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FUSIMOTOR REFLEXES IN TRICEPS SURAE ELICITED BY NATURAL STIMULATION OF MUSCLE AFFERENTS FROM THE CAT IPSILATERAL HIND LIMB

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SUMMARY

1. Experiments were performed in forty-one cats anaesthetized with chloralose.

2. The aim of the study was to investigate whether activity in stretch-sensitive muscle receptors may cause reflex effects in fusimotor neurones.

3. Activity in fusimotor neurones was studied indirectly by recording from primary and secondary muscle spindle afferents of the triceps surae muscle. The mean rate of firing of the afferents as well as either dynamic index (during ramp extension) or modulation (during sinusoidal extension) was determined. This was done under control conditions, with the posterior biceps–semitendinosus muscles relaxed, and under test conditions, with the same muscles extended.

4. All together, seventy-one primary afferents were studied quantitatively. Pure or predominantly dynamic effects were observed in twenty-two, pure or predominantly static effects in nine and no statistically significant effects in forty of the units. Amongst seven secondary afferents studied, two showed weak fusimotor activation, the other five were not influenced.

5. Electrical stimulation of the posterior biceps–semitendinosus or medial gastrocnemius nerves at group II strength was observed to cause dynamic fusimotor reflexes on a number of occasions.

6. The reflex effects observed were, on many occasions, recorded in spinalized preparations.

7. The reflex effects were not accompanied by any detectable e.m.g. activity in triceps, as judged from surface e.m.g. recordings. The reflex effects observed are therefore tentatively ascribed to activation of γ-motoneurones, yet a contribution from β-motoneurones cannot wholly be excluded.

8. On the basis of available evidence concerning reflex connexions to γ-motoneurones from various muscle afferents, it is suggested that the effects observed were caused by activation of muscle spindle secondary endings.

† Where all the experimental work was done.

INTRODUCTION

Ever since the classical investigations by Lloyd (1946) and Laporte & Lloyd (1952) reflex pathways from various sensory afferents to α-motoneurones have been studied in considerable detail. On the other hand, information concerning the reflex activation of static and dynamic fusimotor neurones is still comparatively scarce. There seem to be two main reasons for this. First, γ-cells are small and difficult to record from. Secondly, for micro-electrode recordings from the spinal cord a convenient method of classifying γ-motoneurones has, until recently, been missing.

A comprehensive study, using both electrical and natural stimulation, was carried out by Grillner and co-workers (cf. Grillner, 1969). These studies implied that indirectly classified γ-motoneurones are influenced by muscle as well as by skin and joint afferents. The reflex pattern seemed similar to what was already known for α-motoneurones apart from the effects of Ia spindle afferents. More recently most of the work concerned with reflexes to γ-motoneurones has been devoted to studies of autogenetic effects of spindle primaries on γ-cells using both electrical and natural stimulation in widely denervated hind limb preparations (Ellaway, 1971; Ellaway & Trott, 1978; Fromm & Noth, 1976; Trott, 1976).

It seems to be well established that inhibition as well as weak excitation of γ-motoneurones from muscle spindle primary afferents may occur. The inhibitory effects have also been ascribed to recurrent inhibition from Renshaw cells acting not only on α- but also on γ-motoneurones. The excitatory effects were likely to be mediated by polysynaptic pathways (Ellaway & Trott, 1978) and seem to furnish a positive feed-back loop, the functional significance of which has yet to be established.

In a recent series of experiments antidromically identified γ-cells were classified as static or dynamic on the basis of selective influences exerted upon the dynamic cells by electrical stimulation of a particular mesencephalic region (for further details cf. Appelberg, Jeneskog & Johansson, 1975; Appelberg, 1981; Johansson, 1981). Using electrical stimulation of peripheral nerves the distribution of synaptic inputs to these cells was then determined for a range of receptor types. Unexpectedly, it was found that group II (but only rarely group Ia) fibres of muscle nerves exerted a potent excitatory influence on dynamic cells innervating extensor muscles (Appelberg, Johansson & Kalistratov, 1977; Appelberg, Hulliger, Johansson & Sojka, 1982*a*, *b*). Such group II action on triceps γ-cells could be elicited from homonymous and heteronymous (both synergistic and antagonistic) muscle nerves.

Clearly, electrical stimulation of peripheral nerves at group II strength may excite fibres from functionally heterogeneous receptor types. The group II effects observed could therefore not with necessity be attributed to muscle spindle secondary afferents. Yet most fibres within the group II range of the particular muscle nerves used were in fact likely to be secondary spindle afferents. This has been shown for the gastrocnemius–soleus and the semitendinosus nerves, but not for the posterior biceps nerve (cf. Boyd & Davey, 1968). Nevertheless, it seemed desirable to examine whether natural stimulation of group II afferents by muscle stretching could increase dynamic sensitivity of Ia spindle afferents, indicating that dynamic fusimotor neurones were excited. For such indirect recording of fusimotor reflexes, triceps was

chosen to monitor spindle afferent responses and the posterior biceps–semitendinosus muscles (p.b.s.) were selected for natural stimulation. This particular choice was motivated by the earlier finding of a powerful group II excitatory input from p.b.s. to triceps dynamic γ-cells (Appelberg *et al.* 1977; Appelberg *et al.* 1982*b*). Clearly, these cells also receive strong *autogenetic* group II excitation (Appelberg *et al.* 1977; Appelberg *et al.* 1982*b*; Noth & Thilman, 1980). Yet, no attempt was made to investigate the effectiveness of the latter pathway during natural stimulation, since in practice it would have been considerably more difficult to assess the contribution of autogenetic fusimotor reflexes to the responses of spindle primary afferents to stretching of their own muscle.

The main result of the present work was the demonstration of a clear enhancement of dynamic sensitivity of triceps primary spindle afferents by p.b.s. muscle stretch. In all likelihood this effect was caused by a segmental reflex involving secondary muscle spindle afferents from p.b.s. acting on dynamic γ-motoneurones to triceps.

Preliminary accounts of this work have been previously published (Appelberg, Hulliger, Johansson & Soja, 1978*a*, *b*, 1981).

METHODS

Animals and preparation. The experiments were performed in forty-one cats weighing between 2·5 and 4·5 kg. The animals were initially anaesthetized with chloralose (55–60 mg/kg). In addition, during denervation and spinalization, small amounts of pentobarbitone (Mebumal, ACO;4 mg/kg) were injected intravenously. If necessary, the anaesthesia was maintained by the administration of nitrous oxide or additional doses of chloralose.

Arterial blood pressure was continuously monitored using a cannula tied into the brachial artery of the right forelimb, into one of the carotids or, during the initial experiments, into the contralateral femoral artery. Blood pressure was maintained above 80 mmHg, if necessary by the infusion of sodium chloride acetate, dextran (Macrodex, Pharmacia) or metaradrin (Aramin, MSD; 0·01 mg/ml). End-expiratory CO_2 was continuously monitored and maintained at around 4 % by suitably adjusted artificial respiration.

In the left hind limb a conventional nerve muscle preparation was performed either for soleus alone, or for the lateral gastrocnemius, plantaris and soleus together (triceps). The medial gastrocnemius muscle was routinely removed and its nerve made available for electrical stimulation. Further, the posterior biceps and semitendinosus muscles (p.b.s.) were also prepared with intact nerve supply. For triceps and p.b.s. the slack resting and maximum physiological lengths were determined *in situ* and marked by appropriate reference labels in the surrounding tissue. The tendons were then disconnected from their points of insertion and, later, tied to two separate stretching devices (see below, *Stimulation*). Apart from the nerves to the muscles mentioned the limb was extensively denervated. In the hip region the branches of the femoral, obturator and sciatic nerves were cut at their exit points from the pelvis.

The animals of the present report were also studied for another series of experiments which involved surgical preparation and mechanical stimulation of the contralateral hind limb (Appelberg, Hulliger, Johansson & Sojka, 1979 and in preparation). Yet, normally the contralateral limb was left intact during the initial preparation. Later, during the course of the experiment, the skin was occasionally removed from the thigh downwards, and either the knee or the ankle joint were locally anaesthetized by intra-articular injection of lidocaine (Xylocard, Hässle).

The animal was mounted in a rigid metal frame and the left hind limb was carefully immobilized with horizontal pins which were firmly inserted into the bones of the hip, knee and ankle regions. A laminectomy, exposing the spinal cord between L3 and S1 was routinely performed, and some of the animals were spinalized at L3, either during the initial operation or later during the course of the experiment. Functionally single afferent fibres from triceps or p.b.s. were isolated from small ipsilateral dorsal root filaments which were cut. Otherwise, dorsal and ventral roots were left intact on both sides. Exposed tissues were covered with liquid paraffin which was kept at around 37 °C.

In two cats, when fusimotor reflexes from the p.b.s. muscles could not be elicited in a spinal preparation, the animals were injected with Nialamid (50 mg/kg) and, half an hour later, with DOPA (maximum dosage 100 mg/kg, cf. Bergmans & Grillner, 1969).

Stimulation. The triceps or soleus tendons were connected to an electromagnetic puller with length and velocity feed-back (stiffness 0·06 mm/N). These muscles were continuously stretched (to 2 mm below the maximum physiological length) and released to 10 mm below maximum length, using ramp and hold command signals (1–2/min) with a velocity of 10 mm/sec and a plateau duration of 15 sec. Superimposed on this were repetitive sinusoidal stretches at 1 Hz with a half peak-to-peak amplitude of usually 1 mm (standard measurements). A few units were also studied with 2 mm sinusoidal stretching (cf. Fig. 3) in addition to the standard measurements.

For the investigation of reflex effects on triceps spindles the p.b.s. muscles were subjected to static stretch and release. The amplitude of stretch was normally 40 mm, which corresponded to an alternation between approximate resting length and maximum physiological length (cf. Goslow, Reinking & Stuart, 1973). On a few occasions intermediate values of muscle length were also used in addition to the physiological extremes. When muscle spindle afferents from p.b.s. were investigated (determination of their static position sensitivity, cf. Fig. 1) the length of the muscle was systematically varied in an ascending series using steps of 5 mm. For all these positions the length was adjusted with a mechanical slide which could be locked in any position to maintain constant muscle length. The application of such maintained stretches to p.b.s. was always completed 10–15 sec before the onset of data collection during sinusoidal or ramp stretching of triceps.

Recording and analysis. The activity of muscle spindle afferent units was recorded from small dorsal root filaments. The units were classified as primary or secondary afferents on the basis of their conduction velocity (division line at 72 m/sec). Gross e.m.g. activity was recorded with surface electrodes placed on the belly of the receptor bearing muscle. Any alteration of fusimotor activity was assessed indirectly by monitoring the responses of muscle spindle afferents to large ramp and hold and/or sinusoidal streches. *Control* observations were made with p.b.s. at resting length and in the absence of any electrical stimulation of peripheral nerves. *Test* observations were made when the p.b.s. muscles were subjected to maintained stretch or during graded electrical stimulation of peripheral nerves. For all units, control and test responses were first assessed qualitatively using the criteria listed below. With time and stability of any stretch-induced effects permitting, control and test responses were then subjected to quantitative analysis. To this end the responses to a number of successive stimuli (usually five or ten) were averaged on line by constructing cycle histograms with the aid of an averaging computer (Didac 800, Intertechnique). The numerical analysis was also performed on line with a desk calculator (Hewlett Packard 9810A) which was linked to the averaging device with a specially designed interface. Ramp responses were quantified by measuring the dynamic index and the mean rate of discharge of the averaged responses (Matthews, 1972). The averaged responses to sinusoidal stretching were analysed by fitting a simple sinusoid to the histogram using a least square algorithm which ignored periods of afferent silence (Hulliger, Matthews & Noth, 1977*a*). The measures of mean rate of discharge (in short: fitted mean), depth of modulation and phase of the response (relative to the phase of the stimulus) were then used for the construction of scatter diagrams (see Fig. 4). Such analysis of *averaged* responses seemed justified since normally the responses during both tests and controls were sufficiently stationary during the sampling period (5 or 10 sec).

Based on earlier investigations with controlled electrical stimulation of functionally single γ-fibres (Crowe & Matthews, 1964*a*, *b*; Appelberg, Bessou & Laporte, 1966; Matthews, 1972; Hulliger *et al.* 1977*a*, *b*; Emonet-Dénand, Laporte, Matthews & Petit, 1977; Hulliger, 1979) the occurrence of predominantly dynamic fusimotor reflex activation was inferred when at least the first three of the following criteria were met: for individual units (1) increase of the dynamic sensitivity of primary afferents, with the dynamic index of ramp responses and/or the depth of modulation of responses to sinusoidal stretching clearly raised above the level of the control responses; (2) moderate increase of the maintained rate of discharge during the static phase of the ramp and hold stretches and/or moderate increase of the fitted mean of sinusoidal responses; (3) occurrence of afferent silence during the release phase of both ramp and sinusoidal stretching, and for the whole sample; (4) manifestation of spindle excitation with primary but not with secondary afferents.

An increase of the predominantly static fusimotor activity was inferred when there was (1) an appreciable decrease in dynamic sensitivity, (2) a sizeable increase in the mean rate of discharge,

(3) absence of afferent silence during release, for primary afferents, and, for the whole sample, (4) excitation of secondary afferent units.

An increase in mixed (static and dynamic) fusimotor activity was inferred when primary afferents showed (1) a relatively small change in dynamic sensitivity (increase or decrease), combined with (2) a large increase in the mean rate of discharge, and with (3) an absence of afferent silence during release, and when (4) secondary afferents were also excited.

For the assessment of static position sensitivity of muscle spindle afferents from p.b.s. the mean rate of discharge was determined at each muscle length by counting the number of afferent impulses over a period of 10 sec beginning 5 sec after the muscle had been brought to a new steady position. The measurements were performed using the computational facilities already described above.

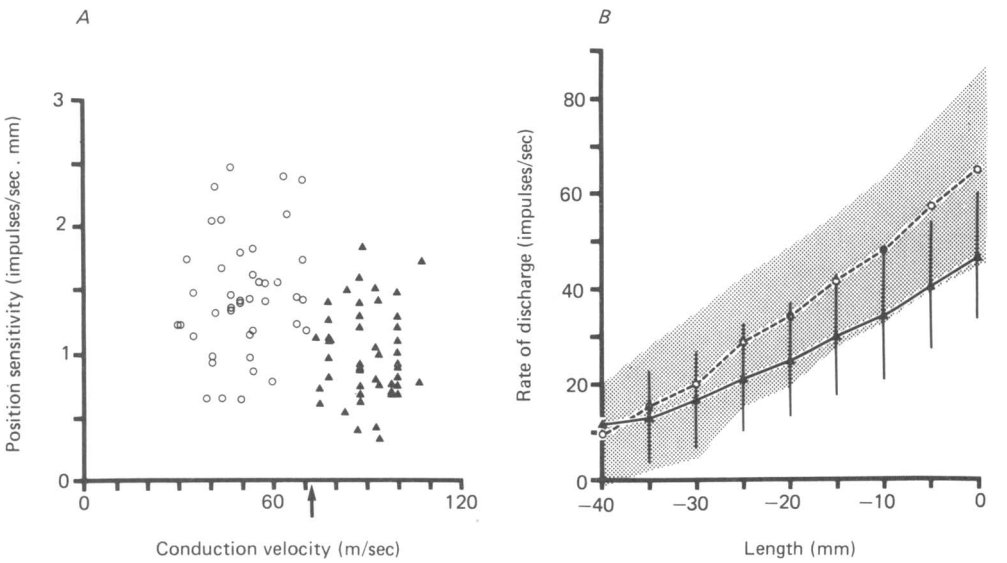

Fig. 1. Position response of muscle spindle afferents from p.b.s. In *A*, the values of slope of the regression line fitted to the length–discharge relationship of each afferent unit (position sensitivity) is plotted against conduction velocity for forty-two secondary (○) and forty-eight primary (▲) muscle spindle afferents. In *B*, the mean rate of discharge, averaged separately for primary (▲) and secondary (○) afferents, is plotted against the length of the p.b.s. muscle between the physiological minimum (−40 mm) and maximum (0 mm). The vertical bars (primaries) and the width of the shaded area (secondaries) give, for each length, the value of S.D. of the rate of discharge.

RESULTS

The purpose of the present experiments was to investigate whether natural stimulation of muscle afferent units could excite dynamic fusimotor neurones. For technical reasons (see Introduction) the occurrence of any activation of dynamic fusimotor neurones was *assessed indirectly* by monitoring any alteration of dynamic sensitivity of primary afferents from triceps resulting from stretch of the p.b.s. muscles. The results obtained with graded electrical stimulation of peripheral nerves (Appelberg *et al.* 1977, 1982*a*, *b*, *c*) suggested that muscle spindle afferents (in particular secondaries) *from p.b.s.* should effectively excite dynamic fusimotor neurones *to triceps*. Since the literature appeared to lack any accounts of the basic

properties of muscle spindle afferents from p.b.s. it was desirable for the present purpose to determine the dependence of their mean rate of discharge is on maintained muscle length.

Static position sensitivity of spindle afferents from p.b.s.

For forty-eight primary and forty-two secondary spindle afferents which were investigated in thirteen animals it was found that the mean rate of discharge increased with increasing muscle length. Since in most cases the relationship between muscle length and rate of discharge was approximately linear, straight lines were fitted to the data using conventional methods of linear regression analysis. For each unit the slope of this regression line is a measure of its static position sensitivity.

In Fig. 1*A* the values of position sensitivity are plotted against the conduction velocity of the afferent fibres. Secondary afferents on the average had higher values of static position sensitivity than primary afferents (mean 1·45 impulses/sec . mm $\pm$ 0·47 S.D. for secondaries, compared with 0·98 impulses/sec . mm $\pm$ 0·35 S.D. for primaries). In spite of the considerable overlap of the values obtained for the two groups of afferents the difference of the mean values for each group was significant ($t = 5{\cdot}39$, $P < 0{\cdot}001$). The data in Fig. 1*B* were obtained by averaging, separately for primary and secondary afferents, the mean discharge rates at each muscle length studied. At long muscle lengths the mean rate of discharge was on the average higher for secondary than for primary afferent units, whereas at short lengths the two groups of afferents did not differ with respect to the mean level of firing. This again demonstrates that the secondary spindle afferents had a higher position sensitivity than the primary afferents.

These data indicate that maintained stretch of the p.b.s. muscles within their physiological range of muscle lengths was an effective stimulus of their muscle spindle afferents, and that it was justified to use it for an investigation of the question whether natural stimulation of muscle afferents and especially of spindle receptors could elicit fusimotor reflexes.

The present values of static position sensitivity for muscle spindle afferents from p.b.s. are considerably lower than those reported in the literature for soleus spindle afferents. A number of investigators found mean values of between four and six impulses/sec . mm (Harvey & Matthews, 1961; Lennerstrand, 1968; Brown, Lawrence & Matthews, 1969). However, the p.b.s. muscles are appreciably longer than soleus (by a factor of about three in the present animals), so that the value of relative position sensitivity (increase in afferent firing per percentage change in muscle length) appears to be comparable for p.b.s. and soleus (cf. also Newsom Davis, 1975).

Effects of p.b.s. stretch on triceps spindle sensitivity

Fig. 2 shows averaged responses of a primary spindle afferent from triceps to ramp and hold stretches applied to the same muscle. In *A* the p.b.s. muscles were kept at the resting length. The response of the afferent unit exhibits a number of features which are typical of ramp responses of primary afferents deprived of fusimotor drive: a dynamic index of 50 impulses/sec (for stretching at 10 mm/sec), a negative acceleration response at the end of the dynamic phase of stretching, only moderate adaptation of the rate of discharge during the hold phase of the stretch (Matthews, 1963, 1972). Since, however, the ventral roots were intact, an unknown amount of

spontaneous fusimotor drive to the spindle could have been present. Given the size of the dynamic response and the fact that the animal was spinalized (at L3), any fusimotor activity presumably involved mainly dynamic fusimotor neurones (cf. Alnaes, Jansen & Rudjord, 1965). No matter what the size and type of any spontaneous fusimotor activity was, it can be seen from Fig. 2*B* that the size of the dynamic response to identical ramp stretches was considerably increased after the

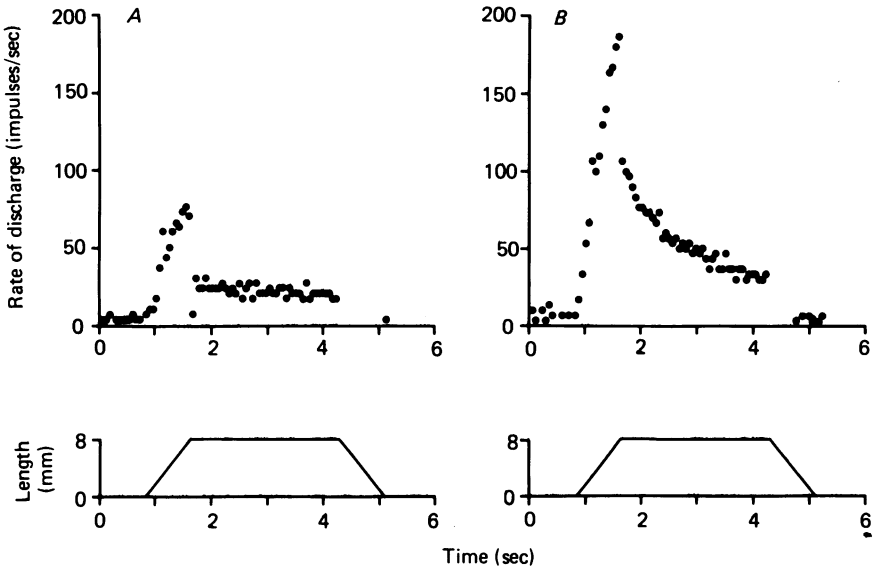

Fig. 2. Responses of a primary spindle afferent to ramp and hold stretches applied to triceps, with p.b.s. either relaxed (at −40 mm, *A*) or stretched to the physiological maximum (at 0 mm, *B*). The responses to five successive stretches (between −10 mm and −2 mm, velocity 10 mm/sec) were averaged and are displayed as cycle histograms (top row) showing the probability density of afferent discharge throughout a stretch cycle (bin width of the histograms: 60 msec). The time course of triceps length is schematically indicated in the bottom diagrams. The values of dynamic index and mean rate of discharge during the hold phase of muscle stretch (the latter measured over 0·54 sec, beginning 0·54 sec after the completion of the dynamic phase of stretching) were 50·4 impulses/sec and 23 impulses/sec in *A*, and 123 and 60·4 in *B*. The rate of discharge at the end of the hold phase, also measured over 0·54 sec, was 22·6 impulses/sec in *A* and 32·6 impulses/sec in *B*. The animal was spinalized at L3.

p.b.s. muscles had been stretched up to their maximum physiological length (10 sec before the onset of data collection). Compared with Fig. 2*A* the dynamic index was increased, by a factor of 2·5, to 123 impulses/sec. Moreover the dynamic phase of the ramp response was followed by a roughly exponential decay of the rate of the discharge, and the maintained increase of the rate of firing at the end of the hold phase of the stretch was only rather moderate (9 impulses/sec). Finally, the afferent unit fell silent during the release of the stretch. These observations suggest that the maintained stretch applied to the p.b.s. muscles caused an increase in predominantly dynamic fusimotor activity in triceps. Since this increase in dynamic fusimotor activity was not accompanied by any detectable e.m.g. activity in triceps (not illustrated), it is likely that it was mainly mediated by dynamic γ-fibres. The

responses of Fig. 2 were obtained in a *spinal* preparation during light anaesthesia. All together, similar dynamic fusimotor reflexes were found in thirteen primary afferent units in eight spinal preparations.

Fig. 3 illustrates that the dynamic fusimotor reflex elicited by steady stretch of the p.b.s. muscles was also observed in animals with intact spinal cord which were lightly anaesthetized (cf. Fig. 3*A* and *B*). In this case the occurrence of increased

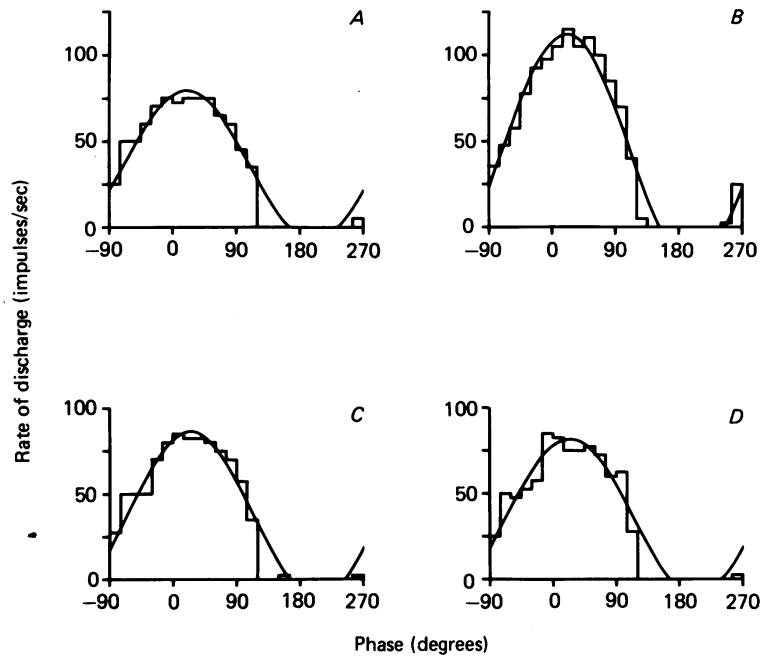

Fig. 3. Cycle histograms showing averaged responses of a primary spindle afferent from triceps to 2 mm sinusoidal stretching of the receptor bearing muscle. The probability density of firing (along the ordinate, in impulses/sec) is plotted against the phase of the stretch cycle (abscissa). The sinusoidal stimulus (not illustrated) began at 0°. Thus all responses exhibited a clear phase advance on the stimulus. In *A* and *C* the p.b.s. muscles were completely relaxed (at −40 mm), whereas in *B* and *D* they were stretched to their maximum physiological length (0 mm). *A* and *B*, light chloralose anaesthesia; *C* and *D*, deeper anaesthesia following the administration of an additional dosage of chloralose (10 mg/kg). The continuous lines superimposed on the histograms are simple sinusoids fitted to the data using a least squares algorithm (cf. Methods). The values for fitted mean, depth of modulation and phase of the response relative to the stimulus were 33·4 impulses/sec, 43·6 impulses/sec and 69·8° in *A*; 44·1, 66·4 and 69·2 in *B*; 35·6, 48·6 and 65·1 in *C* and 34·1, 45·7 and 65·7 in *D*. Non-spinalized preparation.

dynamic sensitivity of a triceps primary afferent during stretching of p.b.s. was demonstrated with responses to 2 mm sinusoidal stretching of triceps. The following observations, equivalent with those described above for ramp responses, suggest that the change in spindle sensitivity in Fig. 3*B* (compared with Fig. 3*A*) was attributable to an increase in predominantly dynamic fusimotor activity: the depth of modulation of the sinusoidal response increased from 43·6 to 66·4 impulses/sec, there was an only moderate increase in fitted mean (from 33·4 to 44·1), and there was clear silence during

the release of stretching which began at 90°. Since this increase in dynamic sensitivity again was not accompanied by any detectable e.m.g. activity in triceps (not illustrated), it may also be tentatively attributed to a predominant excitation of dynamic γ-motoneurones, rather than dynamic β-motoneurones (see also Discussion).

Fig. 3*D* shows that the increase in dynamic fusimotor activity could no longer be elicited by an identical stretch of p.b.s. when the level of anaesthesia was increased. This finding provides an important control, since it indicates that the change in sinusoidal response by the stretching of p.b.s. (Fig. 3*B*) could not be explained by any mechanical coupling between p.b.s. and triceps, which conceivably might have altered the mechanical properties of triceps, and thus, possibly, the dynamic sensitivity of its muscle spindle afferents.

Looking at the present data as a whole, there are four lines of evidence which suggest that the increase of dynamic sensitivity of triceps spindle afferents was due to a genuine fusimotor reflex rather than to some accidental mechanical interaction between the two muscle groups. First, it was always ensured that the mechanical fixation of the femur and the tibia on the left hind limb was very rigid (cf. Methods), so that stretching of p.b.s. alone did not evoke any visually detectable movements in triceps. Secondly, the excitatory effect was frequently abolished, under otherwise identical experimental conditions, when the level of anaesthesia had to be increased (as with the example of Fig. 3). Thirdly, with thirteen primaries from ten animals the stretch-induced increase of dynamic sensitivity was found to wax and wane spontaneously or even to disappear completely, again with identical mechanical stimulation of the muscles (see also below and Fig. 4). Fourthly, cutting of the p.b.s. nerve (five animals) completely abolished the excitatory action of p.b.s. stretching.

Variability in reflex size and character

It was a common finding that the size of the excitatory effect from p.b.s. varied to a greater or lesser degree from one test to the next, although for individual tests the reflexes were sufficiently stationary to permit averaging over up to 10 sec. All units were therefore investigated with a number of pairs (usually at least five) of successive control (p.b.s. relaxed) and test measurements (p.b.s. stretched). Fig. 4 shows the results obtained with another two primary spindle afferents with such repeated control and test responses. Both units were studied in anaesthetized preparations with intact spinal cord. The results of the quantitative analysis of cycle histogram responses are displayed as scatter diagrams, by plotting the *change* in depth of modulation and phase (test response compared with control) against the *change* in fitted mean for the same pair of histograms, each histogram being the result of ten averaged consecutive cycles. This form of display corresponds to the scatter diagrams for dynamic index introduced by Crowe & Matthews (1964*b*). It was chosen, since the interest lay in the *change* of response elicited by p.b.s. stretching, rather than in the absolute size of the test responses. Moreover, throughout a whole series of measurements the control responses could exhibit considerable variability (see Fig. 6) which, most likely, was due to slow drifts in spontaneous fusimotor drive (see below). Using the present analysis of *changes* in response such effects on the reflex measurements could at least be reduced. A more detailed account of this method of

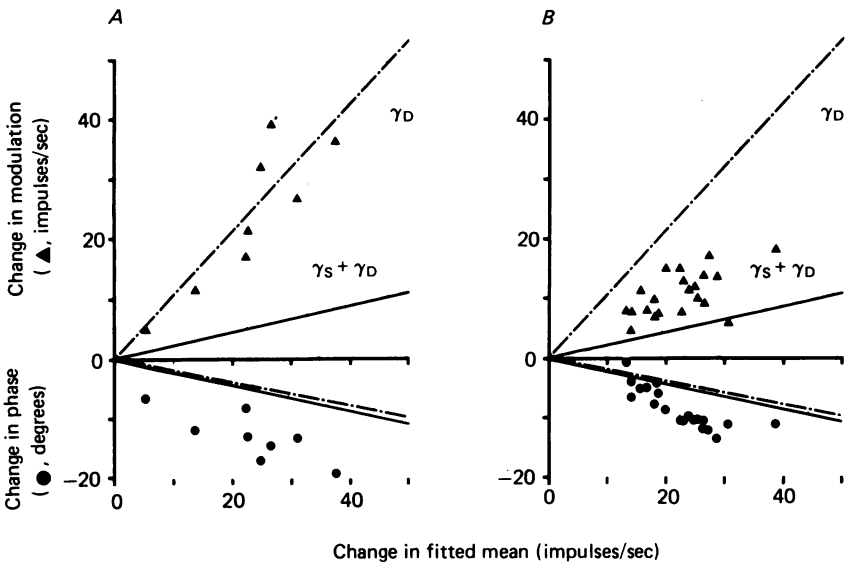

Fig. 4. Scatter diagrams showing the *change* in sinusoidal response (at 1 Hz, 1 mm) of two primary afferent units from triceps during maintained stretching of p.b.s. A number of pairs of control and test responses were separately averaged to give cycle histograms for each of which the mean, modulation and phase of the best fitting sinusoid were determined. For each pair the change in depth of modulation (i.e. test minus control value) and the change in phase are plotted against the change in fitted mean (abscissa). The slopes of the lines in the upper quadrant give the ratio of mean change in modulation: mean change in fitted mean, which have been found with electrical stimulation of dynamic fusimotor fibres alone (–·–, ratio: 1·07) and with combined stimulation of static and dynamic fusimotor fibres (—, ratio; 0·24); (cf. Fig. 7, data from Hulliger *et al.* 1977*b*, replotted). The slopes of the lines in the lower quadrant give, for the same data, the ratios of the mean change in phase: mean change in fitted mean during dynamic fusimotor stimulation (–·–, ratio: −0·22) and during combined static and dynamic stimulation (—, ratio: −0·25).

In *A*, the mean values of the response parameters were, for the controls: 33·1 impulses/sec ± 3·8 S.D. (fitted mean), 38·8 ± 6·8 (modulation) and 60·8 degrees ± 4·1 (phase), and for the test responses: 56·1 ± 10·7 (fitted mean), 62·5 ± 10·8 (modulation) and 47·9 ± 4·8 (phase). The changes induced by p.b.s. stretching were, for fitted mean: 23 ± 9·9 (S.D.), $t = 6·5$, $P < 0·05$ (paired t test, $n = 8$), for modulation: 23·7 ± 12·1, $t = 5·5$, $P < 0·05$, and for phase: −12·9 ± 4·2, $t = 8·7$, $P < 0·05$. In *B*, the mean response parameters were, for the controls: 51·7 ± 8·3 (fitted mean), 62·3 ± 7·2 (modulation) and 67·8 ± 4·6 (phase), and for the test responses: 73·9 ± 7·2 (fitted mean), 73 ± 6·5 (modulation), and 49·5 ± 2·7 (phase). The induced changes were, for fitted mean: 22·3 ± 6·5, $t = 15·3$, $P < 0·05$ (paired t test, $n = 20$), for modulation: 10·6 ± 3·7, $t = 12·8$, $P < 0·05$, and for phase: −8·3 ± 3·4, $t = 10·9$, $P < 0·05$. The two units were studied in separate animals, both with intact spinal cord and during light anaesthesia.

reflex assessment using scatter diagrams as in Figs. 4, 5 and 7 has recently been published (Appelberg *et al.* 1981). For both units in Fig. 4 the change in modulation was always positive, indicating a consistent increase in dynamic sensitivity. Further, it increased with increasing change in fitted mean brought about by stretching of p.b.s. In contrast, the change in phase was always negative, yet its magnitude also increased with increasing change in fitted mean. For both units, the alterations in

fitted mean, modulation and phase were statistically significant at the 5% level (cf. legend to Fig. 4). Thus with increasing size of the reflex, there was an increasing change in fitted mean and the test responses showed, compared with the controls, a progressive increase of depth of modulation and an increasing phase lag. Qualitatively these findings agree with the effects of electrical excitation of dynamic fusimotor fibres with progressively increasing rate of stimulation (Hulliger *et al.* 1977*a*) so that, at first sight, both units of Fig. 4 seem to reveal the occurrence of dynamic fusimotor reflexes of variable size.

However, there are important quantitative differences between the response of Fig. 4*A* and *B*. In *A*, the increase in modulation and the increase in fitted mean were of the same size (ratio of the means: 1·02). This is in close agreement with the data obtained with electrical stimulation of identified dynamic γ-fibres (Hulliger *et al.* 1977*a*, cf. also Fig. 7). In Fig. 4 the slope of the interrupted reference line labelled γ_D indicates in fact the ratio of the average change in modulation: average change in fitted mean of these reference data. Furthermore, the test responses of Fig. 4*A* all showed clear silence during release of stretching (not illustrated but evident in the original histograms). In contrast, in Fig. 4*B*, the increase in modulation was considerably less than the increase in fitted mean (ratio: 0·48), and the data points for modulation lie clearly below the line of pure dynamic action and much closer to the line of mixed static and dynamic action labelled $\gamma_S+\gamma_D$ (see also Fig. 7). This is in line with the observation that the test responses of Fig. 4*B* did not, in the original histograms, exhibit the silence during the release of stretching, which is typical of uncontaminated dynamic action. Rather, they were very similar to the 'trough' responses which are characteristic of mixed fusimotor action (cf. Hulliger *et al.* 1977*b*, Fig. 1). The changes in phase in Fig. 4*A* and *B* differed to a lesser degree, yet for both units they are larger than for the average reference data. However, this was not a general trend but rather a manifestation of variability (see Figs. 5 and 7). Thus, taken together, the present data suggest that Fig. 4*A* shows a relatively pure dynamic fusimotor reflex elicited by stretching of p.b.s., whereas the unit of Fig. 4*B* reveals a mixed, albeit predominantly dynamic, fusimotor reflex.

The scatter diagrams of Fig. 5 show, for primary afferent units, the size of the reflex evoked by stretch of p.b.s. Only those units are illustrated, which were tested with 1 mm sinusoidal stretching at 1 Hz (standard measurements) and for which test responses exhibited statistically significant alterations in modulation and/or fitted mean (paired *t*-test, 5% significance level). The data of each unit are based on usually at least five consecutive pairs of control and test responses, each averaged over ten cycles. As in Fig. 4 the changes in modulation and phase are plotted against the change in fitted mean. For the twenty units of Fig. 5*A* the fusimotor reflex enhanced the dynamic sensitivity, i.e. it increased the depth of modulation of the test responses. It was a common finding that this effect was not accompanied by manifest e.m.g. activity in triceps. On the contrary, the weak spontaneous e.m.g. activity, which on a few occasions was present, was regularly inhibited by tonic stretch of p.b.s. As above (Figs. 2 and 3) the change in spindle afferent sensitivity may therefore be attributed to a fusimotor reflex. Comparison with the reference lines (same as in Figs. 4 and 7) indicates that the fusimotor activity elicited by stretch of p.b.s. was purely or predominantly dynamic (cf. Methods for criteria). In contrast, for the nine units of

Fig. 5*B* the fusimotor reflex evoked a slight decrease in modulation and thus in dynamic sensitivity. For the majority of units (8) this was accompanied by an increase in fitted mean (lower right hand quadrant) and may therefore be attributed to an enhancement of pure static (cf. reference line labelled γ_S) or mixed static and dynamic fusimotor activity. However, for one unit the reduction of dynamic sensitivity was accompanied by a decrease in fitted mean (lower left hand quadrant

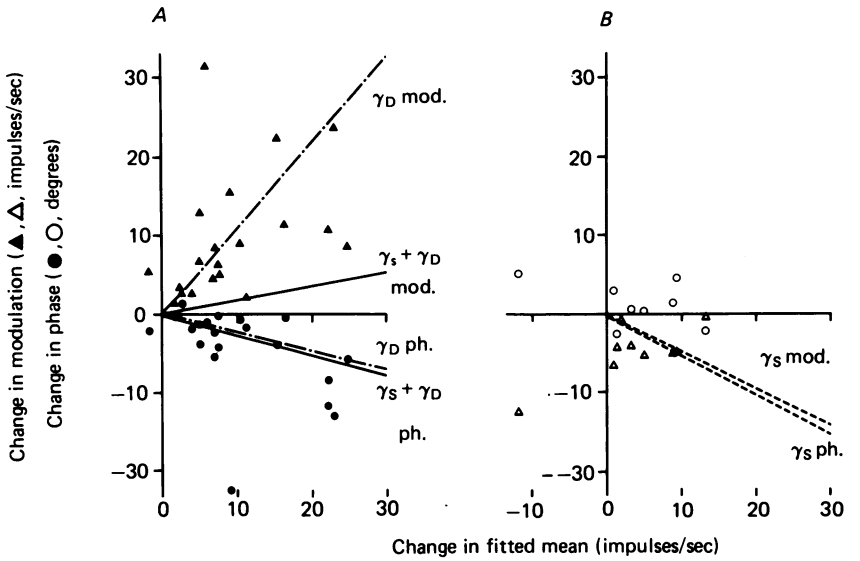

Fig. 5. Scatter diagrams to show the average change in sinusoidal response (at 1 Hz, 1 mm) of twenty-nine primary spindle afferent units from triceps, for which statistically significant reflex effects were elicited by stretch of p.b.s. (cf. text). In *A*, the average change in modulation and change in phase of twenty units, which in test responses exhibited an increase in modulation over the control values, are plotted against the average change in fitted mean. Same reference lines as in Fig. 4. In *B*, the average change in modulation and phase are shown for nine units, which exhibited a decrease in modulation in the test responses. The slopes of the reference lines in *B* give the ratio of the mean change in modulation: mean change in fitted mean (ratio: −0·47; labelled γ_S mod.), and the ratio of mean change in phase: mean change in fitted mean (ratio: −0·5; labelled γ_S ph.), which were found with electrical stimulation of single fusimotor fibres (for details cf. legend to Fig. 7). In each diagram the mean values for all units were, in *A*, for change in fitted mean: 9·3 impulses/sec ± 7·4 S.D., for change in modulation: 9·7 ± 8·1, and for change in phase: −4·2 ± 7·5. In *B* the mean values were, for change in fitted mean: 3·6 impulses/sec ± 7·1, for change in modulation: −4·9 ± 3·5, and for change in phase 1·0 ± 2·7.

of Fig. 5*B*). This effect was confirmed by qualitative observations in another five primary afferents and it may be attributed to an inhibition of spontaneous dynamic fusimotor drive.

Finally it should be emphasized that the size of the fusimotor reflexes induced by tonic stretch of p.b.s. was considerably smaller than the size of the effects evoked by conventional electrical stimulation of individual fusimotor fibres. Thus the average changes in fitted mean and modulation of the units of Fig. 5*A* were 9·3 impulses/sec ± 7·4 S.D. and 9·7 ± 8·1, whereas the reference responses of Fig. 7 during electrical stimulation of dynamic fusimotor axons at 100 Hz exhibited an average

change in fitted mean of 44·5 impulses/sec ± 15·7 (S.D.), and a change in modulation of 47·7 ± 30·5 (for additional quantitative detail cf. legends to Figs. 5 and 7).

The standard data of Fig. 5 were complemented by measurements of significant reflex effects at larger amplitudes of 1 Hz stretching. Altogether, pure or predominantly dynamic fusimotor reflexes were observed in twenty-two primary afferent units (including those of Fig. 5*A*) whereas pure or predominantly static effects were seen in nine primaries. Finally, forty primary units which were also studied quantitatively did not show statistically significant effects evoked by stretch of p.b.s. It should be pointed out that the sample of those units, which were studied quantitatively, was clearly biased in favour of those which exhibited manifest reflex effects. Therefore, in all together thirty-one animals, the quantitative measurements were supplemented by *qualitative observations* (cf. Methods), which were not subjected to such selection bias. Taken together forty-one out of 202 primary afferents (20 %) showed predominantly dynamic reflexes (nineteen in spinal preparations out of which six showed inhibitory reflexes), eleven out of 202 primary units (5 %) showed predominant static effects (one in a spinal preparation), and 150 out of 202 primary afferents (75 %) showed no significant reflex activation (fifty-one in spinal preparations). Amongst secondary spindle afferents two out of seven showed weak fusimotor activation, whereas five out of seven were not excited by stretch of p.b.s.

Thus the number of units which failed to show fusimotor reflexes during tonic stretch of p.b.s. was considerable, indicating that the reflex excitability with the present anaesthetized preparation was quite low. A major factor responsible for this seemed to be the level of anaesthesia, since it was a common observation that with increasing depth of anaesthesia fusimotor reflexes diminished in size or disappeared altogether (cf. also Fig. 3). It was also noted that the excitability appeared highest in those preparations which showed signs of spontaneous fusimotor drive. Although this could not directly be measured, it was nevertheless possible to infer its occurrence from the observation that control responses often showed considerable variability of fitted mean and depth of modulation of sinusoidal responses. This was assessed by measuring the co-efficient of variation of these parameters in control responses. The values obtained usually were clearly higher in responsive preparations than in non-responsive preparations or in units which, e.g. during deep anaesthesia, appeared to lack significant fusimotor drive. Moreover, for reflex responsive primary afferent units there was a positive correlation between the size of the reflex from p.b.s. and the variability of the control responses. Thus the changes in fitted mean as well as in modulation increased with increasing variability of fitted mean of the controls, both for predominantly dynamic and predominantly static action.

Additional observations

It was a common observation that the size of the fusimotor reflex depended on the degree to which the p.b.s. muscles were extended. In most instances a nearly maximal extension was neccessary, but at times a clear gradation of the reflex could be obtained by graded extensions of p.b.s. An example is given in Fig. 6 where the average change in peak rate of discharge (sum of fitted mean and modulation, filled squares) and the values for change in modulation (open triangles) and phase (open circles) which were obtained at different p.b.s. lengths, are shown. From the cycle histogram responses (inset) it is clear that the effect was of a dynamic nature. This again indicated that the reflex excitability was generally rather low, since maximum stretch of p.b.s. was mostly neccessary for clear effects. Yet observations like those in Fig. 6 also show that, in sensitive preparations, the reflex indeed was a p.b.s. *length dependent* feature.

The results described so far did not provide any information on the types of afferent

fibres from p.b.s. that were responsible for the stretch-induced reflex activation of triceps fusimotor neurones. However, indirect evidence strongly suggests that secondary spindle afferent units were substantially contributing (cf. Discussion). Experimental evidence to support this interpretation was obtained in experiments where the proximal ends of the cut nerves to the p.b.s. or to the ipsilateral medial gastrocnemius muscles were activated by graded electrical stimulation. Repetitive

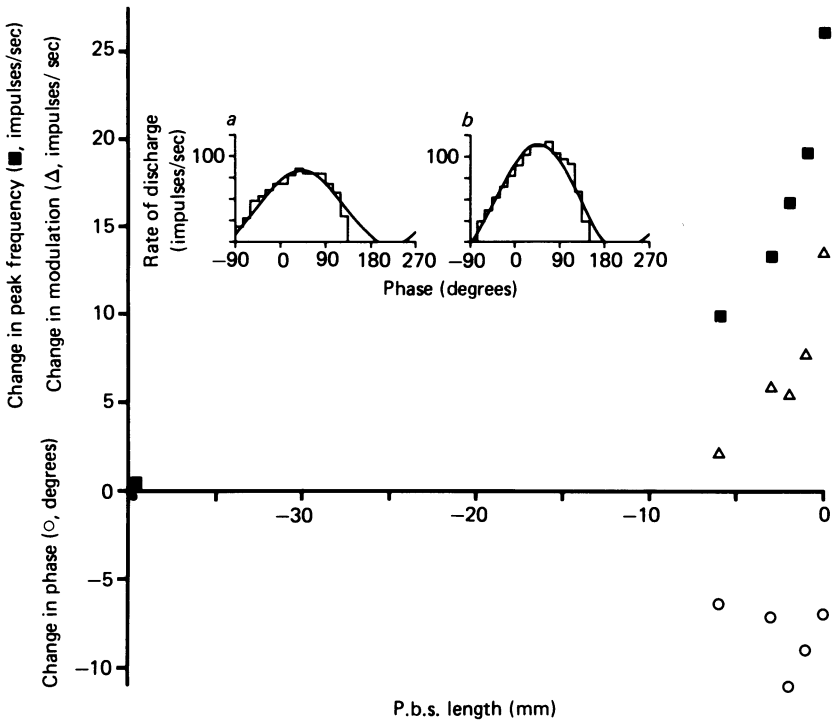

Fig. 6. The dependence of the increase in sinusoidal sensitivity of a primary spindle afferent from triceps on the size of the tonic stretch applied to p.b.s. For each length, mean changes in sinusoidal response (at 1 Hz, 1 mm) of six consecutive pairs of control and test responses, each averaged over ten cycles, are shown. The typical changes in peak rate of discharge, depth of modulation and phase were elicited when the p.b.s. muscles were stretched close to their maximum physiological length (0 mm; inset *b*). The control measurements were always taken with p.b.s. at resting length (−40 mm; inset *a*). The averaged response of the inset was obtained with p.b.s. stretched to the physiological maximum. The values of fitted means, depth of modulation and phase of the histograms of the inset were, for the control, 39·6 impulses/sec, 43·5 impulses/sec and 49°, and for the test response, 45·3, 69·7 and 43·5. Spinal preparation.

stimulation (200/sec) of either nerve at an intensity below group II threshold (1·3 times I a threshold, T) failed to alter the dynamic sensitivity of primary afferent units from lateral gastrocnemius–soleus. However, at minimum group II threshold (1·5 T, cf. Fu, Santini & Schomburg, 1974) a weak increase in dynamic sensitivity was sometimes observed. From the work of Fu *et al.* (1974) it can be assumed that at this intensity the group I fibres were already maximally activated. When the intensity of stimulation was further increased to 3 T strong reflex effects of predominantly

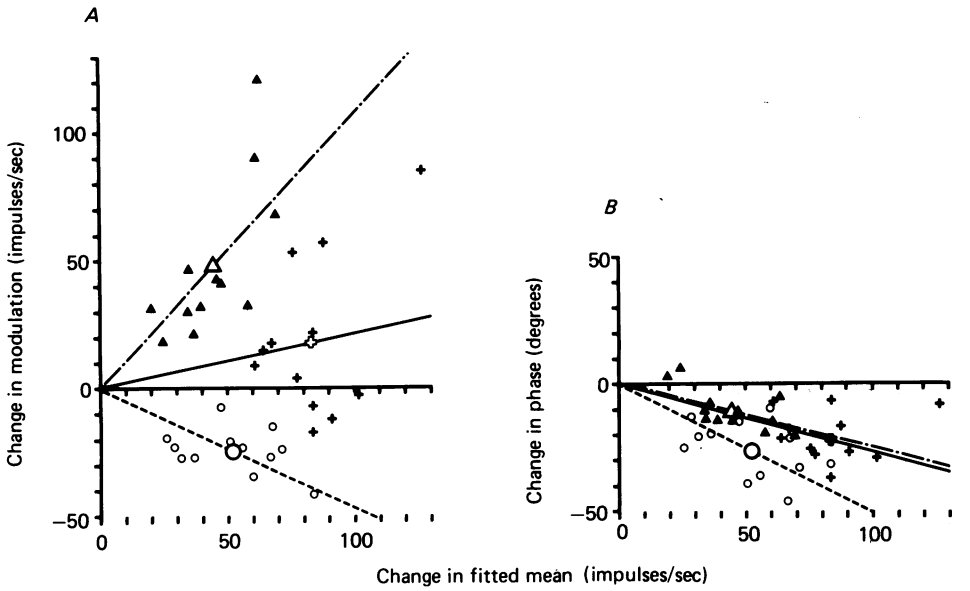

Fig. 7. Scatter diagram to show the *change* in sinusoidal response (at 1 Hz, 1 mm) of twelve primary spindle afferents from soleus during electrical stimulation of functionally single fusimotor fibres. Data from Hulliger *et al.* (1977*b*) replotted and recalculated. For each unit (de-efferented spindle afferents) control responses (in the absence of stimulation) and test responses (during stimulation) were averaged over ten stretch cycles and displayed as cycle histograms, for which mean, modulation and phase of the best fitting sinusoid were determined. The change in modulation (test minus control, in *A*) and the change in phase (*B*) are plotted, for each unit, against the change in fitted mean (abscissa), for the same pair of histograms. Each afferent was investigated during stimulation of dynamic (▲) fusimotor fibres (range of rate of stimulation: 66–120 Hz), during static (○) fusimotor stimulation (range of rates: 30–100 Hz), and during combined (+) static and dynamic stimulation at the same rates. The mean values for the changes in response parameters were, for *dynamic* stimulation (△): 44·5 ± 15·7 (S.D.) impulses/sec (t = 9·8) for fitted mean, 47·7 ± 30·5 impulses/sec (t = 5·4) for modulation and −10·7 ± 8·3° (t = −4·5) for phase; with *static* stimulation (○): 52·1 ± 18·7 (t = 9·7) for fitted mean, −24·4 ± 8·7 (t = −9·7) for modulation and −25·8 ± 11·3 (t = −7·9) for phase; with *combined* stimulation (✪): 83·7 ± 17·9 (t = 16·2) for fitted mean, 18·5 ± 31·3 (t = 2·1) for modulation and −20·8 ± 9·5 (t = −7·5) for phase. All these changes (except for modulation during combined stimulation) were statistically significant ($P < 0·05$, paired t test).

dynamic fusimotor nature was observed. Such observations were made in four units of three separate experiments. For three of the units p.b.s. nerve was stimulated.

DISCUSSION

The present results show that excitation of muscle afferents from a flexor muscle (p.b.s.) can enhance the dynamic sensitivity of primary spindle afferents from an extensor muscle (triceps or soleus). These findings could be obtained in spinal preparations, and the excitation was abolished by cutting the muscle nerve to p.b.s. or by deep anaesthesia. The most likely interpretation is that muscle afferents from p.b.s. caused an activation of dynamic fusimotor neurones to triceps via a segmental

reflex loop. In contrast, reflex activation of static neurones was considerably smaller than for dynamic fusimotor neurones (Fig. 5). This inference is based on a quantitative comparison of the present reflex data with the findings obtained with electrical stimulation of single fusimotor fibres (Hulliger *et al.* 1977*b*; see Fig. 7).

For these reference data, the change in mean rate of discharge and the change in modulation of sinusoidal responses was of the same size with pure dynamic action. In contrast, with mixed dynamic and static action or with pure static action the relative change in mean discharge rate is considerably larger than the change in modulation. The fusimotor activation of the present experiments was not accompanied by manifest gross e.m.g. activity in triceps. If anything, weak spontaneous e.m.g. activity in this muscle was abolished by p.b.s. stretching. Therefore the present reflex activation seems to involve γ- rather than β-motoneurones. However, this interpretation can only be tentative, since our e.m.g. recording technique (using surface electrodes) probably was not sufficiently sensitive to monitor remote potentials of small motor units. Thus any activation of small β-motoneurones, which are known to exert dynamic fusimotor effects (Emonet-Dénand, Jami & Laporte, 1975; Laporte, Emonet-Dénand & Jami, 1981) would not necessarily have been detected. On a few occasions, when spontaneous – mainly dynamic – fusimotor drive appeared to prevail, clear inhibition rather than excitation of fusimotor neurones by tonic stretch of p.b.s. could be observed. This seems of considerable interest, since it confirms the finding of alternative – excitatory and inhibitory – pathways from muscle receptors to dynamic γ-motoneurones (Appelberg *et al.* 1982*b*, *c*).

Reflex mechanisms

Which then are the muscle afferents causing this reflex? Clearly, primary as well as secondary spindle afferents were excited by the tonic stretch of p.b.s. (cf. Fig. 1). Yet Golgi tendon organs and group III and IV afferents may also have been activated. As to primary spindle afferents it is known that they may weakly excite or inhibit unclassified homonymous γ-motoneurones (Ellaway & Trott, 1978; Fromm & Noth, 1976). It is also known that muscle group II fibres, most likely secondary spindle afferents, may strongly excite γ-motoneurones. Their action seems to be widely distributed, covering both homonymous as well as synergistic and antagonistic γ-motoneurones (Appelberg *et al.* 1977, 1982*b*). Moreover, in these studies it has also been shown that excitation of dynamic lateral gastrocnemieus, soleus γ-motoneurones by muscle group II afferents from p.b.s. was about twice as frequent as for static γ-cells. Evidently, this is in good agreement with the present findings with natural stimulation of secondary afferent fibres from p.b.s. (cf. above). Also, in the present experiments, electrical stimulation of muscle nerves at group II but not at group I strength could mimic the effect caused by muscle stretch. As to Golgi afferents from triceps it has been shown that they can elicit autogenetic inhibition of unclassified γ-motoneurones (Ellaway, Murphy & Trott, 1979). Also, heteronymous Golgi inhibition has been demonstrated in triceps γ-motoneurones (Ellaway & Murphy, 1979). In our own experiments on γ-cells (Appelberg *et al.* 1982*a*) short latency excitation or inhibition of triceps γ-cells by electrical stimulation of the p.b.s. nerve at group Ib strength was never observed.

As to the possible contributions of group III and IV afferents to the present fusimotor reflex, there are three lines of evidence indicating that any excitatory effect

from these fibres was less significant than the group II effects. First, the stretch responses of group III and IV afferents to muscle stretch are less frequent and considerably weaker than the responses of secondary spindle afferents (Paintal, 1960; Kniffki, Mense & Schmidt, 1978; cf. Fig. 1). Secondly, with electrical stimulation of the p.b.s. nerve the reflex actions of group III and IV afferent fibres are strikingly different from those mediated by group II fibres. With the latter there is a clear prevalence of excitatory effects in lateral gastrocnemius, soleus γ-motoneurones, particularly with dynamic γ-cells (Appelberg *et al.* 1982*b*), whereas with group III and IV fibres excitatory and inhibitory effects are roughly balanced (Appelberg *et al.* 1982*c*). Thirdly, group III and IV responses to stretch often occur with latencies up to 1 min (Paintal, 1960; Kniffki *et al.* 1978), whereas the present reflex excitation was observed within seconds. In conclusion, it seems reasonable to suggest that the reflex effects observed were mainly caused by activation of secondary spindle afferents.

Functional significance

Significance of natural stimulation. Natural stimulation of muscle spindle secondary afferents within the physiological range of muscle lengths may thus reflexly activate dynamic and to some extent static fusimotor neurones. Under the experimental conditions used nearly maximal physiological stretching was required for a clear manifestation of the reflex. However, under physiological conditions the excitability and gain of the fusimotor reflex may be appreciably higher than in the anaesthetized and widely denervated preparations of the present experiments. Also, under normal conditions static fusimotor drive may well be higher and secondary spindle afferents would then discharge at higher rates, thus providing a more powerful excitatory input. It seems therefore likely that the spinal pathway demonstrated may indeed be operative in normal motor tasks.

Functional specificity of the dynamic fusimotor system. The findings with electrical stimulation of skin-, joint- and muscle nerves (Appelberg *et al.* 1977, 1982*a*, *b*, *c*) and with natural stimulation of afferents (Appelberg *et al.* 1978*a*, *b*, 1979, 1981, and the present report), all show that dynamic fusimotor neurones may be operated by rather specific reflex pathways. An additional observation in the present experiments is of interest in this context. The spontaneous e.m.g. activity which was occasionally present in triceps was often abolished by stretching of the p.b.s. muscle. This is presumably a manifestation of the well known Ib inhibitory pathway from p.b.s. to triceps (Laporte & Lloyd, 1951; Eccles, Eccles & Lundberg, 1957), although the participation of other afferents can by no means be excluded. Yet at the same time the dynamic γ-motoneurones were clearly activated, although most likely by different types of receptors. Thus, under the present conditions, the dominant reflex action on α- and dynamic γ-motoneurones was in opposite directions and did not conform with the frequently encountered pattern of coactivation of α- and γ-motoneurones. This could indicate that such coactivation may not be a general feature. It might be restricted to static γ-motoneurones and dynamic fusimotor neurones may be operated in a more independent manner. Such an arrangement would enable the central nervous system to make more effective use of the rather specific properties of the dynamic fusimotor system.

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