SUMMARY AND CONCLUSIONS

1. The responses of 11 individual motoneurons, the muscle to which each projected, plus all other muscles in the anterior thigh of the cat, were recorded following single nonnoxious electrical stimuli to cutaneous nerves while the intact animal walked on a treadmill.

2. The various excitatory and/or inhibitory responses were qualitatively similar for stimuli within the range 1.1-10 times threshold for group I fibers in the stimulated nerve (usually saphenous).

3. Monarticular knee extensor muscles in the vastus group and their motoneurons were usually inhibited in the period 10- to 25-ms poststimulus. The faster contracting vastus medialis and lateralis muscles tended to have an excitatory rebound at ~25- to 40-ms poststimulus that was confined to the stance phase of the step cycle when these muscles were normally active.

4. Biarticular hip flexor muscles rectus femoris and both the anterior and medial parts of sartorius and their motoneurons all had similar bimodal excitatory responses, including an early period 3- to 18-ms poststimulus and a later period 20- to 35-ms poststimulus.

5. The short-latency excitatory responses appeared to be proportional to the normal recruitment of the muscles in the step cycle, whereas the long-latency responses tended to be phase advanced with respect to normal recruitment.

6. Motoneurons projecting to muscles with two excitatory peaks tended to have similar excitatory responses at both latencies and occasionally responded at both latencies to a single stimulus.

INTRODUCTION

The anterior thigh muscles of the cat are comprised of pure extensors, pure flexors, and mixed biarticular muscles that are capable of contributing to both extension and flexion. The vasti group (vastus intermedius, VI; vastus medialis, VM; vastus lateralis, VL) are anatomic ally pure knee extensors and are recruited during only the stance phase of locomotion. The sartorius pars medialis (SA-m) acts as a flexor of both the hip and knee and is recruited only during the swing phase. The rectus femoris (RF) and sartorius pars anterior (SA-a) are hip flexors and knee extensors. Both are recruited during both the swing and stance phases of fast trotting, although only the SA-a is normally recruited in both phases of slower gaits (10, 22).

In the companion papers, we have reported on the normal recruitment patterns of individual motoneurons that project to these muscles. These records suggest that the SA-a motoneuron pool is divided into two functionally distinct groups that contribute only to one or the other of the two motor tasks performed by this muscle during locomotion (16). In this report, we describe the recruitment of anterior thigh motoneurons and their parent muscles in response to cutaneous stimuli delivered during walking.

Activation of the flexor-reflex afferent (FRA) system has long been known to cause a flexion response in the ipsilateral limb and extension in the contralateral limb. Recently, cutaneous pathways constituting parts of this system have been stimulated during locomotion, revealing muscle responses that depended particularly on the phase of the step cycle in
which they were delivered (9, 11, 12, 25). The details of the responses in anterior thigh muscles reported here are similar to those reported previously for other, unifunctional muscles (1, 8). The two bifunctional muscles SA-a and RF both were reflexly recruited as if they were simple flexors. This recruitment included motoneurons that participated normally in the swing as well as the stance phase of unperturbed walking.

Preliminary reports of this work have been published elsewhere (23).

METHODS

The records described here come from three of the adult cats described in the companion papers (see Ref. 14 for detailed description of the implanted devices and unit identification methods).

Briefly, the fifth lumbar ventral root (L5 VR) was chronically implanted with up to 12 floating microelectrodes, some of which recorded stable discriminable unit activity during normal motor behavior over a period of 1–2 mo postoperatively. The conduction direction and velocity of these presumed fiber recordings was identified by spike-triggered averaging of neurograms recorded by a chronically implanted multipolar cuff electrode on the femoral nerve that provided two tripolar sites—15 mm apart (15). The muscle to which the efferent units projected was determined by comparing the spike-triggered averages obtained from chronically implanted bipolar or multipolar EMG electrodes in all of the muscles to which the femoral nerve projects (14). Usually one such record was much larger and contained higher frequency components than all of the others, indicating that the muscle fibers innervated by the triggering unit were closest to that particular recording electrode.

Identification of units during responses

All of the analog signals from the microelectrodes, nerve cuff, and EMG electrodes were recorded on an FM tape recorder (DC to 10-kHz bandwidth) so that these identification procedures could be carried out off-line on the actual records analyzed for experimental results. This is particularly important for reflex responses because of the possibility that stimulation may provoke responses in other VR fibers adjacent to the identified motoneuron. The presence of other fibers generating similar unitary waveforms is difficult to rule out because such units may not have been recruited during the unperturbed behavior. We used two variations of the normal unit identification procedures to try to eliminate this possibility. First, a storage oscilloscope was triggered to overlay multiple sweeps of the amplified and expanded complete unitary waveform that was accepted by the window discriminator (using the analog delay line configuration described in Refs. 4 and 5). Two waveforms occurring spontaneously (not in response to stimuli) were compared with all of the so-called reflex responses that occurred from 1- to 30-ms poststimulus (see Fig. 1, top).

The unit waveforms were generally distinctive enough in shape and amplitude that identification seemed unambiguous. However, to prevent the possible coincidence of a similar waveform from a previously silent unit, we used a second method when the reflex responses included enough spikes to make this feasible. We compared the spike-triggered averages of the two femoral nerve cuff electrodes for all of the reflex spikes with averages triggered by a similar number of spontaneous spikes, as shown in the bottom half of Fig. 1. Although we usually used 500 sweeps to obtain accurate measures of fiber conduction velocity, averaged responses usually began to emerge at ~100 sweeps, and the corresponding features of the two sets of averages can be discerned for each unit (dashed vertical lines). Spike-triggered averages of EMG during reflex responses were not useful because of the large-amplitude synchronized activity evoked in the muscles.

Stimulus delivery

Stimuli were delivered by chronically implanted bipolar patch electrodes on the saphenous nerve (10 out of 11 units studied) or on the sural nerve and subcutaneously in the dorsum of the foot (unit B10B18, see Table 1). The saphenous patch consisted of a U-shaped sheet of Dacron-reinforced Silastic (Dow Corning #570-1000 Dura Film, 0.25 mm thick × 10 mm wide × 15–20 mm long) with stranded Pt-Ir wire contacts sewn to the inner face so as to contact the nerve at 5-mm intervals along its course. The saphenous nerve, a cutaneous branch of the femoral, was partially mobilized over 20–25 mm along the medial thigh. The flexible patch electrode was folded around the nerve and sewn to overlying fascia. Interelectrode impedances were in the 1–5 kΩ range. The use of this design rather than a sealed nerve cuff enabled the small fragile saphenous branch to remain attached to local connective tissue and blood supply, preserving viability. The threshold for group I cutaneous fiber activation was determined by noting the lowest current that produced an evoked potential in the proximal femoral nerve cuff electrodes. All stimuli were photoisolated, current-controlled, balanced biphasic pulses with 0.1-ms duration per phase.

Various stimulus amplitudes from threshold to 10 times threshold were delivered at a constant interval of 2 s while the cat walked at a steady rate somewhat faster than one step per second. Visible responses usually began at two to three times group
Discrim. Units

CUTANEOUS REFLEXES ONTO MOTONEURONS

FP

Spike

FD

Triggered Averages

N=15R+2S

N=106R

N=128S

VR

FP

FD

N=132R+2S

N=132R

N=128S

VR

FP

FD

FIG. 1. Criteria used for confirming the identity of spikes recorded during responses to stimuli for the two most responsive units. Oscilloscope photographs at top show the number (n) of superimposed traces of filtered input to the window discriminator showing accepted spikes occurring in the response period 1–30 ms poststimulus (R) overlaid by spontaneously occurring spikes (S). Spike-triggered averages below show averaged waveforms from the unfiltered ventral root (VR) microelectrodes and femoral nerve proximal (FP) and distal (FD) tripolar recording electrodes used to obtain conduction velocity, for similar numbers of sweeps from reflex response spikes (R) and spontaneous spikes (S).

I threshold and became somewhat more noticeable at 10 times threshold but were always confined to slight hesitations or flexion movements that did not break the stride or cause apparent discomfort. Over the course of a typical run of 5–10 min of steady walking, 150–300 responses distributed randomly over the step cycles were recorded on video and 18-track FM tape. Also recorded were stimulus and step cycle timing information, the latter in the form of the analog signals from chronically implanted length gauges across the vasti and sartorius-rectus muscle groups.

Data analysis

The response rasters shown in Figs. 2–5 were produced by a PDP-11/23 computer from the taped data. The raw microelectrode recording (1–10 kHz) was further filtered if indicated, and the acceptance pulses from a window discriminator (see above) provided one input to the computer. The six EMG records (50–5,000 Hz) were full-wave rectified and integrated into discrete 2-ms bins that were sampled once per bin by the computer. The digitization was buffered so that the digitized files included 30 ms of data before and 100 ms after each stimulus synchronization pulse. In a separate digitization of the same data sequence, the recording from a length gauge (usually the vastus gauge across the knee) was digitized in a continuous record and the various inflections associated with footfall, footlift, and the flexion-extension boundary during swing were marked by hand while examining the corresponding video stills from videotape. These times were associated with the stimulus times recorded in the response file to obtain the phase of each stimulus as a fraction of the mean duration of the corresponding segment between marked inflections. Stimuli occurring in step cycles that were 15% longer or shorter than the mean step cycle were rejected. In Table 1, n refers to the number of accepted stimuli used to make up the resultant raster. Typically about three-fourths of the stimuli were accepted.

Each raster shows the actual peristimulus data (unit spikes are shown as 4-ms triangles) with each
trace vertically positioned in order of the phase of the stimulus since footfall. A histogram of all of the traces is shown at the top. The control periods from -30- to 0-ms prestimulus have been integrated and smoothed into the bar graph shown along the right edge of each raster. Amplitudes of these two bar graphs and of the set of data traces were scaled for visual clarity and should be used only for relative amplitude and timing information within a particular raster. It is also important to remember that the 130-ms length of each trace represents a substantial fraction of the total step cycle duration (typically 700-850 ms), so that long-latency responses actually occurred significantly later in the step cycle than the stimulus. Thus the control for the normal activity at a long latency in one trace would actually correspond to the prestimulus activity several traces down in the raster.

RESULTS

The general patterns of EMG response to stimulation of cutaneous nerves were similar at all tested stimulus intensities and in all three animals, including those elicited by sural nerve and paw dorsum stimulation in one animal. In some of the rasters, we have combined stimuli at various intensities to improve the representation of the step cycle.

Pure extensor muscles were inhibited during stance, commencing at ~12- to 15-ms latency and persisting until 20- to 35-ms poststimulus depending on the particular muscle and stimulation level. This was sometimes followed by a rebound to slightly greater than control levels, particularly in the vasti muscles VM and VL, which contain a mixture of muscle fiber types including fast-twitch units. At the higher stimulus intensities, this late excitatory activity had a larger amplitude and shorter latency, perhaps indicating a direct excitatory component of the reflex. There could also be a brief short-latency excitation before the inhibitory response. However, all excitatory responses were confined to and tended to be in proportion to the normal level of recruitment for these muscles at any given point in the step cycle. No significant excitatory responses were seen outside of the stance phase, when these muscles are normally active.

The responses of the remaining biarticular muscles SA-a, SA-m, and RF were all quite similar, despite their considerable differences in normal EMG activity associated with the step cycle. Only excitatory responses were seen (although inhibitory influences may have been obscured), and these tended to have a bimodal latency. We have designated the short-latency responses as P1 (EMG latency usually ~8 ms) and the long-latency responses as P2 (EMG latency usually ~25 ms). P1 responses occurred mainly when the muscle was normally active in the step cycle and tended to increase with stimulus strength. P2 responses tended to occur mostly during the flexion phase of the swing, often largest before the normal activity
of the muscle had reached its peak (including RF, which had no unperturbed swing phase activity) and usually disappearing early in the E₁ phase while the normal activity was still in progress.

Unit responses to stimuli were always similar to that of the parent muscles, but earlier in latency by 3–4 ms. They are summarized in Table 1, which groups the motoneurons by muscles, with those muscles and units demonstrating the most excitatory responses placed first. All unit spikes occurring in each of two 15-ms windows identified as P₁ (3- to 18-ms poststimulus) and P₂ (20- to 35-ms poststimulus) were counted, although the reflex responses often were considerably more tightly clustered in the rasters (see Figs. 2–5). The total spike count in the 30-ms prestimulus control periods was divided by two to obtain comparable control spike (CS) rates. The

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**FIG. 2.** Peristimulus rasters for motoneuron B10B18 and parent VI muscle and for motoneuron L4A4 and parent VM muscle. Each trace shows unit responses (4-ms triangles) or rectified bin-integrated EMG (2-ms sample intervals) for 30 ms before and 100 ms after stimuli (dots lined up at 0 ms). Occasional unit spikes possibly attributable to false acceptance of stimulus artifact have been filled in. Traces have been reordered based on step cycle phase at time of stimulus, with Phillipson step cycle phases (26) shown at left (down arrow indicates footfall, up arrow indicates footlift, vertical bar indicates F-E₁ transition during swing phase). Control activity preceding stimulus has been integrated and smoothed in the bar graph at right to show the naturally occurring activity patterns in the absence of stimuli. Solid histograms at top are summations of all traces synchronized to the stimulus. Vertical scales are constant within each raster, but have been scaled for visual clarity. In all figures, the corresponding traces in each row of rasters were recorded simultaneously.
number of individual stimulus presentations with spikes in both the \( P_1 \) and \( P_2 \) windows are indicated along with a corresponding control for the number of control periods in which there were two spikes in the 30-ms prestimulus period [control pairs (CP)].

Only three of the units had large net excitatory responses at both the \( P_1 \) and \( P_2 \) latencies: L2A42, H1A16, and L4A4. However, all three of these had many more incidences of spikes at both latencies following a single stimulus than control incidences of such paired spikes prior to the stimulus (CP in Table 1). Unit L9B6 probably also had a \( P_1 \) excitatory response, but this is obscured in these totals by what appears to be a short-lived inhibition in the remainder of the \( P_1 \) window (see Fig. 3). This unit also had a large number of paired responses. Two of the VI units (all of whose reflex responses were exclusively inhibitory) had doublets early in their normal stance phase activity, resulting in the unusually high count of control pairs for one unit (L2A33).

**Extensor motoneurons**

Figure 2 shows typical response patterns for a motoneuron projecting to the predominantly slow-twitch red vastus intermedius muscle (top) and a motoneuron projecting to the mixed vastus medialis muscle (bottom). The top two rasters show pooled responses to stimulation of the paw dorsum and sural nerve at levels about twice threshold for visible flexion responses during the swing phase. The weak inhibition of the stance phase EMG of the VI muscle (top right) was mirrored in the motoneuron responses (top left). The bottom two rasters present responses to saphenous nerve stimulation at four times threshold for the group I fibers. The somewhat more pronounced inhibition in the VM EMG (bottom right raster) was followed by a postinhibitory excitation (and perhaps even a subsequent decrease below control values before returning to normal stance phase activity). The unit responses (bottom left) included a similar inhibi-
Fig. 4. Periodic stimuli for RF motoneuron 111A16 and various muscles in response to saphenous nerve stimuli at 1-3 times threshold (top row). Adsorbed thresholds (bottom row). Changes are mostly quantitative. With increasing threshold, eventually overwhelming or obscuring
ity and excitatory pattern, plus clearer evidence for a brief excitatory event at very short latency. The presence of longer-latency responses extending into the F phase for this unit was unusual and is only barely discernible in the EMG traces from the parent muscle (bottom right). It may be significant that this unit was recruited normally only at relatively high threshold (56%).

Rectus femoris motoneurons

Figure 3 shows the responses of two RF motoneurons (top and bottom rows) plus the simultaneous responses of the parent RF muscles and the anatomical synergist SA-a. These records came from the same animal in response to similar stimulus levels (3–4 times group I) on different days. Both motoneurons had weak excitatory responses at short latency during stance phase and more diffuse long-latency activity in both stance and swing phases. Both RF EMG rasters show similar patterns, perhaps including a significant pause between the early and late excitation during stance phase. Both RF and SA-a muscles had long-latency excitatory responses in early swing phase, corresponding to observed unit activity, despite the fact that RF was normally silent during this phase (see control histograms along right edges) and control SA-a activity peaked later in the E1 phase, when the reflex was absent.

Figure 4 shows the responses of an RF motoneuron and parent muscle plus functional stance phase synergists (VI and VM) and anatomical synergist SA-a. As the stimulus intensity was increased (from top row down), the responses generally become more excitatory. Note that to accommodate the very large excitatory peaks, the vertical scale in individual rasters has been made so small that the control activity is barely discernible. At the highest intensities, the cumulative rasters at the top tend to obscure the bimodal pattern of excitatory unit responses that remained during swing phase. In the bottom left raster,
five traces with unit responses at both latencies can be discerned (see DISCUSSION). At all intensities, the RF responses tended to be most similar to SA-a rather than to either of the vasti muscles. Note that the excitatory activity in the vasti obscured the inhibitory responses at higher stimulus intensities but never developed the large coherent peaks found in the biarticular muscles.

Sartorius motoneurons

Figure 5 contrasts the reflex responses of three functionally distinct motoneuron groups in the anterior thigh musculature. The top row shows a pure extensor motoneuron with a predominantly inhibitory response to saphenous stimuli over the range 1.5–10 times group I threshold. The second row shows a motoneuron projecting to SA-a that was normally active during stance but was excited during the swing phase in response to saphenous stimuli at three to four times group I threshold. The motoneuron responses occurred at two distinct latencies following stimulation, corresponding to the two somewhat longer-latency responses noted in the parent muscle EMG (second raster). The third row shows another motoneuron projecting to SA-a, but which was part of the swing phase task group. The reflex responses were obtained during a wider range of stimulus strengths (over half of the traces represent responses to stimuli at 5–10 times group I threshold). The short-latency excitatory responses were more distinct in both the motoneuron and SA EMG responses, but the bimodal pattern and its gating during the step cycle were essentially the same. This contrasted sharply with the excitatory responses in the VL muscle. L2A42 unit responses at both latencies to a single stimulus can be discerned in the individual traces.

DISCUSSION

During locomotion, the motor units of the anterior thigh muscles of the cat appear to be organized into several functional task groups (16, 17, 19, 20, 24) including the following: 1) monarticular knee extensors active during stance phase (VI, VM, and VL), 2) biarticular flexors active during flexion phase (SA-m), 3) motor units with mixed biarticular action that are normally active only during stance phase shortening (RF and some SA-a motoneurons), and 4) motor units with mixed biarticular action that are normally active only during E1 phase shortening (other SA-a motoneurons). The reflex responses elicited by activation of FRAs can be grouped into two types of responses: 1) mostly inhibitory responses in pure extensors (VI, VM, and VL), and 2) bimodal excitatory responses in all units with some flexion action (RF, SA-m, and both groups in SA-a).

With regard to locomotion, it is possible to divide the motoneurons into those that are active during stance and those that are active during swing. However, the FRA recruitment cuts across such lines: RF and some SA-a motoneurons that are normally recruited during stance with the vastus muscles generate excitatory reflex responses similar to SA-m and swing-phase SA-a motoneurons.

We have argued elsewhere that during locomotion the task group organization in these muscles may provide kinematically homogeneous periods of recruitment (e.g., active lengthening vs. active shortening) rather than being related to the half-centers of a hypothetical step cycle generator (20). In contrast, the reflex recruitment patterns described here appear to be dictated more by the potential contribution of the muscles to flexion or extension of the whole limb than by the groupings operating during locomotion. The apparent discrepancy can be resolved by noting that the flexor reflex represents an entirely different motor control problem from those of normal locomotion, being largely an open-loop response to an unexpected perturbation. Thus it should not be surprising that the projections via these pathways appear to be distributed in patterns unlike those from the locomotor pattern generator. For related reasons, the flexor reflex recruitment patterns in α-motoneurons appear not to be accompanied by similar patterns in fusimotor neurons (21).

The locomotor pattern generator does appear to interact in several ways with the FRA pattern generator. First, the appearance and mechanical effects of inhibition can manifest themselves only when the muscles are normally recruited and operating under some mechanical load (e.g., vastus muscles during stance). (Such mechanical effects may then give rise to longer-latency excitation via stretch reflexes that may be difficult to distinguish from direct excitatory projections in the FRA circuitry; see Refs. 1, 8.) Second, excitatory
reflexes will be modulated by the level of polarization of the motoneuron groups to which the reflex EPSP's must add (2). Interestingly, the individual SA-a and RF motoneurons that are normally active only during swing or stance phases appear to be close enough to threshold at other phases to respond vigorously to flexor reflex excitation. Third, reflex pathways involving interneurons that are modulated by the locomotor pattern generator may exhibit phase-dependent modulations in throughput that are out of phase with the step cycle recruitment (e.g., phase lead of the long-latency flexor excitation during swing phase; see Refs. 27, 28).

It is interesting to note that the interval between the two FRA excitatory waves is similar to that between the M1 and M2 responses to muscle stretch (30). The participation of a single motor unit at both latencies (see Table 1) corresponds to a relatively high instantaneous discharge rate (33–67 pps), which may be sufficient to lead to a brief potentiation of force output identified as the “mammalian catch property” by Burke et al. (7). It should also be noted that these high spike rates must result from excitatory synaptic input that is sufficient to overcome the postspike hyperpolarization that usually serves to stabilize motoneuron discharges at lower spike rates.

The predominantly inhibitory pattern seen in the slow VI muscle and its motoneurons contrasts with the more complex mixed inhibition/excitation seen in the mixed VL and VM muscles, particularly at stronger stimulus intensities [see Ariano (3) for fiber histochemistry profiles of these muscles]. Selective net excitation from sural nerve onto fast rather than slow motoneurons in the triceps surae has been reported (18), although it is not clear whether this apparent reversal of the orderly size-ranked recruitment (13) reflects a reversed excitatory strength or a normal ranking of EPSP's superimposed on a very strong selective inhibition of slow motor units. At least some of the long-latency excitation reported here in VM and VL may reflect proprioceptive feedback as a result of preceding inhibition of the loaded muscles. In analogy to the ankle extensor muscles, the relative absence of such responses in the slow VI, which probably receives stronger monosynaptic Ia input than the faster VM and VL, would argue for the existence of a preferentially strong inhibition from the cutaneous reflex pathway. This may be related to the general undesirability of having slow muscles (with long relaxation times) participating in potentially fast motor behaviors, as noted for paw shaking (29).

In general, the cutaneous reflex generator appears to be organized on the basis of the skeletal mechanics of the individual motor units and independently from the functional groupings of other generators. The FRA generator interacts with the locomotor generator via interneuronal circuits whose transmission properties are determined on a moment-to-moment basis by the locomotor circuitry of the spinal cord and, presumably, by various descending pathways. This gives rise to the complexly modulated and quite specialized motoneuron recruitment patterns that underlie the mechanically well-adapted responses of the hindlimb to perturbations of the locomotor step cycle.

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