

The distal hindlimb musculature of the cat

Cutaneous reflexes during locomotion

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Summary. In order to better understand the organization of the locomotor control system, we examined the temporal patterns of distal hindlimb muscle responses to brief electrical stimulation of cutaneous nerves during walking on a treadmill. Electromyographic recordings were made from twelve muscles; stimuli were applied individually to three nerves at random times throughout the step cycle. A new graphical technique was developed to assist detailed examination of the time course and gating of complex reflex patterns. The short latency reflexes were of two primary types: inhibition of extensors and excitation of flexors; these responses were only evident during locomotor phases in which the respective motoneuron pools were active. Longer-latency response components were gated in a similar but not identical manner, suggesting some independence from the basic locomotor influence on the motoneuronal pool. The phase-dependent gating of reflexes appeared to be consistent with a functional role for reflex responses during locomotion. The reflex responses of muscles with complex anatomical actions were often correspondingly complex.

Key words: Muscles – Locomotion – Reflexes

Introduction

The roles of central and peripheral inputs in the control of locomotion have been studied widely (e.g. Grillner and Zangger 1979; Forssberg et al. 1975; Forssberg et al. 1980; Stuart 1981; Engberg and Lundberg 1969). Most evidence suggests that

peripheral inputs serve to modify or correct centrally generated patterns of EMG activity (Wand et al. 1980; Rasmussen et al. 1982; Forssberg 1979a and 1981). Such effects may be studied in isolation from the usual afferent input by recording directly from ventral root filaments during “fictive” locomotion (paralyzed, spinal preparation; Andersson and Grillner, 1981 and 1983). The effects of identical peripheral inputs may vary, depending on the states of the presumed central pattern generators (Forssberg et al. 1975; Duysens and Loeb 1980; Schomburg and Behrends 1978; Schomburg et al. 1981).

Chronic recording techniques can be used to monitor continuously and simultaneously the activity of many muscles. Using these techniques, Forssberg et al. (1976) found that muscle electromyographic (EMG) reflex responses to cutaneous stimuli varied consistently according to phases in the locomotion step cycle. Further investigation has suggested that the alterations in reflex responses reflect gating of afferent signals to the motoneuronal pools (Forssberg 1979a; Duysens and Loeb 1980; Duysens et al. 1980; Wand et al. 1980) as well as changes in the excitability of those pools consequent to their normal recruitment and inhibition by the pattern generator. The result of this modulation of reflex input to the motoneurons is functional to the locomoting animal – reduced limb extension during stance and increased limb flexion during swing, both strategies likely to minimize the consequences of the perturbation.

As a part of a project to generate detailed kinesiological information for the cat distal hindlimb (see Abraham and Loeb 1985), we examined reflex EMG responses to electrical stimulation of cutaneous nerves in the foot during treadmill walking. The overall reflex response of the limb can be described as both coordinated and functional, but perhaps with different kinematic goals than occur normally during unperturbed walking. The contrasting patterns of

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muscle activation should provide evidence of the different ways muscles are grouped and controlled functionally by the nervous system (see Loeb 1982 and 1984). Preliminary results of this study have been reported elsewhere (Abraham et al. 1981).

Methods

Most of the methodological details of this study are provided in the preceding paper (Abraham and Loeb 1985). One female and five male cats were used (3.0–4.5 kg). All animals were trained for several weeks to walk steadily on the treadmill for intermittent food reward. Electromyographic recordings were made from twelve muscles: classical extensors – medial gastrocnemius (MG), lateral gastrocnemius (LG), plantaris (PLT), soleus (SOL), and flexor digitorum brevis (FDB); the deep medial compartment – flexor digitorum longus (FDL), flexor hallucis longus (FHL), and tibialis posterior (TP); the anterior compartment – tibialis anterior (TA) and extensor digitorum longus (EDL); and two of the peroneals – peroneus longus (PL) and peroneus brevis (PB). Length gauges were implanted to obtain records of knee and ankle joint position so that phases of the step cycle could be accurately identified. The EMG electrodes and length gauges are described in detail in the preceding paper (Abraham and Loeb 1984), as are the basic data collection procedures and equipment.

In order to elicit reflex responses to electrical stimulation of cutaneous nerves in the foot, stimulating "patch" electrodes identical to those used for EMG recording (see above) were placed so that the exposed wires lay at right angles against a nerve bundle. In five animals a stimulating patch was placed over the lateral sural nerve (LSN) on the lateral surface of the LG, in four animals a stimulating patch was placed on the medial plantar nerve (MPN) dorsal to the FDB, and in two animals a patch was placed on the superficial peroneal nerve (SPN) against the undersurface of the skin overlying the anterolateral aspect of the ankle.

Stimulation procedure

Single biphasic square wave shocks were delivered to the selected cutaneous nerve via a pulse generator and photoisolated constant current stimulator (Bak Electronics BPG-1 and BSI-1). Each pulse had a total duration of 1 msec. We informally examined the responses to varying intensity of electrical stimulation before settling on a particular stimulus current for the complete experimental series, and found no qualitative or temporal differences as current increased from twice threshold for any response to about 10 times threshold. The intensity of the stimulation was adjusted, while the cat was quietly standing on the treadmill, to be just below the level at which the animal appeared to notice the shock. (Raising the stimulation intensity would typically first lead to the cat's turning quickly as if seeking the source of the cutaneous stimulation.) No attempt was made to identify the stimulus strength in terms of reflex thresholds, since that depends on the particular muscle and behavioral state. However, it was clear that varying the stimulus intensity affected the amplitude of the reflex responses, but had little effect on their qualitative nature or latencies until very high and clearly noxious intensities were reached. Therefore we have limited our observations to the qualitative nature (excitatory or inhibitory) and temporal details of the reflex responses in various muscles to a single stimulus of relatively low intensity. Stimuli of this intensity produced reliable EMG responses in all muscles without distracting the animal or interfering with steady gait.

Table 1. Number of surveys of reflex responses in each muscle for stimulation of each nerve. Each survey consisted of 80–120 stimulus presentations distributed randomly over 200–300 step cycles. LSN: Lateral Sural Nerve; MPN: Medial Plantar Nerve; SPN: Superficial Peroneal Nerve

Abbrev.	Name	(LSN)	(MPN)	(SPN)
MG	Medial gastrocnemius	4	2	1
LG	Lateral gastrocnemius	3	1	1
SOL	Soleus	4	2	1
PLT	Plantaris	4	3	1
FDB	Flexor digitorum brevis	3	3	0
FDL	Flexor digitorum longus	4	2	1
FHL	Flexor hallucis longus	5	3	1
TP	Tibialis posterior	3	3	0
TA	Tibialis anterior	5	3	1
EDL	Extensor digitorum longus	2	1	1
PL	Peroneus longus	3	2	1
PB	Peroneus brevis	1	0	1

EMG data and length gauge records, along with a time code and stimulation markers, were stored on FM tape while the animal walked on the treadmill. Stimuli were delivered at regular intervals, usually 2.5 s, which did not coincide with the animal's step frequency and which permitted about two unperturbed step cycles between stimuli. Higher intensity stimuli did entrain the stepping frequency, but the conditions reported here produced an even distribution of stimuli over all phases of the step cycle. Data was collected over a three to six minute session for each nerve stimulation, so that over one hundred stimuli were delivered to assure a complete sampling of the step cycle. Each animal was tested at its preferred walking speed (ranging from 0.6 to 0.8 m/s) in order to provide stable walking patterns throughout the session. The order of nerves stimulated was varied; each animal had stimulating electrodes on only two nerves. The Table contains a summary of the number of observations of each nerve/muscle combination (no observations were available in a few cases because of unacceptable EMG signal quality and/or limitations in the number of devices that could be implanted in each animal).

Data analysis

Analog length gauge and rectified integrated EMG signals were digitized (at 500 Hz) for 20 ms preceding and 100 ms following each stimulus and stored on hard disk files using a PDP-11 laboratory computer. Continuous records suitable for analysis were identified using the videotape records synchronized to the analog records with the digital time code. Length gauge records were digitized directly; EMG signals were rectified and integrated into 2 ms resettable bins zeroed after each sampling, using a pulsed EMG integrator (Bak and Loeb 1979). At the same time, a record of the times of stimulus occurrence was also generated and stored.

A computer-generated video display showing a continuous analog record of the ankle length gauge was compared with frame-by-frame video records to identify step cycle phases. A joystick-driven cursor on the display locked to a digital clock readout (which could be compared to the digital time display on the videotape) was used to mark the times of transition between step cycle phases. Three phases, corresponding closely to those of Phillipson (1905), were marked for each step: pre-stance limb extension (E_1), stance (E_2 , E_3), and limb flexion (F). This procedure allowed for step duration normalization and the iden-

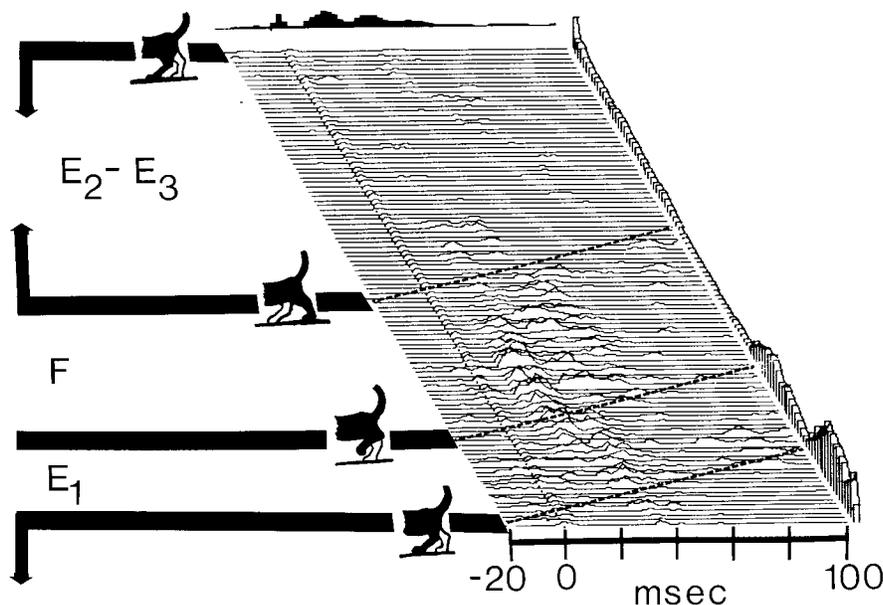


Fig. 1. Sample data presentation consisting of normalized peristimulus EMG records ($n = 104$) from EDL arranged vertically according to the time of stimulus (superficial peroneal nerve) presentation relative to locomotor phase (stages of locomotor cycle are indicated at left, time progressing downward). Stimulus occurrence = time 0 on scale at bottom. Combined peristimulus activity is represented by histogram at top. Pre-stimulus (unperturbed) activity throughout the step cycle is shown along right side. Diagonal, dashed lines indicate isotemporal borders of normal activity. Stimulus artifact appears as a deflection of consistent amplitude just following the dot denoting the stimulus occurrence in each trace and also in the histogram at the top.

tification of stimulus occurrence by phase in the step cycle. For each data set of 200 to 300 steps, the average duration of each of the step phases was computed. For each stimulus, the time in ms since the most recent footfall was computed based on the assumption that the duration of each intervening phase or fractional phase was equal to the average duration for its type. This determined a relative onset time for each stimulus, ranging in value from 0 to the average step duration. Stimuli which fell in phases differing from the norm by $\pm 20\%$ were not used. Generally the effects of a stimulus were brief and barely, if at all, perceptible on videotape, with no apparent resetting of the step cycle pattern generator.

Figure 1 contains a typical set of peristimulus EMG records, from 20 ms before each stimulus to 100 ms after it, displayed as a series of horizontal sweeps. The sweeps are displaced evenly down the display, and have been arranged sequentially in order of their relative onset time, so that early stance peristimulus EMG traces appear at the top, and late swing EMG traces appear at the bottom. The horizontal traces have been successively offset to create a diagonal perspective view which enhances visualization of the response pattern. Step cycle phase transitions are indicated along the left edge of the figure; the raster begins at foot contact (E_{2-3}), the next bar indicates foot lift (start of F), and the next the beginning of pre-stance extension (E_1). At the top of the figure is an average response histogram which was created by combining all traces. Along the right edge of the figure is a smoothed histogram of the prestimulus (control) activity, obtained by integrating the EMG in the first 20 ms of each trace. This can be read down from the top to give the normal pattern of EMG activity for this muscle (EDL) corresponding to the locomotor cycle phases along the left margin.

An important feature of this type of display is that isotemporal lines may be drawn diagonally from upper right to lower left at about 20° to the horizontal (dashed lines overlaying traces in Fig. 1). Thus the onset and offset of normal activity can be seen first to the extreme right (at the end of the traces that begin in late E_2) and then moving progressively downward and leftward through the reflexes response periods.

The amplitude of these EMG records has been normalized to represent percentages of the maximum rectified and smoothed EMG signal encountered in each raster (regardless of whether part

of the reflex response or normal activity). Where large reflexes occur, control EMG amplitude may be barely perceptible in the raster, but it is rescaled upward in the prestimulus histogram at the right.

Results

Qualitative assessment of the effect of stimulating each of the three cutaneous nerves in the foot revealed similar results: a coordinated approximation of limb flexion. The stimulus strength was not high enough to elicit actual flexion consistently (though increasing the stimulus would clearly increase the extent or likelihood of hip, knee, and ankle flexion). However, during F and early E, a hesitation or exaggerated flexion would at times be visible. No kinematic differences in this flexion reflex response were observed among the responses to stimulation of different nerves.

General response patterns

Although complex, the response patterns of the muscles were highly repeatable whenever a particular muscle was studied with a particular stimulus locus in more than one animal. In order to obtain an overview of the form of the reflex response in each muscle independent of the influences of step cycle phasing, we have collected the peristimulus histograms (top lines) from a number of rasters in Fig. 2. Each histogram represents over 100 stimulus presentations to a single animal during constant speed walking, and

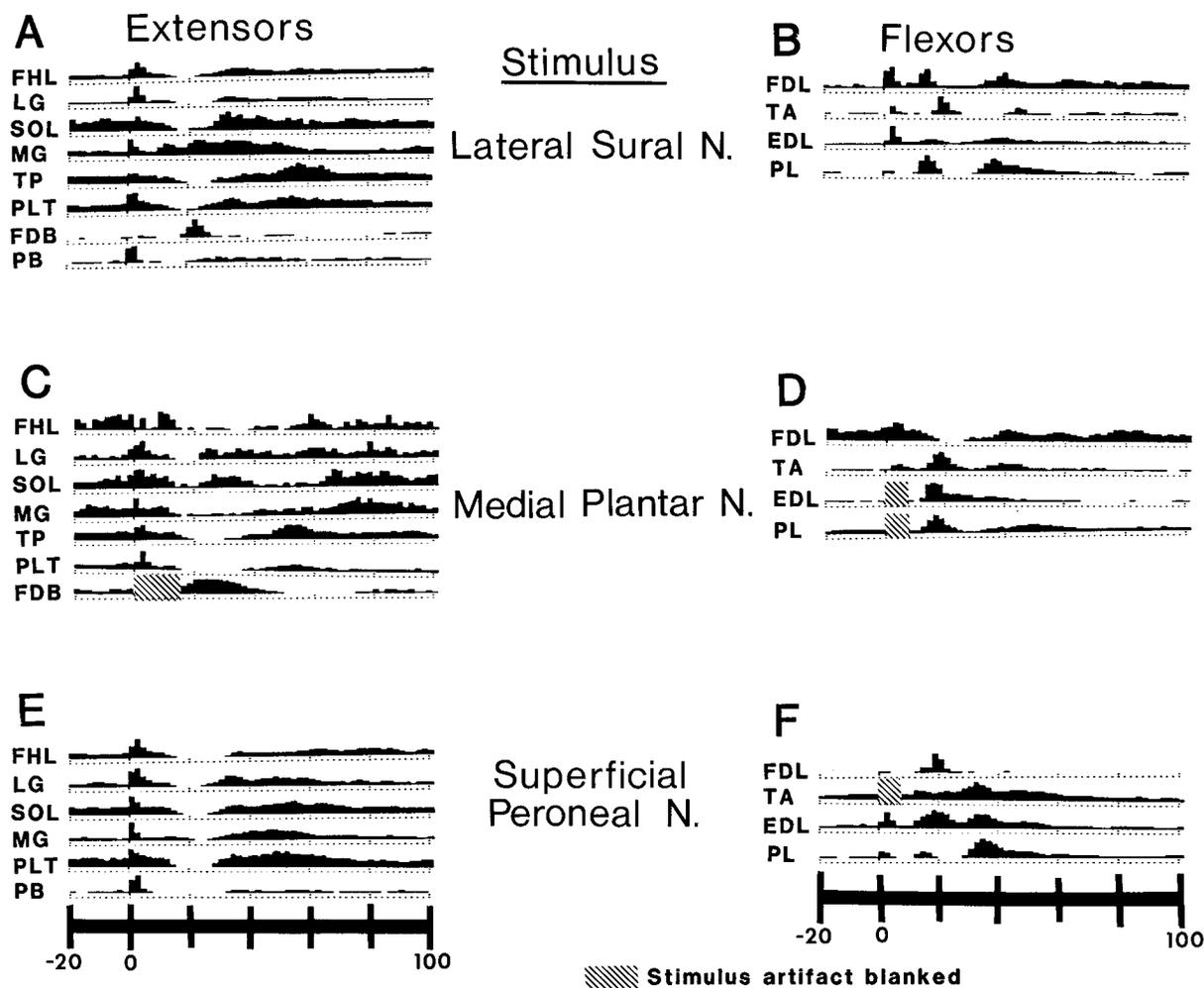


Fig. 2A-F. Peristimulus histograms of normalized EMG responses to brief stimuli applied (at $t = 0$) to the sural nerve (A and B), the medial plantar nerve (C and D), and the superficial peroneal nerve (E and F). Extensor muscles are on the left, flexors on the right. Most histograms show stimulus artifacts in the first two or three bins after stimulus onset; these have been blanked out in some traces to avoid confusion. Data in each histogram were collected from a single cat

includes 20 ms of prestimulus (control) activity followed by 100 ms of poststimulus (response) activity.

Two basic patterns of EMG responses emerged: a *flexor* pattern of two distinct excitatory bursts, and an *extensor* pattern of inhibition. The latencies of the reflex responses were remarkably consistent across muscles as well as within rasters; the first excitatory response occurred about 7–10 ms, and the latency of the second excitatory response was about 27–31 ms. Later waves of response were also seen, but these are more difficult to interpret because they may include proprioceptive reflexes resulting from the mechanical effects of the short latency reflexes.

The muscles crossing the ankle joint can be grouped into those that are normally active during

the stance phase and those that are normally active during swing. We have here identified these as extensors and flexors, respectively, a classification which is in general agreement with their participation in the classical flexor reflex (Sherrington 1910) and which corresponds to the basic division of response types to cutaneous nerve stimuli during walking as seen in Fig. 2. In general, the reflex responses of the flexors were quite homogeneous, with the notable exception of muscles such as FDL and PL, for which this simple categorization might be expected to break down. FDL is anatomically both an ankle extensor and toe plantarflexor, and is in fact anatomically synergistic with the FHL muscle despite their opposite recruitment in the swing and stance phases,

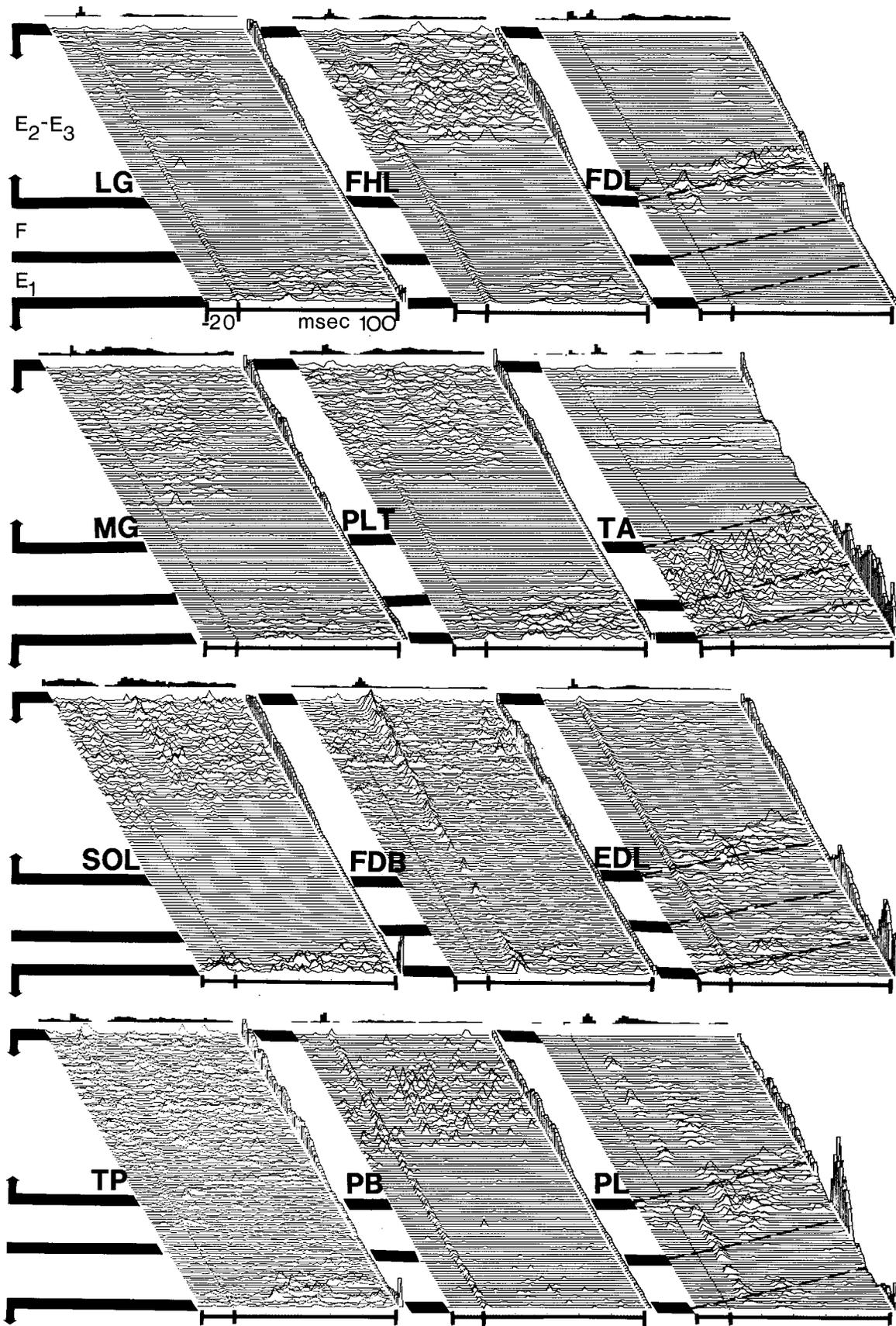


Fig. 3. Peristimulus rasters and histograms of typical responses of twelve muscles to lateral sural nerve stimulation at random points throughout the step cycle. See Fig. 1 for detailed explanation of format

respectively (O'Donovan et al. 1982; Abraham and Loeb 1985). Thus it is interesting to note that its response to MPN stimuli was an inhibition similar to that seen in the extensor group, whereas the response to LSN and SPN stimuli was excitatory (although note absence of a long latency response to SPN stimuli). Peroneus longus acts to invert as well as flex the ankle, which may be related to the absence of a clear second excitatory burst to MPN stimuli, despite the more usual response to LSN and SPN stimuli.

The responses of the muscles active in the stance phase (extensors) were less homogeneous. Inhibitory responses, while often very strong, were less consistent in both onset and offset, and were sometimes followed by excitatory responses. This was most notable with LSN stimulation, and may represent rebound from the preceding inhibition as a result of post-inhibitory synchronization of normal recruitment and/or stretch reflexes elicited by the relaxation of loaded muscles.

Reflex gating

In order to examine interactions between the locomotor cycle and the reflexes, the data from the complete rasters as described in the Methods has been presented for selected muscles during LSN (Fig. 3) and SPN (Fig. 4) stimulation.

The phasing of reflex responses by the step cycle may have two causes. The simplest is the state of activation of the motoneuron pool by the step cycle generator at the time the stimulus was presented. Obviously, inhibitory reflexes can be seen in the EMG signals only if the muscle is already recruited. The inhibition of the stance phase muscles was quite strong, usually completely silencing the muscle even during the peak of its normal recruitment. It is impossible to know whether these inhibitory effects on the motoneuron pools were modulated by the central pattern generator or whether they persisted during periods of EMG silence.

The short latency excitatory reflexes in the swing phase muscles were generally present in proportion to the level of recruitment apparent in the EMG. In some cases, this meant that reflex responses were discernible only when the muscle was at or near the peak of its recruitment (e.g. TA in Fig. 3). In other cases, the reflexes broke through in phases where the muscle was not normally active, but the reflex amplitude still peaked when the muscle was most active (e.g. PL and EDL in Fig. 3). In both cases, the simplest (but not only) explanation is a constant excitatory input whose EMG expression depended on the closeness to threshold of the motoneurons.

The more interesting source of reflex phasing is gating of transmission in the premotor relays, which has been demonstrated for short latency responses during fictive locomotion (Andersson et al. 1978; Schomburg and Behrends 1978). Our methods do not permit us to distinguish premotor from motor pool gating unless the pattern of the reflex responses is out of phase with the normal muscle recruitment. In using these rasters to assess this possibility, it is important to remember that, particularly for long latency reflexes, the control level that is pertinent to the observed response is best found on a trace occurring later in the step cycle (perhaps 5–8 lines lower) than that on which the reflex is observed. Bearing this in mind, at least some of the longer latency excitatory responses of the flexor muscles (e.g. EDL, TA, and PL) appear to begin earlier or cease earlier in the step cycle than the control EMG. Note the peak of the long latency reflexes in TA (Fig. 3) early in the swing phase whereas both the normal EMG and short latency reflex excitation are more sustained throughout the swing phase. The long latency excitatory reflex to the flexors occurred only rarely for stimuli delivered more than 100 ms into the flexion phase, although short latency reflexes were more often persistent (e.g. FDL in Fig. 4, EDL and PL in Fig. 3). This suggests that transmission in the pathway responsible for mediating this longer latency excitation was gated by the step cycle pattern generator so as to peak around the time of foot lift, when the limb is not bearing significant weight and when there is time left in the swing for adaptation of the following footfall to correct for changes in swing trajectory. This is consistent with the behavioral observation that overt movements occurred only for stimuli delivered early in the swing phase, and usually included a hesitation in the ensuing foot placement.

Multifunctional muscles

Two multifunctional muscles (PL and EDL) were unusual in having both normal activity as well as reflex responses during both stance and swing. Furthermore, EDL was recruited twice during swing, in F (ankle dorsiflexion) and E₁ (digit dorsiflexion in preparation for stance). The predominant period of recruitment in F was accompanied by both short and long latency excitatory reflexes, the latter apparently phase-advanced as noted above. The lesser recruitment in E₁ was accompanied by little or no reflex excitation in this or any muscle at that point in the step cycle.

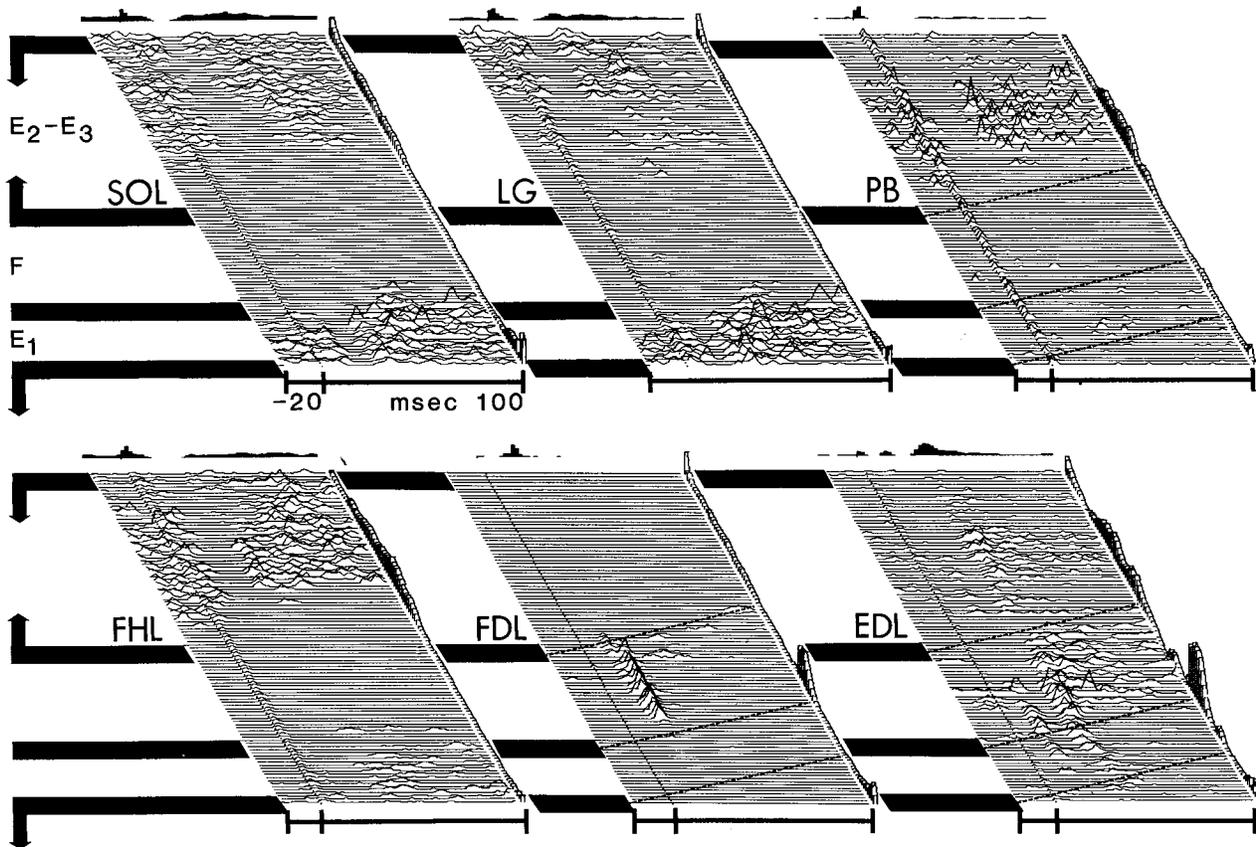


Fig. 4. Peristimulus rasters and histograms from six muscles responding to superficial peroneal nerve stimulation at random points throughout the step cycle. See Fig. 1 for detailed explanation of format

Both PL and EDL demonstrated occasional weak recruitment during the stance phase as well as during swing, perhaps related to their actions as ankle inverter and toe stabilizer, respectively. These periods of recruitment during stance were accompanied by typical double-peaked excitatory reflexes, providing virtually the only excitatory responses seen during stance that could not be attributed to the effects of rebound from inhibition. Thus the various responses appeared to be more a function of the predominant work of the muscles (both presumably flexors) than of the general nature of responses occurring at any given point in the step cycle (e.g. inhibition during stance phase).

Comparison of PLT and FDB responses is also of interest because of the close anatomical synergy between these - series muscles. The data in Fig. 3 reveal that although the normal walking EMG patterns were similar for these two muscles, the extent as well as the type of reflex response was quite different. PLT displayed a typical *extensor* pattern of inhibition, while the short latency excitation of FDB was occurring almost simultaneously. This would be

most consistent with a combination of ankle dorsiflexion and digit plantar flexion, particularly if, as noted in the previous paper (Abraham and Loeb 1985), the calcaneus pulley is operating against its anatomical stop at this point in the cycle.

Stimulus locus

The stimulation of different cutaneous nerves had relatively little effect on the patterns of responses in the various muscles. It is difficult to make quantitative comparisons because of differences in the total numbers of afferents in those nerves and their fiber diameters, which would be important to their threshold to electrical stimulation. However, it seems that the reflex generation machinery responds similarly to inputs from various regions of skin with very different relationships to the motions of walking. The plantar nerve includes afferents from surfaces that normally contact the ground during walking. The sural (LSN) and peroneal (SPN) nerves innervate the anterior and posterior surfaces of the limb, respec-

tively, which might be expected to encounter different types of obstruction in different points of the step cycle. In each case the muscle recruitment seemed to depend most on the phase of walking, and seemed to serve the general purpose of reducing dependence on the stimulated limb, either by unloading it or by getting it into the air faster or longer. This is consistent with a previous study from this laboratory which examined more diverse stimulation and recording sites but in considerably less detail (Duysens and Loeb 1980).

The MG response pattern to LSN, but not SPN, stimulation included excitatory peaks with latencies similar to those seen in the flexion phase responses of ankle dorsiflexors, rather than the typical *extensor* inhibition. A similar excitation of ankle extensor motoneurons by sural but not saphenous nerve stimuli has been reported in decerebrate cats (Hagbarth 1952). It may reflect some local effect associated with an attempt to move medially in response to a lateral stimulus, or perhaps a *flexor* action at the knee in which the other muscles did not participate. This may also reflect a previously reported selective sural excitation of fast twitch MG units (Kanda et al. 1977). Failure to see such a pattern in LG might arise either from a true difference in sural nerve projections or, more likely, from selective sampling from the slow compartments of LG (English and Letbetter 1982). A similar fractionation of the knee extensor reflexes (vastus intermedius, medialis, and lateralis) has been noted for saphenous nerve stimuli during walking (Loeb et al. 1983).

Certain small, multiarticular muscles also had patterns of reflex recruitment that were not consistent with the responses of their locomotor synergists. In fact, depending on the stimulus, they could switch between patterns characteristic of either the swing or stance synergistic groups. Most striking in this regard was FDL, as noted earlier.

Discussion

The basic reflex pattern, regardless of locomotor phase or stimulus locus, could best be described as limb flexion, with coordinated activation of flexors and inhibition of extensors, resembling in many respects the classic flexor reflex of Sherrington (1910) and the ballistic flexion that occurs during rapid locomotion or jumping (Abraham and Loeb 1985). This would be entirely consistent with the suggestion that cutaneous reflexes during locomotion act to prevent stumbling by producing an exaggerated limb flexion (Forssberg et al. 1975). The primary variation

from this pattern was the addition of a late excitatory response in the ankle extensor muscles. Although this might be interpreted in a manner similar to that of reports of "reflex reversal" involving limb extension during stance (Forssberg et al. 1975 and 1976; Forssberg 1979b), the late excitation exhibited in the ankle *extensor* pattern followed a clear inhibitory response and was less marked than the ankle *flexor* excitation caused by the same stimuli. Thus this late extensor excitation might better be construed to be a proprioceptive reflex to correct exaggerated yielding of the limb caused by the preceding inhibition.

A major limitation of this study was the artificial nature of the reflex-eliciting stimuli and the restricted set of muscles from which data were collected. The stimuli used cannot be compared to actual cutaneous stimulation of the foot (e.g. Wand et al. 1980), either in intensity or quality. Thus some physiological relevance was sacrificed in order to have reproducibly consistent stimuli with precise temporal control. This limitation may have been responsible for the failure to clearly differentiate reflex response patterns to stimulation of different nerves. Also, data were collected in these experiments only from the distal musculature of the hindlimb ipsilateral to the stimulus. Duysens and Loeb (1980) and Duysens et al. (1980) have reported on the ipsi- and contralateral reflex responses above and below the knee during locomotion. The ipsilateral response latencies and patterns reported here were similar to those found by Duysens and Loeb (1980), who also found relatively little specificity for stimulus locus.

While it is logical to suspect that reflex pathways might interact with phasic recruitment patterns, we were unable to distinguish between the phasic changes in motoneuron excitability and premotor pathway modulation for the shortest latency responses. We did, however, find some evidence for premotor modulation of the longer latency responses. Demonstrations of modulation of motoneuronal EPSP's in fictive preparations (e.g. Schomburg and Behrends, 1978; Andersson et al. 1978) are difficult to compare to these EMG reflexes in intact cats. When EPSPs are below threshold for motoneurons that are hyperpolarized in the phases between normal recruitment times, their modulations go undetected in EMG records (and are functionally irrelevant). Long latency responses probably go through so many interneurons that little of relevance to the normal can be learned from the various, quite different reduced preparations (see Sherrington and Sowton 1915). In fact, most reflexes of the type described here do not occur at all for similar stimuli delivered during decerebrate walking (Duenas et al. 1984).

The fact that most of the reflex responses reported here occurred during periods in which the muscle was usually active (or might have been active) seems to reflect a very functional scheme. When a muscle is active during locomotion, it is in the best position to affect the movement in a meaningful way: *Extensors* can "produce" limb flexion during stance by simply relaxing; *flexors* can produce limb flexion during swing by additional contraction from a "primed" state. The central locomotor pattern and reflex pathways appear to be arranged synergistically so that calamitous actions, such as complete limb flexion with loss of support just before or during stance, are very unlikely to occur. Rather a yielding occurs, which effectively unweights the foot and flexes the limb with minimal disturbance of overall posture. At the same time, the contralateral limb simply works harder in whatever state it is in (Duysens et al. 1980). The reflex response to stimulation of cutaneous afferents appears to be gated both temporally and anatomically so that a functional, whole-limb action occurs which employs coordinated activity in all of the muscles in the cat distal hindlimb. Usually, this entails patterns of synergy that are not dissimilar from those seen during the normal locomotor recruitment of the various muscle groups.

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References

- Abraham LD, Loeb GE, Marks WB (1981) Comparison of normal use and reflex response patterns of cat distal hindlimb muscles. *Soc Neurosci Abstr* 7: 688
- Abraham LD, Loeb GE (1985) The distal hindlimb musculature of the cat: patterns of normal use. *Exp Brain Res* 58: 580-593
- Andersson O, Forsberg H, Grillner S, Lindquist M (1978) Phasic gain control of the transmission in cutaneous reflex pathways to motoneurons during "fictive" locomotion. *Brain Res* 149: 503-507
- Andersson O, Grillner S (1981) Peripheral control of the cat's step cycle. I. Phase dependent effects of ramp-movements of the hip during "fictive locomotion" *Acta Physiol Scand* 113: 89-101
- Andersson O, Grillner S (1983) Peripheral control of the cat's step cycle. II. Entrainment of the control pattern generators for locomotion by sinusoidal hip movements during "fictive locomotion". *Acta Physiol Scand* 118: 229-239
- Bak MJ, Loeb GE (1979) A pulsed integrator for EMG analysis. *Electroenceph Clin Neurophysiol* 47: 738-741
- 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, Loeb GE, Weston BJ (1980) Crossed flexor reflex responses and their reversal in freely walking cats. *Brain Res* 197: 538-542
- Engberg I, Lundberg A (1969) An electromyographic analysis of muscular activity in the hindlimb of the cat during unrestrained locomotion. *Acta Physiol Scand* 75: 614-630
- English AW, Letbetter WD (1982) A histochemical analysis of identified compartments of cat lateral gastrocnemius muscle. *Anat Rec* 204: 123-130
- Forsberg H (1979a) On integrative motor functions in the cat's spinal cord. *Acta Physiol Scand Suppl* 474
- Forsberg H (1979b) Stumbling corrective reaction: a phase-dependent compensatory reaction during locomotion. *J Neurophysiol* 42: 936-953
- Forsberg H (1981) Phasic gating of cutaneous reflexes during locomotion. In: Taylor A, Prochazka A (eds) *Muscle receptors and movement*. MacMillan, London, pp 403-411
- Forsberg H, Grillner S, Halbertsma J (1980) The locomotion of the low spinal cat. I. Coordination within a hindlimb. *Acta Physiol Scand* 108: 269-281
- Forsberg H, Grillner S, Rossignol S (1975) Phase dependent reflex reversal during walking in chronic spinal cats. *Brain Res* 85: 103-107
- Forsberg H, Grillner S, Rossignol S, Wallen P (1976) Phasic control of reflexes during locomotion in vertebrates. In: Herman RM et al. (eds) *Neural control of locomotion*. Plenum, New York, pp 647-674
- Grillner S, Zanger P (1979) On the central generation of locomotion in the low spinal cat. *Exp Brain Res* 34: 241-261
- Hagbarth K-E (1952) Excitatory and inhibitory skin areas for flexor and extensor motoneurons. *Acta Physiol Scand* 26: Suppl 94: 1-58
- 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
- Loeb GE (1982) Task groups - a proposed functional unit for motor control. *Soc Neurosci Abstr* 8: 947
- Loeb GE (1984) The control and responses of mammalian muscle spindles during normally executed motor tasks. *Exp Sport Sci Rev* 12: 157-204
- Loeb GE, Marks WB, Hoffer JA (1983) Reflex recruitment of individual cat hindlimb motoneurons by cutaneous shocks during normal walking. In *Reflex organization of the spinal cord and its descending control*. IUPS Satellite, Canberra, Australia, Abstr 1.9
- O'Donovan MJ, Pinter MJ, Dum RP, Burke RE (1982) The actions of FDL and FHL muscles in intact cats: Functional dissociation between anatomical synergists. *J Neurophysiol* 47: 1126-1143
- Phillipson M (1905) L'Autonomie et la centralisation dans le systeme nerveux des animaux. *Trav Lab Physiol Inst Solvay, Bruxelles* 7: 1-208
- Rasmussen SA, Goslow GE, Hannon PR (1982) Locomotion of partially deafferented cats. *Am Col Sports Med Abstr*.
- Schomburg ED, Behrends H-B (1978) Phasic control of the transmission in the excitatory and inhibitory reflex pathways from cutaneous afferents to α -motoneurons during fictive locomotion in cats. *Neurosci Lett* 8: 277-282
- Schomburg ED, Behrends H-B, Steffens H (1981) Changes in segmental and propriospinal reflex pathways during spinal locomotion. In: Taylor A, Prochazka A (eds) *Muscle receptors and movement*. MacMillan, London, pp 413-426