

Functionally complex muscles of the cat hindlimb

I. Patterns of activation across sartorius

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Received February 16, 1990 / Accepted January 22, 1991

Summary. The cat sartorius (SA) can be divided functionally into an anterior (SAa), knee extensor portion and a medial (SAM), knee flexor portion; it can be further subdivided anatomically by multiple nerve branches into parallel longitudinal columns that terminate in a distributed insertion at the knee with a continuous range of moment arms. Thus, SA may be controlled by a discrete number of motoneuron task groups reflecting a small number of central command signals or by a continuum of activation patterns associated with a continuum of moment arms. To resolve this question, the activation patterns across the width of the SA were recorded with an electrode array during three kinematically different movements – treadmill locomotion, scratching and paw shaking, in awake, unrestrained cats. Uniformity of activation along the longitudinal axis was also examined because individual muscle fibers do not extend the length of the SA. In addition, the cutaneous reflex responses were recorded throughout all regions of the SA during locomotion. Two fascial surface-patch arrays, each carrying 4–8 pairs of bipolar EMG electrodes, were sutured to the inner surface of the SA, one placed proximally and the other more distally. Each array sampled separate sites across the anterior to medial axis of SA. During locomotion, two basic EMG patterns were observed: the two burst-per-step-cycle pattern typical of SAa and the single burst pattern typical of SAM. There was an abrupt transition in the pattern of activation recorded in the two parts of SA during locomotion, and no continuum in the activation pattern was observed. Stimulation of both sural and saphenous cutaneous nerves during locomotion produced reflex responses that were uniformly distributed throughout SA, in contrast to the regional differences noted during unper-

turbed walking. Similarly, during scratching and paw shaking all parts of the SA were active simultaneously but with regional differences in EMG amplitude. The abrupt functional border between SAa and SAM coincided with the division of the SA into a knee flexor vs. a knee extensor. In all cases, the quantitative and qualitative differences in SAa and SAM EMGs were uniformly recorded throughout the entire extent of SAa or SAM; i.e., there was no segregation of activity within either SAa or SAM. Furthermore, the time course of EMG from each proximal recording site was nearly identical to the corresponding distal site, indicating no segregation of function along the longitudinal axis of SA. These results indicate that SAa and SAM constitute the smallest functional modules that can be recruited in SA. The functional subdivision of the SA motor nucleus is reflected in the central pattern generators for these movements to permit a task-dependent recruitment of any combination of SAa and SAM. Our data indicate that the number of task groups even in an anatomically and functionally complex muscle like the SA is small and appears to be related to the kinematic conditions under which the muscle operates.

Key words: Sartorius – Muscles – Task groups – Kinesiology – Electromyography – Reflexes – CPGs – Differential activation – Cat

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Introduction

The traditional view of motor unit recruitment tacitly assumes that neural inputs are uniformly distributed throughout a motor nucleus, resulting in a unidimensional control of the muscle expressed as the orderly recruitment of all of its motor units (reviewed by Henneman and Mendell 1981). The word “muscle” denotes a singular entity; the musculature of a body part, such as a limb, is divided into an integral number of individual

muscles. Gross anatomical dissection often establishes a range of more or less well-defined fascial planes between muscle tissue. Furthermore, the spinal motor nuclei, defined by the locations of the motoneuronal cell bodies projecting to individual muscle nerves are, for the most part, dense and contiguous anatomical entities (Romanes 1953), further reinforcing the apparent biological relevance of this working definition of "muscle". However, it has long been known that some muscles have regions that are differentially recruited during various motor tasks (Sherrington 1910, Engberg and Lundberg 1969). More recently, it has been reported that motor units within a given muscle region may tend to participate selectively in different motor behaviors (Desmedt and Godaux 1981; Ter Haar Romeny et al. 1984; Hoffer et al. 1981, 1987c). Thus, it is clear that at least some motor nuclei are functionally subdivided by some species of pre-motoneuronal inputs that are not distributed uniformly to all of the motoneurons within that nucleus.

While it is generally agreed that traditionally defined anatomical entities (e.g., muscles and motor nuclei) do not define functional units of recruitment in all muscles (see reviews by Windhorst et al. 1989, 1990; Burke 1990; Loeb 1990), it is not clear what determines the organization of the pre-motoneuronal inputs that sculpture functional subsets of motoneurons. In this series of papers (Papers I-V, this journal), we have studied ten anatomically complex muscles of the cat hindlimb and attempted to relate their functional organization to the mechanical and/or anatomical complexity of the muscle.

We have used the adjective "functionally complex" to describe any muscle in which the motor units do not form one homogeneous recruitment group over the entire extent of the muscle. Multiple, simultaneous, gross electromyographic (EMG) recordings were obtained from restricted regions within most of the thigh muscles and one calf muscle (tibialis anterior) of intact cats during a wide range of natural behaviors and in response to electrical stimulation of cutaneous afferents. Differential activation, defined here as heterogeneity in the timing and/or amplitude of the EMG recorded from different regions within a muscle, has been interpreted relative to the gross innervation and histochemical composition of the intramuscular regions (see Discussion of Paper V) for evidence of functional subsets of motoneurons. We have then tried to relate the organization of these subsets to any mechanical, architectural or histochemical heterogeneities that could be found in these muscles, as well as to any previously described segmental circuitry involving their motoneurons and muscle afferents. By comparing intramuscular activation patterns recorded in individual muscles across several natural movements we can gain insight into the relative importance of anatomical vs. mechanical factors in organizing functional units of recruitment.

Attempts to relate the functional organization of muscle/motor unit activation to muscle architecture are not straight-forward; muscles can be as complex and ambiguous anatomically as they are functionally. In fact, it is not always obvious where and how the subdivisions that define individual muscles should be made. The

fascial planes revealed by gross anatomical dissection (as distinct from internal tendinous inscriptions and aponeurotic sheets) serve the function of permitting differential mechanical slippage between regions of muscle tissue. They also appear to be related to ontogenetic subdivisions of mesenchymal tissue that are often preserved as the basis for the phylogenetic homologies in muscular architecture that are easily observed among even widely separated species. For these reasons, in the present series of papers, we have adopted such a strictly gross morphological definition of "muscle". Thus, sartorius, biceps femoris, tensor fasciae latae, and semitendinosus are referred to as four individual muscles regardless of the heterogeneities in their internal neuromuscular architecture. Similarly, a motor nucleus is defined herein as the set of motoneurons innervating a given muscle.

Teleologically, functional complexity might be expected to arise in muscles that have broad origins and/or insertions on the skeleton, which would result in different mechanical conditions in and actions by different regions of the muscle. Five of the ten muscles studied in this set of papers, including sartorius, the subject of this paper, have such a musculoskeletal architecture (see below), which we call "mechanically heterogeneous". During some motor behaviors, the muscle units in different regions seem to call for and, indeed, receive different command signals, despite the fact that their motoneurons may originate from relatively homogeneous motor nuclei (Pratt et al. 1984; Gordon et al. 1991).

Physiologically, such functional complexity can arise only if the individual motor units occupy relatively restricted territories within the whole of the muscle. English and Letbetter (1982) noted that the muscle nerve innervating lateral gastrocnemius in the cat was divided into four primary branches, each of which innervated all of and only muscle fibers contained within these "neuromuscular compartments". However, it was still possible that the axons of the individual motoneurons might bifurcate proximally and innervate more than one such primary nerve branch. In a subsequent paper (English and Weeks 1984), this was shown not to be true in this muscle as individual motor unit territories also were confined to neuromuscular compartments.

The lateral gastrocnemius of the cat is a multipinnate muscle that is naturally divided by intramuscular aponeurotic septae into mechanically heterogeneous regions that correspond to the neuromuscular compartments defined by its clear and consistent primary nerve branches. This has given rise to much speculation and some experimentation regarding the possibility of preferential "partitioning" of the proprioceptive feedback to homonymous compartments (reviewed by Windhorst et al. 1989). However, the extent to which these definitions and hypotheses can be generalized to the neuromuscular architecture of many other muscles remains to be determined. In particular, it may be impossible to identify "primary nerve branches" in muscles that have multiple, separate nerves (e.g., semitendinosus; Bodine et al. 1982) or inconsistent patterns of complex serial and parallel branching (e.g., sartorius; Loeb et al. 1987b). Furthermore, anatomical demarcations of mechanical heteroge-

neity may be absent (e.g., sartorius) or related to in-series rather than in-parallel compartments (e.g., semitendinosus and many axial muscles).

The relationship between functional subunits and neuromuscular compartments has been examined in detail in two muscles, sartorius (this paper) and biceps femoris (Chanaud et al. 1991a, b; Chanaud and Macpherson 1991) in this series of papers. We have used the term "neuromuscular compartment" to denote the muscle territory controlled by the motor axons of any gross anatomical nerve branch, without considering whether the branch is "primary" and without presuming whether or not these axons might bifurcate proximally to innervate other nerve branches. Such a general, gross anatomical definition is useful experimentally to define sets of afferents and efferents for electrophysiological and anatomical tracer studies. In particular, it avoids criteria such as "smallest anatomical unit" (English and Weeks 1987) which themselves require extensive experimentation and may be meaningless if the muscle fibers innervated by separate nerve branches are partially intermingled in the muscle (Thomson et al. 1990). A return to the more conservative definition (English and Letbetter 1982) seems wise, at least for our purposes. Whether or not neuromuscular compartments, defined in any manner, correlate with gross musculoskeletal architecture (e.g., moment arms), intramuscular design (e.g., aponeurotic sheets, fascicle length, pinnation angle), natural recruitment, or control circuitry remains to be determined for most muscles (see reviews by Windhorst et al. 1989, 1990; Burke 1990; and Loeb 1990).

This paper deals specifically with the sartorius (SA) muscle, a biarticular muscle that spans the hip and knee joints. It originates on the anterior iliac crest and has a broad and continuous insertion, extending from the dorsal margin of the patella medially and distally along the tibia. Thus, the fascicles along its anterior margin exert torques that flex the hip and extend the knee, whereas the fascicles along its medial margin flex both the hip and the knee. There is no intramuscular feature to mark the point at which the gradually changing moment arm at the knee reverses sign. The muscle nerve bifurcates into two sets of nerve branches roughly dividing SA into anterior (SAa) and medial (SAm) regions. The two sets each consist of a series of longitudinally running branches that innervate narrow strip-like territories. These territories contain multiple, short muscle fibers in series (Loeb et al. 1987b).

It has long been known that SAa has a different EMG pattern during locomotion than SAm (Engberg and Lundberg 1969; Hoffer et al. 1981, 1987c; Loeb et al. 1985a, 1987a). However, it is not known whether there is a small number of activation patterns associated with the different actions of SA on the skeleton (i.e., hip flexion coupled with either knee extension or knee flexion) or, instead, a continuum of activation patterns associated with a continuum of moment arms. That is, the functional subunits within SA could correspond to the division of SA by the two main sets of longitudinal branches or there could be further subdivisions within those sets. In addition, it is not known whether the func-

tional subdivision of the SA motor nucleus observed during locomotion is a special case or is typical of SA motoneuron recruitment during all or most movements.

The present study addresses the following questions: What is the relationship between the functional organization of SA and muscle architecture (gross vs. micro anatomy)? Is the functional subdivision of SA movement-specific? If so, what is the relationship between the functional organization of SA and the kinematic conditions under which different regions of SA operate in each movement? The activation of multiple regions of the SA muscle was recorded during three rhythmic movements (locomotion, scratching, and paw shaking) and in response to electrical stimulation of two hindlimb cutaneous nerves. For all conditions, the SA muscle appeared to consist of no more than two independently controlled regions whose mutual boundary corresponded consistently with the line of neutral action at the knee joint. Preliminary results of this study have been reported previously (Loeb et al. 1984).

Methods

Experiments were performed on 9 adult cats (2.0–3.5 kg) of either sex. Each cat was trained, using affection and food rewards, for several weeks prior to surgery to walk on an enclosed treadmill belt (about 1.3 m long and 0.3 m wide) at a range of speeds. In addition, the cats selected for use were screened for their ability to produce scratching and shaking movements (see below). Various combinations of chronic EMG recordings were obtained from localized subvolumes of the SA muscle in awake, freely moving animals. The EMG activity of the ipsilateral quadriceps (vastus lateralis, VL; vastus intermedius, VI; vastus medialis, VM; and rectus femoris, RF), tibialis anterior (TA) and lateral gastrocnemius (LG) muscles was also recorded in some experiments to provide controls for assessing possible crosstalk and information regarding task-related muscle synergies. An implanted length gauge recorded the angular motion of the knee joint and was used off-line to identify cycle boundaries for each movement. All movements during recording sessions were filmed by video cameras. Limb kinematics for each behavior were calculated subsequently by digitizing video stills. Joint angle information and muscle morphometric data collected in post-mortem dissections were fed into a mathematical model of the cat hindlimb to generate curves describing the length changes in SAa and SAm. In addition, the saphenous and sural cutaneous nerves were electrically stimulated during locomotion to assess the similarity of SAa and SAm connections to the locomotor central pattern generator (CPG) and flexion reflex afferents. Most of these procedures have been described extensively in previous publications from our laboratory, as noted below, and will be described only briefly herein. Only procedures that were specific to this study or were not published previously will be described in detail.

Surgery

All recording devices were surgically implanted under aseptic conditions and deep barbiturate anesthesia. Animals were anesthetized initially with an intraperitoneal dose of Nembutal (30 mg/kg) that was supplemented intravenously throughout surgery. Antibiotics (Ancef) were administered routinely pre- and post-operatively. Animals were placed in a temperature and humidity-controlled chamber immediately following surgery for 14–24 h and then transferred to their home cages. Typically animals were sufficiently recovered within two days to walk on the treadmill and were fully recovered after five days.

Implanted devices

Electromyograms were recorded using bipolar patch electrodes positioned on the fascial surface of selected muscles. The design of these patch electrodes has been described in detail elsewhere (Hoffer et al. 1980; Abraham and Loeb, 1985; Loeb et al. 1985a; Loeb and Gans 1986; Hoffer et al. 1987a). Briefly, they consisted of exposed sections of two Teflon-insulated multi-stranded wires that were sewn into a flexible sheet of Dacron-reinforced Silastic material. The exposed electrode contacts were usually 5 mm long with a 5 mm interelectrode separation in all electrodes except the distributed patch electrodes that were implanted on SA (see below). Each patch was anchored to the fascial sheath of the target muscle so that the electrode contacts were oriented with the axis of the dipole parallel to the apposed muscle fibers. The dielectric sheet provided insulation of the electrodes from signals generated by surrounding muscles (see Loeb and Gans 1986). This electrode design records EMGs from localized subvolumes of muscle with excellent protection from crosstalk. This was a particularly significant concern in recording from the very thin, sheet-like medial part of SA which sits atop the large, active quadriceps muscles.

Distributed patch arrays with multiple pairs of bipolar electrodes were specially designed to record from restricted subvolumes of the SA muscle. In initial experiments, arrays with four 3 mm × 3 mm electrode pairs, spaced 5–7 mm apart, were used. In four animals, two such patch arrays were positioned along the transverse axis against the internal surface of the SA muscle (between SA and the underlying quadriceps muscles), one proximally and the other located more distally (see Fig. 1A). Both patches were placed distal to the primary nerve entry point. The electrodes were situated such that the electrode pair near one edge of each patch sat under the most anterior border of SA (SAa); the pair near the other edge was positioned under the most medial border of SA (SAm). Thus, it was possible to detect regional differences in EMG patterns both in the longitudinal (interpatch comparisons) and transverse (intrapatch comparisons) axes of this long and broad muscle. In later experiments, arrays with 5–8 bipolar recording sites were used to sample with finer resolution along the transverse axis of SA. The data obtained with these latter arrays were similar to those obtained with the 4-electrode arrays and, thus, will not be presented separately.

An additional pair of contacts facing in the opposite (inward) direction was usually attached near the most anterior SA electrode providing a "doublesided" patch that could record from SAa and VL simultaneously. This arrangement provided a convenient check against crosstalk between these two muscles. This was especially important in interpreting the stance phase activity in SAa.

Two of the patch electrodes were situated over the saphenous and sural cutaneous nerves to permit testing of electrically evoked cutaneous reflexes during locomotion (see also Abraham et al. 1985; Loeb et al. 1985b, 1987a; Pratt et al. 1991). The patch used to record LG EMG was aligned over the sural nerve as it passes across the LG muscle and could be used for both recording and stimulation.

A length gauge, also described in detail in previous publications (Hoffer et al. 1980, 1981; Abraham and Loeb 1985), was positioned across the knee joint to record changes in joint angle during movement. Proximally the length gauge was tied to a stainless steel screw inserted in the lateral surface of the femur just below the greater trochanter; distally it was sewn into the patellar tendon. The path of this length gauge approximates the attachments of the vasti muscles, and records presented in figures from the gauge are designated LV. In the figures, an upward deflection in the LV trace indicates knee flexion which causes an increase in the length of the gauge and the knee extensors, such as SAa. See Fig. 1 of Loeb et al. (1985a) for a more detailed explanation of the relation of LV inflections to the phases of the step cycle.

The wire leads from all implanted devices plus a ground wire anchored in the left thigh were passed subcutaneously to a small exit hole in the skin near the site of the backpack connector. Each wire was soldered to contacts on the backpack connector which sat on the animal's back, anchored by two heavy synthetic sutures placed between the spinous processes and passing through the skin and the

paravertebral muscles. The design of the backpack "saddle" connector and its interface with the recording equipment has been described in detail previously (Loeb et al. 1985a; Hoffer et al. 1987a). The contacts and the wires were protected by a metal cover that was removed during recording sessions to access the connector. The animals gave no evidence of discomfort from the external connector, and the arrangement remained free of infection.

Animals were sacrificed immediately following the conclusion of data collection, usually 4–6 weeks post-surgery. A post-mortem inspection of all implanted devices was performed to verify that no post-surgical migration of the patch electrodes had occurred.

Signal recording

All signals from the implanted devices were led to various amplifying and signal conditioning devices and thence to an 18-channel FM tape recorder (DC–10,000 Hz bandpass) through a 1 m flexible ribbon cable. The following signals were recorded on tape for off-line analysis: one length-gauge channel (DC–100 Hz); ten to fourteen channels of EMG (bandpass 50–5,000 Hz); an IRIG-B time code (Datum 9300–100); a monitor of treadmill speed multiplexed with a marker of cutaneous nerve stimulation; and a voice commentary.

The animal's movements were videotaped from both the right and left sides using two Telemation plumbicon cameras displayed on a split-screen and stored on a Panasonic VO-2800 video cassette recorder. Marks were placed on the skin overlying the lateral aspect of the metatarsal/phalangeal joint, ankle (lateral malleolus), hip (femoral greater trochanter), iliac crest and ischial tuberosity in order to extract kinematic data from the video records (see Kinesiological Analysis below). Stroboscopic illumination was used to minimize blurring of the marks. The digital time code was also recorded on the video record in order to synchronize the simultaneously recorded video and analog signals.

Electrical stimulation

The procedures used to electrically evoke cutaneous reflexes with chronically implanted patch electrodes on the saphenous or sural nerves during locomotion have been described in detail in previous reports from this laboratory (Abraham et al. 1985; Loeb et al. 1985b, 1987a). The stimuli consisted of balanced, biphasic square wave pulses (0.1 ms/phase) delivered by a photoisolated, constant-current stimulator. The stimulation series consisted of single biphasic pulses delivered at 1.5 s intervals for 3–5 min. This interval did not coincide with the animal's stepping frequency, and thus the stimuli occurred randomly throughout the different phases of the step cycle. Stimulus intensity was referenced to the threshold current level that consistently evoked time-locked excitatory or inhibitory EMG responses observed in single synchronized sweeps on a storage oscilloscope while the animal walked on the treadmill. The use of a nerve cuff positioned proximal to the stimulating electrode provides a more sensitive measure of stimulus threshold (see Loeb et al. 1985b, 1987a; Pratt et al. 1991), but the large number of channels devoted to recording EMGs in this study precluded using nerve cuffs to monitor the volleys evoked by electrical stimulation of the cutaneous nerves. All stimuli used in these experiments ranged from 2–5 times threshold based upon inspection of the EMG responses. Experiments in which reflex thresholds were determined by recording the electrically evoked volley in a femoral nerve cuff (Pratt et al. 1991) have shown that current intensities in this range are about 1.5–2 times threshold recruitment of group I fibers. This level of stimulation was usually well below that which interrupted steady gait as evidenced by limb withdrawal or a turning of the head towards the left hindlimb.

Data collection

Animals were monitored daily in the laboratory post-operatively, and data were collected for analysis when the cats were able to perform all necessary movements with no sign of discomfort (usually 5–7 days after surgery). Data were collected over two to three consecutive days. The in situ impedance of each implanted lead wire was measured at the beginning of each recording session. The normal range for impedances was 0.5–5.0 kOhm measured with a 1 kHz test signal. The first series of data were recorded while the animal walked steadily on the treadmill at a slow-to-moderate speed (0.5–0.8 m/s) for 10–15 min. During this time, data were collected both with and without cutaneous nerve stimulation. Following recording of EMG responses during slow-to-moderate speed walking, the speed of the treadmill was steadily increased until the animal could no longer maintain its position on the center of the treadmill belt. The fastest speeds attained varied across animals (3.0 to 3.5 m/s) and could be maintained for only 15–30 s.

Two other high speed movements studied in these experiments were reflex paw shaking and scratching. To elicit the paw shake, a sticky piece of tape was placed on the plantar surface of the left hindpaw while the animal stood on the treadmill belt (Smith et al. 1980; Abraham and Loeb 1985a; Loeb et al. 1985b; Carter and Smith 1986). The treadmill was then activated, and the animal would step and shake the paw during the normal swing phase of the left hindlimb. The posture and planar orientation of the left hindlimb during the paw shake varied across animals, especially in the extent of backward extension vs. abduction (see also Smith et al. 1985). Kinematic analysis was restricted to animals in which abduction of the limb was minimal. Light cutaneous stimulation of the ipsilateral pinna, with the animal stationary, was used to trigger reflex scratching of the left ear. This response was more variable than the paw shake and locomotion both across and within animals and ranged from a vigorous scratching of the left ear to a rather aimless waving of the left limb near the left shoulder. Cats adopted either a sitting or a standing posture when scratching, similar to the postures described by Carlson Khuta and Smith (1990) in their Figs. 1B and C. Only scratch cycles in standing cats in which the cat's paw contacted the ear and the hindlimb appeared roughly planar, as determined by inspection of video stills, were selected for digitization and kinematic analysis.

EMG analysis

After each recording session, all of the analog and videotape records were reviewed and segments of data, identified by the digital time code, were selected for further analysis. A 10-channel oscillographic recorder (Honeywell, 1858 CRT Visicorder) was used to make permanent records of selected segments. The video signal was viewed field-by-field (temporal resolution of 17 ms) with an Eigen Video Disc to identify the times for footfall and footlift during locomotion and cycle inflections during paw shaking and scratching. The transition times in step cycles corresponding to the Phillipson (1905) phases of pre-stance limb extension (E1), stance (E2–E3), and flexion (F) were marked during locomotion trials, whereas for the scratch and shake cycles the propulsive (extension) and withdrawal (flexion) phases were marked. The relationship of the length gauge to cycle boundaries was determined by marking the boundary times on the oscillographic records. This information was used subsequently (see below) to mark critical cycle boundaries on digitized computer records preliminary to generating gated reflex rasters and cycle-triggered, normalized EMG averages (see Fig. 2 of companion paper IV, Pratt et al. 1991).

The EMG signals were rectified and analog integrated into resettable 2 ms bins, as described previously (Bak and Loeb 1979; Hoffer et al. 1987b). A PDP-11/73 laboratory computer, equipped with a multichannel digitizing program, sampled the value of each preceding bin's integration plus length gauge records at a rate of 500 samples per second that was synchronized by the digital time code.

A joystick-driven cursor was used to mark significant phases in the movement cycles on the continuous analog records of the length gauge and multichannel EMGs viewed on a computer-generated video display. Cycle boundaries were marked on the basis of inflections in the length gauge record, as described above.

Reflex rasters

The gating of reflexes during locomotion (Andersson et al. 1978; Forssberg 1979; Duysens and Loeb 1980; Abraham et al. 1985) makes it necessary to sample reflex responses throughout the step cycle. The peristimulus EMG rasters, shown in Fig. 4, display all of the reflex responses recorded throughout the various phases of the step cycle during two minute sessions of cutaneous nerve stimulation. The procedures used to construct these reflex rasters have been described in detail in previous reports from this laboratory (Abraham et al. 1985; Loeb et al. 1985b, 1987b). Briefly, each trace represents the rectified and bin integrated EMG from 30 ms preceding to 100 ms following each stimulus. The traces were reordered by the computer and displayed according to the phase of the step cycle during which the stimulus occurred. The stance and swing phases of the normalized step cycle are indicated along the left border of the rasters; the upward-pointing triangle indicates footlift and the downward-pointing triangle indicates footfall. All rasters are arranged with the swing phase starting at the top.

Kinesiological analysis

It was of interest in the present study to determine the relationship between muscle activation patterns observed across SA and the kinematic conditions under which different parts of the muscle operated during various movements. Length changes in different longitudinal regions of SA were calculated on the basis of the moment arms for different muscle regions at the hip and the knee and changes in angles at both joints. Joint angle changes were obtained by digitizing skeletal landmarks in consecutive fields of the video records for each movement using a joystick-driven cursor on the computer. The knee joint position was calculated trigonometrically (to avoid errors caused by skin slippage) from the ankle and hip positions and post-mortem measurements of thigh and shank lengths. In post-mortem dissections the path lengths (path length = muscle length + tendon length) for the anterior and medial borders of SAa and SAM were measured along with the distance of each path from the approximated center of rotation at each joint. A pulley radius for SAa at the knee was also measured.

The SA muscle morphometric data and joint angle data were fed into a computerized mathematical model of the cat hindlimb, under joint development by our Laboratory and W.S. Levine of the Electrical Engineering Department at the University of Maryland (Levine 1986), in which each muscle of the cat hindlimb has been modeled on the basis of its gross anatomy and mechanical constraints on tendon path, i.e., pulleys and tethers. The model calculated the short and long path length changes (corresponding to the small and large moment arms at the knee at the edges of SAa and SAM). However, since no differentiation was seen in activation within either region, only the long path length curves showing the largest length changes are used herein to describe each muscle, as shown in Fig. 3B. (Note that because SAa and SAM are contiguous, the short path of SAa is identical to the short path of SAM and both are taken from the line through the muscle at which the moment arm at the knee becomes zero).

Results

Sartorius EMG during locomotion

The EMG records illustrated in Fig. 1A are representative of those seen in the 9 cats studied in this series of

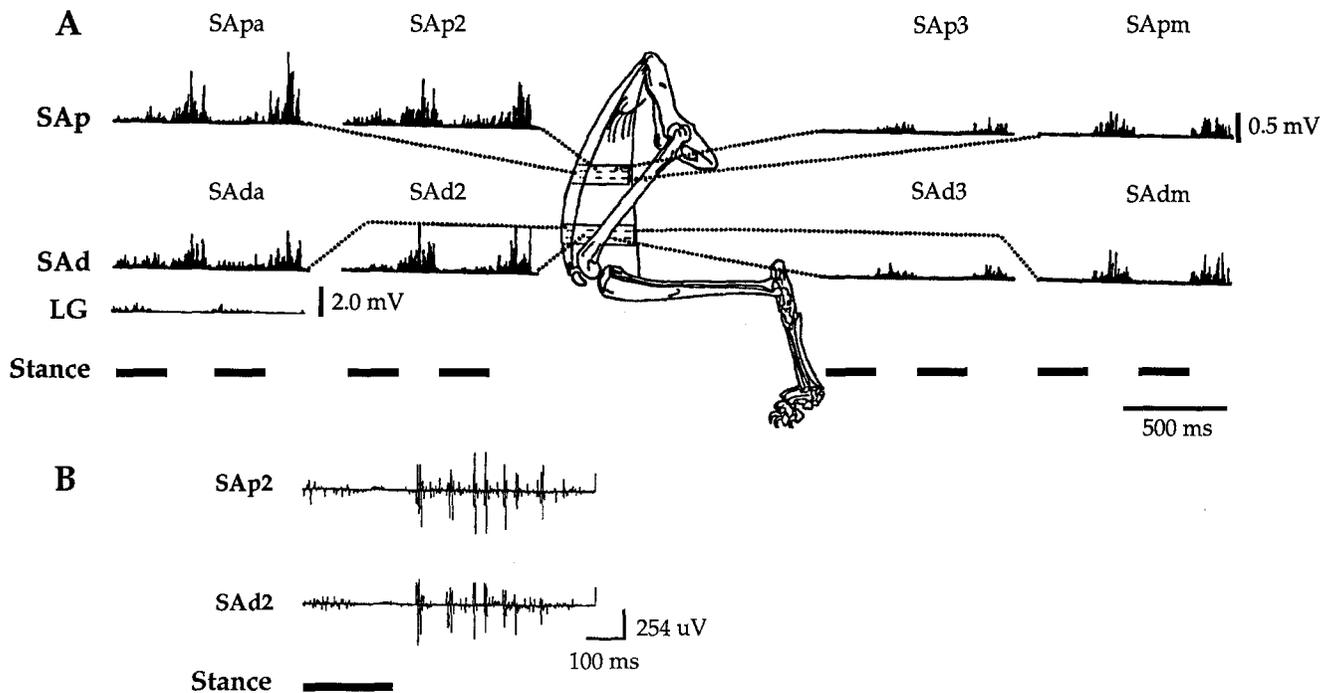


Fig. 1. A Sartorius (SA) activity during trotting in cat CP2 recorded with two 4-electrode EMG patch arrays. The placement of the proximal (p) and distal (d) arrays on sartorius is shown in the diagram. Electrodes pa and da were situated on the most anterior border, and pm and dm were on the most medial border of sartorius. **B** Records from electrodes #2 in a proximal (SAP2) and

distal (SAD2) 5-electrode patch array in cat CP3 recorded during treadmill walking. Note the large action potentials that appear during the swing phase burst but not the stance phase burst and the appearance of these potentials in both the proximal and distal records

experiments. As previously described (Engberg and Lundberg 1969; Hoffer et al. 1980, 1987c), the biarticular, bifunctional SAA displays two bursts of EMG per step cycle, one during the stance phase and one during the swing phase. Because there is no anatomical demarcation dividing SA into its anterior and medial portions, SAA could be defined functionally during locomotion (as shown in Fig. 1A) on the basis of the EMG recordings as that portion of the muscle lying over electrodes 1 and 2 in the proximal (pa and p2) and distal (da and d2) patches. Electrodes 3 and 4 (p3, pm, and d3, dm) recorded the single swing phase burst of EMG that is typical of SAM. The border between sites 2 and 3 corresponds approximately to the part of the muscle having essentially neutral action on the knee joint.

Use of distributed, multi-electrode patches with as many as eight pairs of electrodes did not reveal patterns of EMG intermediate between the well-described patterns for the anterior and medial edges of the muscle. As shown in Figs. 1 and 2 during the trot, only the two basic patterns of EMG were recorded at all gait speeds. No evidence of a continuum from the double burst to the single burst of EMG per step cycle was seen. The abrupt transition between the two patterns can be seen in Figs. 1 and 2 to have occurred between electrodes 2 and 3 in both the proximal and distal patches. The center-to-center interelectrode spacing for all adjacent electrode pairs (p1-p2, p2-p3, etc.) was 7 mm in these records.

The patterns of activation described above in SAA and SAM during locomotion were observed in all 9 ani-

mals. In all cats, a double burst pattern of activation was recorded in SAA and a single burst pattern in SAM, and there was an abrupt transition between the two patterns (the transition occurred between two adjacent electrode pairs). While the amplitude of the flexor burst in SAA was always larger than the extensor burst during treadmill locomotion, the ratio of the amplitude of the two SAA bursts varied across cats but was consistent within each cat across recording sessions. In all cats the amplitude of the extensor burst in SAA increased with treadmill speed, as reported by others (Engberg and Lundberg 1969; Hoffer et al. 1987c).

The reason for implanting the proximal and distal patches was to examine the functional homogeneity/heterogeneity along the longitudinal axis of this long muscle with short muscle fibers (Loeb et al. 1987b). It is apparent from Fig. 1A that the EMG patterns recorded in longitudinally equivalent pairs of electrodes, i.e., SAPa and SAda, were similar. This was such a consistent finding in the first four animals in which proximal and distal patches were implanted that we discontinued implanting two patches in subsequent cats. Furthermore, it can be seen in Fig. 1B that even the individual electrical events in the unrectified record from proximal electrode 2 were also recorded more distally by electrode d2 (compare records SAP2 and SAd2 in Fig. 1B; note that data in Figs. 1A and B are from different cats). Because parts of SA are very thin, it is possible occasionally to record single unit activity with the relatively low impedance patch electrodes, as we have previously reported (Loeb

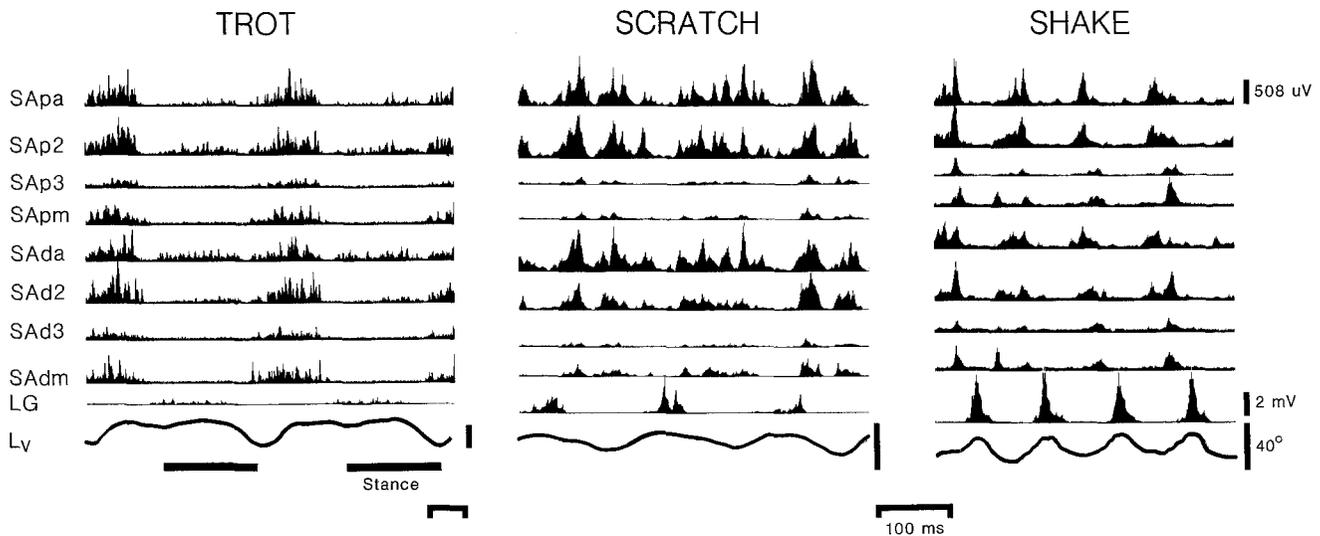


Fig. 2. Comparison of sartorius (SA) activation during three fast cyclical movements in cat CP2. Records pa-pm are from the proximal array and da-dm are from the distal EMG patch array. For reference, the EMG activity of lateral gastrocnemius (LG) is presented in the bottom trace and, during the locomotion sequence, the stance phase is indicated by the horizontal bars in the bottom

record. The last trace (L_v) is from an implanted length gauge; knee flexion (corresponding to an increased length of the gauge) is indicated by an upward deflection. The rectified and integrated sartorius EMGs are presented at the same gain across the three movements; note the lower gain for the LG records and the faster time scale for the scratch and shake records

et al. 1987a). In the recording presented in Fig. 1B, electrodes SAp2 and SAd2 were approximately 2.5 to 3.0 cm apart. Since SA muscle fibers are usually 1.0–3.0 cm long and apparently interdigitated (Loeb et al. 1987b), it is likely that the proximal and distal electrodes recorded the activity of different muscle fibers within the same motor unit. Thus, the patterns of natural activation of SA observed in this study confirm previous anatomical studies (Pratt et al. 1986; Loeb et al. 1987b) indicating that the SA muscle is organized into functionally homogeneous longitudinal columns.

Activity during scratching and paw shaking

Different patterns of activation than those seen during locomotion occurred in SA when the limb was involved in scratching the ear or shaking the paw. EMGs recorded in the same cat as shown in Fig. 1A (four electrodes in a proximal patch, SAp2–SAp4, and four in a distal patch, SAd2–SAd4) during three rapid, cyclical movements are shown in Fig. 2. There are several important observations to note from these records: 1) A single activation pattern was always observed within SAA and SAM. 2) The time course and pattern of EMGs recorded at the proximal electrode sites were virtually identical to those recorded at the corresponding distal sites, again indicating no segregation of function along the longitudinal axis of the muscle. 3) Differential activation of SAA and SAM was movement-specific. 4) The movement-specific differential activation of SAA and SAM includes both differences in the phasing (trot) and amplitude (scratch and paw shake) of their recruitment. The general pattern of activity in each region of the muscle for each behavior was consistent for all animals and all trials.

During trotting, the main difference between SAA and SAM was the presence or absence, respectively, of stance phase activity. In contrast, during both ear scratching and paw shaking, SAA and SAM were active synchronously, but differences in the relative amplitudes of the EMGs were often seen in the two regions of the muscle. During scratching, the difference in amplitude could be slight to large, but, when present, the difference was always in the direction of a smaller SAM EMG compared to SAA (example in Fig. 2). The differences between SAA and SAM activations were more complex during paw shaking, varying from cycle to cycle (see below), but a consistent pattern was always found across sequences and days within a cat.

There was more variability in the details of the bursts during scratching and paw shaking from cycle to cycle and across cats than was true of the locomotor activation patterns. An example of this variability can be seen in the EMGs recorded during the scratch and shake in Fig. 2. Two full scratch cycles and part of a third are presented in the middle panel of the figure. In the first and third cycles, there was a pause in the SAA and SAM EMG when the knee was approaching peak extension (see length gauge trace, L_v). This pause was not seen during the middle cycle where the EMG appears segmented (multiple peaks) but was essentially continuous throughout the burst. Typically the EMGs in SAA and SAM were not smoothly modulated during scratching in most cats. Differences in the level of activation in SAA and SAM during scratching were also variable across cats. The pattern shown in Fig. 2 was seen most often, but smaller differences and even equal magnitudes of activity in SAA and SAM were observed in some cats (see also Loeb et al. 1985b).

Variability in the intraburst details of the EMG in

both SAa and SAM is also evident in the paw shake records presented in Fig. 2. In the first two paw shake cycles, SAa EMG peaked at the end of the burst, whereas in the third cycle SAa activity was maximal early in the burst. The level of activation in SAM during paw shaking was, in general, lower than in SAa, but there were also cycle to cycle variations in the details of the SAM bursts that were not coupled to the variations seen in SAa. For instance, note that in both the first and third shake cycles shown in Fig. 2, SAM EMG peaked at the end of the burst. Maximal activity in SAa and SAM was thus in phase in the first shake cycle but out of phase in the third cycle. In contrast to locomotion, there were no consistent patterns across cycles or cats in the correlation between the peaks in the SA EMGs and deflections of the length gauge during scratching and shaking.

Relationship of sartorius EMG to kinematics

Analysis of the kinematics associated with each movement provides some insight into why different strategies of neural control might be required in SA in certain movements. There are significant differences in the postures, limb kinematics, and cycle times associated with the three movements, as shown in Fig. 3A. The cycle durations for ear scratching (150–180 ms) and the paw shake (80–100 ms) were much faster than those for even the fastest treadmill locomotion (trot, 380–400 ms); there was not sufficient length to our treadmill to induce cats to gallop with any consistency. For ear scratching, cats reached forward with their ipsilateral hindlimb while they either sat or stood on the stationary treadmill belt. These scratch postures correspond to the postures described in Carlson Khuta and Smith (1990) in their Figs. 1B and C, respectively. For paw shaking, the left hindpaw was extended backwards during the swing phase of the step cycle in order to produce 5–7 shake cycles. The kinematic analyses presented in Fig. 3A were obtained in a cat (M10) that had a minimum of hindlimb abduction during paw shakes and assumed a standing posture during ear scratching. Video stills were inspected to select for kinematic analysis scratch cycles in which the hindpaw made contact with the head/ear. We could not determine directly the strength of the paw contact, which may provide proprioceptive feedback that determines the duration of extensor activity within each scratch cycle (Carlson Khuta and Smith 1990). However, in these studies, ankle extensor (LG) activity occupied 30% (Fig. 2) to 45% of the scratch cycle across cats during cycles in which paw contact was made. According to data presented by Carlson Khuta and Smith (1990), these extensor burst durations are probably associated with light-to-firm paw contact, respectively. The kinematic analyses presented in Fig. 3A are typical of those observed in two other cats performing similar movements, although the hip and knee were kept in a slightly more flexed position during paw shaking in this cat than was usually seen.

Joint angle changes occurring in the hip and knee joints during representative cycles for each of the three

movements are shown in Fig. 3A; each cycle is defined as starting with hip extension in these plots. It can be seen that the joint angle excursions for both joints are greater during the trot than during scratching or paw shaking, but the velocities (not shown) are more similar. Smith and colleagues have reported similar ranges of joint angle excursions in their studies of ear scratching (Carlson Kuhta and Smith 1990) and pawshaking (Carter and Smith 1986) with the exception of the more flexed position of the knee in cat M10 during paw shaking (Fig. 2A). Another significant difference involves the phasing of hip and knee actions; the hip and knee move in phase with one another during the trot and scratch but are out of phase with one another during the paw shake. The knee leads the hip in transition from extension to flexion in the scratch (see also Carlson Kuhta and Smith 1990) and paw shake (see also Carter and Smith 1986). Data on the joint angle changes at the ankle are not presented in Fig. 3A because, in this study, we were interested primarily in the actions of the joints spanned by the SA; the ankle moved in phase with the hip and knee during the trot and scratch and out of phase with the knee during the paw shake. This coupling among the joints during paw shaking is typical in normal, standing cats (Carter and Smith 1986). In contrast, in chronic spinal cats held pendant during paw shaking, the hip and knee move in phase and both joints are out of phase with the ankle (Hoy et al. 1985; Smith et al. 1985).

The approximate relationships of SAa and SAM activation to displacements of the hip and knee joints during all three movements are indicated schematically in Fig. 3A. The periods of SAa and SAM activity are superimposed (solid symbols in each curve) on the joint angle curves for the knee and hip, respectively. The activation periods were averaged over 5 cycles of each movement in the cat whose records are shown in Figs. 1 and 2. The EMGs were averaged over normalized cycles and were synchronized with the knee joint angle changes on the basis of the length gauge records. During the trot, SAa was first active during stance when the hip and knee were extending and then, simultaneously with SAM, during hip and knee flexion. In contrast to locomotion, both SAa and SAM were electrically active prior to maximal hip *extension* during scratching and paw shaking. Given typical delays for mechanical rise-time and fall-time (50–100 ms), their maximal active force would be expected to occur near the peak of muscle length in both regions. There was biphasic motion at the knee during SA activity during both scratching and paw shaking; the knee first extended and then flexed during scratching with the opposite sequence occurring during paw shaking. Thus, the primary activity in SAa and SAM occurred in phase with their combined flexor action at the hip. Iliopsoas, another hip flexor, also is active to decelerate hip extension during scratching (Carlson Khuta and Smith 1990) and paw shaking (Smith et al. 1985).

Further insight into understanding the movement specific strategies used by the nervous system to control the SA muscle can be gained by relating the activation of SAa and SAM to the kinematic conditions under which each region of the muscle operates during each move-

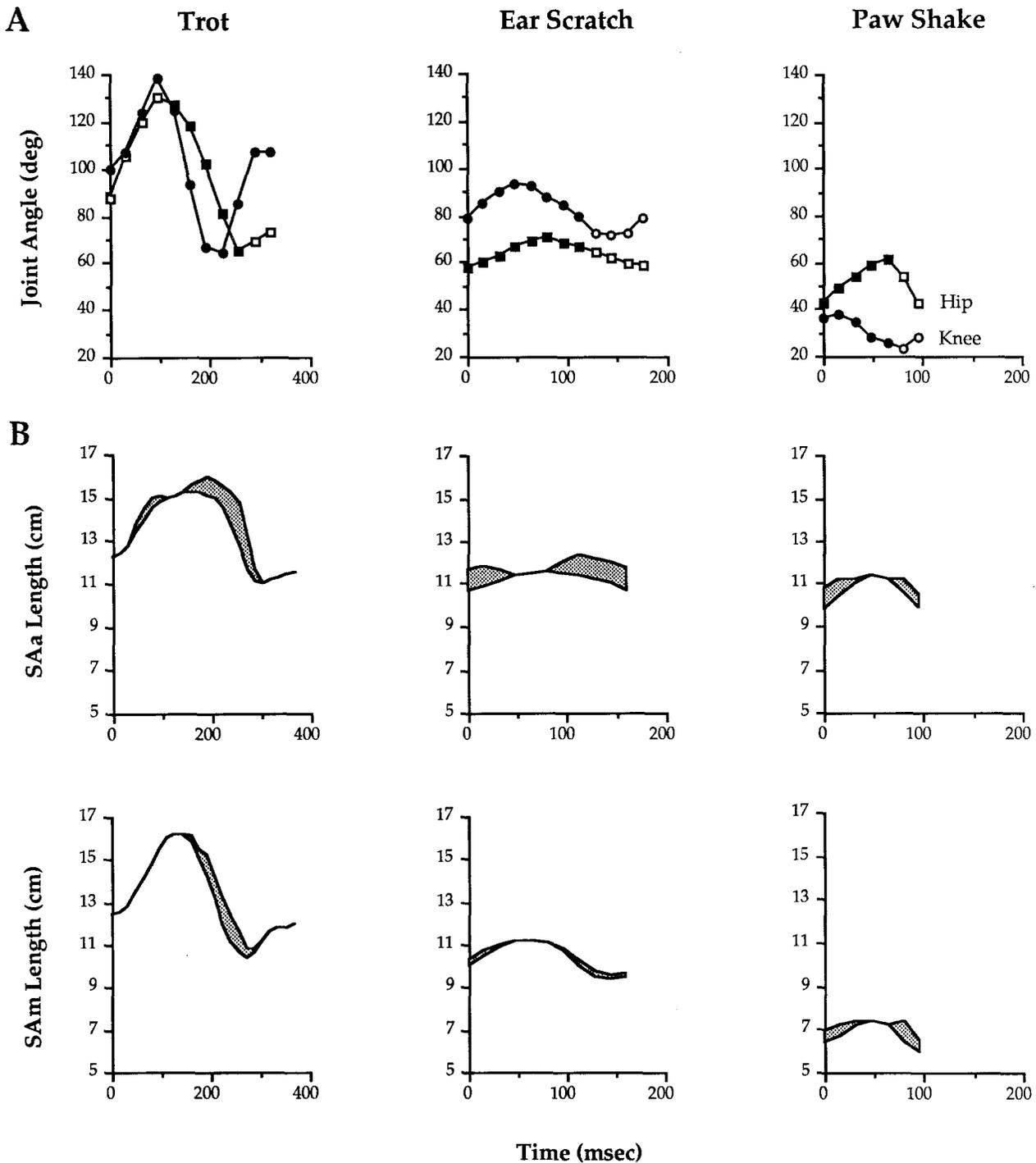


Fig. 3. A Joint angle changes in the hip and knee during three cyclic movements. Data were recorded in cat M10 and digitized from video stills. For each movement, displacements are plotted from the onset of hip extension. The approximate time of SAa and SAM activation are indicated by the solid symbols on the knee and hip joint angle curves, respectively. Muscle activations are normalized averages from cat CP2 that were synchronized with joint displacements on the basis of length gauge records. Note different time scale for scratch and shake plots. B Length changes in SAa and SAM

during three cyclic movements. Muscle lengths were calculated with a mathematical model on the basis of muscle morphometric and joint displacement data (see text for details). The shaded area superimposed on each muscle length curve indicates representative SAa and SAM EMG recorded in cat CP2 and processed as in A. The EMGs were recorded at the same gain across all three movements; the maximum amplitude of sartorius EMG recorded during these movements was about 1 mV (see Fig. 2)

ment. Both the magnitude and phasing of motion at the hip and knee joints will affect the resultant length changes in SAa and SAM. Because the moment arms for both SAa and SAM are greater at the hip than the knee, displacement of the hip will have a relatively greater

effect on SA muscle length than action at the knee. The consequence of the phasing of hip and knee joint displacement on SAa and SAM is described in Table 1. The fact that SAa has an opposite action at the hip and knee means that the length changes induced in SAa by dis-

Table 1. Effect of hip and knee joint angle change on SAa and SAM length

	SAa	SAM
Hip-Ext.	+	+
Hip-Flex.	-	-
Knee-Ext.	-	+
Knee-Flex.	+	-

Increase in length (+); decrease in length (-)

placement of the hip and knee joints are offset when they are in phase and sum when they move out of phase; the opposite holds true for the SAM.

Based on the trigonometric relations of SAa and SAM skeletal attachments at the hip and knee joints and other data (see Methods), a mathematical model (Levine 1986) was used to translate the joint angle displacements shown in Fig. 3A into SAa and SAM muscle length changes. One representative cycle, referenced to the onset of lengthening in SAa, for the trot, ear scratch, and paw shake are presented in Fig. 3B. Normalized averages of SAa and SAM activation (see above) during each movement have been superimposed on the muscle length curves. Several interesting observations can be gleaned from Fig. 3B. 1) It is obvious that the length changes in SAa and SAM were much larger during the trot than in the other two movements. 2) The relationship between muscle activation and muscle length change was similar in both SAa and SAM during the scratch and paw shake. During both movements, SAa and SAM activity was balanced over periods of active lengthening and active shortening; neither muscle region was active when it was at its longest length. The length changes in both regions of the muscle were very modest, however, during both movements. 3) The active lengthening contraction that occurred during the trot in SAa but not in SAM when the hip and knee were extending remains the distinctive asymmetry between these two parts of SA observed over these three cyclical movements.

Cutaneous reflex responses in sartorius during locomotion

The electrically evoked cutaneous reflex response patterns were different for the two cutaneous nerves (sural or saphenous), but each response pattern was qualitatively similar across the width of SA. In addition, no differences were seen in the responses at equivalent electrode positions between the proximal and distal EMG patch arrays; therefore, only the data from the proximal patch is presented in Fig. 4. At the slow walking speeds needed to sample reflex responses for at least a two min. test period (see Methods), there was little stance phase EMG activity in SAa. Thus, the prestimulus (C) EMGs presented in the reflex rasters in Fig. 4 for the four regions of SA look fairly similar, particularly after scaling the amplitudes to accommodate the large flexor reflex bursts recorded in all parts of the muscle.

Sural stimulation evoked a double peaked excitatory response throughout the SA that was very similar to that recorded in distal hindlimb flexor muscles (Abraham et al. 1985). The latency of the first excitatory burst (P1 response, see Duysens and Loeb 1980) was about 6–8 ms, and the second burst (P2) occurred about 18–20 ms after the stimulus. Typically, the cutaneous reflex response was highly gated during the step cycle, occurring during late E3 and the swing phase. The amplitude of the later P2 response was consistently larger than that of the first burst in both SAa and SAM. Similar results were obtained in all three cats implanted with sural stimulating electrodes.

The reflex effects evoked in SA by Saph nerve stimulation were very consistent in the nine animals tested here (see also Loeb et al. 1987a). Typical results are presented in Fig. 4. Again, the reflex responses recorded were similar in SAa and SAM. Reflex responses evoked by Saph stimulation differed from sural reflexes in two respects: 1) The P1 excitatory burst was present during most of the step cycle, including the stance phase, even though it was smaller in amplitude than the P1 burst resulting from sural stimulation during the swing phase. 2) The P2 excitatory burst was attenuated or even absent, being replaced by an inhibition of any background activity. Interestingly, these complex, stimulus-dependent reflex patterns were expressed similarly in all regions of SA despite their different patterns of recruitment by the locomotor CPG that was responsible for the ongoing motor behavior on which they were superimposed. However, see companion paper by Pratt et al. (1991) for examples of compartment-specific reflexes in other thigh muscles following similar stimuli.

Discussion

Functional subdivisions of sartorius

Based on gross anatomy, the SA muscle can be divided transversely into anterior and medial parts depending on whether the insertion is on the patellar tendon (SAa) or the proximal tibia (SAM). Histological (Pratt et al. 1986) and electrophysiological mapping studies (Loeb et al. 1987b) have shown, however, that the SA can be further subdivided into multiple longitudinal columns of muscle units, each innervated by a longitudinally running nerve branch, arranged in parallel across the width of the muscle. The present study has shown that the functional subdivisions of SA, when present, are determined by the muscle's gross rather than micro anatomy. Only two activation patterns, one in SAa and one in SAM, were observed in SA in all of the movements analyzed. Recordings from distributed arrays of EMG electrodes showed that there was a discrete functional border between these activation patterns (Figs. 1 and 2). This border roughly corresponds to the division of the SA muscle into regions having knee flexor vs. knee extensor action.

The uniformity in activation patterns observed along longitudinal strips of the SA is particularly interesting in

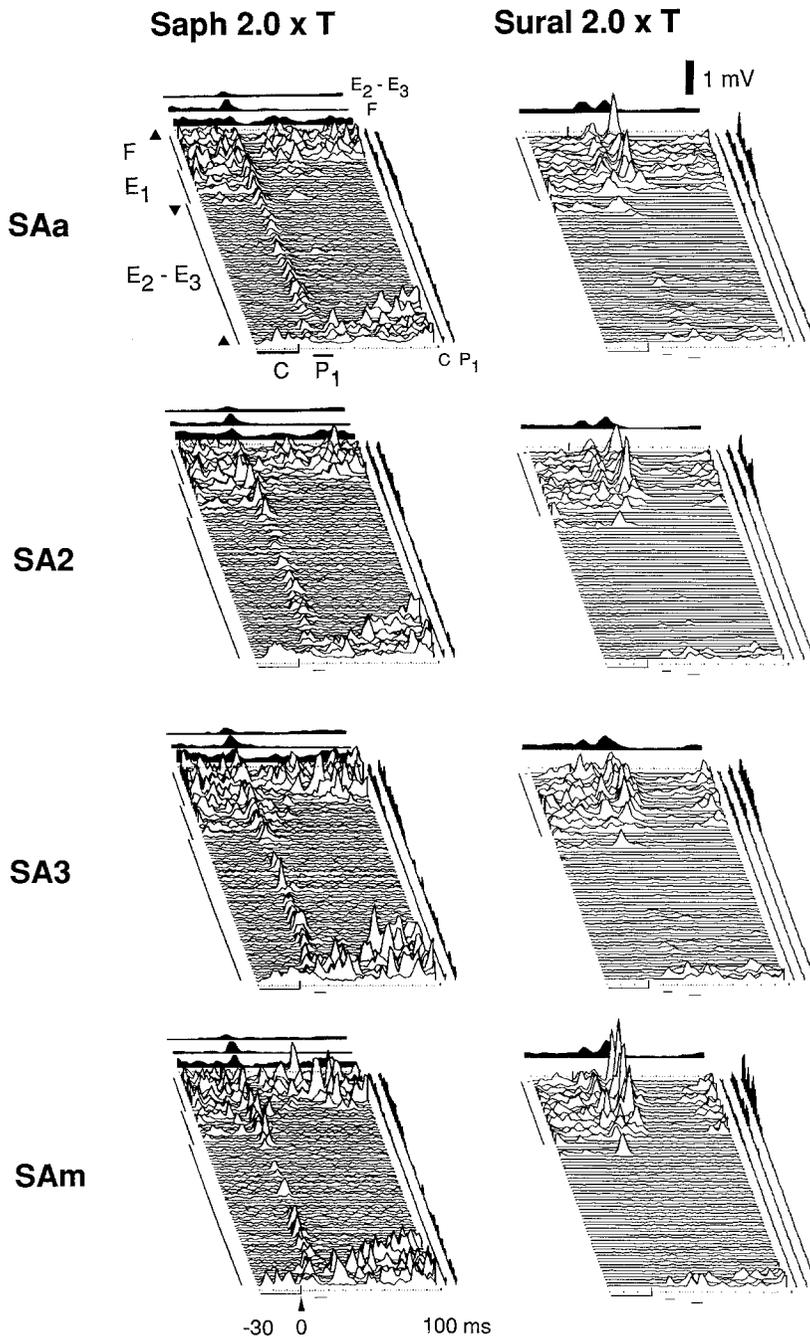


Fig. 4. Peristimulus rasters of reflex responses recorded across the width of sartorius to stimulation of the saphenous (Saph) and sural cutaneous nerves during treadmill locomotion. A total of about 60–80 responses are included in each raster. Each trace presents a total of 130 ms of EMG; 30 ms of normal locomotor activity (control, C) is shown to the left, and 100 ms of post-stimulus EMG is shown to the right of the stimulus (vertical mark at time = 0). The traces in each raster are ordered relative to the phase of the step cycle in which the stimulus occurred; the top of the raster starts with footlift (upward triangle). The summary histograms presented at the top of each raster show responses averaged over selected step cycle epochs marked by the solid lines along the lefthand border of the raster (see top left raster for relationship between summary traces and markers of selected epochs). See Methods for a more detailed description of raster format. Note that the reflex responses for the two cutaneous nerves were quite different, but that they were similar in all four regions of sartorius

view of the fact that it has recently been shown (Loeb et al. 1987b) that the individual muscle fibers in SA are much shorter than the muscle length (8–12 cm), averaging only 2.5 cm (range = 1.0 to 3.0 cm). Mechanical stability within a motor unit is preserved, however, since motor axons branch repetitively to innervate muscle fibers distributed from origin to insertion (Pratt et al. 1986; Loeb et al. 1987b). Our present results confirm that during natural activation the SA is functionally organized into longitudinal columns. This architectural design appears to be an optimal solution to the mechanical instability that would result from slow conduction in long muscle fibers (see Loeb et al. 1987b for further discussion) without sacrificing the length conservation

benefits associated with long muscle fibers (Loeb and Gans 1986). However, it should be noted that we have not recorded EMGs from the less accessible portions of SAa lying proximal to the nerve entry zone, whose pattern of innervation remains unclear (Thomson et al. 1990).

These results suggest that SAa and SAm constitute two basic, functional modules that can be recruited in various combinations in different movements. However, in a previous study of individual motoneuron recruitment during locomotion in SA, there was evidence of three functional task groups (Hoffer et al. 1987c) based on the correlation between motor unit firing rates and the envelope of gross EMG activity in SAa and SAm during

the two phases of locomotor activity. Specifically, individual SAa motor units were active during either the stance or swing phase of locomotion, but not both (except when reflexively recruited by cutaneous nerve stimulation; Loeb et al. 1987a), indicating that SAa motoneurons were functionally subdivided into two separate task groups. Furthermore, the SAa units that were active during the swing phase had subtle but consistent differences in the modulation of that activity from those recruited in SAM during the swing phase, suggesting that these two groups could not be collapsed into one functional entity. The present data further support the notion that, at least in some muscles, the functional units of organization may be based on the kinematics of muscle action rather than on visible structural boundaries (Loeb 1985).

Is recruitment determined by segmental reflexes or by central pattern generators?

Differences in the fine detail in SAa vs. SAM EMGs, as well as cycle-to-cycle variations, may be due to movement-dependent proprioceptive inputs to SA motoneurons. It has been shown that Ia inputs from knee flexors and knee extensors are preferentially distributed to SAM and SAa motoneurons, respectively (Eccles and Lundberg 1958). Thus, moment-to-moment changes in knee position could dynamically shift the relative magnitude of Ia excitation of SAa and SAM motoneurons. Both homonymous and heteronymous Ia drive would be affected and not necessarily in the same way. The homonymous Ia input from SA is a function of muscle length (and fusimotor control) which, in turn, is determined by the combined motions at the hip and knee joints (see Table 1). During the E1 portion of the swing phase, knee extension is coupled with hip flexion. The out-of-phase motions at the two joints will tend to conserve SAM muscle length. Conversely, muscles such as gracilis, a hip extensor and knee flexor, will be stretched by the actions at both joints. Thus, SAM motoneurons would receive significant heteronymous Ia excitation from the knee flexors despite a relatively modest homonymous Ia drive. Similarly, during the flexion portion of the swing phase, there could be a differential heteronymous Ia excitation of SAa but not SAM motoneurons from the stretched uniaxial knee extensors. These effects could be important in all of the movements analyzed in this study since we have shown previously that there is a high level of fusimotor support during fast cyclical movements, especially scratching and paw shaking (Loeb et al. 1985b). Smith and colleagues (Hoy et al. 1985; Smith et al. 1985; Smith and Zernicke 1987) have also presented evidence indicating that proprioceptive inputs are particularly important in the recruitment of muscles acting at the knee during fast, cyclical movements.

The selective recruitment of SAa and SAM during the various phases of locomotion seems more clearly to require at least some specific commands from the CPG. During mid- to late-stance, when SAa is active, but SAM is not, the knee is extending, which shortens knee extensor spindles that project to SAa and stretches the knee

flexor spindles that project to SAM. The large moment arm and large angular excursion (extension) at the hip dominate the effects related to knee joint angle changes, however, resulting in a net lengthening of all parts of SA. Thus, homonymous Ia excitation might be responsible for the stance phase recruitment of the stretched SAa, but the absence of recruitment in SAM, which is actually stretched to a greater length than SAa (Fig. 3B), would then require a selective inhibition (or withdrawal of excitation), presumably from the CPG, as has been reported during fictive locomotion in decorticate, paralyzed cats (Perret and Cabelguen 1980). Stretch of SA, especially SAM, at the end of stance could help to initiate its flexion phase activity, but this EMG is sustained during the rapid shortening of the muscle. Interestingly, spindle primary afferents from SA also exhibit sustained activity during the swing phase. However, this spindle activity can be abolished by blocking fusimotor axons with low doses of lidocaine without affecting the swing phase EMG (Loeb et al. 1985b), suggesting that at least some alpha and gamma motoneurons projecting to SA receive direct drive from the locomotor CPG during the swing phase.

What are the mechanical consequences of the recruitment patterns?

The selective recruitment of SAa and SAM during different phases of different motor behaviors should be related to the mechanical actions on the skeleton that are required to perform those behaviors, whether the recruitment patterns result directly from excitatory inputs from the CPG or indirectly from segmental reflexes that have not been blocked by the CPG.

During rapid oscillatory movements, such as shaking and scratching, it is efficient to use muscles as springs coupled to the inertial masses of the limb segments. A muscle used in such a manner should produce maximal active force during the transition from maximal rate of stretching to maximal rate of shortening. When the EMG activities of SAa and SAM are superimposed on the calculated muscle lengths for shaking and scratching and allowances are made for electromechanical coupling delays in the muscle fibers, such a pattern emerges (Fig. 3B). The simultaneous recruitment of SAa and SAM may be related to their common action to slow and reverse hip motion (extension) during rapid oscillations, as suggested by Smith et al. (1985).

During slower locomotor movements in which momentum and power are passed gradually from one limb to the other and from one skeletal segment to another, biarticular muscles can perform a special function (Van Ingen Schenau 1989). If the two joints crossed by the muscle move such that the motion at one joint tends to stretch the muscle while the motion at the other joint tends to shorten the muscle, tension in the muscle provides a highly efficient mechanism for transmitting excess kinetic energy from one segment to another without having to dissipate it as heat (through active lengthening). At the end of stance, SAa is being stretched by hip extension and shortened by knee extension. Its

force output (together with the simultaneously active, synergistic rectus femoris) would tend to decelerate hip extension prior to footlift while providing a final extensor thrust at the knee. This push-off thrust would be difficult to generate in the monoarticular knee extensors; the vasti muscles are highly pinnate and their muscle fibers would be operating at highly suboptimal length and shortening velocity. Activation of the biarticular SAM would be mechanically inappropriate at the end of stance since this muscle region would act to flex rather than extend the knee.

Muscle synergies

The muscles of the cat hindlimb and their functional subdivisions exhibit shifting patterns of synergy, depending on the nature of the ongoing motor behavior. The reorganization of inter- and intramuscular synergies associated with the three movements analyzed in this study is illustrated in Fig. 5. The activity periods of SA, the biarticular ankle extensor, LG, and the uniarticular VL, recorded during trotting, ear scratching, and paw shaking, are shown schematically in normalized form in Fig. 5. For each movement, the onset of LG activity represents the beginning of the normalized cycle. During trotting, the ankle and knee extensors, including SAa, are active in phase. However, during the swing phase of trotting and for scratching and paw shaking, both parts of SA work together as hip flexors. As reported by Smith et al. (1985), the kinetics of paw shaking require an unusual uncoupling of ankle and knee extensors (LG and VL, respectively, in Fig. 5). This results in yet another pattern of synergy in which both parts of SA work together with VL, a pattern never seen during locomotor or reflexive recruitment.

Sherrington (1910) classified the various muscles, including some of their anatomically obvious compartments, into groups of extensors and flexors on the basis of the response of decerebrate cats to noxious cutaneous stimuli. However, he and many subsequent researchers (e.g., Bernstein 1967) have commented on the mechanical complexity of multiarticular limbs and muscles and the likelihood that natural patterns of recruitment and reflexes during such recruitment would depend on limb dynamics rather than such invariant synergistic groups. The flexible, movement-specific inter- and intramuscular synergies observed in SA and other thigh muscles (Pratt et al. 1991, paper IV in this series) most likely result from a complex interplay between CPG circuits and afferents providing movement-dependent feedback. Identification of the afferents mediating this information and the mechanisms involved in dynamically remodeling basic CPG outputs to produce the detail and finesse of muscle recruitment exhibited by the functioning limb remains a major challenge to motor physiologists.

The present study indicates that the nervous system distributes different species of inputs selectively to the SA motor nucleus, presumably to match the mechanical effects of different regions to the mechanical requirements of the movement. Some, but not all, CPG and Ia (Eccles and Lundberg 1958) inputs are apparently dif-

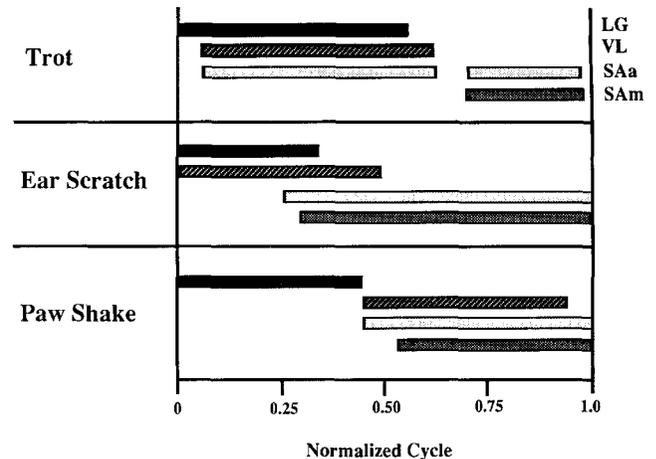


Fig. 5. Summary of intermuscular synergies of anterior (SAa) and medial (SAM) sartorius, vastus lateralis (VL), and lateral gastrocnemius (LG) activation during three fast, cyclical movements from cat CP2. The bar diagrams indicate the activity periods for each muscle averaged over 5–10 cycles and presented in normalized form. For each movement, the onset of activity in LG defines the beginning of the cycle

ferentially distributed to SAa and SAM motoneurons, whereas inputs from all cutaneous afferents appear to be similarly distributed to all SA motoneurons. The question of how neural inputs come to develop selective connections to SA motoneurons remains intriguing given the fact that there is extensive overlap in the central locations of SAa and SAM motoneurons (Pratt et al. 1984; Gordon et al. 1991). The fact that the functional organization of SA motoneurons depends on the particular species (or combination) of premotoneuronal inputs that are activated cautions against functionally classifying mechanically heterogeneous muscles on the basis of any single input system or movement.

Acknowledgements. The technical assistance of Michele Manley and the thoughtful comments on previous versions of this manuscript by Drs. Robert Burke and Jane Macpherson are gratefully acknowledged.

References

- Abraham LD, Loeb GE (1985) The distal musculature of the cat: patterns of normal use. *Exp Brain Res* 58: 580–593
- Abraham LD, Marks WM, Loeb GE (1985) The distal hindlimb musculature of the cat: cutaneous reflexes during locomotion. *Exp Brain Res* 58: 594–603
- Andersson O, Forssberg H, Grillner S, Lindquist M (1978) Phasic gain control of the transmission in cutaneous reflex pathways to motoneurons during “fictive” locomotion. *Brain Res* 149: 503–507
- Bak MJ, Loeb GE (1979) A pulsed integrator for EMG analysis. *Electroencephalogr. Clin Neurophysiol* 47: 738–741
- Bernstein N (1967) *The coordination and regulation of movement*. Pergamon, New York
- Bodine S, Roy RR, Meadows DA, Zernicke RF, Sacks RD, Fournier M, Edgerton R (1982) Architectural, histochemical, and contractile characteristics of a unique biarticular muscle: the cat semitendinosus. *J Neurophysiol* 48: 192–201
- Burke RE (1990) Selective recruitment of motor units. In: Humphrey DR, Freund H-J (eds) *What are the output units of motor behavior and how are they controlled?* Dahlem Konferenzen. John Wiley & Sons, LTD, Chichester (in press)

- Carlson Kuhta P, Smith JL (1990) Scratch responses in normal cats: hindlimb kinematics and muscle synergies. *J Neurophysiol* 64:1653–1667
- Carter MC, Smith JL (1986) Simultaneous control of two rhythmic behaviors. I. Locomotion with paw-shake response in normal cat. *J Neurophysiol* 56:171–183
- Chanaud CM, Macpherson JA (1991) Functionally complex muscles of the cat hindlimb. III. Differential activation within biceps femoris during postural perturbations. *Exp Brain Res* 85:271–280
- Chanaud CM, Pratt CA, Loeb GE (1991a) Functionally complex muscles of the cat hindlimb. II. Mechanical and architectural heterogeneity within the biceps femoris. *Exp Brain Res* 85:257–270
- Chanaud CM, Pratt CA, Loeb GE (1991b) Functionally complex muscles of the cat hindlimb. V. The roles of histochemical fiber-type regionalization and mechanical heterogeneity in differential muscle activation. *Exp Brain Res* 85:300–313
- Desmedt JE, Godaux E (1981) Spinal motoneuron recruitment in man: rank deordering with direction but not with speed of voluntary movement. *Science* 214:933–936
- Duysens J, Loeb GE (1980) Modulation of ipsi- and contralateral reflex responses in unrestrained walking cats. *J Neurophysiol* 44:1024–1037
- Eccles RM, Lundberg A (1958) Integrative pattern of Ia synaptic action on motoneurons of hip and knee muscles. *J Physiol (Lond)* 144:271–298
- Engberg I, Lundberg A (1969) An electromyographic analysis of muscular activity in the hindlimb of the cat during unrestrained locomotion. *Acta Physiol Scand* 75:614–630
- English AW, Letbetter WD (1982) Anatomy and innervation patterns of cat lateral gastrocnemius and plantaris muscles. *Am J Anat* 164:67–77
- English AW, Weeks O (1984) Compartmentalization of single muscle units in cat lateral gastrocnemius. *Exp Brain Res* 56:361–368
- English AW, Weeks O (1987) An anatomical and functional analysis of cat biceps femoris and semitendinosus muscles. *J Morph* 191:161–175
- Forssberg H (1979) Stumbling corrective reaction: a phase-dependent compensatory reaction during locomotion. *J Neurophysiol* 42:936–953
- Gordon DC, Loeb GE, Richmond FJR (1991) Distribution of motoneurons supplying cat sartorius and tensor fasciae latae, demonstrated by retrograde multiple-labelling methods. *J Comp Neurol* 304:357–372
- Henneman E, Mendell LM (1981) Functional organization of the motoneuron pool and its inputs. In: Brooks VB (ed) *Handbook of physiology, Sect. I. The nervous system. Vol II, Part 1. American Physiological Society, Washington DC* pp:423–507
- Hoffer JA, Loeb GE, O'Donovan MJ, Pratt CA (1980) Unitary activity patterns during walking confirm the existence of two functionally distinct classes of sartorius motoneurons in cats. *J Physiol (Lond)* 308:20P
- Hoffer JA, O'Donovan MJ, Pratt CA, Loeb GE (1981) Discharge patterns of hindlimb motoneurons during normal cat locomotion. *Science* 216:466–468
- Hoffer JA, Loeb GE, Marks WM, O'Donovan M, Pratt CA, Sugano N (1987a) Cat hindlimb motoneurons during locomotion. I. Destination, axonal conduction velocity and recruitment threshold. *J Neurophysiol* 57:510–529
- Hoffer JA, Sugano N, Loeb GE, Marks WM, O'Donovan MJ, Pratt CA (1987b) Cat hindlimb motoneurons during locomotion, II. Normal activity patterns. *J Neurophysiol* 57:530–553
- Hoffer JA, Sugano N, Loeb GE, Marks WM, O'Donovan MJ, Pratt CA (1987c) Cat hindlimb motoneurons during locomotion. III. Functional segregation in sartorius. *J Neurophysiol* 57:554–562
- Hoy MG, Zernicke RF, Smith JL (1985) Contrasting roles of inertial and muscle moments at knee and ankle during paw-shake response. *J Neurophysiol* 54:1282–1294
- Levine WS (1986) Kinesiological modeling of the cat hindlimb musculature during locomotion. Final Report, NIH Contract #NO1-NS-3-2348, Univ. of Maryland, College park, MD 20734
- Loeb GE (1985) Motoneuron task groups: coping with kinematic heterogeneity. *J Exp Biol* 115:137–146
- Loeb GE (1990) The functional organization of muscles, motor units, and tasks. In: Binder MD, Mendell LM (eds) *The segmental motor system. Oxford Univ Press, New York*, pp 23–35
- Loeb GE and Gans C (1986) *Electromyography for experimentalists. The University of Chicago Press, Chicago*, pp 66–67
- Loeb GE, Hoffer JA, Pratt CA (1985a) Activity of spindle afferents from cat anterior thigh muscles. I. Identification and patterns during normal locomotion. *J Neurophysiol* 54:549–564
- Loeb GE, Hoffer JA, Marks WM (1985b) Activity of spindle afferents from cat anterior thigh muscles. III. Effects of external stimuli. *J Neurophysiol* 54:578–591
- Loeb GE, Marks WB, Hoffer JA (1987a) Cat hindlimb motoneurons during locomotion. IV. Participation in cutaneous reflexes. *J Neurophysiol* 57:563–573
- Loeb GE, Pratt CA, Chanaud CM, Richmond FJR (1987b) Distribution and innervation of short, interdigitated muscle fibers in parallel-fibered muscles of the cat hindlimb. *J Morph* 191:1–15
- Loeb GE, Pratt CA, Marks WM (1984) Segregation of normal and reflex activity in the cat sartorius muscle. *Soc Neurosci Abstr* 10:629
- Perret C, Cabelguen J-M (1980) Main characteristics of the hindlimb locomotor cycle in the decorticate cat with special reference to bifunctional muscles. *Brain Res* 187:333–352
- Phillipson M (1905) *L'autonomie et la centralisation dans le système nerveux des animaux. Trav Lab Physiol Inst Solvay, Bruxelles* 7:1–208
- Pratt CA, Yee WJ, Chanaud CM, Loeb GE (1984) Organization of the cat sartorius motoneuron pool. *Soc Neurosci Abstr* 10:629
- Pratt CA, Chanaud CM, Loeb GE (1986) Single motor unit territories in the cat sartorius. *Soc Neurosci Abstr* 12:1083
- Pratt CA, Chanaud CM, Loeb GE (1991) Functionally complex muscles of the cat hindlimb. IV. Intramuscular distribution of movement command signals and cutaneous reflexes in broad, bifunctional thigh muscles. *Exp Brain Res* 85:281–299
- Romanes GJ (1953) The motor cell columns of the lumbo-sacral spinal cord of the cat. *J Comp Neurol* 94:313–363
- Sherrington CS (1910) Flexion-reflex of the limb, crossed extension reflex, and reflex stepping and standing. *J Physiol* 40:28–121
- Smith JL, Betts B, Edgerton VR, Zernicke RF (1980) Rapid ankle extension during paw shakes: selective recruitment of fast ankle extensors. *J Neurophysiol* 43:612–620
- Smith JL, Hoy MG, Koshland GF, Phillips DM, Zernicke RF (1985) Intralimb coordination of the paw-shake response: a novel mixed synergy. *J Neurophysiol* 54:1271–1281
- Smith JL, Zernicke RF (1987) Predictions for neural control based on limb dynamics. *TINS* 10:123–128
- Ter Haar Romeny, Denier van der Gon BM, Gielen CC (1984) Relation between location of a motor unit in the human biceps brachii and its critical firing level for different tasks. *Exp Neurol* 85:631–650
- Thomson DB, Scott SH, Richmond FJR, Loeb GE (1990) Complex motor unit architecture of anterior sartorius muscle in the cat. *Abstr First World Congress of Biomechanics*
- Van Ingen Schenau GJ (1989) From rotation to translation: constraints on multi-joint movements and the unique action of bi-articular muscles. *Human Movem Sci* 8:301–337
- Windhorst U, Hamm TM, Stuart DG (1989) On the function of muscle and reflex partitioning. *Behav Brain Sci* 12:629–681
- Windhorst UR, Burke RE, Dieringer N, Evinger C, Feldman AG, Hasan Z, Hultborn HRA, Illert M, Lundberg AP, Macpherson JM, Massion J, Nichols TR, Schwarz HRM, Vilis T (1990) What are the output units of motor behavior and how are they controlled? In: Humphrey DR, Freund H-J (eds) *Motor control: concepts and issues. Dahlem Konferenzen. John Wiley & Sons Ltd, Chichester*