Tonic and Phasic Discharge Patterns in Toe Flexor γ-Motoneurons During Locomotion in the Decerebrate Cat

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Murphy, P. R. Tonic and phasic discharge patterns in toe flexor γ-motoneurons during locomotion in the decerebrate cat. J Neurophysiol 87: 286–294, 2002; 10.1152/jn.00917.2000. To investigate the specificity of fusimotor (γ) drive during locomotion, γ-efferents were recorded from the flexor digitorum longus (FDL) and flexor hallucis longus (FHL) nerves in a decerebrate cat preparation. These nerves innervate hindlimb muscles that differ in some aspects of their mechanical action. For both FHL and FDL, two stereotyped patterns of γ activity were distinguished. Tonic units fired throughout the step cycle and had less modulation, but higher minimum rates, than phasic units, which were mainly recruited with ankle extensor (soleus (SOL)) electromyogram (EMG) activity. Differences in the relative timing of these patterns were apparent. In FHL the activity of phasic and most tonic neurons peaked after EMG onset. With FDL, tonic units generally reached maximum rate before, while phasic units peaked after, the beginning of EMG activity. During locomotion FHL and FDL α activity were rhythmically recruited with SOL. However, consistent with previous reports, FHL and FDL differed in their patterns of α activity. FHL was stereotyped while FDL was variable. Both FHL and FDL had activity related to ankle extensor EMG, but only FDL exhibited a peak around the end of this phase. No corresponding γ activity was observed in FDL. In conclusion, 1) FHL and FDL received tonic and phasic fusimotor drive; 2) there was no α/γ linkage for the late FDL α burst; 3) phasic γ-efferents in both muscles received similar inputs, linked to plantar flexor α activity; and 4) tonic γ-efferents differed, to the extent that they were modulated at all. The FHL units peaked with the plantar flexor alphas. The FDL neurons generally peaked before α activity even began.

INTRODUCTION

Muscle spindles are stretch receptors that have an important role in proprioception and the control of muscle activity. Through the two types of γ-efferent (fusimotor neuron), static and dynamic (Matthews 1962), the CNS is capable of powerfully influencing spindle afferent feedback during movement (for review, Prochazka 1996). Currently, however, the rules that govern γ discharge are not fully understood (e.g., Gandevia and Burke 1992; Kakuda et al. 1997; Loeb et al. 1985; Murphy 2000; Prochazka 1996; A. Taylor et al. 2000; J. Taylor et al. 1985), in large part due to the lack of a technique that allows stable, direct recordings from identified γ-efferents during movement in intact animals. A major unresolved issue in this field concerns the incidence and functional significance of variation in γ drive to different muscles during the same behavior (i.e., muscle-specific γ drive). One credible proposal is that its nature (i.e., static or dynamic) depends on the action of the parent muscle and there is evidence, in support of this idea, based on direct γ and spindle afferent recordings during locomotion in cat preparations (for review, Murphy and Martin 1993). Thus, for example, the ankle flexor, tibialis anterior, receives powerful phasic static γ drive that is coactivated with homonymous α-motoneurons (Cabelguen 1981; Murphy and Hammond 1993), while in its antagonist (triceps surae), dynamic γ-efferents exhibit this pattern of discharge (Bessou et al. 1990; Cabelguen 1981; Murphy et al. 1984; Perret and Berthoz 1973; Taylor et al. 1985). It should be noted, however, that a different interpretation of phasic static γ activity to tibialis anterior has been suggested (Taylor et al. 2000).

An important test of such muscle-specific γ drive would involve muscles that share some common action but differ in others. FDL and FHL fulfill these requirements since both produce toe flexion, while only FHL generates substantial extensor torque at the ankle joint (Lawrence et al. 1993; Young et al. 1993). These hindlimb muscles have been intensively studied over the last 20 years, particularly by Burke’s group, and the data highlight their differential properties (Chin et al. 1962; Dum et al. 1982), control (Bonasera and Nichols 1994; Fleshman et al. 1984; Loeb 1993; McCurdy and Hamm 1992), and patterns of usage (Fleshman et al. 1984; Loeb 1993; O’Donovan et al. 1982; Trank and Smith 1996). A notable absence, however, concerns the locomotor discharge patterns and nature of the γ activity to FDL and FHL. Indeed, there have been no previous recordings of fusimotor activity to toe muscles during locomotion.

In the present study the specificity of γ drive to FDL and FHL during locomotor activity has been investigated by recording directly from γ-efferents in a decerebrate cat preparation. Although similar profiles of γ activity were recorded in both muscles, differences in their timing were apparent, consistent with muscle-specific γ drive. This information permits a fuller interpretation of the nature of the fusimotor drive to FDL and FHL during locomotion based on spindle afferent recordings (unpublished observations). A brief account of some of this work has been published in abstract form (Murphy 2001).

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METH ODS

Preparation

Seven adult cats of either sex were anesthetized with halothane delivered in a mixture of 40% oxygen and 60% nitrous oxide. Both carotid arteries were tied and one was cannulated for recording blood pressure. The left hindlimb was denervated below the hip except for the SOL nerve. In three experiments the nerve to FHL was also left intact up to the time of γ recordings. The animal was supported over a treadmill, with the head in a stereotaxic apparatus and with pins at the iliac crests. Local anesthetic [lignocaine (lidocaine) hydrochloride, 2%] was infiltrated around the hip supports. The left knee and ankle were supported by clamps. Premammillary decerebration was performed, with complete removal of the forebrain, by a section from just rostral to the superior colliculus to just in front of the mammillary bodies. This procedure renders the animal incapable of feeling or awareness. Blood pressure, rectal temperature, and the temperature of a paraffin pool in the popliteal fossa were maintained within physiological limits throughout the experiment. Death was induced at the end of the experiments by an iv-administered barbiturate overdose.

Recordings

After recovery from anesthesia spontaneous locomotor movements could occur but were not maintained. Sustained locomotion was evoked during treadmill movement. Three legs walked on the treadmill while the innervated muscles of the fixed leg gave appropriately timed bursts of EMG activity. Recordings of both α- and γ-efferent discharges were made in dissected filaments of the cut FHL (n = 3) or FDL (n = 4) nerves, using twin platinum wire electrodes, in separate experiments. EMG was recorded from SOL, via a pair of implanted silver wires, in all experiments, as was the homonymous ENG (i.e., FDL or FHL). In three experiments involving FDL γ-efferents, simultaneous recordings were made of FDL ENG, SOL ENG, and FHL EMG prior to γ recordings. Initial recordings were made from functionally single units. These were frequently followed by simultaneous recordings of a γ- with α-motoneurons (usually 1), in which the separate filaments containing functionally single units were placed on the same electrode (e.g., Fig. 7). Initial investigation indicated relatively little background γ-efferent activity in FDL and FHL nerves. Therefore in the present experiments, units were selected for study by searching for activity during locomotion. To ensure γ recording stability, a single bipolar electrode was used in the muscle pool. The same electrode was used alternately for single unit and ENG recordings. A Silastic cuff (Dow Corning, Midland, MI) containing three electrodes was placed around the sciatic nerve to monitor its neural activity. Axonal conduction latency was determined by pre-triggered averaging. Action potentials recorded in peripheral filaments were used to trigger averaging of the same signal and the sciatic recording, both of which were delayed by equal amounts (e.g., Murphy et al. 1984). Units were identified as either α-motoneurons (52–80 m s⁻¹) or γ-motoneurons (17–40 m s⁻¹) on the basis of conduction velocity. Occasionally, the axonal conduction latency of α-motoneurons was not determined and these units (n = 2) were identified by the presence of short-interval double-discharges, which are a well-known characteristic of α-, but not γ-, motoneurons.

Data were amplified by conventional means, recorded with an FM tape recorder and monitored on storage oscilloscopes and a UV paper recorder (Thorn-EMI, Feltham, UK, frequency response DC, 5 kHz). The γ rate was monitored on the UV recorder by converting action potentials into standard pulses, which were fed to a leaky integrator (time constant, 100 ms).

Analysis

Further analysis was performed using a computer. Action potentials of γ-efferents were converted to standard pulses, which were used to generate cycle histograms and histograms of impulse rate. Histograms were constructed from periods of locomotor activity in which step-cycle durations were similar. A step marker was generated whenever the filtered SOL EMG (time constant, 50 ms) exceeded a preset level. The markers were used to trigger histogram sweeps. A histogram consisted of 250 bins, each of 4 ms width. For the cycle histogram, the number of spikes in each bin was divided by the number of cycles (range, 7–32) and the binwidth to convert it to units of impulses s⁻¹. In a separate histogram, every time a spike occurred the values of all bins since the last spike were incremented by the interspike interval. After sampling all steps the average interval (ms) in each bin was calculated by dividing by the number of cycles. The reciprocal of this value was then computed to give an average rate (impulses s⁻¹).

A feature of this method of generating rate histograms is that a finite minimum rate (low) is produced when units are recruited with EMG bursts. For example, in Fig. 2A there are no action potentials between EMG bursts. Nevertheless, the corresponding impulse rate histogram (Fig. 3A) shows a constant, low level at this time, reflecting the relatively long interspike interval (i.e., the approximate time between EMG bursts). Data from the two types of histogram were similar. However, the impulse rate histograms were considerably smoother and were used to illustrate the data (e.g., Fig. 3) and quantify discharge characteristics such as maximum and minimum discharge rates. Modulation of neuronal firing was expressed as half the difference between these parameters. The timing of peak γ firing was normalized with respect to mean step-cycle duration (Fig. 5). EMG and ENG were sampled at 5 kHz. Averages of EMG and ENG were triggered from the SOL step marker (see above) and smoothed with a five-point moving average (e.g., Fig. 6). The statistical significance of differences between mean values was analyzed by Student’s two-tailed t-test. In all statistical tests, P < 0.05 was accepted as being significant. Results are expressed as means ± SE, unless otherwise stated.

RESULTS

α Locomotor activity

FDL or FHL γ-efferents were recorded in separate experiments. In experiments (n = 4) involving FDL γ-efferents, simultaneous recordings were made initially of ENG activity from the cut FDL nerve, SOL EMG, and FHL EMG (3 experiments). During locomotion rhythmic bursts of α activity occurred in each case (Fig. 1A). While FHL was recruited in a stereotyped fashion with the ankle extensor SOL (extension phase), the pattern of FDL activity was variable. Independent activation of FHL and FDL was first reported in the intact walking cat (O’Donovan et al. 1982) and subsequently during fictive locomotion in the paralyzed, decerebrate preparation (Fleshman et al. 1984).

In the present experiments, FDL ENG activity was recruited with FHL/SOL EMG and ended just after these muscles became inactive. Generally, a single period of activity was apparent. However, closer inspection indicated the presence of a brief, late FDL burst around the end of its activity (Fig. 1A, arrows). This is more obvious in the integrated neural record, which also shows that the relative magnitude of the “late” and the preceding extension-related (“early”) components could vary markedly, even on a step-by-step basis. Variability was also apparent in single α-motoneuron recordings from FDL (Fig. 7), but not FHL, in confirmation of previous results involving intracellular recordings during fictive locomotion.
Such variability in FDL ENG was not always the case, as illustrated in Fig. 1B. This recording was made 10 min before that in Fig. 1A, when the early and late components of FDL activity were quite consistent. A late FDL peak was recorded in each experiment (\(n = 4\)) and occurred 55–74% of the step cycle after the onset of SOL EMG. The current patterns of activation of FDL and FHL are similar to those described by Burke and co-workers (see DISCUSSION).

### γ Discharge characteristics

During recordings from single FDL (\(n = 21\)) or FHL (\(n = 17\)) γ-efferents, both parent nerves were cut and locomotor activity was monitored from SOL EMG, which is recruited with FHL and FDL in the present preparation (Fig. 1A). Homonymous α motor pool activity was not simultaneously recorded. However, ENG activity from the parent muscle nerve was periodically sampled (see later). Figures 2 and 3 illustrate the two basic firing profiles that were recorded in FDL and FHL during locomotion. The γ-efferents in Fig. 2, A (FHL unit) and B (FDL unit), were strongly phasically activated with EMG activity, while those in Fig. 2, C (FHL) and D (FDL), had high levels of tonic firing throughout the step cycle and relatively little modulation. Units showing similar firing patterns will be referred to as phasic (FDL, \(n = 9\); FHL, \(n = 8\)) and tonic (FDL, \(n = 11\); FHL, \(n = 9\)), respectively. These patterns were stable, could be recorded in the same animal, and did not appear to depend on the degree of EMG activity in a given experiment.

In FHL and FDL, tonic and phasic units were most clearly distinguished by their modulation (half-peak-to-peak) and minimum discharge rates during walking. These parameters, derived from histograms of average rate (e.g., Fig. 3; see METHODS), are plotted against each other in Fig. 4. Two groups are apparent, with little overlap, in each muscle and their mean...
values were significantly different (Table 1). In both muscles, therefore, tonic units fired throughout the step cycle and had less modulation, but higher minimum rates, than that of phasic units. Phasic γ-efferents were mainly recruited with EMG activity, although four units (2 FDL, 2 FHL) sometimes fired at low rates between EMG bursts. Hence, although FHL and FDL have different mechanical actions (see INTRODUCTION), they nevertheless receive similar profiles of γ discharge during locomotion. Exceptionally, one unit (FDL) had intermediate locomotor values for modulation (23 impulses s⁻¹) and minimum rate (27 impulses s⁻¹) and was not categorized as either tonic or phasic.

In general, other discharge characteristics were less consistent in distinguishing tonic and phasic units in both muscles. For example, the mean rate during walking of tonic units was significantly greater than that of phasic units in FHL but not in FDL (Table 1). Regarding discharge rates in the resting state, with the treadmill off and in the absence of movement, the ranges of tonic and phasic units overlapped in both muscles but tonic units had a narrower range and lower mean values. Tonic units in FHL and FDL had resting frequencies in the ranges 0–5 and 0–8 impulses s⁻¹, respectively, while the corresponding values for phasic units were 0–40 and 0–50 impulses s⁻¹. It is also worth noting that a large proportion of the present sample of FDL (57%) and FHL (59%) γ-efferents had no background discharge at rest, and included both phasic and tonic units. The low resting rates of tonic units resulted in a large increment in their firing during walking in both muscles (Table 1). In contrast, since phasic neurons could have high or low rates at rest, individual units could show an increase or a decrease in mean rate when moving between these states.

In Fig. 2 the phasic and tonic units appear to differ regarding the timing of their maximum discharge rate, but this feature is more clearly illustrated in the averaged records of Fig. 3. The phasic units fire at maximum rate during early extension, while the tonic units peak before EMG commencement. Figure 5 shows a bar histogram of the time of peak rate relative to EMG onset, normalized with respect to the mean step-cycle duration. With FHL, phasic and most tonic neurons reached the maximum rate after the beginning of EMG activity and their mean values were not significantly different (Table 1). For FDL, phasic neurons again peaked after, but most tonic units peaked before, EMG onset and their mean values of 29% and 9% of the step cycle, respectively, differed significantly (Table 1). It should be noted that the late peak in FDL ENG activity, recorded in separate trials (see previous section), occurred 55–74% of the step cycle after EMG onset and was thus not associated with any peak in homonymous γ activity. Two FHL and one FDL tonic units showed little modulation during locomotion with no consistent maximum.
procedure from relatively large nerve fi
EMG/ENG or FDL ENG were generated (see METHODS, Fig. 6). The onset of SOL EMG in Fig. 6B occurred at about 128 ms (time difference, 1 ms). FHL EMG/ENG onsets ranged between 0 and 6 ms after the beginning of SOL EMG [2.8 ± 2.1 ms (mean ± SD); n = 6]. Simultaneous recordings of FDL ENG and SOL EMG were made in four experiments. In each case SOL preceded FDL activity (range, 10–19 ms; mean, 15 ms; n = 4). The mean differences in timing of FHL (3 ms) and FDL (15 ms) with respect to SOL were small, relative to a typical step-cycle duration of 650 ms, and indicate a closely related coactivation in the present preparation. These time differences would not have altered the histograms in Fig. 5 had they been constructed with reference to the onset of homonymous α activity.

Simultaneous α/γ recordings

As described above, in separate recordings during locomotion FDL ENG activity was variable, while its patterns of γ discharge were stereotyped. This contrast is emphasized by simultaneous α/γ recordings from nerve filaments (see METHODS) that were made during the present study. Thus in Fig. 7A, the phasic γ is consistently recruited with extensor (SOL) EMG and shows little variation in its firing pattern. In contrast, two α-motoneurons show a variable recruitment pattern. The smaller unit (α1) is active during the first EMG burst; fires only a single double-discharge, with a short interspike interval (about 2.5 ms) near the end of the next burst; and is inactive in the last. The larger unit (α2) is active only in the first step cycle, where it gives a double-discharge near the end of EMG activity. Double-discharges were frequently seen when FDL α-motoneurons fired only at the end of the extension phase and are a common feature in decerebrate preparations during locomotor activity (e.g., Zajac and Young 1980). The timing of such firing is reminiscent of the late component of FDL ENG activity and probably represents the same central synaptic drive (c.f. Fleshman et al. 1984 and Fig. 1 in Schmidt et al. 1988).

Both phasic and tonic FDL γ-efferents were recorded with α-motoneurons when the discharge was restricted to the end of the extension phase and when it occurred earlier. The units in Fig. 7A were recorded again shortly thereafter (Fig. 7B). Here the γ discharge pattern was unchanged but α-motoneuron firing differed. The larger unit (α2) now consistently fires near the beginning of extension and variably thereafter. The discharge of α1 spans extension over the two initial step cycles but, subsequently, is restricted to the onset of EMG activity. A total of 15 FDL α/γ pairs were recorded during locomotion, involving 13 α-motoneurons, 7 phasic, and 8 tonic γ-motoneurons. In all cases the pattern of γ firing was consistent, despite clear variations in the activity of simultaneously recorded α-motoneurons. Nine α/γ pairs were recorded from FHL and confirmed the stereotyped activity patterns of both types of motoneuron to this muscle, and their coactivation during locomotor activity. FHL α-motoneurons never displayed firing that was restricted to the end of the extension phase. Simultaneous recordings of α and γ activity involved the γ-efferents, whose characteristics were described in the previous section when recorded individually. No obvious difference was noted in γ discharge in these two situations.

These neurons were not included in the analysis of timing of peak firing rates.

During the present experiments, since γ-motoneurons were selected for study on the basis of firing during locomotion (see METHODS), recordings were frequently made during the search procedure from relatively large nerve filaments containing multunit α discharges, together with SOL EMG. Further, ENG was periodically recorded from approximately half the parent nerve and confirmed the coactivation of FHL/FDL with SOL EMG, and the presence of a late component in FDL activity (e.g., Fig. 6A; see also next section).

In Fig. 5 and Table 1 the time of peak γ rate is expressed relative to the onset of SOL EMG. Although the relative timing of individual γ firing is unlikely to have been affected by this procedure, it is possible that the absolute values relative to the onset of parent α activity differ. To estimate the difference, averages of simultaneously recorded SOL EMG and FHL EMG/ENG or FDL ENG were generated (see METHODS, Fig. 6). The onset of SOL EMG in Fig. 6B occurred at about 128 ms (arrow). The FDL ENG average shows a rapidly increasing trend that commences at about 138 ms (Fig. 6B) and was taken to represent the onset of α activity. In Fig. 6D the onsets of SOL and FHL EMG activity occur almost simultaneously (time difference, 1 ms). FHL EMG/ENG onsets ranged between 0 and 6 ms after the beginning of SOL EMG [2.8 ± 2.1 ms (mean ± SD); n = 6]. Simultaneous recordings of FDL ENG and SOL EMG were made in four experiments. In each case SOL preceded FDL activity (range, 10–19 ms; mean, 15 ms; n = 4). The mean differences in timing of FHL (3 ms) and FDL (15 ms) with respect to SOL were small, relative to a typical step-cycle duration of 650 ms, and indicate a closely related coactivation in the present preparation. These time differences would not have altered the histograms in Fig. 5 had they been constructed with reference to the onset of homonymous α activity.

**FIG. 4.** Two groups of γ-motoneurons in FHL and FDL based on locomotor discharge characteristics. The modulation (half-peak-to-peak) and minimum discharge rate of individual phasic (●) and tonic (○) γ-efferents in A, FHL and B, FDL. In both muscles, tonic units had higher minima, but less modulation, than phasic units. One unit (FDL, star symbol) had intermediate locomotor values for modulation and minimum rate. Values were taken from averaged data, such as those shown in Fig. 3.


In that study a stereo-

The relative sizes of these components could vary, consistent with a degree of independent control, and they frequently overlapped in time, giving the appearance of a single period of activity approximately coactivated with ankle extensor muscles. These results are similar to those of Burke and co-workers, who originally described the independent activation of FHL and FDL during locomotion in the intact cat (O’Donovan et al. 1982). In that study a stereotyped burst was recorded from FHL during stance, while the most consistent activity in FDL was of short duration, around the onset of the swing phase (c.f. present late component). In contrast, any earlier, stance-related activity (c.f. present early component) was generally of a low level (see also Fleshman et al. 1984; Trank and Smith 1996). Thus the basic patterns of activation of FHL and FDL in the present preparation resemble the intact animal, with differences mainly in the balance between the two components in FDL. These observations are consistent with results during fictive locomotion in paralyzed cats that indicate both a central origin for the extension- and early flexion-related drives to FDL and a dependence of their balance on the degree of peripheral afferent input/descending activation (Fleshman et al. 1984).

**DISCUSSION**

**Differential activation of FDL/FHL**

SOL, FHL, and FDL were rhythmically coactivated during locomotion. However, the pattern of activation of FHL and FDL differed. FHL was characterized by a single, consistent EMG burst in time with SOL (extension phase). In contrast, FDL ENG was variable and two components were distinguished. One commenced around the onset of FHL activity and continued during the extension phase (early component). The other was brief and occurred around the end of SOL/FHL activity (late component). The relative sizes of these components could vary, consistent with a degree of independent control, and they frequently overlapped in time, giving the appearance of a single period of activity approximately coactivated with ankle extensor muscles. These results are similar to those of Burke and co-workers, who originally described the independent activation of FHL and FDL during locomotion in the intact cat (O’Donovan et al. 1982). In that study a stereotyped burst was recorded from FHL during stance, while the most consistent activity in FDL was of short duration, around the onset of the swing phase (c.f. present late component). In contrast, any earlier, stance-related activity (c.f. present early component) was generally of a low level (see also Fleshman et al. 1984; Trank and Smith 1996). Thus the basic patterns of activation of FHL and FDL in the present preparation resemble the intact animal, with differences mainly in the balance between the two components in FDL. These observations are consistent with results during fictive locomotion in paralyzed cats that indicate both a central origin for the extension- and early flexion-related drives to FDL and a dependence of their balance on the degree of peripheral afferent input/descending activation (Fleshman et al. 1984).

**Tonic and phasic γ discharge patterns**

In contrast to the α activation of FHL and FDL during locomotion, their basic patterns of γ firing had a similar profile. Thus for both muscles, two stereotyped patterns were distinguished whose characteristics are summarized in Table 1. Tonic units fired throughout the step cycle and had less modulation, but higher minimum rates, than those of phasic units, which were generally recruited with SOL EMG activity. The relative timing of these γ profiles did, however, differ in the two muscles. With FHL, the activity of phasic and most tonic units peaked after the onset of EMG activity (means, 10% versus 2% step cycle). In FDL, tonic units usually reached a maximum rate before (mean, −9% step cycle), while phasic

![Figure 5](http://jn.physiology.org/)

**FIG. 5.** Timing of maximum rate of γ-efferents in FHL (A) and FDL (B) during locomotion. Phasic (filled bars) and most tonic (open bars) units in FHL peaked after extensor (SOL) EMG onset, at time 0. In FDL, tonic neurons generally reached maximum rate before, while phasic neurons peaked after, the beginning of EMG activity. Timing was normalized with respect to mean step cycle duration.

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**Table 1. Summary of characteristics of FHL and FDL γ-motoneurons**

<table>
<thead>
<tr>
<th>Component</th>
<th>FHL</th>
<th>FDL</th>
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<tbody>
<tr>
<td>α Resting rate (1, 9)</td>
<td>1 ± 1</td>
<td>1 ± 1* (11)</td>
</tr>
<tr>
<td>α Mean walking rate (2, 1)</td>
<td>69 ± 5 (9)</td>
<td>42 ± 4 (11)</td>
</tr>
<tr>
<td>γ Peak – EMG onset (2, 4)</td>
<td>2 ± 4</td>
<td>10 ± 1</td>
</tr>
<tr>
<td>γ Conduction velocity, m/s–1 (2, 1)</td>
<td>21 ± 1</td>
<td>25 ± 2</td>
</tr>
<tr>
<td>Total number of units (2, 9)</td>
<td>9</td>
<td>11</td>
</tr>
</tbody>
</table>

γ-efferents in both muscles showed tonic (γ_1) or phasic (γ_2) patterns of discharge during locomotion. Values are expressed as means ± SE unless otherwise stated. * Statistically different for tonic and phasic units within each muscle at the P < 0.05 level, using a Student’s t-test. The number of units is shown in parentheses.
units peaked after (mean, 29% step cycle), EMG onset. Interestingly, the peak firing of FDL tonic units was probably more closely related to dorsi-, as opposed to plantar, flexor α activity (e.g., Carlson-Kuhta et al. 1998; Degtyarenko et al. 1998). These features suggest that FHL and FDL γ-efficients differ in synaptic input during locomotion and are consistent with the notion of muscle-specific fusimotor drive (e.g., Murphy 2000). However, discussion of its functional significance requires evidence concerning the nature of the neurons involved. In other words, is there a direct correspondence between tonic/phasic γ patterns and the functional classification by Matthews (1962) into static and dynamic types? If so, is this the same in FDL and FHL?

For both FHL and FDL the pattern of discharge of phasic γ-efficients was more closely related to extensor EMG activity than the tonic type. However, even with phasic neurons there were indications in FDL of α/γ independence. Thus two components of FDL α activity could be distinguished (see above).

**FIG. 6.** Closely related recruitment of SOL and FDL/FHL α activity during locomotion. A and B: averages (52 sweeps) of SOL EMG (top trace) and FDL ENG (bottom trace). The horizontal bar in A represents the period that is shown in B on an expanded time scale. The beginning (arrows) of the increasing trends in EMG and ENG were taken to represent the onsets of α activity. SOL preceded FDL by about 10 ms. Step markers, derived from filtered SOL EMG, were used to trigger averaging. The averages in A and B are from the experiment illustrated in Fig. 3, B and D. The vertical gains of respective traces in A and B are the same. C and D: averages (26 sweeps) of SOL EMG and FHL ENG. The onsets (arrows) of α activity occurred almost simultaneously. Traces are presented as in A and B.

**FIG. 7.** Contrasting locomotor activity patterns in FDL α- and γ-moteuneurons during simultaneous neural recordings. A and B: the phasic γ-effenter is consistently recruited with extensor (SOL) EMG, while two α-moteuneurons show variable activity. The same neurons were recorded in A and B, but in separate trials.
While FDL phasic $\gamma$-efferents were recruited around the onset of, and peaked during, the earlier $\alpha$ component, there was no corresponding $\gamma$ activity related to the later component, which peaked 55–74% through the step cycle. The late component of FDL $\alpha$ activity may be too brief to be functionally linked with a distinct $\gamma$ burst to this muscle. This, of course, does not preclude the possibility that preset fusimotor drive plays a role in the control of afferent feedback at this phase and, indeed, tonic $\gamma$-efferents have a marked level of firing throughout the step cycle. Independence of FDL $\alpha/\gamma$ activity is also emphasized by its consistent $\gamma$, but variable $\alpha$, discharge patterns and advanced timing (mean, $-9\%$ step cycle) of peak tonic $\gamma$ firing relative to EMG activity (see Fig. 5). In contrast, a greater degree of $\alpha/\gamma$ coactivation is apparent with FHL, since both types of motoneuron showed stereotyped discharge patterns and $\gamma$ firing (tonic and phasic units) generally peaked during EMG activity.

“Tonic” and “phasic” $\gamma$ activity have been reported in three types of rhythmic movement: respiration, jaw movements, and locomotion (for reviews, Murphy and Martin 1993; Prochazka 1996). In the last case, both patterns have now been recorded in the nerves to a variety of muscles, including ankle extensors (Bessou et al. 1986; Murphy et al. 1984), ankle flexor (Murphy and Hammond 1993), and toe flexors (present results), but it should be noted that these neuronal firing patterns do not appear to be a consistent feature throughout the hindlimb. Thus recordings from intact nerve branches to the medial sartorius muscle (hip/knee flexor), in the thalamic cat, indicated that $\gamma$-motoneurons are generally coactivated with homonymous $\alpha$-motoneurons during locomotion, and there was little sign of $\gamma$ firing that persists throughout the step cycle (Bessou et al. 1990). This observation again highlights the potential for variation in $\gamma$ drive to different muscles during the same behavior.

Functional implications

There have been no previous recordings of $\gamma$ activity to FHL or FDL muscles during locomotion. Spindle afferent recordings, under isometric conditions in thalamic cats, suggest a degree of $\alpha/\gamma$ coactivation (Perret and Cabelguen 1980), consistent with the present results. In the intact cat, few such recordings exist (Loeb and Duysens 1979; Prochazka and Gorassini 1998; Prochazka et al. 1976) and are difficult to interpret, in terms of fusimotor drive, in view of uncertainty regarding the contribution of muscle length changes. However, the locomotor patterns of decerebrate preparations are strikingly similar to those of the intact animal (Grillner 1975). In addition, the available data from fictive locomotion in the paralyzed state suggest a central origin for the basic $\gamma$ rhythms (Bessou et al. 1986, 1990; Murphy and Hammond 1990), which are likely to be strongly represented in the intact animal. Nevertheless, it should be noted that the effect of fixation and denervation of the test leg on $\gamma$ locomotor drive is unknown. Indeed, electrical stimulation of low-threshold skin afferents from the foot does affect $\gamma$ activity during locomotion in decerebrate cats (e.g., Murphy 1999), but the net effect of peripheral afferent input remains to be determined.

As $\gamma$-motoneurons exert their effects via muscle spindle afferents, the functional significance of fusimotor drive depends on the sensorimotor role of these receptors during a given task. In terms of a possible contribution to the reflex control of homonymous muscle activity, it is striking that during the extension phase of locomotion in the intact cat (O’Donovan et al. 1982; Trank and Smith 1996), and in the current preparation (unpublished observations), FHL is strongly recruited, while any FDL activity is generally weak. In contrast, the present results suggest that both muscles experience strong levels of fusimotor drive at this time. Although the different patterns of muscle recruitment are centrally generated (Fleshman et al. 1984), it is plausible that spindle afferent feedback, which is normally present from both muscles during extension (Loeb and Duysens 1979), is similarly controlled and serves to reinforce the central pattern of activation of $\alpha$-motoneurons. One potential peripheral mechanism that arises from the present study, but remains to be established, is differential static/dynamic fusimotor drive to FHL and FDL. It is also interesting that disynaptic hindlimb extensor $\alpha$-motoneurons is facilitated in the extension phase of fictive locomotion (McCrea et al. 1995). This regulation occurs in both FDL and FHL during extension (Degtyarenko et al. 1998) and may be functionally related to the phasic $\gamma$ drive that has been described in the present study. The heteronymous monosynaptic Ia connections between these muscles (Fleshman et al. 1984) may also be relevant in this context.

In summary, tonic and phasic $\gamma$ drive was recorded in the nerves to FHL and FDL. While both muscles shared a common pattern of phasic $\gamma$ drive linked to plantar flexor $\alpha$ activity they differed in the timing of tonic $\gamma$-efficients. Peak firing occurred with plantar flexor alphas in FHL but generally preceded $\alpha$ onset in FDL.

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