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Functionally complex muscles of the cat hindlimb

IV. Intramuscular distribution of movement command signals and cutaneous reflexes in broad, bifunctional thigh muscles

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Summary. Similarities between the muscle synergies associated with the flexion reflex and locomotion in reduced preparations have suggested that spinal circuits subserving these two motor tasks might share common interneurons. To test this hypothesis in functionally complex muscles, we studied the interaction between low-threshold cutaneous afferents and the locomotor central pattern generator (CPG) during treadmill locomotion in awake, intact cats. Electrical stimuli were delivered via implanted nerve cuff electrodes at all phases of locomotion, and EMGs were recorded from fourteen intramuscular subregions in eight bifunctional thigh muscles (adductor femoris, biceps femoris, caudofemoralis, gracilis, semimembranosus, semitendinosus, tensor fasciae latae, and tenuissimus). In addition, the EMG patterns recorded during locomotion were compared with those recorded during two other centrally driven rhythmical behaviors, scratching and paw shaking, to determine whether the functional relationships among these intramuscular subregions were fixed or task dependent. Four of the five broad, bifunctional muscles studied (biceps femoris, gracilis, semimembranosus, and tensor fasciae latae) had functional subunits that could be differentially activated in one or more of the three movements studied; adductor femoris was consistently uniformly activated despite its distributed skeletal attachments. The pattern of recruitment of the intramuscular functional subunits was movement-specific. The locomotor CPG and cutaneous reflex pathways both similarly subdivided some bifunctional muscles, but not others, into intramuscular subregions. The results of the present study confirm that some combinations of muscle subregions and cutaneous nerves constitute simple reciprocal categories of flexors and extensors, as described originally by Sherrington (1910). "Typical" low threshold excitatory or inhibitory reflex responses were produced in muscles or muscle subregions that were recruited as "net" flexors of extensors, respectively. However, muscles with complex activation patterns during walking often had very individualized, complex reflex responses during locomotion that did not conform to the background locomotion synergies. All of the reflex responses observed were mediated by low threshold cutaneous afferents. These data indicate that there are multiple, low threshold, excitatory and inhibitory cutaneous reflex pathways that have highly specialized connections with flexor and extensor muscles and even their intramuscular subregions. It is also clear that the premotoneuronal circuits mediating these cutaneous reflex effects are not necessarily synonymous with those of the locomotor CPG. These two systems do interact powerfully, however, suggesting some convergence. The nature of the convergence between the CPG and the many independent subsets of spinal interneurons mediating cutaneous reflexes is specialized and muscle subregion-specific.

Key words: Cutaneous reflexes – Bifunctional muscles – Differential activation – Muscle compartments – CPG – Muscle recruitment – EMG – Cat

Abbreviations: Muscles: adductor femoris – AF; biceps femoris – BF; caudofemoralis – CF; gracilis – G; semimembranosus – SM; semitendinosus – St; tensor fasciae latae – TFL; tenuissimus – TEN; *Nerves:* saphenous – Saph; superficial peroneal – Sup Per

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Introduction

The first systematic, functional classification of the muscles in the cat hindlimb by Sherrington (1910) was based on their reflex responses to cutaneous inputs. Each of the muscles in the hindlimb was classified as either a flexor or extensor depending on whether it reflexly contracted

or relaxed, respectively, in response to electrical stimulation of cutaneous nerves. The reciprocal effects on antagonists led Sherrington (1906) to conclude that the excitation of flexors and the inhibition of extensors were "part and parcel of the same reflex" and to suggest that these reflex circuits could operate as a neural substrate for the generation of movements featuring alternating activity in antagonists, such as locomotion (Sherrington 1908).

Sherrington (1910) and his contemporary, Graham-Brown (1911), also provided the initial evidence that the basic rhythms of alternating movements, such as locomotion, could be generated and controlled by the isolated feline spinal cord. What emerged from the intersection of these investigations was the theoretical concept that the central pattern generator (CPG) for locomotion consisted of two half-centers, one driving flexors and the other the extensors with reciprocal inhibition linking the two (Graham-Brown 1911). These observations, and supporting reports by later investigators (e.g. Eccles and Lundberg 1959; Jankowska et al. 1967a, b), profoundly influenced scientific thought on the organization of segmental neuromotor circuits (Lundberg 1969, 1975, 1979). The economy of design that would result from a sharing of reflex and CPG interneuronal circuitry has obvious appeal teleologically and developmentally.

The similarity between the muscle synergies associated with the flexion reflex and locomotion suggested the possibility that spinal circuits subserving these two motor tasks might share common interneurones. The observation that hindlimb joint, cutaneous and high-threshold muscle afferents evoked similar ipsilateral flexion reflex effects in interneurons and motoneurons prompted Eccles and Lundberg (1959) to functionally classify this heterogeneous population as "flexion reflex afferents" (FRAs). Lundberg and his colleagues further suggested that the spinal pathways mediating long-latency effects from FRAs could serve as the locomotor CPG (Eccles and Lundberg 1959; Holmqvist and Lundberg 1961; Jankowska et al. 1967a, b; Lundberg 1969, 1979; Lundberg et al. 1987). Alternate models of locomotor CPGs with more complex behavior have also been proposed (Grillner 1981).

Exceptions to the general rule of excitation of flexors and inhibition of extensors by cutaneous and other FRA afferents have been reported by many investigators including Sherrington (Graham-Brown and Sherrington 1912; Hagbarth 1952; Eccles and Lundberg 1959; Holmqvist and Lundberg 1961; Duysens and Stein 1978; Duysens and Loeb 1980; Abraham et al. 1985; Drew and Rossignol 1987). Excitation of extensors is the most common "atypical" response. Intracellular recordings of extensor motoneurons have shown that at least some of the excitatory responses in extensors are mediated by low threshold cutaneous afferents (Eccles and Lundberg 1959; Burke et al. 1970; Pinter et al. 1982; Omeniuk et al. 1986; LaBella et al. 1987; Fleshman et al. 1988; Schmidt et al. 1988). Inhibition of flexors is less common but has been reported (Duysens and Loeb 1980; Fleshman et al. 1984; Abraham et al. 1985; Yang and Stein 1990 (humans)). In acute spinal cats treated with L–DOPA, a preparation that exhibits spontaneous locomotor-like behavior, short latency FRA effects appear to be depressed, but there are long latency responses that appear to be closely associated with the locomotor CPG (Jankowska et al. 1967a, b). Both "typical" and "atypical" short latency cutaneous reflex responses have been observed during locomotion in intact cats (Duysens and Stein 1978; Duysens and Loeb 1980; Abraham et al. 1985; Drew and Rossignol 1987; Pratt and Loeb 1991) and in humans (Yang and Stein 1990).

Some cat hindlimb muscles have intramuscular subregions that can be differentially activated during locomotion (English 1984; English and Weeks 1987; Hoffer et al. 1981, 1987; Chanaud et al. 1991b; Pratt and Loeb 1991), indicating that CPG inputs can be heterogeneously distributed within some motor nuclei. In the present study, we have compared the distribution of reflex effects from low threshold cutaneous afferents and locomotor CPG inputs across fourteen intramuscular subregions in the cat thigh to test the hypothesis that the two systems share common interneurons. In order to determine whether the relationship between locomotor CPG and low threshold cutaneous inputs is invariant to all populations of motoneurons, we have compared the distributions of inputs from the two systems in functionally homogeneous vs. functionally complex muscles, particularly those with kinematically distinctive intramuscular subregions. We have recorded the activity at multiple sites of four broad, biarticular, bifunctional muscles (biceps femoris, gracilis, semimembranosus, and tensor fasciae latae), one broad, uniarticular (adductor femoris), and three biarticular, bifunctional muscles with relatively discrete origins and insertions (caudofemoralis, semitendinosus, and tenuissimus) in awake, intact cats during three kinematically distinct (Pratt and Loeb 1991) movements: treadmill locomotion, ear scratching, and paw shaking. Each of these motor behaviors is thought to be driven by spinal CPGs (Grillner and Zangger 1979; Deliagina et al. 1975; Sabin and Smith 1984).

The intramuscular locomotor synergies were compared with the intramuscular distribution of cutaneous reflex responses evoked during walking. In addition, the intramuscular synergies were compared across the three movements to determine whether the functional recruitment of complex muscles is primarily dictated by muscle anatomy or movement kinematics. These data provide information on the neural control of functionally complex muscles and the relationship of intramuscular specializations to the organization of central neural control circuits. Some of these results have been reported in preliminary form (Chanaud et al. 1986; Pratt et al. 1987).

Methods

Experiments were performed on five adult cats (2.0–3.3 kg) of either sex. The methods used in these experiments to produce locomotion, scratching, paw shaking, and cutaneous reflexes during locomotion were, in general, identical with those described in the Methods of the companion paper, Pratt and Loeb (1991). The following methods were specific to experiments presented in this paper.

Implanted devices

The number of devices that could be implanted in a given cat was limited by the number of solder contacts (40) on the backpack connector. Implanting all four cutaneous nerves, the femoral and sciatic nerves, and all of the muscle regions of interest (14) required a minimum of 43 leads. Thus, in all but one experiment, different combinations of nerves and muscle regions were selected for implantation. All of the devices shown in Fig. 1 were implanted in one animal, cat CP30, which enabled us to compare the effects of well-controlled electrical stimulation of the four cutaneous nerves on the same 14 muscle regions, eliminating possible variabilities associated with locations of the patch electrodes across cats. In this cat, all of the devices were implanted in one surgical procedure, but only 40 of the leads were soldered to the backpack; the extra leads were tucked under the backpack and secured. After recording the effects of each cutaneous nerve at 4–5 levels of stimulation during locomotion, the cat was anesthetized with ketamine, and the extra leads were substituted for those that had been used in stage one.

The bipolar patch electrodes used in these experiments had 3 mm long contacts with a 3 mm interelectrode spacing. The design of the patch electrodes was customized for the individual muscles based on the anatomical and functional complexity of the muscles of interest. The designs most often used are illustrated in Fig. 1A along with a schematic representation of the muscles that were implanted. Muscles with broad attachments (i.e., gracilis (GR), semimembranosus (SM), tensor fasciae latae (TFL), and biceps femoris (BF)) were fitted with distributed patch arrays consisting of 2–6 contact pairs. Intramuscular regions within these broad muscles are indicated by abbreviations a, m, and p for anterior, middle and posterior, respectively. TFLa and TFLp subregions correspond to Sherrington's (1910) longus and brevis divisions, respectively. SMa and SMp correspond to designations used previously by other investigators of femoral and tibial, respectively (Engberg and Lundberg 1969; see also Botterman et al. 1983). Single bipolar electrodes were used to record the activity of tenuissimus (TEN), caudofemoralis (CF), adductor femoris (AF), and semitendinosus (St). Previous recordings in preliminary studies from this latter group of muscles indicated that they are not functionally heterogeneous with the exception of St. There is a quantitative differentiation in the activity of the deep vs. superficial regions of St which parallels the histochemical regionalization of the muscle (Chanaud et al. 1991b). Similar quantitative differences were observed in the reflex responses recorded from the deep and superfical portions of St, but the responses were qualitatively the same. Thus, only the St reflexes recorded from patch electrodes situated over the deep portion of St, which contains all major muscle fiber types, are presented in this paper.

Because of the delicate anatomy of TEN, a bipolar electrode embedded in a silastic cuff was used that effectively shielded the TEN electrode from signals produced by the neighboring synergists, BFp and St (note differences in EMG patterns of first three traces in Fig. 2). The dielectric shielding and individualized designs of the patch electrodes effectively guarded against cross-talk as evidenced in Fig. 2 by the unique features seen in the EMGs recorded in adjacent muscles (e.g., BFa vs. CF during scratching and paw shaking; St vs. TEN during walking and paw shaking). The location of all electrodes was always confirmed by a thorough post mortem dissection.

Bipolar nerve cuffs were implanted on the Saph, sural, Sup Per and plantar cutaneous nerves for stimulation. The approximate placements of the stimulating cuffs are shown in Fig. 1B. The cuff on the Saph nerve was placed distal to the bifurcation of the muscle nerves to anterior and medial sartorius, and Sup Per was instrumented distal to the branch point of the most distal muscle nerve branches. Tripolar nerve cuffs were placed on the sciatic nerve in two cats (CP29 & CP30) and the femoral nerve in one cat (CP30). When recording nerve cuffs were implanted, stimulus intensity was expressed in multiples of the threshold (T) current at which an evoked nerve response could first be detected in either the sciatic or femoral cuff (see Fig. 10). In experiments without recording nerve cuffs, reflex threshold was defined as the current at which consistent short latency EMG reflex responses appeared in flexor muscles while the cat walked steadily on the treadmill. In the latter case, either a Nicolet 1120 averager or a storage oscilloscope was used to determine the first consistent appearance of a reflex response. Slightly larger absolute current strengths were needed to reach reflex threshold when threshold was determined by the latter method, but the relative thresholds for excitatory and inhibitory reflex responses were similar in all experiments regardless of the method for determining threshold current strengths.

Identification of activated afferents

The grouping of a multi-modal population of afferents into the common functional classification of FRAs is consistent with their primary central action in acute spinal cats (Jankowska et al. 1967a, b), but it is also likely that each species of afferents convey modality specific information through "private" spinal interneuronal circuits. Thus, we were interested in this study in whether there was evidence of any specialization in the distibution of reflex effects from different classes of cutaneous afferents. Measurements of the conduction velocity of afferents activated at different stimulus intensities were used to identify roughly the classes of constituent fibers. At the conclusion of the initial surgery, while the cat was still under the anesthetic, the threshold (T) currents needed to evoke neural volleys in the femoral and sciatic nerves by stimulation of each of the four cutaneous nerves were determined in two cats instrumented with tripolar recording cuff electrodes (see above). Neural volleys evoked at 1.0, 1.2, 1.5, 2.0, 4.0 and 8.0 × T were averaged and photographed. Conduction distances from the stimulating electrodes to the recording electrodes were determined in a post mortem dissection. The evoked potentials and conduction velocity estimates for each population of activated afferents are shown in Fig. 10 for cat CP30. Each triphasic waveform, or distortion from a smooth triphasic shape, was assumed to represent a distinct class of afferent fibers.

Results

Intramuscular regionalization during natural movements

Four (BF, GR, SM, TFL) of the eight muscles sampled in this study had at least one wide tendinous skeletal attachment. As shown in Fig. 1, BF, SM, and GR have wide insertions on the femur, and TFL and GR have wide origins at the hip. Thus, BF, GR, and SM muscles have a range of knee flexor moment arms across their width, and there is a range of hip extensor and hip flexor moment arms across GR and TFL, respectively. Muscles with broad attachments are often differentially activated (see definition in Pratt and Loeb 1991, this volume) reflecting the mechanical heterogeneity that results from a distributed attachment (Engberg and Lundberg 1969; Perret and Cabelguen 1980; English and Weeks 1987; Hoffer et al. 1981, 1987; Chanaud et al. 1991b; Pratt and Loeb 1991).

The activity of eight thigh muscles during locomotion, ear scratching, and paw shaking is shown in Fig. 2. The records illustrated in Fig. 2 are averages of five consecutive, normalized cycles; in each movement, the cycle was normalized relative to the onset of AF activity. AF is a uniarticular hip extensor. Thus, each normalized locomotor cycle starts with the onset of the stance phase, and the scratch and shake cycles begin with the onset of the propulsive phase of the movement. Two normalized

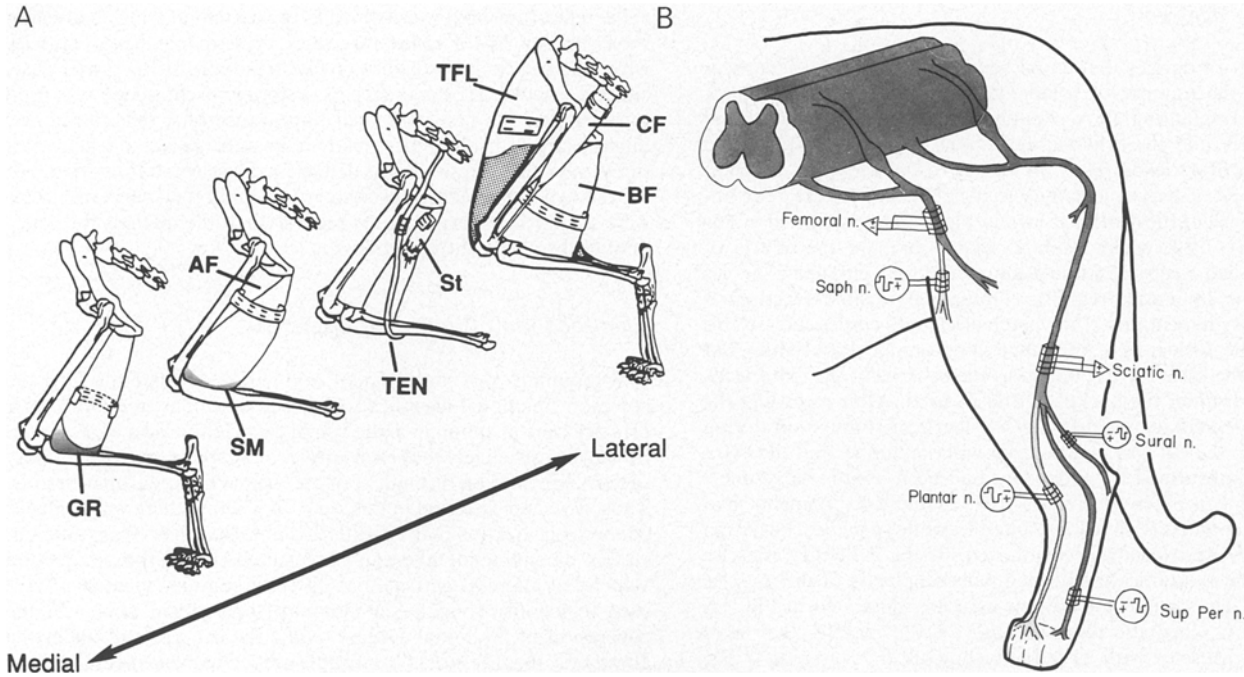

Fig. 1.A, B. Schematic summary of implanted devices. The muscles that were implanted and their customized patch electrodes are shown in **A**. The muscle diagrams are presented from left to right in order of each muscle's location in the hindlimb along the medial-lateral axis, respectively. **B** Shows the four cutaneous nerves that were implanted with bipolar stimulating electrode cuffs (saphenous, sural, superficial peroneal and plantar nerves) and the tripolar recording nerve cuffs placed on the femoral and sciatic nerves to record electrically evoked nerve volleys

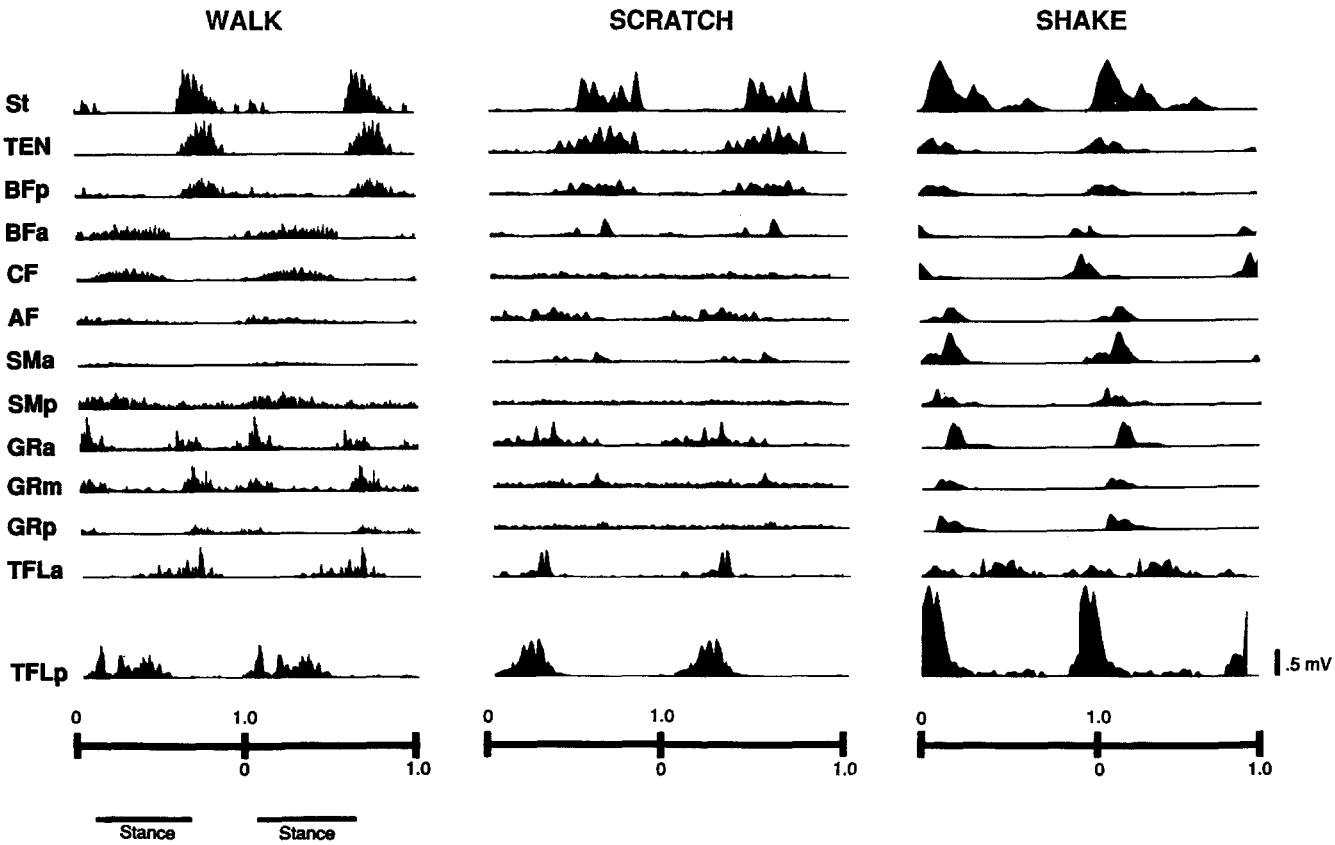

Fig. 2. Activation patterns of muscle regions during natural movements. Each trace represents the rectified and bin integrated (2 ms intervals) *EMG* averaged over five consecutive cycles, during treadmill walking, scratching of the ear, or hindlimb paw shaking. Two normalized cycles are presented for each movement. In each panel, the onset of *AF* activity marks the beginning of the cycle. All traces are displayed at the same vertical calibration. Data are from cat CP29 except for TFL records which are from cat CR03. The mean cycle durations were: walk – 528 ms; scratch – 166 ms; and shake – 84 ms

cycles are presented for each movement to make the temporal relationships across muscles and muscle regions more evident. Because it was not possible to record from all muscle regions of interest in each cat, normalization of movement cycles enabled us to integrate data recorded in different cats, all of which exhibited similar EMG patterns during these behaviors except as noted below. All of the data in Fig. 2 is from cat CP30 with the exception of the TFL records, which are from cat CR03. The locomotor EMGs shown in Fig. 2 were recorded at brisk walking speeds (cycle durations = 520–540 ms). Slower speeds of walking were used when recording cutaneous reflex responses (see below). Average cycle durations for scratching were 160–170 ms, and paw shaking cycles were the shortest (80–90 ms) of the three movements. In addition to differences in cycle duration, these three centrally driven movements are kinematically distinct from one another (see Pratt and Loeb 1991). Analysis of muscle synergies across these movements thus provides an excellent comparison of the intramuscular distribution of the outputs of CPGs associated with three mechanically distinct motor tasks.

In interpreting Fig. 2, it is useful to distinguish the main trends that appear to be consistent among animals from those details that may be labile. For most muscle regions, the synergies recorded during locomotion were quite consistent across animals. The following synergies were typically seen during walking: flexors – St, TEN, and BFp; extensors – AF, BFa, CF, and TFLp. The activity of GR, SM and TFLa did not fit neatly into either classification and was variable across, but consistent within, cats. Lability during locomotion seemed mainly to arise from the threshold speeds at which secondary bursts of EMG activity started to appear in muscles such as GR and St. Interestingly, the burst that could disappear at slower walking speeds in St was the one at footfall (see also Fig. 8), whereas for GR, it was the one at footlift. In TFLa, the appearance of a distinct burst at footlift at faster speeds could be accompanied by a diminution of its mid-stance-phase activity at slower speeds (compare Figs. 2 and 7, from same animal), reversing its apparent functional synergies. A similar lability may affect SM, which shows mid-stance-phase activity in Figs. 2 and 9, but which could have a double-burst pattern similar to St at faster speeds (also described by Engberg and Lundberg 1969).

Muscle synergies during scratching and paw shaking were more variable across cats. Cats adopted either sitting or standing postures when scratching that were similar to those described in Figs. 1B and C, respectively of Carlson Khuta and Smith (1990). The EMG records shown in Fig. 2 were obtained in two cats (CP29 and CR03), both of whom assumed sitting postures while scratching. During ear scratching, AF, GRa, and TFL (TFLa and TFp were coactive) were usually recruited together. The coactivation of TFL with the hip extensors AF and GRa indicates that TFLa and TFLp were both recruited as knee extensors, forming an extensor synergy. CF and SMp were usually not recruited or were active at relatively low levels (i.e., compare CF activity in scratch vs. walk and shake, all presented at equal gains in Fig. 2). The knee flexors (BFp, TEN, and St) were always coactive during scratching. Activity in the knee flexor synergy consistently commenced after the onset of the AF–GRa–TFL synergy, but its timing relative to the other posterior thigh muscles (SM, GRm, GRp, and BFa) was variable across cats; it could either precede or follow the onset of activity in SM, GRm, and GRp, and could either follow or occur simultaneously with BFa activity (Fig. 2). Similar variability in the timing of the St burst during scratching has also been reported by Carlson Khuta and Smith (1990). During paw shaking, an extensor synergy consisting of AF and SM and a knee flexor synergy of BFp, St, and TEN were observed consistently across animals. The knee flexor synergy consistently commenced after the AF–SM synergy, but as was observed during scratching, the timing of the flexor synergy was variable relative to activity in other muscles.

The exact posture and trajectory of these fast movements were subtly, but visibly different among animals (although usually consistent among trials within an animal). In particular, differences in lateral motion (abduction at the hip) may have contributed to the complex relationships between the two compartments of TFL, which in Fig. 2 appear to be cyclical antagonists during walking, cyclical synergists during scratching, and cyclic vs. tonic (negligible amplitude modulation) during shaking. The variable timing of the knee flexor synergy during ear scratching and paw shaking also may reflect subtle differences in movement kinematics. This explanation would be consistent with evidence from Smith and colleagues that knee extensor muscles function primarily to produce torques to control intersegmental dynamics and are, therefore, particularly affected by motion-dependent feedback (reviewed in Smith and Zernicke 1987). Our data suggest that the activity of the biarticular knee flexor muscles also may be flexible and strongly influenced by movement-related feedback. Further interpretation of these different EMG patterns would require a detailed, three-dimensional kinematic and dynamic analysis of these movements with a higher temporal resolution than can be achieved with conventional video equipment.

In summary, the patterns of synergy during voluntary recruitment depended on the behavioral task and could include switches from synergistic to antagonistic relationships among the intramuscular subregions of individual muscles, particularly for those muscles that sometimes contributed to the stance phase of locomotion (BF, SM, GR, and TFL). All four of these broad muscles were differentially activated during one or more of the three movements analyzed in the present study. BF and TFL were differentially activated during all three movements, and differential activation in SM and GR was movement specific. During locomotion at the speeds studied, temporal differences in the recruitment of intramuscular subregions, which could reflect different sources of central command signals, were observed in BF and TFL but not in GR or SM.

General features of cutaneous reflexes during locomotion

Cutaneous reflex responses basically fell into three categories on the basis of their latency and polarity (excit-

Table 1. Cutaneous reflex responses in posterior thigh muscles

		1.2 x T[a]		1.5 x T		2.0 x T		4.0 x T	
FLEXORS	BFp[b]	E6[c]			E10			E18, 36	
				E8				E35	
	St	E6						E20, 30	I10
				E8				E18, 36	
	TEN				E10	E8		E30	
		E8						E35	
EXTENSORS	BFa						I12	I10	
						I10			
	CF						I12	I10	
						I10			
	AF						I12	I10	
						I10			
MIXED	SMa					I14		E8	I14
						E8 / I14			
	SMp					I14		E8	I14
						E8 / I14			
	GRa					E6	E8 / I24	I20	
				E8 / I20					
	GRp					E6	E8 / I24	I20	
				E8 / I20					
	TFLa			E8		E20	I10		E20
	TFLp					I10	I10	Saph	sural
								Sup Per	plantar

[a] Stimulus intensity in multiples of threshold (T) for appearance of neural volley

[b] Muscle region where EMG response was recorded. See Methods for abbreviations and criteria for functional groupings of muscles

[c] The letters in each box indicate the sign of the response: E = excitatory; I = inhibitory. The numbers indicate the latency (ms) of the response first evoked at the stimulus intensity indicated at the top of each column. The four boxes for each muscle region, at each stimulus intensity, indicate the response to one of four sensory nerves, formatted as shown in bottom two rows under 4.0 × T at lower right. Note that in some cases (e.g., SMa response to SP stimulation at 2.0 × T), biphasic responses were evoked. All data are from cat CP30 except TFL data, which is from cat CR03 (see Fig. 7)

atory or inhibitory) of response: short (P1) and long (P2) latency excitation and short latency inhibition (N1), as has been reported by others (Duysens and Loeb 1980; Abraham et al. 1985; Pratt and Loeb 1991). The latencies of excitatory and inhibitory reflex responses, determined from the peristimulus rasters, that were evoked at four standardized levels of stimulation for each of the four cutaneous nerves in cats CP30 and CR03, are presented in Table 1. The response latencies in Table 1 are presented at the stimulus intensity at which the response was first observed. For each muscle/stimulus intensity combination there are four boxes in which the responses evoked by the four cutaneous nerves are presented, as indicated in the key in the lower right of Table 1. In the left-hand column, muscles and muscle subregions are grouped according to their pattern of activation during locomotion (see Fig. 2); "net" flexors are listed at the top followed by "net" extensors, and lastly, muscle regions that did not fit neatly into either category. Table 1 shows that, in general, the earliest excitatory responses had shorter latencies and durations and were evoked at lower stimulus intensites than the N1 responses. The data presented in Table 1 are representative of the latencies of excitatory and inhibitory responses and the thresholds at which they were evoked in other animals. The patterns of responses recorded in some muscle subregions varied across cats, however, as discussed below.

Because long periods of treadmill walking were needed to sample adequately cutaneous reflex responses in all phases of the step cycle, relatively slow walking speeds were used in these experiments. Thus, the muscle activation levels in the reflex rasters are lower than those recorded during brisk walking (Fig. 2). The differences between the EMG patterns shown in Fig. 2 and those presented in the reflex response rasters (discussed below) are mostly quantitative in nature, however.

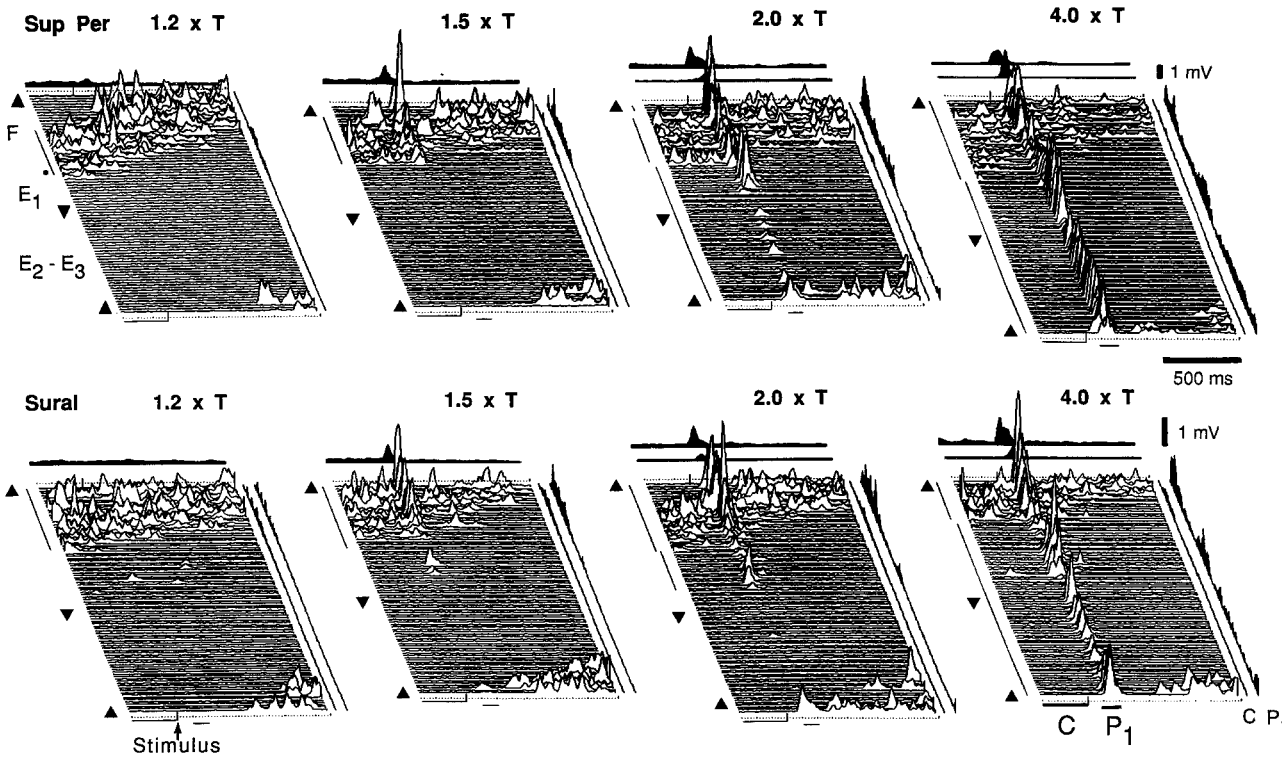

Fig. 3. Example of cutaneous reflex responses in a "pure" flexor. Each peristimulus raster presents the responses recorded in the knee flexor muscle, TEN, in cat CP30 to stimulation of either the Sup Per or sural nerve at one of four levels of stimulation. In this and all subsequent figures with rasters, stimulation intensity is indicated in multiples of threshold (T), determined as described in Methods. Each trace displays the peristimulus EMG record, from 30 ms before to 100 ms following the stimulus (vertical hash mark along row of tick marks at bottom of each raster). Traces are arranged from top to bottom relative to standard divisions of the step cycle shown along the left border of top left raster; footlift is indicated by an upward-pointing triangle and footfall by a downward-pointing triangle. The summary traces at the top show averaged activity across selected step cycle epochs, indicated by the solid lines along the left border of the raster, and those along the right border of each raster show the averaged activity at selected peristimulus intervals, indicated by solid bars along the bottom of the raster (see selected epochs *C* and *P1* in lower right raster). See Methods and Fig. 4 of Pratt and Loeb (1991) for a more detailed description of normalization procedures and interpretation of rasters. Note modulated excitatory P1 responses evoked at lower stimulation strengths which become less modulated at intensities of 2.0–4.0 × T

Responses in typical flexors and extensors

In general, BFp, St, and TEN had similar excitatory responses, and AF, BFa and CF had similar inhibitory responses to electrical stimulation of cutaneous nerves in all animals. All of these muscle regions, except AF, are biarticular hip extensors with varying moment arms at the knee. In each case, the classification of each muscle region as a "net" flexor or extensor reflects the action of the muscle at the joint at which the moment arm is the greatest.

The flexor responses recorded in TEN, shown in Fig. 3, were typical of the "net" knee flexors and were observed in all cats. Reflex responses evoked in TEN by electrical stimulation of either the Sup Per or sural nerve at four levels of stimulus intensity are presented in Fig. 3; similar responses were produced by stimulation of Saph ($> 1.5 \times$ T) and plantar ($8.0 \times$ T) nerves (not shown). Typically, low threshold ($1.2–1.5 \times$ T) stimulation produced short latency, modulated excitatory (P1) responses confined to the flexion phase of the step cycle when the muscle was normally active. At higher stimulus intensities ($1.5–2.0 \times$ T), the P1 response appeared during the E1 phase and, with further increases ($4.0–8.0 \times$ T), extended into the stance phase.

In both "net" flexors and "mixed" muscles, the amplitude of the P1 response was usually maximal around footlift and then declined throughout the swing phase (Figs. 3, 4, and 9). Often, as the P1 response spread into all phases of the step cycle, a longer-latency excitatory response (P2) would appear, and, occasionally, even a P3 response was observed (i.e., Sup Per effects in St in Fig. 4). The P2 or P3 responses usually remained modulated in a fashion similar to the phasing of the P1 response evoked at lower stimulus intensities (Figs. 3, 4, and 9). However, we occasionally found P2 responses without P1 (TFLa, sural stimulation in Fig. 7) or P2 responses less modulated than the P1 response (BFp, sural stimulation in Fig. 7).

Within the group of muscles that were excited by cutaneous afferents there were nerve-specific differences in the details of the excitatory responses. For example,

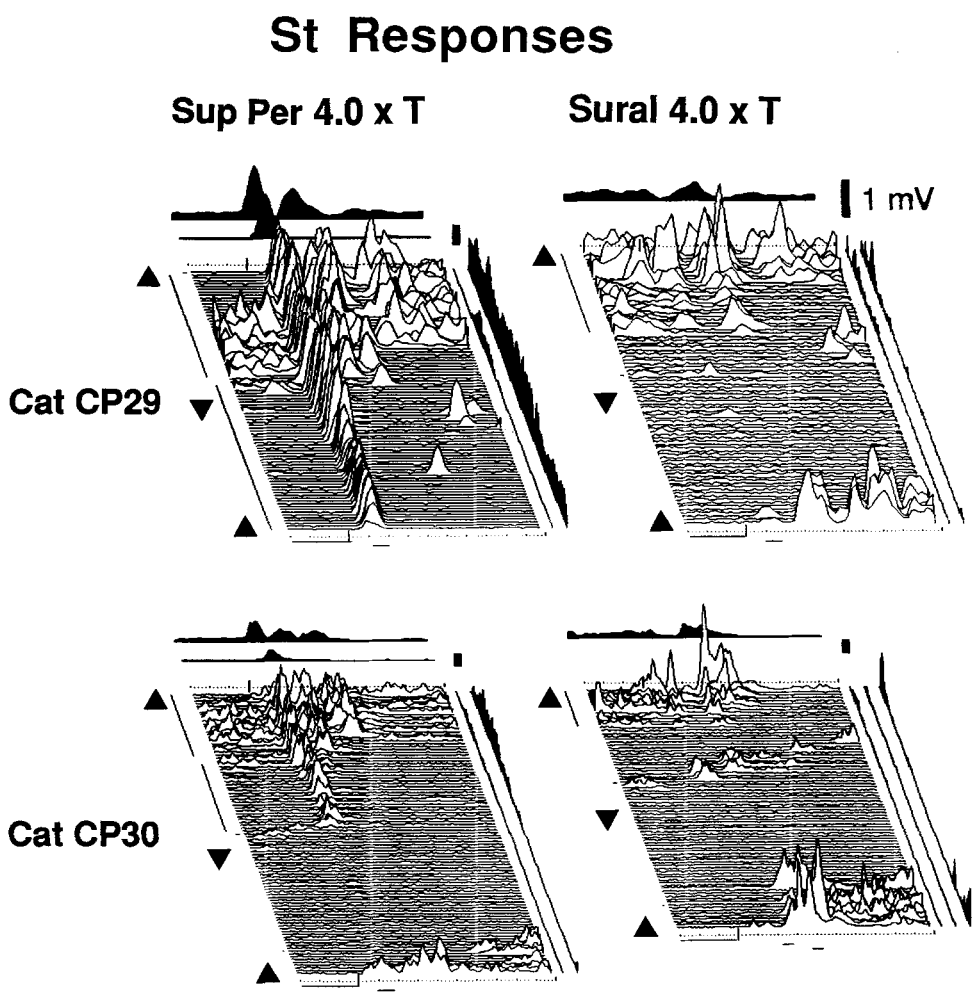

Fig. 4. EMG reflex responses recorded in the flexor, St, in two cats, *CP29* and *CP30*. Note that in both cats Sup Per stimulation evoked multiphasic excitatory responses in St while the effect of sural stimulation was predominantly inhibitory. Note also the difference in the details of the flexor response produced by Sup Per in St and its synergist TEN (monophasic excitation, Fig. 3)

Sup Per stimulation evoked a triphasic excitatory response in St in cat CP30 (Fig. 4) that differed markedly from the mostly single-peaked excitation produced concurrently in TEN in the same cat (Fig. 3, 4.0 × T). Other examples are the differential effects of: sural and Saph stimulation on TFLa (Fig. 7); Sup Per on GRa and SMa (Fig. 9); and sural vs. Sup Per on GRa (Fig. 9). There were also differences in the sensitivity of synergistic motor nuclei to particular cutaneous inputs. For instance, the threshold for Sup Per excitation was lower in TEN than in BFp and St, but the reverse was true for Saph inputs in cat CP30 (Table 1). Similar variations were observed in all animals, but there did not appear to be patterns that were consistent across cats. The variations observed among synergists within individual animals suggest the presence of a significant amount of individualization in the excitatory circuits mediating reflex inputs from cutaneous afferents to hindlimb motoneurons. This is in contrast to the inhibitory responses that were more uniform across muscles and nerves, as discussed below.

A notable exception to the general excitation of flexors by cutaneous afferents was the consistent finding that sural stimulation resulted in a short-latency inhibition of the knee flexor St. As shown in Fig. 4, the normal locomotor activity of St during the swing phase of the step cycle was inhibited about 12 ms following sural stimulation in cats CP29 and CP30. The summary histograms, presented along the top of each sural reflex raster, show no evidence of an excitatory response preceding an obvious inhibition of St activity. The summary histograms were averaged over periods of St locomotor activity only and did not include periods of St inactivity when inhibitory inputs to this motor nucleus would not be detectable (see lines along the left border of each raster). This peculiar response in St was not seen in its synergist, TEN (Fig. 3) or in St following Sup Per stimulation (Fig. 4) and was observed in all four animals in which sural reflexes in St were recorded.

The inhibitory responses in extensors (Figs. 5–9) typically first appeared at stimulus intensities of 2.0 × T (except plantar nerve, which required 4–8 × T in all cats). There were several features of the N1 inhibitory responses that were significantly different from their P1 excitatory counterparts: 1) slightly higher stimulus intensities were required to evoke detectable inhibition; 2) the earliest inhibitory responses had longer latencies than P1 responses (see above); and 3) the duration of the inhibition (15–30 ms) usually exceeded that of short-latency excitatory responses (10–15 ms). Activation of higher threshold cutaneous afferents at stimulus intensities > 4.0 × T often resulted in a significant prolongation of the inhibition in extensors, as shown in Fig. 6. Like the

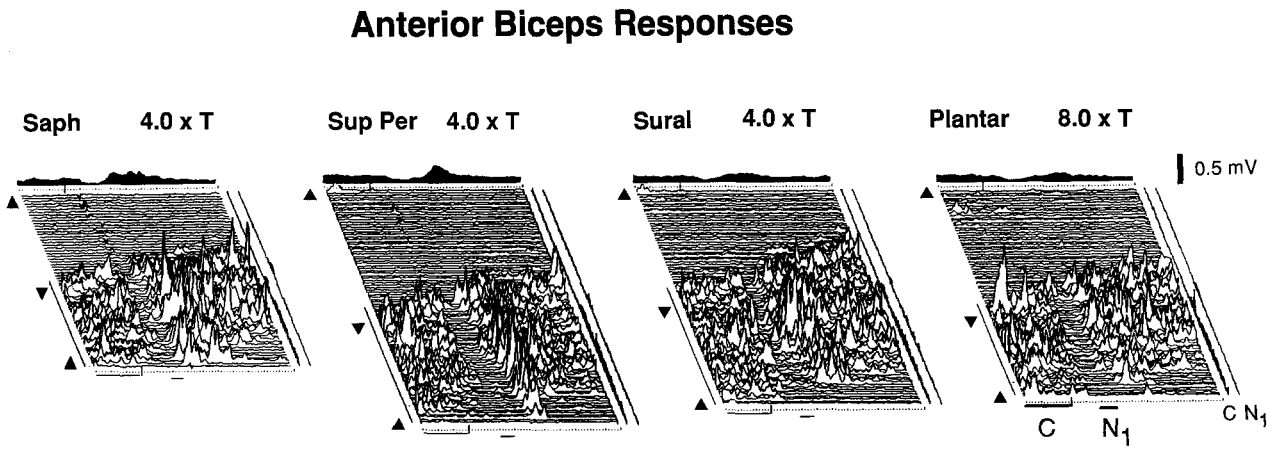

Fig. 5. Example of cutaneous reflex responses in a "pure" extensor. Stimulation at 4.0 × T of all four cutaneous nerves produced a significant short latency inhibition (*N1*) of the background stance phase EMG activity in the extensor, anterior biceps (BFa in text) in cat CP30. Note that a higher stimulus intensity (8.0 × T) was needed with plantar stimulation to produce significant inhibition. Note also the tendency for the pre-footfall activity to be less susceptible to inhibition than the activity during stance

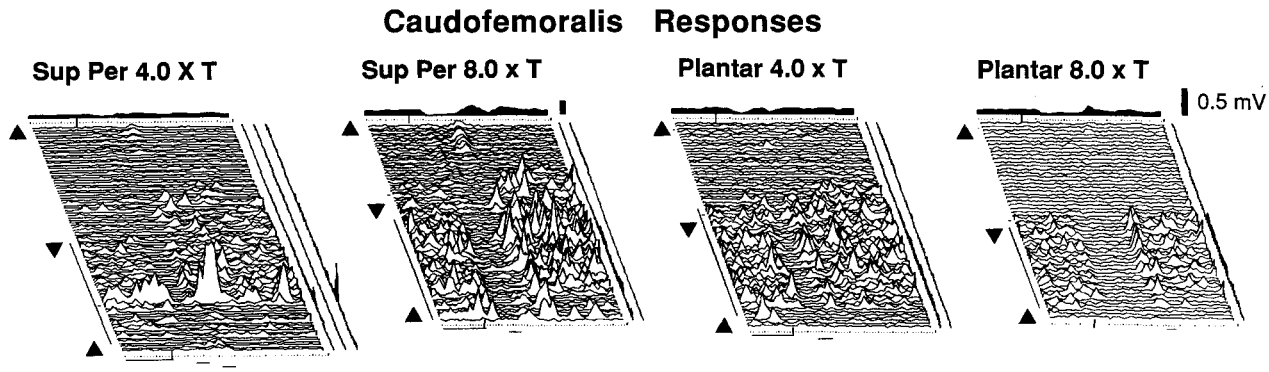

Fig. 6. Inhibitory responses in the extensor CF (cat CP29) evoked by moderate (4.0 × T) and high threshold (8.0 × T) stimulation of Sup Per and plantar nerves. Note the significant increase in the duration of the inhibition at 8.0 × T

excitatory responses in flexors, the inhibitory responses could be affected by the phase of the step cycle. At moderate stimulus intensities (2.0–4.0 × T), the inhibition of extensors was often less pronounced during E1 than during E2–E3 (Figs. 5–9). An increase in the baseline EMG was often observed immediately following inhibition (Figs. 4–9) that most likely reflects a post-inhibitory rebound (see Discussion).

Responses within broad muscles that were functionally heterogeneous during walking

As discussed previously, both BF and TFL were differentially activated during locomotion. In general, the nature of the cutaneous reflex responses in these functionally heterogeneous muscles was correlated with the phasing of their activation during locomotion (but see Fig. 8 and below). BFa and BFp reflex responses fell into classic categories of extensors and flexors, respectively (Fig. 7), i.e., BFa was always inhibited and BFp was always excited by all cutaneous inputs. TFLa and TFLp usually responded differently to stimulation of cutaneous afferents, but neither muscle region responded consistently as either a "typical" flexor or extensor. In cat CR03, inhibitory responses were evoked in TFLp by stimulation of both Saph and sural nerves, but the responses in TFLa were complex (Fig. 7). Saph stimulation (4.0 × T) evoked a short latency excitatory response in TFLa throughout the step cycle, while sural stimulation produced a mixture of inhibition and long latency (P2) excitation. The fact that the excitatory response in TFLa evoked by sural stimulation was largest during late stance and early swing when TFLa had low levels of activity suggests that the excitation was an active excitation and not due to post-inhibitory rebound. In another cat with similar locomotor EMGs (CR02, not shown), sural stimuli excited TFLa and produced a mixture of short latency excitation followed by inhibition in TFLp, while Saph elicited similar excitatory responses in TFLa and TFLp throughout the step cycle.

An interesting exception to the general rule that the sign of the cutaneous reflex response was correlated to the phasing of a muscle region's locomotor activity is presented in Fig. 8. As shown in the EMG recordings of BFa and BFm activity during locomotion in two cats

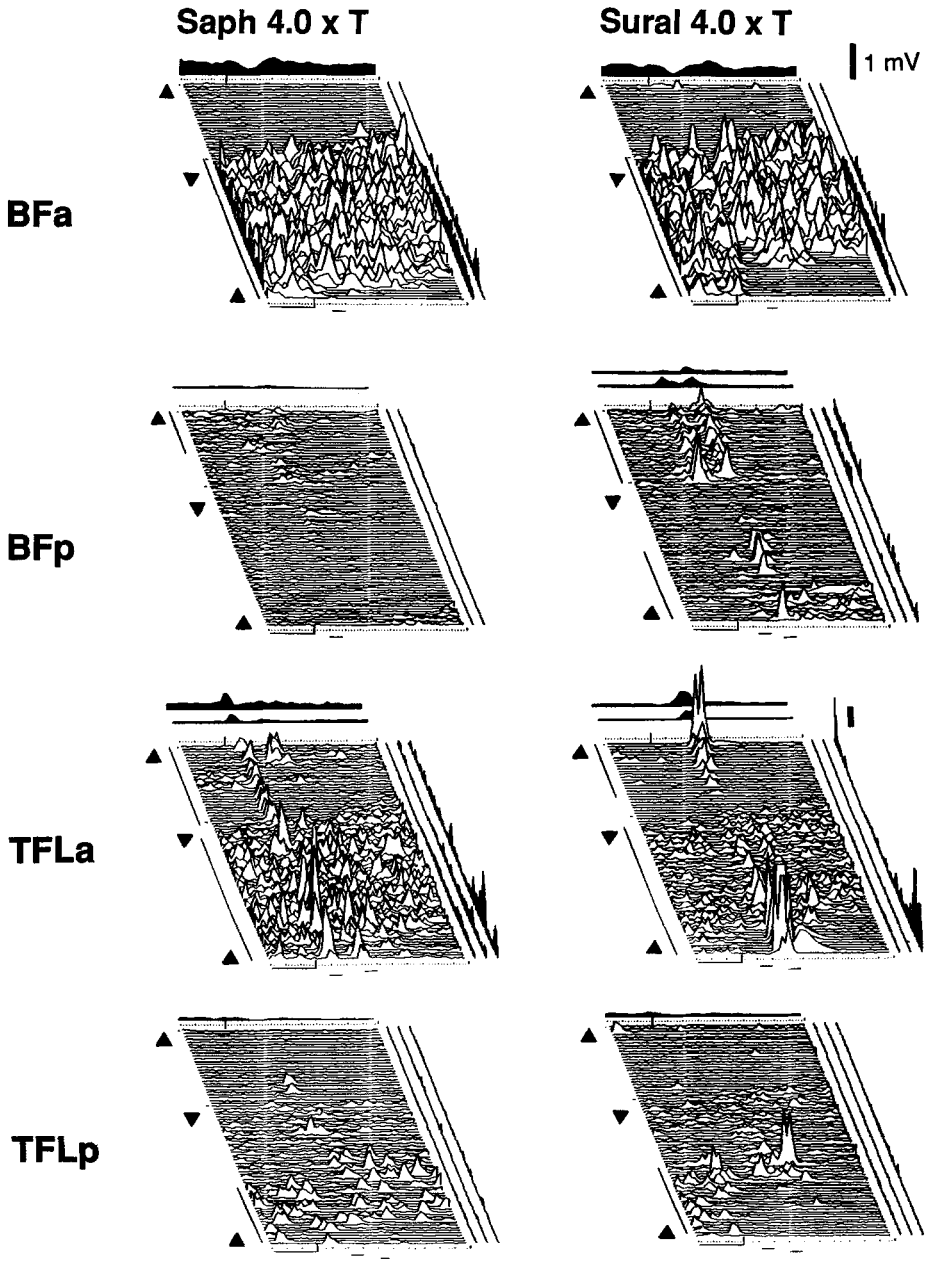

Fig. 7. Nerve-specific intramuscular heterogeneity of cutaneous reflex responses. Stimulation of Saph and sural nerves in cat CR03 evoked different responses within the anterior and posterior regions of the biarticular muscles BF and TFL that are differentially activated during locomotion. The activity of TFL during a fast walk in cat CR03 is shown in Fig. 2; *BFa* and *BFp* locomotor activity in cat CR03 was similar to that of cat CP30 shown in Fig. 2 (also see BFa activity in cat CR03 in Fig. 8). Both nerves produced only inhibition in *BFa* and *TFLp*, regions that were active during the stance phase of the step cycle. *BFp* and *TFLa*, regions with more flexor activity during locomotion, displayed excitatory responses to both cutaneous nerves. Note the inhibition preceding the excitatory response produced in *TFLa* by sural stimulation. Note also the dissimilarity in the excitatory responses evoked by the two nerves in *TFLa* and *BFp*

(CR03 and CR02), presented in the bottom of Fig. 8, BFm was coactive with the hip extensor BFa. Like BFa, Saph stimulation inhibited BFm in cat CR03, but in cat CR02, Saph (and sural, not shown) stimulation evoked an unmodulated, *excitatory* P1 response. BFp was excited by both nerves in both cats (see BFp responses in cat CR03 in Fig. 7). In both cats, however, the P1 excitatory responses in BFp (and St) were primarily confined to the swing phase of the step cycle, so it is unlikely that the P1 response recorded in BFm was due to cross talk from either BFp or St. Thus, the architecturally distinctive middle region of BF (Chanaud et al. 1991a) may be treated as an extensor by CPG recruitment and as a flexor by cutaneous reflex pathways.

Responses within broad muscles that were functionally homogeneous during walking

Cutaneous reflex responses from all nerves were homogeneously distributed to all regions of GR and SM in all cats. Unlike TFL and BF, which also have broad attachments, GR and SM were not differentially activated during locomotion at the walking speeds used in these experiments (Fig. 2). Thus, a correspondence in the intramuscular distribution (i.e., differential vs. uniform) of cutaneous reflexes and locomotor activity was consistently observed in the four broad muscles studied in these experiments.

Neither GR or SM responded to cutaneous input as

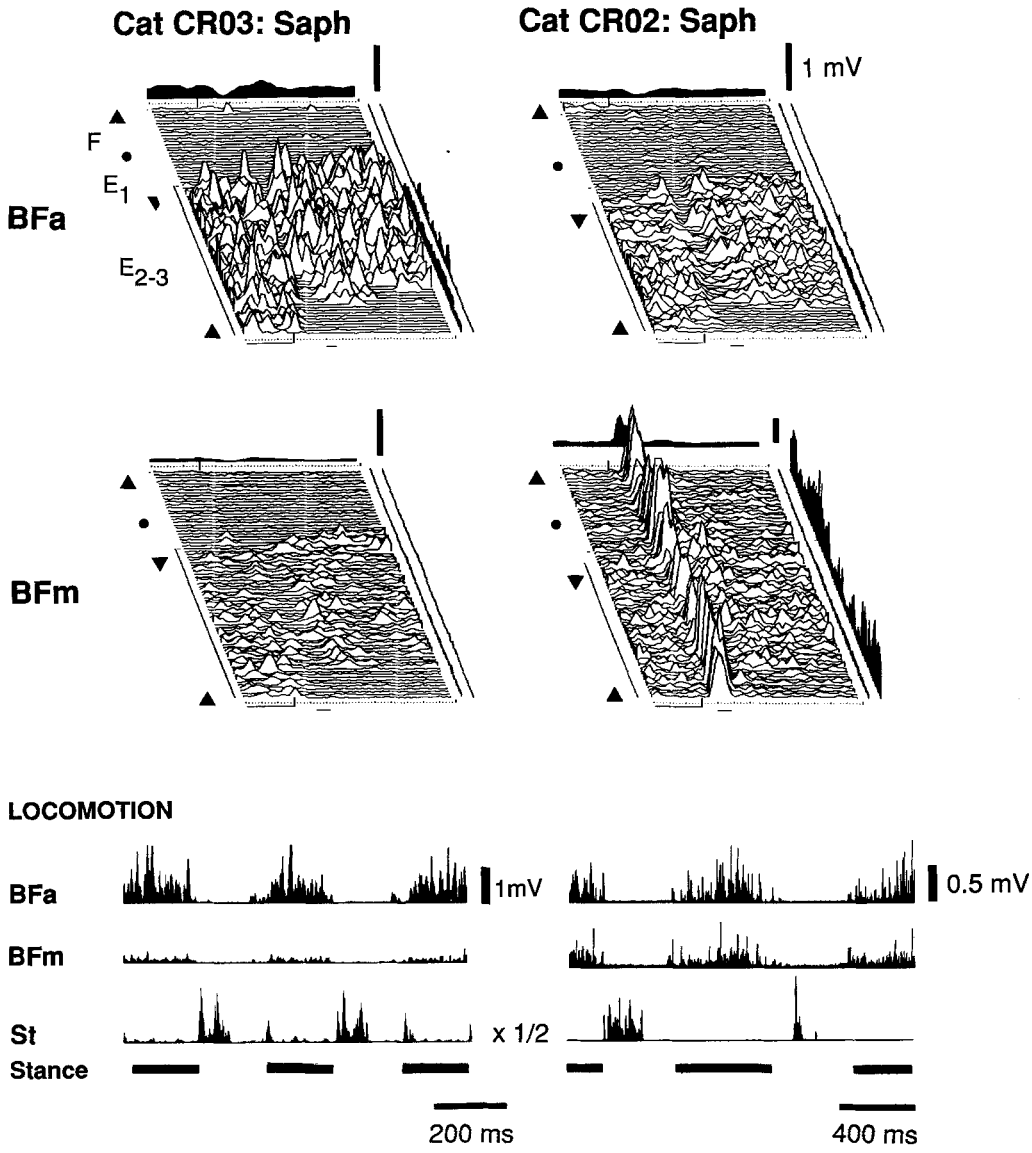

Fig. 8. Unusual flexion reflex response evoked in a functional extensor muscle. The locomotor EMG records shown in the bottom panels were rectified and bin integrated; the St records are at half the gain of the *BFa* and *BFm* traces for both the right and left-hand panels. In both cats (CR02 and CR03), BFm was co-active with *BFa* as an extensor during locomotion. Saph stimulation produced inhibition in both *BFa* and *BFm* in cat CR03 but an unusual excitatory response in *BFm* in cat CR02

a typical flexor or extensor, however, as shown in Fig. 9. In cat CP30, Saph, Sup Per, and sural stimulation evoked a mixture of excitation and inhibition in GR. The P1 response evoked by Sup Per and Saph occurred throughout most of the step cycle but was curiously absent during the pre-footfall burst. Similar results were obtained in two other cats that also exhibited a double burst pattern of activity during walking. Inhibition in the absence of excitation was observed in one cat which had only a pre-footfall burst of activity. The inhibition in GR had a longer latency ($\sim$20 ms) than the P1 excitatory response even during the pre-footfall burst when the P1 response was absent. Both excitation and inhibition were evoked in GR at similar Sup Per and sural stimulus intensities, but higher Saph stimulus currents ($4.0 \times$ T), perhaps recruiting Aδ fibers, were needed to produce inhibition than excitation (see Table 1). The long latency ($\sim$38 ms) excitatory response produced by Sup Per and sural (but not Saph) during early flexion could be due to either a longer latency excitatory input or postinhibitory rebound, that is, release of a subliminal excitatory drive to GR motoneurons that were temporarily hyperpolarized by the cutaneous afferent input. Sural effects on GR were modest even at $8.0 \times$ T in cat CP30, and were negligible in another cat.

The most common reflex response observed in SM consisted of a short latency excitation during swing that reversed to a short latency inhibition during the stance

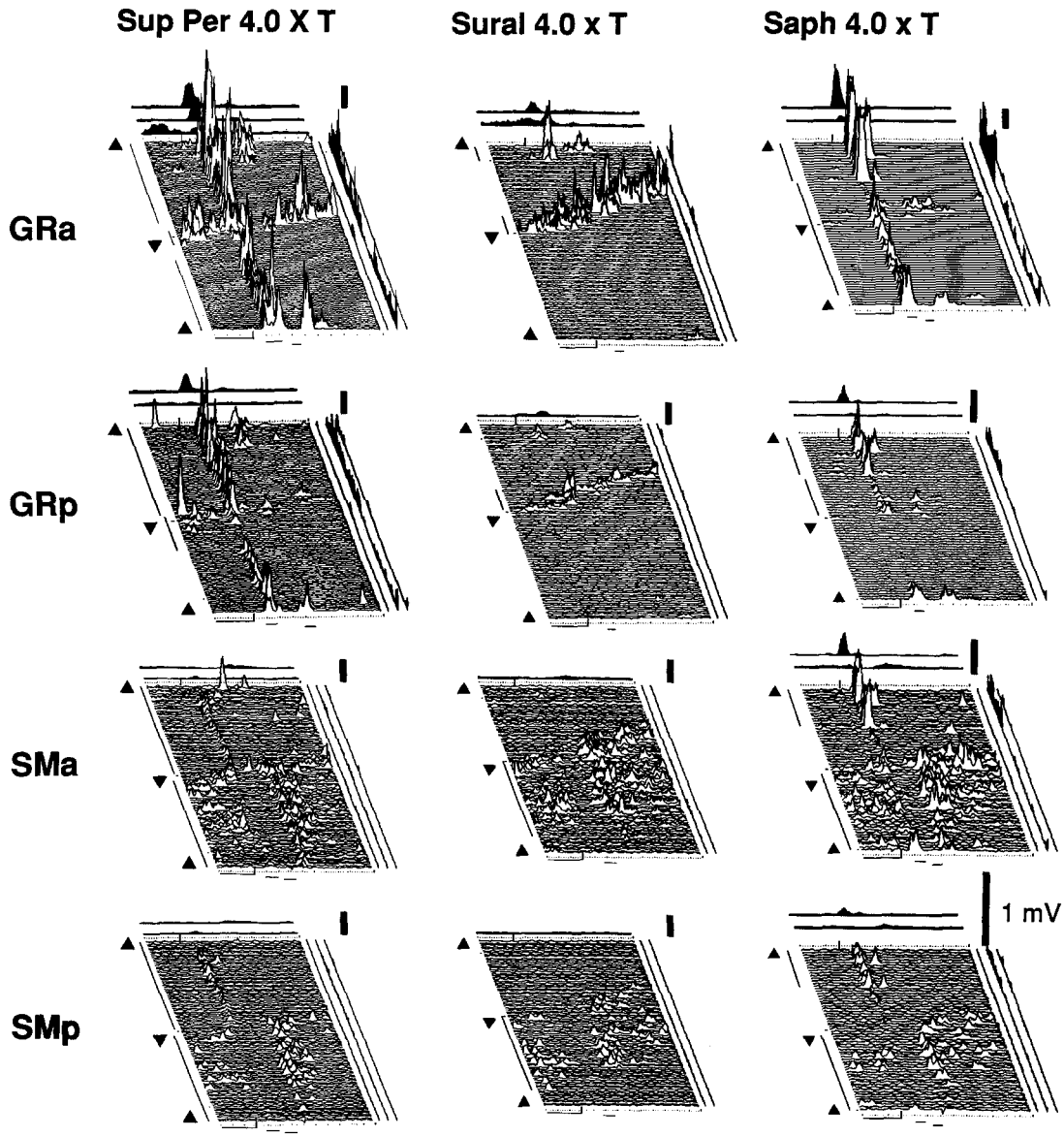

Fig. 9. Homogeneity of cutaneous reflex responses in broad muscles that were not differentially activated during slow walking. The anterior and posterior subregions of the bifunctional muscles GR and SM responded similarly to stimulation of all cutaneous nerves in cat CP30. Plantar stimulation, even at 8.0 × T, had no effect on any of these muscle regions in this cat. Note the complex responses consisting of mixtures of excitation and inhibition produced in both muscles by Saph and Sup Per stimulation. Note also the nerve-specific responses in GR to stimulation of all cutaneous nerves and the different effects of Sup Per and Saph vs. sural stimulation in SM

phase (Fig. 9). Similar responses were observed in SM by Duysens and Loeb (1980), but the opposite pattern was seen during fictive locomotion in high-spinal cats (Schomburg et al. 1981). Both Sup Per and Saph nerves produced a combination of stance-phase inhibition and swing phase excitation in SM in cat CP30 (Fig. 9). The swing phase excitation in SM appears to be a true reflex and not due to crosstalk from the flexor responses in the adjacent GR since: 1) SM was inhibited during stance and showed no sign of the stance phase excitation recorded in GR; and 2) the large excitation evoked in GR in early flexion by sural stimulation was not reflected in SM. Similar results were obtained in another cat (CR03) with Saph stimulation. Cat CR03 had a double burst pattern of activity during slow walking, one burst occurring in late stance and the second during E1. Pure inhibition or excitation was never observed in SM. Sural stimulation had only negligible effects on SM in all cats.

Classes of afferents activated by electrical stimulation

The use of recording nerve cuffs implanted on the femoral and sciatic nerves in cat CP30 enabled us to determine reflex thresholds for all four cutaneous nerves during locomotion on the basis of the evoked neural volley (Fig. 10) rather than the appearance of a reflex response in the muscle (see Methods). The conduction velocity of the population of afferents activated at each stimulus intensity was determined by measuring the lat-

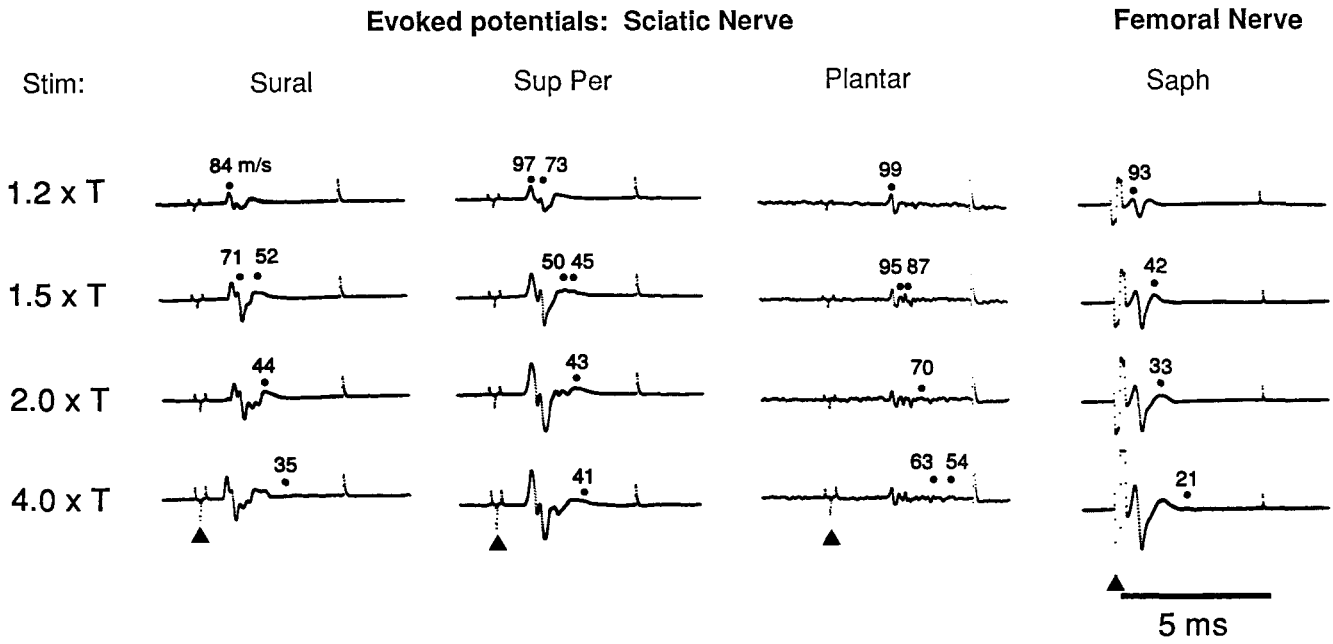

Fig. 10. Nerve fibers activated at different stimulus intensities in cat CP30. Each trace shows the averaged evoked potential recorded in either the sciatic or femoral (far right panel) nerve for 64 stimuli delivered at the indicated multiple of threshold (*T*). Onset of the stimulus is indicated by the solid triangle (bottom trace). The numbers above each trace are conduction velocity estimates for the afferents associated with each triphasic waveform (marked by dot over upgoing spike). Conduction velocities were measured between the stimulating cuff on each of the cutaneous nerves and the recording cuff on either the sciatic or femoral nerve cuffs (see Methods for more detail). All traces are displayed at the same vertical calibration. The late upward-going spike in each trace is a calibration pulse occurring 5 ms after the stimulus. Note the continued growth in the amplitude of some short latency responses evoked at 1.2–1.5 × T (and beyond 2.0 T in sural) as stimulus intensity was increased. The proportion of large diameter fibers recruited by plantar nerve stimulation consistently appeared to be lower than in the other three cutaneous nerves

ency of each separate triphasic waveform in the recording cuff and the distance between the stimulating and recording cuffs. These data provided information on the classes of cutaneous afferents involved in mediating the reflexes observed during locomotion.

The profile of cutaneous reflex responses recorded in cat CP30, presented in Table 1, shows that consistent excitatory reflex responses were usually produced by all but plantar stimulation at stimulus intensities of 1.2–1.5 × T. Inhibitory responses in extensors usually had slightly higher thresholds ($\geq 2.0 \times$ T) than excitatory responses (but see Sup Per and sural effects of GR). Similar results were obtained for the sural, Sup Per, and plantar nerves in cat CP29 which also had a recording cuff implanted on the sciatic nerve. The conduction velocities of cutaneous afferents activated at different multiples of threshold in cat CP30 are indicated in Fig. 10. Threshold excitatory responses were mediated by rapidly conducting fibers (99–42 m/s), whereas afferents with slower conduction velocities (44–21 m/s) had to be recruited before thresholds for inhibitory responses were reached. The conduction velocities of all of the cutaneous fibers recruited at stimulus intensities $\leq 4.0 \times$ T fall in the range of myelinated Aβ or Aδ fibers (≥ 5 m/s). Thus, none of the responses reported in this paper involved unmyelinated C fibers. The cut-off between the more rapidly conducting Aβ and Aδ fibers is about 30 m/s (Burgess et al. 1968). In cat CP30, most of the shortest latency excitatory and inhibitory responses were mediated by Aβ fibers. An exception could be the inhibition evoked in GR by Saph stimulation which first appeared when Aδ fibers (conduction velocity = 21 m/s) were recruited at 4.0 × T. Both excitation and inhibition in GR were evoked by Aβ fibers by Sup Per and sural stimulation, however. The reflexes evoked by Saph stimulation at intensities $\geq 2.0 \times$ T and by sural at 4.0 × T (inhibition in St and SM) could have involved Aδ fibers.

Discussion

Intramuscular synergies during natural movements

In the present study, all four of the bifunctional thigh muscles with distributed origins or insertions (BF, GR, SM and TFL) were differentially activated in one or more of the three movements studied. Differential activation could be manifested by differences in either the timing or amplitude, or both, of the EMG recorded in different subregions within a muscle. Quantitative differences in EMG could reflect differences in spatial facilitation centrally or a nonuniform distribution of muscle fiber types peripherally (see Chanaud et al. 1991b). In this paper, we are primarily interested in temporal differences in the activation of intramuscular subregions insofar as they provide indirect information regarding the central sources of command signals. That is, it can be inferred that muscles or muscle subregions with synchronous onsets of activation share a common central drive. Conversely, significant differences in the temporal charac-

Table 2. Temporal heterogeneity in activation of intramuscular subregions in broad, bifunctional muscles during natural movements and cutaneous reflexes

Muscle	Cutaneous reflexes	Slow walking	Scratching	Paw shaking
BF	D	D	D/U	D
TFL	D	D	U	D/U
GR	U	U	D	U
SM	U	U	D	U

D: Differential activation; U: uniform activation; D/U: different results in different animals

teristics of muscle activation suggest different sources of central drive. The temporal patterns of activation observed across muscles have been used traditionally to describe muscle synergies with the implication that muscles belonging to a synergy are grouped centrally into a functional unit, thereby reducing the degrees of freedom (total number of muscles) to be controlled (Lee 1984; Macpherson 1990).

Temporal differences in the onsets of activation of intramuscular subregions were observed in BF, GR, SM, and TFL muscles during some movements. This evidence indicates that central circuits involved in the control of the three movements studied in this report can be differentially distributed among the motoneurons associated with each of these broad, bifunctional muscles. Temporal heterogeneity in the activation of intramuscular subregions was not invariant, however. As shown in Table 2, which summarizes the results obtained across cats, the occurrence of temporal differences in EMG onsets within a given muscle depended on the particular movement studied. Similar results were obtained in sartorius, another broad, bifunctional muscle (Pratt and Loeb 1991).

In contrast to the broad, bifunctional muscles, a single command signal, distributed uniformly throughout the associated motor nuclei, could explain the activation of adductor femoris, a uniarticular hip extensor muscle with a distributed origin and insertion, and bifunctional muscles with relatively discrete skeletal attachments (CF, St, TEN) during the motor behaviors studied in these experiments. As described in detail in the last paper in this series (Chanaud et al. 1991b), the differential activation observed in St can be explained by a nonuniform distribution of motor unit types in the deep and superficial regions of the muscle and probably does not represent a central partitioning of command signals; equivalent in-series proximal and distal compartments of St also were always activated similarly. These results provide information regarding the conditions that require a differential distribution of synaptic inputs within motor nuclei in order to most effectively utilize the action of muscle subregions to meet the mechanical requirements of the task. In the three movements we have studied, differential activation would appear to be necessary only in biarticular muscles composed of mechanically dissimilar compartments arranged in-parallel and only for some, but not all, tasks.

During slow walking, temporal heterogeneity in the activation of intramuscular subregions was consistently observed in BF and TFL but not in SM or GR. Our results on BF, TFL, and GR are consistent with those reported previously by Engberg and Lundberg (1969) and others (TFL cat, Sherrington 1910; TFL human, Paré et al. 1981; BF cat, English and Weeks 1987). In contrast to our data, however, Engberg and Lundberg (1969) reported temporal differences in the activation of SMa and SMp during locomotion. In their study, SMa was active as a classical extensor while SMp was primarily active during flexion at slow speeds and at faster speeds (trot and faster) exhibited one burst during late extension and another during E1. While SM activity during slow walking was variable across cats in the present study, temporal differences in the activation of SMa and SMp were not seen in any of the three cats studied. It is possible that differences in electrode design were responsible for the different results obtained in the two studies; intramuscular wire EMG electrodes, which are more subject to crosstalk than the patch electrodes, were used in the earlier study. A more detailed study of SM in a larger number of cats would be needed to resolve this issue conclusively.

The relationship between locomotor and reflex recruitment patterns

As noted in the Introduction, the suggestion that the circuits for spinal reflexes might be an integral part of the locomotor CPG has provided a basis for many hypotheses and experiments in the cat hindlimb. This study provides somewhat greater detail than previously available on the distribution of both locomotor and reflex activity recorded simultaneously in a particularly complex group of muscles in the posterior thigh. Thus, it is useful to consider whether these data are easily subsumed into such a unified view of muscle recruitment.

The pattern originally described by Sherrington (1910) of flexor excitation and extensor inhibition can account for much of the data presented here as well as elsewhere (Duysens and Stein 1978; Duysens and Loeb 1980; Schomburg et al. 1981; Abraham et al. 1985; Lennard and Hermanson 1985; Loeb et al. 1987; Schmidt et al. 1987; 1988). However, the general trend for certain groups of muscles to be recruited homogeneously during both locomotion and reflex responses may arise coincidentally because these muscles are mechanically best suited to perform similar roles in both types of movements, rather than on the basis of common drive. It is particularly interesting to look at muscles that are bifunctional (recruited twice during the step cycle) and/or mechanically heterogeneous (with neuromuscular compartments that have a range of skeletal actions). As was noted above, the synergies among these compartments change readily, depending on the kinematics of various motor tasks. The interactions between the locomotor and flexor reflex pathways can be studied in great detail in the intact cat by the simple expedient of applying stimuli to the cutaneous FRAs at all possible phases of

ongoing step cycles. This, in turn, can shed light on the classes of spinal circuitry that might account for any deviations from strict extensor-flexor synergies.

In general, there was a close correspondence between the synergies observed and the profiles of reflex responses recorded across muscles/muscle subregions during walking. That is, muscles that were active during walking as relatively "pure" extensors (BFa, AF, CF, and TFLp) or flexors (BFp, St, and TEN) were typically inhibited or excited, respectively, by low threshold cutaneous afferents. Similarly, muscles/muscle subregions (GR, SM, TFLa) that exhibited more complex patterns of activation, i.e., more than one burst of activity per step cycle or variable patterns across cats, had complex responses to cutaneous nerve stimulation that did not fall into traditional categories of flexors or extensors. These complex responses included both phase-dependent reversals in sign during the step cycle (see SM responses in Fig. 9) as well as complex mixtures of excitation and inhibition (see responses in TFLa, Fig. 7; GR, Fig. 9; and sartorius, Fig. 5 of companion paper (Pratt and Loeb 1991)). The latter resemble cutaneous postsynaptic potentials (PSPs) recorded intracellularly in many flexor and extensor motoneurons consisting of a short latency EPSP followed by an IPSP (Schomburg et al. 1978, 1981; Fleshman et al. 1984; Omeniuk et al. 1986; Schomburg and Steffans 1986; Schmidt et al. 1987, 1988; Leahy and Durkovic 1988).

The agreement between the first two columns of Table 2 indicates that both the locomotor and reflex recruitment systems tend similarly to subdivide certain muscles by regions and not others. Table 1 shows a clear pattern of excitatory reflexes (E) in the locomotor flexors and inhibitory reflexes (I) in the locomotor extensors that would be consistent with a close integration of the two sources of motoneuronal drive. The scattering of excitatory and inhibitory responses in the muscle regions designated "mixed" suggests more independent and specialized circuitry. However, even this might be consistent with a common drive system because, as noted above, many of these subregions can switch their locomotor recruitment pattern at different speeds in different animals.

Thus, it is important to look at the interaction of a given reflex with the ongoing locomotor recruitment in a particular muscle compartment. This reveals at least some striking dissociations between locomotor and reflex synergy, but not all of these have the same implications for circuitry. The reflexes in SM (Fig. 9) suggest a hybrid of classical extensor inhibition during stance, when the muscle was recruited normally, plus flexor excitation during swing. The muscle was not actually recruited by the CPG during the swing phase, but it was probably receiving subliminal excitation from the CPG (a swing phase EMG burst was seen at faster walking speeds in two cats; see above). The inhibition of St following sural stimulation (Fig. 4) is less easily explained and would seem to call for a special circuit. Kinematically, it would be useful to modify the usual flexion reflex in response to a sural input; this nerve innervates the posterior surface of calf, and knee flexion produced by St would only increase contact with the presumed offending object.

The reflex excitation of BFm, a muscle compartment that was coactive with BFa as an extensor during locomotion (Fig. 8), was an exception to the typical parallelism in locomotor and cutaneous reflex recruitment patterns. Botterman et al. (1983) have shown that there are two subgroups of motoneurons innervating BFm that differ in their Ia receptivity with the knee flexors. Ia inputs from BFp and St project to some BFm motoneurons and not to others, in contrast to Ia inputs from the hip extensors that are uniformly distributed to all BFm motoneurons. The mixed locomotor and cutaneous reflex synergy observed in BFm suggests that BFm motoneurons receive extensor inputs from the locomotor CPG and flexor inputs from FRAs, similar to the mixture of flexor and extensor Ia receptivity that exists in BFm. The distribution of flexor and extensor coupled inputs to BFm motoneurons may allow BFm to function flexibly as a transitional unit sandwiched between a classical extensor (BFa) and flexor (BFp) (see also Chanaud and Macpherson 1991). The flexible synergic coupling of BFm with either BFa or BFp observed during walking, scratching, and paw shaking is consistent with this interpretation. BFm activity was recorded in two cats in this study. Only the activity of BFm during walking is shown in Fig. 8, but in both cats, BFm was coactive with BFa during walking, with BFp during scratching, and all three compartments had different onsets during paw shaking. In addition, BFm was recruited differently than either BFa or BFp during postural perturbations (Chanaud and Macpherson 1991).

The mechanisms of reflex recruitment and modulation

Both excitatory and inhibitory cutaneous reflexes to flexor and extensor muscles were modulated during treadmill locomotion. The modulation of cutaneous reflexes may reflect either motoneuronal polarization or premotoneuronal processes. Use of EMG activity to estimate the excitability of the motoneurons (upon which reflex inputs must be superimposed) carries several limitations. When there is no background activity, it is impossible to say whether the motor pool is deeply hyperpolarized and largely refractory to excitatory input, or sitting just subthreshold and capable of a brisk response to a relatively small input. Obviously, in the absence of background activity, inhibitory inputs cannot be seen at all, and any excitatory reflexes that are smaller than those seen during background EMG activity may reflect "breakthrough" of large EPSPs riding on changing levels of hyperpolarization. Less obviously, the possible existence of "task groups" of motoneurons in double-bursting muscles (Hoffer et al. 1987) makes it difficult to compare reflex amplitude between EMG bursts because they may be generated by different populations of motoneurons. Even if both groups of motoneurons are affected similarly by the reflex input (as they appear to be in the case of sartorius motoneurons; Loeb et al. 1987), the numbers of motoneurons close enough to threshold to respond to the input may not be the same even during

EMG bursts of similar amplitude at different phases of the step cycle (see also Kernell and Hultborn 1990).

Taking these limitations into account, there were at least some patterns of reflex modulation that suggest premotoneuronal gating (e.g., response of TFLa to sural stimulation, Fig. 7; response of TEN to Sup Per stimulation, Fig. 3). There are two categories of premotoneuronal gating: presynaptic inhibition directly onto cutaneous afferents and hyperpolarization of interneurons interposed in the reflex pathway. Modulation of presynaptic depolarization of cutaneous afferents has been described during presumed cycling of the locomotor CPG in reduced preparations (Bayev and Kostyuk 1982; Dubuc et al. 1985, 1988; Gossard et al. 1987; Gossard and Rossignol 1988). Recent recordings of spontaneous (Gossard et al. 1987) and evoked dorsal root potentials (Gossard and Rossignol 1988) during fictive locomotion suggest that presynaptic inhibition is maximal during the flexion phase, at least in some afferents. This would be consistent with the decrease of the P1 amplitude in TEN during the middle of swing phase (Fig. 3). However, other excitatory reflexes were largest during the mid-swing phase, sometimes even when the muscle was not recruited (e.g., BFm in Fig. 8; GR and SM in Fig. 9). These would seem to require premotoneuronal facilitation of the sort found by Schmidt et al. (1987) for Sup Per EPSPs onto flexor motoneurons and argue against motoneuronal polarization determining reflex modulation. Another pattern of modulation, excitation during the active phase and inhibition during the inactive phase in both flexor and extensor motoneurons, was reported by Schomburg et al. (1981) in a reduced preparation. The variable patterns of modulation observed in different muscle regions and different experimental preparations most likely reflect the influence of descending pathways on interneurons mediating cutaneous reflexes (reviewed by Lundberg 1979 and Baldissera et al. 1981).

In unifunctional muscle regions, spread of excitatory reflex responses into the extension phases of the step cycle typically occurred only when the stimulus intensity was increased to levels of $\geq 2.0 \times T$ (Fig. 3). Since most reflex responses observed were mediated by the same class of afferents (as judged by latency), the excitation of muscles during their inactive phase of the step cycle was probably due to a spatial facilitation of excitatory inputs to motoneurons that exceeded their levels of reciprocal (or other) inhibition. Another possibility is alternative cutaneous reflex pathways that require spatial facilitation for their interneurons before they can excite motoneurons (see also Jankowska et al. 1973 and Lundberg 1979).

It seems likely that the interneuronal circuits for these short-latency, low-threshold reflexes are quite simple, perhaps consisting of a single interneuron onto which inputs from the primary afferents and the CPG must converge. The amplitude of these reflexes seemed to correspond to the relative amplitude of the compound nerve potential associated with fibers conducting around 70 m/s (compare Figs. 3 and 10). For an afferent conduction distance of 220 mm from the Sup Per nerve to the spinal cord, this represents an ascending delay of 3.1 ms. The motor delay would be about 2.3 ms (about 100 mm at 80 m/s plus 1 ms delay for neuromuscular transmission). The reflex latency was about 8 ms (± 1 ms uncertainty due to the bin integrators), leaving only 1.6–3.6 ms for interneuronal relays in the spinal cord.

The half-center model of the locomotor CPG proposed by Jankowska et al. (1967a, b) was based on the late (≥ 100 ms), long-lasting effects of FRAs on interneurons and motoneurons that were disinhibited by the administration of DOPA in acute spinal cats. The short latency effects produced by FRAs were reported to be depressed by DOPA. However, this and other studies of cutaneous reflexes in awake, freely walking cats (Abraham et al. 1985; Loeb 1987; Loeb et al. 1987; Pratt and Loeb 1991) have shown that short latency excitatory and inhibitory effects are produced in leg muscles by stimulation of low threshold cutaneous afferents. Thus, the short latency pathways from low threshold cutaneous afferents do not appear to be depressed during locomotion in intact, awake animals. In fact, the similarity in locomotor and reflex synergies and the modulation of the observed reflex responses during locomotion suggests that at least some of the interneurons receiving input from the locomotor CPG also receive inputs from low threshold cutaneous afferents. This indirect evidence is consistent with the observation made by Jankowska and her colleagues (1967b) that many of the reciprocally coupled interneurones activated at long latencies after DOPA were also excited at short latency by FRAs. The fact that both short latency and alternative pathways from FRAs to flexor and extensor motoneurons are more evident in normal cats than in acute spinal cats (Holmqvist and Lundberg 1961; Lundberg 1969) suggests that descending inputs play an important role in determining which FRA pathways are activated.

Stimulus specificity of cutaneous reflexes

Our data clearly indicate that there are specializations in the projections of certain species of cutaneous afferents and their target motoneurons. In the present study, low to medium threshold plantar afferents had little effect on the thigh muscles. These observations are consistent with Engberg's (1964) observation that the plantar pad had little synaptic effect in BFp and St. While sural, Saph and Sup Per all had powerful effects on thigh muscles, there were significant differences among these cutaneous nerves in both the quantitative and qualitative features of their evoked reflexes, as shown in Figs. 3, 7 and 8. These results are consistent with the differential effects of various cutaneous nerves observed by others in hindlimb muscles (Hagbarth 1952; Loeb 1987, but see Abraham et al. 1985) and in hindlimb motoneurons (Fleshman et al. 1984; Omeniuk et al. 1986; Schomburg and Steffans 1986; LaBella et al. 1987; Schmidt et al. 1988, but see Schomburg et al. 1981).

As noted previously, the reflex responses evoked by sural stimulation were exceptional in their bias towards inhibition in some flexors (St, GR and TFLa). The synergists St, BFp and TEN, typically receive very sim-

ilar profiles of synaptic input. The inhibition of St, but not BFp or TEN, by sural afferents cannot be explained on the basis of differences in motoneuron properties, since all three muscles have similar histochemical profiles (Ariano et al. 1973; Lev Tov et al. 1988; Chanaud et al. 1991b). Distinctive inhibition of the flexors, tibialis anterior (Hagbarth 1952) and flexor digitorum longus (Fleshman et al. 1984; Abraham et al. 1985), by sural afferents has also been reported.

The knee flexors, BFp, St and TEN, displayed similar activation patterns during locomotion. TFLa also was usually activated as a flexor during locomotion, but its phase relationship with the three hip extensor, knee flexor synergists was variable. The reflex responses evoked in these four flexors were highly specialized. Only BFp and TEN were consistently excited by all four cutaneous nerves. Among the three tightly coupled synergists (BFp, St and TEN), only St was inhibited by sural stimulation. All three muscle regions were excited by cutaneous afferents, but there were significant qualitative differences in the form of the excitatory response evoked in these motor nuclei. For example, Sup Per stimulation evoked a triphasic excitatory response in St (Fig. 4) and a monophasic response in TEN in the same cat (Fig. 3). Other examples include the differential effects of Sup Per and sural on TFLa (Fig. 7) and of Saph, sural, and Sup Per on GR (Fig. 9). Differential effects of other FRA afferents (group II and III muscle afferents) on ankle and knee flexor synergists have also been reported (Holmqvist and Lundberg 1961; Lundberg et al. 1987).

Conduction velocity measurements of cutaneous afferents activated at different stimulus intensities indicated that, in most cases, both the excitatory and inhibitory components of complex reflex responses were mediated by the lowest threshold ($A\beta$) cutaneous fibers. Occasionally, the appearance of additional long latency reflex components may have involved the recruitment of higher threshold $A\delta$ fibers, but recruitment of a larger percentage of the faster fibers cannot be ruled out. Leahy and Durkovic (1988) reported that the reflex effects evoked from both classes of afferents in flexor motoneurons were similar. None of the responses reported in this paper involved high threshold, unmyelinated cutaneous fibers. The fact that some muscle regions were both excited and inhibited by the same class of afferents within a given nerve is consistent with available data indicating that there are multiple, parallel excitatory and inhibitory pathways from cutaneous (and other FRA) afferents to flexor and extensor motoneurons (Hagbarth 1952; Holmqvist and Lundberg 1961; Lundberg 1975, 1979; Pinter et al. 1982; Fleshman et al. 1988). Our data indicate that during locomotion in intact cats the alternative cutaneous reflex pathways have a greater influence on motoneurons innervating bifunctional than unifunctional muscle regions.

These data indicate that while some spinal interneurons receive input from the wide receptive field of FRAs, it is also apparent that some premotoneuronal neurons receive selective input from subgroups of cutaneous afferents. Furthermore, despite the tremendous convergence of multiple sensory input systems onto spinal interneurons (for review see McCrea 1986), their net effects are generally manifested as consistent and distinctive reflexes in specific muscle subregions. An appreciation of both the global and specialized actions of cutaneous afferents is necessary, therefore, to understand fully their contribution to the control of natural movements. The parallel specializations in the intramuscular distribution of CPG and cutaneous afferent inputs observed are consistent with the suggestion that low threshold cutaneous afferents (and other FRAs) function to provide movement-related multisensory reinforcement of FRA pathways selectively activated by descending commands and projecting to different "functional units" (Lundberg et al. 1987; Hultborn and Illert 1990). Since all of the reflex responses observed in this study were evoked by myelinated, low threshold cutaneous afferents, it is likely that the population of cutaneous afferents that were electrically evoked in this study could be activated naturally during movement, as suggested by others (Lundberg 1979; Lundberg et al. 1987).

Functional classification of muscles

Evidence has accumulated over many studies that inputs from proprioceptive afferents, cutaneous afferents, and CPGs can be differentially distributed among the motoneurons that control muscles with heterogeneous mechanical actions on the skeleton. Five thigh muscles in the cat, BF, GR, SM, TFL and sartorius (SA) have intramuscular subregions that are differentially activated during natural movements (Engberg and Lundberg 1969; Hoffer et al. 1987; English and Weeks 1987; Chanaud et al. 1991b; Pratt and Loeb 1991). At present, no consistent pattern in the intramuscular distribution of reflex inputs to these bifunctional muscles is apparent, however. There is a differential distribution of cutaneous reflex inputs during walking in BF and TFL but not GR, SA or SM (Eccles and Lundberg 1959; Pratt and Loeb, 1991). Conversely, projections from various sources of spindle primary afferents are differentially distributed within BF, SA and SM, but not GR or TFL (Eccles and Lundberg 1958; Botterman et al. 1983; Hamm et al. 1985).

Because no common patterns exist as to which species of inputs are differentially distributed, and because the differential activation of functionally complex muscles is movement-specific, no simple functional classification of broad, bifunctional muscles, or their intramuscular subregions, is appropriate. It appears that the central nervous system can use differentially distributed input systems to subdivide these muscles into functional modules or homogeneously distributed sources of inputs to recruit the anatomical whole as a functional unit depending upon the mechanical requirements of the intended movement.

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