

## Fusimotor neurone responses to medial plantar nerve stimulation in the decerebrate cat

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1. The effect of single shock electrical stimulation, up to  $20 \times$  threshold ( $T$ ), of the medial plantar nerve on the discharges of single medial gastrocnemius static and dynamic  $\gamma$ -efferents has been investigated in the decerebrate cat.
2. The neurones were classified as static (15) or dynamic (8) indirectly on the basis of their locomotor and/or resting discharge characteristics.
3. All  $\gamma$ -efferents were affected by stimulation of the medial plantar nerve. Dynamic units showed net inhibition while facilitation dominated the responses of static neurones.
4. The responses of dynamic units consisted of powerful short latency ( $15 \pm 1.2$  ms, mean  $\pm$  s.d.) spinal inhibition followed by weaker facilitation that was difficult to characterize due to concomitant rephasing of neuronal discharge.
5. Static neurones showed two patterns of response. Some units (7 of 15) were facilitated at medium latency ( $39.9 \pm 12.2$  ms) while the remainder showed mixed effects in which short latency ( $18 \pm 3.6$  ms) spinal inhibition was followed by stronger facilitation (latency,  $38.1 \pm 5.3$  ms).
6. Fusimotor facilitation and inhibition were generally present at  $2T$ . The inhibition of dynamic and static  $\gamma$ -efferents, and the facilitation of the latter type, increased with stimulus intensity. Thus low and high threshold afferents contributed to the effects without changing their qualitative nature.
7. We conclude that low threshold cutaneous mechanoreceptors in the plantar surface of the foot are capable of influencing the discharges of medial gastrocnemius static and dynamic  $\gamma$ -efferents. Further, the cutaneous responses of fusimotor neurones appear to vary according to both the source of the afferent input and the type of unit involved.
8. The results are discussed in relation to the control and function of fusimotor neurones and the possible existence of subdivisions within the static system.

The fusimotor ( $\gamma$ ) system, which innervates the muscle spindle, receives a wide variety of inputs from peripheral, spinal and supraspinal structures (for review, see Hulliger, 1984). Although many previous investigations in animal preparations have shown that cutaneous afferents produce potent reflex effects on  $\gamma$ -motoneurones, no consistent pattern of response has emerged and a functional interpretation of such sensorimotor control has been difficult to achieve (Hunt, 1951; Eldred & Hagbarth, 1954; Hunt & Paintal, 1958; Voorhoeve & van Kanten, 1962; Bergmans & Grillner, 1969; Grillner, Hongo & Lund, 1969; Catley & Pascoe, 1978; Bessou, Joffroy & Pages, 1981; Johansson & Sojka, 1985; Davey & Ellaway, 1989; Murphy & Hammond, 1991, 1992). The reported responses have ranged from a 'simple' flexor reflex pattern (i.e. flexor excitation, extensor inhibition; Hunt, 1951) to those that appeared individualized for a given  $\gamma$ -motoneurone

(Johansson & Sojka, 1985). Various factors may have contributed to the diversity of effects in previous studies, including differences in preparation, afferent input and  $\gamma$  sampling. In addition, the presence of two functionally distinct types of fusimotor neurone, static and dynamic (Matthews, 1962), is likely to have contributed, since direct studies of the reflex behaviour of the  $\gamma$  system have mainly involved recordings from unclassified units.

The plantar surface of the foot is a major source of cutaneous sensory feedback during posture and movement and, as such, might be expected to play an important role in the control of the fusimotor system. We have investigated this problem in the present study by examining the responses of medial gastrocnemius (ankle extensor) static and dynamic  $\gamma$ -efferents to electrical stimulation of the medial plantar nerve which supplies the

sole of the foot. Our results indicate that cutaneous afferents from the plantar surface of the foot are capable of exerting powerful reflex effects on the discharges of ankle extensor fusimotor neurones. Such influences vary with the type of  $\gamma$ -efferent and are consistent with the existence of two subgroups within the static system that differ in synaptic input. The functional implications of these findings are discussed in relation to the role of the fusimotor system. A brief account of some of this work has been published (Murphy, Martin & Hammond, 1994).

## METHODS

### Preparation

Seventeen adult cats of either sex were anaesthetized with halothane delivered in a mixture of oxygen and nitrous oxide (1:2). Both carotid arteries were ligated and one was cannulated for recording blood pressure. The left hindlimb was denervated below the hip except for the lateral gastrocnemius and soleus muscles and the animal was placed in a stereotaxic headholder with pins at the iliac crests and clamps on the left knee and foot. 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 was discontinued.

Six animals were paralysed with gallamine triethiodide ( $10 \text{ mg kg}^{-1} \text{ i.v.}$ , repeated as required) and artificially ventilated after decerebration. The end-expiratory  $\text{CO}_2$  of these cats was maintained at 3.5–4%, which was similar to those animals which breathed spontaneously throughout the experiment. Blood pressure, rectal temperature and the temperature of paraffin pools in the popliteal fossa and the sole of the foot were maintained within physiological limits throughout the experiment.

### Recordings and stimulation

Functionally single  $\gamma$ -efferents with background discharges were recorded from dissected filaments of the cut medial gastrocnemius 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, Stein & Taylor, 1984). Units were identified as  $\gamma$ -motoneurones on the basis of their conduction velocities ( $16\text{--}35 \text{ m s}^{-1}$ ; Fig. 1A) and discharge characteristics (Murphy *et al.* 1984). Electromyogram (EMG) recording was via a pair of silver wires, inserted in the lateral gastrocnemius muscle, which were insulated except for 2 mm at the tips. The central end of the cut medial plantar nerve was electrically stimulated with single shocks ( $0.1 \text{ ms}$  width,  $1/1.3\text{--}4 \text{ s}$ ) through bipolar platinum wire electrodes and the ingoing volley was continuously monitored from the sciatic cuff. The threshold ( $T$ ) of the most excitable afferent fibres was determined by stimulating the medial plantar nerve with single shocks and averaging the signal recorded from the sciatic cuff. Threshold was assessed after each stimulus run but showed little variation during the course of an experiment. For each  $\gamma$ -motoneurone a range of stimulus strengths up to  $20T$  was tested. A storage oscilloscope was triggered by the stimulus and used to monitor single sweeps of neuronal discharge. Coincident spikes and exceptionally short interspike intervals were never observed thus precluding the possibility

of recruitment of additional units during stimulation. Data were amplified by conventional means and monitored on oscilloscopes. The rate of  $\gamma$  discharge was monitored on a UV recorder by converting action potentials into standard pulses which were fed to a leaky integrator (time constant, 100 ms).

### Analysis

A Victor Vi computer was used to construct peristimulus time histograms (PSTHs) from standard stimulus and  $\gamma$  pulses. PSTHs generally comprised 1000 1 ms bins. These histograms give the probability of firing of a cell in relation to a stimulus. The computer also generated the cumulative sum (cusum) of the PSTH (Ellaway, 1978). Cusums assist in threshold and latency determinations and in the interpretation of complex responses which may be due to a combination of excitatory and inhibitory effects. The cusum is formed by subtracting a reference level from the contents of each bin of the PSTH in turn and summing the differences. A cusum plot is the sequential display of the accumulated differences. The reference level was the mean bin count during the control period and consisted of 249 1 ms bins ending 1 ms before the stimulus.

## RESULTS

A total of twenty-three  $\gamma$ -efferents were recorded from the medial gastrocnemius nerve in seventeen cats (6 with and 11 without paralysis). Since the patterns of response in the paralysed and the unparalysed animals were similar, the results will be considered together.

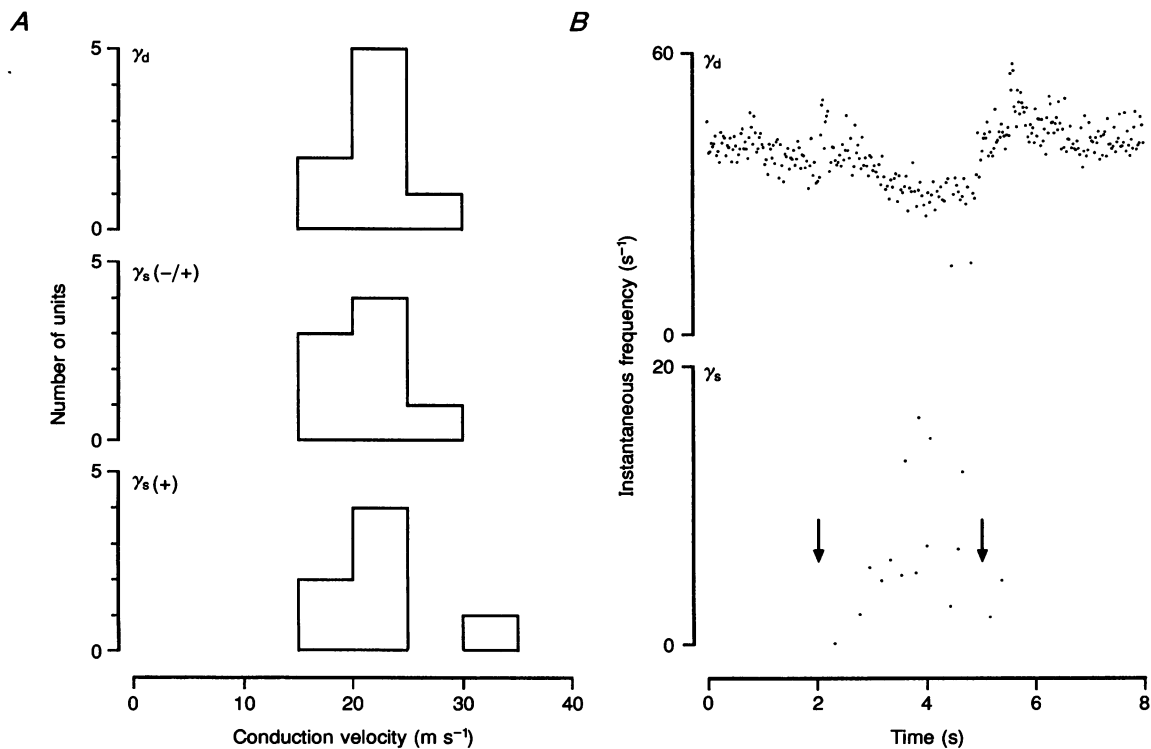
### Classification of $\gamma$ -motoneurones

As a preliminary to describing the present method of classification of  $\gamma$ -efferents it is perhaps pertinent to consider the behaviour of the premammillary decerebrated cat as observed in our experiments. This preparation, unlike the classical intercollicular animal, exhibits two basic states. In the 'resting' state the limbs are stationary, with little or no EMG activity in ankle extensor muscles. The resting state may be transformed into the 'locomotor' state, which is characterized by movement of the limbs, either spontaneously or in response to an external stimulus (e.g. a moving treadmill). In this condition the preparation is capable of showing prolonged periods of regular locomotor activity.

Fusimotor neurones were classified as static (15) or dynamic (8) on the basis of their locomotor and/or resting 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  $\gamma$ -motoneurones fell into two groups on the basis of their discharge characteristics. Tonicity modulated units had low resting rates but greatly increased their discharges 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  $\gamma$ -axons had mean resting rates  $\geq 20 \text{ impulses s}^{-1}$ , while tonically modulated

axons had rates below 20 impulses  $s^{-1}$ . Thus, on the basis of mean resting rate alone, the two groups of  $\gamma$ -motoneurons could be distinguished. In other experiments the resting discharges of classified static and dynamic  $\gamma$ -efferents were recorded directly and found to correspond to those of tonically modulated and phasically modulated units, respectively (Murphy *et al.* 1984). Further, this correspondence was supported by experiments in which the stretch sensitivity and the discharge rates of muscle spindle afferents were investigated (Taylor, Stein & Murphy, 1985). In the present study six  $\gamma$ -efferents were classified as static or dynamic on the basis of their resting and locomotor discharge characteristics as follows. For static units (2), mean resting rates were 8 and 6 impulses  $s^{-1}$ , modulations were 10 and 14 impulses  $s^{-1}$  (half peak-to-peak), mean rates during walking were 60 and 44 impulses  $s^{-1}$ , changes in mean rate from resting to locomotor states were 52 and 38 impulses  $s^{-1}$ . The equivalent values for dynamic units (4) were 36–44, 28–40, 22–37 and  $-4$  to  $-18$  impulses  $s^{-1}$ , respectively. These discharge characteristics are similar to those reported in previous studies for static and dynamic  $\gamma$ -efferents (Murphy *et al.* 1984; Murphy & Hammond, 1991).

The remaining fusimotor neurones (17) were not recorded during locomotion and their classification was based on mean resting discharge rates. Regarding the use of this parameter as the sole criterion for classification it may be appropriate to consider a wider division between the two types of  $\gamma$ -efferent in order to minimize the possibility of misclassification of units with resting rates around 20 impulses  $s^{-1}$ . We therefore propose the following working classification where mean resting rate is the sole criterion: static  $\gamma$ ,  $< 15$  impulses  $s^{-1}$ ; dynamic  $\gamma$ ,  $> 25$  impulses  $s^{-1}$ ; unclassified, 15–25 impulses  $s^{-1}$ . In the present study units which were classified on the basis of resting rates alone had frequencies in the ranges 0–9 or 30–70 impulses  $s^{-1}$  and were thus classified as static (13) or dynamic (4), respectively. It should be noted that mean resting discharge rates, as judged from the output of a leaky integrator (time constant, 100 ms), were stable over the recording periods. Further, no difference in the pattern of responses to medial plantar nerve stimulation was evident for fusimotor neurones that were classified on the basis of resting and locomotor discharge characteristics as opposed to those for which resting rate was the sole criterion. In common with all indirect methods of classifying fusimotor



**Figure 1. Characteristics of fusimotor neurones**

*A*, histograms of the distribution of axonal conduction velocities of medial gastrocnemius dynamic ( $\gamma_d$ ) and static ( $\gamma_s$ ) fusimotor neurones. Static neurones which showed mixed effects ( $-/+$ ) in response to stimulation of the medial plantar nerve are displayed separately from those which were purely facilitated ( $+$ ). Note that the mean conduction velocities of the three groups were not statistically different ( $P > 0.1$ ). *B*, reciprocal effect in the discharges of a dynamic and a static  $\gamma$ -efferent, recorded simultaneously from the medial gastrocnemius nerve, in response to stroking the fur over the thorax. Stimulus onset and removal are indicated by the arrows. The traces are efferent instantaneous frequency.

neurones, the present use of discharge characteristics cannot be regarded as wholly definitive. Indeed, even with a full range of direct testing procedures  $\gamma$ -axons cannot be classified unambiguously as static or dynamic in every case (Emonet-Denand, Laporte, Matthews & Petit, 1977).

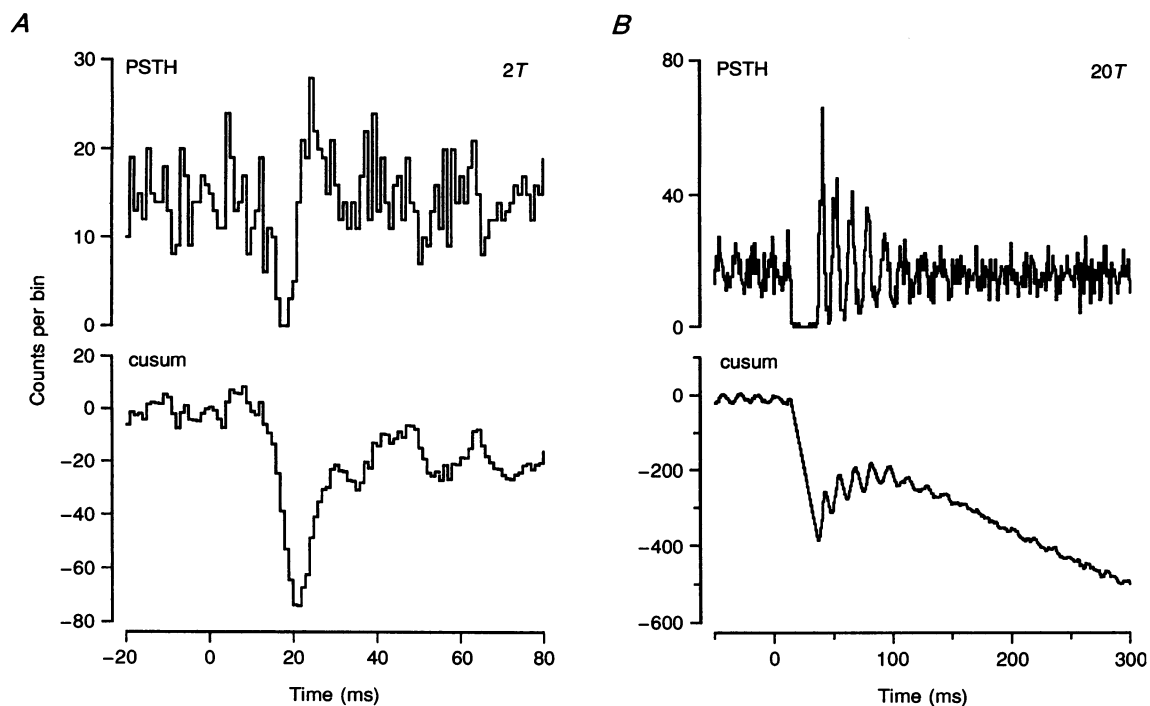
A second line of evidence in support of the present classification of neurones concerns the responses of  $\gamma$ -efferents to natural stimulation (stroking fur over the thorax and abdomen). In the current investigation such stimuli uniformly facilitated static and inhibited dynamic units. The reciprocal effect is illustrated in Fig. 1*B*. This pattern of behaviour is consistent with previous reports of the responses of medial gastrocnemius fusimotor neurones for the same stimulus/preparation. Thus in a study in which resting discharge rates were also used to classify neurones (Murphy & Hammond, 1992), all static efferents (a total of 12) were facilitated while the majority of dynamic neurones (6 of 7) were inhibited; the remaining unit was not obviously affected. Similarly, in an earlier investigation in which fusimotor classification was based on resting and locomotor discharge characteristics (Murphy & Hammond, 1991) we found (P. R. Murphy & G. R. Hammond, unpublished observations) the same pattern of static facilitation (15 of 15 units) and dynamic inhibition (8 of 8 units) in response to stroking the fur over the thorax and abdomen. Collectively, these results suggest that static

and dynamic  $\gamma$ -efferents differ qualitatively in their responses to certain natural stimuli. However, such reciprocal effects may only occur for specific stimulus loci. Indeed, a variation in responses, depending on stimulus location, may explain the previous report by Murphy *et al.* (1984) of inhibition and facilitation of triceps surae dynamic  $\gamma$ -efferents in response to innocuous cutaneous inputs since, in that study, the area of stimulation was not restricted.

## Response characteristics

### Dynamic $\gamma$ -efferents

The responses of dynamic fusimotor neurones to medial plantar nerve stimulation were characterized by powerful short latency inhibition which generally resulted in a silent period (Fig. 2*A* and *B*), even at low stimulus intensities (i.e. 2*T*). A typical response is illustrated in Fig. 2*A*. The dynamic unit had, characteristically, a high discharge rate (57 impulses  $s^{-1}$ ) during the control period prior to stimulus application (2*T*) at time zero. At a latency of 13 ms the cusum begins a negative trend indicating net inhibition which corresponds to a brief silent period in neuronal discharge (see PSTH). The negative trend continues for 8 ms, the duration of the response. The cusum indicates that, during the period of the response, a total of eighty fewer impulses occurred relative to the control level, in



**Figure 2.** Reflex responses of a dynamic  $\gamma$ -efferent

*A* and *B*, responses to electrical stimulation (0.1 ms width) at time zero, of the medial plantar nerve at 2*T* (1/1.3 s) and 20*T* (1/3 s), respectively. In both cases, powerful inhibition occurs at short latency (ca 13 ms), followed by weaker facilitation with concomitant rephasing of neuronal discharge. Note the late (latency, 100 ms), diffuse inhibition which was present at the higher stimulus strength. Upper traces, PSTHs derived from 250 sweeps; bin width, 1 ms. Lower traces, the cusums of the PSTHs.

response to 250 stimuli. Thus the  $\gamma$ -efferent can be said to have fired 0.32 fewer impulses per stimulus. We have used this ratio in the present study as a measure of the potency of inhibitory responses. It should be noted that this index probably underestimates the strength of inhibition that results in a silent period. In a similar manner excitation, when quantified, has been expressed as the excess in firing, relative to the control period, per stimulus trial. Inhibition of dynamic  $\gamma$ -efferents was followed by weaker facilitation (positive trend in cusum, Fig. 2A and B); however, this response was difficult to characterize due to concomitant rephasing of neuronal discharge which is evident as a rhythmic variation in firing. Such resetting reflects the fact that the cell is the site of origin of the rhythm of fusimotor discharge (Ellaway, 1972).

Inhibition and facilitation were present in dynamic fusimotor neurones at  $2T$ , which was invariably sub- $A\beta$  maximum (range of  $A\beta$  maxima,  $2.2$ – $3.5T$ ), indicating that the largest afferents in the medial plantar nerve contribute to the effects. Both the strength and the duration of inhibition were graded with stimulus intensity (Fig. 2A versus 2B; Fig. 3). The potency of inhibition varied from  $-0.2 \pm 0.1$  impulses per stimulus (mean  $\pm$  s.d.,  $n = 8$ ) at  $2T$  to  $-0.8 \pm 0.5$  impulses per stimulus ( $n = 7$ ) at  $20T$ , with corresponding durations of  $6.5 \pm 2$  and  $20.1 \pm 5.3$  ms. For low threshold stimulation (i.e.  $2T$ ) a brief silent period (2–4 ms) was observed with five units ( $n = 8$ ). Long latency (95–180 ms) inhibitory responses (see cusum of Fig. 2B) often occurred at stimulus strengths  $\geq 5T$  and were diffuse in nature. Their durations varied from 220–340 ms at  $5T$  to  $\geq 570$  ms at  $20T$ . Since, in the latter case, responses had generally not ceased at the end point of PSTHs, we were in most cases unable to define their precise durations. Such long latency effects may involve spinal and/or supraspinal structures and definite conclusions concerning their nature are not possible on the basis of the present data. It should be noted, however, that the durations of such responses, as judged from interspike intervals, were less than the time between shocks so that  $\gamma$  discharge rate had returned to control levels before subsequent stimuli were applied. In the present study long latency effects will not be

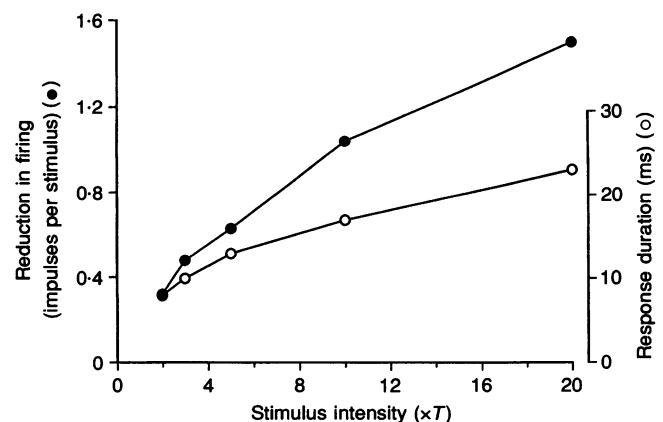
considered in detail due to their diffuse nature and variable occurrence; rather we will focus mainly on short and medium latency effects.

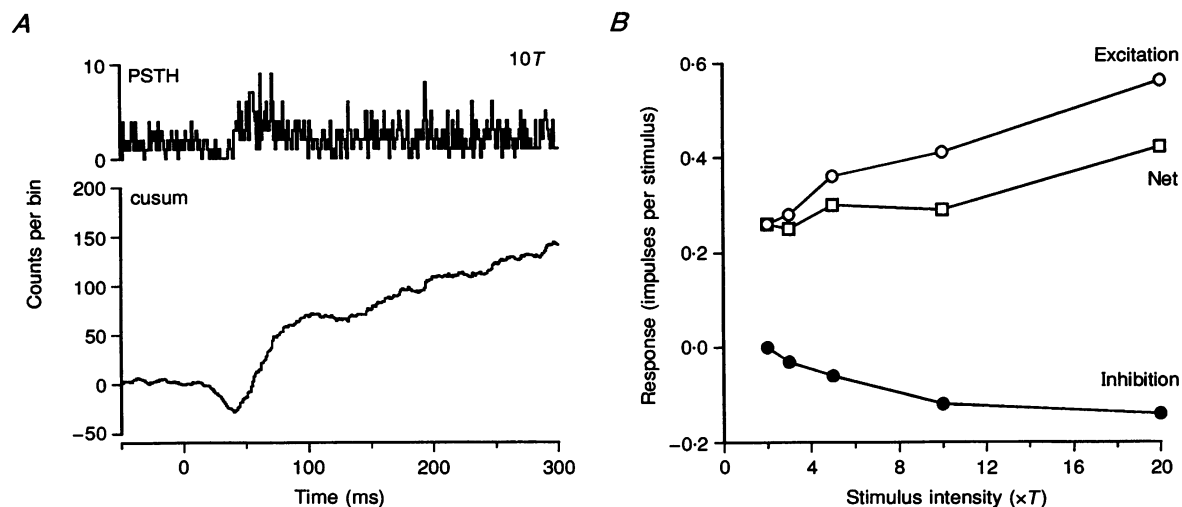
### Static $\gamma$ -efferents

In contrast to dynamic fusimotor neurones, the responses of static efferents were dominated by facilitation. However, these neurones did not exhibit a homogeneous reflex profile and two patterns of response, which could be recorded in the same animal (3 experiments), were observed. About 50% of static neurones (8 of 15) showed mixed responses comprising early inhibition followed by more powerful facilitation. Thus, for the neurone in Fig. 4A, the cusum begins a negative trend, indicating net inhibition, at a latency of 19 ms. This response is terminated by a positive trend (i.e. facilitation, latency, 40 ms) lasting *ca* 65 ms after which the neurone returns to the control level of discharge, as indicated by an approximately horizontal cusum. Most commonly (4 of 8 units) the initial inhibitory response was present at  $2T$ . For the remaining neurones the effect first appeared at  $3T$  (2 units) or  $5T$  (2 units). Although the degree of inhibition increased with stimulus intensity (Fig. 4B), generally (never at  $2T$ ) it did not produce a silent period in neuronal discharge, in contrast to the inhibition of dynamic  $\gamma$ -efferents. The potency of inhibition of static neurones ranged from  $-0.04 \pm 0.01$  impulses per stimulus ( $n = 4$ ) at  $2T$  to  $-0.11 \pm 0.04$  impulses per stimulus ( $n = 8$ ) at  $20T$ , with corresponding durations of  $11.5 \pm 3.7$  and  $18.8 \pm 6.7$  ms, respectively. For stimuli  $>5T$  facilitation generally curtailed inhibition but for lower intensities it occurred as a separate response. Facilitation was always present at  $2T$  and increased with stimulus strength (Fig. 4B). For each stimulus, intensity facilitation was stronger than initial inhibition and the net effect was always facilitation (Fig. 4B). The potency of facilitation varied from  $0.3 \pm 0.1$  impulses per stimulus ( $n = 8$ ) at  $2T$  to  $1 \pm 0.7$  impulses per stimulus ( $n = 7$ ) at  $20T$ , with corresponding durations of  $84.9 \pm 32.3$  and  $137.9 \pm 82.2$  ms, respectively. Periods of long-latency (110–296 ms), diffuse facilitation (e.g. Fig. 4A) often occurred at stimulus intensities  $\geq 5T$ . Their durations varied from 322–407 ms at  $5T$  to  $\geq 475$  ms at  $20T$ .

**Figure 3.** The effect of increasing stimulus intensity on the potency and duration of short latency inhibition of a dynamic  $\gamma$ -motoneurone

Note that both parameters increased with intensity and were greatest at  $20T$ . A given stimulus was tested on one occasion. The neurone is the same as in Fig. 2.



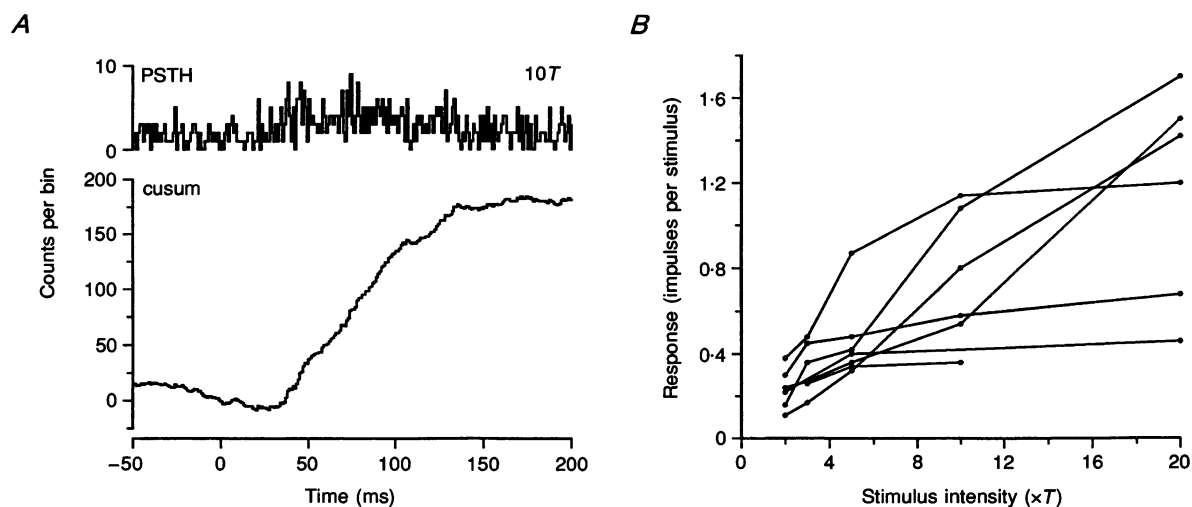


**Figure 4. Example of a static fusimotor neurone that showed mixed reflex effects**

*A*, short latency inhibition (19 ms) is followed by stronger facilitation at medium latency (40 ms) in response to medial plantar stimulation (10T, 0.1 ms width, 1/3 s). Note the presence of diffuse, late facilitation (see cusum) commencing at *ca* 145 ms latency. Traces are presented as in Fig. 2. Sweeps, 250. Bin width, 1 ms. *B*, the potency of short latency inhibition (●) and medium latency facilitation (○) of a static  $\gamma$ -efferent at increasing strengths of stimulation of the medial plantar nerve. Note that the net effect (□) was always facilitation. A given stimulus intensity was tested on one occasion. The neurone is the same as in *A*.

The second pattern of static  $\gamma$  behaviour (7 units) was characterized by medium latency, pure facilitation, and a typical example is shown in Fig. 5A. This static fusimotor neurone had, characteristically, a low discharge rate (4 impulses  $s^{-1}$ ) during the control period prior to stimulus application at time zero. At a latency of *ca* 37 ms the

cusum begins a gradual positive trend (facilitation) lasting about 95 ms. Figure 5B shows the potency of such responses at different stimulus levels for individual static neurones. Invariably, increasing stimulus intensity produced larger responses, indicating a net excitatory effect of recruited afferent fibres. Facilitation was present

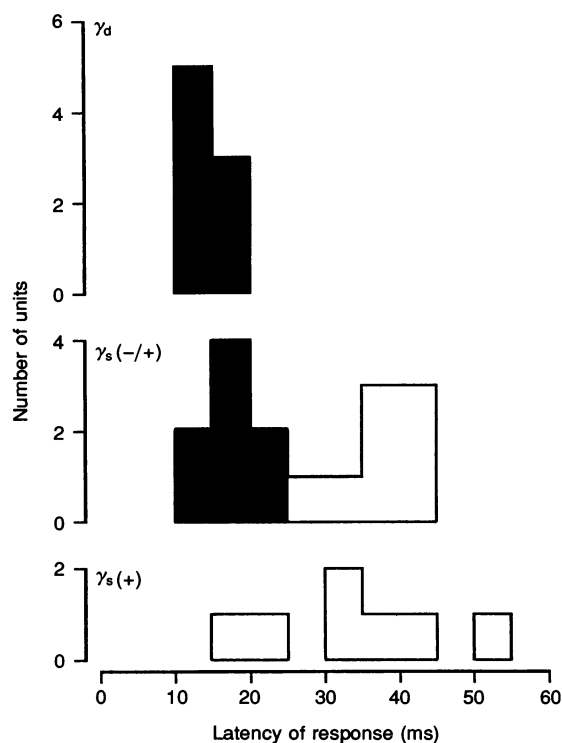


**Figure 5. Static  $\gamma$ -efferents showing pure facilitation**

*A*, example of a static fusimotor neurone that was purely facilitated by stimulation (10T, 0.1 ms width, 1/3 s) of the medial plantar nerve. Facilitation (see cusum) occurs at medium latency (37 ms) and continues for *ca* 95 ms. Traces are presented as in Fig. 2. Sweeps, 500; bin width, 1 ms. *B*, the potency of medium latency responses of individual static neurones (total, 7) that were purely facilitated by medial plantar stimulation. Response size increased with stimulus intensity and there was no sign of mixed or purely inhibitory effects. For each neurone a given stimulus was tested on one occasion.

**Figure 6. Histograms of the distribution of latencies of response of  $\gamma$ -efferents to stimulation of the medial plantar nerve**

Four responses are characterized: the short latency inhibition (■) of dynamic ( $\gamma_d$ ) and those static fusimotor neurones that showed mixed responses ( $\gamma_s(-/+)$ ); the medium latency facilitation (□) of static neurones that were purely facilitated ( $\gamma_s(+)$ ) and those which exhibited mixed effects.



at  $2T$  (potency,  $0.2 \pm 0.1$  impulses per stimulus; duration,  $76.3 \pm 57.7$  ms;  $n = 6$ ) and was strongest at  $20T$  (potency,  $1.2 \pm 0.5$  impulses per stimulus; duration,  $253.7 \pm 132.8$  ms;  $n = 6$ ). Fusimotor neurones, which were facilitated by medial plantar nerve stimulation, also exhibited late facilitation which was similar to that of static neurones showing mixed effects. Thus, latencies were in the range 62–220 ms and durations ranged from 266–330 ms at  $5T$  to  $\geq 617$  ms at  $20T$ . The conduction velocities (Fig. 1A) of static  $\gamma$ -motoneurones that showed mixed responses (range, 16–28  $\text{m s}^{-1}$ ) and those which were facilitated (range, 17–35  $\text{m s}^{-1}$ ) by medial plantar stimulation overlapped widely.

### Central delays

A range of stimulus strengths (up to  $20T$ ) were tested for each neurone. At each intensity the latency of effect(s) was measured as the time between stimulus application and the first visible sign of a change in probability of firing as judged from the PSTH or its cusum (e.g. Fig. 2A). For an individual unit, the shortest consistent latency was taken to represent the response. It should be noted that the measurement of the latency of facilitation in those static neurones which displayed mixed effects was not affected by preceding inhibition since facilitation generally occurred as a separate response. In all, four different responses were characterized with respect to latency (Fig. 6): the short latency inhibition of dynamic ( $15 \pm 1.2$  ms;  $n = 8$ ) and a subgroup of static ( $18 \pm 3.6$  ms;  $n = 8$ )  $\gamma$ -efferents; the medium latency facilitation of those static neurones which

showed mixed responses ( $38.1 \pm 5.3$  ms;  $n = 8$ ) and those that were purely facilitated ( $39.9 \pm 12.1$  ms;  $n = 7$ ).

The latencies of inhibition of dynamic and a subgroup of static  $\gamma$ -efferents were similar. The corresponding central delays were estimated by subtracting afferent and efferent conduction times from the overall latency. The resultant values therefore represent intraspinal conduction time and synaptic delay. Afferent and efferent conduction times were calculated on the basis of conduction velocities estimated from peripheral nerve recordings. Afferent conduction time was assumed to correspond to the most rapidly conducting fibres in the medial plantar nerve. This seemed justified since inhibition was generally present at low ( $2T$ ) stimulus levels. However, for four static fusimotor neurones inhibition appeared at higher intensities and central delays have not been calculated for these units. The central delays of inhibition of dynamic ( $3.2 \pm 0.6$  ms;  $n = 8$ ) and static ( $3 \pm 0.6$  ms;  $n = 4$ )  $\gamma$ -efferents were similar and their respective ranges (2.1–4 and 2.2–3.5 ms) overlapped widely. These values are within those reported for spinal cutaneous reflexes to fusimotor neurones in previous studies (Hunt & Paintal, 1958; Grillner *et al.* 1969; Johansson & Sojka, 1985; Davey & Ellaway, 1989). The central delays, based on conduction in the fastest afferent fibres, of the medium latency responses of purely facilitated ( $22 \pm 11.8$  ms;  $n = 7$ ) static  $\gamma$ -efferents and those showing mixed effects ( $24.4 \pm 7.1$  ms;  $n = 8$ ) were also similar; however, their wide ranges (6–42.5 and 12.2–31.1 ms, respectively) are consistent with diffuse polysynaptic pathways, possibly involving supraspinal structures.

## DISCUSSION

### General pattern of responses

The present study indicates that ankle extensor static and dynamic  $\gamma$ -motoneurons are influenced by afferents that supply the skin of the plantar surface of the foot. The pattern of responses was complex and consisted of facilitation and mixed effects. However, reflex profile was related to unit type. Thus dynamic  $\gamma$ -efferents showed net inhibition while facilitation predominated with static neurons. In addition, the responses of static units indicated the presence of two subdivisions: one showed only facilitation while the other exhibited mixed responses. The possibility that these subgroups may be functionally distinct will be considered later.

Previous reports (Hunt, 1951; Eldred & Hagbarth, 1954; Hunt & Paintal, 1958; Grillner *et al.* 1969; Johansson & Sojka, 1985) of the effects of cutaneous afferents, supplying the sole of the foot, on fusimotor neurons are difficult to interpret for two main reasons. Either unclassified  $\gamma$ -efferents were recorded or the tibial nerve, which also contains a significant component of muscle afferent (and efferent) axons, was stimulated. Since muscle afferents influence  $\gamma$  discharge (for review, see Hulliger, 1984) we cannot be confident that fusimotor responses to tibial nerve stimulation are dominated by cutaneous inputs. In the earlier studies, involving spinal, decerebrate and anaesthetized preparations, inhibitory, excitatory and mixed responses were observed; however, no consistent pattern of reflex behaviour is evident, possibly due to the limitations mentioned above.

### Nature of effects

The responses of dynamic  $\gamma$ -motoneurons were dominated by powerful inhibition at short latency (mean, 15 ms), followed by weaker facilitation that was difficult to characterize due to concomitant rephasing of neuronal discharge. Static  $\gamma$ -efferents with mixed responses (*ca* 50%) also showed short latency inhibition (mean, 18 ms), which was followed by stronger facilitation (mean latency, 38.1 ms). For the other static units, only medium latency facilitation was observed (mean, 39.9 ms). The short central delays of the inhibitory responses of dynamic (mean, 3.2 ms) and static (mean, 3 ms) efferents indicate spinal oligosynaptic connections and their similarity raises the possibility of common interneuronal pathways. One possible mechanism for the generation of such short latency inhibition of fusimotor discharge is recurrent inhibition (Ellaway, 1971) subsequent to activation of homonymous/synergistic, but not antagonistic (Noth, 1971),  $\alpha$ -motoneurons. This was considered unlikely since there was generally little or no  $\alpha$  activity in the parent muscle nerve (medial gastrocnemius) or in a synergistic muscle (lateral gastrocnemius). Furthermore, stimulation of the medial plantar nerve at intensities up to  $20T$  did not activate  $\alpha$ -motoneurons, as judged from recordings in

which single units could be distinguished and from signal averaging. Facilitation, alone or following a period of inhibition, occurred at medium latency over a wide range, suggesting the involvement of diffuse polysynaptic pathways that may include supraspinal structures.

Both inhibition and facilitation were generally present at  $2T$  and increased in size as the stimulus intensity was raised to  $20T$ . Thus low and high threshold myelinated afferents in the medial plantar nerve contributed to the effects, but without changing their qualitative nature. In each experiment a stimulus of  $2T$  was submaximal for the  $A\beta$  nerve fibre group (range of  $A\beta$  maximums,  $2.2$ – $3.5T$ ) which contains predominantly non-nociceptive afferents (Janig, Schmidt & Zimmermann, 1968; Janig, 1971). It is therefore likely that the pathways underlying the present fusimotor effects are utilized during 'normal' posture and movement. Since stimuli  $> 2T$  may recruit both non-nociceptive and nociceptive fibres we cannot comment on the functional implications of the effects except to note their greater potency relative to  $2T$  (e.g. Fig. 5B).

### Two types of static fusimotor neurone?

Boyd (1986) postulated the existence of two types of static  $\gamma$ -motoneuron on the basis of their pattern of innervation of intrafusal muscle. One type innervated the bag<sub>2</sub> fibre, while the other supplied chain fibres, in all affected spindles. Although this classification remains controversial (Gladden & Sutherland, 1989; Banks, 1991; Celichowski, Emonet-Denand, Laporte & Petit, 1993; Durbaba, Taylor, Rodgers & Fowle, 1993), one source of support for the notion of subpopulations of static  $\gamma$ -efferents comes from studies of the effect of stimulation of the CNS on the activity of intrafusal fibres, either observed directly or deduced from spindle afferent recordings (Gladden & McWilliam, 1977; Wand & Schwarz, 1985; Dickson & Gladden, 1990; Rodgers, Durbaba, Taylor & Fowle, 1994). Perhaps most strikingly, reciprocal effects, consisting of recruitment of the bag<sub>2</sub> fibre and simultaneous inhibition of chain fibre activity, have been observed in some spindles in response to electrical stimulation in the area of the red nucleus, leading to the suggestion that the CNS may control subpopulations of static  $\gamma$ -efferents independently (Dickson & Gladden, 1990). These observations are also consistent with the existence of subgroups within the static system that differ in synaptic input. The present results, involving peripheral afferent stimulation, support this notion. Thus in response to stimulation of the medial plantar nerve, some static  $\gamma$ -efferents were facilitated at medium latency while the remainder showed mixed effects consisting of early inhibition followed by facilitation. Considering the above results together it appears that an increasing body of evidence indicates that the static fusimotor system is not a homogeneous entity with regard to both central and peripheral control. However, whether these observations correspond to the existence of two types



of static  $\gamma$ -efferent, as envisaged by Boyd (1986), or the presence of other functional units remains to be established.

### Muscle spindle afferent recordings

Any functional interpretation of the present fusimotor reflex effects in the decerebrate cat presupposes that the underlying neuronal pathways are utilized during normal posture and/or movement. Is there any evidence to support this supposition? Most studies in this field have involved recordings from muscle spindle afferents, from which fusimotor firing is indirectly inferred. In general, fusimotor responses to innocuous cutaneous stimulation have been difficult to demonstrate (Prochazka, 1983; Loeb, Hoffer & Marks, 1985; see also Taylor & Gottlieb, 1985); however, this paucity may be a reflection of the indirect methods employed. Thus a given spindle afferent is influenced by length changes, which are difficult to gauge (Hoffer, Caputi, Pose & Griffiths, 1989), and by up to ten  $\gamma$ -efferents with actions that summate in a non-linear fashion (for review, see Hulliger, 1984). In addition, evidence from recordings of  $\gamma$ -efferents in the cat (Hammond & Murphy, 1989; Murphy & Hammond, 1991) and from spindle afferents in man (Gandevia, Aniss, Diener, Hore & Burke, 1989; Aniss, Diener, Hore, Burke & Gandevia, 1990) indicate that the reflex responses of fusimotor neurones are task dependent and may be absent in certain conditions. Nevertheless, there are some reports in the literature that are consistent with the notion that afferents from the sole of the foot do produce reflex responses in fusimotor neurones during normal behaviour (Prochazka, Westerman & Ziccone, 1977; Loeb & Duysens, 1979; Aniss *et al.* 1990). Thus in a recent study in man pretibial spindle afferents were activated by innocuous electrical stimulation of the posterior tibial nerve (Aniss *et al.* 1990). In another investigation, in the intact cat, Loeb & Duysens (1979) describe the response of a medial gastrocnemius secondary afferent upon manually lowering the animal onto a stationary surface. The unit responded with a large increment in discharge rate (up to 100 impulses  $s^{-1}$ ) approximately 60 ms after foot contact when passive stretch of the parent muscle had just started (their Fig. 3B). It is quite possible that this effect was produced by excitation of static  $\gamma$ -efferents subsequent to activation of receptors in the plantar skin.

### Functional significance

In the present study static and dynamic fusimotor neurones differed in their net responses to stimulation of the medial plantar nerve. Thus dynamic neurones showed net inhibition while facilitation predominated with static units. These opposite responses reflect the domination of short- (spinal) and medium-latency (polysynaptic, possibly supraspinal) effects, respectively, and raise the possibility that the reflex control of fusimotor neurones involves different levels depending on the type of unit involved. The functional significance of any such difference in the

level of control of static and dynamic  $\gamma$ -efferents must await further information concerning its incidence.

Although the *net* effect of medial plantar nerve stimulation on medial gastrocnemius static and dynamic  $\gamma$ -efferents differed (i.e. facilitation and inhibition, respectively), their *temporal* profiles of response were similar. Thus both types showed short latency spinal inhibition (followed by facilitation). This pattern of spinal effects is the *opposite* to that which has been found for fusimotor neurones in the same nerve/preparation in response to electrical stimulation of the sural nerve (Murphy & Hammond, 1992), which innervates the hairy skin of the lateral posterior leg from the knee to the ankle and the lateral and proximal plantar surface of the foot. In that study both types of  $\gamma$ -efferent exhibited short-latency, low-threshold (generally  $\leq 2T$ ) spinal facilitation, with no sign of mixed or purely inhibitory effects. Thus the responses of static and dynamic fusimotor neurones to cutaneous inputs vary according to both the stimulated nerve and the type of unit involved. This variation probably reflects a variety of central (e.g. different interneuronal pathways) and peripheral (e.g. different types of receptor in hairy *versus* glabrous skin) factors. In the absence of such information it is not possible to provide a complete rationale for the different fusimotor patterns of cutaneous response. Nevertheless, we suggest that the opposite cutaneous spinal effects on ankle extensor  $\gamma$ -motoneurones may be functionally appropriate as follows.

Low threshold mechanoreceptors with afferents in the sural and the medial plantar nerves produce spinal facilitation and inhibition, respectively, of medial gastrocnemius fusimotor neurones. Thus if the afferent feedback from both receptive fields increases (or decreases), opposing spinal reflex effects will occur, and a degree of cancellation. Conversely, if the changes in afferent feedback are of opposite sign then summation will result. During the maintenance of a standing posture any yielding at the ankle joint (e.g. due to increased load) will enhance the activity of low threshold mechanoreceptors in the sural receptive field (due to skin stretch) leading to spinal facilitation of extensor  $\gamma$ -efferents. However, if yielding is resisted by enhanced force at the sole of the foot then sural facilitation of fusimotor neurones will be opposed by spinal inhibition due to increased activation of plantar afferents. Thus where yielding at the ankle joint is accompanied by a corrective increase in torque it may be the case that no net change in the spinal drive to fusimotor neurones occurs. However, if plantar afferent activity remains unaltered then net spinal facilitation of static and dynamic  $\gamma$ -efferents will occur, resulting in elevated Ia afferent feedback which will oppose the shift in posture via monosynaptic excitation of ankle extensor  $\alpha$ -motoneurones. Appropriately, such reflex compensation will be maximal when yielding is accompanied by a decrease in plantar force (i.e. 'give way') since fusimotor facilitation (i.e. sural input) will be augmented by disinhibition consequent upon

a reduction in plantar afferent activity. In a similar manner a shift in posture in the opposite direction (e.g. due to reduced load) would produce appropriate changes in  $\gamma$  activity. We therefore suggest that net changes in the spinal drive to ankle extensor fusimotor neurones serve to adapt Ia afferent feedback so as to maintain a steady posture. Further, in this context, the opposite spinal effects from the sural and medial plantar receptive fields ensure that the level of spinal drive to fusimotor neurones is appropriate for the degree of postural deviation.

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