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STATIC AND DYNAMIC FUSIMOTOR ACTION ON THE RESPONSE OF IA FIBRES TO LOW FREQUENCY SINUSOIDAL STRETCHING OF WIDELY RANGING AMPLITUDE

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SUMMARY

1. Single fusimotor fibres were stimulated repetitively to test their action on the responsiveness of muscle spindle primary endings in the cat soleus to sinusoidal stretching of both large and small amplitude. Frequencies of 0·06–4 Hz were used at amplitudes from 10 μm to 3 mm.

2. The response was assessed by fitting a sinusoid to the cycle histogram of the afferent firing throughout the course of the cycle; this linear approximation measures the fundamental of the response and ignores any harmonics. The sine was allowed to project to negative values and any empty bins in the histogram were ignored when fitting.

3. With small amplitudes of stretching the histograms were reasonably sinusoidal, but with large amplitudes they showed appreciable distortion of the wave form for the passive ending and during dynamic fusimotor stimulation. Non-linearity of response manifested itself also, with increasing amplitude of stretching, by an increase in the phase advance of the response, by increasing r.m.s. deviation of the histogram points from the fitted sine and (for dynamic stimulation) by an increase in the mean value of the fitted sine.

4. With increasing amplitude the response modulation ceased to increase proportionately with the stimulus, so that the sensitivity of the ending to a large stretch (defined as afferent modulation/stretch amplitude) was appreciably less than for a small stretch. This effect was most pronounced for the passive ending.

5. Whatever the amplitude of movement the modulation during static stimulation was less than that for the passive or during dynamic

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stimulation. For small amplitudes the response during dynamic stimulation was less than that of the passive, but for large amplitudes the response during dynamic stimulation was always the greater. At some intermediate cross-over amplitude the two responses were the same size, though still differing slightly in other respects. The value of the cross-over amplitude was usually about 200 μm at 1 Hz, and increased on lowering the frequency. Thus dynamic fusimotor action does not uniformly produce either an increase or a decrease in the sensitivity of the ending in relation to the passive.

6. Bode plots, for each amplitude, of sensitivity and phase against frequency suggested that

(*a*) under all conditions the ending is relatively insensitive to frequency in the range studied, for the slope of the log-log sensitivity lines was only 0·15–0·2 (3·5–6 db/decade);

(*b*) the mechanism which makes for non-linearity is not particularly frequency sensitive;

(*c*) static fusimotor stimulation does not change the frequency sensitivity of the ending;

(*d*) dynamic fusimotor stimulation very slightly increases the frequency sensitivity of the ending for large amplitudes.

In reaching these conclusions more attention was paid to the slope of the sensitivity lines than to the values of phase.

7. It appears that the major effect of fusimotor action, whether static or dynamic, is to regulate the sensitivity of the primary ending to stretching for all amplitudes of movement (i.e. gain) rather than to control the relative values of its sensitivity to length and to velocity (i.e. crudely, the damping in a feed-back loop).

INTRODUCTION

On using low-frequency sinusoidal stretching of sufficiently small amplitude to fall within the 'linear range' Goodwin, Hulliger & Matthews (1975) found that fusimotor stimulation, whether of single static or dynamic fibres, reduced the sensitivity of the primary ending below that shown by the same ending in the absence of fusimotor stimulation. The phase of the response also remained constant in both cases. The effect on sensitivity was large for static stimulation and in line with previous findings (see also, Chen & Poppele, 1973). The reduction in sensitivity on dynamic stimulation was small but consistent, and was paradoxical in the light of the well-documented action of dynamic fibres in increasing the 'dynamic sensitivity' of the primary ending to a ramp stretch of large amplitude (Crowe & Matthews, 1964*a*). It seemed of interest, therefore, to study the effect of a wider range of amplitudes of sinusoidal stretching using broadly the same methods as before. This has raised new problems both of analysis and interpretation since the ending no longer behaves linearly (cf. Hasan & Houk, 1975*a*, *b*; Matthews & Stein, 1969). With higher frequencies these difficulties become progressively more severe and others have already documented the complicated and abrupt changes which may then occur in the pattern of response with quite small changes in the frequency and amplitude of stretching (Grüsser & Thiele, 1968; Eysel & Grüsser, 1970; Stuart, Ott, Ishikawa & Eldred, 1965). We have concentrated our attention on frequencies of 0·06–4 Hz and in spite of the non-linearities have quantified the response of the ending to the stretching by the parameters of the sinusoid of the correct period which best fits its firing throughout the cycle; this linear approximation is tantamount to measuring the fundamental of the response and ignoring the harmonics. The findings support the idea that the major fusimotor action on the primary ending, in addition to the familiar direct excitatory effect, is the control of the absolute value of its sensitivity to stretching rather than the regulation of the relative amounts of velocity and positional information that it provides the C.N.S. In addition, as already noted elsewhere (Hulliger, 1976; Hulliger, Matthews & Noth, 1976), the results provide a formal description of the way in which the effect of dynamic fusimotor stimulation does indeed progress, with increasing amplitude of stretching, from being a reduction to being an increase in the response in relation to the passive.

METHODS

In all essential respects the methods followed those of Goodwin *et al.* (1975) except for the present employment of large stretches as well as small ones (10 μm to 3 mm, half peak-to-peak amplitude) and the restriction of the frequencies studied to low frequencies (0·06–4 Hz). The stretcher had been slightly improved by increasing its stiffness (from 20 to 10 μm N^{-1}) with consequent reduction in certain small friction-dependent errors in the measurement of phase; these were reduced to below 3°. In outline the methods were as follows.

Preparation. The discharges of single afferent fibres from muscle spindle primary endings of the soleus were recorded from dorsal root filaments in the anaesthetized cat (pentobarbitone sodium). They were classified on the basis of their conduction velocity ($>$ 70 m/sec), their dynamic responsiveness to large ramp stretches (dynamic index $>$ 40 impulses/sec for 7 mm at 10 mm/sec), and on their vibration sensitivity (driven at 200 Hz by peak-to-peak movements of below 25 μm). Functionally single fusimotor fibres were stimulated in ventral root filaments at twice threshold, after isolating the spindles from central control by severing the appropriate spinal roots. Occasionally more than one gamma spike could be recorded from the filament on stimulating the muscle nerve but various tests then led us to believe that the effect on the ending studied was none the less due to a single efferent, or at the very worst to two with equivalent action (i.e. sharpness of threshold of effect on the afferent and typical nature of the response). The efferents were classified into static and dynamic fibres by virtue of their effect on the response of the afferent to a large ramp stretch, but no attempt was made to further subdivide them into the various intermediate categories of Emonet-Dénand, Laporte, Matthews & Petit (1977). However, we endeavoured to select 'typical' static and dynamic fibres, so most of our effects probably correspond to their types I and VI, which in peroneus brevis together comprise two-thirds of the population. In one case a dynamic β fibre was studied in place of a dynamic γ fibre (conduction velocity 58 m/sec, tetanic tension 30 mN) but its extrafusal action was not considered to have a significant effect on the afferent responses; since these showed no overt differences, they were pooled with the rest of the dynamic actions (the threshold for tension detection was 3 mN). In total, twenty-two primary afferents were studied in twenty-one preparations during stimulation of thirty-five single fusimotor fibres sixteen of which were static fibres and nineteen dynamic fibres (including the β); in twelve cases the action of a static and of a dynamic fibre were compared on the same afferent.

Usually only a single rate of fusimotor stimulation was employed in an experiment. Values of 70–120/sec were used for the dynamic fibres and of 30–100/sec for the static fibres. Higher values were chosen for the dynamic stimulation so as not to elicit too great a disparity in the mean level of afferent firing in the two cases. Even so, in the main systematic studies the mean increase in steady firing elicited by the static fibres was 55 ± 15 S.D. impulses/sec ($n = 13$) and that for the dynamic fibres only 24 ± 7 S.D. ($n = 17$). In any given experiment all measurements were made with the muscle at the same length, which was 1–2 mm short of physiological maximum.

Because of the extended time required for data collection the experiments commonly lasted 15–20 hr, 10 hr of which might be occupied with recording from the same afferent on stimulation of one or more fusimotor fibres. Particular care was taken to check the constancy of the various responses to ensure that the effects attributed to specific fusimotor actions had not arisen from temporal change. Constancy was favoured by the I.V. infusion of Dextran to maintain the mean arterial pressure above 80 mm Hg, and by bubbling $O_2 + CO_2$ into the Ringer overlying the muscle and its nerve. In addition, the root filaments were periodically treated with Ringer solution. The temperature of the cat and of the paraffin pools was maintained between 35 and 38° C.

Analysis. The data collection and a substantial part of the numerical analysis were performed 'on line' with a PDP 12 computer. The averaged response to an integral number of cycles of sinusoidal stretching was displayed in a cycle histogram where the number of spikes occurring in each of 24 bins of constant width was plotted against the phase of the cycle to give the probability density of firing (frequency) throughout the stretch cycle. Normally each histogram was based on 10 sec recording, beginning 1–2 sec after commencing fusimotor stimulation and 3–5 sec after tautening the muscle by stretching it to just short of its maximum in situ length from a resting length some 7 mm shorter. Longer periods of analysis were used for frequencies below 0·1 Hz and even so only a single cycle was studied, as was also often done for 0·1 Hz. The histogram was fitted with a sinusoid of the same frequency using the least squares method. When firing continued throughout the cycle and all bins contained spikes, the value for each bin was given the same weight in the fitting procedure. But when, with the larger amplitudes of stretching, the ending fell silent for part of the cycle the empty bins were ignored in the fitting rather than given the value of zero; this was done because empty bins would appear to indicate an undefined frequency rather than true zero since negative frequencies are not available to the ending to enable it to continue to signal its degree of excitability. The rejection of the empty bins was done manually by setting cursors on the oscilloscope display of the histogram to select the cycle segment for fitting. This element of personal judgement was preferred to simply programming the computer to ignore all empty bins, since it allowed a single spike in the middle of a period of silence to be neglected, thus helping to reduce errors due to any noise pulses. Also, as a control, it allowed us to fit the sine to more restricted positive-going parts of the cycle histogram (cf. Fig. 4), but this was not done routinely. The computational and analytical details are described elsewhere (Hulliger, 1976).

In order to assess the goodness of fit between a histogram and the fitted sinusoid the root mean square deviation (e_1) between the two was always computed. This term gives an averaged measure of the point by point difference between the two functions and it can be shown to be proportional to the residual harmonic power contained in all the Fourier coefficients (m_k) beyond the fundamental

$$e_1 = \sqrt{\left(\frac{1}{2\pi}\int_0^{2\pi}\left\{h(t)-[f_0+m_1\sin(t+p_1)]\right\}^2 \mathrm{d}t\right)}$$
$$= \frac{1}{\sqrt{2}}\sqrt{\left(\sum_{k=2}^{\infty} m_k^2\right)},$$

where $h(t)$ denotes the histogram, whereas f_0 (the fitted mean), m_1 (magnitude of the fundamental) and p_1 (phase of the fundamental) describe the fitted response (Hulliger, 1976). Very high harmonics, however, would not contribute because of the finite number of bins (24) employed in the cycle histogram to sample the data. When the least-square fit was based on only a fraction of the cycle, the same window was used for the computation of the r.m.s. deviation. The magnitude and phase values for the higher harmonics were only occasionally calculated. From the above expression it can be deduced, however, that in the case of obviously distorted histograms the magnitude of any harmonic could not be higher than $e_1\sqrt{2}$.

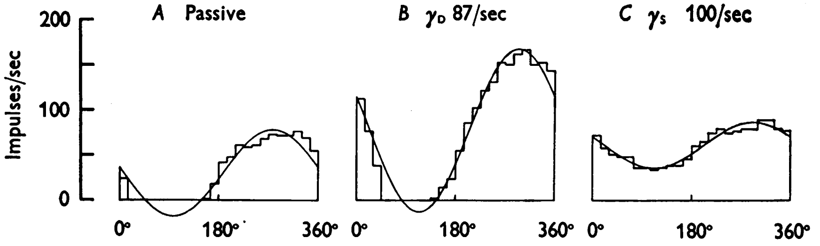

Fig. 1. Cycle histograms showing the response of a primary ending to 1 Hz sinusoidal stretching of large amplitude (1 mm half peak to peak). *A*, in the absence of fusimotor stimulation. *B*, during repetitive stimulation of a single dynamic fibre at 87/sec. *C*, during stimulation of a single static fibre at 100/sec. The smooth sine was fitted to the histograms by a procedure which gave no weight to the empty bins rather than treating them as having the true value of zero. 360° on the abscissa corresponds to the point of maximum extension; thus in all cases the response shows appreciable phase advance upon the stimulus of stretch (*A*, 81°; *B*, 66°; *C*, 68°).

RESULTS

Fig. 1 shows typical responses to large amplitude stretching at 1 Hz together with the fitted sine, the parameters of which were taken as the measure of the afferent response. In all three responses the peak firing occurred before the peak of the stretch at 360°, indicating that the ending was responding to the velocity and/or acceleration component of the stimulus over and above its response to the length component of the extension. When the ending was passive (i.e. in the absence of fusimotor stimulation) the actual rate of firing varied between zero and 75/sec, but because of the projection of the sinusoid below zero its peak-to-peak value exceeded this figure and was 96/sec. During dynamic stimulation both the actual modulation of firing and the amplitude of the fitted sine were in-

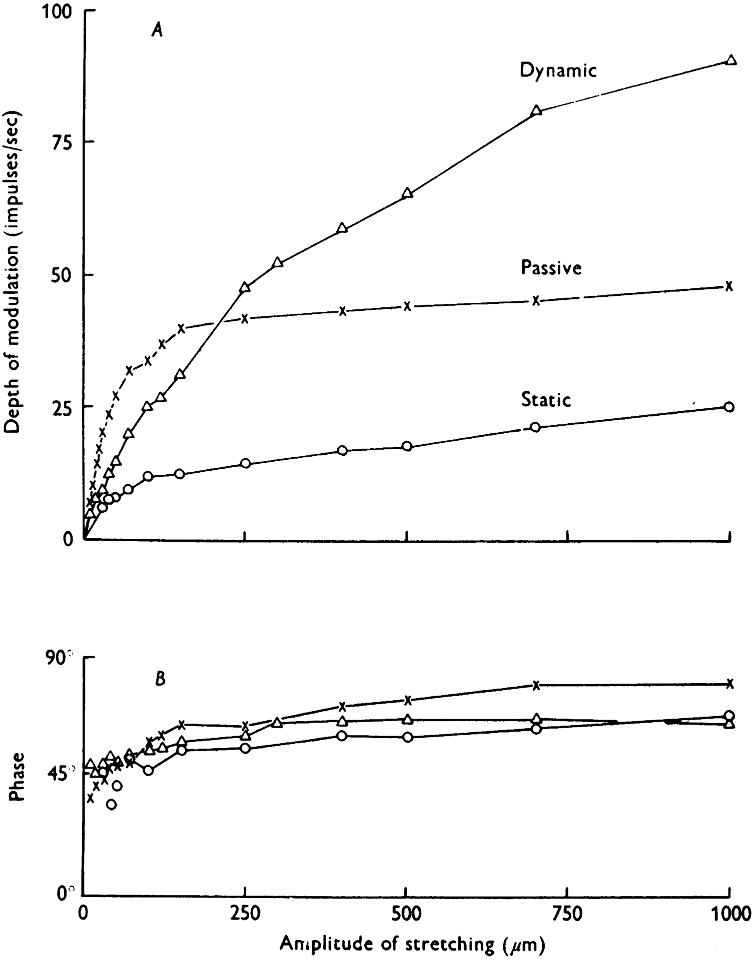

Fig. 2. The effect of the amplitude of stretching at 1 Hz on the depth of modulation and on the phase of the afferent response, as given by the parameters of the fitted sine. Same experiment as Fig. 1. Positive values of phase indicate that the ending fired in advance of the length stimulus.

creased above their passive value, whereas during static stimulation both were decreased. Thus the fitted sine would appear to provide a reasonable indicator of the responsiveness of the ending to sinusoidal stretching.

Fig. 2 shows similar data plotted systematically for the same ending. In all three amplitude plots, the response at first increased in approximate direct proportion with the stimulus for amplitudes up to 50 μm (half the peak-to-peak movement); this is the so-called linear range. Thereafter, the relation becomes less steep and the curve progressively flattens so that the overall relation deviates from direct proportionality. A particular feature of the responses is that the curving off is much more abrupt for the passive ending than it is during dynamic activation and these two curves cross over at an amplitude of stretching of about 200 μm; such behaviour will be discussed in detail below. The phase plot in Fig. 2*B* shows the related finding that as the amplitude of stretching was increased so also was the phase advance of the response on the stimulus, although the effect was relatively small.

In this experiment, as always, the ending fired throughout the whole of the cycle for amplitudes of below 100 μm irrespective of whether or not it was being activated by fusimotor stimulation. Again there appeared a typical short period of silence during the releasing phase for the passive ending at an amplitude of 100 μm, and at an amplitude of 250 μm during dynamic activation, though this latter value was rather variable in different experiments (modal value 700 μm, range 250–1400 μm at 1 Hz). Once silence appeared for a given amplitude of stretching it remained for all larger stretches. Silence did not occur during static fusimotor stimulation.

Non-linear features

The graphs of Fig. 2 show that the system possesses non-linear features. A linear system, when tested with sinusoidal inputs of increasing amplitude, should respond with a pure sinusoidal output of proportionally increasing magnitude, constant phase and constant mean. The spindle commonly violated one or more of these conditions of linearity, as will be discussed for each in turn so as to help assess the significance of the main measurements of amplitude and phase which represent linear approximations.

(1) *Departure from proportionality of the input–output relation.* We confirm that for the magnitude of the response a proportional relationship holds for small movements (Goodwin *et al.* 1975), at least as a first approximation. But as illustrated in Fig. 2, a proportional relation is not found for larger stretches, although the response continues to increase monotonically and may exhibit segments which can be approximated by straight lines.

(2) *Inconstancy of phase.* For all amplitudes the response shows phase advance over the stimulus. Large movements elicit an additional phase advance of 20–30° above that found for small movements (Figs. 2, 5).

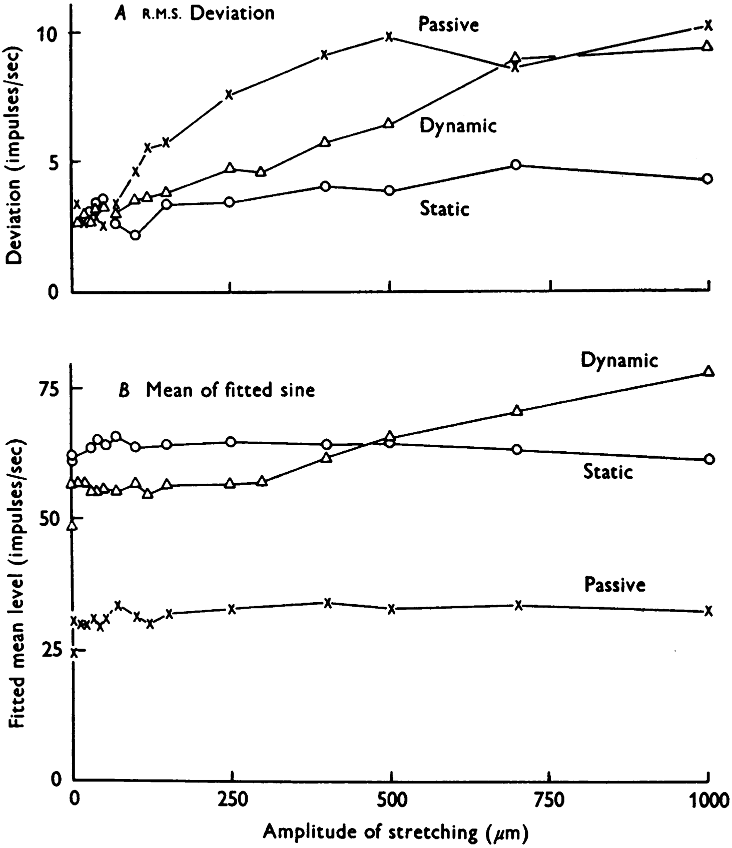

Fig. 3. Manifestations of non-linearity. The effect of the amplitude of stretching *A*, on the root mean square (r.m.s.) deviation of the fitted sine from the histogram, and *B*, on the mean level of the fitted sine, for the experiment of Fig. 2.

This occurs both in the presence and absence of fusimotor stimulation. It should be noted that measurements of the phase of the response are readily influenced by asymmetries in the cycle histogram.

(3) *Distortion of wave form.* Afferent silence during part of the cycle was the commonest reason for the cycle histogram to deviate from a sinusoid. But this of itself provides no impediment to linearity once the empty bins are ignored and the fitted sine is allowed to project below zero. In addition, after ignoring the lack of fit for the zero segments, the remaining portions

of the cycle histogram often deviated from the appropriate pure sinusoid. As illustrated in Figs. 1 and 4 such distortions were regularly found for larger amplitudes of stretching for the passive and for the dynamically activated ending. During static activation, however, the wave form was normally entirely above zero and reasonably sinusoidal for all amplitudes. With passive endings 'square wave' type of responses or histograms with bifid peaks were commonly seen for larger amplitudes (Figs. 1*A*, 4*A*). During dynamic stimulation the falling phase of the response tended to be appreciably steeper than the rising phase, mainly with large amplitudes (Figs. 1*B*, 4*B*). Such asymmetry was also found when the ending fired throughout the cycle and was particularly marked at low frequencies with abrupt transition between a steep falling phase and a flat trough (Figs. 4*C*, *D*).

Harmonic distortion assessed by the r.m.s. deviation. The extent of any deviation of the response from a pure sinusoid could be expressed in terms of the parameters of the higher harmonics that would be required to improve the goodness of fit. Yet since there appeared to be no obvious physiological significance which could be attached to such individual harmonics we have preferred to make an overall assessment of the harmonic distortion by determining the r.m.s. deviation of the cycle histogram from the fitted sine. This figure will, of course, contain a component attributable to the noisiness of the response as well as components relating to the systematic amplitude-specific distortions of its wave form. As in Fig. 3*A* the r.m.s. deviation tended under all conditions to be constant for a range of small amplitudes, spanning approximately the linear range defined on the basis of amplitude-modulation plots. Here its value provides a measure of the variability of the response. However, with further increase of the amplitude the r.m.s. deviation term increased appreciably, particularly for passive endings and during dynamic stimulation. This may be attributed to distortions occurring during specific phases of the response cycle. As formally described in Methods the value of the r.m.s. deviation sets an upper limit to the magnitude of any higher harmonic. For example, in Fig. 3 the response during dynamic stimulation and 1 mm stretching exhibited a deviation of approximately 10 impulses/sec, as was typical. If this value were due entirely to the appearance of a first harmonic then its amplitude would be 14 impulses/sec, in comparison with an amplitude of the fundamental of 85 impulses/sec. During static activation the absolute values at the same amplitudes were lower, though the relative values would be higher. But in this case most of the r.m.s. deviation would appear to be attributable to stretch-independent noise rather than to distortions linked to the stretch cycle, since the term increased only moderately with increasing amplitude. Generally, measurements of the deviation term confirmed the qualitative assessment by inspection of the goodness of fit by the fundamental.

(4) *Change in the mean level of the fitted sine.* With passive or statically activated endings the mean level of the response was either approximately constant (as in Fig. 3*B*) or tended to decrease with increasing amplitude of stretching. In contrast, as also shown in Fig. 3*B*, during dynamic stimulation the mean level of the fitted sine regularly increased for movements above a certain threshold, which was usually outside the linear range (average increase on 1 mm stretching at 1 Hz, 14·1 ± 12·1 s.d., $n = 17$). When an ending is firing throughout the whole of the cycle the value of the fitted mean of a sinusoid is the same as the average rate of firing, as given by the number of spikes per cycle. When the ending falls

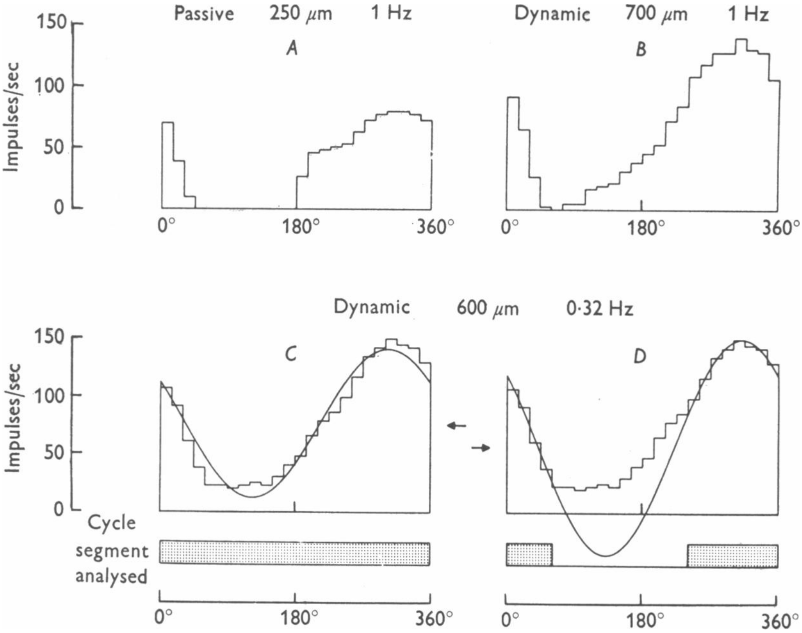

Fig. 4. Cycle histograms from various endings showing responses that deviate from a sinusoid, apart from any absence of firing during a part of the cycle. *A*, typical passive response seen with large amplitudes. *B*, asymmetry of rising and falling phases of response seen during dynamic stimulation. *C*, *D*, flattening of the trough of the response accompanied by slight asymmetry. *C*, sine fitted as usual to all data points. *D*, same data fitted by a sine based only on the peak of the response, and ignoring the trough, as indicated below. The arrows show the mean value of the fitted sine (77 and 57 impulses/sec in *C* and *D* respectively; the values for modulation and phase were 65 and 93 impulses/sec and 57 and 48° in each case; and the r.m.s. errors were 9 and 2 impulses/sec).

silent for part of the cycle, the average firing rate is greater than the fitted mean, because the physically impossible negative values are replaced by zero. Although the average rate may rise with amplitude there is no necessary reason for the fitted mean to do so. Yet, such stretch-induced increase in the fitted mean during dynamic stimulation was found both in the presence and absence of partial silence. We initially hoped that this phenomenon would throw light on the intrafusal mechanisms associated with dynamic action, since appreciable effects were specific for dynamic fusimotor stimulation and thus seemed unlikely to depend on any general properties of the sensory terminals, of intrafusal mechanics, or of the analytical methods. In particular, we suspected that the increase in the fitted mean might depend upon a specific tendency of certain intrafusal muscle fibres to show some kind of stretch activation in which their contractile activity was augmented by stretching itself. Unfortunately, as discussed below, the complexities arising from other non-linearities in the system invalidate such simple reasoning.

This is illustrated by Fig. 4*C* and *D*, where two different sinusoids have been fitted to the same histogram. In Fig. 4*C* the usual sine, based upon the whole cycle, has been determined and shows a mean level of 77 impulses/sec, which as usual is appreciably above the value obtained in the absence of stretching (65 impulses/sec). In Fig. 4*D* the sine has been fitted only to the peak of the histogram whilst its trough was ignored. This leads to a reduction of the fitted mean (57 impulses/sec) to a level which is now slightly below the value in the absence of stretching. Thus the increase in the value of the fitted mean with amplitude seems related to a progressive distortion of the wave form consisting partly of a relative flatness of its trough and partly of an elevation of the initial part of its rising phase.

It may also be noted that on fitting the sine to the peak of the response, then its amplitude was greater than the value obtained with the normal analysis utilizing the whole of the histogram. For example, in Fig. 4 it increased from 65 to 93 impulses/sec. A similar effect was found when the same procedure was applied to the passive, but altering the method of analysis did not interfere with the conclusion that dynamic fusimotor stimulation increases the response to sufficiently large amplitudes of stretching above its passive value. For small stretches, within and close to the linear range, the cycle histogram was approximately sinusoidal so that changing the mode of analysis made little difference to the measured parameters.

Restricting the period of analysis also influenced the measurement of phase and tended to indicate less phase advance than the normal analysis. In Fig. 4 the advance decreased from 57 to 48° on restricting the fitting to the peak. Such observations indicate the danger of attaching much importance to small differences in phase under different conditions. Unremarkably, restricting the period of analysis to the peak tended to give a lower value for the normalized r.m.s. error term (measured over the restricted sampling period only), thus indicating that the peak of the response was relatively more sinusoidal than the over-all response.

Consistency of responses

The underlying system expresses itself with remarkable consistency from preparation to preparation in terms of our measurements. This is shown by the pooled values in Fig. 5 which gives the mean figures for twelve endings each of which was studied with both a static and a dynamic fusimotor fibre. In its general attributes Fig. 5 differs little from the example of Fig. 2 and, in particular, confirms the paradoxical effect of dynamic stimulation in reducing the response at small amplitudes while increasing it at large amplitudes. Moreover, for the whole population a correlation was found between the reduction of sensitivity at small amplitude and the increase at large amplitude, indicating that both effects are linked to the 'strength' of dynamic action. The pooled phase measurements can bear more detailed scrutiny than the example of Fig. 2, since

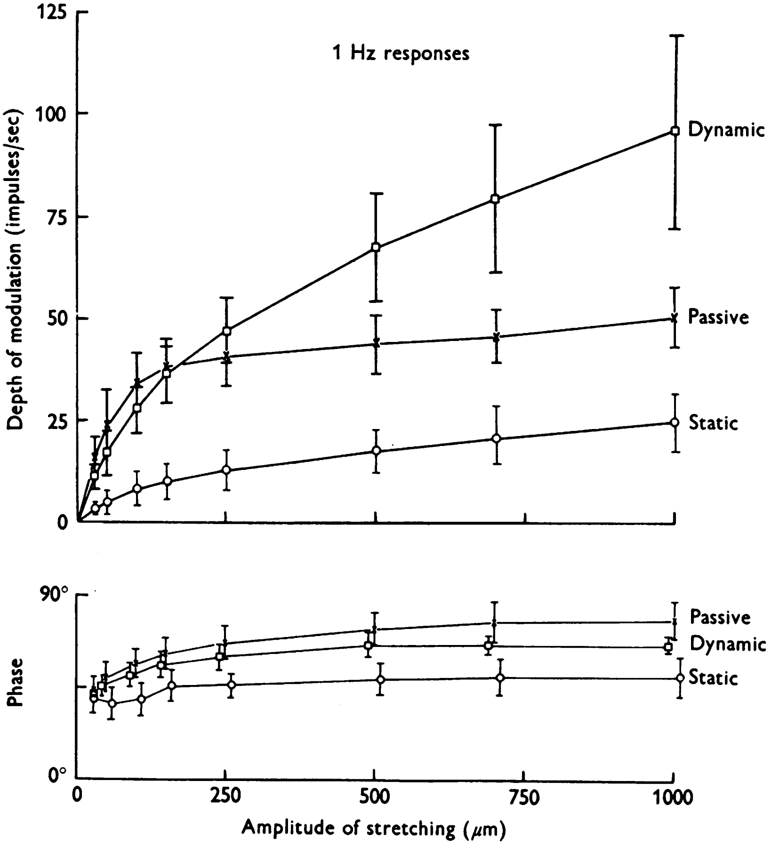

Fig. 5. Averaged amplitude response curves to show the degree of consistency of the findings. Data from twelve primary endings for each of which both a static and a dynamic fibre were stimulated. The bars show the standard deviation. The phase data has been staggered slightly laterally to avoid overlap (in four cases data was not obtained for 30 μm stretching during static stimulation).

their inherent variability has to some extent been overcome by the averaging. For the small amplitudes of the linear range the phase can be seen to be essentially the same under all conditions (Goodwin *et al.* 1975). All three curves show increasing phase advance with increasing amplitude of stretch, to reach an approximate plateau for the larger amplitudes. However, the values of phase now differ, with the passive showing the greatest phase advance and the static the least. More particularly, during dynamic activation the phase is some 15° in advance of that during static activation. In a truly linear system such a figure could be taken to show a difference in the velocity sensitivity (strictly, sensitivity to higher derivates of length in relation to length sensitivity) during the two types of activation. But under the present conditions the small phase difference might equally be attributable to differences in the distortion of the wave form of the responses in the two cases, since this was much more severe during dynamic activation.

When the phases of Fig. 5 were plotted against the corresponding values of modulation there was little difference in phase between the three conditions for depths of modulation up to about 30/sec. With deep modulation, which was not reached during static stimulation, the passive response showed some 20° more phase advance than that obtained during dynamic stimulation eliciting the same modulation; this occurred only outside the linear range.

Cross-over amplitude observed with dynamic stimulation

A notable feature of the amplitude response curves is that the dynamic curve starts below the passive but then crosses over the passive so as to lie above it at larger amplitudes of stretching, as first described by Hulliger (1976). Measurement of the parameters of this cross-over point helps to delimit the somewhat paradoxical effect of dynamic stimulation, at any rate in terms of the present measures, in first reducing the stretch responsiveness of the ending at low amplitudes and then augmenting it at large amplitudes. In the population of Fig. 5 the mean amplitude at which cross-over occurred at 1 Hz was 200 μm. As Fig. 6 illustrates, this value depends upon the frequency of stretching. In the particular case of Fig. 6*A*, lowering the frequency from 1 to 0·1 Hz increased the cross-over amplitude from 150 to 330 μm. The point of cross-over depends upon the relationship between the behaviour shown under active and under passive conditions. In this case, as was usual, the major change on lowering the frequency can be seen in the dynamic curve which was scaled down by over one third, whereas the passive curve was reduced by only about 10 %; in both cases the detailed shape of the curve also changed so the effect of frequency was not simply a matter of scaling. It follows that the depth of afferent modulation at the cross-over amplitude was rather similar at the two frequencies. But, as emphasized by Fig. 7, this does not mean that the actual patterns of firing were the same in the two cases, since both the absolute levels of firing and the shapes of the histograms differed. Fig. 6*B* shows, for a number of different preparations, that the value of the cross-over amplitude increased progressively with reduction in the frequency of stretching. The rather different slopes of the lines joining the points for each ending is related in part to the strength of fusimotor action; those dynamic fibres which caused the larger increases in the ratio of active/passive modulation for 1 mm at 1 Hz kept the cross-over amplitude small at all frequencies, while the steep slopes were due to dynamic fibres with a weak action. In view of the complexities involved in relating two curves of differing shape, no precise meaning should be attached to the particular values of the slopes in Fig. 6*B*. It may also be noted that for the whole population of endings there was wide variation in the depth of modulation at which cross-over occurred (range, 22–62 impulses/sec).

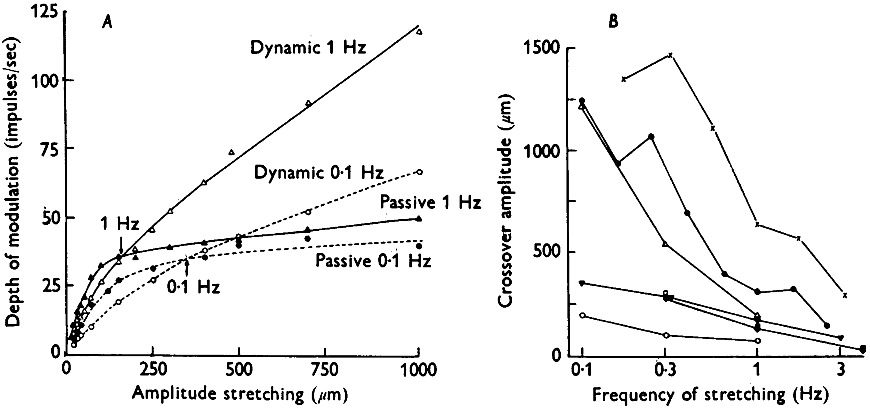

Fig. 6. The effect of varying the frequency of stretching on the amplitude at which the depth of modulation of the dynamically activated ending first reaches that of the passive ending (cross-over amplitude). *A*, shown for one particular ending in amplitude–response plots for 1 Hz and for 0·1 Hz stretching (rate of fusimotor stimulation 87/sec). *B*, shown for a number of endings by relating the cross-over amplitude to the frequency of stretching, the latter plotted logarithmically. Both *A* and *B* show that the lower the frequency and thus the velocity of stretching, the larger the movement that is required before the response of the dynamically activated ending surpasses that of the passive ending.

Rate of fusimotor stimulation

Systematic studies were of practical necessity restricted to a single rate of fusimotor stimulation. The value chosen was such as to elicit 'typical' static and dynamic effects but was generally set lower for static than for dynamic fibres. However, control experiments in which the rate of stimulation was varied confirmed that this was not an important variable for determining the overall type of response. This is illustrated in Fig. 8. With dynamic stimulation, increasing the rate progresively increased the response to a large stretch while it reduced that to a small stretch; in this case the latter fell to an approximate steady level, but in other experiments the effect was progressive (cf. Fig. 7, Goodwin *et al.* 1975). At a given amplitude of stretching, however, the phase did not show any progressive shift with change in the rate of stimulation, although there was the usual greater phase advance with the larger stretch (Fig. 8*A*). This argues that the effect of increasing strength of dynamic action is simply upon the magnitude of the afferent response rather than in altering the balance of its components of length and velocity sensitivity, etc.

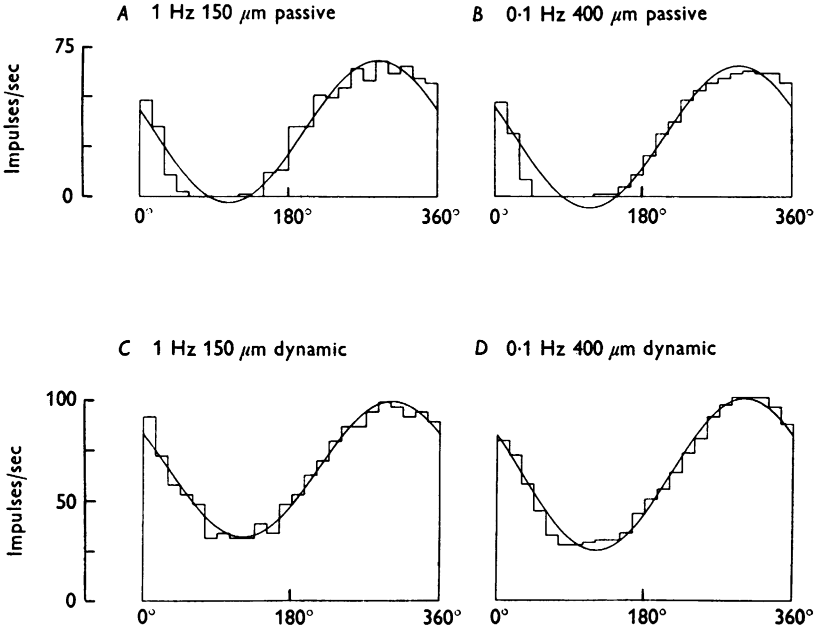

Fig. 7. Cycle histograms comparing the responses of the same ending while passive and during dynamic activation, when the amplitude of stretching was set so that the modulation of the fitted sines was approximately equal. *A*, *C*, 1 Hz stretching when the requisite amplitude was 150 μm. *B*, *D*, 0·1 Hz stretching when the appropriate amplitude was 400 μm. Same ending and same rate of γ_D stimulation as Fig. 6*A*. In the order *A* and *C*, *B* and *D* the parameters of the fitted sines were: mean level 33, 66; 30, 63; modulation 35, 34; 36, 38; phase 71, 59; 65, 59.

As shown in Fig. 8*B*, increasing the rate of static stimulation causes the magnitude of the response to fall to an approximately constant value for each amplitude of stretching. The phase also settles to a more or less steady level. The smallness of the modulation during stretching at small amplitude made the phase measurements relatively inaccurate; in addition, the aberrant value in Fig. 8*B* was associated with a tendency for the fusimotor stimulation to 'drive' the afferent firing at its own value. Altogether, the effect of varying the rate of stimulation was studied for one or other amplitude of stretching on nine occasions during static stimulation (all for 1 Hz) and on sixteen occasions during dynamic stimulation (for 0·3–1 Hz) – in this terminology each fibre of Fig. 8 was studied on two occasions.

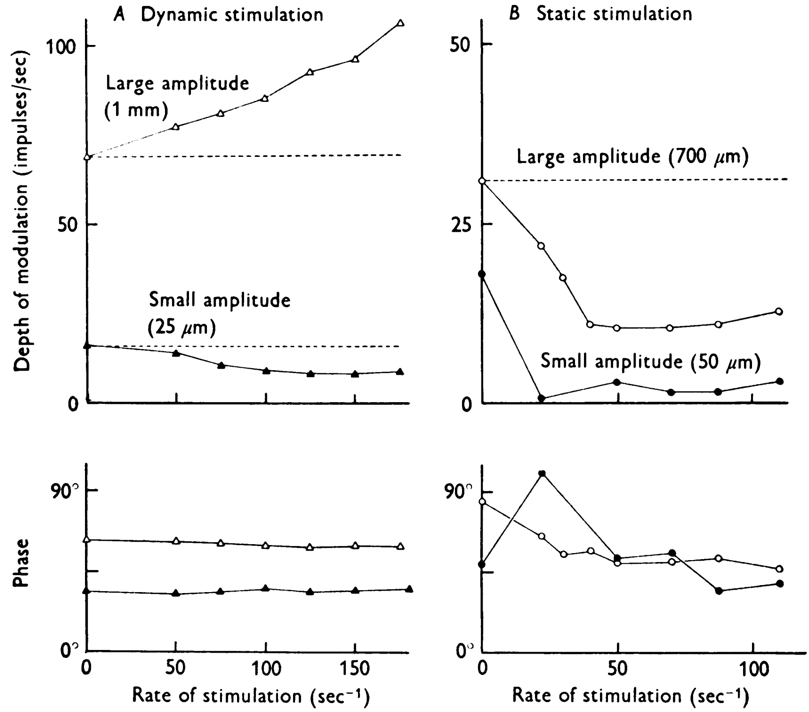

Fig. 8. The effect of varying the rate of fusimotor stimulation on the responses to large- and to small-amplitude stretching. The dashed lines indicate the values for the passive. The results for *A*, dynamic and *B*, static stimulation were from two different preparations, both with 1 Hz stretching but with slightly different amplitudes.

Thus at all amplitudes increasing the rate of stimulation enhances the characteristic effects of both kinds of fusimotor fibre; in particular, with dynamic action it sharpens the contrast between the effects at large and small amplitudes of stretching.

Bode plots – effects of frequency of stretching

The behaviour of a linear system can be completely described by Bode plots, giving, for a sinusoidal input, the gain and phase of its response in relation to the frequency of the input. Such curves have already been published for the spindle primary ending operating within its small-amplitude linear range (Goodwin *et al.* 1975). They are independent of the amplitude of stretching if the magnitude of the response is expressed as sensitivity, that is as the initial slope of the amplitude–response curve. Because of the non-linearities seen with large stretches the sensitivity, calculated by dividing the depth of modulation by the amplitude, becomes amplitude-dependent. Thus at any frequency the behaviour of the system has to be described separately for each amplitude.

By their curvature, the typical amplitude–response plots (Figs. 2, 5) show that at 1 Hz the amplitude-specific sensitivity (i.e. the ratio modulation/amplitude) decreases with increasing amplitude of stretching. This effect is most pronounced for passive endings and least conspicuous during static activation. The phase of the response at 1 Hz, on the other hand, becomes more advanced on the stimulus with increasing amplitude, the effect being again largest with the passive and smallest with static action (Figs. 2, 5). All this is equally seen in the Bode plots of Figs. 9 and 10, which show further that the same pattern occurs at all frequencies between 0·06 and 2·5 Hz. The extent of the reduction of the 'large amplitude sensitivity' from the linear range value is given by the degree of separation of the various lines. The new information in Figs. 9 and 10 lies in the way in which the 'sensitivity' for each amplitude of stretching varies with its frequency.

Passive ending. On increasing the frequency of stretching at any particular amplitude the sensitivity and phase can both be seen to increase (Figs. 9*A*, 10*A*), suggesting that the system is responding to velocity and/or acceleration as well as to extension *per se*. The relative flatness of all the curves, however, deserves emphasis though it should be reiterated that the stretching has been confined to low frequencies. If, in the frequency range studied, the ending were to be responding predominantly to the velocity component of the stimulus, the lines in Figs. 9*A* and 10*A* should rise with a slope of 1 (with a tenfold increase in sensitivity on a tenfold increase in frequency) and the phase advance should approach 90°. However, the average slopes of the sensitivity plot range from about 0·15 to 0·2 (3·5–6 db/decade). In contrast to the behaviour of a linear system, the relative constancy of slope with amplitude is accompanied by an increasing phase advance with amplitude for every frequency; yet on its own, the latter would indicate an increase in velocity sensitivity. All in all, it would appear that whatever the mechanism responsible for such amplitude-specific non-linearities it is one that is not particularly frequency sensitive.

Static activation. Fig. 9*B* shows the Bode plots during static fusimotor stimulation. The sensitivity is now relatively independent of amplitude,

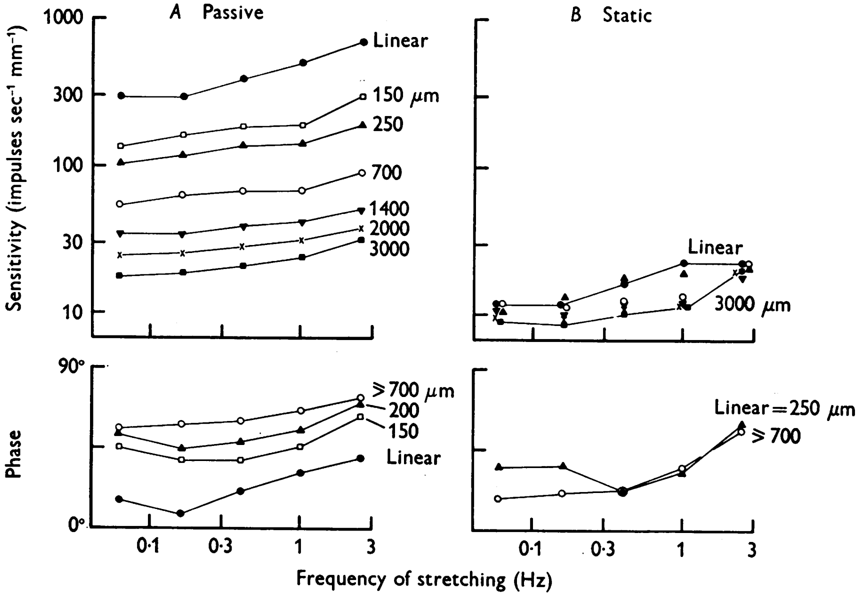

Fig. 9. The frequency dependence of 'sensitivity' and phase for a number of amplitudes of stretching. The term 'sensitivity' is used for the ratio of modulation/amplitude; the linear range sensitivity is based on the slope of the amplitude response curve whereas the 'large-amplitude sensitivity' is based on one-point measurements. *A*, passive responses. *B*, same ending during static fusimotor stimulation at 58/sec. The numbers against each line give the amplitude employed. The linear range of the passive ending was 30 μm, but during static stimulation this was extended to 250 μm.

so that the various curves are bunched together, and only two sets of connecting lines have been drawn in. The lines were, however, more widely spaced on the two other occasions when full Bode plots were obtained with static stimulation. The slopes of the frequency–sensitivity plots are all low, are not appreciably influenced by amplitude, and are not substantially different from the slopes when the ending was passive (i.e. around 0·15). The phase, again, shows only moderate increase with frequency for all amplitudes. On this evidence the degree of velocity sensitivity of the ending, relative to its length sensitivity, would not appear to have been changed dramatically from its passive value by static fusimotor action; the only reservation in this is that at large amplitude static activation does decrease the amount of phase advance from the passive.

Dynamic activation. Fig. 10*B* shows the corresponding plots during dynamic activation of a different primary ending. The family of curves during dynamic activation is grossly similar to the passive family, but shows important differences of detail. First, increasing amplitude of stretching produces less change in the level of both the sensitivity and of the phase curves in comparison with those of the passive, showing that in this respect the active curves are less non-linear. Secondly, the slope of the dynamic curves shows a tendency to increase with amplitude, though never appreciably above the maximum value of 0·2 shown by the passive in its linear range as was also seen in the two other similar experiments. This is to say that during dynamic activation changing the frequency of stretching

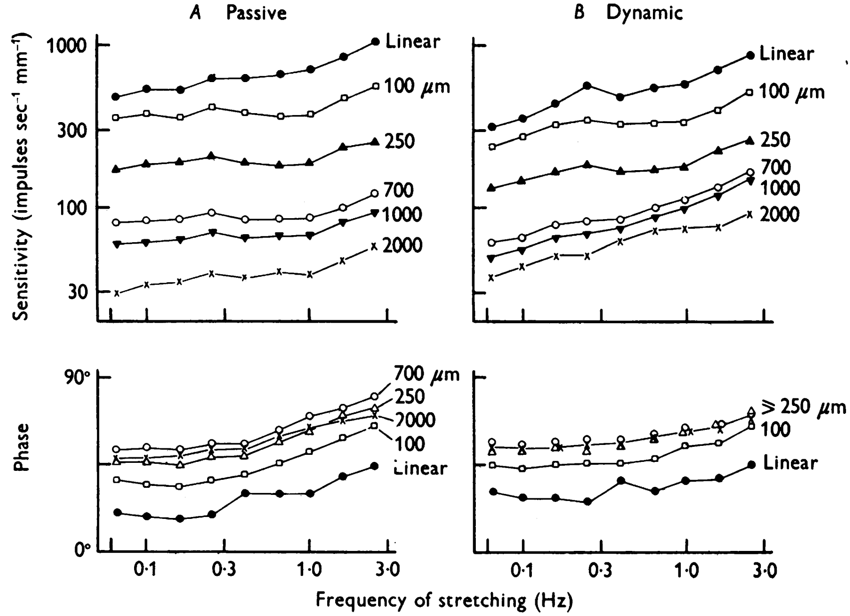

Fig. 10. The effect, during dynamic action, of varying the frequency of stretching at a constant amplitude. Same arrangement as in Fig. 9, but a different experiment with a dynamic fusimotor fibre stimulated at 100/sec. In both *A* and *B* the linear range values were based on amplitudes of 20, 30 and 50 μm.

has a very slightly greater effect on the response to a large stretch than it does on the response to a small stretch.

Active/passive ratios. The comparison of the sensitivity curves during fusimotor activation with the corresponding passive curves is more strongly brought out in Fig. 11 in which each active value has been expressed as a ratio of the passive value obtained at the same frequency and amplitude of stretching. In Fig. 11*A* for the static activation the most prominent feature is that the active and passive responses become progressively more alike as the amplitude increases. More significantly, the various curves in Fig. 11*A* are nearly flat, arguing as before that, irrespective of amplitude, static activation changes the absolute size of the response but does not alter its relative components of length and velocity. In contrast, the curves in Fig. 11*B* show an upwards slope for the larger amplitudes of stretching, indicating that dynamic action produced a slight increase in the ratio of velocity sensitivity to length sensitivity of the ending. It should be noted that the ordinate in *B* is on a much larger scale than in *A*; this has been done because of the numerically small changes involved. Finally, Fig. 11*B* further illustrates the complex pattern of dynamic action in sometimes increasing and sometimes decreasing the sensitivity in relation to the passive depending on the precise parameters of stretching. Within the linear range the sensitivity was reduced at all frequencies, while for the largest amplitude the sensitivity was always increased. With the intermediate amplitudes of stretching increases in sensitivity occurred for the highest frequency of stretching,

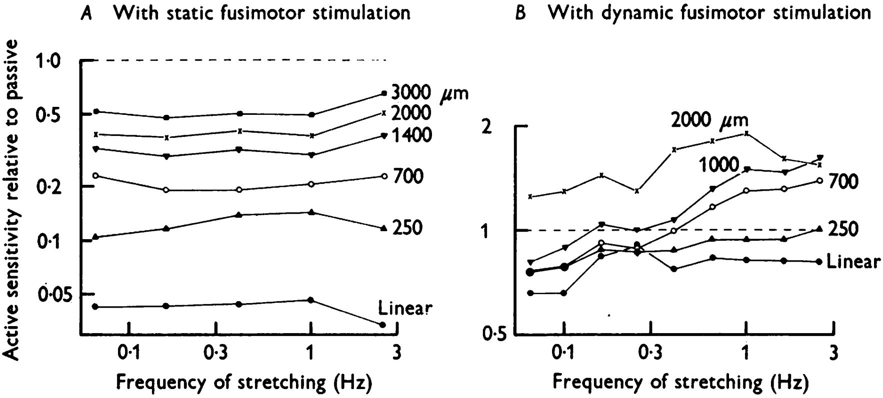

Fig. 11. The change induced by fusimotor stimulation in the magnitude of the spindle response in relation to its passive value for a number of amplitudes and frequencies of stretching. Data of Figs. 8 and 9 replotted as the sensitivity ratio (active/passive). See text.

and decreases for the lowest frequency; the cross-over of sensitivity in relation to the passive then occurred at a frequency that was the higher the smaller the amplitude.

DISCUSSION

Assessment of linear analysis

The non-linearities in the spindle responses on using large amplitudes of sinusoidal stretching are such that the validity of the present approach requires some justification. The rhythmicity and alternation of sinusoidal movement is of course physiologically meaningful and the stretches themselves are certainly all of physiological magnitude, whether in relation to tremor or to walking, and, except for the lowest values, of a physiologically relevant frequency. In defence of the actual measurements it may be said that we have used methods which rely on averaging and numerical analysis to make more exact the things which physiologists commonly assess more qualitatively, such as the peak to peak change in firing elicited by stretching. In this respect it should be noted that we have allowed the fitted sine to project below zero, whereas in direct measurements from frequency displays this is not usually done. This method was chosen since it seems the most appropriate in relation to transducer action. From the point of view of the receptor potential, for example, afferent silence during part of the response cycle appears simply as half wave rectification by the spike generating process, and so analysis restricted to the positive going segments of the cycle histogram is the most appropriate to recover its over-all form (cf. Mann & Chapman, 1975). The C.N.S., however, can only see zero as zero, and reflex responses, etc., are unlikely to be based on an extrapolation to negative frequencies. But it would have made little difference to our main observations if we had operated otherwise (cf. Fig. 7 especially) for our sines rarely projected far below zero even when the ending showed a significant period of silence; rather, the actual values of our various parameters would have been slightly altered. The various additional non-linearities (Figs. 3, 4) that we have observed certainly appear as unattractive peculiarities of response from the formal analytical point of view. Yet they may provide valuable clues to the internal functioning of the spindle and they presumably occur for good functional reasons, such as extending the range of response of the ending beyond that which could be signalled without saturation by a linear system with a uniformly high initial sensitivity.

Fusimotor classification. Sinusoidal stretches have been widely used for classifying fusimotor actions as dynamic or static with the underlying assumption that increases in the response above the passive can always be attributed to dynamic action and decreases to static action. As Fig. 12

emphasizes, this is not universally true. Static action, on our measures, invariably reduces the modulation, but the effect of dynamic action depends critically upon the amplitude of stretching. In our sample the well-known dynamic sensitizing action of dynamic γ efferents was confined to amplitudes of stretching well above 200 μm at 1 Hz, and to even higher values with lower frequencies. However, stretching soleus at 1 mm, 1 Hz seems to be a reliable test for classifying 'pure' static and dynamic fibres since all seventeen dynamic fusimotor fibres studied then increased the response of the ending, whereas the fifteen static fibres studied all reduced the sensitivity appreciably. In applying this test, however, it should be remembered that the passive ending normally fell silent for part of the cycle, thus enhancing the measured modulation in relation to that seen during static activation when the ending fired throughout the cycle. Thus the static-evoked reduction would be appreciably less if sole reliance was placed upon measurements of instantaneous frequency, and this might even prevent accurate classification with low rates of static activation. In addition, some static fibres appear to produce a degree of dynamic action along with their main static action and require more detailed testing for classification (Emonet-Dénand *et al.* 1977).

Intrafusal mechanisms and the dynamic paradox. The present results provide a formal description of the way in which, with increasing amplitude, dynamic fusimotor action first reduces and then increases the sensitivity in comparison with the passive. However, we have not achieved a unique explanation for this paradox, and many factors require to be taken into account. Goodwin *et al.* (1975) and Hulliger (1976) have considered various possible mechanisms underlying the effects of fusimotor stimulation on the behaviour of the ending within its linear range, but the present paradox must depend further upon the factors making for the obvious non-linearity in the response of the ending with large stretches. Simple linear mechanical models of the spindle are clearly inadequate to provide an explanation. Some of the non-linearities, particularly for passive intrafusal fibres, probably arise from the yielding of cross-bridges between the actin and myosin filaments within the sarcomere (Brown, Goodwin & Matthews, 1969; Hasan & Houk, 1975*b*), when their kinetics becomes crucial. In addition, stretching of itself might change the mechanical properties of the system by inducing extra contractile activity of certain intrafusal muscle fibres, whether by a stretch evoked depolarization of their membrane (Boyd, 1976) or by a 'stretch activation' of the contractile process at the myofilament level as described for certain insect muscles (Pringle, 1972). Finally, there seems every possibility that the afferent terminal may have more than one pacemaker site for impulse initiation (Crowe & Matthews, 1964*a*, *b*; Brokensha & Westbury, 1974), and that these could respond differently at various phases of the stretching cycle, when their competitive interaction could produce a variety of patterns of response and so contribute to the paradox. Thus for the moment the matter must remain open, but some of the main points are developed in more detail below.

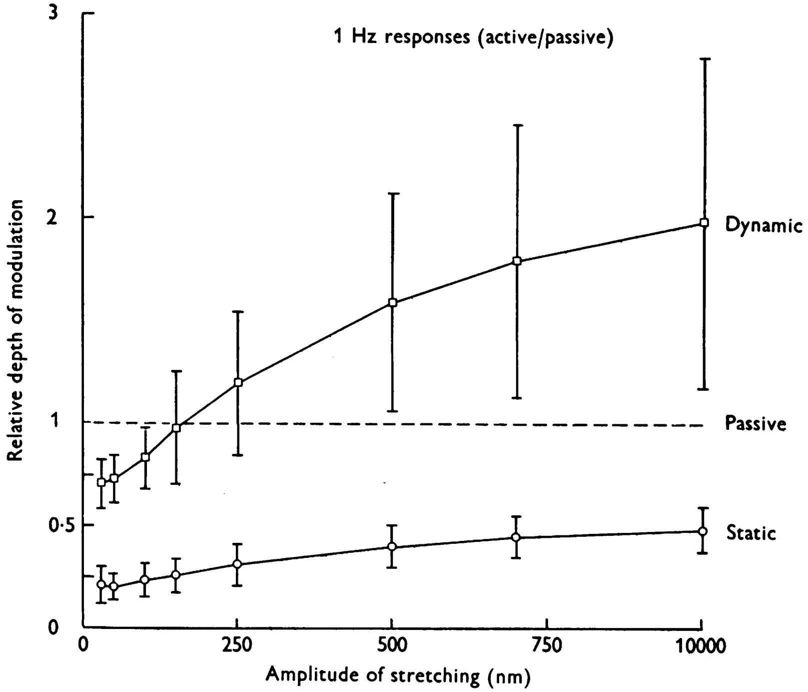

Fig. 12. The significance of the amplitude of stretching in classifying fusimotor actions as static or dynamic by their effect on the response to sinusoidal stretching. Averaged results for twelve endings for each of which both a static and a dynamic fibre was studied. For each ending at any amplitude the depth of modulation during fusimotor stimulation was divided by the passive value, and the mean ratio then determined (bars give S.D.; same endings as Fig. 5).

The amplitude of movement at which the processes responsible for the paradox begin to manifest themselves can be defined to a first approximation, and lies somewhere between the end of the linear range and the cross-over amplitude. At 1 Hz this is to place it usually between 50 and 200 μm, and probably nearer the lower value. In this region a sharp decline in the passive response is always found which has been attributed to the breakage of stable-cross-bridges presumed to be responsible for the higher linear range sensitivity of the passive ending (Goodwin *et al.* 1975*a*; Hasan & Houk, 1975). This would deprive the intrafusal fibre of its most rigid structure and so explain the reduction in sensitivity. Dynamic action might then be seen as a means of preventing this decline at the end of the linear range. It might do this by a stiffening spring effect in the following way:

The force generated by local activation with dynamic fibres is likely to lead to an extension of passive intrafusal elements in series (permanent elastic structures, sarcolemma). If this caused a shift towards higher stiffness values (due to the typical curvature of the passive length–tension curve) sinusoidal stretching would cause deeper tension modulations than in the absence of such stiffening spring effects with the passive ending. The cross-over amplitude would be determined by the magnitude of such stiffening. Its frequency dependence would, however, not be expected, since both the reduction of small-amplitude sensitivity and the stiffening elastic springs fail to show it. Moreover, the velocity-dependence of the dynamic phase of the ramp response would not be accounted for either.

An alternative possibility is a stretch-induced type of enhancement of force modulation of the dynamically activated region, as described for insect flight muscle, but also seen with mammalian muscle (Pringle, 1972). Because of the time-dependent processes likely to be involved in stretch-induced activation (cf. also Proske's (1975) stretch induced potentiation), the requisite frequency characteristics of dynamic action present no conceptual problem here. Moreover, the slow component of adaptation at the end of a dynamic phase of a ramp stretch might represent the decay of stretch activation. Such enhancement of contractility in phase with the stretch cycle could obviously lead to an increase in the modulation of the afferent response. It could also be accompanied by an increase in the mean level of contractile force, above that found in the absence of stretching, leading to an increase in the mean firing rate. As noted earlier, our finding that during dynamic stimulation the mean of the fitted sinusoid rose initially seemed to support this idea.

However, the finding can be equally explained by the competitive interaction of two or more pacemakers. If one of them had a high sensitivity and were brought into relief by dynamic activation (by virtue of an upwards shift in its mean level of firing) this pacemaker could then dominate the ending during the peak of the response, while it could be expected to fall silent during the trough of the response, because of its high innate sensitivity. The second pacemaker, presumed substantially less sensitive, would continue to fire during the release phase of the cycle and therefore prevent the manifestation of negative response components of the sensitive pacemaker by substituting more positive values. This would obviously lead to an increase in the mean level of the over-all response and it might account for the observed increase in the fitted mean. Thus this observation, whilst being compatible with the concept of stretch activation, cannot be taken as evidence for it.

Functional implications. From the point of view of motor function the paradoxical amplitude-dependent effect of dynamic stimulation, in relation to the passive, may well prove to be immaterial. Perhaps the slight decrease in sensitivity at small amplitude is the price that has to be paid during dynamic action to keep the response increasing progressively with amplitude throughout the physiological range instead of running almost flat as it does for the passive (Fig. 5); with such flatness the Ia fibre provides very little information to the C.N.S. about the size of the stretch, other than that it has exceeded 200–300 μm. The more significant finding would seem to be that at all amplitudes the response during dynamic stimulation is very appreciably greater than it is during static stimulation. Thus static and dynamic fibres may both be seen as providing a gain control for the primary ending, without prejudice to any other functions they may have – such as providing a biasing signal or controlling the behaviour of the secondary ending. On their combined stimulation, variation in their relative strengths can produce a continuous regulation of sensitivity to any particular amplitude of stretching (Hulliger, Matthews & Noth, 1977).

A further question is whether either type of fusimotor fibre should be seen as controlling the balance between the length and velocity component of the Ia response and thus perhaps as regulating the damping of the stretch reflex; this was tentatively suggested by Jansen & Matthews (1961, 1962) at the very outset of interest in such matters. The evidence, however, both now and for some time past seems against such an idea. For small amplitudes of movement, falling within the linear range, there can be no question on the matter since the phase of the response is the same for the passive and during stimulation of either kind of fusimotor fibre (Goodwin *et al.* 1975 and presently confirmed) and during the combined stimulation of a static and of a dynamic fibre (Hulliger *et al.* 1977). For the present large sinusoidal movements there are indeed small differences of phase under the various conditions (Fig. 5 especially), but the largest effect was produced simply by increasing the amplitude of stretching. We feel that the small differences seen between static and dynamic action (average 15° at 1 mm, 1 Hz) are also better seen as non-linearities rather than as indicating a specific physiologically significant fusimotor regulation. This is supported by similar findings during the combined stimulation of a pair of fibres (Hulliger *et al.* 1977).

The slope of the lines in the Bode plots of sensitivity against frequency (Figs. 9–11) perhaps provides a more reliable guide to the relative sensitivities to length and its higher derivatives. Under all conditions these were low (0·15–0·2), suggesting that in the range 0·06–2·5 Hz the ending is mainly length rather than velocity sensitive (on this measure pure velocity sensitivity gives a value of 1); yet the velocity stimulus was of reasonable size, at least with the larger amplitudes of movement (1 mm at 1 Hz corresponds to a peak velocity of 6 mm/sec). Static action produced no appreciable change in slope from the passive. However, dynamic action did produce a small increase in slope relative to the passive for the larger amplitudes of movement, though not for the linear range (which is all in agreement with the systematic change in cross-over amplitude with frequency, as illustrated in Fig. 6). Lennerstrand & Thoden's (1968) 'slow' velocity response, observed with large amplitude triangles stretching, appears to show a similar frequency-dependence. None the less, we again consider such effects too small to be considered as a major physiological feature of dynamic fusimotor action, and taken as definitive evidence that its proper function is to increase the ratio of velocity to length sensitivity.

Instead, the slight increase in slope at low-frequency in the Bode plot seems likely to relate to a characteristic feature of dynamic action seen with ramp stretching. This is that after an initial abrupt fall in frequency at the end of the dynamic phase of the ramp the afferent firing then decays slowly over the next 1–2 sec in an approximately exponential manner with a time constant of about 0·5 sec (Crowe & Matthews, 1964*a*). Such behaviour is absent or very slight both for the passive and during static stimulation. For a linear system such a slow component of adaptation would inevitably be associated with an increase in the slope of the frequency–response curve above the value it would otherwise have had; thus for the spindle, in spite of its non-linearities, the slope during activation might also be expected to be above that for the passive or during static activation. Moreover, with a time constant of 0·5 sec the range of frequencies where this might be expected would be centred upon 0·3 Hz, which is nearly in the middle of the present range. The underlying basis of this slow component of adaptation would seem to be the slow creeping movement, with relaxation of the primary afferent terminals, that occurs in certain intrafusal fibres at the end of a step-stretch and which in the one case studied was particularly marked during dynamic activation (Boyd, 1976). The biophysical origin of this creep remains uncertain, though as noted it might represent the relaxation of a stretch-induced contraction.

In terms of motor function, however, it seems possible that what is important is not the creep itself and any effect it produces on the frequency – response curves. Rather, importance may lie in the fact that before the spindle has yielded and the creep occurred, the ending has a very high value of what is now best termed 'position sensitivity' (increase in firing per unit extension at constant velocity). This was first shown by Crowe & Matthews (1964*a*), who measured its value during the course of ramp stretches and found it relatively independent of velocity above 5 mm/sec. They emphasized that on dynamic fusimotor stimulation the position sensitivity, when measured dynamically, was much greater than the similarly measured value for the passive, and that its value increased with the rate of fusimotor stimulation; moreover, it was much higher than the value obtained during dynamic stimulation with the spindle at a constant length, when any process associated with the creep would be at equilibrium. Rather similarly, Lennerstrand & Thoden (1968) subsequently described, as a principal feature of dynamic activation, an increase in the magnitude of their 'slow' velocity response observed with triangular stretching; this appears to be simply a measure of position sensitivity in another guise (it has units of impulses/sec firing per mm of stretching). It seems possible that an important variable for motor control is the value of the position sensitivity at velocities above those influenced directly by the creep, rather than the presumed frequency-dependent effects of the creep occurring at relatively low frequencies. By analogy, in a human engineered system the d.c. response to a particular variable may sometimes be most expeditiously provided by an a.c. device with a time constant sufficiently long not to obtrude itself in to the useful working range (i.e. high-pass filter properties); thus, in particular, at functionally important higher frequencies such a device could respond largely to position, although at lower functionally irrelevant frequencies it might show an unwanted and un-needed degree of velocity sensitivity. But the spindle certainly also appears to have a genuine velocity response which increases with dynamic activation (cf. also Crowe & Matthews, 1964*a*; Lennerstrand & Thoden, 1968), so that on present evidence it would be premature to reach a conclusion about the effect of dynamic stimulation on their ratio during more rapid stretches. Among other things we need to achieve better quantitative understanding of the effects of fusimotor stimulation on the response to large stretches of higher frequency, although here yet more formidable difficulties are involved in handling non-linear behaviour of the system. None the less, for the moment it seems more reasonable to view the physiological significance of fusimotor action as providing a gain control of the primary ending rather than as a regulator of its frequency-dependence and phase advance.

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REFERENCES

Boyd, I. A. (1976). The response of fast and slow nuclear bag fibres and nuclear chain fibres in isolated cat muscle spindles to fusimotor stimulation, and the effect of intrafusal contraction on the sensory endings. *Q. Jl exp. Physiol.* **61**, 203–254.

Brokensha, G. & Westbury, D. R. (1974). Adaptation of the discharge of frog muscle spindles following a stretch. *J. Physiol.* **242**, 383–403.

Brown, M. C., Goodwin, G. M. & Matthews, P. B. C. (1969). After-effects of fusimotor stimulation on the response of muscle spindle primary afferent endings. *J. Physiol.* **205**, 677–694.

Chen, W. J. & Poppele, R. E. (1973). Static fusimotor effect on the sensitivity of mammalian muscle spindles. *Brain Res.* **57**, 244–247.

Crowe, A. & Matthews, P. B. C. (1964*a*). The effects of stimulation of static and dynamic fusimotor fibres on the response to stretching of the primary endings of muscle spindles. *J. Physiol.* **174**, 109–131.

Crowe, A. & Matthews, P. B. C. (1964*b*). Further studies of static and dynamic fusimotor fibres. *J. Physiol.* **175**, 132–151.

EMONET-DENAND, F., LAPORTE, Y., MATTHEWS, P. B. C. & PETIT, J. (1977). On the sub-division of static and dynamic fusimotor actions on the primary endings of the cat muscle spindle. *J. Physiol.* In the Press.

EYSEL, U. TH. & GRÜSSER, O. J. (1970). The impulse pattern of muscle spindle afferents. A statistical analysis of the response to static and sinusoidal stimulation. *Pflügers Arch. ges. Physiol.* **315**, 1–26.

GOODWIN, G. M., HULLIGER, M. & MATTHEWS, P. B. C. (1975). The effects of fusimotor stimulation during small amplitude stretching on the frequency–response of the primary ending of the mammalian muscle spindle. *J. Physiol.* **253**, 175–206.

GRÜSSER, O. J. & THIELE, B. (1968). Reaktionen primärer und sekundärer Muskelspindelafferenzen auf sinusförmige mechanische Reizung. I. Variation der Sinusfrequenz. *Pflügers Arch. ges. Physiol.* **300**, 161–184.

HASAN, Z. & HOUK, J. C. (1975*a*). Analysis of response properties of deefferented mammalian spindle receptors based on frequency response. *J. Neurophysiol.* **38**, 663–672.

HASAN, Z. & HOUK, J. C. (1975*b*). Transition in sensitivity of spindle receptors that occurs when a muscle is stretched more than a fraction of a millimeter. *J. Neurophysiol.* **38**, 673–689.

HULLIGER, M. (1976). Some quantitative studies on muscle receptors. Doctoral Thesis, Oxford University.

HULLIGER, M., MATTHEWS, P. B. C. & NOTH, J. (1976). The response of spindle primary afferents to 1 Hz sinusoidal stretching during paired fusimotor stimulation. *J. Physiol.* **263**, 182–183*P*.

HULLIGER, M., MATTHEWS, P. B. C. & NOTH, J. (1977). Effects of combining static and dynamic fusimotor stimulation on the response of the muscle spindle primary ending to sinusoidal stretching. *J. Physiol.* **267**, 839–856.

JANSEN, J. K. S. & MATTHEWS, P. B. C. (1961). The dynamic responses to slow stretch of muscle spindles in the decerebrate cat. *J. Physiol.* **159**, 20–22*P*.

JANSEN, J. K. S. & MATTHEWS, P. B. C. (1962). The central control of the dynamic response of muscle spindle receptors. *J. Physiol.* **161**, 357–378.

LENNERSTRAND, G. & THODEN, U. (1968). Position and velocity sensitivity of muscle spindles in the cat. II. Dynamic fusimotor single-fibre activation of primary endings. *Acta physiol. scand.* **74**, 16–29.

MANN, D. W. & CHAPMAN, K. M. (1975). Component mechanisms of sensitivity and adaptation in an insect mechanoreceptor. *Brain Res.* **97**, 331–336.

MATTHEWS, P. B. C. & STEIN, R. B. (1969). The sensitivity of muscle spindle afferents to sinusoidal stretching. *J. Physiol.* **200**, 723–743.

PRINGLE, J. W. S. (1972). Arthropod muscle. In *The Structure and Function of Muscle*, vol. I, ed. BOURNE, G. H., pp. 491–541. London: Academic Press.

PROSKE, U. (1975). Stretch-evoked potentiation of responses of muscle spindles in the cat. *Brain Res.* **88**, 378–383.

STUART, D., OTT, K., ISHIKAWA, K. & ELDRED, E. (1965). Muscle receptor responses to sinusoidal stretch. *Expl Neurol.* **13**, 82–95.