FREQUENCYGRAMS OF
SPINDLE PRIMARY ENDINGS ELICITED BY STIMULATION
OF STATIC AND DYNAMIC FUSIMOTOR FIBRES

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SUMMARY

1. Frequencygrams of cat spindle primary endings, obtained by the method described by Bessou, Laporte & Pagès (1968), were elicited by the stimulation of single static and dynamic fusimotor fibres.

2. Stimulation of static fibres by single stimuli may elicit: (i) no response, (ii) responses of small amplitude, (iii) responses of large amplitude with a pause after the rising phase.

3. Stimulation of static fibres by repetitive stimuli gives frequencygrams resembling records of tetanic contraction of skeletal muscle. At a frequency of stimulation of 180–200/sec periodic oscillations are perceptible on the plateau of the frequencygram.

4. Stimulation of dynamic fibres by single stimuli may elicit: (i) no response, (ii) responses smaller and longer than the responses given by static fibres.

5. When the muscle is stretched the amplitude of the responses elicited by dynamic fibres decreases whereas the amplitude of the responses given by static fibres increases.

6. Frequencygrams obtained by repetitive stimulation of dynamic fibres show periodic oscillations only at low rates of stimulation. At rates of stimulation higher than the minimal rate giving frequencygrams with a smooth contour, the amplitude of the frequencygram increases.

INTRODUCTION

In a preceding paper (Bessou *et al.* 1968) a method of analysing discharges of spindle primary endings was described. This method which gives indirect information on the contraction of intrafusal muscle fibres leads to construction of graphs called 'frequencygrams'. It is based on superposition of records of 'instantaneous' frequency of discharges from primary

endings obtained during stimulation of single fusimotor fibres. The stimuli must be delivered at all possible intervals with respect to the resting discharge of the ending. The superposition is made on the screen of a storage oscilloscope whose time base is synchronized with the stimulation. In the present paper, frequencygrams of cat's primary endings obtained during stimulation of static and dynamic single fusimotor fibres will be described in detail and some deductions on the contraction of intrafusal muscle fibres elicited by these two types of motor fibres will be presented.

METHODS

Twenty-six experiments were carried out on adult cats under Nembutal anaesthesia. In each experiment a single Group I fibre connected to a spindle located in the distal third of a tenuissimus muscle was prepared by splitting L_7 or S_1 dorsal roots and several single fusimotor fibres innervating this spindle were prepared by splitting L_7 and S_1 ventral roots.

Single fusimotor fibres were identified as static or dynamic (Matthews, 1962) by the effects that their repetitive stimulation at 100/sec exerted on responses of primary endings to phasic stretch. Stimulation of static fibres decreases both the response of the ending during the period of phasic stretch and the dynamic index (Crowe & Matthews, 1964), while dynamic fibres exert opposite effects. The distal segment of the tenuissimus muscle in which the analysed spindles were located was stretched over 3 mm at constant velocities ranging from 10 to 18 mm/sec.

Single fusimotor fibres were stimulated by single stimuli and repetitively with rates of stimulation between 20 and 200/sec.

RESULTS

Among all the single fusimotor fibres whose repetitive stimulation at 100/sec increased the rate of discharge of the primary endings only fifty, i.e. approximately two fibres per spindle, were systematically analysed. Thirty-seven fibres were identified as static, thirteen as dynamic.

Static fusimotor fibres

(1) *Frequencygrams obtained during stimulation by single stimuli*

The frequencygrams (Fig. 1) varied from fibre to fibre:

(i) Some static fibres did not increase the frequency of discharge of primary endings. In this case the frequencygram is a horizontal band whose width results from small random variations in the frequency of discharge of the ending (record 1).

(ii) Some static fibres produced an increase in the frequency of discharge in only one out of two or three stimuli. The frequencygram shows a response of moderate amplitude superimposed on the base line of the resting discharge (record 2). Its rising phase lasts 5–8 msec, its decreasing phase 15–30 msec. As it has been verified that single fusimotor fibres were effectively excited by every stimulus, this response suggests that trans-

mission of a single impulse at the neuromuscular junction was intermittent and 'all-or-none' in these cases.

(iii) Some static fibres produced a moderate increase each time they were stimulated. The frequencygram shows a response (record 3) with approximately the same time course as the response illustrated by record 2 (note the time scales are different), but since the discharge of the primary ending was accelerated after each single stimulus, the base line is interrupted by the response.
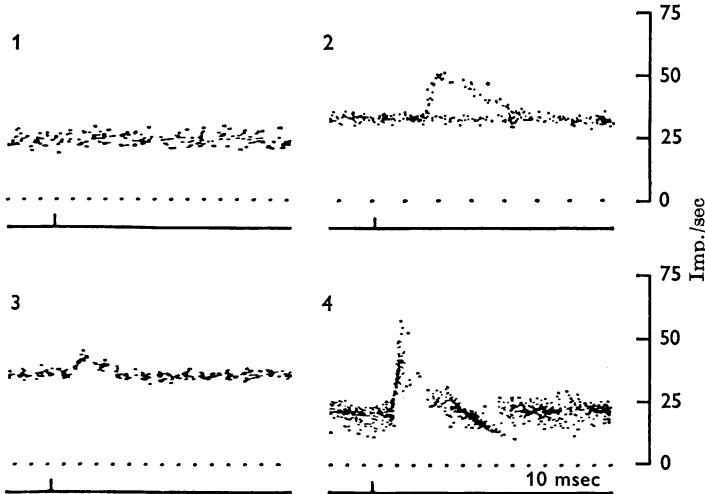

Fig. 1. Frequencygrams of four primary endings recorded during stimulation of single static fusimotor fibres by single stimuli. Upper trace, frequencygram; lower trace, stimulus; middle trace, time in 10 msec periods; this trace gives the zero line of the frequencymeter. The same disposition has been used in all figures. Records 1, 2, 3 were obtained by the superposition of about 30 traces, record 4 of 80 traces. Conduction velocity in m/sec: Group I fibres, (1) 75, (2) 91, (3) 91, (4) 74. Fusimotor fibres, (1) 26, (2) 30, (3), 33, (4) 31.

(iv) Some static fibres elicit responses of greater amplitude (record 4), the increase in frequency being often greater than 50 impulses/sec. The rising phase of these responses, whose duration can be as short as 5 msec, is followed by a period during which no impulses are initiated by the ending. The declining phase lasts 30–45 msec. These large responses which served for developing the frequencygram method have been described in detail by Bessou *et al.* (1968).

Of the thirty-seven static fibres studied, ten gave no response, fourteen gave small responses such as the ones illustrated by records 2 and 3 and thirteen gave large responses. These values do not give an accurate estimate of the actual proportion of the different types of responses because, at the beginning of this study, we had the tendency to select fibres eliciting large

responses. More recently P. Bessou & B. Pagès, in the course of other experiments (unpublished data) have aimed at preparing all the fusimotor fibres which activated individual spindles by repetitive stimulation and have recorded systematically the frequencygrams elicited by single stimuli. In twelve tenuissimus spindles, they prepared an average of four fusimotor fibres per spindle, three static and one dynamic. One static fibre out of five gave a large response, two a small one and two no response. Fusimotor fibres eliciting large responses with a pause after the rising phase were not found in every spindle. On the other hand, the three types of responses could be observed in the same spindle innervated by at least three static fibres.

Effect of static stretch. Changing the length of the muscle modifies considerably the amplitude and the duration of the response. This effect, which is more prominent with large responses than with small ones, is illustrated by Fig. 2.
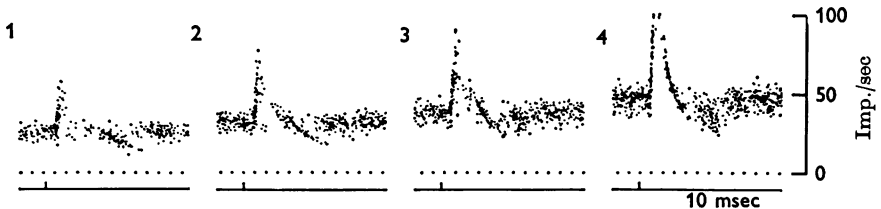

Fig. 2. Effect of muscle stretch on the responses to stimulation of a single static fibre by single stimuli. Length of the tenuissimus muscle segment: (1) 28 mm, (2) 30 mm, (3) 32 mm, (4) 34 mm. 100 superposed traces for each frequencygram. Conduction velocity in m/sec: Group I fibre, 106; fusimotor fibre, 39.

When the tenuissimus segment was relaxed (28 mm, record 1) the resting frequency was about 30/sec. The peak of the response reached a frequency of 70/sec; the duration of the rising phase was 6 msec with a slope of 7·1 impulses/sec/msec and the duration of the response (parts 2, 3 and 4) was approximately 70 msec. When the muscular segment was stretched to 34 mm so as to increase the resting frequency to a value of 50/sec (record 4), the response to stimulation underwent a large change; the rising phase lasted 5 msec with a much faster slope (12 impulses/ sec/msec). The maximal frequency reached a value above 100/sec, and the duration of the response (parts 2, 3 and 4) was only 30 msec. Records 2 and 3 obtained with intermediate lengths (30, 32 mm) show the progressive development of these modifications.

(2) *Frequencygrams obtained during repetitive stimulation*

Figure 3 shows the frequencygrams obtained by stimulating at various rates a single static fusimotor fibre which produced a response of large size
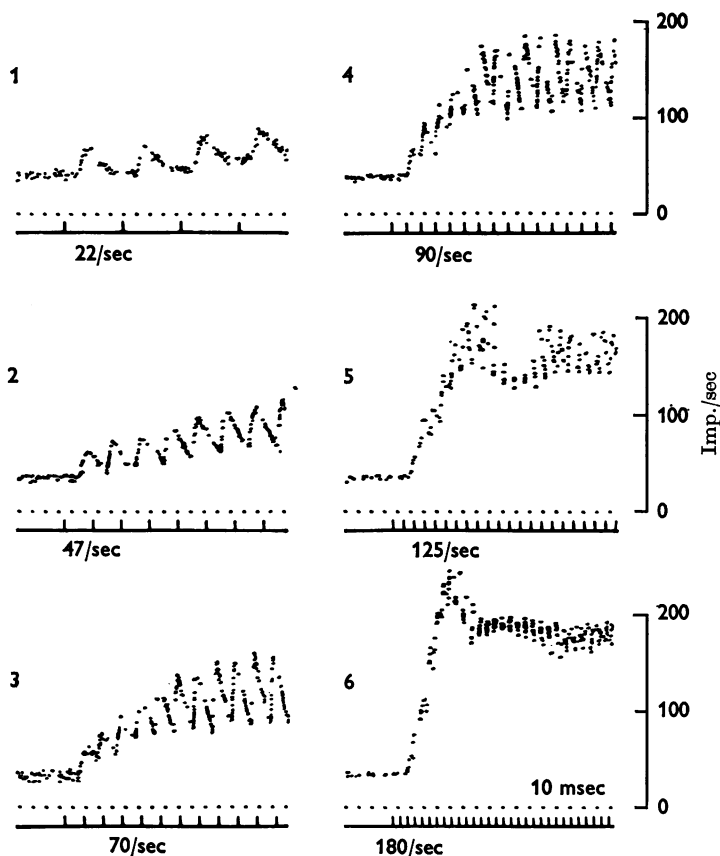
Fig. 3. Frequencygram of a primary ending recorded during repetitive stimu-
lation of a single static fibre. Note that the first stimulus was always giving a
response. Thirty superposed traces for each frequencygram. Conduction velocity
in m/sec: Group I fibre, 81; fusimotor fibre, 36.

to a single stimulus. The frequencygrams somewhat resemble records of
incomplete tetani of skeletal muscles. Each stimulus produces a frequency
increment which sums with the preceding one depending on the time
interval between stimuli. The frequencygrams show a rising phase and a
plateau on which periodic peaks corresponding to the stimuli are super-
imposed. The faster the rate of stimulation, the steeper is the rising phase
and the higher the level of the plateau. For rates of stimulation below
100/sec (records 1, 2, 3, 4) the plateau is attained after about 7 to 9 stimuli.
The amplitude of successive peaks increases during the rising phase and
stays approximately constant during the plateau. For example, with a
rate of stimulation of 90/sec (record 4), the first peak has an amplitude of

4-2

30 impulses/sec while the ninth has an amplitude of 80 impulses/sec. At higher rates of stimulation (records 5, 6) the maximal frequency of discharge is reached more quickly, and the subsequent periodic increments become smaller. At 180/sec (record 6), the frequency of discharge of the primary ending rises to 250/sec in about 35 msec. After a short period of high frequency discharge, a limited fall in the frequency is observed. Small
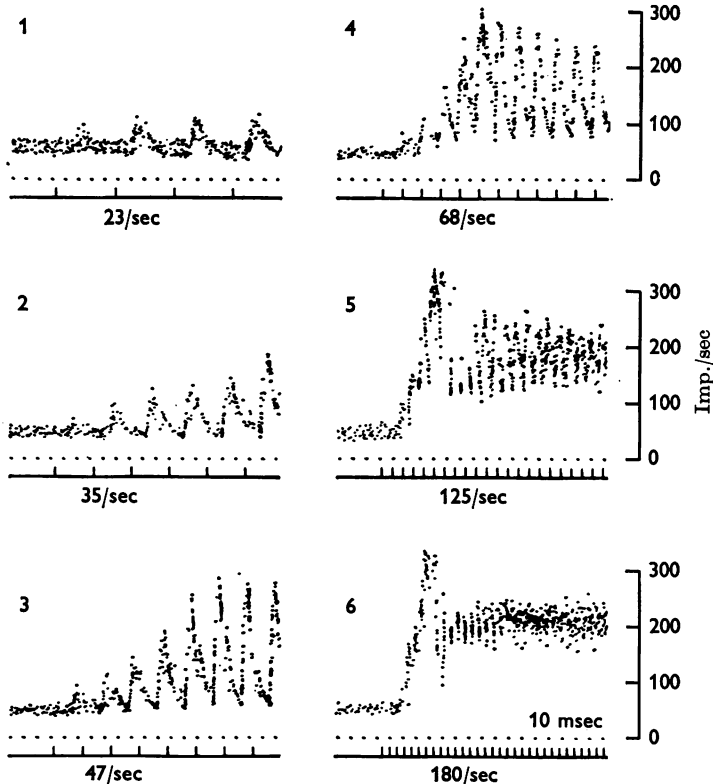

Fig. 4. Frequencygrams of a primary ending recorded during repetitive stimulation of a single static fibre. Note the occasional responses given by the first stimulus. Fifty superposed traces for each frequencygram. Conduction velocity in m/sec: Group I fibre, 71; fusimotor fibre, 26.

increments are still discernible during the plateau probably because the elongation of the primary ending by the intrafusal muscle fibres is not constant, suggesting these fibres were not in a state of complete tetanus in spite of the high rate of stimulation.

The frequencygrams illustrated by Fig. 4 were obtained by stimulating repetitively a static fibre which produced intermittent responses to the first stimulus, as shown in nearly all records. The progressive increase in

amplitude of individual peaks at the beginning of stimulation is very pro-
nounced; for example, the sixth stimulus in record 3 is responsible for an
increment of nearly 200 impulses/sec whereas the first one was either
ineffective or gave an increase of about 30 impulses/sec.

Figure 5 illustrates the frequencygrams elicited by a static fibre whose
stimulation by single stimuli had no effect. An increase in the rate of dis-
charge could not be observed before the third stimulus, as shown by each
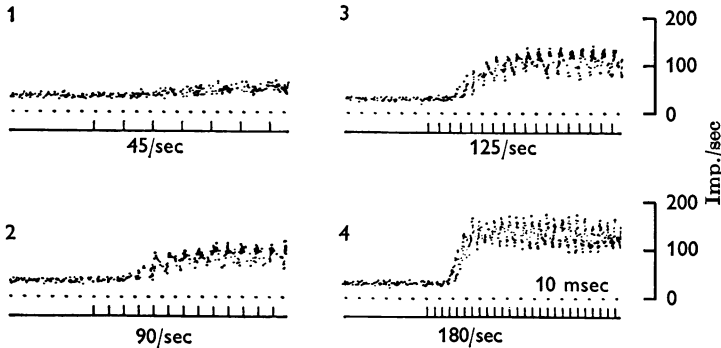record of this figure. Following this first stage, periodic increments of

Fig. 5. Frequencygrams of a primary ending recorded during repetitive stimu-
lation of a single static fibre. The two or three first stimuli do not elicit responses.
Fifty superposed traces for each frequencygram. Conduction velocity in m/sec:
Group I fibre, 86; fusimotor fibre, 37.

frequency of only relatively small amplitude were detected after each
stimulus, even for stimulation at 180/sec. The maximal frequency of
discharge reached by this ending was much lower than in the two pre-
vious cases and no peaks of large amplitude were observed during the
rising phase.

The activity of primary endings when the repetitive stimulation was
over was studied in fourteen cases. Two types of frequencygram were
observed. After the stimulation of the majority of static fusimotor fibres
(ten out of fourteen) the primary ending stopped discharging impulses and
did not resume its activity for some time (Fig. 6, records 1 and 2). Follow-
ing this pause, grouping of impulses was observed. The duration of the
pause increased with the rate of stimulation; at rates of stimulation lower
than 50/sec there was usually no pause but only an undershoot in the
frequencygram. In four cases, although the rate of stimulation of the
fusimotor fibre was high, the frequencygram showed a progressive decay
lasting about 0·3 sec (Fig. 6, record 3) without any undershoot before the
resting level of activity was reached. These different time courses of post-
tetanic decay cannot be attributed to differences between primary endings

because in three of the four spindles in which a slow return to resting conditions was observed another single static fibre produced a typical posttetanic pause.

No correlation could be established between the mode of decay and the characteristics of the responses elicited by single stimuli.
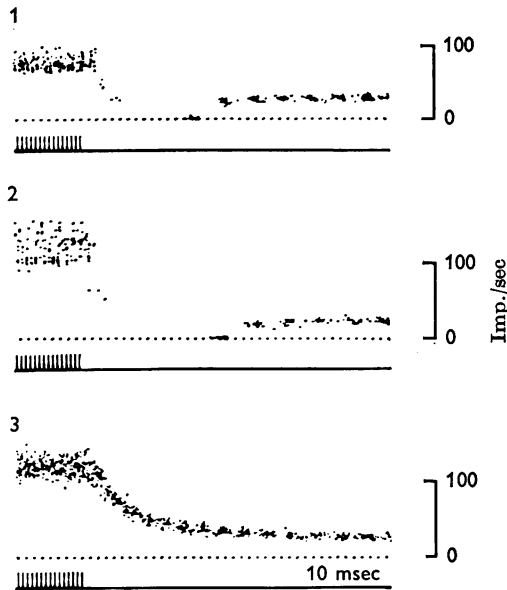

Fig. 6. Frequencygrams of three primary endings observed after a period of repetitive stimulation of a single static fibre. Stimulation at 175/sec during 1 sec. Twenty superposed traces for frequencygram 1, 10 for frequencygram 2, 30 for frequencygram 3. Conduction velocity in m/sec: Group I fibres, (1) 76, (2) 82, (3) 86. Fusimotor fibres (1) 42, (2) 40, (3) 37.

Observations on 'driving'. 'Driving' is very commonly produced by repetitive stimulation of static fibres which give large responses after single stimuli. An example of driving is illustrated by record 2 of Fig. 7 which was obtained when the length of a segment of tenuissimus muscle in which the spindle under study was located was 32 mm. The maximal physiological length of this segment, measured before it was separated from the rest of the tenuissimus muscle during complete extension of the knee, was 36 mm. After the first two stimuli the ending's discharge followed exactly the frequency of stimulation (55/sec). The accuracy of this 'driving' can be appreciated from the fact that each of the points of record 2 results from the superposition of about eighty points which appeared exactly at the same position on the screen for the eighty consecutive repetitive stimulation. When the length of the muscular segment was either shortened or

lengthened by 2 mm (Fig. 7, records 1 and 3) the 'driving' was not as
precise. For instance, in the first half of record 1, instead of a 1:1 ratio
between impulses and stimuli, the driving had a 1:2 ratio. When the
muscle was stretched at maximal physiological length (Fig. 7, record 4) a
typical frequencygram of tetanic stimulation reappeared with individual
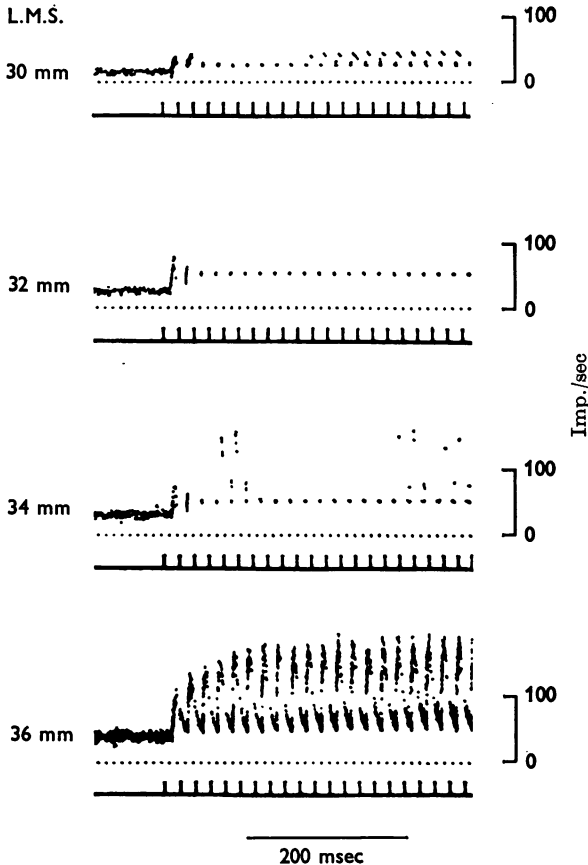peaks starting from a constant low level. The comparison of records 2 and

Fig. 7. 'Driving' of a primary ending by the repetitive stimulation of a single
static fibre. Note the effect of stretching the tenuissimus muscle segment con-
taining the spindle. L.M.S.; length of muscular segment. Eighty superposed traces
for each frequencygram. Conduction velocity in m/sec: Group I fibre, 106; fusi-
motor fibre, 39. Frequency of stimulation: 55/sec.

4 shows that the points resulting from the 'driving' of the ending corre-
spond to the origin of each individual peak. Eight similar cases of 'driving'
were observed. All of them were obtained with single fibres giving large
frequencygram responses after single stimuli. Single fibres eliciting a small

response or no response at all when stimulated by single stimuli did not produce 'driving' of the ending.

Dynamic fibres

(1) *Frequencygrams obtained during stimulation by single stimuli*

Four dynamic fusimotor fibres out of the thirteen which were studied produced no increase in the rate of discharge of the endings when stimulated by single stimuli (Fig. 8, record 1). The nine others gave a response showing approximately the same time course and amplitude; five of these
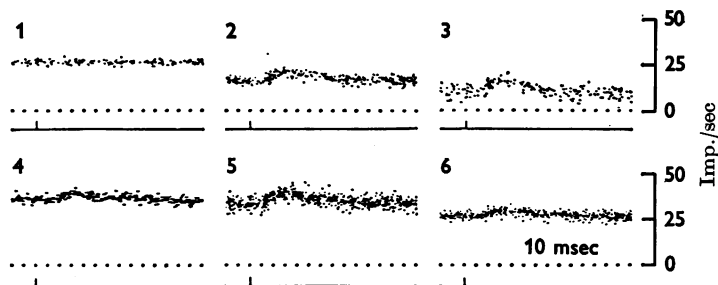

Fig. 8. Frequencygrams of six primary endings recorded during stimulation of single dynamic fusimotor fibres by single stimuli. Conduction velocity in m/sec: Group I fibres (1) 75, (2) 72, (3) 99, (4) 81, (5) 84, (6) 110, fusimotor fibres (1) 31, (2) 35, (3) 42, (4) 32, (4) 39, (6) 37.

responses are illustrated by records 2–6. Their latency was about 10–15 msec, the duration of their rising phase, although difficult to measure accurately was between 15 and 25 msec. The increase in frequency was often less than 10 impulses/sec. The declining phase lasted 40–60 msec.

The responses given by single stimuli could be markedly augmented when the single stimuli were applied after a period of repetitive stimulation. Records 2 and 5 of Fig. 9 show that after a 1 sec period of repetitive stimulation of two single dynamic fibres the rate of discharge of two primary endings, respectively activated by each one of these fibres, did not return to its original value for several tenths of a second. The stimulation of one dynamic fibre by single stimuli (Fig. 9, record 1) had no effect on the ending's discharge, while the stimulation of the other fibre (Fig. 9, record 4) elicited a response of small amplitude. When the single stimuli were applied just before the increase due to repetitive stimulation had subsided, a typical response was produced by the first fibre (Fig. 9 record 3) and the response to the second fibre was markedly increased (Fig. 9, record 6).

Effects of static stretch. The responses elicited by dynamic fibres decrease or even disappear when the muscle is stretched. This effect is opposite to the effect exerted on the responses to static fibres which increase markedly in amplitude (see Fig. 2).

The frequencygram in record 1 of Fig. 10 shows a typical response to a dynamic fibre. It was obtained when the tenuissimus muscle segment was relaxed, its length being 9 mm shorter than the maximal physiological length. When the muscle segment was lengthened by 3 and 6 mm the
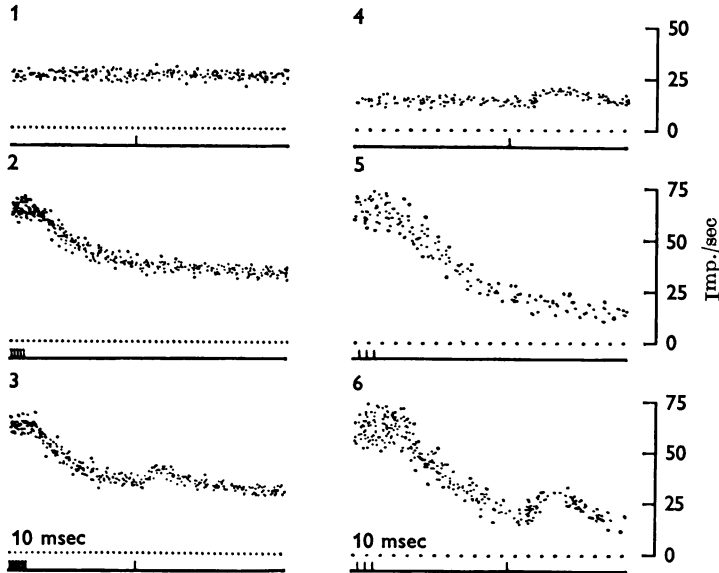

Fig. 9. Increase of the responses to stimulation of single dynamic fibres by single stimuli produced by a preceding period of repetitive stimulation. Two experiments are illustrated. One of the dynamic fibres produced no response when stimulated by single stimuli (record 1). In the same conditions, the other dynamic fibre gave a small response (record 4). Twenty-five superposed traces for frequencygrams 1, 2, 3; 15 for frequencygrams 4, 5, 6. Conduction velocity in m/sec: Group I fibres 85 and 72. Fusimotor fibres 37 and 35.
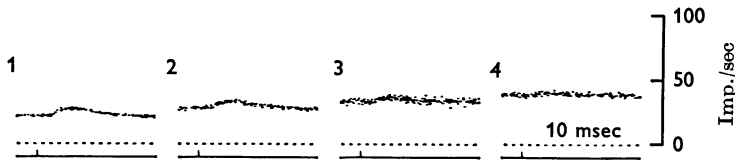

Fig. 10. Effect of muscle stretch on the responses to stimulation of a single dynamic fibre by single stimuli. Length of the tenuissimus muscle segment: (1) 38 mm, (2) 41 mm, (3) 44 mm, (4) 47 mm. 30 superposed traces for each frequencygram. Conduction velocity in m/sec: Group I fibre 91, fusimotor fibre 42.

resting rate of discharge increase and the response to the dynamic fibre diminished in size (Fig. 10, records 2, 3), Finally, this response disappeared when maximal physiological length was reached after a further stretch of 3 mm (Fig. 10, record 4).

(2) *Frequencygrams obtained during repetitive stimulation*

As would be expected from the relatively long duration of the rising phase of the responses elicited by single stimuli the frequencygrams recorded during repetitive stimulation showed discrete increments only for very low rates of stimulation. This is the case for record 1 of Fig. 11 which was obtained at 25/sec. With a rate of stimulation as low as 47/sec (record
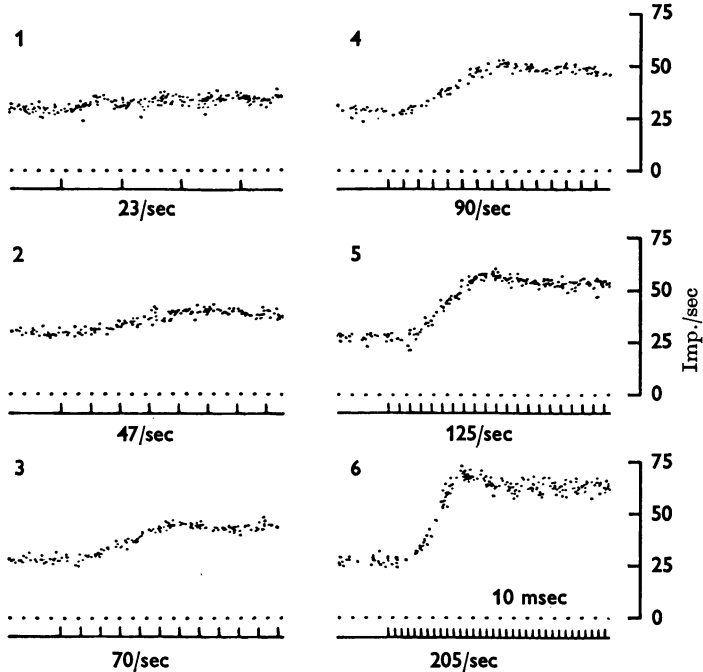

Fig. 11. Frequencygram of a primary ending recorded during repetitive stimulation of a single dynamic fibre. Twenty-five superposed traces for each frequencygram. Conduction velocity in m/sec: Group I fibre 110, fusimotor fibre 37.

2) the frequencygram had already a smooth contour. For higher rates (Fig. 11, records 3, 4, 5, 6), the amplitude of the frequencygram rose from 15 impulses/sec (record 3) up to 35 impulses/sec (record 6), and its rising phase became progressively shorter, 35 msec in record 6, compared with 70 msec in record 3.

After a period of repetitive stimulation, the frequency of discharge of the primary endings returned slowly to the resting level. Pauses in the discharge were never observed. The longest relaxation phase (Fig. 9, record 2) that we found lasted half a second, the shortest 0·1 sec. In this case the frequency showed a slight undershoot of about the same duration before the resting level was attained.

DISCUSSION

The frequencygrams of primary endings obtained during the stimulation of static fusimotor fibres by single stimuli differ from one another. Stimulation of about two axons out of five produces no response in the frequencygram. Several explanations, not mutually exclusive, can be proposed to explain this lack of response: (i) some fusimotor axons have so few terminal branches innervating some spindles that the contraction they induced in these spindles is weak; (ii) the contraction elicited by single stimuli is localized and the region which contracts is distant from the sensory ending; the energy of contraction is absorbed by inactive parts of intrafusal muscle fibres situated between the contracted region and the sensory ending; (iii) single impulses may fail to be transmitted across some neuromuscular junctions as it is suggested by the 'all-or-nothing' behaviour (see record 2, Fig. 1) of some responses.

The frequencygrams elicited by single stimuli differ in their amplitude and time course. Large responses very likely result from the contraction of several intrafusal muscle fibres innervated by the same fusimotor axon. Possibly they are elicited by fusimotor axons which innervate both poles of intrafusal muscle fibres (see Fig. 2 in Barker, 1966) and which elongate the equatorial region more than the axons producing the contraction of only a single pole. When individual records (the superposition of which gave rise to the frequencygram) were examined, it was observed that most of them had a dot (corresponding to an action potential) during the period corresponding to the rising phase in the frequencygram, showing that the transient increase of generator potential resulting from the contraction is large enough to increase rapidly the rate of discharge of the ending. The succession of two impulses at a short interval increases markedly the refractoriness of the ending, as shown originally by the mode of resetting of the rhythmic discharge after an antidromic impulse (Matthews, 1933). This explains, at least partly, the reason why no impulse can be initiated for a certain time after the rising phase (see Bessou *et al.* 1968).

Responses of small amplitude, i.e. responses in which the rate of discharge increased moderately, are very likely due to a weaker muscle contraction, possibly because fewer muscle fibres are involved or because the contraction occurs only at one pole thus producing a small transient increase of generator potential. In the individual records of which these frequencygrams were made up, there is in many cases no dot in the period corresponding to the rising phase of the frequencygram showing that, in this case, the increase of generator potential cannot rapidly drive the ending to the level of firing. As the time between successive impulses in

individual records is relatively long the lowering of excitability of the ending is less pronounced and no pause is observed in the frequencygram.

Our observations on the effect of single stimuli show that about three static fibres out of five may activate intrafusal muscle fibres and produce an increase in the rate of discharge of the ending when stimulated by single stimuli. Direct confirmation of these contractions has been recently obtained by Bessou & Pagès (1967) who recorded, by an optical method, movements of a spindle pole elicited by a single stimulus applied to single axons which had been identified as static. In some isolated spindles, after stimulation of a muscle nerve, Boyd (1966b) has observed local contractions which were sometimes capable of extending the portion of intrafusal muscle fibres close to the equatorial region and which he ascribes to static axons.

When static axons are stimulated repetitively the frequencygram consists of a fast rising phase followed by a plateau on which peaks corresponding to each stimulus are superimposed. The plateau results from the sensitivity of the primary endings to maintained extension, the elongation being maintained by tetanic contraction of intrafusal muscle fibres. The small peaks are probably due to small periodic changes of length resulting from the incompletely fused tetanus, which are very effective because primary endings are sensitive to velocity of stretching.

When the rate of stimulation is lower than 100/sec, large and progressive increases in the size of the first individual responses can often be observed (see Fig. 3, records 3 and 4), indicating that each of the consecutive contraction produces a greater deformation of the sensory endings. These incremental changes are probably due to alteration in the muscular elements situated between the site of contraction and the sensory endings, but synaptic properties of the neuromuscular junctions may also participate in this phenomenon.

The required rate of stimulation for completely fused contractions seems to be very high, since at rates as high as 180–200/sec the plateau of the frequencygrams still shows small phasic increments with each stimulus. This is in agreement with the time interval, of about 6 msec, for which complete summation of two responses is obtained (Bessou et al. 1968) and with the observations of Harvey & Matthews (1961) and Bessou, Emonet-Dénand & Laporte (1962) on the rate of stimulation giving maximal activation of the primary endings.

The observations we made on the discharge of primary ending immediately after the cessation of repetitive stimulation confirm the findings of Eyzaguirre (1960). In most cases the discharge stopped abruptly suggesting a fast relaxation of the intrafusal muscle fibres but in some cases (4 times out of 14) the discharge slowed down gradually. Since in our experiments all the sensory endings analysed were identified as primary

endings, such slow post-tetanic declines indicate a slow relaxation of at least some intrafusal muscle fibres. During the repetitive stimulation of these four static axons the frequencygram was not different from those produced by axons whose repetitive stimulation was immediately followed by a pause.

Static fusimotor fibres also differ in their ability to 'drive' primary endings. Only the axons which elicited large responses when stimulated by single stimuli induced 'driving'; other static axons, even if they had a powerful action when repetitively stimulated, did not.

It is possible that the heterogeneity of the response given by static fusimotor fibres is only the consequence of stimulating single axons differing in the way they innervate individual spindles, but it cannot be excluded that this heterogeneity is also due to the activation of intrafusal muscle fibres with different speed of contraction and of relaxation. Such a possibility has to be considered since Barker (1966) maintains that the same motor axon may innervate both nuclear chain and nuclear bag muscle fibres, which were shown by Smith (1966) and Boyd (1966a) to differ in the velocity of their contraction. Differences in junctional potentials (local or spikes more or less propagated) such as the ones found in crustacean muscle fibres (Fatt & Katz, 1953a, b; Furshpan, 1955; Hoyle & Wiermsa, 1958) could also account for these differences.

Dynamic axons, on the other hand, give more homogeneous results. The small amplitude and long duration of the responses given by single stimuli show that the contraction elicited by these fibres is weaker and slower than the contraction elicited by static fibres. When the muscle is stretched these responses decrease in amplitude or even disappear (see Fig. 10) whereas the responses to static fibres, on the contrary, increase (see Fig. 2). The opposite effect exerted by stretch on the responses to the two kinds of fibres suggests that the contractions elicited by static and dynamic fibres are of different nature. In the ileofibularis muscle of the frog, Kuffler & Williams (1953) found that the optimal initial tension for tension development in 'slow' fibres was notably smaller than the optimal tension for twitch fibres.

During repetitive stimulation of dynamic fibres frequencygrams show smooth contours even for low rates of stimulation, but their amplitudes increase markedly for higher rates of stimulation, as is also the case for 'slow' muscle fibres of the frog (Kuffler & Williams, 1953).

The comparison of our results with recent cinematographical observations of contractions of intrafusal muscle fibres (Diete-Spiff, 1966; Smith, 1966; Boyd, 1966a, b) is difficult mainly because these contractions were elicited by direct stimulation or by stimulating muscle nerve, whereas in our experiments intrafusal muscle fibres were activated by stimulating single fusimotor axons of known function.

Diete-Spiff (1966) found in spindles of dog lumbrical muscles that a
1 sec period of direct repetitive stimulation produced a strong contraction
lasting several seconds; so far, we have never recorded frequencygrams of
such long duration.

Smith (1966) made the important observations on rat lumbrical spindles
that small diameter intrafusal muscle fibres (presumably nuclear chain
fibres) twitched vigorously when directly stimulated while large diameter
fibres (presumably nuclear bag fibres) gave only a small movement in
response to a single stimulus. Comparing the time course of contraction
of small and large intrafusal muscle fibres with the time course of the
frequency increase of afferent discharges elicited by repetitive stimulation
of static and dynamic fusimotor axons, Smith suggested that the small
muscle fibres could be responsible for static effects and the large ones for
dynamic effects. Such a suggestion is certainly of interest, although the
single traces of 'instantaneous' frequency which were used for this com-
parison do not give a very accurate picture of the time course of the
activity of the sensory endings. At the frequency used by Smith (1966),
the rising phase of the frequencygram produced by stimulation of static
fibres (see, for example, Figs. 3 and 4) shows successive peaks of large
amplitude whereas single traces would give too few points to allow the
peaks to be observed.

More recently, Boyd, using cats' tenuissimus spindles (1966 a, b), suc-
ceeded in observing the contraction of intrafusal muscle fibres elicited by
stimulation of the muscle nerve and confirmed that nuclear chain fibres
contract and relax more rapidly than nuclear bag fibres, but he expresses
the opinion that the fusimotor axons responsible for all these contractions
are static.

The responses we obtain with the frequencygram method strongly sug-
gest that the contractions responsible for static and dynamic actions have
different velocities: static fusimotor axons elicit very fast contractions and
dynamic fusimotor axons slower ones. Therefore we could propose, as
Smith did (1966), that nuclear chain fibres are responsible for static effects
and nuclear bag fibres for dynamic effects. We prefer not to do this, partly
because the variations among responses to static fusimotor axons we found
(large and small responses to single stimuli, axons which elicit driving and
axons which do not, abrupt stop of the ending discharge after repetitive
stimulation of some axons contrasting with progressive slowing down
observed with others), are not yet clearly explained and because we think
that direct evidence is needed to understand the mechanism of action of
fusimotor fibres. Direct optical observations are necessary to ascertain
whether static fusimotor axons activate only chain fibres and dynamic
axons only bag fibres. It would be equally important to know whether or

not the contractions elicited by the two kinds of fusimotor axons are of an entirely different nature as some of our observations suggest and also, since Barker states (1967) that different varieties of motor endings may coexist on the same muscle fibre, to know whether an intrafusal muscle fibre may contract in different ways according to the kind of fusimotor fibre which activates it.

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