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Functionally complex muscles of the cat hindlimb

V. The roles of histochemical fiber-type regionalization and mechanical heterogeneity in differential muscle activation

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Summary. Several cat hindlimb muscles that exhibit differential activation (activity that is restricted to a specific region of muscle) during natural movements were studied to determine the possible roles of 1) non-uniform distribution of histochemically-identified muscle fiber-types (semitendinosus, ST; tibialis anterior, TA) or 2) mechanical heterogeneity (biceps femoris, BF; tensor fasciae latae, TFL). Using chronic recording techniques, electromyographic (EMG) activity was recorded from multiple sites of each muscle during treadmill locomotion, ear scratch, and paw shake. Standard histochemical analysis was performed on each muscle to determine fiber-type distribution. The histochemically regionalized muscles (ST and TA) were differentially active during slow locomotion; the deep regions (high in type I [SO] fibers) were active, but the superficial regions (high in type IIB [FG] fibers) were inactive. Vigorous movements (fast locomotion, ear scratch, paw shake) produced additional, synchronous activation of the superficial regions. In all movements, ST and TA activation patterns were consistent with the existence of identically timed synaptic inputs to all motoneurons within each motoneuron pool, resulting in an orderly recruitment of each whole pool. The differential activation recorded from ST and TA during slow locomotion was presumably a consequence of the non-uniform distribution of the different muscle fiber types. In contrast, differential activation of the histochemically nonregionalized, mechanically heterogeneous muscles (BF and TFL) resulted from non-synchronous activation of different muscle regions. The selective activation of BF or TFL compartments was indicative of differential synaptic inputs to, and selective recruitment of, subpopulations of the motoneuron pool, with each motoneuron subpopulation exclusively innervating physically separate regions of the muscle consistent with the regions defined by the neuromuscular territories of the major nerve branches supplying each muscle. Individual neuromuscular compartments of BF and TFL differ in their mechanical arrangements to the skeleton and in their contribution to mechanical action(s) at the hip and knee joints. Selective neural activation of mechanically distinct compartments within a mechanically heterogeneous muscle can provide highly advantageous mechanical "options" for animals that perform kinematically diverse movements. With regard to EMG recording techniques, the results of this study emphasize the need for carefully chosen EMG sampling sites and the value of knowing the muscle histochemistry, neuromuscular and musculoskeletal anatomy and possible mechanical functions *prior* to recording EMG.

Key words: Differential activation – Kinematics – Muscles – Electromyography – Histochemistry –Neuromuscular compartments – Cat

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Introduction

One of the central concepts of neuromuscular organization is the principle of orderly recruitment, which states that the musculature of the body can be subdivided functionally into groups of motor units, each of which is usually, if not invariably, recruited in a consistent sequence (Henneman et al. 1974). It is attractive to suppose that such functional groupings have a one-to-one correspondence with the individual muscles that can be distinguished anatomically by blunt dissection, particularly in those muscles that are anatomically simple and have single, homogeneous actions upon the skeleton. In simple muscles such as the soleus and medial gas-

trocnemius, there is ample evidence in favor of this correspondence (for reviews see Henneman and Mendell 1981; Burke 1981).

However, the skeletal musculature of mammals offers a wide range of architectural and functional complexity. At the opposite extreme, there are muscles that have been described classically as having multiple "heads" or "parts" on the basis of obvious heterogeneity in their skeletal actions. It has long been known that different regions of such muscles may be recruited independently of each other in various natural behaviors and reflexes, although there has rarely been any systematic attempt to identify exactly how many such independent regions a given "complex" muscle might actually contain. In this series of papers, we have attempted to address this question in two such muscles in which the classical identification of two heads does not correspond to any obvious dichotomy in terms of innervation, architecture of skeletal action: sartorius (Pratt and Loeb 1991) and biceps femoris (Chanaud and Macpherson 1991).

In between these architectural extremes, there are many muscles (perhaps the majority) in which there are anatomical features that suggest at least the possibility that these muscles may contain more than one recruitment group (reviewed in Loeb 1989):

- multiple nerves or pronounced nerve branching (e.g. lateral gastrocnemius; English and Letbetter, 1982)
- multiple motor nuclei (e.g. stapedius; McCue and Guinan 1988)
- gradients of muscle-fiber architecture or moment arm (e.g. masseter; Herring et al. 1979)
- effects upon multiple degrees of freedom in the skeleton (e.g. first dorsal interosseus; Desmedt and Godaux 1981)
- internal tendinous inscriptions (e.g. splenius; Richmond et al. 1985)
- heterogeneous distributions of different histochemical fiber-types and/or proprioceptors (e.g. flexor carpi radialis; Richmond and Stuart 1985)

There have been many reports of selective recruitment in different regions of muscles having one or more of the above features (e.g. Herring et al. 1979; Henderson-Smart et al. 1982; English 1984; English and Weeks 1987; Lev-Tov and Tal 1987). However, the implications of such reports regarding the principle of orderly recruitment remain unclear. Partly, this is because muscles may have more than one of the above types of features. Partly, it is because the EMG techniques usually employed to quantify activation are susceptible to electrical and mechanical artefacts such as cross-talk and shifting electrode geometry as well as stochastic problems from sampling small, perhaps unrepresentative populations of randomly asynchronous signal sources. In this paper, we consider two types of differential activation: i) reciprocal activation, in which the relative amplitude relationship between two sites tends systematically to be reversed during different behaviors or phases of behaviors; ii) subset activation, in which the activity recorded at one site can always be construed as a subset of the envelope of activity recorded at the other site, but the temporal features of the two envelopes may be quite different. We specifically exclude fluctuations that may occur in occasional examples of a single behavior phase (e.g. English 1984) because these may arise stochastically, particularly at the low levels of recruitment that obtain for behaviors such as locomotion.

In this study, we have selected four muscles (tibialis anterior, semitendinosus, tensor fasciae latae and biceps femoris) that express various interesting combinations of the above features. In particular, we have combined improved EMG techniques with systematic characterization of histochemical and musculoskeletal architecture to try to identify the relative importance of various structure-function relationships and their possible significance for sensorimotor control. We conclude with a synthesis of the findings of this study, the other reports in this series, and the many related studies and reviews into a proposed set of definitions for anatomical and functional terms that might provide a reasonable compromise among the various historical proposals, the needs of working neuroscientists, and the emerging picture of biological diversity.

A preliminary report has appeared previously (Chanaud et al. 1986).

Methods

Experiments were performed on 7 adult cats (2.0–3.5 kg) of either sex. Prior to surgery, cats were trained to walk on an enclosed treadmill at a range of speeds. Chronic recording electrodes were surgically implanted at 2–8 recording sites on each of the four muscles studied: tibialis anterior (TA), semitendinosus (ST), tensor fasciae latae (TFL) and biceps femoris (BF). Each muscle was implanted in a minimum of 4 cats, and following surgery, the EMGs were recorded during locomotion, paw shaking and ear scratching. The lateral gastrocnemius (LG) or soleus (SOL) was implanted as a reference EMG.

Surgery and implanted devices

All recording devices were surgically implanted under aseptic conditions into pentobarbital anesthetized cats (initial dose 30 mg/kg). Antibiotics (Ancef) were administered daily pre- and post-operatively. EMG patch electrodes (Hoffer and Loeb 1980; Abraham and Loeb 1985; Loeb and Gans 1986; Hoffer et al. 1987a; Pratt and Loeb 1991) were sutured to the fascial surfaces of the muscles. Each bipolar electrode site consisted of two Teflon-coated stainless steel wires sewn into the Silastic (Dow Corning) patch material (providing a dielectric backing to reduce possible cross-talk from adjacent muscles, Loeb and Gans 1986).

The EMG patch size and shape and the arrangement of the electrode contacts were designed specifically for each muscle, as listed in Table 1. The basic shape of all patches was a simple rectangle unless the muscle anatomy dictated otherwise, as in the case of TFL (see explanation below). All patch widths were determined by the spacing between each contact of a bipolar electrode plus an extra 5 mm on all edges to provide insulation from extraneous electrical signals.

Patch lengths for TA, proximal ST and distal ST were determined by the muscle circumference. Two bipolar contact pairs were sewn into each patch and the spacing between sites was determined by the circumferential distance between the deepest and the most superficial surfaces of the muscle. During surgery, each patch was wrapped completely around the muscle belly and the first site was positioned on the deepest, underside portion of the muscle, and the

Table 1. EMG patch dimensions and electrode arrangements

Muscle[a]	Patch *Shape*	Patch dimensions *(W X L) (mm)*	Number of *Electrodes*	Distance (mm) between *Electrodes*	Contact *Length*	Distance between *Contacts (mm)*
Proximal ST	rectangular	15 × 55	2	15	5	5
Distal ST	rectangular	15 × 55	2	15	5	5
TA	rectangular	15 × 52	2	12	5	5
BFa, BFm, BFp	rectangular	15 × 65	3	15	5	5
BFa, BFm, BFp	rectangular	15 × 90	4	10	5	5
BFa, BFm, BFp	rectangular	15 × 92	8	4	5	5
TFL	double-lobe	15 × 45	2	27	3	3
LG	rectangular	15 × 15	1	–	5	5
SOL	rectangular	15 × 15	1	–	5	5

[a] *Abbreviations:* ST – semitendinosus; TA – tibialis anterior; BF – biceps femoris; TFL – tensor fasciae latae; LG – lateral gastrocnemius; SOL – soleus

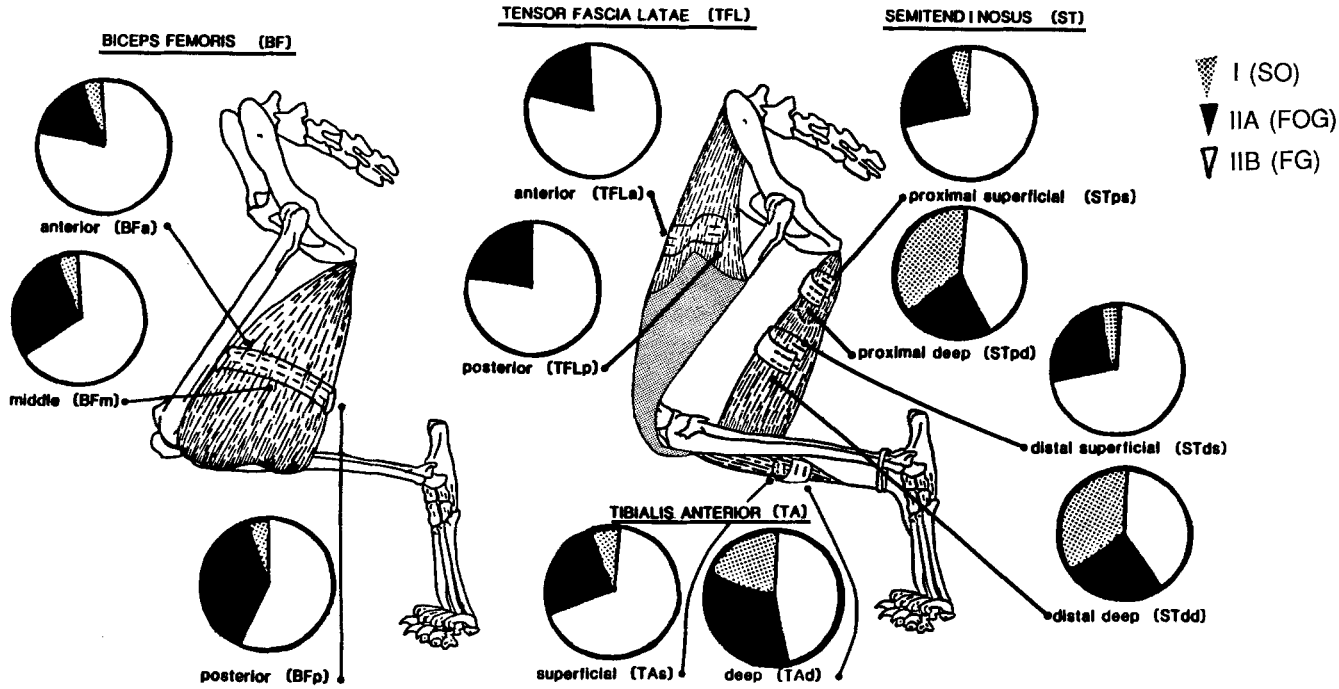

Fig. 1. Muscle Anatomy, Histochemistry and EMG Recording Sites. The TA (tibialis anterior), proximal ST (semitendinosus), distal ST, BF and TFL (tensor fasciae latae) were implanted with single Silastic patches containing electrodes at 2–8 recording sites. ST and TA patches were wrapped around the muscle such that one electrode sampled EMG from the deepest region of muscle and the second electrode sampled EMG from the most superficial region. The TFL electrodes were positioned to record from the anterior and posterior regions. BF (biceps femoris) was implanted with a single patch consisting of electrodes at 3–8 recording sites spanning the width of the muscle from anterior to posterior edges. Patch dimensions and electrode arrangements are listed in Table 1. Pie charts display the proportions of the three major fiber types (Fast-Intermediate's were combined with Fast-Oxidative-Glycolytic's) for selected muscle regions. See Table 3. for exact values

second site was positioned on the outermost, superficial portion of the muscle (Fig. 1).

Due to the unusual anatomy of TFL the patch shape was cut as a doublelobe to conform to the curvature of the distal muscle/tendon boundary (Fig. 1). The contacts were angled slightly to insure that each site would be positioned perpendicular to the direction of the muscle fibers (Loeb and Gans 1986). The superficial position of TFL relative to other hip muscles allowed placement of the patch underneath the muscle with the contacts facing the muscle mass. The face-up contacts were spaced such that one bipolar site was positioned under anterior TFL (TFLa) and the other site was positioned under the posterior TFL (TFLp). Prior to this study, TFL compartment territories had been determined by maximal stimulation of each of the two branches of the main TFL muscle nerve and mapping the occurrence and location of surface EMG.

Patch length for all BF patches was equal to the muscle width, at approximately two-thirds the distance from the origin, plus an extra 10 mm at either end. The BF patches consisted of 3, 4 or 8 bipolar sites spaced evenly across a length of patch equal to the muscle width. The BF patches consisting of 3 or 4 sites were found to be insufficient for recording from all three anatomical compartments (anterior – BFa; middle – BFm; posterior – BFp), therefore two additional patches were constructed with eight sites. Each patch was placed underneath this superficial limb muscle with the contacts facing up and spanning the width of the muscle (Fig. 1).

All wire leads, including a ground wire, were passed sub-

cutaneously to an exit site in the skin over the lumbar vertebrae. Wires were soldered to a 40-pin connector assembly on a backpack sutured percutaneously to the lumbosacral fascia (Hoffer et al. 1987a).

Recording

Each pair of leads was connected to a differential EMG amplifier (50–5000 Hz filtering). All signals were recorded simultaneously with identical gain settings and saved on tape (FM tape recorder with DC–10000 Hz bandpass). Cat movements were videotaped at 60 fields/sec and synchronized to the FM tape by a digital time code generator (DATUM 9300). Recordings were made during steady walking at a range of treadmill speeds (0.5–3.0 m/s) and during paw shaking and hindlimb scratching of the ear. Paw shaking was triggered by placement of adhesive tape around the pad while the animal walked on the treadmill (Smith et al. 1980). Ear scratching was initiated by cutaneous stimulation of the ipsilateral pinna and varied in form and intensity from vigorous scratching of the ear to half-hearted paw waving towards the ear.

Data analysis

Each video was reviewed for segments of consistent locomotion, vigorous paw shaking and repeated ear scratching. Selected tape sections of EMG activity were rectified, bin integrated with 2 ms bin widths (Bak and Loeb 1979), and digitized at 2 ms intervals by a PDP 11/73 computer. Two to five samples of each type of movement per cat were examined and compared.

Terminal experiment

Following completion of chronic EMG data collection, a terminal experiment was performed on each cat (using pentobarbitol anesthesia) to verify electrode placement and to remove muscles for histochemical analysis. Prior to muscle removal, supplemental recordings were made from the two cats implanted with the 8-electrode BF patches. To correlate the neuromuscular compartments of BF to the EMG recorded during normal movement, each primary BF nerve branch was stimulated maximally and the resulting EMG was recorded from the eight BF recording sites. In addition, the BF primary nerve branches were dissected to verify compartment territories (Chanaud et al. 1991).

Histochemistry

Following removal from the animal, muscles were tied to a metal stick or plate, quickly frozen in liquid nitrogen and stored in a freezer at − 20° C. Muscle blocks were cut into 10 μm thick sections with a Hacker Instruments cryostat. Whole muscle blocks from 2–4 specimens of TA, TFL, proximal ST, and distal ST were sectioned, however, it was necessary to divide the wide BF muscles into two blocks. Adjacent sections were stained with alkaline ATPase at pH 10.0, acid ATPase at pH 4.15 and NADH. Histochemical evaluation was performed on regions of muscle close to the EMG recording sites. Fascicles of the deep regions and superficial regions were analyzed from TA, proximal ST and distal ST and fascicles of the anterior and posterior TFL compartments were sampled. The BF muscle showed a slight deep to superficial gradient of oxidative to glycolytic fibers, therefore the region chosen for histochemical evaluation was midway between the deep and superficial surfaces. According to the histochemical staining patterns, individual fibers were classified into one of four categories (Burke 1981) as listed in Table 2. The distribution of fiber types was similar in all specimens of a single muscle region; therefore, only a single specimen of each was selected for classification of 50–200 fibers. Thus, these data provide an indication of general trends and differences in fiber distribution (which were immediately obvious macroscopically in the stained sections) but are not meant to constitute a definitive study of inter-fascicular or inter-animal variability.

Table 2. Muscle fiber histochemical classifications

Fiber type Motor unit type (presumed)	I/SO *S*	IIAB *FI*	IIA/FOG *FR*	IIB/FG *FF*
Histochemical Sain:				
Alkaline ATPase	low	high	high	high
Acid ATPase	high	medium	low	low
NADH	high	medium	medium-high	low

Results

In the following sections the term "mechanically homogeneous" refers to a muscle in which all anatomical regions possess nearly identical relationships to the skeleton (i.e., lever arms from points of origin or insertion to center of joint rotation, direction of active muscle pull, etc.) and serve a similar mechanical function(s) when activated. Conversely, a "mechanically heterogeneous" muscle is comprised of anatomical regions with qualitatively different mechanical relationships to the skeleton which, upon activation, contribute to different biomechanical actions. "Histochemical regionalization" refers to a non-uniform distribution of the histochemically identified fiber-types across a transverse section of muscle.

In the following, the patterns of EMG activity reported hold true across all cats. Individual variations occurred for such things as the locomotion speed at which the second ST burst appeared (see below).

Differential activation of mechanically homogeneous muscles with histochemical regionalization

Semitendinosus (ST). ST is a biarticular hamstring muscle which originates at the ischium, crosses the hip and knee joints, and inserts on the medial side of the tibia (Fig. 1, right). Two serial compartments, proximal (STp) and distal (STd), are delineated by a tendinous inscription and innervated by separate nerve branches from the sciatic nerve (Bodine et al. 1982; English and Weeks 1987). Previous studies of the architectural, contractile and mechanical properties of the two compartments revealed no differences in mechanical function (Peters and Rick 1977; Bodine et al. 1982). Our additional examination of different regions of ST uncovered no apparent mechanical differences, leading us to classify ST as a mechanically homogeneous muscle.

Gross observations of regional differences in ST muscle color (dark red in the deep regions and pale red in the superficial regions) were paralleled at the microscopic level by a regionalization of the different histochemically identified fiber types (Fig. 1, right and Table 3.). Consis-

Table 3. Fiber-type distribution within the ST, TA, BF and TFL muscles[a]

MUSCLE[b]	*I (SO)%*	*FI%*	*IIA (FOG)%*	*IIB (FG)%*
STpd	23	8	12	57
STps	3	6	17	74
STdd	22	7	33	38
STds	3	12	15	70
TAd	11	8	35	46
TAs	5	5	25	65
BFa	3	–	16	81
BFm	6	–	26	68
BFp	4	–	32	64
TFLa	0	0	21	79
TFLp	1	0	21	78

[a] Due to the similar distribution of fiber types in the samples taken from each subsection of a muscle, only the values from one specimen are recorded in the table

[b] *Abbreviations:* STpd – semitendinosus proximal deep; STps – semitendinosus proximal superficial; STdd – semitendinosus distal deep; STds – semitendinosus distal superficial; TAd – tibialis anterior deep; TAs – tibialis anterior superficial; BFa – biceps femoris anterior; BFm – biceps femoris middle; BFp – biceps femoris posterior. TFLa – tensor fasciae latae anterior; TFLp – tensor fasciae latae posterior

tent with a previous report (Bodine et al. 1982), the analysis showed that the deep regions of the proximal (STpd) and distal (STdd) compartments consisted of a greater percentage of fibers high in oxidative enzyme than the superficial proximal (STps) and distal (STds) regions. Each deep region had a greater percentage of fiber types I, IIAB and IIA (presumed motor unit types S, slow oxidative; FI, fast intermediate; and FR, fast fatigue-resistant, respectively) and the superficial regions had a greater percentage of fiber type IIB (presumed motor unit type FF, fast fatiguable).

EMG recordings from ST during slow treadmill walking (Fig. 2, Locomotion with 750 ms and 720 ms cycle durations) revealed that activity was present only in the two deep regions of the muscle (STpd, STdd). Each deep region exhibited a single burst during the flexion phase of the step cycle, an activation pattern that is consistent with a primary muscle function of knee flexion (Engberg and Lundberg 1969; English and Weeks 1987). As the speed of locomotion increased (Fig. 2, 500 ms and 340 ms), the amplitude of this flexor burst increased progressively and a brief second burst (per step cycle) appeared just prior to footfall. As the limb swings forward and approaches footfall, flexion of the hip and extension of the knee results in lengthening of ST. An activated ST at this point in the step cycle provides a taut line of muscle down the posterior surface of the limb and functions to decelerate the fast forward swing of the shank in preparation for foot strike (Engberg and Lundberg 1969; Rasmussen et al. 1978). Similar to the flexor burst, this second burst increased in amplitude as gait speed increased (Fig. 2, 340 ms). A similar progression was also observed by Grillner and Zangger (1984) in decerebrate cats walking on a treadmill following stimulation of the mesencephalic locomotor region.

Activation patterns of the superficial regions (STps, STds) were similar to the deep regions, but comparable activation levels were elicited at different gait speeds. The deep ST regions were active during slow walks but a flexor burst did not appear in the superficial regions until a relatively fast walking speed was attained (Fig. 2, 340 ms). The second burst, prior to footfall, appeared in the superficial regions only at the fastest walking speeds (not shown). Regardless of the particular gait speed, activation of the corresponding regions (superficial or deep) in both the proximal and distal compartments always occurred in-phase.

During the quick, ballistic movements of ear scratch and paw shake (Fig. 2, Scratch and Shake), both the deep and superficial regions of ST were activated. Although burst amplitude varied during these movements, the major components of the EMG occurred synchronously in all ST regions. During shake, the presence of a second burst in the deep regions of ST and its absence in the superficial regions, appeared to be related to intensity

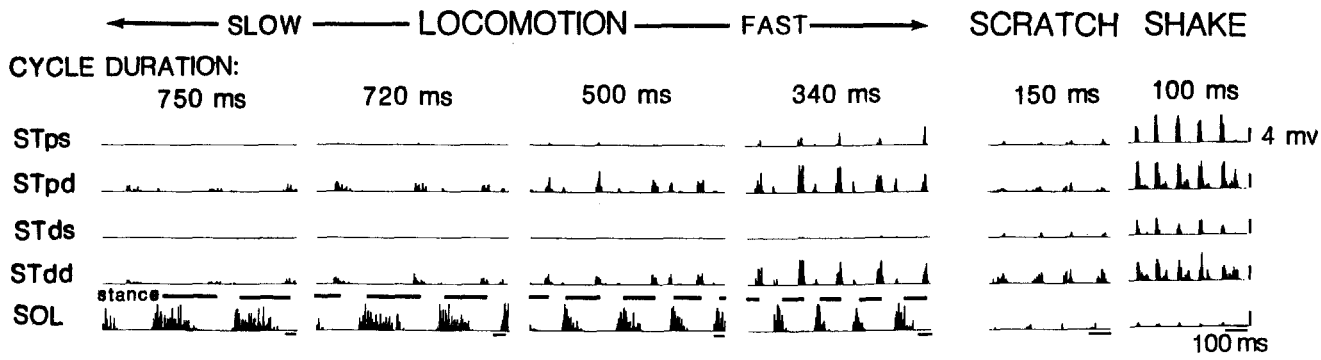

Fig. 2. Semitendinosus (ST) EMG Activity During Locomotion, Ear Scratch and Paw Shake. During slow walk (750 ms and 720 ms cycle duration) EMG was present during flexion only in the deep regions (*STpd, STdd*). At moderate speeds (500 ms) the deep regions added a second burst just prior to footfall and, at the fastest walking speeds (340 ms), the superficial regions (*STps, STds*) became active during flexion, in-phase with the deep regions. During scratch and shake the deep and superficial regions of both compartments were activated synchronously. *Abbreviations:* pd – proximal deep; dd – distal deep; ps – proximal superficial; ds – distal superficial; SOL – soleus

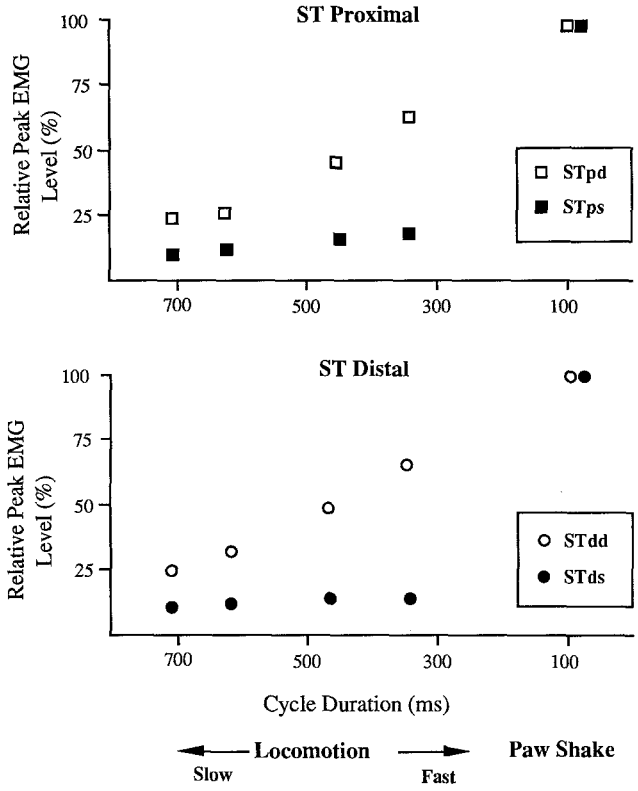

Fig. 3. ST Relative Peak EMG Level vs. Cycle Duration. Peak EMG during shake was assigned an arbitrary maximum value (100%) and the locomotion values were normalized accordingly. The graphs show similar peak activation profiles for the proximal *(top)* and distal *(bottom)* ST compartments. As speed of locomotion increased, peak EMG in the deep and superficial regions increased progressively. At all speeds, peak activation levels were greater in the deep regions than the superficial regions. During shake, these activation levels were equal. *Abbreviations:* pd – proximal deep; ps – proximal superficial; dd – distal deep; ds – distal superficial

and amplitude; slower, less intense shakes resulted in lower amplitude, single bursts in both the deep and superficial ST regions.

Figure 3 summarizes the peak EMG levels recorded from each ST region during the different gait speeds and paw shake; peak values obtained during locomotion were normalized to shake. During treadmill walking, active ST regions showed a progressive increase in peak EMG level as gait speed increased. At any particular walking speed the deep regions of both compartments showed higher peak activity than the superficial regions. During paw shake this relationship changed in that the activity levels of the deep and superficial regions were equal (Fig. 2, Shake). At no time did activity in the superficial regions exceed that of the deep regions. Thus, this represents an example of subset activation rather than reciprocal activation. However, note the very different temporal patterns of activity that are consistent with this interpretation. Summaries of muscle work based on such onset and offset times would come to very different conclusions about the work of these different regions of each compartment.

Tibialis anterior (TA). The TA muscle, originating on the proximal tibia and head of the fibula and inserting on the first metatarsal (Fig. 1, bottom), functions as an ankle dorsiflexor (Engberg and Lundberg 1969; Rasmussen et al. 1978; Abraham and Loeb 1985). The muscle is innervated by two branches of the peroneal nerve, an anterior branch and a posterior branch (Dum and Kennedy 1980b). The TA, with its discrete insertion and single mechanical action, can be classified as mechanically homogeneous.

The TA muscle histochemistry revealed a deep-to-superficial gradient similar to the ST muscle (Fig. 1), as reported previously (Dum and Kennedy 1980a; Van Winkle et al. 1978). The deepest region of the muscle (TAd), located adjacent to the tibia, possessed a greater composition of fibers high in oxidative enzyme than the outermost, superficial region (TAs) (Table 3.). The deep region had a greater percentage of type I, IIAB and IIA fibers (presumed motor unit types of S, FI and FR, respectively) and the superficial region had the higher percentage of type IIB fibers (presumed motor unit type FF).

EMG recordings from TA during slow walking revealed that the deep portion of TA was active during the flexion phase while the superficial region remained inactive or only slightly active (Fig. 4, Locomotion, 630 ms cycle duration). As gait speed increased, the burst amplitudes increased progressively and proportionately in both regions (Fig. 4, 440 ms and 350 ms), however, TAd

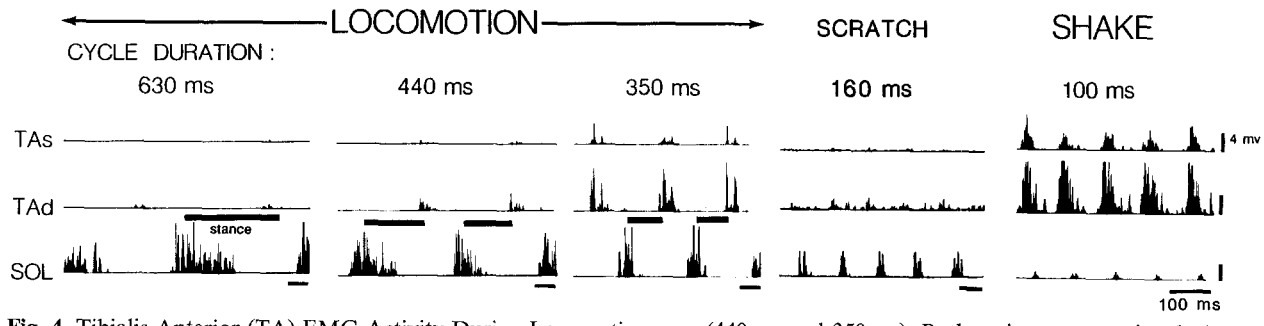

Fig. 4. Tibialis Anterior (TA) EMG Activity During Locomotion, Ear Scratch and Paw Shake. At slow walking speeds (630 ms) only the deep TA (*TAd*) was active. As speed increased, *TAd* EMG amplitude increased and the superficial region (*TAs*) became active (440 ms and 350 ms). Both regions were active during scratch and shake although the *TAd* had higher amplitude activity. All *TAd* and *TAs* activation during locomotion, scratch and shake occurred in-phase. *Abbreviations:* d – deep; s – superficial; SOL – soleus

bursts were always greater in amplitude than TAs bursts. The highest amplitude bursts for both TAd and TAs were recorded during paw shake (Fig. 4, Shake). A weak scratch produced low amplitude, poorly modulated activation of both TAd and TAs (Fig. 4, Scratch). Comparison of TAd and TAs activity during all movements showed that if both regions were active, the activity occurred at the same point in the step cycle (onsets, durations, and offsets of activity were similar in both regions). This is consistent with subset but not reciprocal activation. The timing differences are much less than for ST, although the conclusions that might be drawn about the degree of TA recruitment would be rather different for the two sites, particularly for slow walking.

Differential activation of histochemically unregionalized, mechanically heterogeneous muscles

Biceps Femoris (BF). BF is a biarticular hamstring muscle that originates on the ischial tuberosity, crosses the hip and knee joints, and inserts broadly on the fascia latae, lateral femur, patellar fascia, and crural fascia (Fig. 1, left). Three to four main nerve branches from the sciatic nerve innervate the BF muscle and each branch innervates a distinct neuromuscular compartment: anterior (BFa), middle (BFm) or posterior (BFp) (Botterman et al. 1983; English and Weeks 1987).

Each BF compartment possesses a different mechanical relationship to the skeleton (see also Chanaud et al. 1991). The BFa compartment, with an insertion on the femur and patellar fascia, has significant mechanical advantage only at the hip joint. BFm, inserting on the upper crural fascia, has nearly identical lever arms to both joints. BFp, with an insertion on the lower crural fascia, has a greater mechanical advantage at the knee than at the hip. Differences in probable biomechanical action(s) of the compartments have been inferred from these differences in mechanical arrangement to the skeleton (Chanaud et al. 1991). In addition, previously recorded activity patterns of BFa and BFp have provided experimental evidence of significant differences in compartment function (Engberg and Lundberg 1969; English and Weeks 1987; Chanaud and Macpherson 1991). Based on the biomechanics and physiology of the BF compartments, we have classified this muscle as mechanically heterogeneous.

Regional comparisons from anterior to posterior showed no histochemical differences. The three compartments were composed of nearly identical percentages of three fiber types (Fig. 1 and Table 3.), but predominantly fibers that were high in myofibrillar ATPase, pH 10.0. The low percentage of type I fibers (presumed motor unit type S) and high percentage of type IIB fibers (presumed motor unit type FF) is in agreement with Ariano et al. (1973).

During slow locomotion, the EMG recordings showed that only the BFa compartment was active; the BFm and BFp compartments remained inactive (Fig. 5, Locomotion at 780 ms cycle duration, electrodes BF1–BF3). EMG activity in BFa was present during the entire stance phase of the step cycle, consistent with its previous identification as a hip extensor (Rasmussen et al. 1978; English and Weeks 1987). As gait speed increased, the amplitude of the BFa extensor burst increased progressively. Increased speed also resulted in slight activation (compared to BFa) of the BFm compartment during stance (640 ms and 490 ms, electrodes BF5–BF7), identifying BFm as a hip extensor.

The BFp compartment was activated only at the fastest gait speeds (Fig. 5, 350 ms, electrodes BF7–BF8). Low amplitude activity occurred in BFp throughout the duration of each step cycle. High amplitude double bursts occurred during some swing phases (350 ms). The early swing phase burst is consistent with a BFp knee flexor function (Engberg and Lundberg 1969; English and Weeks 1987). The late swing burst occurred just prior to footfall; BFp may be activated synergistically with ST to decelerate the forward swing of the limb prior to foot strike during fast locomotion. If ST was the only muscle (acting across the knee) activated at this point of the step cycle, it could result in an undesirable medial torque on the knee (ST inserts on the medial side of the shank). Synchronous activation of BFp, which inserts on the lateral side of the shank, would provide a balancing of any medio-lateral torque at the knee.

EMG bursts during ear scratching were present at all eight recording sites, burst amplitudes were relatively uniform across electrodes and all activity occurred synchronously (Fig. 5, Scratch). Paw shake produced low amplitude, synchronous activity in those electrodes recording from the BFa and BFm compartments (Fig. 5, Shake, electrodes BF1–BF6). Activity of the BFp compartment (electrodes BF7–BF8) was greater in amplitude although it occurred in-phase with the BFa and BFm compartment activations. Double bursts per shake cycle occasionally appeared in BFp and this second, low amplitude burst was not matched by activity in either the BFa or BFm compartments. Thus, all three main compartments of BF exhibited reciprocal differential activation with respect to each other, although this would not be completely apparent from the EMG records of any single type of behavior.

Tensor fasciae latae (TFL). TFL originates on the ventral border of the ilium and the fascia of the gluteus medius muscle. The anterior portion of TFL inserts onto the fascia of the rectus femoris on the anterior surface of the thigh, and the lateral portion of TFL inserts onto the fasciae latae of the lateral thigh. The TFL muscle is innervated by two branches of the cranial gluteal nerve; consequently TFL is divisible into two main neuromuscular compartments, anterior (TFLa) and posterior (TFLp) (Fig. 1, center). There are also significant subbranches of TFLp that we did not investigate further.

The anatomical position of TFLa is mechanically advantageous for hip flexion. During post-mortem examinations, manual pulling at the TFLa muscle/tendon boundary produced extension of the knee, a mechanical consequence of the insertion onto rectus femoris fascia. The possible mechanical actions of TFLp were more difficult to discern; it may contribute to hip abduction,

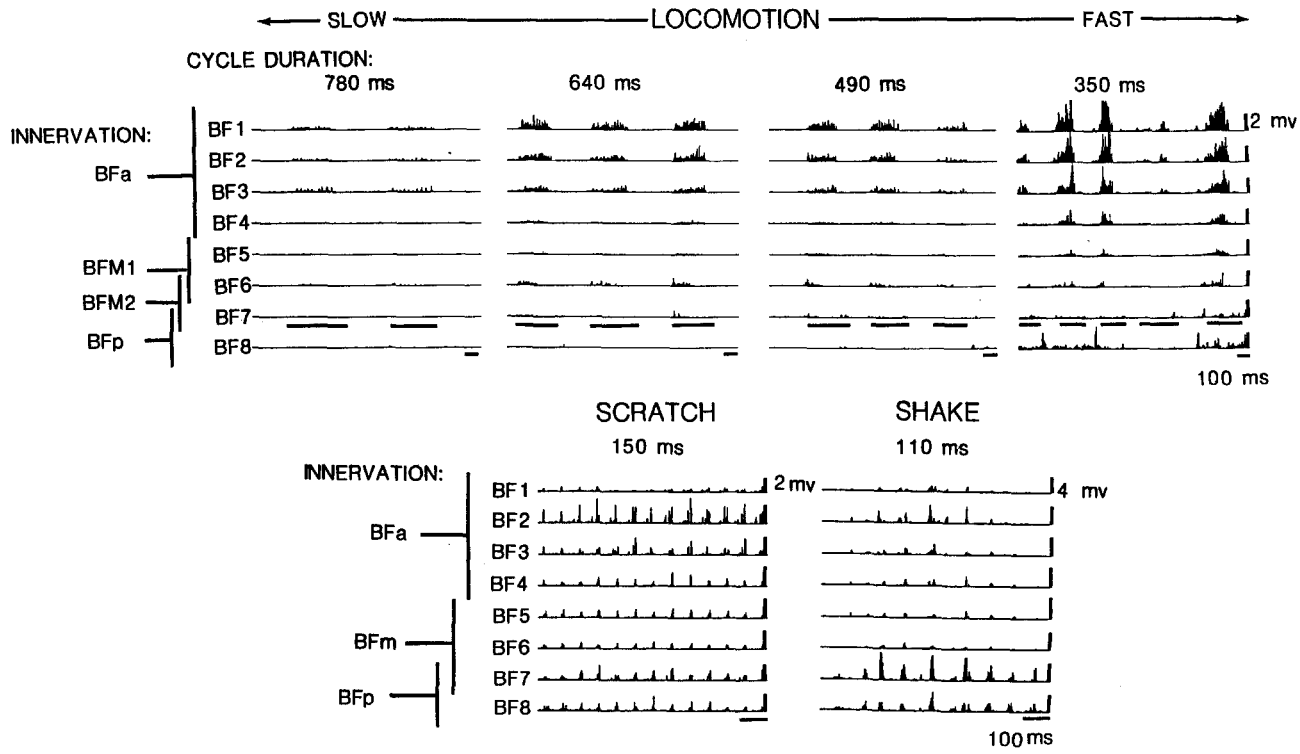

Fig. 5. Biceps Femoris (*BF*) EMG Activity During Locomotion, Ear Scratch and Paw Shake. Electrodes were numbered BF1 to BF8, from the anterior to the posterior regions of the muscle. The relationship between the primary nerve branches and the electrode recordings are shown at the left. The locomotion data and the scratch and shake data were from separate cats. During slow walk only the most anterior region of BF was active (780 ms, electrodes *BF1–BF3*). As speed increased (640 ms and 490 ms) the EMG bursts recorded from BFa increased in amplitude and the middle compartment (*BFm*) became active (electrodes *BF4–BF7*). At the fastest speeds the posterior compartment (*BFp*) became active (350 ms, electrodes *BF7–BF8*). The two *BFp* swing phase bursts were out-of-phase with activity of the BFa and BFm compartments. During ear scratch, synchronous activity with similar burst amplitudes was present at all recording sites. Paw shaking produced low amplitude, synchronous activity in the *BFa* and *BFm* compartments (electrodes BF1–BF6). BFp activity (electrodes *BF7–BF8*) was greater in amplitude but occurred in-phase with BFa and BFm. Note occasional double bursts in *BFp* and the low amplitude burst that was not matched by activity in the *BFa* or BFm compartments

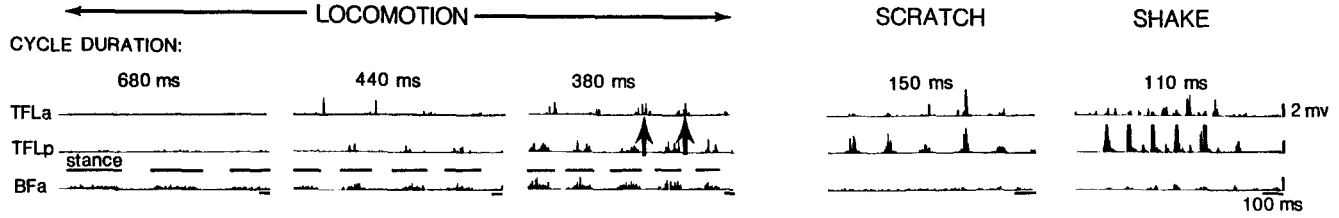

Fig. 6. Tensor Fasciae Latae (TFL) EMG Activity During Locomotion, Ear Scratch and Paw Shake. During slow walk (680 ms) the posterior TFL (*TFLp*) was active during stance and the anterior TFL (*TFLa*) was inactive. At faster speeds (440 ms and 380 ms) *TFLa* became active at the end of stance and first half of swing, partially in-phase with TFLp and partially out-of-phase *(arrows)*. During scratch and shake TFLa and TFLp were active in-phase. *Abbreviation:* BFa – biceps femoris anterior

flexion and/or internal rotation. A similar complexity in TFL anatomy and architecture has been described in humans (Paré et al. 1981). Furthermore, the two compartments of the human TFL were differentially active during locomotion and apparently contributed to different biomechanical actions. The unusual anatomy of the cat TFL, and certain similarities to human TFL, led us to classify this muscle as mechanically heterogeneous.

Histochemical staining revealed that TFLa and TFLp were nearly identical in fiber composition and consisted of 99–100% fibers high in myofibrillar ATPase, ph 10.0 (Fig. 1 and Table 3.). This high proportion of type IIA and IIB fibers (presumed motor unit types FR and FF) and the near-absence of type I fibers (presumed motor unit type S) was also reported by Ariano et al. (1973).

During slow walking TFLp was active during stance and TFLa showed no EMG activity (Fig. 6, Locomotion, 680 ms cycle duration). At a moderate gait speed TFLa also became active, although the TFLa burst occurred at the end of stance and beginning of swing, partially out-of-phase with TFLp (Fig. 6, 440 ms). During fast treadmill walking the TFLp burst nearly matched the duration of stance (Fig. 6, 380 ms). The onset of TFLa activity occurred at approximately 60–80 ms prior to footlift,

overlapping only slightly with the TFLp burst and persisting through the flexion phase (arrows) until mid-swing.

During ear scratch (Fig. 6, Scratch) TFLa and TFLp were active in-phase, although burst amplitude varied. Paw shaking (Fig. 6, Shake) resulted in large amplitude EMG bursts in TFLp and more moderate bursts in TFLa. Both compartments exhibited 1–2 bursts per shake cycle and they were activated synchronously across compartments. Thus, for most but not all behaviors, the two compartments of TFL exhibited some degree of reciprocal activation.

Discussion

Increased muscle activation with increased gait speed

Numerous human and animal studies have established that increased muscle activation during natural movement is a result of two factors: 1) recruitment – an increase in the number of active units and 2) rate modulation – an increase in the frequency of firing of already active units (for reviews, see Burke 1981; Henneman and Mendell 1981). In the current study, both factors presumably contributed to the increased activation recorded from these four cat hindlimb muscles as the speed of locomotion increased.

Orderly recruitment of motoneurons

Hypotheses concerned with the activation of muscle agree on the *orderliness* of motoneuron recruitment, yet differ widely with regard to the critical factor(s) responsible for determining which particular motoneurons are recruited during a movement. Described thoroughly in the literature (Burke 1981; Henneman and Mendell 1981; Stuart and Enoka 1983; Zajac and Faden 1985; Hoffer et al. 1987c; Loeb 1985; Loeb 1989), these proposed factors include motoneuron characteristics (morphological and electrophysiological), motor unit properties (contraction speed, fatigue resistance, contraction strength, etc.), and the kinematic requirements of the movement task. Despite these differences, the experimental evidence overwhelmingly supports (within certain limits, see Stuart and Enoka 1983; Hoffer et al. 1987c) the general statement that small motoneurons innervate motor units of slow contraction speed, low contraction strength and high fatigue resistance, and are the earliest recruited. The largest motoneurons innervate motor units with the fastest contraction speeds, highest contraction strengths and least fatigue resistance, and are the last to be recruited.

Relationships between motoneuron recruitment and muscle activation can be inferred from recordings of muscle force, length and EMG during natural movements. Previous studies of locomoting cats (Walmsley et al. 1978; O'Donovan et al. 1982; Abraham and Loeb 1985; Hoffer et al. 1987b) and humans (Miyashita et al. 1971; Mero and Komi 1986) have found that as gait speed increases, the muscle forces, lengths and EMGs can increase substantially. Walmsley et al. (1978) also proposed a model of recruitment that correlated the type and speed of gait to the percentage of motoneuron pool recruitment and the motor unit type.

The patterns of muscle activation recorded in the current study from the histochemically regionalized muscles (ST and TA) resulted in the following observations:

1) At slow-moderate gait speeds only the muscle regions high in type I (SO) units were recruited.

2) Additional units were recruited as speed increased and this was demonstrated unequivocally by the supplementary activation of the superficial regions at the faster speeds.

3) The muscle regions high in type IIA (FOG) and IIB (FG) units produced detectable EMG signals only at the moderate-high gait speeds. This threshold effect results in the appearance of differential activation by subset criteria but not by reciprocal criteria.

4) Comparison of the EMG levels recorded during locomotion vs. paw shake confirm that only relatively low level muscle activation was necessary for locomotion, as found by Walmsley et al. (1978).

5) High levels of activation of all muscle regions occurred only during the high force, ballistic movement of paw shaking.

These results from the mechanically homogeneous, histochemically regionalized muscles support the well-established view that movement of the intact animal results from an orderly recruitment of motoneurons innervating the different muscle unit types.

Multiple recruitment groups – identification, significance and mechanisms

There is little difficulty in recognizing that some EMG patterns reflect an organization of the motor units that cannot be reconciled with the orderly recruitment of a single group of motoneurons supplying the entire muscle (e.g. reciprocal activation of TFL during rapid walking, Fig. 6). However, as noted above, certain types of quite dissimilar EMG patterns recorded at two sites can be reconciled with such orderly recruitment. The definition of strict criteria for differential activation is necessary if EMG is to be used to make inferences about functional organization. In formulating such criteria, it is useful to consider the biophysical processes whereby the recruitment of motoneurons results in the recording of gross EMG patterns.

Consider a typical neuromuscular compartment with about 100 motor units supplying a mixture of fiber types. Low-level, tonic motor tasks such as postural maintenance seem to require graded activity confined within the type SO units (Walmsley et al. 1978), which typically make up about 10–20% of the muscle fibers (Ariano et al. 1973). Because the innervation ratio for their type I motoneurons may be smaller than for type II units (but see Burke 1981), these tasks may involve a somewhat larger proportion of the motoneurons, perhaps 20–40%. Another 20–30% of the muscle fibers and motoneurons

will be type FOG – IIB, readily recruited during phasic, repetitive activities such as locomotion (Walmsley et al. 1978). The remaining approximately 50% of the motor units will be held in reserve for infrequent ballistic movements such as jumping (Walmsley et al. 1978). If each of the SO and FOG units tends to be distributed over about half the volume of the neuromuscular compartment (Burke 1981), then a gross EMG recording will reflect the activity of about 10 to 25 motor units as the muscle recruitment progresses from low-level tonic activity (if it has any) to phasic, cyclical behaviors. Over this range of recruitment, the spike activity in the various motoneurons will be asynchronous (at least in limb muscles; Loeb et al. 1987b) and frequency modulated over the range of 15–40 impulses per second (Hoffer et al. 1987b). Thus, the gross EMG recording will be composed of about 150 to 600 unitary waveforms per second. Each waveform typically is composed of 2–4 phases with alternating sign lasting about 2 ms per phase, depending on the orientation of the electrode contacts with respect to the motor end-plates (Loeb and Gans 1986). At any point in time, the composite waveform will reflect the random summation of action currents produced by perhaps one to eight muscle units. It should be clear why such recordings have been called "interference EMG" – the signals will reflect neither separable individual events nor the smooth averaging that would result if there were a large number of such events at every point in time.

Because of the biophysical processes underlying spike propagation, the amplitude of the action current associated with each muscle fiber should be related to its caliber, although not necessarily linearly because of the uncertain contribution of the T-tubule system. Because the end-plates of the motoneurons tend to be clustered together in horizontal bands (Loeb et al. 1987a), the currents from all of the fibers comprising a single muscle unit will tend to be synchronous, at least at any single position along the muscle belly. The contribution of a single muscle unit to a gross EMG recording at that position should reflect the activity of the number of muscle fibers that are arranged in parallel (Kosarov et al. 1974), but not fibers in series as motor subunits (Chanaud et al. 1987). Thus, the action current produced by a single motor unit and contributing to a local EMG recording should be approximately proportional to the physiological cross-sectional area of its muscle fibers. If this action current is distributed homogeneously through a region of adjacent tissue that has a constant cross-sectional area, then it should produce an extracellular potential gradient that is approximately proportional to the action current, which potential gradient can be detected by differential recording with a bipolar EMG recording electrode.

Consider a situation in which these action currents are confined within the muscle itself and the resulting potential gradients are well-sampled by the electrode (as tends to be with our large, epimysial, dielectric patch electrodes). Then the amplitude of the gross EMG recording should reflect the percentage of the cross-sectional area of the muscle that has been activated and is contributing active tension (in less confined structures, unit EMG varies as the square root of tension; Milner-Brown and Stein 1975). However, this begs the question of how the amplitude of a complex waveform is to be quantified and how precise the measure will be. Mutual interference among the asynchronous sources of action currents is obviously the largest problem. When examining such records, the eye tends to notice the brief peaks and ignore the valleys; such peaks in a raw, wide-band recording are most likely to result from the fortuitous synchrony of brief, unitary action currents rather than any regular feature of the recruitment process. By averaging the records over longer time frames, the stochastic fluctuations can be minimized, but at the cost of reducing the temporal information that can be extracted from the signal. We have used full-wave rectification and modest integration of area-under-the-curve to produce records that are less biased by such processes (Bak and Loeb 1979); substantially more smoothing and statistical analysis would be required to use even such records to identify the significance of small or occasional differences in EMG envelope. However, when this has been done, gross EMG appears to provide a surprisingly good indicator of the neural input that leads to the recruitment of individual motoneurons (Hoffer et al. 1987b).

The criteria used in this study to determine differential activation were established on the basis of such considerations. We here suggest possible interpretations for three types of differential muscle activation.

Reciprocal activation. This is the strongest criterion, requiring that EMG levels at the two recording sites exhibit large and consistent reversals of relative magnitude for different tasks or phases of behavior. The most easily identified condition meeting this criterion is the case where each site demonstrates strong recruitment while the other site is essentially silent. Such reciprocal patterns form the basis for our classification of differential recruitment in the mechanically heterogeneous muscles BF and TFL, which we believe reflect the presence of independent recruitment groups (see below). However, there are three caveats regarding the more general application of this criterion. First, the absence of such differential activity may reflect only the relative poverty of the particular motor behaviors examined (e.g. all regions of both BF and TFL were recruited together during scratching). Second, a relatively long series of stereotyped behavioral cycles and statistical demonstration of significant differences would be needed to apply this criterion to conditions in which both sites are always active together but with frequent reversals of amplitude. Third, such statistics are unlikely to apply to conditions in which there is any degree of synchronization of motor unit recruitment (e.g. reflex responses to brief stimuli).

Subset activation. This criterion includes differences in EMG envelopes that are consistent but not reciprocal, in which one recording can always be construed as a subset of the other (e.g. later onset times or absence of participation during weak activity at the other site). This may include quite dramatic differences in the shapes and sizes of the envelopes of EMG from two recording sites (e.g.

superficial vs. deep ST in Fig. 2); however, the subset relationship means that the envelopes can always be attributed to the orderly recruitment of a single group of motor units whose muscle territories are not homogeneously or randomly distributed. Muscle-fiber histochemistry is one practical and valuable way to identify such distributions. It is possible to imagine histochemically homogeneous distributions that could give rise to subset activation within one consistently ordered recruitment group, but they seem unphysiologically contrived. Unfortunately, the converse argument that histochemical heterogeneity can be used to exclude the possibility of multiple recruitment groups is not valid.

Envelope fluctuations. This criterion includes differences in timing and/or amplitude of EMG envelopes that are not consistent features of a given behavior, but rather arise occasionally (e.g. English 1984). Because of the above-noted stochastic properties, no two EMG envelopes will be completely and consistently congruent. According to the above biophysical analysis, reversals of relative amplitude should not occur as long as each muscle unit generates an EMG signal whose amplitude is related to the same size-related factors that determine its recruitment order (i.e. physiological cross-sectional area of its muscle fibers). However, the interference EMG reflects this unit amplitude only indirectly and stochastically. Given reasonable assumptions, it is probably possible to determine a probability that an amplitude difference of given magnitude and duration would not arise by chance in a record of given length, but we know of no examples of such an analysis. The problem is certainly of interest because it offers a way to detect the effects of partitioning of sensorimotor feedback (Windhorst 1979; see below).

The above criteria provide a way to determine whether a particular set of EMG records provides evidence for the existence of more than one ordering of recruitment among the complete ensemble of motoneurons innervating a particular muscle. The absence of such phenomena does not preclude such heterogeneous recruitment (e.g. purely functional task groups within anterior sartorius; Hoffer et al. 1987c). If more than one recruitment order has been demonstrated to exist by these criteria, this may reflect either a reversal of orderly (size-related) recruitment in a single recruitment group or the existence of two or more independent but internally orderly recruitment groups of motoneurons. Either of these two possibilities should be reflected in differential synaptic connectivity onto the motoneurons, i.e. synaptic input from a signal source that is not always weighted according to the size and strength of each motor unit supplying the muscle. However, such differential activity may not be reflected in all of the sources of input signals to the motoneurons. Note the homogeneous recruitment of all parts of BF during scratch in Fig. 5 and all parts of sartorius during cutaneous reflexes (Pratt and Loeb, this volume), including motoneurons belonging to different task groups in anterior sartorius (Loeb et al. 1987c). Indeed, differential activity might be created by a single, relatively obscure source of input, such as tonic inhibition via a descending pathway that modulates the recruitment produced by an orderly set of excitatory segmental inputs.

Differential synaptic connectivity has been found in the monosynaptic Ia system of the sartorius (Eccles and Lundberg 1958) and lateral gastrocnemius (Vanden-Noven et al. 1986) motoneuron pools. An early investigation of monosynaptic Ia inputs into motoneuron pools of cat hindlimb muscles (Eccles and Lundberg 1958) found no differential Ia receptivity in TFL motoneurons although the authors note that their sampling of TFL may not have been representative of the entire motoneuron pool. However, this early report did find differential effects within the BF motoneuron pool. BFa, a hip extensor, received its greatest Ia synaptic input from other hip extensors. BFp, a knee flexor, received its greatest Ia input from other knee flexors. In addition, the other extensors of the hip received larger Ia input from BFa than BFp, and the other flexors of the knee received a larger Ia input from BFp than BFa. Botterman et al. (1983) confirmed and extended these findings, showing that individual BF compartments received their largest Ia inputs from themselves and received lesser inputs from the other two compartments. These Ia connectivity studies support the argument that differential activation within certain muscles can be accounted for by a selective recruitment of motoneurons that results from differences in synaptic input.

Although differential synaptic input could provide a mechanism whereby motoneurons are differentially recruited, the biological significance of selective motoneuron recruitment and regional muscle activation becomes evident only when the biomechanical heterogeneity of BF and TFL is considered. Both muscles are comprised of discrete compartments that differ in their mechanical arrangements with the skeleton. Lever arm lengths and mechanical advantages at specific joints differ qualitatively and quantitatively, and the active compartments differ in their contributions to the multiple biomechanical functions. The neural capacity for selectively recruiting motoneurons, and selectively activating biomechanically distinct muscle territories, provides the animal with a greater range of mechanical "options" while performing kinematically diverse movements.

Interestingly, the synaptic connectivity that provides a basis for this strong spatial selectivity among muscle compartments can occur in motor nuclei that reflect little or none of the peripheral neuromuscular organization. Gordon et al. (1991) have shown that motoneurons from all parts of TFL and sartorius are thoroughly intermingled in single, elongated motor nuclei.

Strategies for sampling EMG

The results of this study emphasize the need for careful selection of EMG sampling sites during chronic recordings from intact animals. The presence or absence of EMG in one region of muscle does not necessarily indicate the activity of other regions. Furthermore, the timing of activation may vary across the muscle, particularly in muscles with complex anatomy and multiple

mechanical actions. Knowledge of the histochemical profile, anatomy, and possible mechanical functions of a muscle prior to selection of the recording site(s) will permit an informed decision concerning electrode placement(s) and result in a comprehensive and more accurate survey of neuromuscular function.

Neuromuscular semantics

All five papers in this series have explored the functional implications of relationships between neuromuscular function and different types of structural organization in skeletal muscles. While it would be presumptuous to assume that the small group of muscles that we have sampled from the cat hindlimb reflects the full range of mammalian neuromuscular organization, these muscles do exhibit a remarkable range of structure-function relationships and represent a system that has contributed greatly to current concepts of sensorimotor control. The particular definitions of the organizational terms that we and others have used have important implications for the framing and testing of hypotheses and for the conduct of experiments that rely on convenient anatomical structures (such as nerve branches) whose significance to the organism is often presumed but unspecified. In the course of this work, we have been forced to deal with inconsistencies in both the historical usage and logical relationships among many terms. Therefore, it seems useful to offer for debate a proposed set of terms that seems to capture the meaning and historic development of many key concepts, as well as to deal with the recent concerns of many researchers in this field (see Loeb 1989; Windhorst et al. 1990).

Muscle. An entity defined by connective tissue that is internally continuous and externally separable from adjacent muscles over most or all of its outside surface. The entity encompasses muscle fibers and sense organs contained within the extent of the muscular and connective tissue involved in conveying the tension exerted by the muscle fibers onto a skeletal attachment or a connective-tissue structure that provides a common attachment for more than one muscle. It is tempting to try to define muscles on the basis of their innervation, but this leads to many paradoxes. The serially arranged compartments of ST as well as many axial muscles have separate nerves back to main nerve trunks. The parallel compartments of sartorius sometimes have nerve branches that are separable back to the femoral nerve (Loeb et al. 1987a) and axial muscles such as transversus abdominis and serratus anterior are often comprised of many parallel and serial compartments with separate segmental innervation.

Motor nucleus. The complete set of motoneurons (of all types) supplying axons to a single muscle (Romanes 1951). Motor nuclei are usually (but not necessarily) contiguous and exclusive. At least two types of division into subnuclei are possible: compartmental subnuclei, consisting of the sets of motoneurons supplying different nerve branches in a compartmentalized muscle (see below) and central subnuclei, which arise when discontiguous groups of motoneurons innervate a single muscle (e.g. stapedius; McCue and Guinan 1988). Note that the term "motor pool" is often used as a synonym for motor nucleus, particularly when there is a connotation of function, as in "recruitment pool"; given the complexities discussed in these papers, such ambiguity seems best avoided.

Neuromuscular compartment. The muscle region that is innervated by all of the motoneurons in a single branch of the muscle innervation (English and Letbetter 1982). We would modify their definition of "nerve branches" to include the separate nerves that may arise more proximally than at a single entry point at the hilus of the muscle, as noted above for semitendinosus and many axial muscles. Their distinction into "primary" or other orders may not be generally applicable.

Muscle unit territory. The muscle region that is occupied by muscle fibers innervated by a single motoneuron; may be further subdivided into subunit territories consisting of the groups of muscle fibers innervated in a single end-plate zone in longitudinally distributed series-fibered muscles (Chanaud et al. 1987).

Muscle region. A "functionally neutral" term to designate portions of a muscle on the basis of anatomical coordinates (e.g. proximal-distal, medial-lateral, superficial-deep), whose distinctiveness (or lack thereof) may then be defined by the following criteria:

histochemical – proportional composition by the various muscle fiber types;

kinematic – moment arms at joint(s) crossed;

architectural – length and arrangement of muscle fibers, fascicles and connective tissue;

recruitment – relative amplitude and timing of EMG activity in various regions during various motor behaviors, categorized according to the criteria discussed above.

Task group. The set of motoneurons innervating extrafusal fibers in a single muscle that are recruited in an orderly manner during a single phase of a motor behavior (Loeb 1985; Hoffer et al. 1987c); a purely functional term that may or may not be isorepresentational with any of the above anatomical terms and avoids the ambiguity of "motor pool". Note that this is a more circumscribed version of the original proposal to include gamma motoneurons and proprioceptors contributing to control of the muscle during the subject behavior; the distributed nature of such control among all of the muscles of the limb precludes the drawing of any useful boundaries under the originally proposed definition (Loeb et al. 1989).

Partitioning. A relational term to describe any nonhomogeneous relationship (mechanical or neural) between a set of motor units (defined by one of the above criteria) and a source of afferent signals (sensory or central) (reviewed by Windhorst et al. 1989).

It will be noted that all of these terms are neutral with respect to agonist-antagonist synergies among groups of muscles such as Sherrington's (1910) classification of flexors and extensors. The general applicability of such classifications would seem to argue for their continued utility as a general roadmap to explore entities such as CPGs. However, exceptions such as those described here suggest caution in using them without determining the local conditions.

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