

THE ROLE OF CUTANEOUS AFFERENTS IN THE CONTROL OF γ -MOTONEURONES DURING LOCOMOTION IN THE DECEREBRATE CAT

BY P. R. MURPHY AND G. R. HAMMOND

*From the Division of Neurobiology, Medical School, The University,
Newcastle upon Tyne NE2 4HH*

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SUMMARY

1. The effect of electrical stimulation, up to $20 \times$ threshold (T), of the sural nerve on the discharges of single medial gastrocnemius static and dynamic γ -motoneurones has been investigated at rest and during locomotion in the decerebrate cat.

2. A total of twenty-three γ -motoneurones were recorded. The neurones were identified as static (15) or dynamic (8) on the basis of their discharge characteristics (Murphy, Stein & Taylor, 1984).

3. Low intensity stimulation ($\leq 1.5T$) had no effect on the discharges of most (22 of 23) γ -efferents at rest or during locomotion. Hence the largest afferents in the sural nerve had little influence on the discharges of static or dynamic γ -motoneurones in either condition.

4. Higher intensity stimulation ($> 1.5T$) excited both types of γ -efferent in the resting state and response size was graded with stimulus intensity. For most neurones (20 of 23) excitatory effects appeared in the range 1.5 – $2T$.

5. Stimulation at intensities $> 1.5T$ also excited dynamic and some static γ -motoneurones during locomotion. The responses of dynamic γ -motoneurones were unchanged during locomotion compared to the resting state. In contrast, the responses of static neurones were significantly reduced, or even abolished, during locomotion and stimuli $\leq 3T$ generally (12 of 13) had no effect. Thus the responses of static, but not dynamic, γ -efferents were task dependent. Further, the thresholds of responses indicate that activation of low threshold mechanoreceptors in the sural receptive field excites both types of γ -efferent at rest, and dynamic neurones during locomotion. In contrast, it is proposed that the same peripheral input does not affect static γ -efferents during locomotion.

6. The responses of static and dynamic γ -motoneurones during locomotion were not obviously related to step cycle phase, or γ rate, and responses occurring during or between homonymous electromyogram (EMG) bursts were not significantly different. Thus γ responses during locomotion were not phase dependent.

7. Stimulation at intensities $> 3T$ excited dynamic and some static γ -motoneurones during locomotion but simultaneously inhibited on-going EMG activity. Peripheral inputs are therefore capable of influencing α - and γ -motoneurones independently during locomotion.

8. The significance of the results is discussed in relation to the control and function of γ -motoneurones.

INTRODUCTION

Movement in mammals is ultimately controlled by the discharge of two basic types of motoneurone, α and γ . α -Motoneurones produce muscle activation directly, whereas 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). To date, there have been no direct recordings from identified static and dynamic γ -efferents during normal behaviour, severely limiting the development of theories of γ function. Recently, Murphy *et al.* (1984) identified the patterns of discharge of triceps surae static and dynamic γ -motoneurones during locomotion in a decerebrate cat preparation. Dynamic γ -efferents had high resting discharge rates (≥ 20 impulses s^{-1}) and were deeply modulated during locomotion, with activity linked to the homonymous EMG. In contrast, static γ -efferents had low resting discharge rates (< 20 impulses s^{-1}) and a predominantly tonic locomotor discharge pattern. Thus independent control, not only of the skeletomotor and fusimotor systems, but of the two types of γ -efferent, occurs during locomotion. It was suggested that the discharge characteristics of static and dynamic γ -motoneurones are ideally suited to the functional demands of locomotion (Taylor, Stein & Murphy, 1985).

The distinctive γ locomotor discharge patterns may be produced by central drives, peripheral inputs or, most likely, a combination of both these factors. The aim of the present study was to determine whether cutaneous afferent feedback is capable of influencing hindlimb γ -motoneurones during locomotion. To date there has been no direct study of this problem. The available data, derived from non-behaving preparations, indicates that peripheral afferents, in particular from skin, are capable of exerting powerful effects on γ -efferents in the resting state (for review, see Hulliger, 1984). However, it is conceivable that, like α -motoneurones (for review, see Grillner, 1981), the reflex control of γ -motoneurones depends on behavioural context. Consequently, hypotheses concerning γ function, which are based on observations in the non-behaving state, may not be generally valid.

The present investigation confirms that cutaneous afferents potently affect γ -motoneurones at rest. However, the new observation is made that the efficacy of this reflex to static, but not dynamic, γ -efferents depends on behavioural context. Thus reflex effects on static γ -motoneurones were reduced, or even abolished, during locomotion compared to the resting state, while effects on dynamic neurones were unchanged. Such task dependence must be considered in any theory of the role of the γ system in the control of movement.

A preliminary account of some of this work has been published (Hammond & Murphy, 1989).

METHODS

Preparation

Ten 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 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 -motoneurons with background discharges were recorded from the cut medial gastrocnemius (MG) nerve on twin platinum wire electrodes. A Silastic cuff containing three recording electrodes was placed around the sciatic nerve for monitoring its neural activity. Axonal conduction latency was determined by delaying the signals recorded from the sciatic cuff and from the muscle nerve filaments. The undelayed spike on the muscle nerve was used to trigger signal averaging (Murphy *et al.* 1984). Units were identified as γ -motoneurons on the basis of their conduction velocities ($18\text{--}35\text{ m s}^{-1}$) and discharge characteristics (Murphy *et al.* 1984). 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. The cut sural nerve was electrically stimulated through bipolar platinum wire electrodes and the in-going volley was continuously monitored from the sciatic cuff. Generally, for a given γ -motoneurone, a train of five stimuli (0.1 ms each, 50 s^{-1}) was applied every 4 s at a range of stimulus intensities including 1.5, 2, 3, 5, 10 and $20T$. Higher frequency stimulation was rarely used and not systematically studied. However, responses to such stimuli were consistent with the observations made at a stimulation rate of 50 s^{-1} . For each intensity, stimulation was applied at rest and during locomotion. During locomotion stimulation occurred at all phases of the step cycle. The threshold of the most excitable afferent fibres was determined by stimulating the sural nerve with single shocks and averaging the signal recorded from the sciatic cuff. Threshold was assessed after each period of locomotor activity but showed little variation during the course of an experiment. 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). Stimulus pulses were also converted to standard pulses for recording.

Analysis

Analysis was performed manually from UV records or by digital processing using a Victor Vi computer. In both cases, for each stimulus strength, ten to twenty-five responses were analysed in the resting state and twenty to thirty-five during periods of regular locomotor activity. Responses were assessed by calculating the change in mean γ rate (impulses s^{-1}) which occurred during the 100 ms after stimulus onset compared either to the preceding 100 ms, for responses at rest (Fig. 2), or to the equivalent period of the preceding control step cycle, for responses during locomotion (Fig. 3). During locomotion the onsets of the periods of measurement occurred at the same time (t) in the stimulated (S) and control (C) step cycles. In UV recordings, step cycle onset corresponded to the beginning of extensor EMG activity. With computer analysis this point was defined by a step marker which occurred when the filtered (time constant, 20 ms) EMG exceeded a pre-set level. This method produced a delay of approximately 20 ms in the definition of step cycle onset, which was small compared to a typical step cycle duration of 700 ms. No correction was made for this delay during analysis.

RESULTS

Classification of γ -motoneurons

A total of twenty-three MG γ -motoneurons were recorded in ten experiments. These neurons were classified as static (15) or dynamic (8) on the basis of their discharge characteristics, according to the following rationale. In the same

preparation as that used in the present experiments, Murphy *et al.* (1984) observed that triceps surae γ -motoneurons seemed to fall naturally into two groups on the basis of their discharge characteristics. Tonicity modulated units had low resting rates but greatly increased their discharge during locomotion and maintained them at a relatively steady level. Phasically modulated units had high resting rates that did not change much on average during locomotion but showed a high degree of modulation with each step. All the phasically modulated γ -axons had resting rates ≥ 20 impulses s^{-1} , while tonically modulated axons had resting rates below 20 impulses s^{-1} . Thus, on the basis of resting rate alone, the two groups of γ -motoneurons could be distinguished. In other experiments the resting discharges of classified static and dynamic γ -efferents were recorded directly and found to correspond to that of tonically modulated and phasically modulated units, respectively (Murphy *et al.* 1984). In the present study we used resting discharge rates to classify units as static (< 20 impulses s^{-1}) or dynamic (≥ 20 impulses s^{-1}). Using this method of classification two groups of neurons resulted which had distinctive discharge characteristics, as follows. For static units, resting rate = 3–15 impulses s^{-1} , modulation = 8–20 impulses s^{-1} (half peak-to-peak), mean rate during walking = 48–70 impulses s^{-1} , change in mean rate from resting to locomotor states = 33–66 impulses s^{-1} . The equivalent figures for dynamic units were 25–70, 23–65, 40–60 and –16–25 impulses s^{-1} , respectively. These discharge characteristics are similar to those reported in a previous study for static and dynamic γ -efferents (Murphy *et al.* 1984). The tendency of the present data to fall into two groups of neurons on the basis of their discharge characteristics is illustrated in Fig. 1A. It is, of course, recognized that even with a full range of direct testing procedures γ -axons cannot be classified unambiguously as static or dynamic in every case (Emonet-Denand, Laporte, Matthews & Petit, 1977). The present classification system cannot therefore be regarded as wholly definitive.

Effect of low intensity stimulation ($\leq 1.5T$)

For the vast majority (22 of 23) of static and dynamic γ -motoneurons low intensity stimulation had no detectable effect (i.e. response not statistically different from zero; $P > 0.1$, Student's *t* test) on discharge rate at rest or during locomotion. One static γ -efferent showed a weak response (3.5 ± 1.2 impulses s^{-1} , mean \pm s.e.m.) at $1.5T$ in the resting state, but was unaffected during locomotion. A clear afferent volley was recorded at $1.5T$ from the sciatic nerve in every experiment. Thus it seems likely that the largest afferents in the sural nerve have little effect on the discharges of static and dynamic γ -motoneurons at rest or during locomotion.

Effect of higher intensity stimulation ($> 1.5T$)

Threshold of effects

Higher intensity stimulation ($> 1.5T$) of the sural nerve excited static and dynamic γ -motoneurons in the resting state. For most (20 of 23) neurons excitatory effects appeared with stimulation intensities between 1.5 and $2T$ (Fig. 1B).

There was little or no background EMG activity in the resting state and sural nerve stimulation rarely evoked activity. For four dynamic and six static units some

levels of stimulation were applied at rest in the presence of background EMG activity. The responses were similar to those of other units which were recorded with no resting EMG activity. Further, the resting responses of three static and three dynamic units were assessed, at some stimulus intensities, with and without

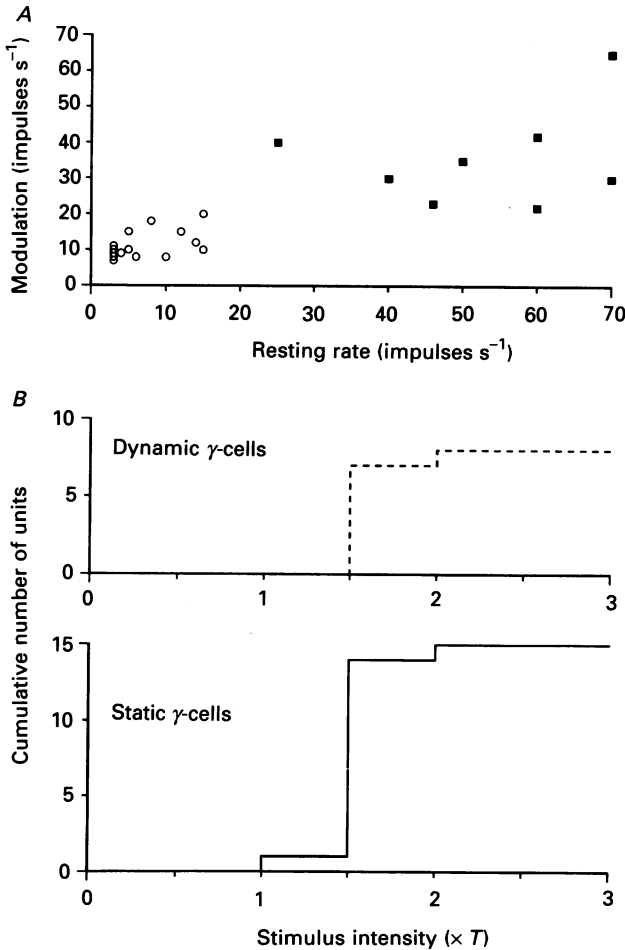


Fig. 1. *A*, the population of static γ -axons (\circ) had lower resting discharge rates and smaller modulations in each step than that of dynamic γ -axons (\blacksquare). *B*, cumulative histograms of the distribution of thresholds for excitation of dynamic (8) and static (15) γ -motoneurons at rest. For both types of neurone excitatory effects generally appeared in the range 1.5–2*T*.

background EMG activity. In each case there was no significant difference ($P > 0.1$) between the responses in the two conditions. These results suggest that the degree of resting reflex activation of static and dynamic γ -motoneurons did not depend upon the level of background EMG activity.

Dynamic γ -motoneurones

Figure 2 shows an example of the response of a dynamic γ -motoneurone to stimulation $> 1.5T$, in this case $20T$, at rest. Powerful excitation was produced in which the mean discharge rate during the 100 ms period after stimulus onset was

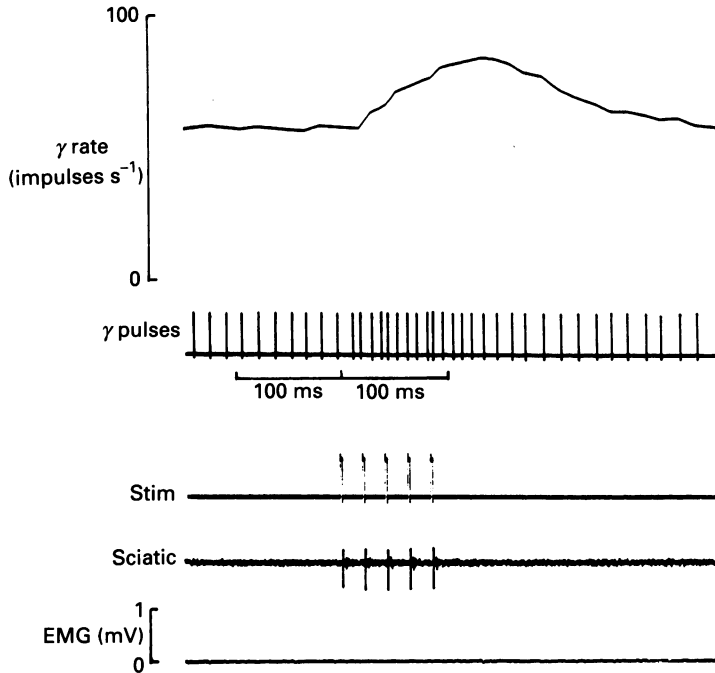


Fig. 2. The excitatory effect of stimulation $> 1.5T$ of the sural nerve, in this case $20T$, on a dynamic γ -motoneurone in the resting state. The γ rate was produced by passing standard pulses, which were triggered by action potentials, to a leaky integrator (time constant, 100 ms). A train of five stimuli (0.1 ms each, $50 s^{-1}$) was applied to the cut sural nerve and the in-going afferent volley was recorded from the sciatic nerve. Stimuli were converted to standard pulses for display. EMG was recorded from the lateral gastrocnemius muscle.

110 impulses s^{-1} . This compares to a mean rate of 70 impulses s^{-1} during the same period preceding stimulus onset, representing a response of 40 impulses s^{-1} (see Methods). Stimulation $> 1.5T$ also excited dynamic γ -efferents during locomotion. Figure 3 illustrates an example for the unit from Fig. 2. Here, the mean frequency of the unit over the 100 ms period after stimulus onset was 120 impulses s^{-1} which compares to 80 impulses s^{-1} during the equivalent period of the preceding control step cycle, giving a response of 40 impulses s^{-1} . In this example the stimulus occurred during an EMG burst and γ excitation was accompanied by simultaneous, powerful inhibition of on-going EMG activity. Inhibition of on-going EMG activity was apparent for intensities of stimulation $> 3T$. When such stimuli fell between EMG bursts the onset of the next EMG burst was generally delayed. At lower stimulus

strengths effects on EMG were less clear cut, but no systematic investigation was made in light of previous studies (e.g. Duysens, 1977).

During locomotion stimulation was generally applied every 4 s and occurred at different times throughout the step cycle. However, for dynamic γ -motoneurons

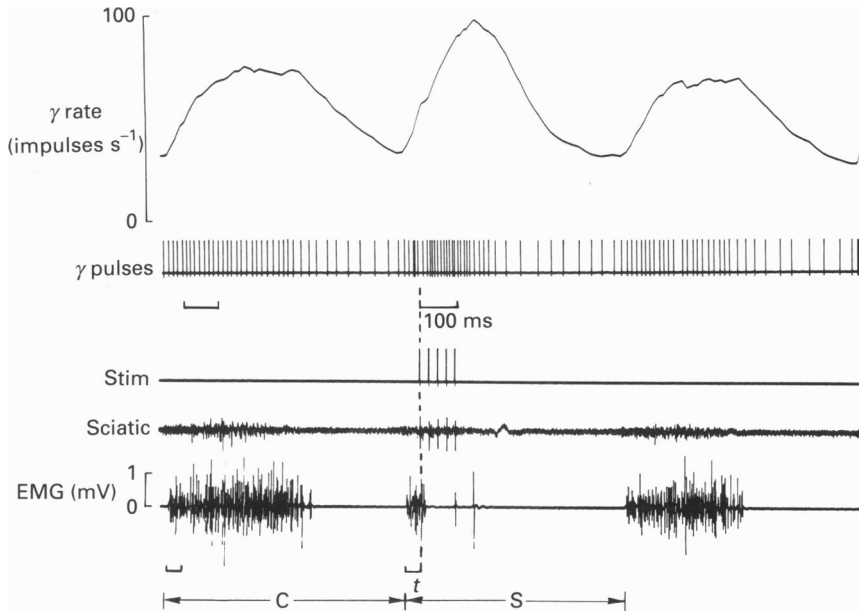


Fig. 3. Response of a dynamic γ -motoneurone (same unit as in Fig. 2) to stimulation ($20T$) of the sural nerve during locomotion. γ -Efferent excitation was accompanied by simultaneous inhibition of on-going EMG activity. Locomotion is indicated by rhythmic bursts of EMG. Traces and stimulus parameters are the same as in Fig. 2. The onsets of the measurement periods occurred at the same time (t) in the stimulated (S) and control (C) step cycles.

there was no obvious tendency for the size of response, to a constant stimulus, to be related to step cycle phase (Fig. 4), and responses occurring during and between EMG bursts were not significantly different ($P > 0.1$). Also plotted for each response in Fig. 4 is the mean γ rate during the equivalent period of the preceding control step cycle. Even though the unit was deeply modulated ($30 \text{ impulses s}^{-1}$) there was little apparent change in the response to sural stimulation. These observations were consistent for all values of stimulation $> 1.5T$ (i.e. 2, 3, 5, 10 and $20T$) tested with this efferent, and with a further seven dynamic units.

A range of values of stimulation $> 1.5T$ was tested for each efferent which generally included 2, 3, 5, 10 and $20T$. For dynamic γ -motoneurons, increasing stimulus intensity produced increasing responses at rest and during locomotion (Fig. 5), suggesting that the predominant effect of successively recruited afferent fibres was excitatory in both conditions. Both $A\beta$ - and $A\delta$ -myelinated afferents would have been activated by the stimulus range employed (Rosenberg, 1970). For each dynamic

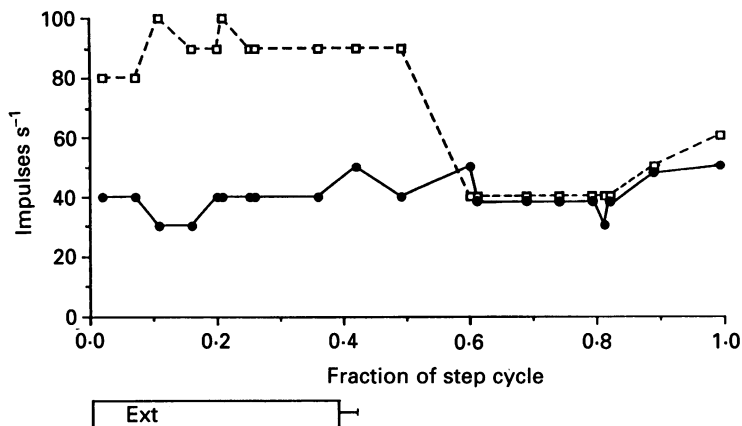


Fig. 4. Responses of a dynamic γ -motoneurone to stimulation $> 1.5T$, in this case $20T$, of the sural nerve at different times (normalized) in the step cycle. Response size (●) was not obviously related to either step cycle phase or γ rate (□), as measured from the preceding control step cycle. Mean responses during (Ext) and between EMG bursts were not significantly different ($P > 0.1$). Points represent single observations and are plotted at the mid-point of the measurement period.

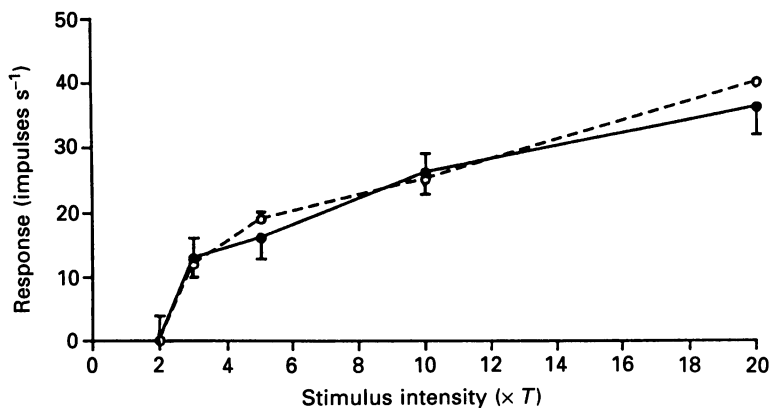


Fig. 5. Mean responses of a dynamic γ -motoneurone in the resting state (○) and during locomotion (●), to increasing intensity of stimulation of the sural nerve. Effects were graded with stimulus intensity and there was no significant difference ($P > 0.1$) between responses in the two conditions at each stimulus intensity. Vertical lines, s.e.m.

γ -efferent, for any given strength of stimulus, there was no significant difference ($P > 0.1$) between mean response at rest and during locomotion (Fig. 5). Hence responses were not task dependent.

Static γ -motoneurones

As with dynamic γ -motoneurones, stimulation $> 1.5T$ of the sural nerve also excited static neurones in the resting state (Fig. 6), and increasing stimulus intensity produced larger effects (Fig. 7). However, in contrast, static γ responses were task

dependent, being reduced, or even abolished, during locomotion. The latter case is illustrated by Fig. 6 in which an excitatory response at rest was absent during locomotion, despite powerful inhibition of on-going EMG activity. The mean response of this unit during locomotion was 1.5 ± 1.8 impulses s^{-1} , which is not

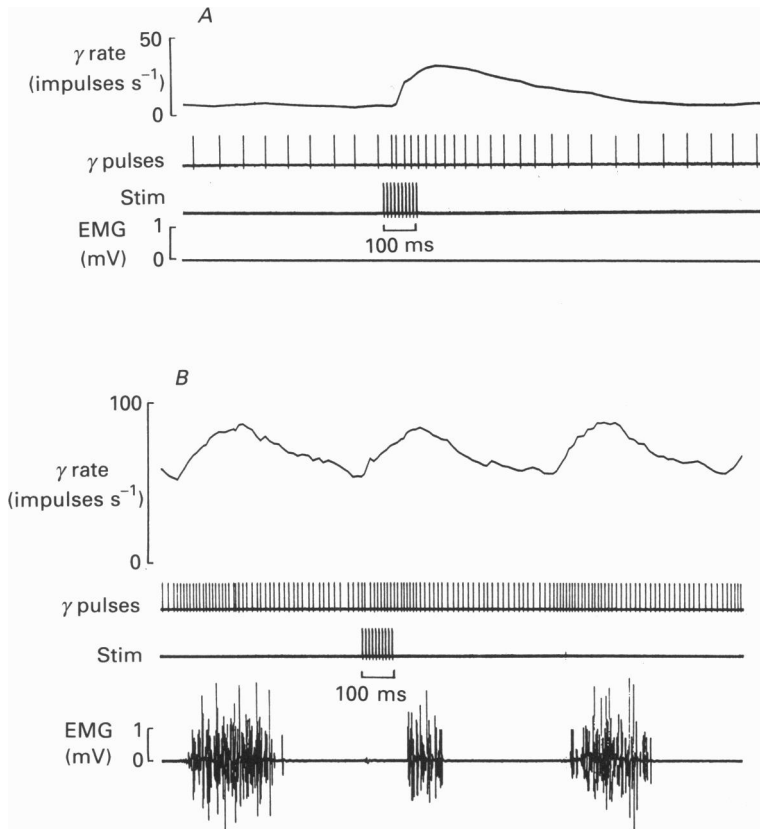


Fig. 6. Example of a static γ -motoneurone in which the excitatory effect of stimulation $> 1.5T$ (in this case ten stimuli, 0.1 ms each, $100 s^{-1}$, $20T$) of the sural nerve, in the resting state (A), was abolished during locomotion (B), despite powerful inhibition of on-going EMG activity. Traces are the same as in Fig. 2 except that the sciatic nerve signal, though recorded, is not shown.

significantly different from zero ($P > 0.1$), compared to a mean response of 38 ± 1.9 impulses s^{-1} at rest. This pattern of response during locomotion was consistent for all values of stimulation $> 1.5T$ and was observed in a further six static units.

For the other eight static γ -motoneurones responses to stimulation $> 1.5T$ were reduced during locomotion with stimuli $\leq 3T$ generally having no effect; only one unit was excited (3.8 ± 1.7 impulses s^{-1}) at a stimulus intensity of $3T$. A typical example is shown in Fig. 7 where the mean response of the γ -efferent during locomotion was reduced ($P < 0.05$ for $1.5T$, otherwise $P < 0.01$) compared to the

resting state at each value of stimulus intensity. Like dynamic neurones, the responses of static units were not related to step cycle phase or γ rate, and mean values during and between EMG bursts were not significantly different ($P > 0.1$).

Potency of effects

A range of stimulus intensities (up to $20T$) was tested at rest and during locomotion for each γ -motoneurone. The most potent responses were elicited in both

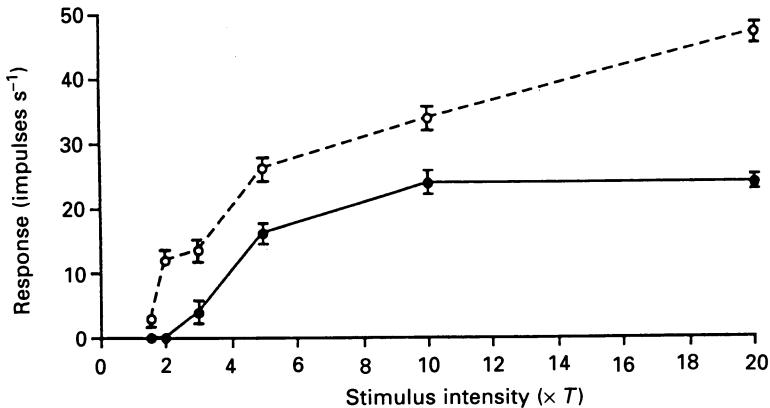


Fig. 7. Example of a static γ -motoneurone in which mean responses to sural nerve stimulation during locomotion (●) were reduced ($P < 0.05$ for $1.5T$, otherwise $P < 0.01$) compared to the resting state (○) at each stimulus intensity. Note that stimuli $\leq 3T$ had little or no effect during locomotion. Vertical lines, s.e.m.

conditions at $20T$ (Figs 5 and 7) and these, presented in Fig. 8, will be considered in order to assess reflex potency. At $20T$ the mean response (42.8 ± 5.6 impulses s^{-1}) of dynamic γ -efferents at rest was not different ($P > 0.1$) from that of static units (40.3 ± 3.7 impulses s^{-1}). During locomotion the mean response (43 ± 5.6 impulses s^{-1}) of dynamic γ -efferents at $20T$ was similar to that in the resting state. In contrast, at the same stimulus intensity, the mean response of static γ -efferents was, on average, reduced by 67% to 13.2 ± 3.8 impulses s^{-1} during locomotion. However, for some of these units (7 of 15), responses to stimulation $> 1.5T$ were abolished (see preceding section) during locomotion. Strikingly, their mean response to $20T$ at rest (31.1 ± 1.7 impulses s^{-1}) was lower ($P < 0.01$) than the remaining static neurones (48.2 ± 5.5 impulses s^{-1}). For other values of stimulation $> 1.5T$ a lower, though not always significantly lower, mean resting response was consistently found. However, the resting responses of units which were unaffected during locomotion could be greater than those of the other static γ -efferents which were excited during locomotion. For example, the unit in Fig. 6 had a mean resting response of 38 ± 1.9 impulses s^{-1} , to a stimulus of $20T$, which was abolished during locomotion. In contrast, other static γ -efferents (e.g. Fig. 7, $10T$), having lower resting responses, were still excited during locomotion. Thus a weaker potency of resting reflex effects *per se* is unlikely to account for the unresponsiveness of some static γ -motoneurones to stimulation $> 1.5T$ during locomotion.

Static γ -motoneurons which showed a reduction or an abolition of response to stimulation $> 1.5T$ during locomotion were affected by the same range of stimulus intensities at rest and there was no obvious difference in their discharge characteristics. The differing patterns of response during locomotion were stable and

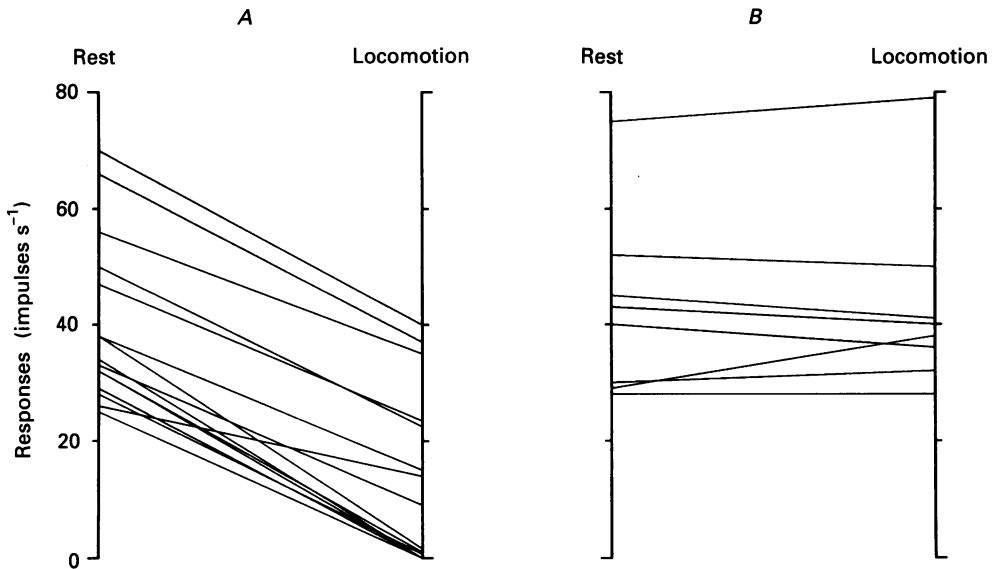


Fig. 8. Mean responses of twenty-three individual static (*A*) and dynamic (*B*) γ -motoneurons at rest and during locomotion to sural nerve stimulation (5 stimuli, 0.1 ms each, 50/s, $20T$). Each line represents one unit. Responses of static, but not dynamic, γ -motoneurons were reduced, or even abolished, during locomotion compared to the resting state.

could be observed in the same experiment. It is therefore unlikely that fluctuating levels of central excitability, within or between experiments, can account for the two patterns of response to stimulation $> 1.5T$. A more probable explanation is a difference in the intrinsic properties and/or synaptic inputs (quantitative and/or qualitative) of the neurones involved. At the moment no definite explanation is possible. However, it is worth noting that two types of static γ -motoneurone have been suggested (Boyd, 1986), and it is conceivable that these may correspond to the two patterns of reflex behaviour observed in the present study. From the above analysis of the potency of reflex responses it is clear that myelinated afferents in the sural nerve are capable of exerting a powerful excitatory influence on the discharges of dynamic and some static γ -motoneurons both at rest and during locomotion.

A comparison of the physiological characteristics (Hunt & McIntyre, 1960) and the electrical thresholds (Rosenberg, 1970) of single sural afferents indicates that stimulus intensities $\leq 2T$ will preferentially excite various types of non-nociceptive afferent, while higher values may, in addition, recruit fibres which signal noxious events occurring at the skin. This level of stimulation (i.e. $2T$) was always

submaximal, in the present experiments, for the $A\beta$ -nerve fibre group (range of $A\beta$ -maximums 2.6 – $3.5T$, $n = 10$) as measured from sciatic nerve recordings of the afferent volley. Since only innocuous stimuli are encountered during 'normal' posture and locomotion it is relevant to assess the potency of reflex effects from this source.

A stimulus intensity of $2T$, presumed innocuous, produced significant excitatory responses in static (10 ± 0.7 impulses s^{-1} , $n = 12$) and dynamic (10.4 ± 0.5 impulses s^{-1} , $n = 7$) γ -motoneurons in the resting state. Only one static and one dynamic neurone were unaffected at $2T$ and these are not included in the above means. Since there are non-nociceptive afferents with thresholds in excess of $2T$, responses at this level of stimulation cannot be considered to represent the maximum possible from this source. While presumed innocuous stimulation (i.e. $2T$) also excited dynamic γ -efferents (11 ± 1.2 impulses s^{-1} , $n = 7$) during locomotion, static units, in contrast, were unaffected (0.2 ± 0.5 impulses s^{-1} , $n = 12$). Indeed, even at $3T$, the mean response (3.8 ± 1.7 impulses s^{-1}) during locomotion of only one static γ -efferent was significantly different ($P < 0.05$) from zero. This stimulus intensity was supramaximal for $A\beta$ -fibres in most experiments (7 of 10) and produced a mean response of 14 ± 0.8 impulses s^{-1} ($n = 13$) for static γ -efferents in the resting state.

DISCUSSION

Effect of low intensity stimulation ($\leq 1.5T$)

Electrical stimulation of the sural nerve at intensities $\leq 1.5T$ had little effect on the discharges of static or dynamic MG γ -motoneurons at rest or during locomotion. It is estimated that a stimulus intensity of $1.5T$ would have activated myelinated afferents with conduction velocities in excess of 54 m s^{-1} (Rosenberg, 1970), comprising a substantial proportion ($> 50\%$) of the $A\beta$ -axon population (Hunt & McIntyre, 1960). In contrast, some previous studies (e.g. Johansson & Sojka, 1985; Davey & Ellaway, 1989) have reported significant effects on γ -motoneurone discharge to sural nerve stimulation $< 1.5T$. However, non-behaving preparations were used and it is possible that the level of excitability in the reflex pathways to γ -efferents was greater than in the current experiments. Hence these results do not necessarily conflict with the conclusion of the present study that activity in the largest afferents in the sural nerve exerts little influence on either type of γ -motoneurone at rest or during locomotion.

Effect of higher intensity stimulation ($> 1.5T$)

Higher intensity stimulation ($> 1.5T$) of the sural nerve produced potent excitatory responses in both types of γ -motoneurone in the resting state. This was also the case for dynamic and some static γ -efferents during locomotion. Thus, although the CNS seems capable of generating the basic locomotor patterns of static and dynamic γ -motoneurons (Murphy & Hammond, 1990), sensory feedback is involved in adapting these patterns to the external environment. The results confirm the conclusion of previous studies (for review, see Hulliger, 1984) that myelinated afferents in the sural nerve exert powerful reflex effects on γ -motoneurons at rest. However, the new observation has been made that the potency of this reflex to static,

but not dynamic, γ -efferents is task dependent. Thus the reflex responses of static neurones were significantly reduced, or even abolished, during locomotion while those of dynamic units were unchanged compared to the resting state.

What factors are responsible for the large reduction (e.g. 67% on average at 20T) in the size of sural reflex effects on static γ -motoneurones during locomotion? There are two possibilities: mechanisms which are premotoneuronal and those which operate postsynaptically at the motoneurone. For α -motoneurones both factors are thought to be involved in controlling reflex efficacy (see e.g. Duenas & Rudomin, 1988; Schmidt, Meyers, Tokuriki & Burke, 1989), however, there have been no specific studies of this aspect of the γ system to date so that a definite conclusion is not possible.

Reflexes involving α -motoneurones also depend on behavioural context (see e.g. Capaday & Stein, 1986; Evans, Harrison & Stephens, 1989). Such flexibility is functionally useful in allowing appropriate motor responses during different tasks. Any assessment (see below: Functional significance) of the implications of the present task-dependent cutaneous reflex to static γ -efferents must consider the nature of the receptors involved. The results suggest that while activity in low threshold mechanoreceptors with $A\beta$ -afferents excites static γ -efferents in the resting state, the same input has no effect during locomotion. A definite conclusion concerning the reflex effects of low threshold mechanoreceptors with afferents in the $A\delta$ range (hair follicle units) is not possible on the basis of the present study, since this group also includes nociceptor and thermoreceptor fibres, which would have been activated non-selectively by electrical stimulation. However, recently, Davey & Ellaway (1989) have investigated the connectivity between myelinated afferents from low threshold mechanoreceptors in the sural receptive field and unclassified MG γ -motoneurones, using a cross-correlation technique in decerebrated, spinal cats. Significant short duration peaks in correlations, indicating connectivity, were observed only with slowly adapting, type 1 mechanoreceptors, which had afferents predominantly in the $A\beta$ range. Strikingly, no such connectivity was observed with hair follicle afferents having $A\beta$ or $A\delta$ velocities. These observations, if applicable to static γ -efferents, considered with the present results, are consistent with the suggestion that input from low threshold mechanoreceptors with myelinated afferents in the sural receptive field does not influence static γ discharge during locomotion. Although we have no data relating to the reflex effects of cutaneous low threshold mechanoreceptors with unmyelinated afferents (C fibres), their sluggish, long latency responses to mechanical events at the skin (for review, see Darian-Smith, 1984) make it unlikely that they are involved in the control of γ discharge during locomotion.

In contrast to static γ -axons, there was no change in the mean responses, to sural nerve stimulation, of dynamic neurones during locomotion compared to the resting state, indicating a constant net effect of the factors (see above) which determine reflex efficacy. Since reflex responses generally (7 of 8 units) appeared at low stimulus intensities (1.5–2T), the results indicate that activation of low threshold mechanoreceptors with myelinated afferents in the sural field excites dynamic γ -motoneurones at rest and during locomotion.

Since stimuli $> 2T$ may activate afferents from low threshold mechanoreceptors,

nociceptors and thermoreceptors, little can be said, on the basis of the present results, about the nature of the afferents which produce excitatory reflex effects at these stimulus intensities. However, it is striking that the most potent reflex responses were observed at intensities $> 2T$ (e.g. Figs 5 and 7). Thus, the mean resting response of dynamic γ -efferents at $20T$ (42.8 impulses s^{-1}) was four times greater than at $2T$ (10.4 impulses s^{-1}). A similar (or greater) difference in potency was apparent when comparing the mean responses, at these stimulus intensities, of dynamic γ -efferents during locomotion, or static γ -efferents at rest, or during locomotion. Thus it is likely that afferents which are recruited by stimuli $> 2T$ are capable of exerting powerful excitatory effects on both types of γ -motoneurone at rest and during locomotion. The strength of such effects relative to those produced by stimuli $\leq 2T$ cannot be gauged, however, in view of the possibility of interactions between the afferent volleys.

During locomotion a variety of reflexes involving α -motoneurons are phase dependent (for review, see Rossignol & Drew, 1985). Thus in the ipsilateral hindlimb extensors of the cat, reflex responsiveness to cutaneous input generally coincides with locomotor EMG activity in the parent muscle, so producing appropriate motor responses throughout the step cycle. In contrast, the responses of static and dynamic γ -efferents to sural nerve stimulation were not manifestly related to step cycle phase, or γ rate, and were constant during and between EMG bursts. This, of course, does not necessarily exclude the possibility that receptors signalling specific modalities do produce phase-dependent reflex effects on γ -efferents. However, as the discharges of γ -motoneurons must be expressed via muscle spindle afferents, which do exhibit phase-dependent effects on α -motoneurons (see e.g. Akazawa, Aldridge, Steeves & Stein, 1982; Capaday & Stein, 1986; Duenas & Rudomin, 1988), phase modulation of responses at the γ -motoneurone level may be redundant. Alternatively, maintained reflex efficacy throughout the step cycle may be functionally advantageous (see below: Functional significance). What are the mechanisms involved in this lack of phase dependence? Both the degree of input to, and the intrinsic excitability of, a γ -motoneurone will determine the size of its reflex response. An invariant level of response during the step cycle could be achieved if these factors varied in an antiphase manner, or if they were constant. However, in view of the lack of information, in the γ system, concerning factors such as membrane properties and premotoneuronal gating mechanisms, further speculation seems premature.

Recordings from muscle spindle afferents and γ -motoneurons in the cat and monkey have indicated that the degree of α and γ activation varies with behaviour (for review, see Hulliger, 1984; Murphy *et al.* 1984). Such independence presumably allows these different neural systems to be used in the most functionally appropriate manner for the task at hand (see e.g. Taylor *et al.* 1985). It also raises the question of the relative contributions of central drives and peripheral inputs. Studies in non-behaving preparations have shown that both factors are capable of influencing α - and γ -motoneurons independently (Hulliger, 1984). In the present preparation triceps surae α - and γ -motoneurons show a degree of independent activation during locomotion (Murphy *et al.* 1984; present results). Thus, static neurons have a predominantly tonic firing pattern while dynamic γ discharge is deeply modulated, with activity linked to homonymous EMG. Further, recordings of γ -efferent activity

during fictive locomotion, in the same preparation, indicate that central drives are capable of generating these basic, distinctive γ locomotor discharge patterns (Murphy & Hammond, 1990). In the present study sural nerve stimulation at intensities $> 3T$ excited dynamic and some static γ -efferents during locomotion but simultaneously inhibited on-going EMG activity. Hence, it would appear that peripheral inputs (as well as central drives) are capable of influencing α and γ discharge independently during locomotion. Since various afferent modalities are activated by stimulus intensities $> 3T$, including pain, temperature and touch (Hunt & McIntyre, 1960; Rosenberg, 1970), the functional significance of such independent control remains uncertain.

Functional significance

The results are consistent with the view that activation of low threshold mechanoreceptors in the sural receptive field excites MG dynamic γ -motoneurons during locomotion but, in contrast, has no effect on static neurons. At rest, the same input excites both types of γ -efferent.

During a steady posture it is likely that some low threshold mechanoreceptors in the sural receptive field are active, due to skin stretch, even in the absence of contact stimulation (Loeb, 1981). Further activation will occur either directly, by contact, or indirectly, where increased skin stretch is produced by a remote stimulus (e.g. during dorsiflexion of the ankle joint, caused by an increased load, during standing). In these circumstances the resultant excitation of static and dynamic γ -efferents will contribute, via muscle spindle Ia afferents, to extensor α activity that is required for the maintenance of a steady posture (see also, Davey & Ellaway, 1989). During locomotion the same cutaneous afferent input will excite dynamic γ -motoneurons at all phases of the step cycle. During stance, the elevated level of dynamic γ activity which occurs at this time (Murphy *et al.* 1984; present results) will thus be augmented by peripheral inputs. The resultant high Ia afferent sensitivity will enhance the stretch reflex and thus assist in supporting the body and propelling it upwards and forwards (Taylor *et al.* 1985). During the swing phase of locomotion dynamic γ activity is low (Murphy *et al.* 1984; present results). The resultant low sensitivity of Ia afferents will help to prevent inadvertent stretch reflexes (Taylor *et al.* 1985). However, these will only occur if extensor α -motoneurons are depolarized to threshold. Indeed extensor Ia afferents normally exhibit significant discharge levels during swing (Prochazka, Westerman & Ziccone, 1977) and this activity, though not producing stretch reflexes, may play an important role in other reflexes (e.g. reciprocal inhibition of ankle flexor muscles) depending on which interneuronal pathways are open and when. Activation of dynamic γ -efferents during swing by inputs from low threshold mechanoreceptors in the sural receptive field will contribute to such reflexes by increasing Ia afferent sensitivity.

Why should static γ -motoneurons be excited by cutaneous low threshold mechanoreceptors at rest but unaffected by the same input during locomotion? A possible explanation involves the role of muscle spindle group II afferents. These afferents have long been regarded as good candidates for providing the CNS with information regarding muscle length. Indeed, direct recordings from normal cats are consistent with this view (Loeb & Duysens, 1979). However, the sensitivity of group

II afferents to length changes can be influenced by static γ -axons (Lennerstrand & Thoden, 1968) so that interpretation of their discharge as muscle length would require information regarding the prevailing level of static γ activity. Such information may be derived centrally via corollary discharges (for review, see McCloskey, 1981), or by way of the driving phenomenon (Kuffler, Hunt & Quilliam, 1951), as suggested by Boyd, Gladden, McWilliam & Ward (1977). In the latter case each static γ impulse evokes one Ia afferent spike. The former mechanism seems more likely during locomotion since the accompanying large muscle length changes may disrupt driving (Boyd, Murphy & Mann, 1985). Further, interpretation of such corollary discharges would be simplified if static γ rate is determined by central drives alone, without influences from peripheral inputs. This rationale would account for the proposed absence of effect of cutaneous low threshold mechanoreceptors on static γ -motoneurons during locomotion. In contrast, during a steady posture, where muscle length changes are relatively small, static γ activity might be monitored directly via driving. This mechanism would provide a highly accurate feedback of static γ drive and permit reflex activation of these neurones by peripheral afferents without increasing the complexity of central length interpretation.

Is there any evidence of the present γ reflex patterns in recordings from muscle spindle afferents during normal behaviour? Although most studies have stressed a lack of effect of innocuous cutaneous stimulation (Prochazka, 1983; Loeb, Hoffer & Marks, 1985), this view may reflect a combination of the difficulties involved in deducing γ activity from spindle afferent discharge (Loeb & Duysens, 1979), together with inappropriate testing procedures. Indeed we have shown that reflexes to γ -motoneurons are task dependent. In addition, it is feasible that, during a particular behaviour, the reflex pattern of these neurones is organized in a specific manner linking, for example, discrete areas of skin with a particular type of γ -motoneurone innervating a particular muscle. However, there are some reports in the literature which may be relevant to the present discussion (Prochazka *et al.* 1977; Loeb & Duysens, 1979; Loeb *et al.* 1985). For example, in a study of the activity patterns of Ia afferents in freely moving cats, Prochazka *et al.* (1977) noted that high discharge rates occurred in ankle extensor units when a light thrust was applied to the animal's back during standing or the stance phase of locomotion (see their Fig. 4). It is possible that, during such loading, the resultant ankle dorsiflexion would enhance the activity of low threshold mechanoreceptors in the sural receptive field (via skin stretch) and reflexly excite γ -efferents, thus contributing to the observed elevated Ia afferent firing and increased extensor α activity. We would predict that any such reflex activation would involve both types of γ -efferent during standing, but only dynamic γ -efferents during locomotion.

Various studies have indicated that sensory transmission to the cerebral cortex exhibits task dependence or 'set' (for review, see Prochazka, 1989). Spindle afferent sensitivity is affected by γ discharge which, in turn, is controlled by central drives and peripheral inputs. Accordingly, the present task-dependent reflex responses of static γ -efferents may be viewed as a further example of such sensorimotor 'set'.

No change in the reflex response of dynamic γ -motoneurons, to cutaneous stimulation, was noted during locomotion compared to the resting state. This, of

course, does not preclude the possibility that the efficacy of this pathway can be altered in other tasks. Indeed, on the basis of Ia afferent recordings in normal cats, it has been deduced that dynamic γ activity varies with behavioural state (see e.g. Prochazka, Hulliger, Trend, Llewellyn & Durmuller, 1989). It is quite possible that such changes in neuronal activity are accomplished, at least in part, by altering the efficacy of cutaneous reflex pathways.

Much of our knowledge concerning the control of γ -motoneurons derives from studies involving direct recordings in non-behaving preparations (for review, see Hulliger, 1984; Gladden & Murphy, 1985). The results indicate that these neurons can be influenced by a wide variety of inputs including skin, muscle, joints and the CNS. Indeed, in the most comprehensive study to date of the effect of peripheral afferent stimulation on γ -motoneurons, the great diversity exhibited by individual neurons led to the proposal of a new hypothesis in which it was suggested that, 'pools of γ -motoneurons should be considered as integrative systems intercalated between descending and reflex pathways on the one hand and skeletomotor neurons on the other' (Appelberg, Hulliger, Johansson & Sojka, 1983). However, it is conceivable that, during movement, such diversity is replaced by a simpler pattern of control, appropriately tailored to the demands of the task at hand. The present results are consistent with this view. Thus theories of γ -motoneurone function which are based on studies in non-behaving preparations are likely to be of restricted functional relevance.

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REFERENCES

AKAZAWA, K., ALDRIDGE, J. W., STEEVES, J. D. & STEIN, R. B. (1982). Modulation of stretch reflexes during locomotion in the mesencephalic cat. *Journal of Physiology* **329**, 553-567.

APPELBERG, B., HULLIGER, M., JOHANSSON, H. & SOJKA, P. (1983). Actions on γ -motoneurons elicited by electrical stimulation of group III muscle afferent fibres in the hind limb of the cat. *Journal of Physiology* **335**, 275-292.

BOYD, I. A. (1986). Two types of static γ -axon in cat muscle spindles. *Quarterly Journal of Experimental Physiology* **71**, 307-327.

BOYD, I. A., GLADDEN, M. H., MCWILLIAM, P. N. & WARD, J. (1977). Control of dynamic and static nuclear bag fibres and nuclear chain fibres by gamma and beta axons in isolated cat muscle spindles. *Journal of Physiology* **265**, 133-162.

BOYD, I. A., MURPHY, P. R. & MANN, C. (1985). The effect of chain fibre driving on the length sensitivity of primary sensory endings in the tenuissimus, peroneus tertius and soleus muscles. In *The Muscle Spindle*, ed. BOYD, I. A. & GLADDEN, M. H., pp. 195-199. MacMillan, London.

CAPADAY, C. & STEIN, R. B. (1986). Amplitude modulation of the soleus H-reflex in the human during walking and standing. *Journal of Neuroscience* **6**, 1308-1313.

DARIAN-SMITH, I. (1984). The sense of touch: performance and peripheral neural processes. In *Handbook of Physiology. The Nervous System*, section 1, vol. III, part 2, pp. 739-788. American Physiological Society, Bethesda, MD, USA.

DAVEY, N. J. & ELLAWAY, P. H. (1989). Facilitation of individual γ -motoneurons by the discharge of single slowly adapting type 1 mechanoreceptors in cats. *Journal of Physiology* **411**, 97-114.

DUEÑAS, S. H. & RUDOMIN, P. (1988). Excitability changes of ankle extensor group Ia and Ib fibers during fictive locomotion in the cat. *Experimental Brain Research* **70**, 15-25.

DUYSSENS, J. (1977). Reflex control of locomotion as revealed by stimulation of cutaneous afferents in spontaneously walking preammillary cats. *Journal of Neurophysiology* **40**, 737-751.

- EMONET-DENAND, F., LAPORTE, Y., MATTHEWS, P. B. C. & PETIT, J. (1977). On the subdivision of static and dynamic fusimotor actions on the primary ending of the cat muscle spindle. *Journal of Physiology* **268**, 827–861.
- EVANS, A. L., HARRISON, L. M. & STEPHENS, J. A. (1989). Task-dependent changes in cutaneous reflexes recorded from various muscles controlling finger movement in man. *Journal of Physiology* **418**, 1–13.
- GLADDEN, M. H. & MURPHY, P. R. (1985). Static and dynamic fusimotor neurones and their reflex control. In *The Muscle Spindle*, ed. BOYD, I. A. & GLADDEN, M. H., pp. 243–254. Macmillan, London.
- GRILLNER, S. (1981). Control of locomotion in bipeds, tetrapods, and fish. In *Handbook of Physiology. The Nervous System*, section 1, vol. II, part 2, pp. 1179–1236. American Physiological Society, Bethesda, MD, USA.
- HAMMOND, G. R. & MURPHY, P. R. (1989). The effect of cutaneous afferent stimulation on γ -motoneurons during locomotion in high decerebrate cats. *Journal of Physiology* **415**, 57P.
- HULLIGER, M. (1984). The mammalian muscle spindle and its central control. *Review of Physiology, Biochemistry and Pharmacology* **101**, 1–87.
- HUNT, C. C. & MCINTYRE, A. K. (1960). An analysis of fibre diameter and receptor characteristics of myelinated cutaneous afferent fibres in cat. *Journal of Physiology* **153**, 99–112.
- JOHANSSON, H. & SOJKA, P. (1985). Actions on γ -motoneurons elicited by electrical stimulation of cutaneous afferent fibres in the hind limb of the cat. *Journal of Physiology* **366**, 343–363.
- KUFFLER, S. W., HUNT, C. C. & QUILLIAM, J. P. (1951). Function of medullated small-nerve fibres in mammalian ventral roots: efferent muscle spindle innervation. *Journal of Neurophysiology* **14**, 29–54.
- LENNERSTRAND, G. & THODEN, U. (1968). Position and velocity sensitivity of muscle spindles in the cat. III. Static fusimotor single-fibre activation of primary and secondary endings. *Acta Physiologica Scandinavica* **74**, 30–49.
- LOEB, G. E. (1981). Somatosensory unit input to the spinal cord during normal walking. *Canadian Journal of Physiology and Pharmacology* **59**, 627–635.
- LOEB, G. E. & DUYSSENS, J. (1979). Activity patterns of individual hind limb primary and secondary spindle afferents during normal movements in unrestrained cats. *Journal of Neurophysiology* **42**, 420–440.
- LOEB, G. E., HOFFER, J. A. & MARKS, W. B. (1985). Activity of spindle afferents from cat anterior thigh muscles. III. Effects of external stimuli. *Journal of Neurophysiology* **54**, 578–591.
- MCCLOSKEY, D. I. (1981). Corollary discharges: motor commands and perception. In *Handbook of Physiology. The Nervous System*, section 1, vol. II, part 2, pp. 1415–1448. American Physiological Society, Bethesda, MD, USA.
- MATTHEWS, P. B. C. (1962). The differentiation of two types of fusimotor fibre by their effects on the dynamic response of muscle spindle primary endings. *Quarterly Journal of Experimental Physiology* **47**, 324–333.
- MURPHY, P. R. & HAMMOND, G. R. (1990). γ -Motoneurone discharge patterns during fictive locomotion in the decerebrate cat. *Experimental Physiology* **75**, 107–110.
- MURPHY, P. R., STEIN, R. B. & TAYLOR, J. (1984). Phasic and tonic modulation of impulse rates in γ motoneurons during locomotion in premammillary cats. *Journal of Neurophysiology* **52**, 228–243.
- PROCHAZKA, A. (1983). Reflex regulation of fusimotor neurones: discussion. In *Reflex Organisation of the Spinal Cord and its Descending Control*, ed. PORTER, R. & REDMAN, S., pp. 25. Roche, Canberra City.
- PROCHAZKA, A. (1989). Sensorimotor gain control: a basic strategy of motor systems. *Progress in Neurobiology* **33**, 281–307.
- PROCHAZKA, A., HULLIGER, M., TREND, P., LLEWELLYN, M. & DURMULLER, N. (1989). Muscle afferent contribution to control of paw shakes in normal cats. *Journal of Neurophysiology* **61**, 550–562.
- PROCHAZKA, A., WESTERMAN, R. A. & ZICCONI, S. P. (1977). Ia afferent activity during a variety of voluntary movements in the cat. *Journal of Physiology* **268**, 423–448.
- ROSENBERG, M. E. (1970). Synaptic connections of alpha extensor motoneurons with ipsilateral and contralateral cutaneous nerves. *Journal of Physiology* **207**, 231–255.

- ROSSIGNOL, S. & DREW, T. (1985). Interactions of segmental and supraspinal inputs with the spinal pattern generator of locomotion. In *Feedback and Motor Control*, ed. BARNES, W. J. P. & GLADDEN, M. H., pp. 355–377. Croom Helm Ltd, London.
- SCHMIDT, B. J., MEYERS, D. E. R., TOKURIKI, M. & BURKE, R. E. (1989). Modulation of short latency cutaneous excitation in flexor and extensor motoneurons during fictive locomotion in the cat. *Experimental Brain Research* **77**, 57–68.
- TAYLOR, J., STEIN, R. B. & MURPHY, P. R. (1985). Impulse rates and sensitivity to stretch of soleus muscle spindle afferent fibers during locomotion in preammillary cats. *Journal of Neurophysiology* **53**, 341–360.