machine language of the computer on which it will run. However, they are all compilers, with certain metastructural similarities deeply embedded in their disparate architectures. The similarities will be apparent only to someone with a broad, intimate knowledge of many different languages and computers, and a clear notion of the high level role of the compiler.

The identification of candidate unifying principles in motor control may be more imminent than one might assume. One approach is to look for performance criteria that might be optimized. At least some of the structure of any system will be dictated

by attempts to optimize specifications such as speed or accuracy, albeit within other constraints. We have proposed that the major function of the fusimotor system in all muscles may be the optimization of the rate of information transmitted by the spindle afferents for the kinematic conditions anticipated during the normal function of the muscle (Loeb and Marks, 1986). Others have proposed that the temporal and spatial patterns of muscle performance during maximal height jumping may be attributed to motor programs optimized for such an experimentally specified criterion (Zajac et al., 1981). The common thread in these suggestions is that sensorimotor systems may be free to adapt control strategies that are in some way optimal for the task at hand rather than being constrained to a limited repertoire of simple, restricted patterns of recruitment. Such performance-based unifying notions seem a priori more encouraging than historical attempts to generalize from single, specific experimental findings.

Summary

A comparison of the control problems inherent in the biomechanics of the oculomotor versus skeleto-motor systems reveals that the skeletal musculature must generally cope with much more diverse kinematic problems, including inertia, elasticity, and external loads. Because of the highly nonlinear properties of muscle, such factors can be expected to require very different and highly specialized structural and functional architectures in both the muscles and their neuronal control circuits. Studies of the cat hindlimb muscles during locomotion have revealed patterns of motoneuron and spindle afferent activity that appear to be segregated based on the kinematics of muscle function (e.g., active lengthening vs. active shortening). It is suggested that these "task groups" of the motor apparatus may represent optimization strategies for the performance and control of kinematically well-defined, frequently recurring motor tasks.

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