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# PROPERTIES OF STRETCH RECEPTORS IN CAT EXTRAOCULAR MUSCLES*

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SUMMARY

1. The properties of fifty-two stretch receptors in the extraocular muscles were studied in thirty cats. Between ten and twenty-eight receptors were observed in each preparation.

2. In four preparations, spontaneously discharging receptors were observed, with afferent fibre conduction velocities ranging from 16·9 to 41·1 m/sec.

3. In the remaining twenty-six cats, the minimal threshold receptors ranged from 3 to 130 g, with a peak distribution between 10 and 20 g, and afferent fibre conduction velocities ranging from 6·5 to 52·0 m/sec, the peak being between 10 and 15 m/sec. Of these receptors, nineteen were quickly adapting and seven were slowly adapting.

4. The dynamic and static indexes of all the receptors were essentially similar; they both increased markedly on increasing the initial length. This suggests that the receptors do not lie in contact with regions of reduced viscosity on the muscle fibres comparable to the equatorial region of the intrafusal muscle fibres.

5. All of the receptors were located in the muscle; none was located in the tendon. Forty-seven of forty-nine receptors were in parallel and two receptors were in series with the contractile elements.

6. The properties of all the receptors studied appeared to be similar, suggesting that a single type of stretch receptor is located in the inferior oblique muscle of cats.

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## INTRODUCTION

Responses from extraocular stretch receptors have been studied in goats (Cooper, Daniel & Whitteridge, 1955; Whitteridge, 1960), which have muscle spindles in these muscles, and in cats and monkeys (Cooper & Fillenz, 1955), which have no extraocular muscle spindles. The presence or absence of extraocular muscle spindles is apparently not related to phylogenetic progression or to the range of eye movements in each species (discussed in Bach-y-Rita, 1959). The present study was undertaken to analyse in detail the properties of the stretch receptors in the eye muscles of a species (cat) that has no extraocular muscle spindles. A preliminary report of this work has been presented (Bach-y-Rita & Ito, 1966*b*).

## METHODS

*Preparation.* Thirty cats (1·8–3·6 kg) anesthetized with sodium pentobarbitone were included in this study. The cat's head was held in a visual model stereotaxic apparatus, and the body temperature maintained at 37–38° C by means of an abdominal heating pad. All experiments were made *in vivo* on an inferior oblique preparation which has been fully described in a previous paper (Bach-y-Rita & Ito, 1966*a*). The muscle was exposed after removal of the frontal sinus and overlying soft tissues. The portion of sclera containing the tendon insertion of the inferior oblique was cut away, and the rest of the globe removed. The tendon of the inferior oblique, together with the portion of the sclera with the muscle insertion, was usually tied with a silk suture. In some experiments the sclera was sutured to a metal bar 0·5 mm in diameter and 8 mm in length, in order to avoid injury to the tendon organs and to keep the normal spread insertion to the sclera. The muscle and nerve were kept immersed in warm paraffin.

*Application of stretch.* At least 5 min were allowed to elapse between applications of stretch, since the majority of the stretch receptors were fast adapting and required up to 3 min for recovery of sensitivity. Three methods of stretching were employed:

1. Loading the muscle. The suture from the tendon of the muscle was passed over a pulley and tied to a ring on which various weights were hung, and the length of the muscle during the loading of various weights was plotted.

2. Stretch at various velocities. The suture on the muscle tendon was attached, as shortly as possible, to a pin of a strain gauge tube mounted on the lever of the stretcher. The stretcher was made from an ink recorder pen motor, and was driven by a sawtooth of electric current producing constant velocities over the distance of the stretch. Ten steps from 0·25 to 200 mm/sec were employed. The calibrated rates were modified by the higher velocity stretches, but corrected values were obtained (e.g. Fig. 7*B*). The range of stretching speeds covered the contraction speeds of the cat's extraocular muscles (Cooper & Eccles, 1930; Robinson, 1964; Bach-y-Rita & Ito, 1966*a*). The distance of stretch was usually set at 3 mm by means of a stopper with a screw adjustment. The initial tension *in vivo* was arbitrarily set at 0·4 g. When the muscle was set at 0·4 g, the initial muscle length was termed '+0 mm'. The term '+5 mm' means that the muscle was lengthened by 5 mm from the initial length.

3. Steady stretching of the muscle: At the end of each experiment the muscle was stretched to its maximal length at a constant speed of 1 mm/sec by means of a rotating gear shaft driven by an electric motor.

*Recording.* The branch of the III nerve to the inferior oblique muscle was cut as close to the ciliary ganglion as possible. In some cases the entire nerve was placed over recording

electrodes and in others the nerve was teased until afferent discharges were obtained from a single receptor. The nerve slip was placed over one or two pairs of platinum electrodes and immersed in warm paraffin; two pairs of electrodes were employed for measuring the velocity of afferent nerve impulses produced by muscle stretch (cf. Ito, Toyama & Ito, 1964). The afferent nerve impulses were led to a differential amplifier and displayed simultaneously on a beam of a cathode ray oscilloscope and on an oscillograph paper recorder. The second and third channels of these recorders were employed for recording muscle tension and muscle length. The muscle tension was transduced by a RAC 5734 tube mounted on the lever of the stretcher. The connecting wires for the RCA tube were sufficiently flexible to avoid affecting the speed of stretch. Displacement of muscle length was recorded with a photo field-effect transistor. By means of a screen, the output of this transistor was kept linear to the movement of the stretcher shaft. The delay of the phototransistor was about 10 $\mu$sec, which was negligible for these experiments. The impulse discharge frequency was averaged for each 0·2 sec after loading in the isotonic stretch experiments. In experiments with stretch at various velocities, the reciprocal values of the impulse intervals were plotted.

*Muscle contraction.* In order to determine whether the receptor was in series or in parallel with the contractile elements, the discharge during muscle contraction was analysed for each receptor studied. All of the teased branches of the nerve to the inferior oblique, except for the branch containing the afferent fibre under study, were placed over three platinum electrodes. Stimuli were delivered to the two proximal electrodes, while the electrode nearest the muscle was grounded to reduce the stimulus artifact. The nerve was stimulated tetanically by electrical pulses of 0·1 msec duration and of maximal intensity, usually at 100 c/s frequency. The tetanic tension of the muscle, detected by the strain gauge tube mounted on the stretcher, was approximately 30 g, which was comparable to that of the intact preparation (Bach-y-Rita & Ito, 1966*a*).

*Site of receptors.* The site of the receptors in each preparation was detected by light pressure along the muscle applied by means of a glass rod with a tip diameter of 1 mm, while observing the muscle with a binocular microscope. The site of the receptor was signalled by a burst of impulses to each tap of the glass rod.

## RESULTS

I. *Muscle loading.* (*a*) Muscle length. The length of the muscle during loading varied approximately linearly with the logarithm of the load between 1 and 5 g. The muscle was 25–26 mm long in its relaxed state and varied from 36 to 42 mm under maximum stretch. The distal part of the muscle appeared to be more extensible than the proximal portion, due perhaps to restraining connective tissue on the proximal end or to the tapered distal ending which lacks the strong tendinous insertion found in limb muscles.

(*b*) Spontaneously discharging receptors. In four of the thirty cats studied, responses from spontaneous afferent discharges were recorded while the muscle was in a relaxed state. Only one of these spontaneously discharging receptors was noted in each of the four muscles. The amplitude of the discharges ranged from 50 to 120 $\mu$V, and the frequencies were 21·0 (cat number P-6), 32·3 (P-19), 16·3 (P-22) and 38·2 (P-25) impulses/sec. These amplitudes and frequencies were similar to those recorded from cat extraocular muscles by Cooper & Fillenz (1955).

The minimum load which produced a detectable change in frequency was 0·4 g. In Fig. 1, responses of a receptor to various loads were plotted against time after loading. All of the time–frequency curves were still descending 10–15 sec after loading, and had not recovered to resting discharge frequencies 10 sec after unloading. These curves were quite different from the response curves obtained from the muscle spindle in the goat's extrinsic eye muscles in which the curves arrived at new levels and recovered to the spontaneous level within 1 sec after on or off loading (Cooper & Daniel, 1957).

The relation of the frequency at 2 sec after loading to the logarithm of the load in the four receptors was almost a straight line in a range below 5 g (as was noted by Matthews, 1933, with frog muscle receptors), but inclined steeply with loads of more than 5 g. As the muscle length changed linearly against the logarithm of the loads between 1 and 5 g, the impulse frequency from the zero threshold receptor appeared to be in a linear relation with the muscle length in a range below 5 g. The sensitivity to the change in muscle length was calculated from the angle of slope of the load–frequency curve and the load–length curve in each muscle. The sensitivity in each receptor was 10·2 (P-6), 4·0 (P-19), 14·1 (P-22) and 9·6 (P-25) impulses. $sec^{-1}$ $mm^{-1}$. When the frequency at 2 sec after loading more than 10 g was represented against the loads (non-logarithmic scale), the load–frequency curves assumed almost straight lines. The sensitivity to load of the spontaneously discharging receptors was 0·2 (P-19), 3·1 (P-6) and 5·55 (P-22) impulses. $sec^{-1}$ $g^{-1}$ in each case, an average of 3·55 impulses $sec^{-1}$ $g^{-1}$. It appears that the spontaneously discharging receptors are sensitive to change of muscle length with loads of less than 5 g, and to change of muscle tension with loads of more than 10 g.

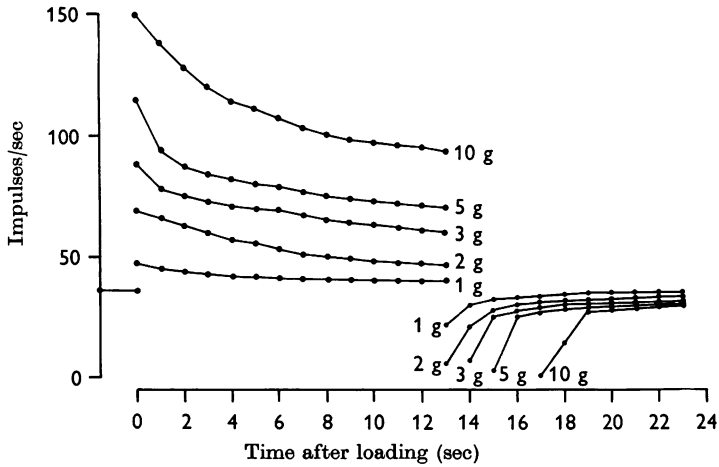



Fig. 1. Frequency of response of a spontaneously discharging receptor (preparation number P-25) after various loads were hung on and removed from the muscle.

The conduction velocities of impulses along the afferent nerve fibres innervating the zero threshold receptors were 41·1 (P-19), 16·9 (P-22) and 20·8 (P-25) m/sec. There was no relation between conduction velocity and sensitivity to muscle length change of the receptor.

(*c*) Non-spontaneously discharging receptors. In twenty-six out of thirty cats, no spontaneous discharges were observed when the muscle was in a relaxed state. The minimal thresholds of receptors observed in those preparations varied from 3 to 130 g, in which a peak distribution lay between 10 and 20 g (Fig. 3*C*). In some preparations, both inferior oblique muscles were studied; in each of these cases similar threshold responses in receptors were recorded from the muscle of both eyes. The receptors were divided into two groups: a group of relatively slowly adapting receptors from which a continuous response could be recorded during loading with some weights (Fig. 2*A*), and a group of rapidly adapting receptors from which the response disappeared a few seconds after loading with even the maximal weight (Fig. 2*B*). There was no relation between the speed of adaptation and the threshold of the receptors. The amplitude of afferent nerve spikes from the slowly adapting receptors was in the same range (50–100 $\mu$V) as that of the spontaneously discharging receptors, but those of the rapidly adapting receptors were relatively large, up to 250 $\mu$V, except in three examples of extremely high threshold receptors (90, 110 and 130 g thresholds). The responses from these three receptors were approximately 50 $\mu$V in amplitude, and disappeared after separating the nerve and the muscle from an underlying large blood vessel. Since they may have been blood vessel receptors, they were excluded from the analysis of stretch receptors.

The responses of the slowly adapting receptors change linearly to changes in muscle load rather than to changes in muscle length. The sensitivity to load, which was calculated from the angle of slope of the load–frequency curve, varied from 0·18 to 1·48 impulses. $sec^{-1}$ $g^{-1}$, with an average of 0·87 impulses. $sec^{-1}$ $g^{-1}$. These values were distinctly lower than those of the zero threshold spontaneously discharging receptors.

Only rapidly adapting responses were recorded in nineteen of the twenty-six cats which did not have spontaneous discharging receptors. Such responses disappeared within 1 or 2 sec, even after the loading of large weights as shown in the time–frequency curve of Fig. 2*B*. Thus, a load–frequency curve could not be drawn, and the sensitivity to load could not be determined. However, the shapes of the time–frequency curves of both the rapidly adapting and the slowly adapting receptors are similar; thus it may be assumed that their properties do not differ markedly, but that the sensitivity to load of the former is lower than that of the latter receptors. There are no significant relations between the thresholds of the receptors in the individual preparations and the conduction velocities of the afferent impulses propagated along the nerve fibres innervating the receptors (Fig. 3*A*). The histogram of the conduction velocities from the receptors included in Fig. 3*A* shows that the velocity varies from 6·5 to

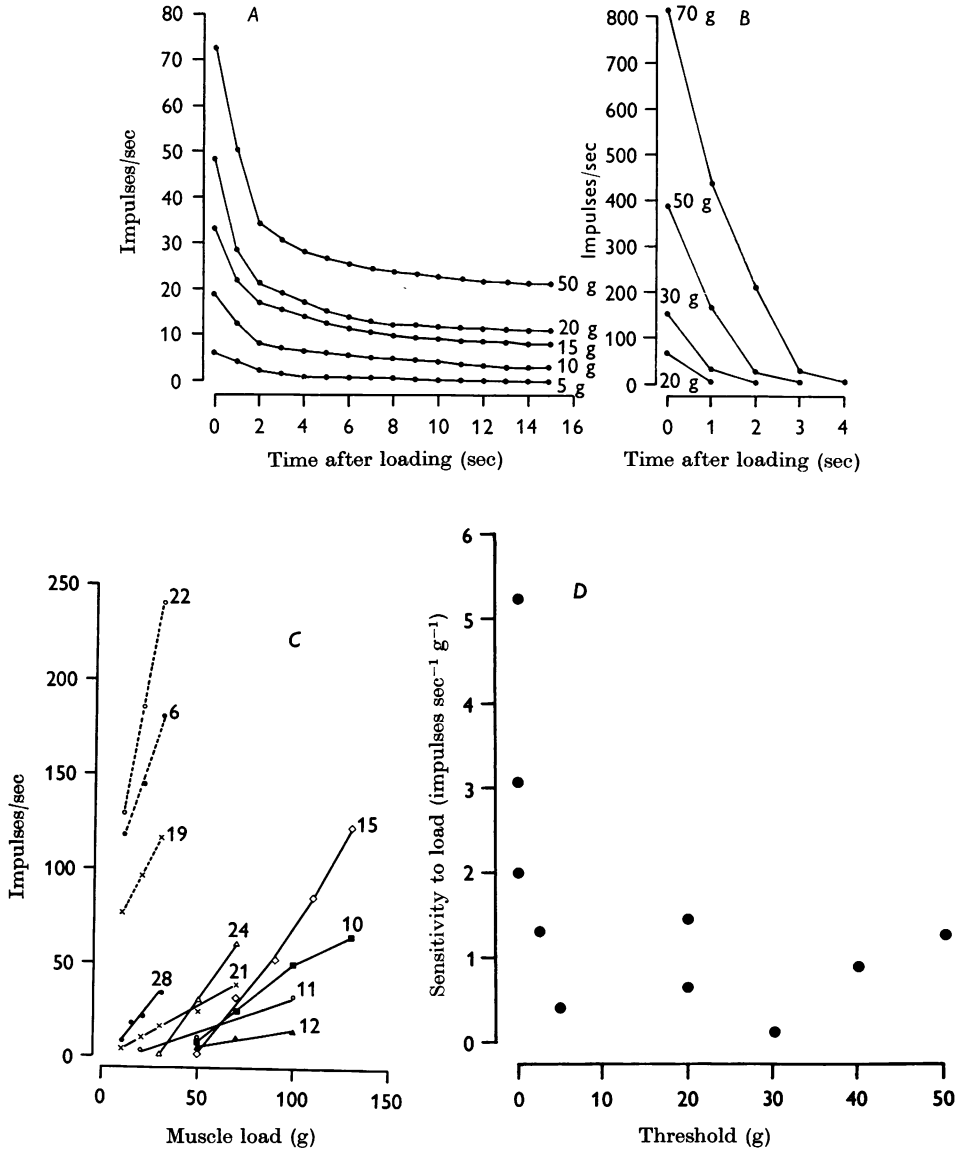



Fig. 2. *A* and *B*. Response frequencies of a slowly adapting (P-28 in *A*) and a rapidly adapting (P-27 in *B*) non-spontaneously discharging receptor, after application of various loads. *C*. The relation of the frequency 2 sec after loading to the load for the seven slowly adapting non-spontaneously discharging receptors illustrated (continuous line), shown in comparison with three curves (between 10 and 30 g load) for three spontaneously discharging receptors (dotted lines). The number on the end of each line refers to the minimal threshold receptor in the indicated preparation. *D*. The sensitivities to load calculated from the slopes of the graphs in *C* plotted against the threshold of corresponding receptors.

52·0 m/sec, the peak being between 10 and 15 m/sec (hatched scale in Fig. 3*B*). It was also noticed that the conduction velocities of the zero threshold receptors fell into the same range. Figure 3*C* is a histogram of thresholds of the 'minimal threshold receptors' in the individual muscles represented in Fig. 3*A*. In each muscle, the 'minimal threshold receptor'

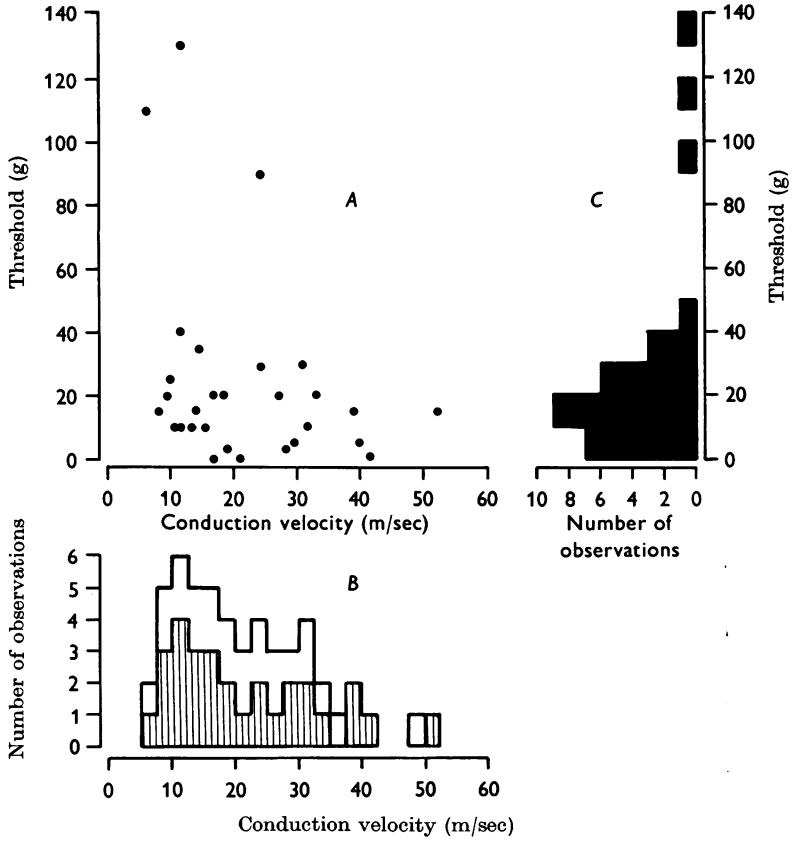



Fig. 3. *A*. Relation between the threshold value and the conduction velocity for the minimal threshold receptors in individual preparations. *B*. A histogram of the conduction velocities of the afferent fibres from the minimal threshold receptors represented in *A* (29 units in the hatched area), and for all receptors tested (fifty-two cases). *C*. A histogram of the threshold distribution for the minimal threshold receptors represented in *A*.

is the receptor with the lowest threshold when the entire nerve was placed over the recording electrodes. When measuring conduction velocities, sufficient weight was applied to activate only the minimum threshold receptor, and thus avoid possible errors due to activation of more than one receptor. Later in the experiment the nerve was divided into several slips in order to eliminate responses of the lower threshold receptors and thus be

able to determine the conduction velocities of impulses from higher threshold receptors. The histogram distributed from 0 to 130 g and the peak appeared between 10 and 20 g. Apparently all receptors (including spontaneously discharging receptors) in the cat extraocular muscles may be included in this category.

II. *Steady stretch.* The total number of sensory units in individual preparations was counted from the record of afferent impulses from each nerve slip at the end of each experiment (some afferent fibres may have been destroyed while splitting the nerve). The muscle was extended at a constant velocity of 1 mm/sec. Each sensory unit could be discriminated by an analysis of the amplitude and the discharge pattern, since we never observed simultaneous discharges from more than seven sensory units. The total number of sensory units observed in individual preparations ranged from 10 (P-21) to 28 (P-19). It was not possible to study in detail the properties of all of these receptors, some of which were observed only during this terminal application of steady stretch. Generally, the preparations with spontaneously discharging receptors included many sensory units. Figure 4*A* illustrates the preparation with the minimum number of sensory units (P-21). In this case, the minimal threshold receptor responded to loading of 5 g, and discharged during muscle extension from 30 to 41 mm. The number of activated receptors increased until the muscle length reached 41 mm, and decreased on further stretch of the muscle (Fig. 4*B*). After the muscle had been stretched to 46 mm, it was allowed to return to a relaxed state for more than 5 min. Stretch was again applied, and it was noted that the threshold of all receptors to extension of the muscle had increased markedly. Apparently the receptors and/or the innervating nerves were damaged or the receptors slipped from their original positions due to the excessive stretch (cf. Ito *et al.* 1964; Catton & PeToe, 1964). The spontaneous discharges and the responsiveness of the zero threshold receptors were also destroyed by excessive stretch.

A histogram of the conduction velocities of afferent nerve impulses from all receptors in which this characteristic was measured is shown in Fig. 3*B*. The range just coincided with the range of conduction velocities of group III muscle afferents innervating pressure-pain receptors (Paintal, 1960).

III. *Stretch at various velocities.* These experiments were undertaken to analyse the dynamic and static sensitivities of extraocular stretch receptors, as compared with those of muscle spindle receptors in cat limb muscles studied by Matthews (1963).

A 3 mm stretch from an initial length (+0 mm) was applied to a typical spontaneously discharging receptor (P-25). Tension development of the muscle increased during the dynamic phase of stretch, as has been shown by Matthews (1963) in limb muscles. Maximum muscle tension at com-

pletion of stretch varied from 2 g to 30 g as the velocity increased from 0·25 to 100 mm/sec. The discharge frequency of the receptor increased progressively as the stretch increased (Fig. 5). At the end of the dynamic

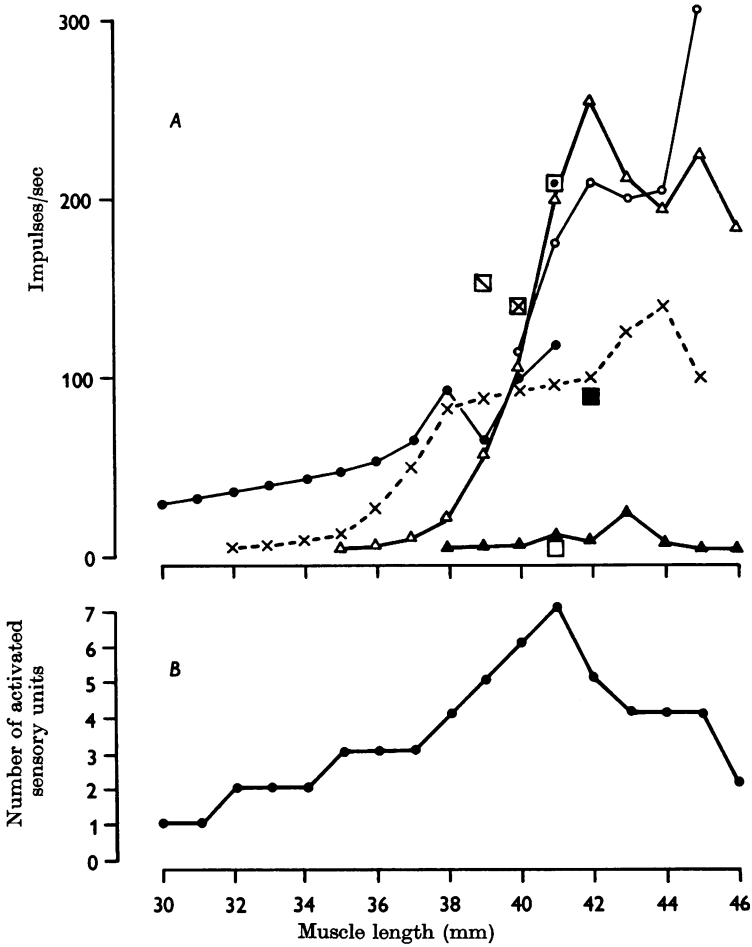



Fig. 4. *A*. Frequencies of responses of individual receptors to muscle length during steady stretching at 1 mm/sec in a preparation (P-21) in which ten non-spontaneously discharging receptors were counted. Each line shows the continuing responses from individual receptors; and each square denotes a burst response which disappeared in less than 1 sec. *B*. The number of sensory units activated plotted against muscle length during steady stretching at 1 mm/sec, from *A*.

phase of stretch the frequency fell to a new level, higher than the initial frequency. Increasing the velocity of stretch resulted in a greater maximal discharge frequency and a greater fall at the end of the dynamic period of stretch. There was no initial acceleration in the discharge frequency at the beginning of the stretch, in contrast to the responses of the primary and

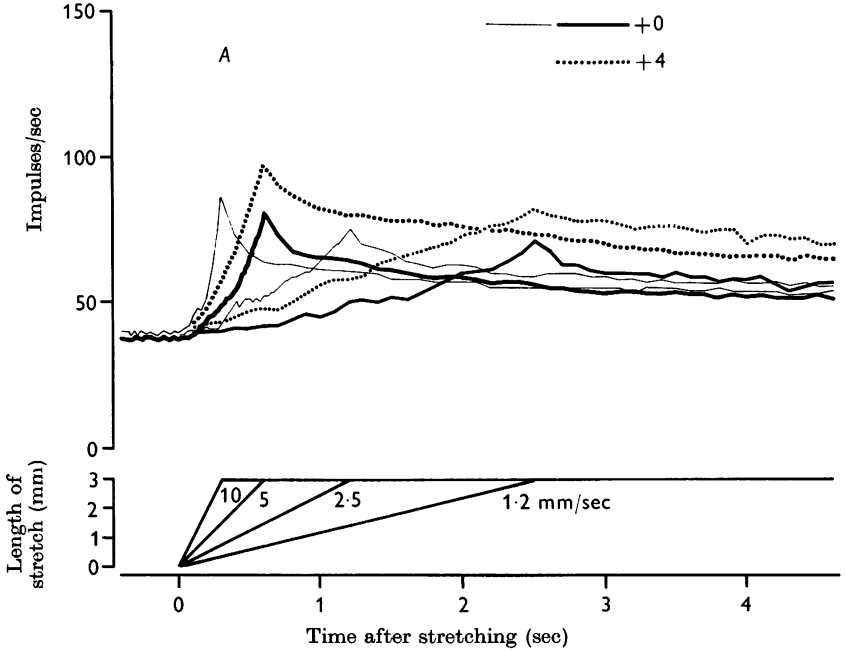
secondary endings in the de-efferented cat limb muscles observed by Matthews (1963). This may result from the absence of an accelerated increase in tension development at both ends of the portion of muscle containing the sensory ending at the beginning of stretch (Fig. 5). This phenomenon is not attributable to non-linearity on mechanical displacement at the beginning of stretch, but is apparently due to a visco-elastic property of the muscle. Another marked difference from the responses of primary receptors and a secondary spindle receptor obtained by Matthews (1963) is that in our studies the falling phase of frequency could not be differentiated into an initial abruptly decreasing phase and a slowly decreasing phase, but appeared to be nearly exponential (Fig. 5). The relative magnitude and the time course of the falling frequency phase would be of importance in a detailed quantitative analysis of the behaviour of an ending, especially since these factors demonstrate the existence of visco-elastic properties of the muscle fibres (Matthews, 1964).

Jansen & Matthews (1962) have called the discharge frequency measured at 0·5 sec after completion of the dynamic phase of the stretch the 'static index', and the difference in frequency between the maximal frequency at final extension and this 'static index' the 'dynamic index'. The lower continuous line in Fig. 6 shows graphically the dependence of the magnitude of the dynamic index upon the velocity of stretch for the same ending (P-25) as in Fig. 1. The dynamic index of spontaneously discharging receptors increased with increasing velocities.

When the muscle was stretched by 3 mm at various velocities from an initial length of +4 mm, the tension development of the muscle increased steeply during the dynamic phase of stretch, and reached a maximum of approximately 10–50 g with velocities of from 0·25 to 100 mm/sec. The discharge frequency during the dynamic phase of stretch also increased more steeply than with stretch from +0 mm initial length. However, 'initial acceleration' of discharge at the beginning of stretch was still not

Legend to Fig. 5

Fig. 5. Responses of a spontaneously discharging receptor (P-25) to an extension of 3 mm from +0 mm (continuous line) and +4 mm (dotted line) initial muscle length at various stretch velocities. The frequency is represented by the reciprocal of the time interval between action potentials. The curves were drawn by connecting the data points. Symbols showing the data points were omitted from *A* for the sake of clarity, but are shown in *B*. The length scales are diagrammatic and represent corrected values derived from the original records. *A*. Velocities of 1·2, 2·5, 5·5, and 10 mm/sec from +0 mm initial length, and of 1·2 and 5 mm/sec from +4 mm initial length. *B*. Velocities of 30, 60, 100 and 200 mm/sec from +0 mm initial length and of 30 and 100 m/sec from +4 mm initial length. Differences between the velocity of stretch at +0 mm and +4 mm initial length are due to the increased load on the stretcher.



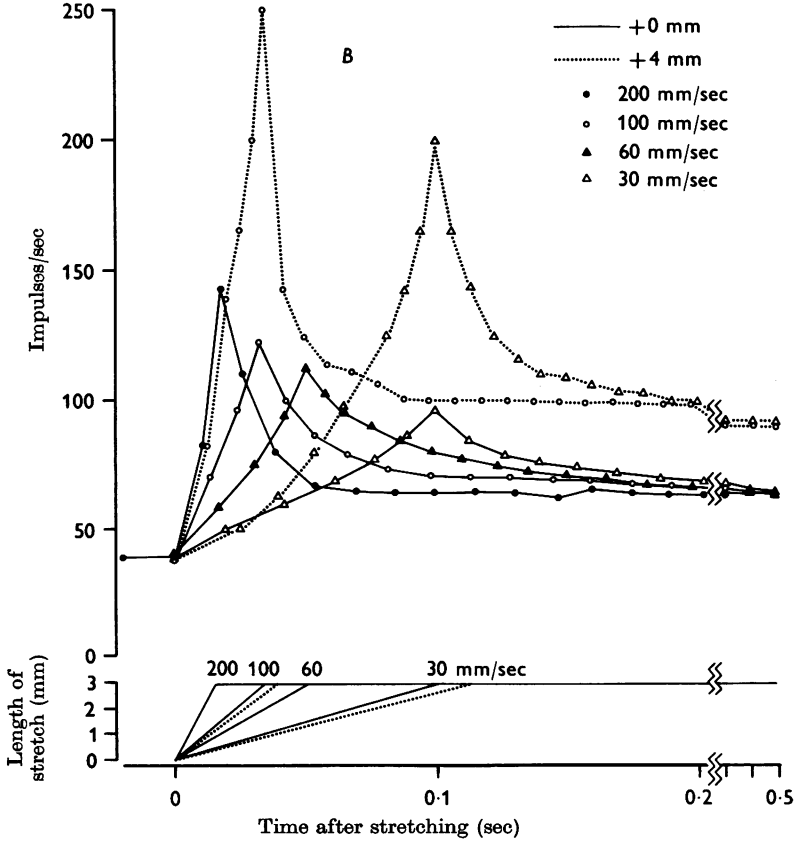




Fig. 5. For legend see opposite page

observed, even with high speeds of up to 100 mm/sec, nor was 'abrupt fall' in frequency observed on completion of the dynamic index on +4 mm initial muscle length of the same receptor as the lower continuous curve (+0 mm) when plotted against the velocity of stretch. For rapid stretches of over 30 mm/sec, the dynamic indexes were up to approximately 2·5 times higher than those observed when the initial length was +0 mm. However, for the slow stretches, below 1 mm/sec, the indexes appeared lower than those on +0 mm muscle length. The magnitude and the time courses of these dynamic indexes were similar to those of primary spindle endings in de-efferented limb muscles of the cat (Matthews, 1963).

Static indexes of a spontaneously discharging receptor were plotted against the velocity of stretch with continuous lines in Fig. 7*A*. The lower continuous line shows the static index on +0 mm initial length of the muscle in which the index was constant at the higher stretching speeds of 5 mm/sec or more. The upper continuous line also shows that the discharge frequency returned to the same level at 0·5 sec after muscle stretch of 3 mm from +4 mm initial length at various velocities of 30 mm/sec or more. The static index values which were constant to stretching at high velocities over 30 mm/sec were represented against the muscle length at completion of the stretch in Fig. 7*B*. At +0 mm muscle length the static index of the spontaneously discharging receptor should be at the frequency of spontaneous discharge (38·2 impulses/sec) when the muscle is not extended. Figure 7*B* illustrates that the static index increases linearly with increases in muscle length.

The slowly adapting high threshold receptors produced a continuous discharge during extension of the muscle by isometric stretch over threshold (Fig. 8). The receptor illustrated did not respond to 3 mm of stretch from +0 mm initial length, but responded to stretch at higher velocities over a critical value from initial length of at least +5 mm. In an example illustrated in Fig. 9*A*, a threshold response (1 spike) was observed on application of a stretch of 3 mm at a velocity of 5 mm/sec from +6 mm initial length. When the initial length was increased to +8 mm, the threshold velocity of stretching decreased to 1·2 mm/sec. The frequency of discharge increased steeply as the stretch increased, without an initial acceleration in the discharge frequency at the beginning of the stretch.

The dynamic indexes of the discharges were plotted against the velocities of stretch with dotted lines in Fig. 6. The lower dotted line shows a dynamic index curve with 3 mm stretch from +6 mm initial length of the muscle. This curve lies between the dynamic index curves of +0 and +4 mm in the spontaneously discharging receptor. When the initial length was increased to +8 mm, the dynamic index increased markedly on increasing the velocity of muscle stretch above a critical value, as shown

with the upper dotted line in Fig. 6. Thus, the dynamic indexes of the non-spontaneously discharging receptors are essentially similar to those of spontaneously discharging receptors, except that the threshold of the former type is higher than that of the latter.

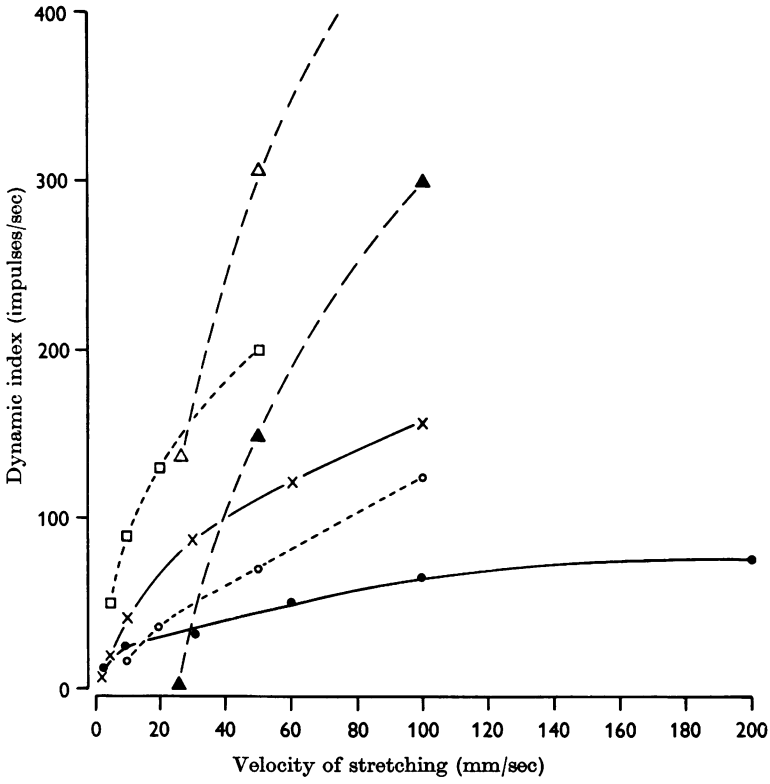



Fig. 6. Relation between dynamic index and velocity of stretching for three representative receptors. The index of a spontaneously discharging receptor (P-25) increased on increase of initial length from +0 mm (lower continuous line, filled circles) to +4 mm (upper continuous line), except on stretching at 1·2 mm/sec. The index on +6 mm initial length (lower dotted line, open circles) of a slowly adapting non-spontaneously discharging receptor (P-28) fell between the upper and the lower continuous lines. The upper dotted line (open squares) shows the index on +8 mm initial length of the same receptor as the lower dotted line. The interrupted lines show the dynamic indexes on +5 mm (lower, filled triangles) and +7 mm (upper, open triangles) of a rapidly adapting non-spontaneously discharging receptor (P-27).

This static index of the discharge was also very low, even with greater initial length of the muscle (+6 and +8 mm), as illustrated with dotted lines in Fig. 7*A*. Figure 7*B* shows that the static index of a receptor increased slightly on increasing the initial muscle length. If the static indexes

are connected with a straight line so as to bear a linear relation to the muscle length, as is the case for the spontaneously discharging receptor, the line crosses a zero index level at 4 mm muscle length. This suggests that impulse discharges from the receptor are never observed with muscle extension below 4 mm, which was confirmed by our observation.

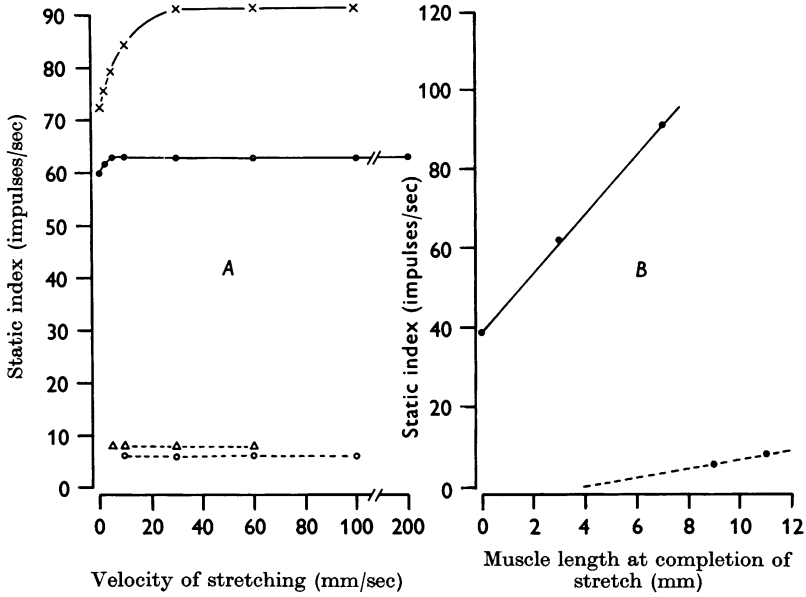



Fig. 7. *A*. Relation between static index and velocity of stretching for two representative receptors. The index of a spontaneously discharging receptor (P-25) increased on increase of initial length from +0 mm (lower continuous line, closed circles) to +4 mm (upper continuous line, crosses). The index of a slowly adapting non-spontaneously discharging receptor (P-28) also increased on increase of initial length from +6 mm (lower interrupted line, open circles) to +8 mm (upper interrupted line, open triangles). *B*. Relation between static index and muscle length at completion of stretching from different initial lengths. The index of the spontaneously discharging receptor (P-25) increased linearly with increases in muscle length (continuous line). The indexes of the slowly adapting non-spontaneously discharging receptor (P-28) were connected with an interrupted line and were assumed to be linear.

In Fig. 7*A*, the static indexes of a non-spontaneously discharging receptor (dotted lines) show a constant value on all stretch velocities above a critical value. If, for the static index lines of the spontaneously discharging receptors, the curves below 30 mm/sec (top continuous line) and 5 mm/sec (lower continuous line) are assumed to be due to visco-elastic properties of the muscle, then similar curves should also be obtained when the non-spontaneously discharging receptors (e.g. lower dotted lines) are studied under high initial lengths. In fact, the curves obtained with initial

lengths of 6 and 8 mm should be more marked than is noted when the response of the spontaneously discharging receptor is recorded on 4 mm initial length (top continuous line). Thus, since more marked curves were observed at higher discharge frequencies, it seems likely that the decrease of the static index at lower velocities of stretching may be attributed to accommodation of the receptor.

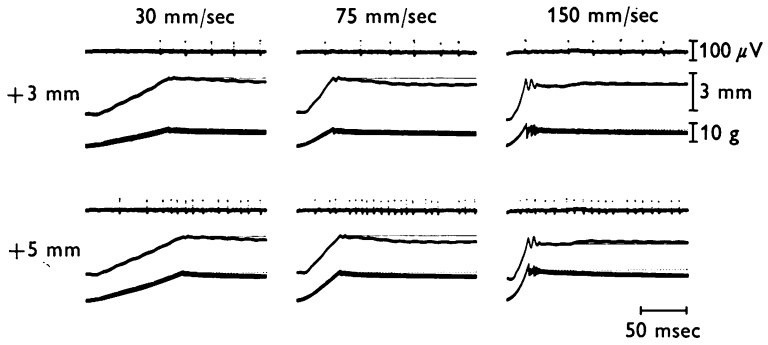



Fig. 8. Response of a slowly adapting non-spontaneously discharging receptor (P-30) to an extension of 3 mm from +3 and +5 mm initial length applied at velocities ranging from 30 to 150 mm/sec, recorded simultaneously with the displacement of the lever of stretcher (middle line) and the tension of the muscle (lower line). The photo-electric displacement recorder showed an apparent movement, due to torsional compliance, after the completion of stretch; thus, straight lines have been inserted to indicate maintained muscle displacement. Superimposed over the tension records (lower lines) dotted reference lines have been drawn.

Figure 9*B* illustrates the responses of a rapidly adapting non-spontaneously discharging receptor. A threshold response was obtained with 3 mm stretch of 40 mm/sec velocity from +5 mm initial length. At this initial length, the first spike always appeared after 2 mm of the 3 mm stretch applied to the muscle. During the dynamic phase of the stretching, 2–5 spikes occurred with marked increase of the frequency related to the increase in muscle length. After completion of the dynamic phase of stretch, the discharge frequency decreased abruptly and the response ceased after only a few spikes, even with the maximal stretching velocity used. The dynamic index inclined steeply with increasing velocity of stretch starting from the threshold initial length of 5 mm, as illustrated with the lower interrupted line in Fig. 6. That the dynamic index fell to zero at approximately 23 mm/sec velocity suggests that the receptor has a high dynamic index threshold, since no responses were produced by stretch velocities below 20 mm/sec. The dynamic index for +7 mm initial length increased more sharply with increases in the velocities of stretch (upper interrupted line).

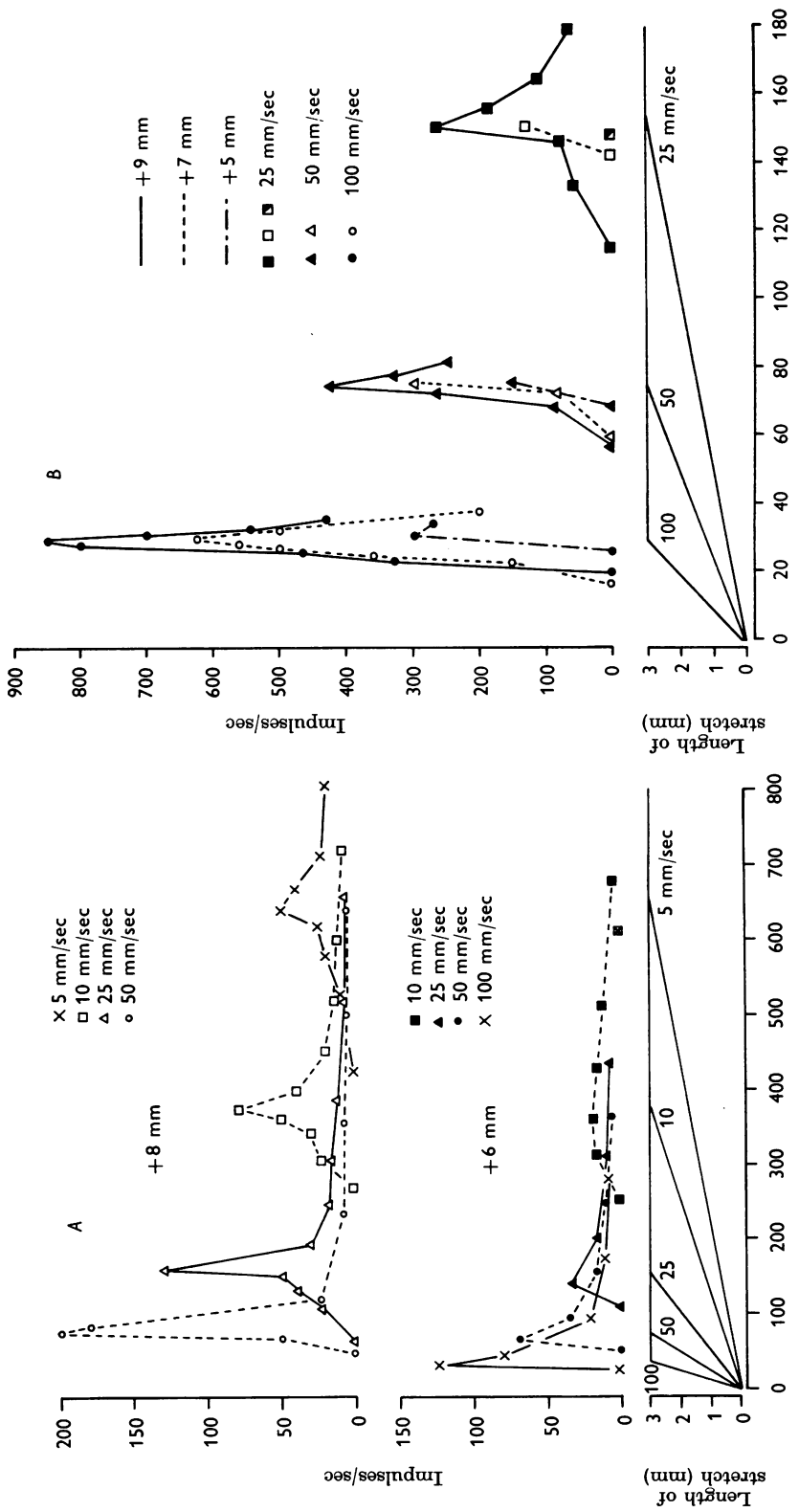



Fig. 9. Responses of a slowly adapting (P-28 in *A*) and rapidly adapting (P-27 in *B*) non-spontaneously discharging receptors to an extension of 3 mm from two initial lengths at various stretch velocities. The frequency is represented by the reciprocal of the time interval between action potentials. The length scales are diagrammatic and represent corrected values derived from the original records.

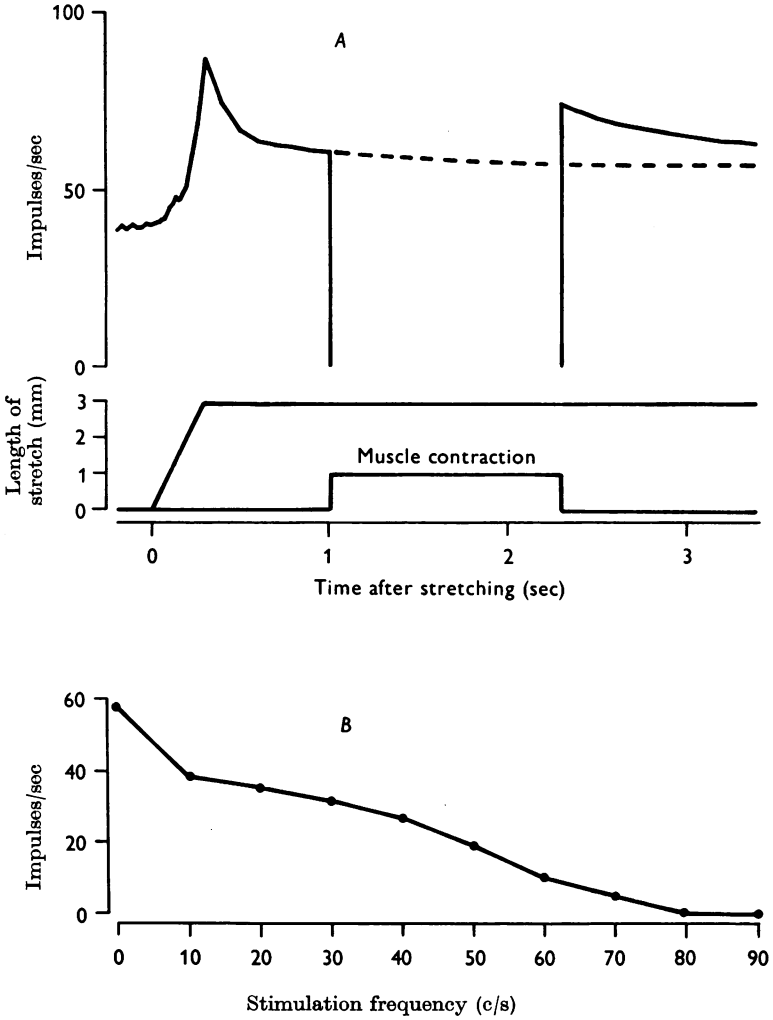



Fig. 10. Effect of tetanic contraction of the muscle on the responses of an in parallel receptor during muscle stretch. *A*. The response of a spontaneously discharging receptor (P-25) to stretching the muscle 3 mm at 10 mm/sec fell to zero frequency during tetanic contraction of the muscle induced by maximal nerve stimulation at 100 c/s (continuous line), in comparison with the control in the absence of nerve stimulation (interrupted line). The diagrammatic representations of the length scale and the muscle contraction are derived from the original records. *B*. Effect of tetanic contraction of the muscle induced by the maximal nerve stimulation at various frequencies on the responses 2 sec after stretching the muscle 3 mm at 10 mm/sec (the same receptor as *A*). With increasing stimulation frequency, the response frequency decreased, and the response disappeared at stimulation frequencies over 80 c/s.

This kind of receptor also has a high static index threshold, but we were unable to measure it since after completion of stretch the response disappeared before 0·5 sec had elapsed. We have concluded from these results that the dynamic and static indexes of all the receptors studied, from the spontaneously discharging receptors to the rapidly adapting non-spontaneously discharging receptors, have similar properties except for differences in their thresholds.

IV. *Response during muscle contraction.* In order to determine whether a receptor was in parallel with the contraction elements of the muscle (like muscle spindle receptors) or in series (like tendon organs), the responses were studied during muscle contraction. The muscle was stretched under isometric conditions and tetanic contraction was produced by electrical stimulation applied to the entire branch of the III nerve to the inferior oblique muscle except for the nerve twig containing the afferent fibre from the receptor under study.

In forty-seven out of forty-nine receptors (excluding the three receptors believed to be related to blood vessels) the response disappeared or the frequency decreased during muscle contraction. Figure 10*A* shows an example of a spontaneously discharging receptor. During maximal tetanic stimulation at 100 c/s, the response disappeared completely. When stimulation ceased, the frequency of the response transiently increased over the normal frequency level (interrupted line) obtained in a preliminary stretch under the same conditions, and then returned to the previously recorded level within 5 sec. Figure 10*B* shows mean frequencies of the response during muscle contractions produced by maximal tetanic stimulations at various frequencies in the same receptor as in Fig. 10*A*. In the absence of muscle contraction, the mean frequency at between 1 and 2 sec after completion of stretch was 57·5 impulses/sec. When stimulation was delivered between 1 and 2 sec after completion of stretching, the frequency of the response during muscle contraction decreased gradually on increasing the frequency of stimulation, and the response disappeared during muscle contraction with stimulation rates over 80 c/s. Similar effects could be demonstrated on all spontaneously discharging receptors studied. However, in slowly adapting non-spontaneously discharging receptors which discharged during stretch from an initial length over +5 mm, the frequency of response decreased during muscle contraction, but did not disappear even during muscle contraction with the maximum fusion frequency stimulation rate of 450 c/s (cf. Bach-y-Rita & Ito, 1966*a*). It might be considered that such reduced effectiveness of muscle contraction is due to a reduction of the contraction force of the muscle; a muscle extended to 8 mm (3 mm stretch from an initial length of +5 mm) has developed approximately the maximal tension (about 50 g), so that the passive ten-

sion may not be cancelled completely even with the maximal contraction (30–40 g, cf. Bach-y-Rita & Ito, 1966*a*). In rapidly adapting non-spontaneously discharging receptors, it was more difficult to demonstrate that the receptors were in parallel with contractile elements of the muscle, because the duration of the discharge burst was often too short to observe the effect of muscle contraction. In such cases the responses during muscle contraction produced at the same time or before stretching of the muscle were compared to the control responses without muscle contraction. The response frequency of these receptors decreased slightly during muscle contraction.

The site of the receptors in each preparation was detected with light pressure on the muscle with a glass rod. All of the forty-seven in-parallel receptors were located in the muscle belly. Most of the receptors with thresholds to loading below 5 g were concentrated in the portion between nerve entry and the globe insertion end, except for a spontaneously discharging receptor (P-22) located at the origin side of the muscle close to the nerve entry. It was noted that the location of the low threshold receptors corresponded to the most extensible portion of the muscle as described in Methods.

In two out of forty-nine receptors, the response was facilitated during muscle contraction. The thresholds of these receptors were 20 g (in cat P-12) and 30 g (in P-15), and both responded with rapidly adapting discharges. The conduction velocities of the afferent impulses were 16·7 (P-12) and 24·2 m/sec (P-15), respectively. When the muscle tetanic contraction was maximal on nerve stimulation during isometric stretch, the afferent discharges, which had disappeared due to adaptation, again appeared (Fig. 11*A*). In Fig. 11*B* the frequency of an in-series receptor during maximal tetanic muscle contraction was plotted against the length at completion of stretch, and also referred to a load scale calculated (approximately) from a load–length relation of the muscle. The frequency during muscle contraction reached maximum at a length comparable to that produced by a 50 g load and then decreased with further stretch.

This suggests that the muscle may develop maximal active tension with stretch comparable to that produced by a 50 g passive load. One of the receptors (P-12) was located in the muscular portion near the insertion end of the muscle, and the other in the origin third of the muscle. No in-series receptors were observed in the preparations in which the normal spread insertion to the sclera was maintained; no tendon organ discharges were observed.

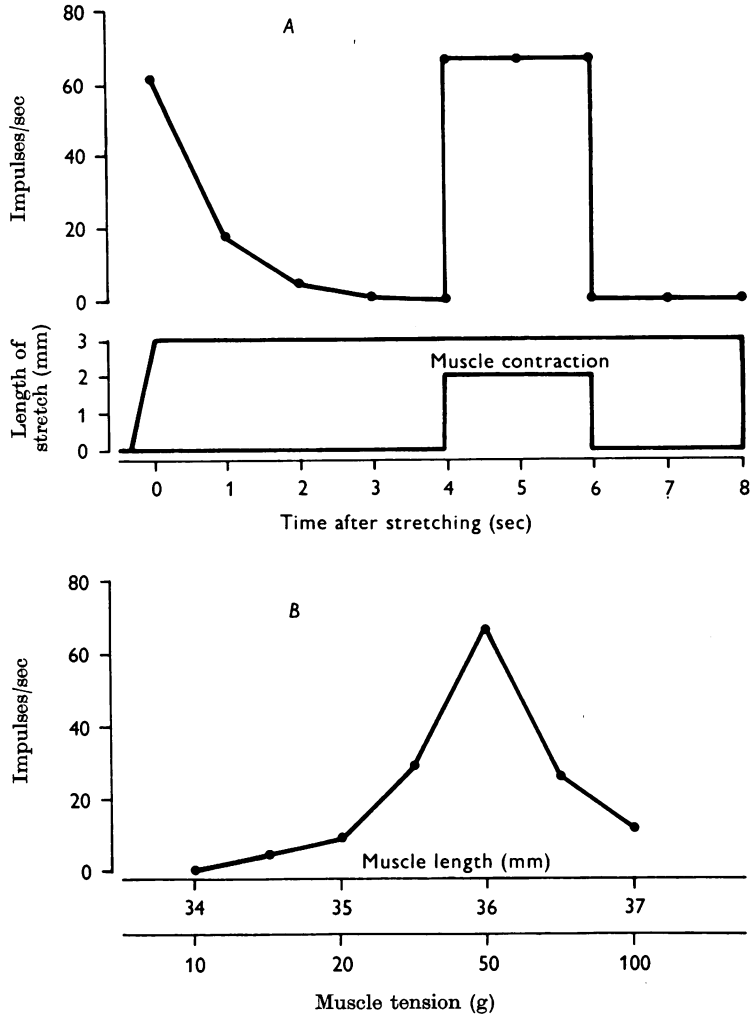



Fig. 11. Effect of tetanic contraction of the muscle on the responses of an in-series receptor during muscle stretch. *A*. The response of a rapidly adapting non-spontaneously discharging receptor (P-12) after 3 mm stretch from +7 mm initial length at 10 mm/sec increased during tetanic contraction of the muscle induced by maximal nerve stimulation at 100 c/sec. *B*. Responses during tetanic contraction of the muscle of the same receptor as *A* plotted to an extension of 3 mm from various initial lengths between +5 and +8 mm (34 and 37 mm total muscle lengths). The muscle length was calculated from the tension, from data on the relation between the muscle loads and muscle length.

## DISCUSSION

Cooper & Fillenz (1955) recorded afferent impulses from spontaneously discharging receptors in cat extraocular muscles and concluded that the responses resembled those of the main sensory endings of muscle spindles. In the present study spontaneously discharging receptors were observed in four of the thirty preparations. The responses from these receptors, however, differed in four ways from those of muscle spindle endings:

(1) the conduction velocities ranged from 16·9 to 41·1 m/sec in the afferent fibres from the eye muscle receptors, whereas group I fibres conduct at between 72 and 110 m/sec and group II fibres conduct at between 24 and 72 m/sec. Thus, there is an overlap of the conduction velocities recorded in this study with group II fibres only in the slower ranges (24–41 m/sec). Cooper, Daniel & Whitteridge (1953) suggested that impulses from goat extraocular muscle spindles are conducted at approximately 100 m/sec.

(2) Increases in spontaneous discharges on stimulation of nerve bundles containing the alpha and gamma fibres were not observed. Thus, annulospiral (A 2) endings are apparently not present in the muscle. However, since the afferent discharges slowed during total nerve stimulation, endings that are in contact with the myotube region, similar to the flower spray (A 1) limb muscle spindle receptors (Matthews, 1933; Harvey & Matthews, 1961), may be located in cat eye muscles.

(3) The dynamic index of the spontaneous discharging receptors increased markedly on increasing the initial length of the muscle, whereas that of the muscle spindle endings appeared to be unchanged on stretching from different initial lengths (Matthews, 1963; Toyama, 1966). Matthews (1964) has suggested that the equatorial regions which are encircled by the primary endings are less viscous in comparison with the other muscle fibre regions (myotube and polar regions) in both intrafusal and extrafusal muscle fibres. In limb muscles, when the initial muscle length was increased, the tension on the equatorial regions scarcely increased. Thus it is likely that the spontaneously discharging receptors in cat extraocular muscles do not lie in contact with regions of reduced viscosity on the muscle fibres similar to the equatorial region of the intrafusal muscle fibres.

(4) The frequency of the spontaneously discharging receptors appeared to decrease exponentially, without a fast falling phase, after completion of stretching in isometric conditions. In contrast, the falls in discharge frequency from primary and secondary endings in limb muscle are divided into fast and slow phases (Matthews, 1963). The absence of a fast-falling phase in the spontaneously discharging receptor suggests that the receptor is not in contact with nor in the vicinity of a region with less viscosity in

parallel with 'extrafusal' fibres of large viscosity. It may thus be assumed that each receptor is in contact with the surface of an extrafusal muscle fibre, as suggested in Fig. 12*A*. The nerve endings may be similar to those

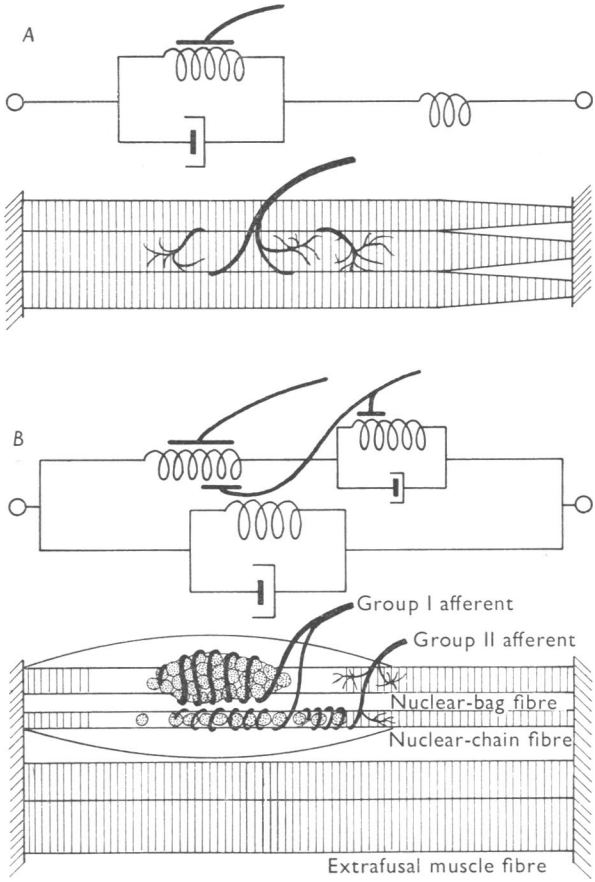



Fig. 12. Schematic diagram of an ending surrounding an extrafusal muscle fibre in the cat's extraocular muscle (lower figure of *A*) with its functional visco-elastic model (upper figure of *A*), in comparison with a simplified diagram of the central region of the muscle spindle after Boyd (1962) and Matthews (1964) (lower figure of *B*) with its functional visco-elastic model (upper figure of *B*). It has not been determined whether the sensory endings in cat eye muscles terminate on the large fast twitch fibres or on the slow multi-innervated twitch muscle fibres (cf. Bach-y-Rita & Ito, 1966*a*), and thus *A* does not show the two types of muscle fibres.

occasionally observed encircling extrafusal fibres in cat eye muscles by Cooper & Daniel (1949), or an essentially similar spiral ending surrounded by a simple non-lamellar capsule described by Pallot (1934). We have no evidence as to whether the receptors are in contact with the large fast

twitch fibres or the slow multi-innervated twitch fibres (Bach-y-Rita & Ito, 1966*a*), or with both types of fibres.

In most preparations, non-spontaneously discharging receptors were found; five possible interpretations merit discussion:

(1) The possibility that some of the receptors normally discharge spontaneously, but have ceased to discharge due to de-efferentation. Cooper & Daniel (1957) have demonstrated that the muscle spindle discharges from goat extraocular muscles either cease or become slow and regular after motor nerve section. We have discounted this possibility on the following grounds: (*a*) Muscle spindles (and therefore intrafusal muscle fibres) have not been observed histologically in cat extraocular muscles (Cooper & Fillenz, 1955). (*b*) The present experiments suggest that even the spontaneously discharging receptors are in contact with the surface of extrafusal muscle fibres as mentioned above. (*c*) All of the non-spontaneously discharging receptors gave rise to threshold responses on application of stretch ranging to 8 mm (5–20 g in load). A previous study has shown that maximal tetanic contraction of slow muscle fibres in the muscle developed a tension of up to 10 g (Bach-y-Rita & Ito, 1966*a*). It would seem that a bundle of slow muscle fibres, which may correspond to intrafusal muscle fibres, would be unable to produce tensions over 1 g.

(2) The possibility that impulses from spontaneously discharging receptors may be carried to the brain through a cranial nerve other than that supplying motor innervation to the muscle and thus have been missed in our study. Cooper *et al.* (1955) have reported that in one cat, stretching the superior oblique muscle produced a low threshold sustained response in the fifth cranial nerve. They also suggested that in the goat the low threshold receptors may transmit impulses centrally through fibres that cross retro-orbitally from the corresponding eye muscle motor nerve to the fifth nerve, while some high threshold receptor discharges are carried in the corresponding motor nerve to the brain stem. In the present experiments the intraorbital portion of the III nerve branch innervating the inferior oblique muscle was always studied, and except for one cat, no branches were observed to emerge from the nerve between the muscle and the ciliary ganglion where the nerve was sectioned. In the one case in which a branch was noted, it was traced centrally and was observed to re-join the III nerve.

(3) The possibility that the spontaneously discharging receptors may be fundamentally different from the non-spontaneously discharging receptors. Cooper & Fillenz (1955) indicated that the two types of responses from cat inferior oblique muscles may be functionally discriminated. The present study, however, suggests that all of the receptors from which responses have been recorded are essentially similar: (*a*) The impulse con-

duction velocities of the non-spontaneously discharging receptors varied from 6·5 to 52·0 m/sec; this range covered the conduction velocities of the spontaneously discharging receptors. It may be concluded that all of the receptors are innervated by a similar range of nerve fibres. (*b*) A histogram drawn from the minimal threshold receptors tested showed that the thresholds of all the receptors (both spontaneous and non-spontaneous) are included in a uniform population distribution. Thus, the spontaneously discharging receptors were observed to be a certain percentage of all receptors, and the preparations with a large number of receptors have a statistically larger probability of including spontaneously discharging receptors. (*c*) Sensitivities to load on the muscle were comparable in spontaneously and non-spontaneously discharging receptors, and no step-like differences between the sensitivities of these receptors were detected. (*d*) Dynamic and static indexes were similar for spontaneously and some of the non-spontaneously discharging receptors.

(4) The possibility that the non-spontaneously discharging receptors are a type of tendon ending. Hosokawa (1961) pointed out that the receptors observed by some investigators in eye muscle tendons are not typical Golgi tendon organs. A number of non-encapsulated tendon endings have been observed histologically in musculotendinous junctions on both ends of mammalian eye muscles (Tozer & Sherrington, 1910; Cooper & Daniel, 1949; Cooper & Fillenz, 1955). Similar endings (so-called 'Ruffini endings') have been observed in cat knee joint ligaments and may produce slowly and rapidly adapting discharges (Boyd & Roberts, 1953) which resemble the responses of the non-spontaneously discharging receptors in the present experiments. In our study only two out of forty-nine receptors tested appeared to be in series (as are the tendon receptors) with the muscular structure. None of the forty-nine receptors that were studied in detail was located in the tendon. It is possible, however, that some of the responses noted during the late phases of the application of steady stretch may have arisen from receptors located in the tendon. It was not possible to study these receptors since the excessive stretch produced irreversible changes in the receptor responses.

(5) The possibility that the receptors in cat eye muscles are similar to the pressure-pain receptors described in cat limb muscles by Paintal (1960). Several similarities and differences between the two types of receptors are evident. (*a*) The pressure-pain receptors were connected to afferent fibres with conduction velocities ranging from 6 to 91 m/sec, with a peak in the 10–15 m/sec (Paintal, 1960). The histogram of the velocity just coincided with that in the present experiment. (*b*) The threshold of the pressure–pain receptors varied considerably and most of them adapted rapidly to the stimulus, as did those in the present study. (*c*) Most of the pressure–pain

receptors were located in the muscle belly near entry of the nerve in the tibialis anterior, and near the musculotendinous region in the gastrocnemius and soleus. Tetanic contraction of muscle produced a low-frequency discharge in about half the pressure–pain receptors (Paintal, 1960). In our study, almost all receptors were also located in the muscle belly near entry of the III nerve, and the discharge frequency usually slowed or disappeared during tetanic contraction of the muscle. (*d*) Paintal (1961) has demonstrated that impulses from pressure–pain receptors connected to group III fibres of the lateral gastrocnemius and soleus muscles facilitated the posterior biceps and semitendinous monosynaptic reflex (flexion reflex), but inhibitied their own. On the other hand, no stretch reflexes have been observed in the cat's eye muscles (McCouch & Adler, 1932) nor in the goat's eye muscles which have many muscle spindles (Whitteridge, 1960). In some cat III nerve nucleus ocular motoneurones, Sasaki (1963) has noted a slight hyperpolarization induced by stimulation of the nerve branch to the inferior oblique. The time course resembled that of the inhibitory post-synaptic potential set up in spinal motoneurones by 'direct' inhibition. (*e*) All of the receptors studied in the eye muscles responded to muscle stretch, while of the pressure–pain receptors described by Paintal (1960) only two of thirty-one gastrocnemius receptors and six of ten tibialis anterior receptors responded to stretch. This may reflect a fundamental difference in the two types of receptors, or it may reflect the differences in experimental methods. In our studies, only the receptors responding to stretch were uncovered by our stimulus procedures.

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