

THE RESPONSES OF PRIMARY SPINDLE AFFERENTS TO FUSIMOTOR STIMULATION AT CONSTANT AND ABRUPTLY CHANGING RATES

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SUMMARY

1. Single fusimotor fibres to de-efferented soleus of the cat were stimulated to investigate the size and time course of the responses elicited in single primary spindle afferents. The muscle was kept at constant length close to the physiological maximum. Constant and alternating rates of fusimotor stimulation were used: (a) repetitive stimulation at constant rate (maintained stimulation); (b) modulated stimulation with the rate of activation alternating between two constant levels at repeat frequencies between 0.09 and 2 Hz (rectangular stimulation). The responses were averaged and displayed as post-stimulus time (pst) histograms (a) or as cycle histograms (b).

2. During static fusimotor stimulation the pst histograms could be clearly modulated over a range of rates of stimulation. However, histogram modulation was not a prerequisite of static action since with different fibres the degree of modulation could range from deeply modulated to completely non-modulated.

3. Dynamic fusimotor stimulation was almost always accompanied by non-modulated pst histograms.

4. Primary spindle afferents responded to rectangular stimulation of either kind of fusimotor fibre with an approximately rectangular modulation of the rate of discharge. At the repeat frequencies studied the size of the responses was appreciably larger with static than with dynamic activation. It was assessed as 'fusimotor rate-sensitivity during alternating stimulation' by the response/stimulus ratio which is defined as change in firing/change in alternating rate of stimulation, in impulses/stimuli. The mean values of rate-sensitivity were 1.35 impulses/stimuli (statics) and 0.29 (dynamics), with a static/dynamic ratio of 4.7.

5. The afferents' 'fusimotor rate-sensitivity during steady stimulation' (change in firing/change in maintained rate of stimulation) was also determined. The mean values were 0.78 (static) and 0.37 (dynamics), with a static/dynamic ratio of 2.1.

6. The time course of the responses to rectangular stimulation was of the same order of magnitude for static and dynamic fibres. It was assessed by fitting a single exponential to the rising and falling phase of cycle histograms. The mean values of the time constants for static fibres were 58 msec (rising phase) and 59 msec (falling phase), and for dynamic fibres 34 msec (rising phase) and 49 msec (falling phase). The differences were statistically non-significant.

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7. The significance of the modulation in pst histograms and the mechanisms and functional implications of the differences in rate-sensitivity are discussed. It is concluded that at constant muscle length static and dynamic fusimotor fibres differ significantly by the size rather than the speed of their action on primary spindle afferents.

INTRODUCTION

Following the initial description of two separate types of fusimotor neurones (Matthews, 1962), a number of functional differences between these two types have been established. Static fibres reduce dynamic sensitivity to muscle stretching, they have a pronounced excitatory action on muscle spindle afferents, and they can either elicit 1:1 driving of primary spindle afferents or increase their variability of rate of discharge. Static fusimotor action affects both primary and secondary spindle afferents (for a review, see Matthews, 1972). In contrast, dynamic fusimotor action maintains a high dynamic sensitivity to stretching over a wide range of amplitudes, and particularly for large amplitude stretching the sensitivity is regularly increased above the level of non-activated primary afferents (Matthews, 1972; Hulliger, Matthews & Noth, 1977*a*). Further, at constant length the excitatory action of dynamic fibres on primary afferents is less pronounced than that of static axons (Lennerstrand & Thoden, 1968*a, b*; Lewis & Proske, 1972; Cheney & Preston, 1976*b*; Hulliger *et al.* 1977*a*; Emonet-Dénand, Laporte, Matthews & Petit, 1977*b*). Dynamic fibres do not elicit 1:1 driving of primary afferents (Brown, Crowe & Matthews, 1965) and they provoke an only moderate increase of the variability of the rate of discharge (Lewis & Proske, 1972; Cheney & Preston, 1976*a*; Emonet-Dénand *et al.* 1977*b*). Finally, dynamic fusimotor action is restricted to primary spindle afferents (Appelberg, Bessou & Laporte, 1966).

As regards the mechanisms of intrafusal action it has been suggested that static axons operate fast intrafusal muscle fibres, whereas dynamic fibres act on slowly contracting fibres (Westbury, 1964; Brown & Matthews, 1966). Later, this interpretation was mainly supported by the finding that static but not dynamic action can cause a rhythmic modulation of afferent discharge, phase-locked to the fusimotor stimulus. This could be shown when successive responses to individual fusimotor stimuli were superimposed and displayed as frequencygrams (Bessou, Laporte & Pagès, 1968; Bessou & Pagès, 1969; Emonet-Dénand & Laporte, 1969). A number of studies have emphasized this difference in the speed of fusimotor action (Brown, 1971, for frog spindles; Goodwin, 1972; Bessou & Pagès, 1975; Boyd, 1976*a, b*; Boyd, Gladden, McWilliam & Ward, 1977). These investigations were based on an analysis of the time course of the rate of afferent discharge or of the shortening of intrafusal muscle fibres at the onset of tetanic fusimotor stimulation. However, this transition from rest to steady activation should be interpreted with caution. The time course of muscle activation in the activated intrafusal segments may well be influenced by initial mechanical transients in the non-activated fibre segments which lie in series. Any short range elastic component (Hill, 1968; Brown, Goodwin & Matthews, 1969; Hunt & Ottoson, 1976) would be broken down, when these segments are passively stretched during the initial shortening in the contracting foci. Indeed, when the time course of excitation was investigated during ongoing stimulation with

sinusoidal or triangular variation of the rate of stimulation, the speed of action seemed to be much the same for static and dynamic axons (Andersson, Lennerstrand & Thoden, 1968; Chen & Poppele, 1978). On the other hand, these studies confirmed that the size of the excitatory effect was appreciably larger for static axons.

This result was paradoxical since the findings with frequency-grams seemed to agree with the concept of static and dynamic axons operating fast twitching and slow non-twitching intrafusal muscle fibres respectively. The present study was therefore undertaken to reinvestigate the speed of fusimotor action. Responses to individual stimuli were assessed with post-stimulus histograms and, for the same fusimotor neurones, compared with the responses to step changes of the level of steady excitation (using repetitive rectangular stimulation). Basically the speed paradox was confirmed, since static and dynamic fibres did not significantly differ in the time course of the responses to rectangular stimulation. Yet they differed significantly with respect to the phasic modulation which was evoked in post-stimulus histograms. It is suggested that this paradox can be resolved if it is accepted that the intrinsic speed of contraction of the intrafusal fibres activated by static and dynamic axons is of the same order of magnitude. But due to a number of mechanisms the phasic properties of the fibres operated by dynamic axons might fail to manifest themselves in the pattern of afferent discharge.

METHODS

The present results were obtained during an investigation of static and dynamic fusimotor action on the sensitivity of primary spindle afferents to sinusoidal stretching of widely ranging amplitude (Goodwin, Hulliger & Matthews, 1975; Hulliger, 1976; Hulliger, Matthews & Noth, 1977*a, b*).

Preparation and single units. The experiments were performed on the soleus muscle of cats weighing 2–3.5 kg which were anaesthetized with pentobarbitone. Single muscle spindle afferent fibres were isolated in dorsal root filaments. Primary afferents were selected on the basis of conduction velocity (≥ 70 m/sec) and high dynamic sensitivity. The latter manifested itself in responses to ramp stretches with a dynamic index ≥ 40 impulses/sec (for stretches of 7 or 8 mm at 10 mm/sec) and by the occurrence of 1:1 driving during vibration at 200 Hz with peak to peak amplitudes $\geq 25 \mu\text{m}$. Fusimotor fibres were first detected when spindle afferents could be excited by electrical stimulation of natural ventral root filaments, both before and during the application of ramp stretches to the muscle. They were classified as static or dynamic if they caused a decrease or pronounced increase of the dynamic index of the afferent's ramp response. No further classification into the six categories of Emonet-Dénand *et al.* (1977*b*) was attempted. However, clear-cut effects, which in most cases would presumably have fallen into their categories I and VI were preferentially selected. Functionally single efferents with conduction velocities in the γ -range were isolated, following standard methods, by subdividing filaments which gave manifest excitation. Because of the initial presence of extrafusal tension the selection of powerful efferents with a pronounced excitatory effect on the mean rate of afferent discharge was clearly favoured (cf. Crowe & Matthews, 1964*a*; Brown *et al.* 1965). This bias should have been equally effective with either kind of fusimotor fibre. It was a common observation that at long muscle lengths static fibres had a stronger excitatory action than dynamic fibres (cf. Results). Often this was quite obvious already during the isolation of single units. In order to achieve some balance between static and dynamic excitation of the same afferent, the most powerful dynamic yet not necessarily the strongest static axons were selected, if there was a choice at all. The difference in the excitatory strength which is emphasized in this paper is therefore likely to be genuine, and the size of the excitation evoked by static fibres is, if anything, underestimated.

Mechanical and electrical stimulation. The muscle was alternately stretched and released using an electromagnetic servo-controlled stretcher (cf. Goodwin *et al.* 1975; Hulliger *et al.* 1977*a*).

Repetitive ramp stretches with amplitudes of 7 or 8 mm and peak plateau durations of 30–120 sec were used to bring the muscle to a length corresponding to 2 mm below the physiological maximum (in short – 2 mm). The level of mechanical noise in the stretcher was kept below 0.1 and 0.5 μm for frequencies below and above 10 Hz. To this end heavily low-pass filtered input signals (ramps) were used. For data collection, fusimotor stimulation was carried out with the muscle held at constant length (– 2 mm). Standard apparatus was used when efferent fibres were electrically stimulated at constant rate. When the pattern of stimulation had a rectangular time course, with the rate of activation alternating between two separate levels (cf. Fig. 4, bottom record), the stimulator was driven by a voltage-controlled oscillator, which performed an undistorted voltage to rate conversion. Its input voltage was rectangular, and generated either by a Digitimer (Devices, 3290) or by a general purpose signal generator (Feedback Ltd, TWG 300). In the experiments with rectangular stimulation both the repeat frequency and the amplitude (difference between two levels of activation) were adjusted individually for each fusimotor fibre, in order to evoke responses which were sufficiently distinct for the analysis of their time course. Owing to this the present data are not fully standardized with respect to these parameters.

Analysis. Data collection and preliminary analysis were carried out on-line with the aid of a PDP 12 computer. At the same time, the afferent impulses and the stimulus markers were recorded as standard pulses on an analogue tape recorder, for additional off-line analysis. Cycle histograms, displaying the averaged response of the afferent fibre to an integral number of cycles of rectangular stimulation, were constructed on-line by counting the number of impulses occurring in each of 360 bins of constant width. Adjacent narrow bins were then lumped together to give histograms of either 60 bins, for the standard display of the responses (cf. Figs. 5 and 6), or of 120 bins, for the quantitative analysis of the time course of the response with exponential curve fitting. For subsequent numerical analysis these impulse counts were then normalized and expressed as a rate of discharge in relation to the phase of the cycle (cf. Fig. 5). Normally each histogram was based on 10–20 sec recording, beginning 1–2 sec after the onset of fusimotor stimulation and 3–5 sec after the stretching of the muscle. Occasionally, when the rectangular stimulation had a repetition frequency below 0.5 Hz, longer periods of data collection (up to 60 sec) were used. Both the original and the lumped cycle histograms were stored on digital magnetic tape for off-line computations.

The time course of the rising and falling phases of the rectangular responses was assessed by the time constant of a single exponential fitted to normalized histograms of 120 lumped bins. In order to reduce the random variability between successive bins the responses were smoothed using a rectangular smoothing window which was moved across the histogram. For each bin which was analysed the window included 3 or 6 adjacent bins on either side. The mean rate of discharge within this window was then calculated and allocated to the centre bin of the window. Thus histograms of 120 bins each displaying the averaged response of overlapping sections of the original histogram were obtained. The width of the windows employed was 21 or 39 degrees. Conventional methods of curve fitting were then used to obtain the time constants of these smoothed responses.

Post-stimulus time (pst) histograms, relating the afferent firing to the time of occurrence of fusimotor stimuli delivered at constant rate, were constructed off-line. They were used to assess the driving tendency exerted upon the afferent by fusimotor impulses (cf. Kuffler, Hunt & Quilliam, 1951; Crowe & Matthews, 1964*b*; Goodwin *et al.* 1975; Emonet-Dénand, Hulliger, Matthews & Petit, 1977*a*). With such maintained fusimotor stimulation the onset of the period of data collection was the same as with rectangular stimulation. The length of the period of sampling was chosen, so as to cover at least 300 inter-spike intervals, and it was usually 10 sec. At low rates of stimulation, when fatigue of fusimotor action did not occur, it was occasionally extended to 20 sec, and if at high rates of activation afferent fatigue was manifest, it was restricted to 6 sec. The pst histograms were normalized by computing the probability of firing (in impulses/sec) for each of the 45 bins normally employed. The extent of modulation (cf. Fig. 1) was assessed by computing the r.m.s. deviation of the histogram from the mean rate of discharge. The latter represents the histogram which would be expected in the absence of any modulation. The r.m.s. deviation gives an averaged measure of the bin by bin difference between the histogram and the mean. It has been shown to be proportional to the harmonic power contained in all the Fourier coefficients (m_n) beyond the zero term (Hulliger, 1976):

$$\text{R.M.S. deviation} = \sqrt{\left(\frac{1}{2\pi} \int_0^{2\pi} \{h(t) - f_0\}^2 dt\right)} = \frac{1}{\sqrt{2}} \sqrt{\sum_{k=1}^{\infty} m_k^2}$$

$h(t)$ denotes the histogram, and f_0 (mean rate of firing or zero term) and m_k (higher harmonics) describe the Fourier coefficients.

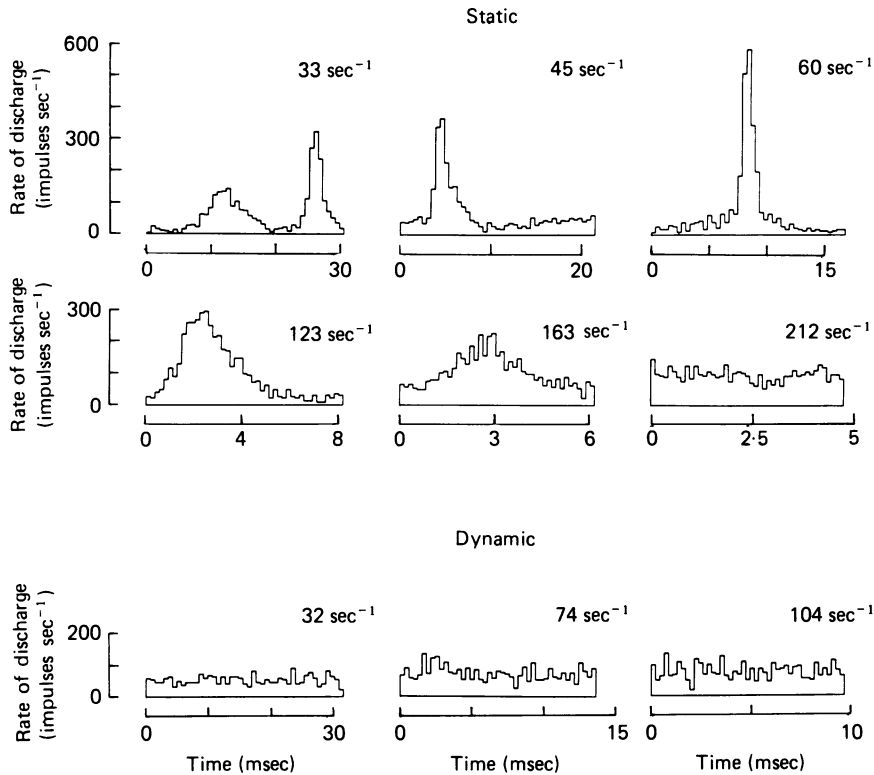


Fig. 1. Pst histograms for fusimotor stimulation of a single static (top and middle row) and dynamic (bottom row) fibre, exciting two separate primary muscle spindle afferents. For different rates of stimulation the duration of the inter-stimulus interval is plotted along the abscissa. The probability of firing (in impulses/sec) is plotted along the ordinate. The duration of the sampling period was 10 sec, except for static stimulation at 33 and 45/sec (20 sec).

RESULTS

Fusimotor stimulation at constant rate

Post-stimulus time histograms. Fig. 1 shows typical examples of pst histograms with increasing rates of stimulation of single static and dynamic fusimotor fibres exciting separate primary spindle afferents. During stimulation the muscle was held at constant length, 2 mm below its physiological maximum. Static fusimotor activation (top and middle row) evoked responses which were clearly modulated for rates up to 163/sec, indicating a consistent time relationship between the afferent discharge

and the fusimotor impulses. At low rates of stimulation the histograms exhibited several peaks (as in Fig. 1: two peaks at 33/sec). Single peaks were found at intermediate and high rates. In contrast, the dynamic fibre did not evoke modulation of histograms at any rate of stimulation. This is indicated by the flatness of the histograms in Fig. 1 (bottom row). In spite of this, the mean rate of afferent discharge increased progressively, showing the familiar dependence on rate of stimulation of the fusimotor excitation. Such absence of manifest phasic modulation was found with eighteen out of nineteen dynamic fibres. In contrast, the static-induced effects (twenty-eight fibres) were not at all uniform. Secure 1:1 driving of the afferent unit could occur over a range of rates of stimulation. Under such conditions the histograms exhibited even sharper peaks than in Fig. 1 at 60/sec, so that the majority of bins remained empty while all the impulses occurred in a narrow segment of the inter-stimulus interval. In other examples of static action the modulation tendency was as pronounced as in Fig. 1, yet much weaker effects were encountered as well, and in the extreme static *pst* histograms could be completely flat at all rates of stimulation. The occurrence of histogram modulation was a feature of static fibres and not of the primary afferent units, since modulation by static action and lack of modulation by dynamic action was repeatedly observed with individual primary afferents when either kind of fusimotor fibre was available for stimulation.

For different rates of static stimulation the dominant peak of the response occurred with approximately constant delay from the fusimotor stimulus, which in the example of Fig. 1 was around 23 msec. This is not immediately obvious since, with the normalized display of histograms the time scale expanded progressively and since at rates above 30/sec the delay usually covered more than one stimulation cycle. For 24 units the histogram modulation was sufficiently distinct at intermediate and low rates of stimulation to permit a reliable estimate of the absolute delays between the stimulus and the onset of modulation. The values ranged from 11.4 to 24.6 msec (mean 17.3, s.d. 3.0). After allowance for efferent and afferent conduction delays between the muscle nerve electrode and the root electrodes, peripheral utilization times ranging from 4.8 to 11.5 msec (mean 8.1, s.d. 2.0) were obtained.

The peripheral utilization time provides only an upper estimate of the intrafusal delays (usually attributed to the neuromuscular transmission and the activation of the contractile apparatus), since it is also affected by additional conduction delays between the peripheral stimulating electrode close to the muscle and the spindle within the muscle. While the distances involved were likely to be small (2–5 cm), any tapering of the peripheral branches, mainly of the γ -fibres (cf. Barker, 1974), could nevertheless render these delays appreciable.

Occasionally the shape of *pst* histograms was not unlike the time course of a muscle twitch, as in Fig. 1 for static stimulation at 123/sec. For a number of reasons it seems, however, unlikely that the histogram could faithfully reflect the time course of unfused tetanic contractions. First, the likely dynamic sensitivity of the mechano-electrical transducer (cf. Hunt & Ottoson, 1976; also Kirkwood, 1972; Smith & Koles, 1974) would distort the transient signal of a twitch. Further, any phase-locking of the afferent impulses to a particular phase of the twitch cycle would cause additional distortions. This could especially happen at rates of discharge close to the rate of fusimotor stimulation or its harmonics and subharmonics (cf. the occurrence of two peaks in the histogram of Fig. 1 with static stimulation at 33/sec). Finally it is not excluded that the phasic component in *pst* histograms could be partly due to direct electrical coupling between intrafusal muscle fibres and the afferent terminals (cf. Ito, Kanamori & Kuroda, 1974).

Measure of histogram modulation. The depth of modulation of *pst* histograms was assessed by computing the r.m.s. deviation of the histogram from a non-modulated horizontal line representing the mean rate of firing (cf. Methods). This term provides a measure of modulation which agrees satisfactorily with the qualitative evaluation

of modulation on the basis of simple inspection. This can be seen from Fig. 2*A* where the values of R.M.S. deviation are plotted against the rate of stimulation. The initially sharply rising and then falling curve (labelled γ_s characterizes the static fibre illustrated in Fig. 1. The nearly horizontal curve at the bottom (labelled γ_D) describes the dynamic fibre of Fig. 1. In the absence of manifest modulation the R.M.S. deviation is low (10–20 impulses/sec) and attributable to the background noisiness, due to

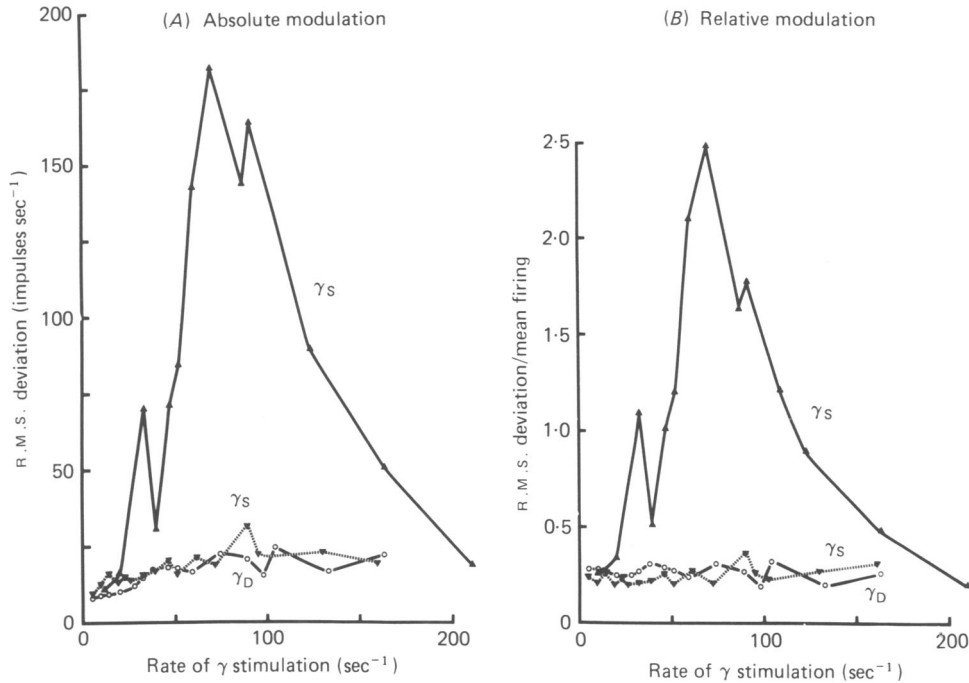


Fig. 2. The effects of varying the rate of fusimotor stimulation on the modulation of pst histograms. The action of two static axons (\blacktriangle — \blacktriangle , modulating, same fibres as in Fig. 1; \blacktriangledown — \blacktriangledown , non-modulating fibre) and one dynamic axon (\circ — \circ , same fibres as in Fig. 1), each on a separate primary spindle afferent, are illustrated. *A*, absolute modulation, measured by the R.M.S. deviation. *B*, relative modulation, expressed as the ratio of R.M.S. deviation and mean rate of firing measured in the same histogram.

the variability between successive bins. In Fig. 1 this is seen for the dynamic histograms and for the static response obtained at 212/sec. In contrast, modulations spanning the whole cycle of stimulation cause an increase of the deviation well above the noise level. Since for a given shape of the whole histogram the absolute value of the deviation increases in direct proportion to the mean rate of discharge (Emonet-Dénand *et al.* 1977*a*), the figures for relative modulation (deviation/mean firing) were also calculated and are illustrated in Fig. 2*B*. Qualitatively there is little difference between the graphs of absolute and relative modulation, as both appear to reflect the degree of histogram modulation satisfactorily. They differ, however, with respect to quantitative detail. For the dynamic fibre the curve of relative modulation runs horizontal, whereas the absolute modulation increases very gradually with the rate of stimulation, paralleling the increase in the mean (not illustrated). Thus the relative

deviation appears to be a more independent indicator of both the degree of modulation and the mere variability of flat histograms. Fig. 2 also contains information on another static fibre whose curves of absolute and relative deviation illustrate the uniform absence of modulation. This renders them hardly distinguishable from the profile of the dynamic fibre. The two static fibres of Fig. 2 indicate the range of effects of static fusimotor action, stretching from deeply modulating to completely non-modulating.

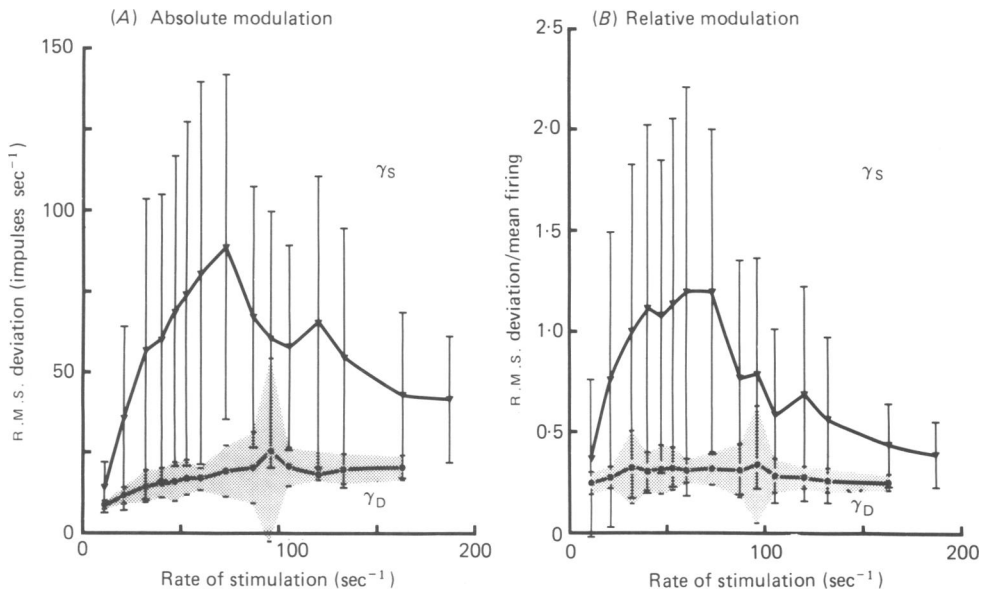


Fig. 3. Averaged histogram modulation curves to show the wide range of static action and the relatively narrow range of dynamic action. Data from thirty-four primary endings, twenty-eight static and twenty dynamic fibres. Fourteen afferents were excited by a pair of two fusimotor fibres, of which twelve by a pair of static and dynamic axons. One dynamic fibre was a beta axon (conduction velocity 58 m/sec, tetanic tension 30 mN). Since not all fibres were stimulated at precisely the same rates, data for narrow classes of rate of stimulation were pooled. The class width was always below 5/sec for rates below 50/sec, and below 10% of the median of the class for rates above 50/sec. Within each class a single fibre is represented not more than once. The mean number of observation per class was 18.1 (range 9–28) for statics, and 12.6 (range 6–20) for dynamics. The analysis is based on 271 histograms for static fibres and 177 histograms for dynamic fibres. For periods of data collection cf. Methods. The bars (and shaded area for dynamics) show the standard deviation of the measure of modulation. *A*, absolute modulation; *B*, relative modulation, as in Fig. 2.

More comprehensive information on the whole sample of fibres studied is given in Fig. 3, where mean and s.d. of absolute (3A) and relative (3B) deviation are plotted against the rate of stimulation. Static fibres clearly gave higher values of absolute modulation than dynamic fibres, over the whole range of stimulation rates (Fig. 3A). This difference persisted in the graphs of relative modulation (Fig. 3B) where allowance is made for the usually larger excitatory effect of static fibres on the mean rate of firing (see below, Fig. 8). Notably the scatter associated with static action is

appreciably larger than with the dynamic effects. This reflects the already mentioned non-homogeneous nature of static action as regards the manifestation of histogram modulation. It bears emphasis that the static fibres examined in the present report were all unambiguously classified by their typical effects on the afferent ramp response (cf. Methods). Moreover, they behaved uniformly as to their effects on the frequency response of the primary afferent for small amplitudes of stretching (Goodwin *et al.* 1975), and as to their action on the primary afferent's sensitivity to low-frequency sinusoidal stretching covering a wide range of amplitudes (Hulliger *et al.* 1977*a, b*). The dynamic fibres of Fig. 3, which were equally homogenous in their effect on the afferent response to stretching, acted much more uniformly on pst histograms, as the consistently low figures for deviation exhibited little scatter for most rates of stimulation. The relatively high values of s.d. at 87 and 96/sec were caused by a single fibre which elicited appreciable modulation at these rates. In this case, as well as with other responses where some, albeit much weaker, modulation occurred, the rate of afferent firing was always close to the rate of stimulation. It is therefore likely that comparatively weak phasic responses to fusimotor stimuli were brought into relief by carrier-dependent resonance. This is a specific enhancement of the response to a repetitive signal, which occurs when the driving frequency of the input is close to the mean rate of discharge (cf. Poppele & Chen, 1972; Goodwin *et al.* 1975).

Rectangular pattern of fusimotor stimulation

Action on single afferents. Single fusimotor fibres were stimulated repeatedly at a rate which alternated between two levels (rectangular pattern of stimulation, cf. Fig. 4, bottom diagrams, repeat frequency 1.9 Hz). The response of primary afferents showed an approximately rectangular time course. This is illustrated in Fig. 4 (top diagrams), where the instantaneous rate of firing alternates between two levels, almost in phase with the rectangular stimulation. Representative examples are given for a dynamic (Fig. 4*A*) and a static fibre (Fig. 4*B*), which excited the same afferent. The responses were obtained with the muscle at constant length (-2 mm). It is obvious that the size of the responses was much larger during static activation, in spite of the appreciably smaller amplitude of rectangular stimulation (difference between the two levels of activation). In contrast, the time course during the rising and falling phase of the responses was very similar for the two types of fusimotor fibres. The present mode of fusimotor stimulation differs from the patterns of rectangular tetanic stimulation widely illustrated in the literature (cf. e.g. Crowe & Matthews, 1964*a, b*; Lewis & Proske, 1972), since the alternation takes place between two separate levels of activation, rather than between a passive and an activated state. Also, the present repeat frequency was appreciably higher. Notably, the rising phases of the responses exhibited no consistent tendency to overshoot with clear transient peaks. In contrast, initial peaks in the instantaneous rate of firing were very prominent in the responses of Lewis & Proske (1972), right at the onset of tetanic stimulation with rectangular time course, following a period of rest.

For quantitative analysis the responses to successive cycles of rectangular stimulation were averaged and displayed as cycle histograms, showing the probability of firing (in impulses/sec) throughout the cycle of stimulation. This is illustrated in Fig. 5 for a separate afferent, which was also excited by both a dynamic and a static fibre.

In this case the rectangular repeat frequencies were 0.5 Hz (Fig. 5*A*) and 1 Hz (Fig. 5*B*). Altogether 117 averaged responses to various amplitudes and frequencies of rectangular stimulation were examined (seventy-two in thirteen dynamic fibres, forty-five in eleven statics). For 101 of the 117 histograms the repeat frequency was between 0.5 and 2 Hz. Within this range no systematic effect of frequency was noted, and the responses were therefore pooled for the quantitative analysis.

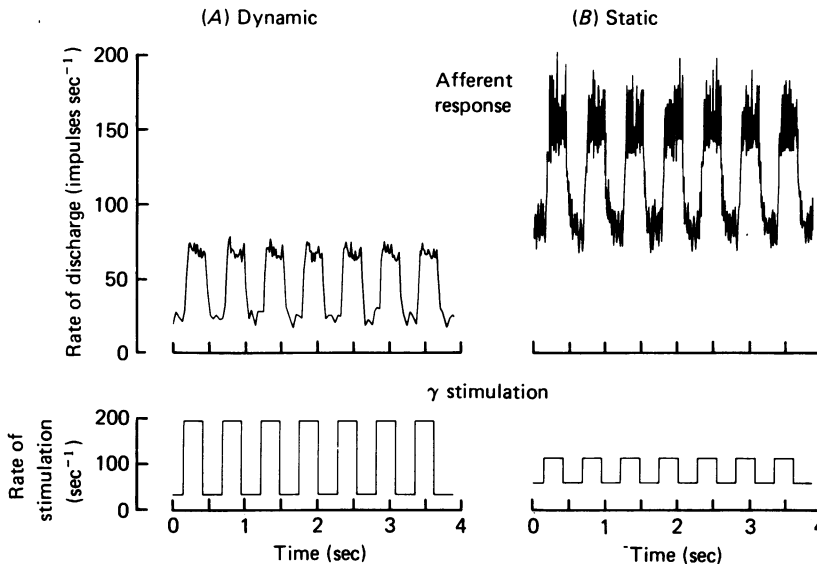


Fig. 4. Responses of a primary spindle afferent to rectangular stimulation of a single dynamic (*A*) and a single static (*B*) fusimotor fibre. The time course of the instantaneous rate of discharge is shown in the upper graphs. The rectangular stimulation with a repeat frequency of 1.9 Hz is illustrated schematically in the lower diagrams.

The most prominent feature in Figs. 4 and 5 is the difference in the excitatory strength of dynamic and static fibres. The afferent responses reveal a sensitivity to rectangular changes in the rate of fusimotor excitation, which is much higher for static than for dynamic axons. This is obvious from the clearly larger changes in afferent firing which were elicited by substantially smaller amplitudes of rectangular stimulation. This fusimotor rate-sensitivity was measured as an output/input ratio (change in maintained firing over change in rate of stimulation, in impulses per stimuli). The changes in the rate of afferent discharge were measured in cycle histograms. Only the maintained levels of firing were relied on, and the transient responses were ignored (for details, cf. Fig. 7, legend). The values of sensitivity for the static axons exceeded the dynamic values by factors of 4.4 (Fig. 4), 7.5 (Fig. 5*A*), and 8.2 (Fig. 5*B*). In agreement with the responses of Fig. 4 none of the histograms examined showed distinct transient peaks in response to the rising phase of rectangular stimulation. Since the cycle histograms were based on a limited number of bins each bin gives the averaged response for an appreciable section (40 msec at 1 Hz) of the cycle of stimulation. This could have obscured small transient peaks which might have been expected with static action. However, the inspection of the raw histograms,

which were based on 360 bins (with a bin width of 2·8 msec at 1 Hz) did not reveal any conspicuous fast transients either.

Fusimotor rate-sensitivity for a range of afferents. The examples of Figs. 4 and 5 were typical for the whole sample of fusimotor axons studied. This is documented in Fig. 6 where the mean response to 1 Hz rectangular stimulation is shown for eight

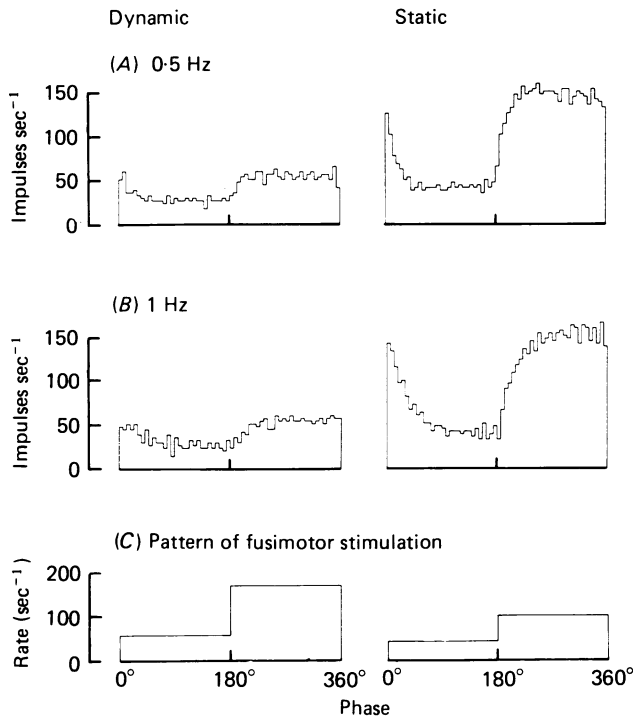


Fig. 5. Cycle histograms showing the responses of a single primary spindle afferent to rectangular stimulation at 0·5 Hz (*A*) and 1 Hz (*B*). Left, activation of a single dynamic axon, right, activation of a single static axon. The pattern of stimulation was the same at either frequency and is illustrated schematically in *C*. The responses were averaged over ten successive cycles of stimulation. The increase in the maintained rate of discharge, measured from the adapted phases of the responses, was 27 impulses/sec (at 0·5 Hz) and 28 (1 Hz) for the dynamic fibre, and 105 (0·5 Hz) and 110 (1 Hz) for the static fibre. The time constants were 43 msec (rising phase) and 94 msec (falling phase) for the dynamic, and 74 msec (rising phase) and 72 msec (falling phase) for the static fibre.

dynamic fibres (Fig. 6*A*) and eight static fibres (Fig. 6*B*). The mean amplitude of rectangular stimulation was $99/\text{sec} \pm 10$ s.d./sec (range 90–114/sec) for the dynamic axons, and 55 ± 6 s.d. (range 44–60/sec) for the static fibres. The mean fusimotor rate-sensitivity of the afferents was 0·25 impulses/stimuli (dynamics) and 1·56 (statics). Thus, on average the fusimotor rate-sensitivity for static axons was 6 times higher than for dynamic fibres.

The pronounced differences in the responses of Fig. 6*A* and *B* might have resulted from a biased selection of primary endings (for instance with an examination of static or dynamic

effects on afferents, which were unduly sensitive or insensitive respectively). This seems unlikely since half of the responses averaged in Fig. 6 are based on pairs of static and dynamic fibres exciting the same afferent. When only these responses were averaged, nearly identical results were obtained. In particular the values for fusimotor rate-sensitivity were 0.28 impulses/stimuli (dynamic) and 1.59 impulses/stimuli (static), with a static/dynamic ratio of 5.6.

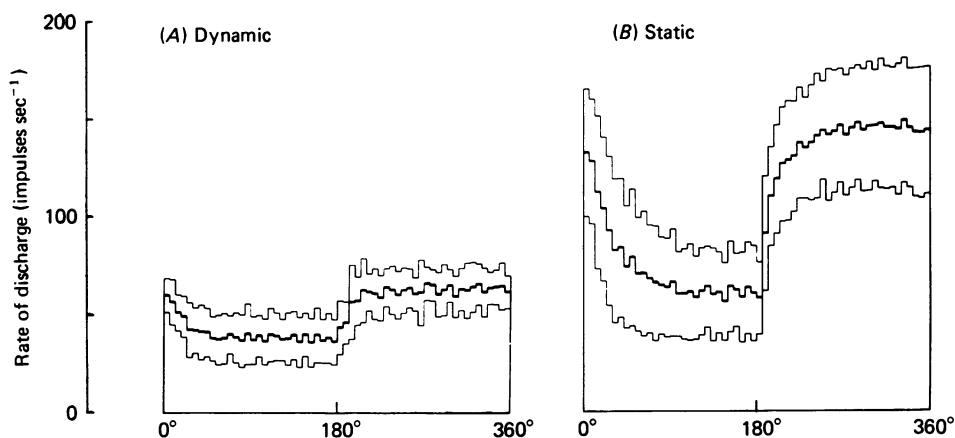


Fig. 6. Averaged cycle histogram responses to 1 Hz rectangular fusimotor stimulation to show the degree of consistency of the findings. Eight dynamic (*A*) and eight static (*B*) fibres, exciting twelve separate primary afferents. The mean amplitude of stimulation was 99/sec (range 90–114) for dynamics and 55/sec (range 44–60) for statics, and all the responses available within a 15% range of the mean amplitude of stimulation were included in the present diagram (both responses of Fig. 5*B* were included; for the fibres of Fig. 4 appropriate 1 Hz responses were available only for the static). The lower and higher stimulation rates of the rectangular pattern (cf. Fig. 5) were 43 ± 17 s.d./sec and 142 ± 23 for dynamics, and 41 ± 14 s.d./sec and 96 ± 11 for statics. Individual cycle histograms were first normalized to give the probability of firing (in impulses/sec) for each bin of the cycle (cf. Fig. 5). Mean (thick line) and s.d. (thin lines) were then calculated for each bin.

For the computation of the averaged responses of Fig. 6 only those units were selected, which had been tested with rectangular amplitudes falling within the 15% range of the mean amplitude of stimulation given above. The required conditions were not met for all endings since during the experiments the amplitude of rectangular stimulation was usually adjusted, in order to elicit responses which were large enough to permit the analysis of their time course (cf. below). Also, not all units were studied at 1 Hz, since initially attention was focused on the possibility that dynamic action might also exhibit slower excitatory components than those demonstrated in Figs. 4–6. Therefore, some fibres were only studied at frequencies between 0.1 and 0.5 Hz. Nevertheless, it is shown in Fig. 7 for a range of rectangular amplitudes, that the data of Fig. 6 reflect the properties of the whole sample of units quite faithfully.

The scatter diagram of Fig. 7 describes the properties of the whole sample of fusimotor fibres examined (thirteen dynamic axons, eleven static axons, acting on sixteen primary endings of which seven were excited by a pair of fibres of either kind, and one by two separate static axons). Each fusimotor fibre is represented by two points (connected by a straight line) which were derived from the histograms with the smallest and largest rectangular amplitudes employed. Notably, the static and dynamic fibres form two almost non-overlapping populations, exhibiting the already

described pronounced differences in fusimotor rate-sensitivity. The mean values of sensitivity for all the points of Fig. 7 are 0.29 impulses/stimuli for the dynamic fibres and 1.35 for the static fibres. These figures were calculated as ratio of the mean values of increase in firing and of amplitude of stimulation, which were 25 ± 15 and 86 ± 14 impulses/sec for dynamics, and 65 ± 31 and 48 ± 24 impulses/sec for statics.

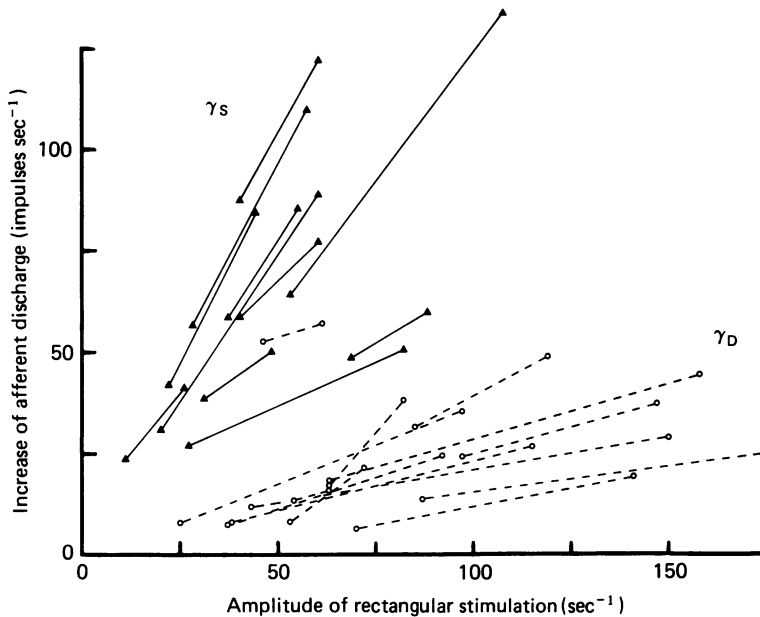


Fig. 7. Scatter diagram to show the difference in the excitatory strength of static ($n = 11$) and dynamic ($n = 13$) fusimotor fibres. Each axon is represented by two points: \blacktriangle — \blacktriangle , static; \circ — \circ , dynamic. The increase in maintained firing was measured from cycle histograms (cf. Fig. 5). The adapted phases of the response were selected by eye (ignoring the transient components of the rising and falling phase). Their length depended on the time constant of the transients, but it was usually more than 70% of a half cycle. Twenty-three of the twenty-four static points were from responses at 1 Hz (one at 2 Hz). Twenty-one of the twenty-six dynamic points were available at 1 Hz (two at 2 Hz, 3 at 0.5 Hz or below). The mean values for the lower and higher rates of the rectangular pattern of stimulation were, for the small amplitude points 55 ± 12 s.d./sec and 89 ± 20 s.d. for statics and 57 ± 14 s.d./sec and 115 ± 24 s.d. for dynamics. For large amplitudes of stimulation, 42 ± 12 s.d./sec and 104 ± 24 s.d./sec for statics and 35 ± 11 s.d./sec and 148 ± 40 s.d. for dynamics.

The static/dynamic ratio of fusimotor rate-sensitivity was 4.7, in agreement with the value for the responses of Fig. 6. Thus the examples of Figs. 4–6 are indeed representative for the present sample. The separation of static and dynamic action in Fig. 7 is very distinct. This does, however, not necessarily imply that rectangular fusimotor stimulation provides an unambiguous method for the classification of the two kinds of fibres, since the present population of axons does not systematically cover the whole range of fusimotor effects (Emonet-Dénand *et al.* 1977*b*; cf. also Methods).

The variations in the amplitude of stimulation in the data of Fig. 7 were mainly achieved by raising the upper level of the rectangular pattern, whereas the lower level was approximately

constant (around 50/sec, cf. legend Fig. 7). Thus with large amplitudes of rectangular activation rates around 200/sec were reached with several of the dynamic fibres. This might have caused saturation of the afferent response. But then extrapolation of the straight lines of Fig. 7 to zero rate should consistently give positive intercepts on the y axis. This seems not to be the case. Also, amplitude curves for units with three or more responses at the same frequency did not show consistent saturation at the higher amplitude (five statics and nine dynamics, examined in sixteen curves). On the whole the linearity in the relationship between amplitude of stimulation and change in the maintained firing appeared satisfactory. Yet the present material is too limited to permit firm conclusions on the question of linearity.

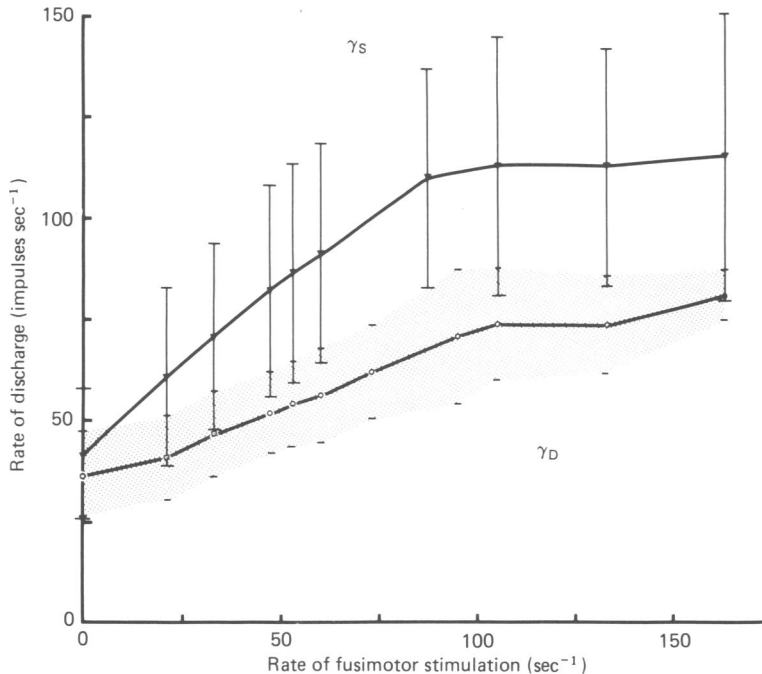


Fig. 8. Averaged curves showing the dependence of the mean rate of discharge on the rate of maintained fusimotor stimulation for the whole sample of twenty-eight static and twenty dynamic axons. Vertical bars (static fibres) and shaded area (dynamic fibres) give the s.d. around the mean rate of firing (solid lines). Same units and same periods of data collection as in Fig. 3. Also same classes of rate of stimulation as in Fig. 3. In contrast to Fig. 3, only those classes with sufficiently high numbers of observations are illustrated to avoid additional scatter due to uneven sampling. The mean number of observations per rate-class was 25 ± 3 s.d. (range 21–28) for statics, and 15 ± 3 (range 11–20) for dynamics.

Fusimotor rate-sensitivity with maintained stimulation

The static/dynamic ratio for fusimotor rate-sensitivity determined with rectangular stimulation is much larger (4.7) than the values reported for stimulation at constant rate (range 1.5–2.5; cf. Lennerstrand & Thoden, 1968*a, b*; Andersson *et al.* 1968; Emonet-Dénand *et al.* 1977*b*). In order to decide whether this was attributable to some bias of the present material or to the difference in the mode of stimulation the averaged sensitivity of the whole sample for changes in the maintained rate of stimu-

lation was also determined. The dependence of the adapted rate of discharge on the rate of maintained fusimotor stimulation is shown in Fig. 8. A nearly linear relationship was found for rates up to 105/sec for dynamic axons, and up to 87/sec for static axons. The slope and thus the fusimotor rate-sensitivity during steady stimulation was determined by linear regression analysis over the linear range. The figures were 0.33 impulses/stimuli for dynamic fibres and 0.75 impulses/stimuli for static fibres, with a static/dynamic ratio of 2.24. Very similar graphs (not illustrated) and nearly the same values for rate-sensitivity were found for the subsample of units which were also tested with rectangular stimulation (cf. Fig. 7). The figures were 0.37 impulses/stimuli for dynamics and 0.78 impulses/stimuli for statics, with a static/dynamic ratio of 2.11.

The comparison of the rates of discharge during rectangular and maintained stimulation at the same rate showed, for static fibres, that with the lower rate of rectangular activation the afferent firing was always below the levels obtained with maintained stimulation (nine units). With the higher rate of rectangular activation, on the other hand, the rate of discharge was usually above the level reached with maintained stimulation (seven out of nine units). Thus the higher value of rate sensitivity during alternating as compared with steady stimulation was due to a depression of firing at the lower and to an enhancement at the higher level of rectangular activation. With dynamic fusimotor stimulation the results of the same comparison were less uniform. However, for eight out of ten units the rate of discharge during rectangular activation was the same or less than with maintained stimulation both at the lower and higher level of rectangular activation.

The considerable scatter around the mean rates of firing in Fig. 8 seems largely attributable to variations in the resting discharge of the primary afferents (cf. s.d. at zero rate). The ranges were 15–72 impulses/sec for the endings stimulated by static axons, and 25–64 for those activated by dynamic axons. In addition, the curves for individual afferents could show appreciable deviations from linearity. In particular, during static stimulation the occurrence of secure driving or some driving tendency by the fusimotor stimuli (cf. Fig. 1, static at 60/sec) could give rise to very non-linear or even non-monotonous relationships.

Time course of rectangular response

Figs. 5 and 6 illustrate qualitatively that significant differences between static and dynamic action as regards the time course of the rectangular responses do not exist, since the time to peak for both rising and falling phase of the responses is rather similar for either type of fusimotor fibre. A quantitative confirmation of this impression was obtained when single exponentials were fitted to the two phases (cf. Methods). For each fibre all the histograms with sufficiently pronounced increases in the maintained rate of discharge were analysed, and the values of the time constants were averaged separately for the rising and falling phase. For the two groups of fusimotor axons the mean values of the time constants of the rising phase were 34 ± 18 s.d. msec (dynamics, $n = 13$) and 58 ± 22 (statics, $n = 11$). The values for the falling phase were 49 ± 27 s.d. msec (dynamics) and 59 ± 22 (statics). The differences between dynamic and static action were not significant for either phase (unpaired t test, $P > 0.05$). Nor were the differences between rising and falling phase significant for either type of fusimotor fibre (paired t test, $P > 0.05$). Thus the values for the two groups of fibres overlapped almost completely (cf. also Fig. 9). When the values for rising and falling phase were compared for individual fibres, a significant correlation was found only for the static axons (correlation coefficient = 0.7, $P < 0.05$; in contrast, dynamics: coefficient = 0.28, $P > 0.05$). The data in Fig. 9 were therefore plotted separately for the two phases.

By the choice of a single exponential for curve fitting it is not implied that this was necessarily the best fitting curve. Yet it appeared to give an adequate approximation of the dominant transient components of the rectangular response. The scatter between successive bins in the present responses (cf. Fig. 5, dynamic fibre) precluded a meaningful evaluation of alternative describing functions.

The use of a smoothing window for the assessment of the time constants could conceivably have distorted the histograms by removing any fast transient components of the response to

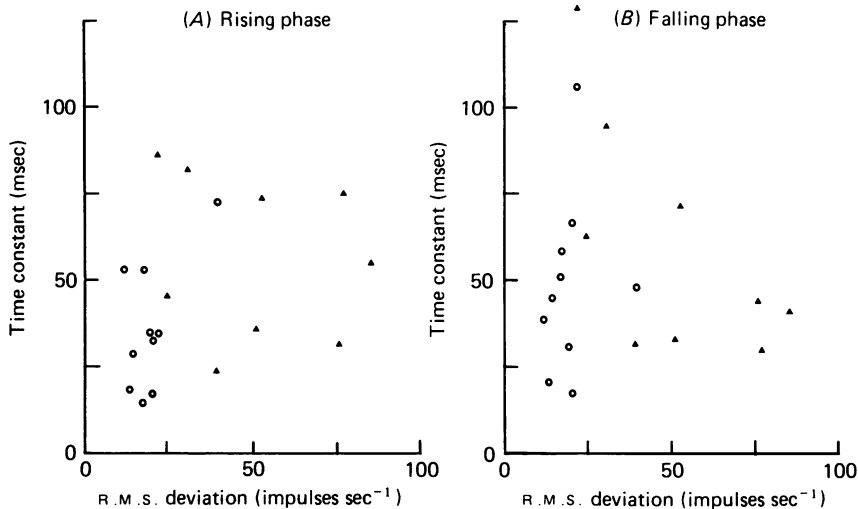


Fig. 9. The relationship between the degree of pst histogram modulation and the magnitude of the time constants of the rectangular responses. Ten dynamic (\circ) and nine static (\blacktriangle) fibres for which either kind of data were available. For each fibre the values of R.M.S. deviation were averaged over the range of rate of stimulation, where static induced modulation was pronounced and sufficiently documented for the present sample (60–105/sec, cf. Fig. 3). For fifteen fibres (including all statics) data from 60, 87 and 105/sec were available, for the remaining fibres data from the nearest rate within this range were taken. The coefficients of correlation were, for *A*, 0.559 (dynamics, $P > 0.05$), -0.191 (statics, $P > 0.05$), and for *B*, 0.202 (dynamics, $P > 0.05$), -0.661 (statics $P < 0.05$). Only absolute modulation illustrated (cf. Fig. 3*A*). The diagrams and statistics for relative modulation (cf. Fig. 3*B*) were nearly identical.

rectangular stimulation. However, inspection of the raw histograms (with a bin width of 2.8 msec at 1 Hz) indicated that such fast components were not present (cf. also text to Figs. 4 and 5), and that the values of the time constants qualitatively agreed with the time course of the responses prior to smoothing.

In initial experiments with dynamic axons responses to rectangular stimulation at lower frequencies (0.09–0.3 Hz) were also investigated, in order to detect any slowly rising or falling components in addition to the transients described thus far. In sixteen responses (four fibres) no significant signs of slower response components could be found. In contrast, responses to stimulation of static axons at 0.5 and 1 Hz did occasionally exhibit slow components in the direction opposite to the fast transients (twelve responses, six fibres). Thus the fast component of the rising phase could be followed by a slow decay which had, however, a much smaller amplitude. A typical example is illustrated in Fig. 5*A* (static fibre at 0.5 Hz). Such slow adaption of the responses was always most pronounced with the largest amplitudes of rectangular stimulation.

The similarity between static and dynamic action as regards the time course of the rectangular responses seems to run counter to the pst histogram data, since the

modulation of the histogram responses by static fibres is usually taken to indicate that their intrafusal action is faster than that of dynamic fibres. The analysis of histogram modulation had shown that the group of static axons was not homogenous in this respect (cf. Fig. 3). It was therefore conceivable that at least those static fibres which caused distinct modulation of pst histograms might evoke faster rectangular responses than dynamic fibres. The scatter diagrams of Fig. 9 show that the expected inverse relationship between the extent of modulation and the magnitude of the time constant was present, but only during the falling phase. Even so, the fast and deeply modulating statics still did not exceed the speed of dynamic action. The scatter of the data and the size of the sample did not warrant further quantitative analysis. Yet it is safe to reiterate that the two samples of fusimotor fibres did not differ significantly in their speed of rectangular responses.

DISCUSSION

Speed of fusimotor action

The investigation of the effects of individual fusimotor stimuli on the discharge from primary spindle afferents agrees with the frequencygram analysis of Bessou *et al.* (1968) and Emonet-Dénand & Laporte (1969). Static fibres could cause appreciable modulation of pst histograms, whereas dynamic fibres did so only very rarely and then to a lesser degree. The present analysis of the modulation of post-stimulus histograms gave a quantitative measure of the extent of modulation, and it indicated that apparently pure static action could be associated with any degree of histogram modulation. This confirms and puts on a broader statistical basis the view that histogram modulation or driving of the afferent by the efferent axon was not a prerequisite of static action (Goodwin *et al.* 1975; Emonet-Dénand *et al.* 1977*a, b*).

If the degree of histogram modulation was interpreted as a faithful measure of the speed of intrafusal contraction the responses to fusimotor stimulation with rectangular time course would be paradoxical, since the groups of static and dynamic fibres did not differ from each other in the time course of the responses. If anything, dynamic fibres were faster. At first sight the findings with rectangular stimulation also seem to be in conflict with reports on the speed of shortening of intrafusal fibres in isolated spindle preparations (Bessou & Pagès, 1975; Boyd, 1976*a*; Boyd *et al.* 1977). But the disagreement is, in fact, with the conclusions drawn from the results, and not with the observations themselves. Bessou & Pagès found that the velocity of displacement of intrafusal reference points with tetanic activation of static axons was appreciably larger than with dynamic activation. However, the absolute velocity, but not the time constant or the time to peak, at the onset of tetanic activation depend on the number of contracting sarcomeres relative to the number of non-contracting sarcomeres in series, and thus on the relative length of the activated segment. This is likely to be substantially longer for fibres activated by static axons (chains and bag 2; cf. Brown & Butler, 1973, 1975; Bessou & Pagès, 1975; Boyd, 1976*a, b*; Barker, Emonet-Dénand, Harker, Jami & Laporte, 1976) than for dynamic activated fibres (bag 1), since statics but not dynamics tend to provoke propagated action potentials and occasionally even full-length activation of intrafusal fibres (Bessou & Pagès, 1972, 1975). Further, the mean length of the bag 2 and the group of chain

fibres is smaller than the length of the bag 1 fibres (Barker, 1974; Barker *et al.* 1976). Indeed, from the published data of Bessou & Pagès (1975) it would appear that the speed of contraction induced by static fibres, measured by its time constant, exceeded dynamic action only by a factor of about 2. This would be in close agreement with the findings of Boyd (1976*a, b*) and Boyd *et al.* (1977), who examined the speed of shortening during tetanic activation on the basis of the contraction and relaxation times. They found that the speeds of bag 2 and chain fibres activated by static axons differed from the speed of bag 1 fibres activated by dynamic axons by similar factors. Thus the present results with afferent responses to rectangular stimulation agree broadly with the findings from isolated spindles. Perhaps the residual differences might be attributed to differences in the dynamic sensitivity of the transducers and encoders operated by static and dynamic axons. The results also agree with the observations of Andersson *et al.* (1968) and Chen & Poppele (1978) on primary afferent responses to sinusoidal modulation of the rate of fusimotor stimulation, covering a range of modulation frequencies. Identical frequency response characteristics were reported for static and dynamic axons, with time constants of 30 msec (Andersson *et al.* 1968) and 20 and 110 msec (Chen & Poppele, 1978).

In the light of this evidence it appears that the description of static and dynamic action as fast and slow, respectively, will provide an only incomplete understanding of the internal spindle mechanisms. The documented differences in speed are rather small and by no means comparable to those found between fast and slow muscle in amphibia (cf. Brown, 1971). Slow excitatory processes, which might occur in addition to the fast responses to rectangular stimulation, were looked for but not found in the present experiments. Thus, it is difficult to imagine, how the small differences in speed could fully account for the large scale differences between static and dynamic action on the dynamic sensitivity of primary spindle afferents.

If, for the moment, one accepts that the speed of contraction elicited by static and dynamic axons is similar it remains to be explained why dynamic fibres and some of the static fibres fail to elicit the phasic modulation of pst histograms which should result from fast and pulsatile intrafusal events. In fact, a number of mechanisms might contribute to this. First, it is known that muscle twitches are prolonged and reduced in size, if the contracting muscle is loaded by compliant springs (Hill, 1951; Bawa, Mannard & Stein, 1976). Given the morphological differences between bag and chain fibres and the occurrence of localized contractions (especially in bag 1 fibres), the compliance of the elastic tissue in series with the foci of contraction is likely to be appreciably larger in bag 1 than in chain fibres. Thus the attenuation of twitch tension by the elastic tissue in series should be more pronounced in bag 1 fibres. In isolated spindle preparations twitching in the sensory region has indeed been observed in chain and bag 2 but not in bag 1 fibres (Boyd, 1976*a*; Boyd *et al.* 1977). This may thus be attributable partly to differences in the filtering by series elastic components rather than exclusively to differences in the intrinsic speed of contraction. Secondly, the afferent discharge of primary afferents may be determined by competitive interaction of multiple pacemakers (Crowe & Matthews, 1964; Matthews, 1972; Hulliger, Matthews & Noth, 1977*c*; Emonet-Dénand *et al.*, 1977*a*). Thus the manifestation of pulsatile patterns of discharge during dynamic fusimotor excitation might be curtailed by pacemaker switching between encoders on non-activated and activated fibres. In particular this might happen at low rates of stimulation, where the unfused pulsatile events would be most clear-cut provided that the resting discharge of the bag 1 pacemaker was below the level of the bag 2 and chain pacemakers. Thirdly, the twitch/tetanus ratio in dynamic-operated fibres might be smaller than in static-operated fibres. Even if the tetanic tension was the same, this would give rise to smaller twitches and thus to a smaller rhythmic modulation of the receptor potential from dynamic-operated fibres. The data of Fig. 8 provide, in fact, some support for this

possibility, since during maintained stimulation static fibres seem to reach maximum tetanic excitation at lower rates than dynamic fibres.

Thus, during submaximal tetanic activation, fast contracting foci in intrafusal fibres need not give rise to rhythmic pulsations at the level of the transducers and in the afferent discharge. The modulation of pst histograms is therefore hardly a faithful indicator of the speed of intrafusal contraction. This is compatible with the finding that it was not correlated with the speed of the responses to rectangular stimulation (Fig. 9).

Fusimotor rate-sensitivity

The present results agree with earlier reports in that under steady conditions (i.e. activation at constant rate) the fusimotor rate-sensitivity with stimulation of static fibres was about twice that found with activation of dynamic fibres (Lennestrand & Thoden, 1968*a, b*; Andersson *et al.* 1968; Lewis & Proske, 1972; Cheney & Preston, 1976*b*; Emonet-Dénand *et al.* 1977*b*). In the present experiments a static/dynamic ratio of 2·1 was found. This also indicates that the present sample was not significantly biased in favour of units with abnormally high rate-sensitivity during static fusimotor stimulation. The difference in sensitivity to stimulation at fixed rate may be most simply related to the observation in isolated spindle preparations that during tetanic stimulation static fibres cause a larger opening of primary sensory spirals than dynamic fibres (Boyd, 1976*a*).

Surprisingly it was found that during rectangular stimulation the differences in rate sensitivity were even more pronounced, with a static/dynamic ratio of 4·7 (compared with 2·1). Earlier investigators may already have noticed this (Andersson *et al.* 1968; Chen & Poppele, 1978), but the direct comparison of the rate-sensitivities during steady and alternating rates of stimulation has so far not been reported. The afferents' sensitivity with rectangular stimulation of static axons was clearly increased relative to the values with maintained stimulation. This was due to a depression of discharge at the lower rate of rectangular activation and to an enhancement at the higher level. The former might be an unmasking of fatigue following a period of intensive firing. The latter may be attributable to the relatively slow adaptation of afferent discharge at the onset of tetanic activation (Emonet-Dénand & Laporte, 1978) or during rectangular stimulation at low frequency (present findings, cf. Fig. 5*A*). In contrast, the rate sensitivity during rectangular stimulation of dynamic axons was slightly decreased. This may be due to the large amplitudes of stimulation used, which might have caused some saturation of the amplitude of the response. The manifestation of such saturation would have been aided by the fact that the discharge of primary afferents at the beginning of tetanic activation usually lacks the adaptation described for static axons (Emonet-Dénand & Laporte, 1978).

Functional implications

The pronounced difference in fusimotor rate-sensitivity, particularly during stimulation at alternating rates is yet another example for the existence of clear functional differences between static and dynamic fusimotor axons. However, the two types of fibres seem not to differ from each other as regards the speed of their action on primary afferents. During physiological motor tasks this should enable either type to exert its specific action on primary afferents equally quickly. Thus, dynamic fibres would accomplish their sensitizing effect without undesirable delays. Static fusimotor fibres

could equally quickly transmit to the spindles command signals or their efferent copies for the performance of servo-assisted movements. The spindle afferents' enhanced rate-sensitivity during alternating activation of single static fusimotor axons would render these particularly suitable for such a role, all the more since several static fibres to a single spindle are normally available. Their coactivation would undoubtedly further increase the static axons' effectiveness for the transmission of central commands.

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