Exp Brain Res (1993) 96:125–140

Experimental Brain Research

The distal hindlimb musculature of the cat: interanimal variability of locomotor activity and cutaneous reflexes

G.E. Loeb

MRC Group in Sensory-Motor Physiology and Bio-Medical Engineering Unit, Queen's University, Kingston, Ontario, Canada K7L 3N6

Received: 21 August 1992 / Accepted: 6 May 1993

Abstract. During stereotyped behaviors such as locomotion, patterns of muscle recruitment are usually quite consistent from animal to animal, even in the face of many surgical and pharmacological reductions. However, as studies of musculoskeletal structure, neuromuscular architecture, and sensorimotor circuitry become more detailed, it is important to ask whether there is some level of organization at which individual differences begin to dominate. This study concentrated on the small muscles of the foot and ankle, using standardized methods that consistently record stereotypical electromyographic activity from prime mover muscles and that permit well-calibrated stimulation of cutaneous nerves to elicit reflexes during treadmill locomotion. Some muscles (particularly the main ankle extensors, triceps surae, and plantaris) had stereotyped activity during both unperturbed locomotion and reflex responses. Others had stereotyped activity during locomotion but variable reflex patterns among animals (tibialis anterior, extensor digitorum longus, flexor hallucis longus, and peroneus brevis). Still others had variable locomotor activity but reflexes that were consistent (flexor digitorum longus) or variable for only peroneal nerve stimulation (peroneus longus), only plantar nerve stimulation (peroneus tertius), or the two (flexor digitorum brevis). Among muscles with interanimal variability, there seemed to be no particular correlation between locomotor and reflexive recruitment in a given animal. This functional heterogeneity is discussed in terms of the development of locomotor and reflex programs and in the context of structural heterogeneity of some of these muscles that is described in the companion paper.

Key words: Muscles – Locomotion – Reflexes – Cat

Introduction

Most musculoskeletal systems contain more muscles than degrees of freedom. In principle, most motor behaviors can usually be accomplished by a large number of different patterns of muscle recruitment. In practice, a more limited range of patterns is usually observed in repeated trials by a single subject and even across subjects with similar physiognomy. It is often assumed that the preferred patterns reflect optimal solutions for an implicit performance criterion such as minimizing energy consumption or mechanical stress, or maximizing speed or endurance (e.g., Chow and Jacobson 1971; Davy and Audu 1987; Pandy et al. 1990; Oguztoreli and Stein 1990).

There are two fundamentally different mechanisms for the discovery and encoding of such optimal solutions:

1. If the behavior is learned, then presumably the nervous system arrives at its preferred motor pattern by a process of trial and error, perhaps by reinforcing synaptic connections according to performance criteria that are sensed during each trial performance.
2. If the behavior is innate, then presumably the pattern of neural connections that produces the desired motor output becomes encoded genetically by evolutionary selection according to performance criteria related to competitive "fitness."

In either case, the application of fixed performance criteria to identical mechanical systems would be expected to lead to identical optimal solutions in all subjects. Variations between individuals would then reflect randomly distributed fluctuations in the expression of the optimal pattern or in the degree of convergence upon that pattern. In studies concerned with either the optimal solution itself or its embodiment in the neural circuitry, it would then be appropriate to pool data from multiple subjects by simply averaging out these random variations.

In complex mechanical systems, however, even a single performance criterion may exhibit multiple local minima in the multidimensional space of all possible motor programs that accomplish the nominal task. For example, the task of the athletic high jump can be performed using two completely different motor strategies that produce almost identical performances optimized for height

Correspondence to: G.E. Loeb, Abramsky Hall, Queen's University, Kingston, Ontario, Canada K7L 3N6

(the Western forward roll and the Fosbury flop). An athlete who starts practicing one particular strategy will come to perform better and to prefer using that strategy, while another athlete may come similarly to prefer and excel with the other. Clearly, it would be inappropriate to average together the optimal motor programs generated by these two athletes; any such average would almost certainly perform the task poorly, if at all.

It is also the case that subtle differences in the mechanical system of a given subject may cause one of several nominally similar programs to be preferred in that subject. The systematic practice of that program might, in turn, induce further modifications of the mechanical system, permitting the subject to explore regions of the performance space that might not be encountered by other individuals. Long-distance runners have been divided into "rearfoot strikers" and "midfoot strikers" on the basis of distinctive temporospatial patterns of loading of the sole of the foot during the stance phase (Cavanagh and Lafortune 1980). Presumably, these patterns require different patterns of torque production by the ankle muscles, particularly the human analogues of several of the muscles described in this study in cats. Unfortunately, it is not clear whether such preferences correlate with the considerable anatomical variability of the human foot and ankle.

The hypothesis of this study is that some of the interindividual variation that is seen in EMG patterns associated with locomotion may arise not from randomly distributed processes distributed around a single mean but from dichotomous processes such as those described above. If this hypothesis is true, it suggests that adaptive processes and functional plasticity may play an important and heretofore unrecognized role in the operation of spinal central pattern generators (CPG; Sherrington 1910; Graham-Brown 1911; Lundberg 1980; for review, see Delcomyn 1980). However, this hypothesis is difficult to test in electrophysiological studies because large differences between subjects can be produced artifactually by surgical and pharmacological procedures required for acute studies and by electrical and mechanical variability of implanted devices required for chronic studies. Over many years of steady improvement in the devices and analytical techniques for chronic kinesiological studies in animals, patterns of recruitment reported for some muscles and some behaviors became more reliably similar. However, for others the problem of interanimal variability has persisted in the face of a decreasing number of plausible methodological explanations (e.g., O'Donovan et al. 1982; Moschovakis et al. 1991).

The devices and analytical techniques employed in this study were selected and designed to minimize and to control for methodological variability between subjects. The study compared electromyogram (EMG) patterns from both small and large muscles of the foot and ankle during unperturbed locomotion and in response to cutaneous nerve stimulation during treadmill walking. The general conclusion is that certain muscles tend to be used consistently but idiosyncratically by different subjects in various behaviors.

Materials and methods

Several preliminary experiments were performed to design stimulating and recording electrode arrays and surgical approaches that would provide the best electrophysiological signals (in terms of signal-to-noise ratio and reproducibility) without interfering with normal behavior. These included cadaver dissections and the fabrication and implantation of electrodes for these nerves and muscles in conjunction with other ongoing experiments. Complete, identical experiments reported here were performed on six adult cats (2.3–3.0 kg) of either sex. Each experiment involved the following steps:

1. A cat was selected and trained to walk continuously with a normal and consistent gait for several minutes on an enclosed, motorized treadmill belt. We used only positive reinforcement (food) and constant belt speeds at the walking rate preferred by the animal, which results in a highly consistent diagonal-couplet gait typical of overground locomotion (Lockard et al. 1976; Blaszczyk and Loeb 1993).
2. A complete, fresh set of recording and stimulation devices was fabricated for the nerves and muscles of each cat (as indicated in Fig. 1 and Table 1). The medial gastrocnemius (MG) muscle was also implanted with length and tendon strain gauges (Loeb et al. 1980); the time courses of their recorded signals were used to

Table 1. Muscles implanted with electrodes

Full name	Abbreviation	Actions[a]	Notes
Tibialis anterior	TA	Ankle dorsiflexor/invertor	EMG from deep surface to avoid fiber-type segregation (Chanaud et al. 1991)
Peroneus longus	PL	Ankle abductor/flexor	Flexor moment arm varies greatly
Extensor digitorum longus	EDL	Ankle flexor/digit extensor	
Flexor digitorum longus	FDL	Ankle adductor/digit flexor	
Flexor hallucis longus	FHL	Ankle extensor/digit flexor	
Peroneus brevis	PB	Ankle abductor/evertor	
Peroneus tertius	PT	Ankle abductor/digit abductor	
Flexor digitorum brevis	FDB	Digit flexor/ankle extensor	Partially in series with PLA
Lumbricals	LUM	Digit adductors	Miscellaneous deep plantar foot muscles
Plantaris	PLA	Ankle extensor/digit flexor	Partially in series with FDB
Soleus	SOL	Ankle extensor	
Medial gastrocnemius	MG	Ankle extensor/knee flexor	
Lateral gastrocnemius	LG	Ankle extensor/knee flexor	

[a] Predominant actions as determined by Young et al. (1993)

determine step cycle phases, but they were not calibrated in absolute units (which requires an acute experiment on the same day as the recordings).

3. Electrodes and transducers were implanted and connected to a percutaneous connector (as described in Hoffer et al. 1987) during aseptic surgery with the animal under deep pentobarbital anesthesia.
4. The cat recovered from surgery for several days, during which we measured daily the impedance of each electrode contact and the threshold at which electrical stimulation of each cutaneous nerve evoked a compound action potential in the proximal nerve trunk.
5. Approximately ten recording sessions of 5–10 min each were conducted over 1–2 days, during which the animal walked on the treadmill while electrical stimuli of graded intensity were delivered to the cutaneous nerves. EMG (50–5000 Hz) and neurograms (1–10 kHz) were recorded from all available channels on an 18-track FM tape recorder (Sangamo Sabre IV) synchronized to a videotape recorder (60 field/s, 400 lines resolution) by a time-code generator (IRIG-B; Datum).
6. A terminal physiological experiment was carried out with the animal under deep pentobarbital anesthesia (within 2 days of the last recording session). A wide range of electrical stimulation amplitudes were applied to the cutaneous nerves through their chronically implanted nerve-cuff electrodes, and precise compound action potentials were recorded by a signal averager from the chronically implanted, nerve-cuff electrodes on the proximal nerve trunks.
7. The locations of the implanted devices were verified by postmortem dissection.

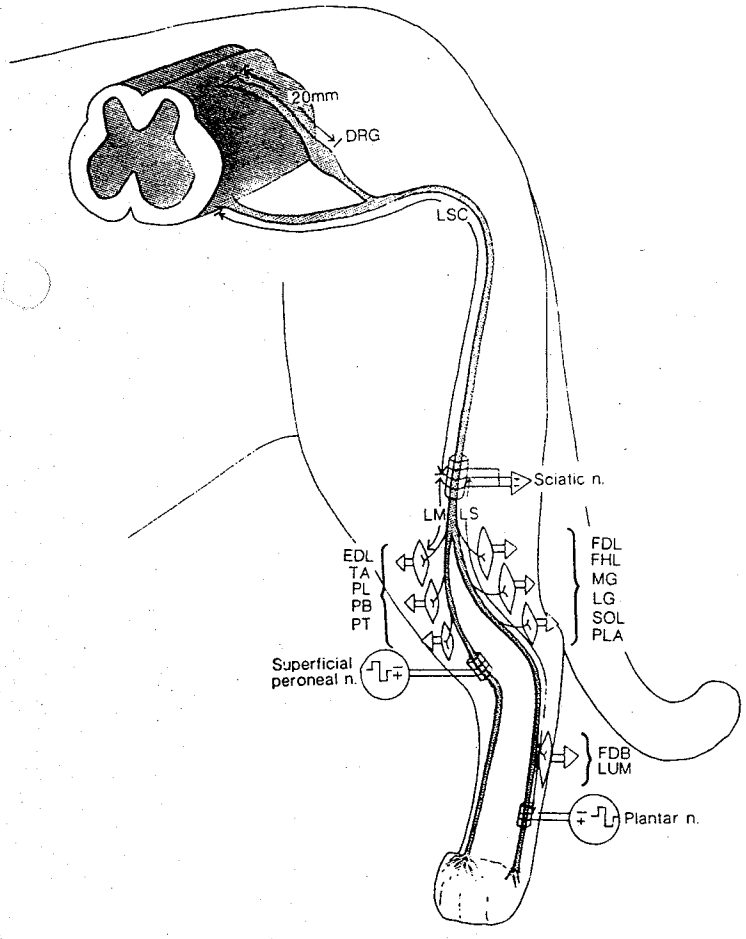

Fig. 1. Schematic arrangement of implanted devices, showing distance measurements used to estimate afferent and efferent conduction delays. *LSC*, distance from recording nerve-cuff on sciatic nerve to spinal cord; *LM*, distance from sciatic nerve to various muscles; *LS*, distance from stimulating nerve-cuffs to sciatic nerve recording site, used to calculate base conduction velocity of afferents; *DRG*, dorsal root ganglion. Muscles: *EDL*, extensor digitorum longus; *TA*, tibialis anterior; *PL*, peroneus longus; *PB*, peroneus brevis; *PT*, peroneus tertius; *FDL*, flexor digitorum longus; *FHL*, flexor hallucis longus; *MG*, medial gastrocnemius; *LG*, lateral gastrocnemius; *SOL*, soleus; *PLA*, plantaris; *FDB*, flexor digitorum brevis; *LUM*, lumbricals

Sequences from videotape were selected in which stimuli of the desired amplitude were delivered while each animal walked with a steady gait. Multichannel data recorded during these periods were digitized using a locally developed PASCAL program on a PDP-11/73 computer that recorded continuous data from certain key channels used to define the onset of various phases of locomotion and from all channels at 1-ms intervals in brief peristimulus bursts. EMG records were full-wave rectified and integrated into synchronous 1-ms bins prior to digitization (Bak Electronics PSI-1; Bak and Loeb 1979). Peristimulus records were selected for regularity of gait preceding the stimulus and ordered into rasters based on phase in the step cycle at which each stimulus occurred. Responses were grouped and averaged into various phases in the step cycle and various peristimulus latencies in order to discern general trends. Peristimulus events occurring near the transitions between step cycle phases were excluded from the means because of uncertainties in the waveform criteria used to estimate phase. Phase boundaries for selecting traces to be averaged were shifted slightly before the actual times of footfall and footlift because the recruitment of the muscles typically leads these mechanical events.

As noted in the references above, each of these methods has been described in detail previously (see also Pratt et al. 1991). Figure 1 shows the arrangement of recording and stimulation electrodes relative to the main nerve trunks of the distal hindlimb. Each animal was implanted with stimulating electrodes on the superficial peroneal nerve (exclusively cutaneous to dorsal paw) and plantar nerve (distal to branches to intrinsic muscles of the foot; exclusively cutaneous to plantar paw). These electrodes were bipolar nerve cuff electrodes with circumferential contacts of stranded stainless steel spaced 4 mm apart within a soft, pliable plastic (Silastic) tube 12 mm long and 2–3 mm inside diameter (selected to be at least 40% larger in diameter than the nerve as measured at surgery). A recording nerve-cuff electrode with three such contacts (4 mm diameter) was implanted on the sciatic nerve proximal to the bifurcation of the tibial and peroneal nerves. This was used in a "tripolar" configuration with an impedance coupling transformer (Hoffer et al. 1981; Stein et al. 1977) to record evoked potentials in the sciatic nerve.

EMG recordings

All of the recording electrodes were bipolar, epimysial "patch" electrodes in which a polyester fiber- (Dacron)-reinforced Silastic sheet was used to position a pair of contacts over each muscle so that the contacts were separated by 3 mm along the fiber direction of each muscle. Each contact was 3 mm long so that it spanned most of the width of the smaller muscles, presumably summing potentials from most of the cross-section of the muscle. Usually a single patch carried two or more pairs of electrodes on both surfaces so that the dielectric patch material served as an insulating shield to reduce cross talk from adjacent muscles (see Loeb and Gans 1986). For superficial muscles, the patch was placed on the deep surface with contacts facing out toward the skin: This would have read more easily with abbreviations only as originally written – the abbrev. have already been well introduced in Table 1 and are used alone elsewhere tibialis anterior (TA), peroneus longus (PL), flexor digitorum longus (FDL), flexor digitorum brevis (FDB), MG, and lateral gastrocnemius (LG). For deep muscles lying directly on bone, the patch was placed on top of the muscle with the contacts facing inward: flexor hallucis longus (FHL), peroneus brevis (PB), lumbricals (LUM) and soleus (SOL). For intermediate muscles, an extension of the patch or another patch was arranged so as to encircle the muscle entirely: extensor digitorum longus (EDL), peroneus tertius

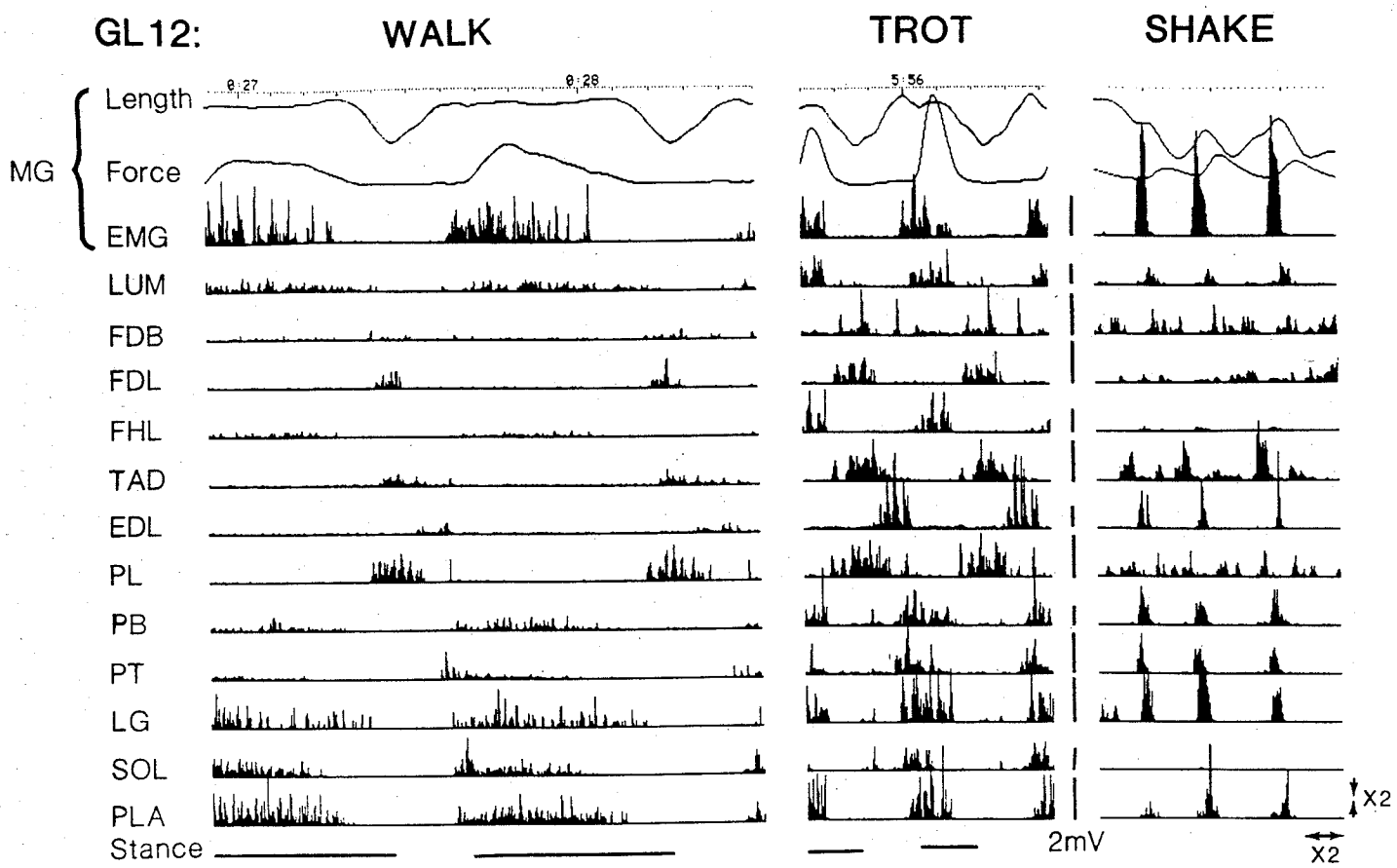

Fig. 2. Typical set of digitized records from implanted devices during unperturbed behaviors (cat GL 12); see Table 1 for muscle abbreviations. Traces *from top*: time scale (seconds, tenths and hundredths); medial gastrocnemius (MG) muscle length and force from implanted transducers (uncalibrated, for timing information only); rectified and bin-integrated electromyogram (EMG) records from all muscles; *stance bars* determined from inflections in length and force records and confirmed by videotaped still fields. *Vertical calibration bars* for EMG traces indicate 2 mV amplitude referred to amplifier input for Walk and Trot records. Shake record expanded $\times 2$ in *horizontal axis* and compressed $\times 2$ in *vertical scale* to accomodate rapidly modulated, intense muscle recruitment

(PT), and plantaris (PLA). In the preliminary experiments, several small changes in the arrangement of these patches were tried to determine whether the EMG recordings were independent of such methodological details. The recorded EMGs seemed to be independent of the patch configurations as long as they adhered to the design principles described in Loeb and Gans (1986), but care was taken always to position the patches similarly in all of the animals reported here. Tibialis posterior was not instrumented in these studies because it is difficult to reach without compromising other muscles, and because its locomotor and reflex activity have been studied previously (Abraham and Loeb 1985; Abraham et al. 1985) and found to be consistent and similar to the major ankle extensors. A two-sided patch electrode was used under FDB to shield it from the underlying, small intrinsic muscles of the foot; the signals recorded from the inner surface presumably arose from the LUM (and perhaps interosseus) muscles.

Figure 2 shows a typical set of transducer and bin-integrated EMG recordings during unperturbed, natural behaviors that tend to recruit these muscles over broad dynamic ranges and different patterns of synergy. Except as noted in Fig. 9 and Table 3, similar recordings were obtained in all six animals. The absence of cross talk between muscles can be verified by identifying times in these records where each muscle is silent while adjacent muscles are recruited vigorously.

Stimulation

The sciatic nerve recordings were used to calibrate the stimulus amplitudes in terms of fiber classes that could be recruited, as shown in Fig. 3. Stimuli were always symmetrically biphasic pulses with a duration of 0.1 ms/phase, delivered via photoisolated, current-regulated stimulator (Bak Electronics BPG-1, BSI-1) with the cathode-first phase on the proximal contact of the bipolar nerve-cuff. They were presented at a regular interval of 1.3 s as the animal walked asynchronously with a step cycle duration of about 0.8 s, so that there was always at least one complete, unstimulated cycle between stimuli and so that 100–120 stimuli were scattered fairly evenly over the step cycle phases in the course of a 2- to 3-min period of regular walking. Individual peristimulus recordings are shown in raster form in Fig. 3A for stimulation of the superficial peroneal nerve at twice threshold for the recruitment of the fastest axons ($2 \times T$). These sciatic nerve signals were rectified and bin-integrated before digitizing and the individual traces ordered according to the relative phase of the step cycle in which the stimulus occurred. The sharp, short-latency waveforms (arrow on time base) indicate constant recruitment by the stimulus in all step cycle phases.

Figure 3B,C shows a full set of averaged evoked potentials (unrectified so that asynchronous interference from EMG is eliminated) recorded at constant gain during eight such stimulus runs. In general, the responses to stimulation of the superficial peroneal nerve conformed to classic divisions of cutaneous nerve fibers from hairy skin (Burgess et al. 1968), with distinguishable and progressively recruitable populations of fast (presumably G1 hair), intermediate (presumably G2 hair), and slow (presumably D hair) receptors. The actual conduction velocities computed from these records have been distorted by partial overlap of the various waveforms and by the fact that they reflect only a segment of the conduction path from

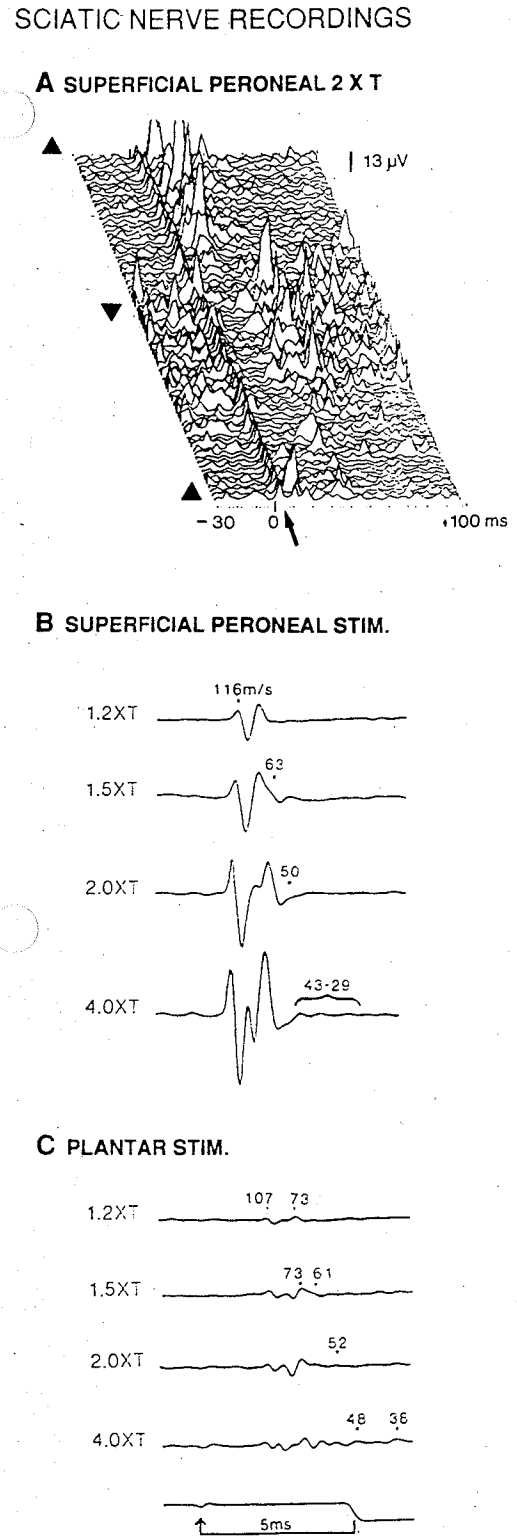

Fig. 3. A Rectified individual peristimulus traces (30 ms before – 100 ms after 2.0 × threshold (*T*) stimulus to superficial peroneal nerve) ordered according to relative step cycle phase (*upward black triangles*, footlift; *downward black triangle*, footfall); *arrow* points to nerve volleys, other deflections reflect EMG pick-up by nerve-cuff electrode. **B,C** Averaged evoked potentials recorded in sciatic nerve (*n* = 64) for different stimulus sites and intensities vs threshold. *Dots above traces* indicate the estimated onset of the longest latency nerve volley associated with that particular stimulus intensity and associated conduction velocity in meters per second. These were normally determined at vertical gains appropriate for each trace; gains shown here are identical for each trace, to facilitate comparison of nerve volley amplitudes

skin to spinal cord, over which conduction velocity changes considerably (Rindos et al. 1984). Note that at gains suitable for showing the large volleys associated with peaks at 116 and 63 m/s conduction, the small, longer latency volleys are barely discernible. The plantar nerve responses were consistently smaller, slower, and less homogeneously recruitable, as evidenced by the ragged, polyphasic waveforms even at 1.2 times threshold for the first detectable evoked potentials, and even with averaging of 64 traces as shown here. The plantar afferents presumably included substantial contributions from the glabrous skin of the foot and toe pads as well as the hairy skin.

Table 2 provides estimated conduction delays in the sensory and motor pathways to and from the spinal cord, which have been used to estimate central transmission delay in various reflex pathways. For each stimulus intensity, the maximal sensory conduction delay has been calculated based on the conduction distances measured in that animal and the conduction velocity of the slowest afferent fiber class just recruited at that intensity. These have been corrected for the changes in conduction velocity that have been documented over various segments of the afferent fibers proximal and distal to the dorsal root ganglion (Rindos et al. 1984). The motor conduction delays are based on estimated conduction delay for motoneurons with an axonal conduction velocity of 80 m/s plus 1 ms for neuromuscular junction delay and 1 msec for conduction along the muscle fibers. They agree generally with delays measured by stimulating the sciatic nerve electrode and recording from the EMG electrodes, but these measurements were not used because they were difficult to interpret in the face of massive but often inhomogeneous activation of the large muscles supplied by the whole sciatic nerve. It should be noted that even with the circumferential cuff electrodes used to stimulate the small cutaneous nerves, fibers of a given caliber tended to be recruited over a fairly broad range of stimulus levels, as indicated by the growth of the various peaks shown in Fig. 3. Thus, changes in reflexes associated with increasing stimulus intensity could be caused either by recruitment of new afferent classes or by recruitment of additional members of a previously recruited class, depending on the connectivity to and thresholds of the various circuits. The method of integrating EMG into 1 ms bins and estimating reflex onset from the raster traces produces an uncertainty of about ±1 ms in the reflex latencies shown in Table 2 and discussed throughout this paper.

Each of the six animals was studied with at least five different stimulus intensities on each of the two cutaneous nerves. For each of the 13 instrumented muscles, rasters were prepared with approximately 90 peristimulus waveforms in each raster. Technical problems rendered unreliable one stimulating cuff in each of three animals and a total of eight EMG recording sites scattered over three animals. Thus, the following results have been extracted from about 700 rasters containing 63 000 events; examples are given to illustrate the most salient and/or general findings, which are summarized in Fig. 8 and Table 3.

Results

General responses to stimulation

In all six animals, short latency (8–30 ms) changes in muscle activity during locomotion were discernible at 1.2 × T for the fastest conducting axons. These reflexes generally became larger in amplitude and more widespread with increasing stimulus intensity. Stimuli up to 4 × T produced only small perturbations in the trajectory of the limb as determined by videotape and MG length-gauge recordings; these were confined to a slight exaggeration of flexion for stimuli delivered in mid-swing with no change in the locomotor rhythm of the cat, which seemed not to notice the stimuli. Stimuli at 8–10 × T produced

Table 2. Latencies of cutaneous reflexes (cat GL 12)

Muscle (motor delay, ms)	Stimulus							
	1.2 × *T*		1.5 × *T*		2.0 × *T*		4.0 × *T*	
	Sup. per. (2.7 ms)	Plantar (3.7 ms)	Sup. per. (5.0 ms)	Plantar (5.5 ms)	Sup. per. (7.0 ms)	Plantar (8.0 ms)	Sup. per. (11.3 ms)	Plantar (10.9 ms)
FDB (6.2)	–	–	E 9	E 11	E 9	E 11	E 11	E 12
FDL (4.3)	E 8	–	E 8	I 12	E 8	I 10	E 8 E 24 (8)	I 12
FHL (4.5)	–	–	I 9	I 11	I 9	I 12	I 9	I 11
TA (4.3)	–	–	E 24 (15)	–	E 10 E 24 (12)	–	E 9 E 23 (11)	E 14
EDL (4.3)	I 7	–	I 11 E 27 (18)	–	I 9	I 12 E 25 (12)	I 9 E 20 (5)	I 13 E 26 (13)
PL (4.3)	–	–	E 9 E 28 (19)	–	E 9 E 24 (13)	E 9?	E 8 E 22 (11)	E 11
PB (4.5)	–	–	–	–	–	I 13	I 10	I 13
PT (4.3)	–	–	–	–	I 9	I 13	I 10	I 12
LG (4.5)	–	–	I 9	–	I 9	I 12	I 9 E 25 (9)	I 12
SOL (4.5)	I 9	–	I 9	I 11	I 9	I 14	I 12	I 14
PLA (4.5)	I 9	–	I 9	I 11	I 9	I 12	I 9	I 12

The numbers in parentheses at the top of each column represent the total afferent conduction delay attributable to the slowest fibers recruited by the stimulus whose intensity is given at the top of each column in multiples of the threshold for the fastest fibers (× *T*). The numbers in parentheses at the beginning of each row represent the estimated efferent conduction delay from spinal cord to recorded EMG for each muscle. The numbers in the table proper indicate total latency in milliseconds for excitatory (E) and inhibitory (I) reflexes; numbers in parentheses indicate the maximal central delay based on the fastest afferent group that evoked the response; ? denotes inconsistent response. Sup. per., superficial peroneal nerve; other abbreviations as in Table 1

Table 3. Variability of activity for various muscles

Muscle	Sagittal action	Recruitment	Locomotion	Plantar reflex	Peroneal reflex
TA	Retraction	Swing	C	Variable	C
PL	Retraction	Swing	Variable	C	Variable
EDL	Retraction	Swing	C	Variable	Variable
FDL	Propulsion	Swing	Variable	C	C
FHL	Propulsion	Stance	C	Variable	Variable
PB	Propulsion	Stance	C	Variable	Variable
PT	Propulsion	Stance	Variable	Variable	C
FDB	Propulsion	Stance	Variable	Variable	Variable
LUM	Propulsion	Stance	C	None	None
PLA	Propulsion	Stance	C	C	C
SOL	Propulsion	Stance	C	C	C
MG	Propulsion	Stance	C	C	C
LG	Propulsion	Stance	C	C	C

C, constant in all animals; muscle abbreviations as in Table 1

more pronounced changes in gait, including yielding during stance and hesitation in paw placement at the end of swing. The animals seemed somewhat surprised and mildly annoyed at these sensations at first, hesitating and glancing toward the ipsilateral foot, but they usually walked regularly thereafter.

Stimuli presented during quiet standing in place had reflex effects that were similar to those for the same stimuli presented during midstance phase of locomotion. However, most of the stance-phase reflexes in response to moderate amplitude stimuli were restricted to inhibition of ongoing extensor activity. Because the recruitment of the extensor muscles was more irregular and generally lower during standing than during walking, these reflexes were sometimes difficult to discern. Paradoxically, the animals seemed much more disturbed by a given stimulus strength applied during standing than during locomotion, glancing repeatedly at their feet, so little testing was done beyond 2 × T.

Muscle recruitment that was common to all animals

The main ankle extensors (triceps surae) and the main ankle dorsiflexor (TA) consistently produced locomotor and reflex activity that agreed with classical studies of their function in both intact and many reduced prepara-

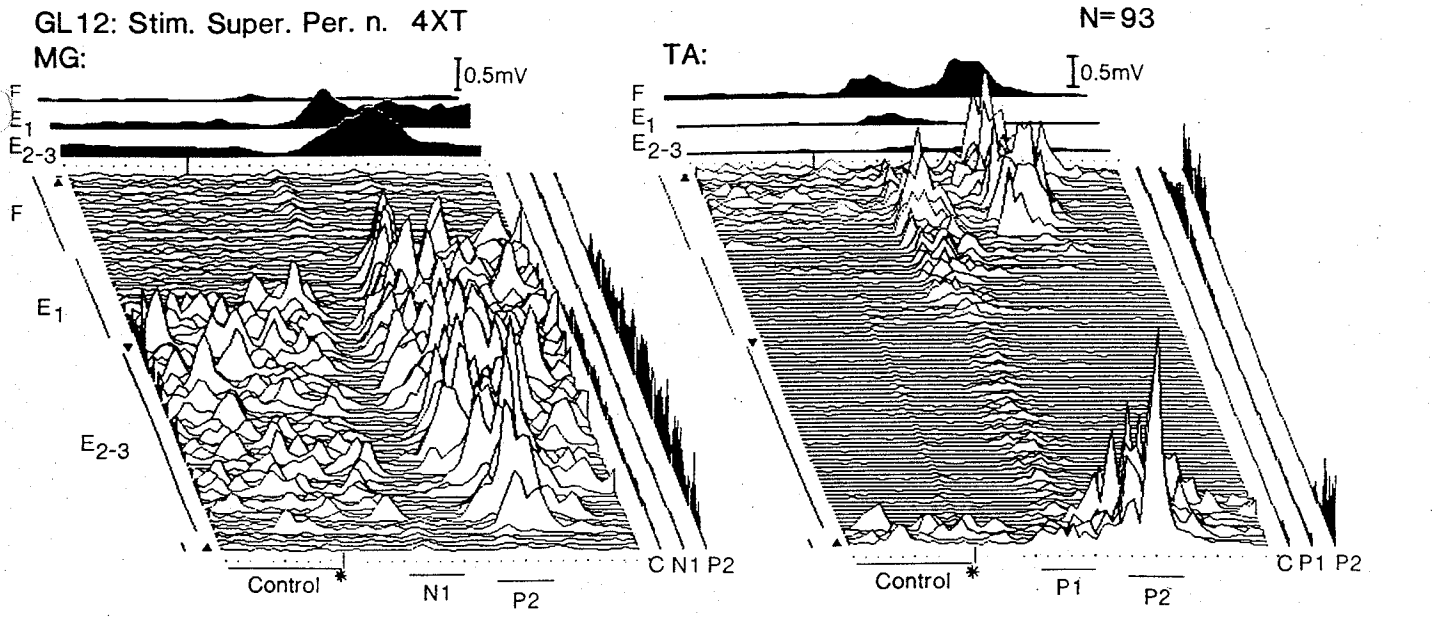

Fig. 4. Peristimulus rasters ordered by step cycle phase showing EMGs recorded simultaneously in medial gastrocnemius (MG) and tibialis anterior (TA) muscles in response to 93 stimuli of superficial peroneal nerve at 4 × threshold for the fastest conducting afferents (cat GL 12). *Time bar at bottom*, 20 ms before and 50 ms after stimulus presentation (*); regions marked *Control* (*C*), *N1*, *P1*, and *P2* correspond to diagonally oriented traces at *right edge* of each raster in which each data point represents the mean EMG value for the corresponding peristimulus period of the adjacent EMG trace. *Bars along the left diagonal edge* indicate Phillipson (1905) step cycle phases during which stimulus was presented (*F*, flexion; E_1, swing phase extension; $E_{2\text{-}3}$, stance); *small black triangles* indicate footlift (*upward*) and footfall (*downward*). The *traces bracketed by the bars* have been averaged to produce the correspondingly labeled, *filled plots at the top*; traces near the transitions have been excluded (note gaps between bars) because of uncertainty in their exact phasing. Bars have been phase-advanced slightly from Phillipson phases because of EMG phase-lead (note *short bar* including the last few traces at the end of the stance period at the *bottom of the rasters*, with the *F bars* at the *top*)

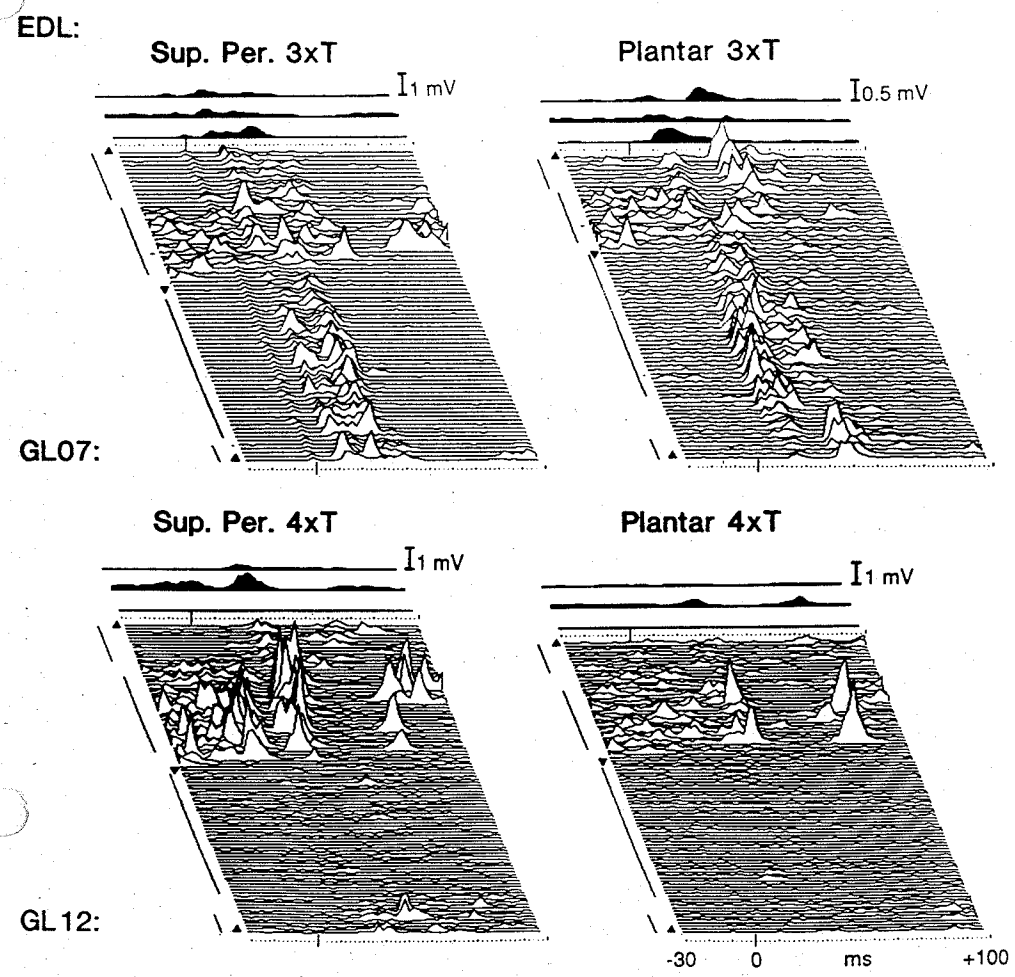

Fig. 5. Peristimulus rasters for extensor digitorum longus (EDL) muscle comparing two stimulus sites in two animals (*top*, cat GL 07; *bottom*, cat GL 12); mean traces at *top* keyed to step cycle phases indicated along *left margin* of each raster. *Sup. Per.*, superficial peroneal nerve; *T*, threshold

tions. Figure 4 illustrates the unusually clear view of their modulation afforded by the generally improved methods employed in this study. The raster for the MG (ankle extensor) shows a strong inhibition of the ongoing activity that normally occurs in this muscle and most ankle extensors during the late E_1 phase and most of the stance phase, followed by an increase that may arise from either postinhibitory rebound or a longer latency excitatory pathway. The TA (ankle dorsiflexor) and several other muscles had excitatory reflexes at two distinctly different latencies. In the example in Fig. 4, the longer latency reflex (P2 in the terminology of Duysens and Loeb, 1980) was much larger than the control activity, and tended to occur only during those periods of the step cycle when the muscle was normally recruited (end of E_3 phase at end of stance and F phase at beginning of swing). The shorter latency reflex (P1) was also quite robust, but it was phase delayed with respect to the control activity, reaching peak amplitude at a point in the step cycle when TA is normally derecruited and persisting as a small response even during stance phase.

Table 2 shows that stimulation of a given nerve at increasing currents above threshold tended to produce little change in the latency or phasing of the various components of the reflex responses in various muscles of a given animal. Most components were well-expressed at $1.5 \times T$ in superficial peroneal nerve and $2 \times T$ in plantar nerve; as stimuli were increased to $8 \times T$, the reflexes tended to become larger in amplitude or less modulated by step cycle phase but did not change qualitatively. One interesting finding was that inhibitory reflexes (N1) during stance-phase recruitment of ankle extensors usually had the lowest threshold of any responses (fully expressed at $1.2 \times T$), while inhibition of the prestance EMG in the triceps surae muscles was complete only at $1.5 \times T$. Both the short- (P1) and long- (P2) latency excitatory responses in ankle and digit flexors usually had slightly higher thresholds than N1 ($1.5 \times T$) and grew substantially up to $2–4 \times T$. In this narrow range of stimulus intensities, these gradients probably reflect spatial summation required to recruit different groups of interneurons rather than stimulation of different classes of afferents (see Fig. 3).

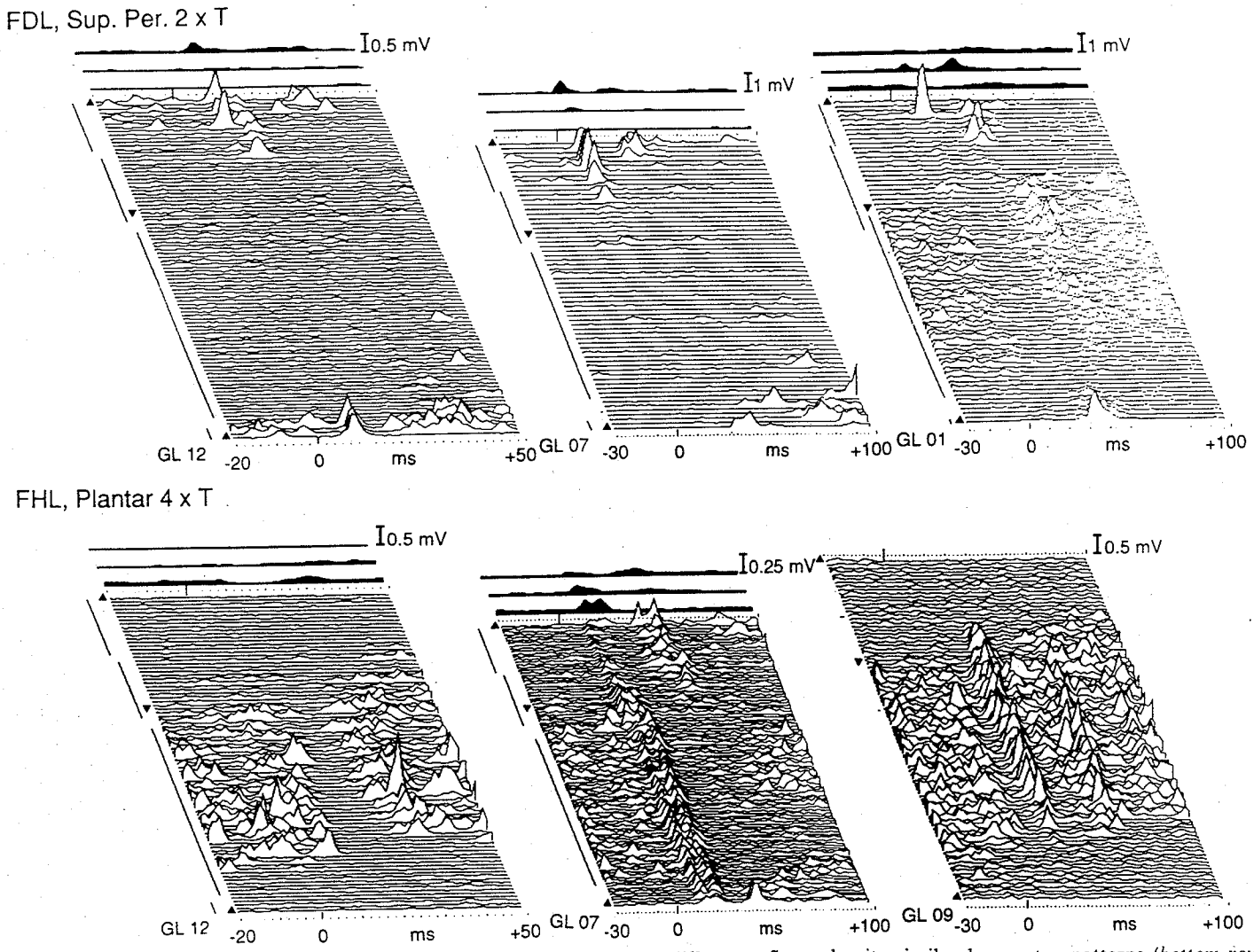

Fig. 6. Peristimulus rasters illustrating similar reflexes despite variable locomotor patterns (*top row*: *FDL*, flexor digitorum longus muscle, responding to stimulation of superficial peroneal nerve at $2\times$ threshold (*T*), in three cats, GL 12, GL 07, and GL 01) and different reflexes despite similar locomotor patterns (*bottom row*: *FHL*, flexor hallucis longus muscle, responding to stimulation of plantar nerve at $4 \times T$, in three cats, GL 12, GL 07, and GL 09). Note expanded time scale in rasters from GL 12 only

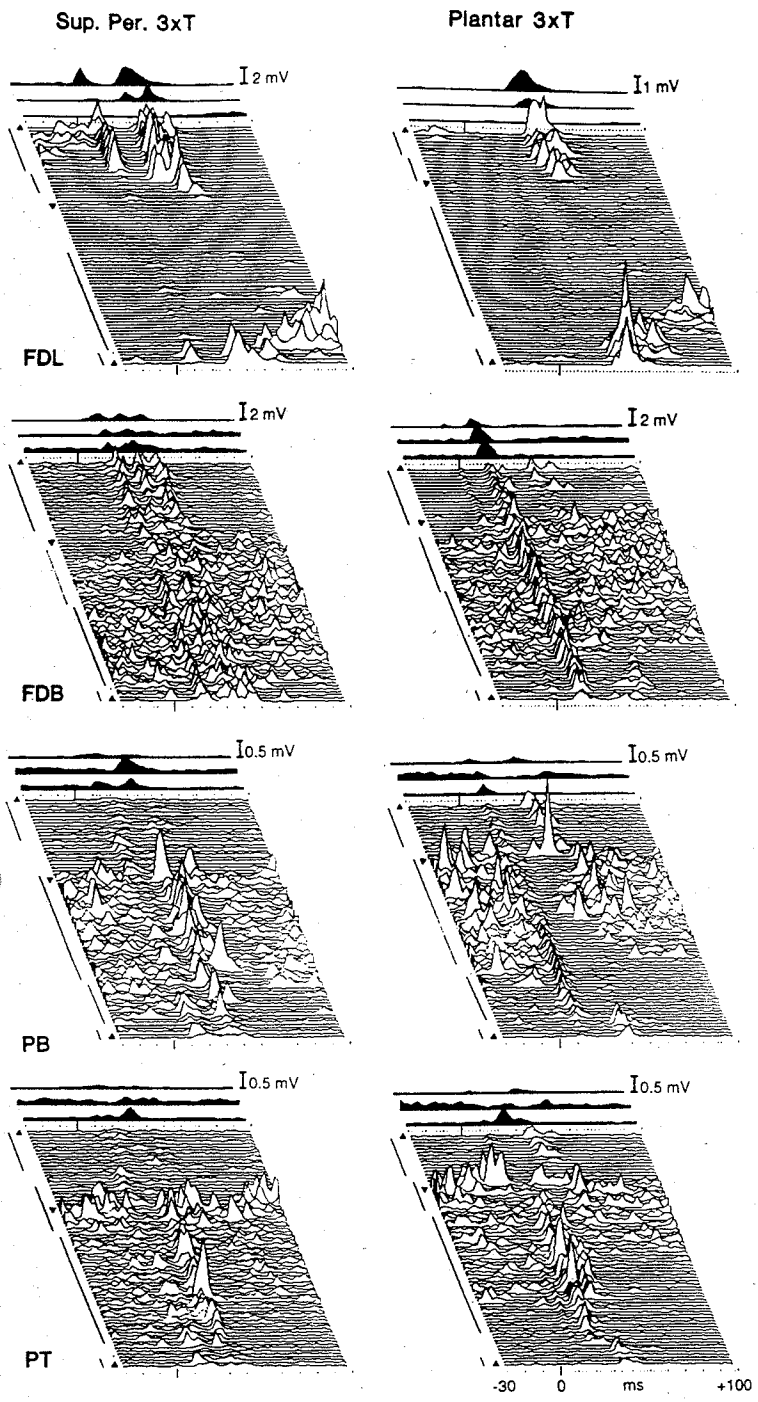

Fig. 7. Simultaneously recorded peristimulus rasters for four muscles (*FDL*, *FDB*, *PB*, and *PT*) in response to stimulation of superficial peroneal (*left*) and plantar (*right*) nerves at 3 × threshold (cat GL 07). Note that traces grouped into means at the *top* have been changed for each muscle to reflect gating patterns that do not always correspond to classical step cycle phases

Muscle recruitment that was animal-specific

Figure 5 shows an example of a muscle that had similar locomotor recruitment in all animals, but very different reflex responses from one animal to the next. EDL in the cat is capable of producing a large flexor moment at the ankle as well as extending the digits dorsally (Young et al. 1993). During unperturbed walking, it was consistently recruited strongly during the E_1 phase, when all other ankle muscles were silent (see prestimulus control activity in all four rasters of Fig. 5). Its reflex responses were quite complex but clear and consistent in a given animal. Cat GL 07 had strong P1 and P2 excitatory reflexes throughout much of the step cycle when stimuli were applied to either cutaneous nerve at 3 × T, although the two peaks were modulated differently through the step cycle (particularly for plantar stimulation). Paradoxically, the excitatory responses seemed to be weakest during E_1 when the motoneuron pool is already partially recruited by the locomotor CPG, perhaps even being replaced by inhibitory pauses (particularly for plantar nerve stimulation). In contrast, cat GL 12 had no excitatory reflexes during stance phase, even at higher stimulus intensities (4 × T shown here). P2 reflexes may have been present during swing phase, but they are difficult to separate from possible postinhibitory rebound following clear N1

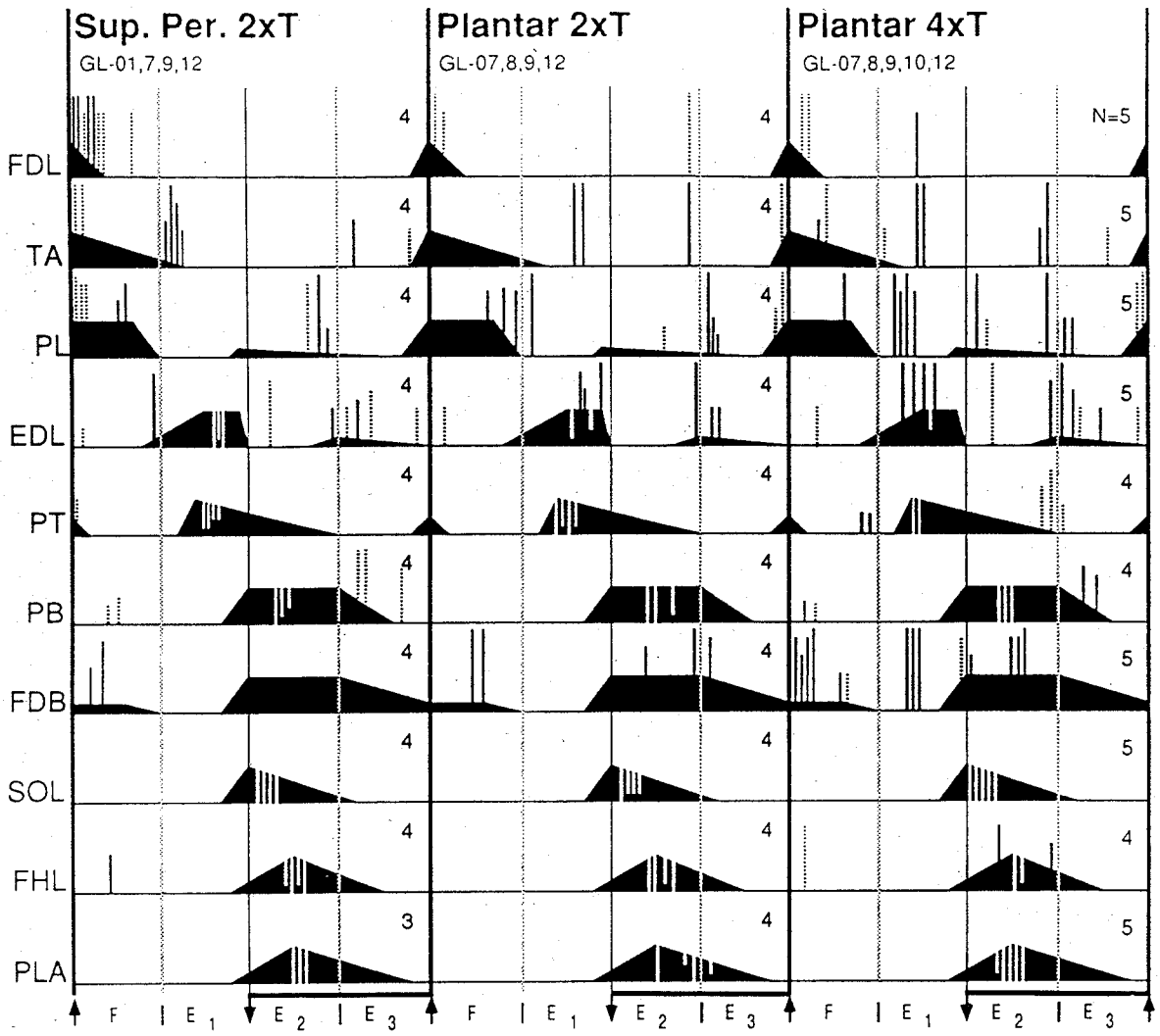

Fig. 8. Summary of reflexes seen across various muscles (*rows*) for three stimulus conditions (*columns*) in *N* animals (*number in upper right of each box*). *Vertical bars* denote phasing and amplitude of peak reflexes with respect to background locomotor activity, *shown as solid black envelopes*; *upward black bars* denote P1 reflexes; *upward striped bars* denote P2 reflexes; and *downward white bars* denote N1 (inhibitory) reflexes. The locomotor EMGs are caricatures of the most commonly observed patterns, with each phase normalized to the same relative duration (*upward and downward arrows and bars along bottom edge* denote footlift, footfall, and stance, respectively with Phillipson phases F and E as in Fig. 4) and the peak amplitudes normalized to the same height for all muscles. Reflex responses were scaled to the peak locomotor EMG, clipped to a maximum of twice the peak locomotor amplitude, and located at the point in the step cycle where the response reached a maximum. Because some muscles in some animals showed relatively little locomotor recruitment, many excitatory bars are so clipped; in terms of absolute EMG amplitude, excitatory reflexes tended to peak at about 1–2 mV in all muscles, about 20–50% of the maximal amplitude noted during paw-shake. Muscle abbreviations as in Table 1

reflexes for both stimuli. Other cats had responses that included various admixtures of these reflex components; no particular pattern seemed to be predominant.

The FDL and FHL muscles have been studied intensively because they have different patterns of locomotor recruitment despite shared skeletal origins and insertions (O'Donovan et al. 1982; Fleshman et al. 1984; Abraham and Loeb 1985; Schmidt et al. 1988). In agreement with previous studies, we found that FDL consistently had a distinctive, brief, flexor EMG burst just at the time of footlift, but that it was quite variable in its tendency to be recruited during stance phase (Fig. 6; see also Fig. 9, and below). Despite this variability, it always had very large and consistent P1 and P2 reflexes confined narrowly to the flexion phase in response to peroneal stimulation (see also Fig. 7). If recruited during stance phase, it was inhibited along with most other ankle extensors (GL 01 in Fig. 6). In contrast, FHL had a completely stereotypical pattern of locomotor activity confined to the stance phase in all cats, but it had remarkably idiosyncratic reflexes (Fig. 6, bottom row). GL 12 showed a simple N1 inhibition typical of ankle extensors; GL 07 showed a strong P1 excitation particularly during stance and an unusually long latency excitation (35–40 ms) confined to swing phase; GL 09 showed a stance phase inhibition apparently interrupted by a typical P2 response that was not present during swing phase, when P2 reflexes in other muscles are usually strongest.

The reflexes in each of the small muscles of a given animal demonstrated much individual detail according to stimulus site and step cycle phase. In Fig. 7, stimulation of a single site at a single intensity can be seen to

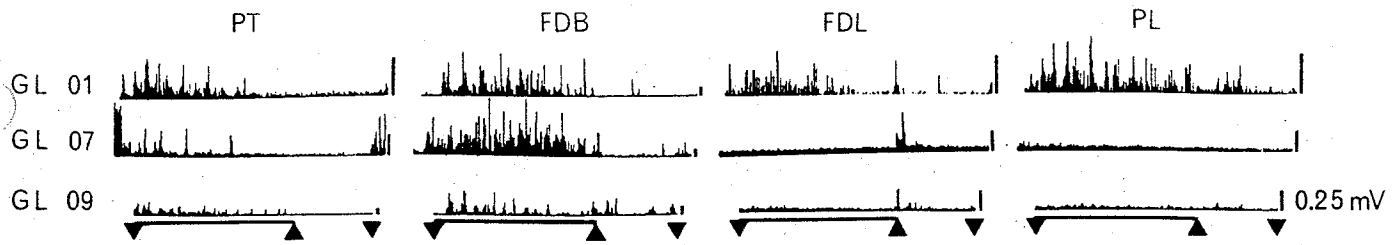

Fig. 9. Rectified, integrated (2-ms bin) EMG from four muscles that had the most variable locomotor recruitment from animal to animal (*PT, FDB, FDL,* and *PL*) in three cats walking at similar speeds (GL 01, GL 07, GL 09; see Fig. 3 for data from GL 12). Traces from each cat taken from a single, typical step cycle during steady treadmill walking without stimulation (*downward triangles*, footfall to footfall; *upward triangles*, aligned to footlifts; *solid bar*, stance phase. Abbreviations as in Table 1)

elicit complex patterns of P1, N1, and P2 reflexes that occur only in certain muscles and for a particular stimulus site. For example, superficial peroneal stimulation produced P1 and P2 reflexes in FDL and FDB, but sural stimuli produced only P2 reflexes in FDL and only P1 in FDB. A strong N1 response occurred in PB for plantar nerve stimulation but not superficial peroneal stimulation, which produced a weak P1 and strong P2 response. These reflexes were often modulated strongly during the step cycle but individually for each muscle, often out of phase with the underlying recruitment of the muscle (see particularly PT). Thus, it was not the case that each individual animal had a simple, global synergy that was expressed in all of its small muscles. Rather, each animal seemed to have a completely idiosyncratic but highly detailed program for recruiting the various small muscles in response to different stimuli in different phases of the step cycle.

Figure 8 attempts to summarize the reflex patterns observed and their consistency across preparations. The numbers of rasters from which these bars were compiled are shown at the upper right of the box (*N*) for each stimulus condition (three columns) and each muscle (ten rows). The number of bars of a particular type in each box may be less than *N* if a particular reflex response did not occur consistently or more than *N* if that response went through two distinct cycles of waxing and waning versus phase. Muscles with consistent reflex patterns will have *N* particular bar types clustered in the same phase of the step cycle. Note that because of the cyclical nature of each diagram, some reflexes in very late stance phase (end of E_3 at the extreme right of the diagram, just before footlift) are really associated with flexor recruitment of the muscle (F phase which wraps around to the extreme left of each diagram). MG and LG muscles have been omitted because their reflexes were consistent inhibitions similar to SOL. LUM was omitted because neither excitatory nor inhibitory reflexes were noted in most preparations over the full range of stimuli, despite strong, consistent locomotor activity confined to the stance phase.

A more systematic analysis of locomotor and reflex variability requires a side-by-side examination of complete sets of EMG tracings and reflex rasters across all animals, the results of which are summarized in Table 3. The muscles here are classified according to whether their net action in the sagittal plane would tend to propel the animal forward and upward (which requires ankle extension and digit plantar-flexion in the digitigrade posture of the cat) or would lead to retraction of the foot towards the body, and according to whether they are recruited primarily during swing or stance phases. Except for the major ankle extensors (SOL, MG, LG and PLA), all muscles exhibited interanimal variability in at least one behavior. Variability in one behavior (unperturbed locomotion or either reflex) was not necessarily linked to variability in the other behaviors. When a muscle exhibited two or more distinct patterns of recruitment for two or more behaviors, there was no tendency for the specific patterns to covary; that is, a muscle that had a similar locomotor or plantar reflex pattern in two animals might exhibit two quite different patterns during peroneal reflexes in the same animals.

The four muscles that had strikingly variable locomotor patterns are examined in detail in Fig. 9. The gains for each trace have been adjusted so that maximal activation of the muscle (e.g., during paw shake) would show similar amplitudes of activity. PT was always active in early stance, but in some animals it had a particularly large peak in E_1 (e.g., in GL 07 in Fig. 9 and GL 12 in Fig. 2), similar to EDL, with which it shares similar mechanical action on the digits and often similar reflexes. FDB was always recruited during most of stance but sometimes weakly and intermittently, with similar amounts of recruitment scattered through the entire step cycle (e.g. in GL 09). As noted in conjunction with Fig. 6, FDL had a consistent burst just at footlift, but could also show strong recruitment during much of stance (e.g., in GL 01). PL was the most variable, sometimes with strong flexion synergy with TA (GL 12 in Fig. 2), sometimes with strong recruitment in both stance and swing (GL 01 in Fig. 9), and sometimes little or no recruitment during unperturbed walking (GL 07 and −09 in Fig. 9); it always had strong, excitatory reflexes that were generally similar to those in TA.

Discussion

The locomotor and reflex EMG patterns described in this paper are qualitatively similar to those described in several previous studies in the intact walking cat (Forssberg et al. 1975 and 1977; Duysens and Stein 1978; Duysens and Loeb 1980; Abraham et al. 1985), hence they will not be discussed in detail here. The improved methods for controlling and monitoring the distribution of stimulated afferents provide clearer evidence that the dif-

ferent components of the reflexes (P1, N1, and P2) in many individual muscles can all be produced by the larger myelinated afferents, frequently designated flexor reflex afferents (FRA; Eccles and Lundberg 1959b). Improved methods for identifying and normalizing the phasing of the step cycle provide a clearer view of the complex modulation of reflex gain, which often depends critically on the phase of the step cycle and the site of the stimulus as well as the presumed level of depolarization in the motoneuron pool. The short latencies of these reflexes (1–3 ms central delay for P1 and N1, 10–20 ms for P2) suggest that they are mediated by oligosynaptic segmental circuits. They seem to reflect a contingency plan for dealing with perturbations to locomotion, which plan is strongly tied to, but may not actually be a part of, the CPG for locomotion, as discussed below.

Artefactual sources of variability and noise

The possibility that neural circuits for a given behavior may differ substantially among animals raises serious methodological problems for studies that depend upon pooling data among animals. At the same time, it opens up a new set of methodological possibilities based upon systematic exploration of the mechanical and behavioral factors that might contribute to the organization of neural circuitry that we otherwise take for granted. The recent and somewhat contentious history of cerebral cortical mapping reflects both of these consequences (Merzenich et al. 1983; Merzenich and Grajski 1990). However, the suggestion that substantial functional adaptation may occur in the much more primitive and stereotyped circuitry of the spinal cord should not be made lightly.

The present study incorporates a number of evolutionary changes in methodology, each of which contributed to substantial improvements in the consistency of signals recorded from the majority of muscles in this study and a similar study of proximal hindlimb muscles (Pratt et al. 1991). Furthermore, even in muscles that showed substantial interanimal variability of locomotor and/or reflex activity, the patterns in an individual animal were strong and consistent from day to day, with an orderly progression of amplitude and timing features over a range of stimulus intensities and locomotor speeds. The following methodological features of this study suggest that at least some of the interanimal variability reported here must be present in the nervous system:

1. EMG electrode design and placement seem to eliminate both cross talk from adjacent muscles and undersampling in which activity confined to a part of the muscle is missed. Even muscles that showed very little activity during locomotion were always observed to have similar absolute amplitudes of EMG when they were intensely recruited by reflexes or by behaviors such as paw-shaking. Recording from virtually all of the muscles in a limb segment makes it possible to rule out cross talk by identifying periods of silence in a muscle even when adjacent muscles are intensely recruited.
2. Nerve cuff electrodes for stimulation constitute a major improvement over subcutaneous hook or patch electrodes, which recruit a mixed and unstable population of afferents as they shift with respect to the major nerve bundles either postoperatively or as a result of deformation of the skin during the step cycle. However, their real advantage comes in combination with recording cuff electrodes that permit precise calibration of thresholds and saturation levels for different fiber populations and confirm constancy of recruitment throughout the step cycle (see Fig. 3).
3. Consistent locomotion was obtained by extensive preoperative training of the animals to walk steadily for long periods of time at a constant and self-chosen pace on the treadmill; it was confirmed and quantitatively phased via kinematic records from implanted transducers. There is a long, contentious literature on the normalcy of treadmill locomotion (Miller et al. 1975; Wetzel et al. 1975; Coss et al. 1978; Halbertsma 1983) and variability and training effects (Lockard et al. 1976; Vilensky and Patrick 1984). When short sequences of various speeds and behaviors are desired, the interactions between the animal and the operator/trainer are complex and difficult to control; animals appear to modify their gaits based on attempts to second-guess what may happen next (Blaszczyk and Loeb 1993). In the present study, the animals were all overtrained to walk for 10–20 min with few or no interruptions. They adopted a distinctive automaton-like appearance characterized by a fixed head position and apparent inattention to visual or auditory stimuli.

Why has interanimal variability not been emphasized in previous studies, including some that have examined some of the same muscles in which variability is reported here (e.g., Abraham and Loeb 1985; Abraham et al. 1985)? The methodological improvements employed here do not reveal variability that was previously undetected; rather they eliminate artifactual sources of variability that add to biological variability. In so doing, they point to a contrast between the majority of muscles, which appear to be remarkably consistent in their recruitment patterns, and a minority that now appear to be so markedly variable that data should not be selected or rejected based upon possible technical problems. In this series, decisions were made to exclude certain blocks of data based upon failed EMG recording sites, damaged cutaneous nerves, and irregular gait, but these decisions were always influenced by unambiguous, objective criteria, including serial impedance tests, evoked potentials, and kinematic and videotape recordings.

In evaluating the significance of differences in EMG patterns, it is important to remember that such signals are removed from the underlying synaptic drive to the parent motoneurons by the nonlinear process of recruitment. The presence of an EMG signal in one case and its absence in another may reflect the same phasic inputs superimposed on relatively depolarized or hyperpolarized motoneurons, respectively. For example, the stance

phase activity of FDL seems to be driven by the CPG (Fleshman et al. 1984), but may or may not reach threshold in different animals (Fig. 9). This problem has been minimized in this study by concentrating particularly on cutaneous reflexes superimposed on locomotor EMG patterns where the motoneuron pool is already partially recruited. However, it is still difficult to interpret quantitative rather than qualitative differences, because the cutaneous pathways do not necessarily follow the size principle of recruitment (Kanda et al. 1977) and because the distribution of relative depolarization in the as-yet unrecruited motoneurons is not determined uniquely by the magnitude of the overt recruitment (Kernell and Hultborn 1990).

Innate versus learned motor programs

Table 3 distinguishes motor programs for locomotion and for reflex responses that were observed to be constant from those that showed variability across a relatively small sample of animals. Programs have been designated as variable only when qualitatively different patterns were observed, but there may well be a continuum of variability involving both qualitative and quantitative features. In trying to understand this continuum, it may be useful to start at the other end and ask what mechanisms account for invariance and why might they be less effective in some muscles and tasks than in others?

Invariance in a given muscle and task might arise either because the neural circuits that recruit that muscle are genetically hard-wired or because the mechanical constraints imposed by the genetic specification of the musculoskeletal system leave little room for idiosyncratic use of that muscle during performance of that task. For the major ankle muscles TA and gastrocnemius, mechanical transposition of the tendons even at an early age results in persistence of the native locomotor EMG pattern despite the fact that it is mechanically inappropriate (Forssberg and Svartengren 1983); this suggests that this part of the CPG is genetically hard-wired. Similar invariance was noted by Sperry in the rat forelimb (1942), but he noted in a subsequent review (Sperry 1945) that there appeared to be a range of plasticity depending on species and muscles. Primates have been reported to exhibit considerable relearning of forelimb motor programs following nerve and tendon transpositions (Sperry 1947; Yumiya et al. 1979). In designing reconstructive procedures for the hand, surgeons draw on the largely subjective clinical impression that some muscles are much more adaptive than others (Leffert 1976).

In the cat hindlimb, genetically fixed wiring of the locomotor CPG to certain muscles does not preclude more flexible arrangements for other muscles. Some of the smaller muscles studied here appear to have considerable variability in their mechanical actions in different specimens (particularly PL and PB; Young et al. 1993), which might make neural hard-wiring inappropriate. Still others may be used only facultatively during locomotion, perhaps to produce intrinsic stiffness in order to resist possible perturbations (Hogan 1984) rather than to produce the overt trajectory of locomotion. Many of the muscles that exhibited the most variability have their predominant moment arms in axes other than the parasagittal, extension-flexion plane (Young et al. 1993). If the genetically hard-wired CPG does not specify the recruitment of these (and perhaps some other) muscles, then functional heterogeneity during locomotion may arise both from architectural pleiomorphism in the musculoskeletal system and from early behavioral experiences that are generally unknown to the investigator. Unfortunately, the functional experiments reported here were completed before we became aware of the complexity and variability of the musculoskeletal mechanics of the feline ankle, so no corresponding anatomical data are available from the same animals. However, some of the most dramatic examples of reflex variability occurred in muscles such as EDL and FDB, which seem likely to be architecturally similar among animals.

What is the relationship between locomotion and the various cutaneous reflexes that can be elicited at different points of the step cycle? Historically, there has been a tendency to see both the proprioceptive and the cutaneous reflexes as integral parts of the CPG (Sherrington 1910). The development of the fictive locomotor preparation showed that the CPG could function without afferent feedback (Grillner and Zangger 1975), but left open the possibility that the reflexes were mediated by interneurons that were an integral part of the CPG itself (reviewed by Burke and Fleshman, 1986), which would account for modulation of reflex gains over the step cycle. However, it is possible that some of the reflex patterns elicited by low threshold afferents (including the FRA) are learned rather than innate. Their tendency to be invariant across animals for most muscles may reflect the considerable constancy of musculoskeletal structure and behavioral experience of the domestic cat, rather than genetic specification of spinal cord circuitry. Variability would then be expected to occur in muscles with weak and/or variable mechanical actions on the skeleton and might not covary with variability in their locomotor patterns, as reported here (Table 3). Interestingly, tendon and nerve crosses such as those that fail to modify locomotor activity (discussed above) have been reported to result in changes in reflexive paw-placing (Yumiya et al. 1979) and long-latency spinal reflexes (McMahon and Wall 1989).

Certainly there are likely to be innate reflexes such as nociceptive withdrawal. However, the kitten may have to learn to associate activity in low-threshold afferents with potentially noxious situations and to develop motor programs to avoid such situations without compromising the stability of ongoing programs such as locomotion. This is not to say that these short-latency reflexes are mediated by supraspinal pathways or that they require learning by spinal neurons, per se. The spinal reflexes have long been known to be under the control of descending systems (Sherrington 1910; for comprehensive review, see Schomburg 1990). The descending tonic input that is required to activate the spinal CPG (Orlovsky and Shik 1976) may, in the intact cat, include carefully distributed biases upon spinal interneurons that mediate

these reflexes. Many (perhaps even all) interneurons receive both CPG and afferent inputs (Lundberg 1975; Burke and Fleshman 1986), which could account for the observed modulations of reflex gain during the step cycle. Absence or abnormality of the descending inputs would account for the striking reductions in FRA-mediated reflexes in some reduced preparations that still exhibit nearly normal locomotor activity (Eccles and Lundberg 1959a; Engberg 1964; Duenas et al. 1984).

The importance of these descending pathways and the possibility that they may be constituted differently in various individuals may underlie the difficulty of relating EMG reflexes such as reported here to synaptic potentials recorded intracellularly from motoneurons following similar cutaneous nerve stimulation during fictive locomotion. Even for muscles such as the triceps surae that produce consistent reflexes in intact animals, intracellular recordings show complex mixtures of excitatory and inhibitory postsynaptic potentials (EPSPs and IPSPs) that may be heterogeneous among different types of motor units in a single compartment, among closely synergistic compartments of a muscle and even among motoneurons with no apparent distinguishing features (Fleshman et al. 1988; LaBella et al. 1989; Schmidt et al. 1989). In FDL, Moschovakis et al. (1990) described trisynaptic EPSPs from the superficial peroneal and plantar nerves whose modulation during the fictive step cycle agrees fairly well with the generally consistent P1 reflexes in the intact, walking cat. However, interanimal variability in the P2 responses in FDL and several other muscles described here cannot be addressed in reduced preparations because of the uncertain biasing of the many interneurons that presumably participate in these longer latency reflexes.

We have suggested elsewhere (Loeb et al. 1990) that the program for a motor behavior such as locomotion must include not only the overt pattern of muscle recruitment required to achieve the nominal kinematic trajectory of the task but also a complete set of contingency responses for dealing with the range of perturbations that *have been experienced*. In the event of a perturbation during a task that is dynamically rather than statically stable (e.g., locomotion), it is important to respond as rapidly as possible. Thus the contingency plan should be located as peripherally as possible. Goal-directed, oligosynaptic reflexes have been implicated in rapid adjustments to perturbations of speech (Gracco and Abbs 1985) and finger manipulation (Cole and Abbs 1987) tasks. An even faster response can be achieved by utilizing the intrinsic length- and velocity-dependency of force in preactivated motor units (Hogan 1984). In the latter case, some part of the EMG patterning observed during unperturbed locomotion would actually constitute part of the contingency plan. Note that all of these rapid response mechanisms might be learned rather than innate because they can be programed by the descending signals (tonic or phasic) rather than generated by the segmental CPG itself. Young et al. (1992) note that coactivation of many of the small ankle muscles that exhibited variable locomotor patterns could produce substantial lateral stability of the foot as a result of both the intrinsic mechanical properties of the active muscle fibers and surprisingly large, joint angle dependent moment arms in the abduction/adduction and inversion/eversion axes. It remains to be determined whether the variable locomotor and reflex patterns reported here can be affected by systematic developmental influences and whether they rely exclusively on descending input or can become embedded in the segmental circuitry itself through long-term association and plasticity (as suggested by Wolpaw and Lee 1989, for modifications of the monosynaptic H-reflex).

Studies of the cat hindlimb and its neural control have often been confined to a few large, relatively accessible muscles and nerves. While this has produced a wealth of insight into some of the motor control functions of the spinal cord, there is no reason to believe that these insights can be extrapolated to the control of all muscles and all behaviors. In particular, theories of higher motor control are often tested in tasks requiring fine control of the smaller, distal muscles of limbs. The spinal circuitry for controlling these muscles may be much less stereotyped than for the larger muscles because of the relatively larger heterogeneity among individuals in the physical actions and functional histories of these distal muscles. Such differences may presage the great phylogenetic elaboration of higher motor circuitry that seems to be responsible for most learned sensorimotor behavior.

Acknowledgements. Some of these data were collected at the author's previous address in the Laboratory of Neural Control, NINDS, NIH, Bethesda, Maryland, with the technical assistance of Michele Manley; a preliminary report has been published (Loeb 1987). Computer software was written by Wayne Yee at the NIH and graphical assistance was provided by Janet Creasy at Queen's University. Drs. F.J.R. Richmond and R.P. Young provided editorial suggestions on the manuscript. Recent research was supported by the Canadian MRC Group in Sensory-Motor Physiology and NIH grant NS27193.

References

Abraham LD, Loeb GE (1985) The distal hindlimb musculature of the cat. Patterns of normal use. Exp Brain Res 58:580–593

Abraham LD, Marks WB, Loeb GE (1985) The distal hindlimb musculature of the cat. Cutaneous reflexes during locomotion. Exp Brain Res 58:594–603

Bak MJ, Loeb GE (1979) A pulsed integrator for EMG analysis. Electroencephalogr Clin Neurophysiol 47:738–741

Blaszczyk JW, Loeb GE (1993) Why cats pace on the treadmill. Physiol Behav 53:501–507

Burgess PR, Petit D, Warren RM (1968) Receptor types in cat hairy skin supplied by myelinated fibers. J Neurophysiol 31:833–848

Burke RE, Fleshman JW (1986) Strategies to identify interneurons involved in locomotor pattern generation in the mammalian spinal cord. In: Grillner S, Stein PSG, Stuart DG (eds) Neurobiology of vertebrate locomotion. Macmillan, London, pp 245–268

Cavanagh PR, Lafortune M (1980) Ground reaction forces in distance running. J Biomech 13:397–406

Chanaud CM, Pratt CA, Loeb GE (1991) 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

Chow CK, Jacobson DH (1971) Studies of human locomotion via optimal programming. Math Biosci 10:239–306

Cole KJ, Abbs JH (1987) Kinematic and electromyographic responses to perturbation of a rapid grasp. J Neurophysiol 57:1498–1510

Coss L, Chan AK, Goslow GE, Rasmussen S (1978) Ipsilateral limb variation in cats during overground locomotion. Brain Behav Evol 15:85–93

Davy DT, Audu ML (1987) A dynamic optimization technique for predicting muscle forces in the swing phase of gait. J Biomech 20:187–201

Delcomyn F (1980) Neural basis of rhythmic behavior in animals. Science 210:492–498

Duenas SH, Loeb GE, Marks WB (1984) A quantitative comparison of hindlimb muscle activity and flexor reflexes in normal and decerebrate cats during walking. Soc Neurosci Abstr 10:628

Duysens J, Loeb GE (1980) Modulation of ipsi- and contralateral reflex responses in unrestrained walking cats. J Neurophysiol 44:1024–1037

Duysens J, Stein RB (1978) Reflexes induced by nerve stimulation in walking cats with implanted electrodes. Exp Brain Res 32:213–224

Eccles RM, Lundberg A (1959a) Supraspinal control of interneurones mediating spinal reflexes. J Physiol (Lond) 147:565–584

Eccles RM, Lundberg A (1959b) Synaptic actions in motoneurons by afferents which may evoke the flexion reflex. Arch Ital Biol 97:199–221

Engberg I (1964) Reflexes to foot muscles in the cat. Acta Physiol Scand 62 (Suppl. 235):46–64

Fleshman JW, Lev-Tov A, Burke RE (1984) Peripheral and central control of flexor digitorum longus and flexor hallicus longus motoneurons: the synaptic basis of functional diversity. Exp Brain Res 54:133–149

Fleshman JW, Rudomin P, Burke RE (1988) Supraspinal control of a short-latency cutaneous pathway to hindlimb motoneurons. Exp Brain Res 69:449–459

Forssberg H, Svartengren G (1983) Hardwired locomotor network in cat revealed by a retained motor pattern to gastrocnemius after muscle transposition. Neurosci Lett 41:283–288

Forssberg H, Grillner S, Rossignol S (1975) Phase dependent reflex reversal during walking in chronic spinal cats. Brain Res 85:103–107

Forssberg H, Grillner S, Rossignol S (1977) Phasic gain control of reflexes from the dorsum of the paw during spinal locomotion. Brain Res 132:121–139

Gracco VL, Abbs JH (1985) Dynamic control of the perioral system during speech: kinematic analyses of autogenic and nonautogenic sensorimotor processes. J Neurophysiol 54:418–432

Graham Brown T (1911) The intrinsic factors in the act of progression in the mammal. Proc R Soc Lond [Biol] 84:308–319

Grillner S, Zangger P (1975) How detailed is the central pattern generation for locomotion? Brain Res 88:367–371

Halbertsma J (1983) The stride cycle of the cat: the modeling of locomotion by computerized analysis of automatic recordings. Acta Physiol Scand [Suppl] 521:1–75

Hoffer JA, Loeb GE, Pratt CA (1981) Unitary axonal conduction velocity from averaged nerve cuff electrodes in cats. J Neurosci Methods 4:211–225

Hoffer JA, Loeb GE, Marks WB, O'Donovan MJ, Pratt CA, Sugano N (1987) Cat hindlimb motoneurons during locomotion. I. Destination, axonal conduction velocity and recruitment threshold. J Neurophysiol 57:510–529

Hogan N (1984) Adaptive control of mechanical impedance by coactivation of antagonist muscles. IEEE Trans Autom Control 29:681–690

Kanda K, Burke RE, Walmsley B (1977) Differential control of fast and slow twitch motor units in the decerebrate cat. Exp Brain Res 29:57–74

Kernell D, Hultborn H (1990) Synaptic effects on recruitment gain: a mechanism of importance for the input-output relations of motoneurone pools? Brain Res 507:176–170

LaBella LA, Kehler JP, McCrea DA (1989) A differential synaptic input to the motor nuclei of triceps surae from the caudal and lateral cutaneous sural nerves. J Neurophysiol 61:291–301

Leffert RP (1976) Patterns of neuromuscular activity following tendon transfer in the upper limb: a preliminary study. J Hand Surg 1:181–189

Lockard DL, Traher LM, Wetzel MC (1976) Reinforcement influences upon topography of treadmill locomotion by cats. Physiol Behav 16:141–146

Loeb GE (1987) Cutaneous reflexes in the cat distal hindlimb and their gating during normal, treadmill walking. Soc Neurosci Abstr 13:1177

Loeb GE, Gans C (1986) Electromyography for experimentalists. University of Chicago Press, Chicago

Loeb GE, Levine WS, He J (1990) Understanding sensorimotor feedback through optimal control. Cold Spring Harb Symp Quant Biol 55:791–803

Loeb GE, Walmsley B, Duysens J (1980) Obtaining proprioceptive information from natural limbs: implantable transducers vs. somatosensory neuron recordings. In: Neuman MR (ed) Physical sensors for biomedical applications. (Proceedings of workshop on solid state physical sensors for biomedical application) CRC, Boca Raton, pp 135–149

Lundberg A (1975) Control of spinal mechanisms from the brain. In: Brady RO (ed) The nervous system, vol 1. Basic neuroscience. Raven, New York, pp 253–265

Lundberg A (1980) Half-centres revisited. Adv Physiol Sci 1:155–167

McMahon SB, Wall PD (1989) Changes in spinal cord reflexes after cross-anastomosis of cutaneous and muscle nerves in the adult rat. Nature 342:272–274

Merzenich MM, Grajski K (1990) Cortical network changes underlying representational plasticity. Cold Spring Harb Symp Quant Biol 55:873–887

Merzenich MM, Kaas JH, Wall J, Nelson RJ, Sur M, Felleman D (1983) Topographic reorganization of somato-sensory cortical areas 3B and 1 in adult monkeys following restricted deafferentation. Neuroscience 8:33–55

Miller S, Van der Burg J, Van der Meche FGA (1975) Coordination of movements of the hindlimbs and forelimbs in different forms of locomotion in normal and decerebrate cats. Brain Res 91:217–237

Moschovakis AK, Sholomenko GN, Burke RE (1991) Differential control of short latency cutaneous excitation in cat FDL motoneurons during fictive locomotion. Exp Brain Res 83:489–501

O'Donovan MJ, Pinter MJ, Dum RP, Burke RE (1982) Actions of FDL and FHL muscles in intact cats: functional dissociation between anatomical synergists. J Neurophysiol 47:1126–1143

Oguztoreli MN, Stein RB (1990) Optimal task performance of antagonistic muscles. Biol Cybern 64:87–94

Orlovsky GN, Shik ML (1976) Control of locomotion: a neurophysiological analysis of the cat locomotor system. Int Rev Physiol Neurophysiol 10:281–317

Pandy MG, Zajac FE, Sim E, Levine WS (1990) An optimal control model for maximum-height human jumping. J Biomech 23:1185–1198

Phillipson M (1905) L'autonomie et la centralisation dans le systeme nerveux des animaux. Trav Lab Physiol Inst Solvay (Bruxelles) 7:1–208

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

Rindos AJ, Loeb GE, Levitan H (1984) Conduction velocity changes along lumbar primary afferent fibers in cats. Exp Neurol 86:208–226

Schmidt BJ, Meyers DER, Fleshman JW, Tokuriki M, Burke RE (1988) Phasic modulation of short latency cutaneous excitation in flexor digitorum longus motoneurons during fictive locomotion. Exp Brain Res 71:568–578

Schmidt BJ, Meyers DER, Tokuriki M, Burke R (1989) Modulation of short latency cutaneous excitation in flexor and extensor motoneurons during fictive locomotion in the cat. Exp Brain Res 77:57–68

Schomburg ED (1990) Spinal sensorimotor systems and their supraspinal control. Neurosci Res 7:265–340

Sherrington CS (1910) Flexion-reflex of the limb, crossed extension-reflex and reflex stepping and standing. J Physiol (Lond) 40:28–121

Sperry RW (1942) Transplantation of motor nerves and muscles in the forelimb of the rat. Neurology 76:283–321

Sperry RW (1945) The problem of central nervous reorganization after nerve regeneration and muscle transposition. Q Rev Biol 20:311–369

Sperry RW (1947) Effect of crossing nerves to antagonistic limb muscles in the monkey. Arch Neurol Psychiatry 58:452–473

Stein RB, Nichols TR, Jhamandas J, Davis L, Charles D (1977) Stable long-term recordings from cat peripheral nerves. Brain Res 128:21–38

Vilensky JA, Patrick MC (1984) Inter and intratrial variation in cat locomotion behavior. Physiol Behav 33:733–746

Wetzel MC, Atwater AE, Wait JV, Stuart DG (1975) Neural implications of different profiles between treadmill and overground locomotion timing in cats. J Neurophysiol 38:492–501

Wolpaw JR, Lee CL (1989) Memory traces in primate spinal cord produced by operant conditioning of H-reflex. J Neurophysiol 61:563–572

Young RP, Scott SH, Loeb GE (1992) An intrinsic mechanism to stablize posture – joint-angle-dependent moment arms of feline ankle muscles. Neurosci Lett 145:137–140

Young RP, Scott SH, Loeb GE (1993) The distal hindlimb musculature of the cat: multiaxis moment arms at the ankle joint. Exp Brain Res 96:141–151

Yumiya H, Larsen KD, Asanuma H (1979) Motor readjustment and input-output relationship of motor cortex following cross-connection of forearm muscles in cats. Brain Res 177:566–570