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THE LOCOMOTOR DISCHARGE CHARACTERISTICS OF ANKLE FLEXOR γ-MOTONEURONES IN THE DECEREBRATE CAT

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SUMMARY

1. The discharge patterns of ankle flexor, tibialis anterior (TA), γ-motoneurones were recorded during locomotion in the decerebrate cat.

2. At rest γ-efferents had no background discharge. During locomotion two patterns of γ activity could be distinguished. Most units (16) were phasically recruited with homonymous electroneurogram (ENG) activity, while the remainder (5) were tonically active throughout the step cycle.

3. The modulation of phasic units was greater ($P < 0{\cdot}01$) than tonic neurones. Phasic units had lower ($P < 0{\cdot}02$) mean, but higher ($P < 0{\cdot}01$) peak, rates during the step cycle.

4. The discharge rate of both types of efferent increased around the onset of ENG activity and peaked during ENG activity, or shortly after its cessation. The conduction velocities of phasic and tonic units overlapped widely.

5. It is proposed, on the basis of muscle spindle afferent recordings during locomotion, that TA phasic and tonic units correspond to static and dynamic γ-motoneurones, respectively. This correspondence is functionally advantageous for the role of ankle flexor muscles during locomotion. Thus phasic static γ discharge during flexion would aid muscle contraction via increased Ia afferent activity, while tonic dynamic γ firing would enhance Ia afferent stretch sensitivity throughout the step cycle. Such enhancement during flexion would oppose unexpected muscle lengthening while, during extension, it would contribute to reciprocal inhibition of ankle extensor muscles.

6. The results are discussed in relation to strategies of γ usage during rhythmic movements. It is postulated that, for such behaviour, muscle contraction is accompanied by coactivity in static and dynamic γ-motoneurones. A functional rationale is suggested for this strategy.

INTRODUCTION

In mammals the control of movement ultimately involves two basic types of motoneurone, α and γ. α-Motoneurones produce muscle activation directly while γ-motoneurones exert their effects indirectly via muscle spindle afferents. In addition there are two types of γ-efferent, static and dynamic, which differ in their functional characteristics (Matthews, 1962). Over the years various theories of γ function have

been proposed (for review, see Matthews, 1972; Stein, 1974; Hulliger, 1984) but they have been difficult to test and develop in view of the lack of direct recordings from classified static and dynamic γ-efferents during normal movement. However, such recordings have been achieved in cat preparations during three types of rhythmic movement: respiration (Eklund, Euler & Rutkowski, 1964; Sears, 1964; Corda, Euler & Lennerstrand, 1966; Euler & Peretti, 1966; Greer & Stein, 1990), jaw movements (Appenteng, Morimoto & Taylor, 1980) and locomotion (Murphy, Stein & Taylor, 1984).

During locomotion the patterns of discharge of static and dynamic γ-motoneurones were identified for the triceps surae muscle, an ankle extensor (Murphy *et al.* 1984). Dynamic γ-efferents were phasically activated with α-motoneurones, while static γ-efferents showed tonic behaviour. These distinctive patterns seemed ideally suited to the role of ankle extensor muscles during stepping (Taylor, Stein & Murphy, 1985). Ankle flexor and extensor muscles are reciprocally active and have different actions during locomotion (Grillner, 1975). Flexors mainly contract isotonically against a relatively small load (i.e. the foot) during swing, while extensors (anti-gravity muscles) are most active while lengthening or nearly isometric during the stance phase, when they support the body and propel it upwards and forwards. Since the locomotor discharges of ankle extensor static and dynamic γ-motoneurones appear to be tailored to muscle function (Taylor *et al.* 1985), a different pattern might be predicted for flexors.

We have investigated this problem by recording from γ-efferents to TA (a direct antagonist of triceps surae) during locomotion in the decerebrate cat. Like ankle extensors, phasic and tonic patterns of γ discharge were encountered in the nerve to TA during stepping. However, spindle afferent recordings (Perret & Berthoz, 1973; Cabelguen, 1981; Taylor *et al.* 1985) suggest the *opposite* correspondence with static and dynamic γ-efferents to that previously demonstrated for ankle extensor muscles (Murphy *et al.* 1984), namely, for TA: phasic units = static and tonic units = dynamic γ-motoneurones. The results are discussed in relation to the function of γ-motoneurones and muscle spindle afferents.

A preliminary account of some of this work has been published (Murphy & Hammond, 1992).

METHODS

Preparation

Nine adult cats of either sex were anaesthetized with halothane delivered in a mixture of 70% oxygen and 30% nitrous oxide. Both carotid arteries were ligated and one was cannulated for recording blood pressure. The nerve supply of the left hindlimb below the hip was sectioned, except for the common lateral gastrocnemius–soleus nerve. The animals were placed in a stereotaxic head holder over a treadmill with pins at the iliac crests and clamps on the left knee and ankle. Decerebration was performed by a section angled from just rostral to the superior colliculus to just in front of the mammillary bodies. Brain tissue above the section was removed and anaesthesia discontinued. When the treadmill was switched on three legs walked spontaneously while the innervated muscles of the fixed leg gave appropriately timed bursts of electromyogram (EMG) activity. Blood pressure, rectal temperature and the temperature of a paraffin pool in the popliteal fossa were maintained within physiological limits throughout the experiment.

Recordings and stimulation

Functionally single γ-motoneurones were recorded from the anterior branch (Iliya & Dum, 1984) of the cut TA nerve on twin platinum wire electrodes. A silastic cuff containing two stimulating

electrodes was placed around the common peroneal nerve. The axonal conduction velocity of each unit was calculated from the latency of response to electrical stimulation (0·1 ms width) of the common peroneal nerve (Fig. 1*A*) and the conduction distance. No allowance was made for the initiation time of the action potential which has a maximum value of 0·1 ms in the preparation used

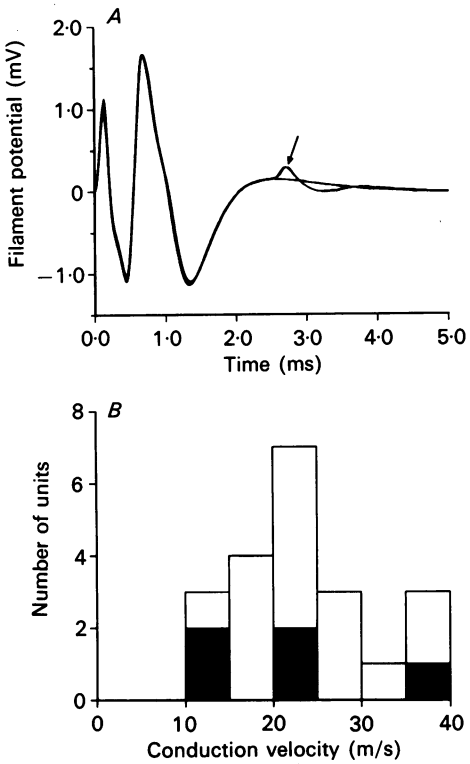

Fig. 1. *A*, axonal conduction latency measurement of a γ-motoneurone. Superimposed compound action potentials recorded from the TA nerve in response to stimulation (time zero) of the common peroneal nerve at 10 ms (arrow) and at 0 ms after a naturally occurring impulse. Both compound action potentials are composed of four superimposed sweeps. The direct γ potential (arrow) fails to occur in the latter case due to refractoriness. The conduction latency of the unit (2·5 ms) was measured from time zero to the earliest point of divergence of the superimposed sweeps. *B*, the conduction velocities of phasic (open bars) and tonic (filled bars) γ-axons overlapped widely. The mean values were 24 and 21 m/s, respectively, which were not statistically different ($P > 0·1$).

(Ellaway, Murphy, Pascoe & Read, 1978). Units were identified as γ-motoneurones on the basis of their conduction velocities (12–40 m/s). EMG was recorded via a pair of silver wires, inserted in the lateral gastrocnemius muscle, which were insulated except for 2 mm at the tips. In addition, in seven experiments the ENG of the cut TA nerve was monitored using bipolar platinum wire electrodes. Data were amplified by conventional means, recorded with a FM tape-recorder and monitored on oscilloscopes and a UV recorder (Thorn-EMI, 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

For further analysis γ pulses were fed to a digital computer to generate cycle histograms and histograms of impulse rate. Each sweep of a histogram was triggered by a step marker which occurred when the filtered ENG (time constant = 50 ms) exceeded a pre-set level. 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, 6–20) and the bin width to convert it to units of impulses per second. 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, an average impulse rate was computed by dividing the number of cycles by the summed interval values in each bin. Similar data were obtained from the cycle histogram and the impulse rate histogram, except that the latter traces were considerably smoother and were used for most of the illustrations in this paper (e.g. Fig. 3). Impulse rate histograms were also used when quantifying discharge characteristics such as maximum and minimum discharge rates. Modulation of neuronal firing was expressed as half the difference between these parameters. For phasic units modulation was, in effect, half of the peak rate since all of these neurones fell silent after the end of TA ENG activity.

RESULTS

At rest, with the treadmill stationary, TA γ-motoneurones had no background discharge and there was no ENG activity. In marked contrast, resting γ firing is high in ankle extensor nerves in the same preparation (Murphy *et al.* 1984). During

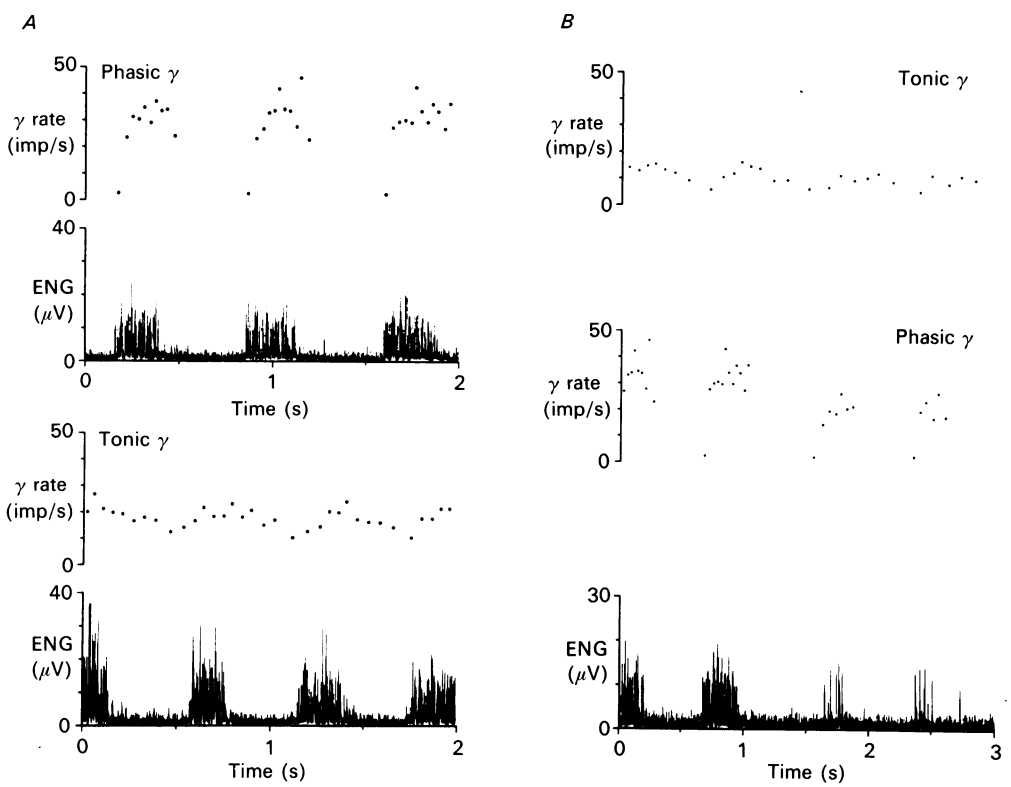

Fig. 2. *A*, two patterns of TA γ-motoneurone discharge during locomotion. The phasic unit was recruited with TA ENG activity while the tonic neurone fired throughout the step cycle. Note the greater modulation of the phasic type. γ-Rate is instantaneous frequency and ENG is rectified but unfiltered. *B*, simultaneous recordings of a tonic and a phasic γ-efferent during a period of irregular locomotion, indicated by variation in the degree of ENG bursts. Although the peak rate of both types of neurone was reduced during less vigorous walking (i.e. last two ENG bursts), there was no change in γ discharge pattern (i.e. tonic/phasic). Neurones are different from those in *A*.

locomotion TA γ-motoneurones showed two patterns of behaviour. Most units (16) were phasically recruited with homonymous ENG activity, while the remainder (5) were tonically active throughout the step cycle (Fig. 2*A*). These patterns were stable, could be recorded in the same animal, and did not appear to depend upon the degree

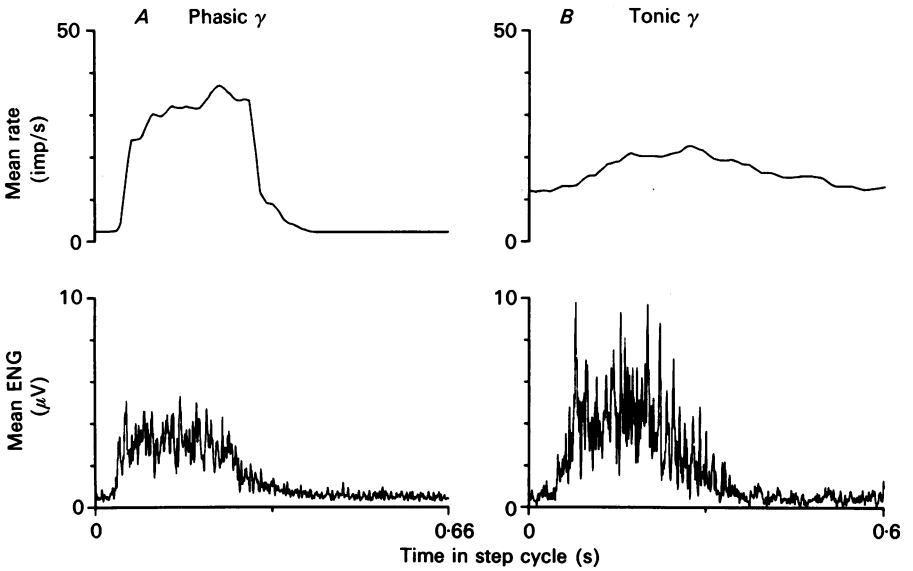

Fig. 3. Average impulse rate of a phasic (*A*) and a tonic (*B*) γ-efferent during the step cycle. In both cases discharge rate increased around the onset of, and peaked during, ENG activity. Neurones are the same as in Fig. 2*A*. Data represent the average of ten (*A*) and eight (*B*) steps, respectively.

of ENG activity in a given experiment. Further, in one instance, an example of each type was recorded at the same time (Fig. 2*B*). The conduction velocities of phasic and tonic γ-motoneurones overlapped widely (Fig. 1*B*), and there was no apparent relation between this parameter and discharge characteristics. Figure 2*A* illustrates another general difference between these neurones, that being the greater modulation of phasic units. The temporal characteristics of these locomotor discharges are more clearly shown by averages of such data (Fig. 3). Although the discharge rate of both units increased around the onset of, and peaked during, ENG activity, only the tonic unit (Fig. 3*B*) was active throughout the step cycle.

The locomotor discharge characteristics of phasic and tonic γ-motoneurones are summarized in Figs 4 and 5. In Fig. 4*A* mean discharge rate during walking is plotted against modulation for individual units. Although the mean rate during stepping of the two types of efferent overlapped, phasic units, on average, had lower ($P < 0{\cdot}02$, Student's *t* test) values ($12{\cdot}5 \pm 4{\cdot}1$ *vs.* $18{\cdot}5 \pm 6{\cdot}1$ impulses/s, mean ± S.D.). Nevertheless, the peak rate of phasic units ($44{\cdot}7 \pm 21{\cdot}7$ impulses/s) during the step cycle was higher ($P < 0{\cdot}01$) than tonic neurones ($25 \pm 9{\cdot}9$ impulses/s). Phasic units (21 ± 11 impulses/s) had greater ($P < 0{\cdot}01$) modulation than tonic neurones (6 ± 4 impulses/s) and their respective ranges (12–46 *vs.* 5–12 impulses/s) showed little overlap. This

difference is more obvious if, for individual efferents, modulation is expressed as a percentage of mean discharge rate during locomotion (Fig. 4*B*). In this form there is a clear separation between the modulation of phasic (110–236%) and tonic (9–50%) γ-efferents.

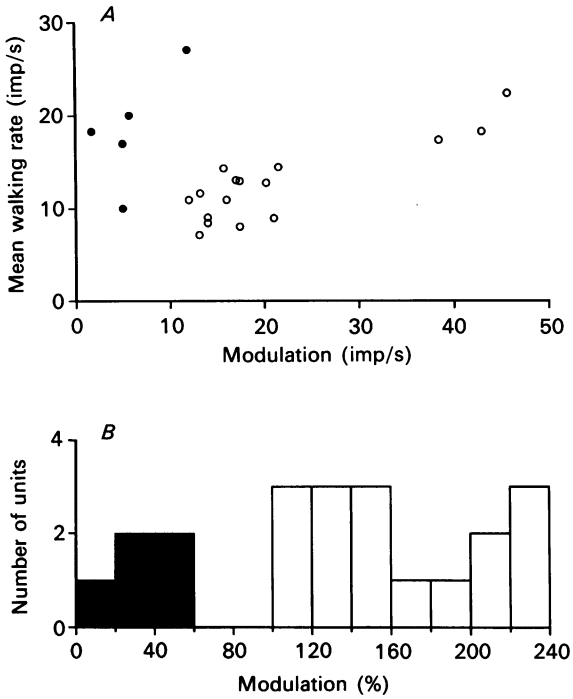

Fig. 4. Modulation and mean discharge rate of individual phasic (○, □) and tonic (●, ■) γ-motoneurones during locomotion. Although the mean rates during walking of the two types overlapped, the modulation of phasic units was greater than tonic neurones (*A*). This difference is more apparent if modulation is expressed as a percentage of mean firing during the step cycle (*B*). Values were taken from averaged data (6–20 steps), such as shown in Fig. 3.

During regular periods of locomotion, which were used for measurement purposes, the peak firing rates of phasic and tonic γ-motoneurones in successive step cycles were relatively constant (Fig. 2*A*). However, during irregular stepping, which generally occurred at the beginning or end of a bout, the peak rates of both types varied and appeared to be related to the degree of ENG activity. This feature is illustrated in Fig. 2*B* in which simultaneous recordings were made from a tonic and a phasic γ-efferent at the end of a period of locomotion. During the first two bursts of ENG activity the peak firing of both efferents was relatively constant; however, in subsequent bursts, which are of lower intensity, their peak rates were reduced, most obviously for the phasic unit. Note that the changes in peak rate during this period of irregular locomotor activity were not accompanied by any variation in the patterns of γ discharge (i.e tonic/phasic). Such invariance was a consistent feature in the present study.

The histograms of Fig. 5 show various features of the timing of TA γ discharge relative to homonymous ENG activity during locomotion. The data was derived from seven experiments in which TA ENG was recorded. Timing is expressed as a percentage of the step cycle and the open and filled bars correspond to phasic and

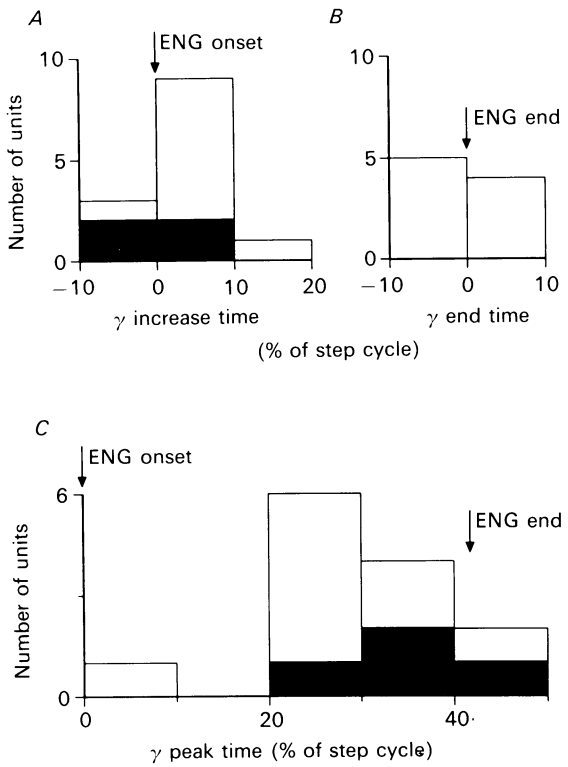

Fig. 5. Temporal characteristics of the locomotor discharge of TA phasic (open bars) and tonic (filled bars) γ-efferents relative to the onset (*A* and *C*) and the end (*B*) of homonymous ENG activity at time zero. *A*, the discharge rate of both types of unit increased around the onset of ENG activity. *B*, phasic γ-efferents ceased firing near the end of ENG activity, while tonic neurones were active throughout the step cycle. *C*, peak rates of phasic and tonic units occurred during or near the end (mean time) of ENG activity.

tonic γ-efferents, respectively. Figure 5*A* represents the time of increased γ rate relative to ENG onset at time zero. The discharge rates of both types of unit increased around the time of ENG onset. While tonic γ-efferents were active throughout the step cycle, the discharge of phasic units ceased around the end (time zero) of ENG activity (Fig. 5*B*). For both types of neurone peak rate occurred during, or shortly after the end of, ENG activity (Fig. 5*C*).

DISCUSSION

Two patterns of TA γ-motoneurone discharge during locomotion

Two patterns of TA γ discharge were distinguished during locomotion in the present study. Most units were phasically recruited with ENG activity while the remainder were tonically active throughout the step cycle. The modulation of phasic units was, on average, much greater (×3·5) than tonic neurones. Phasic units had lower mean, but higher peak, rates during the step cycle. The discharge of both types increased around the onset of ENG activity and peaked during ENG activity, or shortly after its cessation. These observations indicate that tonic and phasic γ-motoneurones differ in synaptic input and/or intrinsic properties, and are consistent with their being functionally distinct.

A direct correspondence between phasic/tonic and static/dynamic γ-motoneurones?

On the basis of TA muscle spindle afferent responses to length changes during locomotion in the cat Cabelguen (1981) reported powerful static, but weak dynamic, γ coactivation with EMG activity. The pattern of static activity was deduced from the large rhythmic bias of spindle Ia and group II afferents during locomotion, coupled with a reduced dynamic sensitivity of Ia afferents to stretch. Weak dynamic coactivation was suggested on the basis of a large increase in the peak frequency, measured at the end of the dynamic phase of stretch, of the velocity component of the response of Ia afferents during muscle contraction. Rhythmic activation of TA dynamic γ-efferents had previously been reported during locomotion, at lower levels of static γ firing when parent extrafusal muscle fibres were inactive, on the basis of increased Ia afferent sensitivity to stretch (Perret & Berthoz, 1973). Since, in the present study, phasic and tonic γ-efferents showed large and small increases, respectively, in their locomotor discharge during ENG activity, the above observations are consistent with the suggestion that, for the TA nerve, phasic units are static and tonic units are dynamic γ-motoneurones. However, other correlations, which seem less likely, are possible and merit further consideration.

In Cabelguen's study (1981) the dynamic sensitivity of all TA Ia afferents (total = 13) showed large rhythmic *decreases* during locomotion, coincident with parent muscle activity. In contrast, the dynamic sensitivity of gastrocnemius (total = 14; Cabelguen, 1981) and soleus (total = 21; Taylor *et al.* 1985) Ia afferents consistently exhibited large *increases* during homonymous muscle contraction under the influence, in the latter case, of coactivated dynamic γ-efferents (Murphy *et al.* 1984) whose modulation (mean, 23 impulses/s) was similar to that of TA phasic units in the present study (mean, 21 impulses/s). The increase in dynamic sensitivity of soleus Ia afferents is particularly striking since it occurred against a background level of static γ-efferent activity (mean, 51 impulses/s; Murphy *et al.* 1984) that is considerably higher than the mean rate during walking of TA tonic units (18·5 impulses/s). Thus with the assumptions, which are not unreasonable (Cabelguen 1979, 1981), that ankle flexor and extensor Ia afferents are influenced through similar degrees of spindle innervation by static and dynamic γ-efferents and have similar sensitivities to these inputs, not only is a direct equivalence between phasic/tonic and dynamic/static γ-efferents, respectively, unlikely but, since TA Ia afferents consistently showed a decrease in dynamic sensitivity during muscle contraction (Cabelguen, 1981), it is

probable that few, if any, of their dynamic γ-efferents, one or two of which are the general supply to a spindle (Boyd, 1980), corresponded to phasic units.

It is feasible that TA tonic and/or phasic units consist of static and dynamic γ-motoneurones. However, in other muscles, including the external intercostals, jaw-closing and ankle extensors, in which tonic and phasic patterns of γ discharge have also been described during rhythmic movements, a direct, though not necessarily the same, correspondence with static and dynamic types has been proposed in each case (Appenteng *et al.* 1980; Murphy *et al.* 1984; Greer & Stein, 1990). The simplest interpretation of the present results is a direct equivalence and this seems particularly appropriate in view of the relatively simple action of the muscle involved (ankle flexor), and since γ-efferents were recorded from a nerve branch (anterior) which supplies, almost exclusively, one of the two intramuscular compartments of TA (Iliya & Dum, 1984). Notwithstanding these comments, we have already discussed the unlikelihood of a significant number of phasic units being dynamic in nature. However, on the basis of available evidence, we cannot exclude the possibility that some tonic units were static γ-efferents. It should be noted that any such relation was associated with *similar* levels of TA Ia afferent discharge, at the end of the plateau phase of ramp stretch (up to maximum muscle length *in situ*), in the resting state and between bursts of muscle activity during locomotion (Cabelguen, 1981), while tonic units were silent and had a mean minimum firing rate of 13 impulses/s in these states, respectively. In conclusion, the results are consistent with, but do not prove, the correspondence: phasic = static and tonic = dynamic for γ-motoneurones in the TA nerve during locomotion. This correspondence will be adopted in the ensuing discussion.

Functional significance

Do the proposed patterns of TA γ discharge offer any functional advantages? During locomotion, activity in this muscle is mainly accompanied by shortening against a relatively small load (i.e. the foot). Powerful phasic static γ activity at this time would prevent spindle afferent silencing and might, depending on its intensity (Appenteng, Prochazka, Proske & Wand, 1982), increase Ia afferent discharge. Muscle contraction would thus be aided by, and responsive to, peripheral feedback. This notion is encompassed in the concept of servo-assistance (Matthews, 1972; Stein, 1974), the functional advantages of which have been discussed elsewhere. In the present experiments, static γ discharge rate appeared to be related to the degree of ENG activity and, presumably, the velocity of muscle shortening *in vivo*. This feature is consistent with the proposed role of static γ-efferents since the degree of activity in these neurones, that is necessary to elevate Ia afferent discharge, will depend on shortening velocity. It should be stressed that, to date, only one TA Ia afferent has been recorded during locomotion in freely moving cats (Loeb & Duysens, 1979) and this unit was most active during flexion (muscle shortening) which is consistent with powerful phasic recruitment of static γ-efferents. Other studies, during fictive locomotion in the cat (Shefchyk, Stein & Jordan, 1984), have indicated that the monosynaptic pathway, from TA Ia afferents to their α-motoneurones, is patent during the flexion phase and thus available for the control of contraction. It is striking that, like TA during locomotion, the masseter muscle during rhythmic jaw movements (Appenteng *et al.* 1980) also exhibits phasic static γ activity while active.

We suggest that the common fusimotor strategy of these muscles, which are involved in different rhythmic movements, reflects their similar mode of action (i.e. predominantly shortening contraction).

During locomotion, tonic dynamic γ-motoneurone activity in TA would enhance Ia afferent stretch sensitivity (Matthews, 1962) throughout the step cycle. During flexion such enhancement would oppose unwanted lengthening via the stretch reflex. Indeed, in intact cats, if an obstacle is brought into contact with the dorsal surface of the foot during the flexion phase of locomotion then a complex response ensues, involving cutaneous and stretch reflexes, which allow the animal to lift the foot over the obstruction (Wand, Prochazka & Sontag, 1980). The initial phase of the response is an enhancement of activity in TA which occurs at short latency (*ca* 9 ms), when the muscle is being lengthened, and which is unaffected by local anaesthesia of the dorsum of the foot. These features are consistent with stretch reflex participation which, we would predict, is enhanced by background activity in dynamic γ-efferents. During the extension phase of the step cycle, when TA is stretched at only moderate rates, enhanced Ia afferent sensitivity would contribute to reciprocal inhibition of ankle extensor muscles. In this context it should be noted that such inhibition has been demonstrated recently during human walking on stimulating the common peroneal nerve (Capaday, Cody & Stein, 1990).

Static γ-motoneurones also influence group II spindle afferents and we would predict an increase in their locomotor discharge in TA during muscle contraction due to powerful phasic fusimotor activation. On the basis of a recent hypothesis proposed by Lundberg and co-workers (Lundberg, Malmgren & Schomburg, 1987), it is possible that such increased group II activity might excite (via excitatory group II interneurones) those muscles whose activity is necessary for the movement, while inhibiting (via the inhibitory group II pathway) others which are not required. The importance of any spindle group II excitation relative to that from Ia afferents remains to be determined. If TA group II spindle afferents do exhibit increased firing during the flexion phase of locomotion, when the muscle is actively shortening, then they do not provide a direct signal regarding muscle length during this behaviour. However, in the resting state TA static and dynamic γ-efferents are quiescent, which is consistent with the passive role of ankle flexor muscles during maintained posture (Rasmussen, Chan & Goslow, 1978), and, under these conditions, group II spindle afferents would be expected to provide ready information regarding muscle length.

The present classification of ankle flexor phasic and tonic units as static and dynamic γ-motoneurones, respectively, is *opposite* to that which has been demonstrated for ankle extensor muscles during locomotion (triceps surae: Murphy *et al.* 1984; Taylor *et al.* 1985). In each case the patterns of static and dynamic γ discharge seem functionally useful for the actions of the parent muscle and spindle afferents during the step cycle. It is, however, pertinent to consider whether there are any common features in these examples that may be of general significance regarding the strategies of γ usage during posture and movement. While recognizing that the timing of changes in γ rate can play an important role in determining spindle afferent discharge (e.g. Appenteng *et al.* 1982) it is striking, nevertheless, that during locomotion α-motoneurone discharge in TA (present results) *and* triceps surae (Murphy *et al.* 1984) is accompanied by *coactivity* in static and dynamic γ-efferents,

albeit to different degrees that, presumably, depend in part on the predominant action (e.g. shortening contraction) of the particular muscle. Such coactivity would enhance the ability of Ia afferents to contribute reflexly to muscle contraction under shortening, lengthening and isometric conditions. We therefore suggest that, for TA and triceps surae, coactivity in both types of γ-efferent during contraction is functionally advantageous in optimizing Ia afferent feedback for reflex contributions to muscle activity during locomotion. Such contributions will depend, in the periphery, on the rate and degree of muscle length variations which will be determined by intrinsic (e.g. muscle fatigue) and extrinsic (e.g. load) factors. In addition, central structures will, or course, exercise significant control over reflex efficacy.

Does static and dynamic γ coactivity occur during contraction in other situations? The discharge patterns of γ-efferents have been classified as static or dynamic in different muscles, with varying degrees of certainty, during three types of rhythmic movement: respiration (Corda *et al.* 1966; Euler & Peretti, 1966; Greer & Stein, 1990), jaw movements (Appenteng *et al.* 1980) and locomotion (Murphy *et al.* 1984; Bessou, Joffroy, Montoya & Pages, 1990; present results). With one exception, these reports indicate coactivity in static and dynamic γ-efferents during activation of homonymous α-motoneurones. In the remaining case (Bessou *et al.* 1990) evidence was presented for coactivation of α- and static γ-motoneurones in the sartorius medialis muscle during locomotion; however, concurrent dynamic γ activity could not be excluded. These studies are, therefore, consistent with the proposal that, during rhythmic movements, muscle contraction is accompanied by coactivity in static and dynamic γ-motoneurones. Further, although different explanations may account for such coactivity, depending on the muscle and type of movement involved, it is also possible that the previously suggested functional rationale regarding TA and triceps surae is generally valid. Whether static and dynamic γ-motoneurone coactivity during muscle contraction is a more general strategy that is employed during other types of behaviour remains to be established.

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