THE DISCHARGE PATTERN OF MUSCLE SPINDLES OF THE RABBIT ON ACTIVATION OF INTRAFUSAL MUSCLE FIBRES

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Histological studies show two types of receptor ending in the muscle spindle. The one has been called annulospiral, nuclear-bag, A 2 or primary; the other has been called flower-spray, myotube, A 1 or secondary. It is generally agreed that the primary endings have larger nerve fibres than the secondary endings, and Hunt (1954) showed that the receptor fibres of the muscle spindle were bimodally distributed, one peak lying in Group I and the other in Group II. There has since been a tendency to classify all spindle receptor fibres conducting at Group I velocity (72–120 m/sec) as coming from primary receptors, and those conducting at Group II velocity (24–72 m/sec) as coming from secondary receptors.

When the intrafusal muscle fibres alone contract the frequency of discharge of the spindle receptors is increased. Moreover, Hunt (1954) showed that there was no qualitative difference in behaviour between the two types of spindle receptor when the intrafusal muscles were made to contract by repetitive stimulation of the small motor fibres in the ventral roots. When the extrafusal muscle fibres alone contract, the strain is removed from the muscle spindles by virtue of their arrangement in parallel with the extrafusal fibres (Fulton & Pi-Suñer, 1928). The spindle receptors therefore stop discharging during the rising phase of the muscle tension record (Matthews, 1933). When both the intrafusal and extrafusal muscle fibres contract, as happens when strong stimuli are applied to the muscle nerve, the resultant of their contractions is such that some endings do not stop discharging during the rising phase of the muscle tension record (Matthews, 1933; Hunt & Kuffler, 1951). These endings are supplied by fibres of fast conduction and hence it is likely that they are primary endings. The response of the secondary endings during supramaximal stimulation of the muscle nerve has, however, remained uncertain. Matthews (1933) showed that certain muscle spindle endings, the A 1 endings which were believed to be identical with secondary endings, could not be activated during contraction of the extrafusal muscle (see also Cooper

1959). Hunt (1954), however, showed that some of the endings with fibres of Group II conduction velocity could be activated by muscle nerve stimulation when the muscle contracted isometrically. In view of these divergent results, it was considered necessary to re-investigate the effect of extrafusal and intrafusal activity on the response of secondary muscle spindle endings.

In this paper, an attempt has been made to provide an explanation of differences in behaviour of muscle spindle receptors, and to discover the conditions in which both types of receptor ending may be activated. It has been found that most of the lower velocity spindle receptor fibres are activated by stimulation of the muscle nerve only if the contraction of the extrafusal muscle fibres is removed or reduced, and when the stimulation is tetanic. If, as seems probable, these fibres are from secondary endings, then the work of Boyd (1959) leads one to suggest that the secondary endings of the muscle spindle are influenced by slow muscle capable of graded contraction, whereas the primary endings lie mainly on muscle capable of all-or-nothing twitches.

A preliminary account of this work has already appeared (Diete-Spiff, 1960).

METHODS

Rabbits were anaesthetized either with a 5% solution of sodium hexobarbitone or with urethane (25g/100 ml.) in 0·9% NaCl solution. When urethane was used, the full dose (1·6–1·8 g/kg body weight) was given into a marginal ear vein. Further doses were administered intraperitoneally as required. When sodium hexobarbitone was used, sufficient was administered initially into a marginal ear vein to induce surgical anaesthesia, and thereafter surgical anaesthesia was maintained by small doses administered through a polythene cannula in the right femoral vein. After the trachea had been cannulated, the left leg was partially denervated by cutting the femoral and obturator nerves, and 5–10 mg of hexamethonium bromide (in 0·9% NaCl) given intravenously to lower the blood pressure. This enabled a relatively bloodless laminectomy to be performed. The blood pressure returned to normal inside 30 min, well before the start of the experiment proper. The cord was usually exposed from the level of L5 to S2 spinous processes. The animal was then fixed rigidly by clamps at the upper ends of both femoral bones, a clamp at the lower end of the left tibia, and a pin through the muscles and spinous processes of the 4th lumbar vertebra. An incision was made in the left popliteal fossa extending inferiorly to the lower limits of this fossa and superiorly to the level of the first sacral spinous process. All the branches of the sciatic and popliteal nerves were then cut, except the nerve to the medial head of the gastrocnemius muscle and the nerve to the plantaris muscle of the left leg. Both the triceps surae tendon and that of the plantaris muscle were prepared for recording tension. After isolating a receptor fibre the muscle containing its ending was identified by stretching it; the nerve to the other muscle was then cut. The tendon of the semi-membranosus muscle was cut through the same incision.

In order to limit the field of action of drugs which were to be injected intra-arterially later in the experiment, the side branches of the femoral and popliteal arteries were tied off as they were revealed during various stages of the dissection. After the tendons had been prepared, the posterior tibial artery was cannulated with a fine heparinized cannula, and the anterior tibial artery tied off at the level of the ankle.

The dura mater was opened under warm paraffin oil (B.P.), equilibrated with water, at 37–38° C. The ventral and dorsal roots from the L 6 to S 1 (at times also L 5) were cut on the left side, after which L 7 or S 1 dorsal root was mounted on a single platinum electrode. The spindle receptor discharges were sampled in split filaments of one of these two dorsal roots, almost always from S 1. The muscle was made to contract by stimulating its nerve. The stimuli used in all instances were of 120 μsec duration, and for tetanic stimulation the frequency was 150–200/sec. The action potentials as well as the tension changes were amplified and recorded by means of a conventional amplifying system. The conduction velocity was calculated from a measurement of conduction time from the stimulus artifact to the start of the evoked spike and the conduction distance, which was measured after killing the animal, without removing the nerve from the body. No correction was made for setting-up time at the stimulating electrodes. The action potentials set up by electrical stimulation were compared in amplitude and duration with those obtained by stretching the muscle (cf. criteria of Paintal, 1953). The experiments were performed at the initial tension which permitted the development of maximum tension. While stimulating the muscle nerve supra-maximally with single nerve shocks, the initial length of the muscle was adjusted until the deflexion on the screen of the oscilloscope which signified tension appeared maximal; the experiment was then continued at that initial tension. The muscle and nerve temperatures were kept at 34–36° C, the rectal temperature at 37–39° C.

When succinylcholine chloride (Scoline; Allen and Hanbury) was used, it was given in Locke's solution by retrograde injection into the posterior tibial artery without occluding the circulation. The success of the method depends, among other things, on a relatively slow rate of injection together with a good blood pressure. Up to six doses of succinylcholine were injected into any one muscle, but the usual number of injections was from three to four. Thirty minutes at least was allowed to elapse between injections. The site of action of the drug is almost completely localized to the gastrocnemius, soleus, and plantaris muscles, as revealed by intra-arterial injection of Indian ink through the same artery before the animal was killed.

Some experiments were performed on rabbits spinalized at the level of the fifth lumbar spinous process.

Nomenclature. 'Spindle receptor fibre' is used in the text to include any nerve fibre from the muscle spindle which conducts impulses towards the spinal cord. It is synonymous with spindle afferent or sensory fibre of other writers. 'Slack muscle' means a muscle which has been freed from its insertion and is not attached to the myograph.

RESULTS

The analysis is based on the discharges in twenty-eight spindle receptor fibres belonging to the gastrocnemius medialis or plantaris muscles. Any fibre whose frequency of discharge slowed or stopped during the rising phase of a just-maximal twitch of the muscle containing its ending was classified as a spindle receptor fibre; fibres whose frequency of discharge increased in similar circumstances were taken to be tendon organ receptor fibres (cf. Matthews, 1933).

It soon became clear that many muscle spindle receptors could not be induced to discharge during the rising phase of the muscle tension record in a maximal twitch. An attempt was therefore made to activate the muscle spindle receptors while stimulating the mixed nerve, but without the complication of extrafusal contraction. This was achieved by reducing or abolishing extrafusal muscle contraction with the drug succinylcholine

chloride, injected intra-arterially into the gastrocnemius and plantaris vessels. Since the administration of succinylcholine chloride forms an essential part of the experiments, its action on extrafusal muscle fibres and on muscle spindles will first be described.

The effect of succinylcholine on extrafusal contraction
and on the discharge of spindle receptors

Within a minute of intra-arterial injection of 25–500 μg of succinyl-choline chloride, paralysis of the extrafusal muscle fibres ensued, the completeness of the paralysis depending on the dose. The degree of reduction in extrafusal tension was observed by stimulating the muscle nerve once every 4–5 sec at the stimulus strength which had previously caused maximal contraction of the extrafusal muscle fibres: recovery from paralysis was studied in a similar fashion. When an adequate stimulus was applied to the muscle nerve during the period of reduced or absent extrafusal contraction, spindle receptor discharges which were previously absent during the rising phase of tension occurred (Fig. 1). Thus the end-plates on the intrafusal muscle fibres are more resistant to succinylcholine than
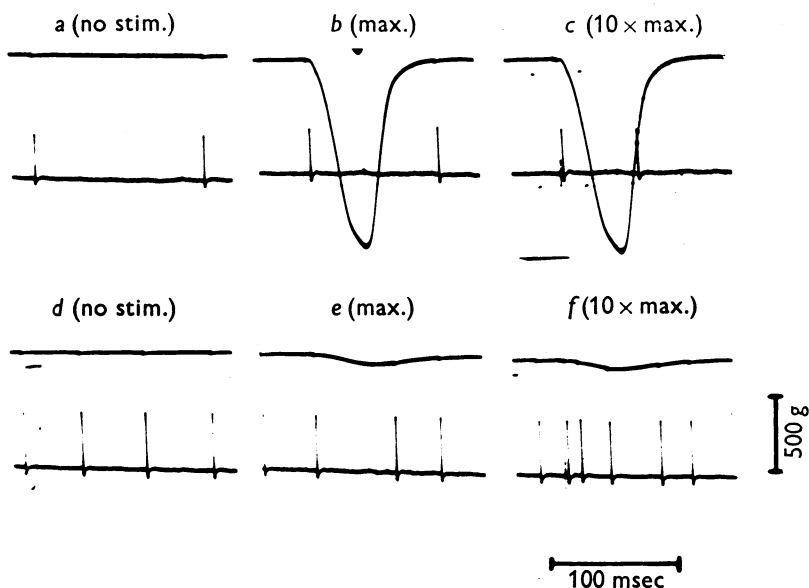

Fig. 1. Selective activation of a spindle receptor (3) (fibre conduction velocity of fibre = 95 m/sec) by single muscle nerve shock after paralysis of the extrafusal muscle fibres. Upper traces are tension records (increase in tension signalled downwards); lower traces are spindle receptor discharges. Plantaris receptor; urethane anaesthesia. *a–c*, before succinylcholine; *d–f*, after 100 μg succinyl-choline. Note acceleration of the receptor discharge in *d* and discharges during contraction in *f*.

are those on the extrafusal muscle fibres. The dose of succinylcholine which was needed to produce extrafusal paralysis varied from 25 to 500 μg. This variation might have been caused by several factors, but was presumably due in part to the difference in the degree of localization of the drug: in most experiments 50–100 μg of succinylcholine was sufficient. By using a larger dose of succinylcholine than was necessary to block extrafusal contraction the intrafusal contraction could also be blocked. However, it was always possible to find a dose of succinylcholine which would block the extrafusal muscles selectively, thereby enabling the intrafusal muscle fibres to be activated on their own.

It was shown by Granit, Skoglund & Thesleff (1953) that succinylcholine excited muscle spindle receptors of the cat but had no effect on tendon organs of the same animal. The action of succinylcholine on similar receptors of the rabbit investigated in this work is in agreement with their findings. Two stages in the action of the drug, an initial and a later phase, may however, be differentiated.

In the initial phase the muscle showed irregular contractions ('fasciculation') which coincided with the time of arrival of the drug. The irregular contractions were clearly visible and tension changes of 100 g or more were recorded, especially in decerebrate animals. During this phase previously tonically discharging muscle spindle receptors stopped firing. In contrast, previously silent tendon organs started to discharge. The effect was presumably due to the fact that the drug caused the extrafusal muscle fibres to contract, thereby unloading the muscle spindle but producing sufficient tension to excite the tendon organs. The initial phase of succinylcholine action lasted a few seconds and led abruptly into the second stage.

In the second phase, that of spindle excitation, the discharge of the spindle receptors built up to a peak within 30 sec and sometimes persisted for 2 min or longer, depending on the dose of succinylcholine. Excitation which lasted over 5 min was seen. The effect was observed usually with 25 μg and invariably with 50 μg of succinylcholine. Spindle receptors whose fibres conducted at Group I as well as those whose fibres conducted at Group II conduction velocity were excited by the drug (Fujimori, Tokizane & Eldred, 1959). The receptors were still sensitive to stretch during and after the stage of excitation, but in some cases, especially with doses over 50 μg of succinylcholine, excitation was followed by complete silencing of the receptor. In a spindle receptor whose fibre was conducting at 36 m/sec 100 μg of succinylcholine caused excitation of the receptor, but this stopped abruptly 3 min after injection of the drug. At this time the receptor was insensitive to stretch, although stretch sensitivity soon returned and the normal behaviour pattern of the receptor was established. The blocking of the receptor by succinylcholine supports the suggestion by Granit et al. (1953) that the drug acts on the sensory terminals themselves.

In none of five tendon organs studied was excitation observed in the second phase, the phase of spindle receptor excitation.

The discharge pattern of spindle receptor fibres
on stimulation of the muscle nerve

In the later experiments the procedure was standardized as follows: After separation of a spindle receptor fibre, the conduction time from the stimulating electrode on the muscle nerve to the recording electrode on the dorsal root filament was recorded. The muscle nerve was then stimulated with single shocks of gradually increasing intensity until the twitch tension

reached a maximum. The intensity of the stimulus necessary to cause a maximal twitch will be referred to as the alpha-maximum voltage throughout the remainder of this paper. The responses of the spindle receptor fibre were observed whilst the alpha-maximum voltage was being determined. In no instances were there action potentials during the rising phase of the muscle twitch when the stimulus to the muscle nerve was below the alpha-maximum voltage. The stimulus intensity was then raised progressively up to ten times the alpha-maximum voltage. If discharges occurred during the rising phase of tension, the threshold voltage at which this took place was determined and expressed as a multiple of the alpha-maximum voltage. The stimulus strength was then set at the alpha-maximum voltage and the muscle nerve stimulated at a frequency of 150–200/sec. Again the stimulus intensity was raised progressively to ten times the alpha-maximum voltage; the threshold voltage at which spindle receptor discharges occurred during the rising phase of tension was determined. Succinylcholine was then injected; as stated previously this excited the receptors in addition to paralysing the extrafusal contraction. When this excitation was seen to be declining, i.e. in about 2 min from the time of injection of the drug, the muscle nerve was stimulated, with single shocks at intensities ranging from the alpha-maximum to ten times this voltage. If spindle receptor discharges occurred during the time, which in the absence of extrafusal paralysis would have been the rising phase of muscle tension, the threshold intensity of muscle nerve stimulation necessary to produce these discharges was determined. The procedure was then repeated, using tetanic stimulation, either immediately after the single shock testing or after a succeeding dose of succinylcholine. At the start of the period of testing the responses of the muscle and its receptor the latter was still obviously excited by the succinylcholine; later in the testing period the excitation was no longer apparent, i.e. the frequency of discharge of the receptor was now at its pre-injection level. The receptor may, however, have been still under the influence of the drug at this stage. In two experiments, therefore, gallamine triethiodide (Flaxedil; May and Baker) was used instead of succinylcholine. Gallamine paralyses the extra-fusal muscle with no concomitant excitation of the spindle receptors. This is referred to again in the Discussion. The procedure detailed above was not followed in all experiments owing to the relatively short life-time of a receptor fibre after isolation. In the later experiments, therefore, if spindle discharges occurred during the rising phase of the muscle tension record to single shocks to the muscle nerve, no time was spent in stimulating tetanically. Instead, the threshold of a spindle receptor activation was determined repeatedly.

The findings are summarized in Table 1. The receptors fell into two

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TABLE 1. Gastrocnemius medialis and plantaris spindle receptor fibres

No.	Conduction velocity (m/sec)	Activated by single stimuli to muscle nerve		Activated by tetanic stimulation of muscle nerve		Threshold of activation (V) alpha-maximum (V)	Early discharge	Spontaneous discharge	Anaesthetic
		Before SCh	After SCh	Before SCh	After SCh				
1	112	+	+	n	+	1·1	+	−	U
2	106	+	n	+	n	<10	+	+	SH
3	95	−	+	n	n	<10	−	−	U
4	91	+	+	n	+	3	−	+	U
5	88	+	+	n	n	2·2	−	+	U
6	87	+	n	n	n	1	−	−	U
7	85	−	+	n	n	1·1	−	−	U
8	80	+	+	n	n	2	−	−	SH
9	75	−	n	n	−	3·5	−	0	U
10X	75	−	n	n	n	<10	−	−	U
11	74	−	n	−	n	−	−	−	U
12	74	−	−	+	+	3	+	+	SH
13	70	−	n	−	+	10	+	+	U
14	58	−	−	−	+	2·6	−	+	U
15	57	−	+	−	+	0·42	−	+	U
16	56	+	+	−	n	1·3	−	+	U
17	52	−	+	−	+	2·6	−	+	U
18X	50	−	n	+	+	2·5	−	+	U
19	48	−	n	−	n	1	−	+	U
20	48	−	n	+	n	−	−	−	U
21	48	−	−	−	n	−	−	−	U
22	48	−	n	+	n	1	−	+	SH
23	42	−	n	−	n	−	−	+	U
24	41	−	−	−	n	−	−	+	U
25	40	−	n	−	n	−	−	+	U
26	36	−	−	−	+	0·13	−	+	U
27	36	−	−	−	+	8·5	−	+	U
28	33	−	n	−	n	−	−	+	U

X, Gallamine, not succinylcholine; *n*, not done; 0, not known; *SCh*, succinylcholine; *U*, Urethane; *SH*, Sodium hexobarbitone.

groups, namely, 13 which were activated by single shocks to the muscle nerve and 8 which were only activated when the muscle nerve was stimulated tetanically.

Spindle receptors activated by single shocks to the muscle nerve. Eight receptors responded to single nerve shocks by giving discharges during the rising phase of the twitch (Fig. 2*d* and *f* large spike). Five more fibres responded to single muscle nerve shocks when the extrafusal contraction was reduced or abolished with succinylcholine or gallamine. Thus a total of thirteen spindle receptor fibres could be activated by single shocks to the muscle nerve.

Eight out of these thirteen were also tested with tetanic stimulation. Two of these (18 and 19) had responded to single shocks only after treatment with succinylcholine, and these likewise responded to tetanic stimulation only after the drug had been given. Four others (1, 2, 4 and 6) also responded to tetanic stimulation (for details see Table 1) but the other two (10 and 17) showed a phenomenon which was unexpected. They were activated after succinylcholine by single but not by tetanic stimulation of the muscle nerve. No experiments were undertaken to discover the cause of this apparently anomalous finding. One possible cause, however, might be the type of depression described by Paintal (1959) and thought by him to be due to stimulation of spindle receptor fibres.

Figure 3*a* is a histogram showing the number of spindle receptor fibres plotted against conduction velocity. Those which could be activated by single shocks to the muscle nerve are shown cross-hatched. It is clear from this figure that almost all the fibres of fast conduction velocity (more than 70 m/sec) and a minority of those of slow conduction could be driven by single stimuli to the muscle nerve.

Spindle receptors activated only by repetitive stimuli to the muscle nerve. Some fibres which were not activated by single shocks to the muscle nerve were activated by tetanic stimulation of the nerve. All the fifteen fibres which were not activated by single supramaximal shocks to the muscle nerves were subjected to repetitive stimulation of the muscle nerve. In three of these fibres (13, 20 and 23), it was possible to set up spindle receptor discharges during contraction with stimuli to the muscle nerve from just maximal to three times the alpha-maximum voltage. In five more fibres activation by this means only occurred when the extrafusal contraction was diminished or abolished in the manner described previously. As extrafusal recovery advanced it was at times necessary to increase the number of stimuli necessary to activate the receptor (Fig. 4).

The fibres activated only by tetanic stimulation of the muscle nerve are shown in Fig. 3*b*. This group of fibres all had conduction velocities in the range 30–70 m/sec.
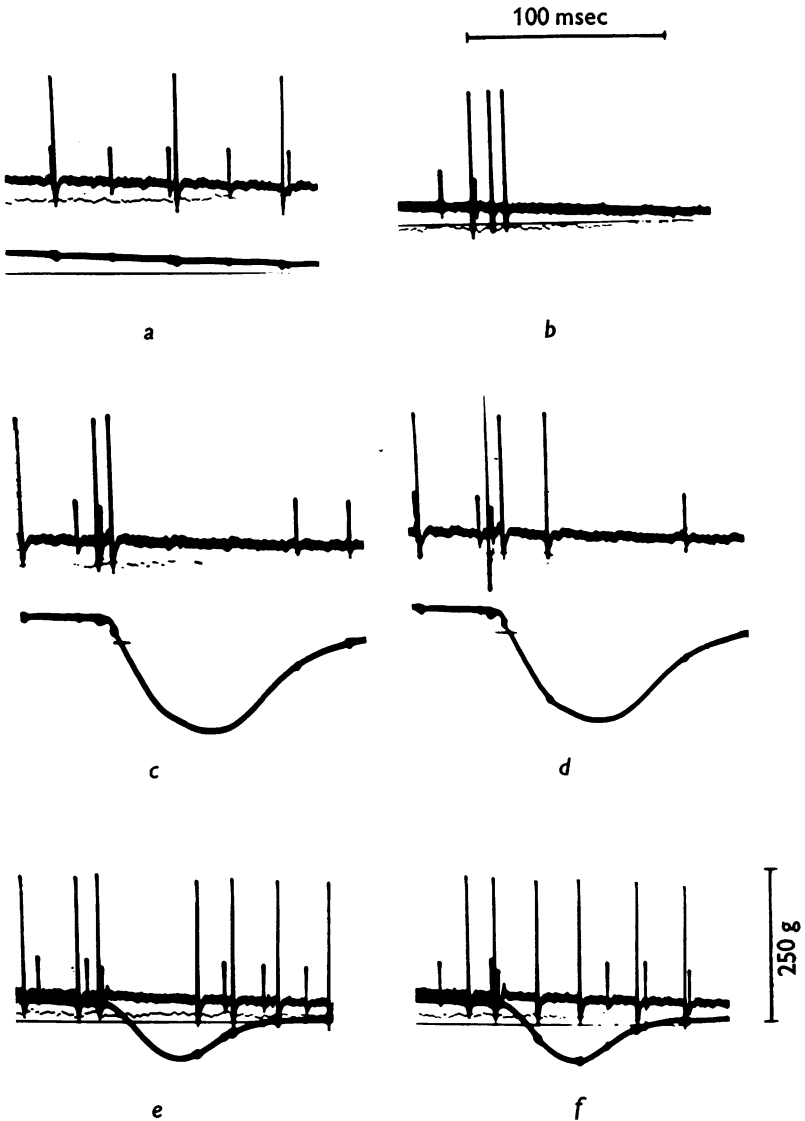
Fig. 2. Spindle receptor discharges during the rising phase of the twitch. Plantaris receptor; spinal rabbit under urethane anaesthesia. The large spike (1) was re-corded from a fibre conducting at 112 m/sec, the small spike (19) from a fibre con-ducting at 48 m/sec. *a*, control, no stimulus; *b*, stimulus strength = alpha-maximum voltage; the muscle was slack; note 'early discharge'; *c*, stimulus strength = alpha-maximum; *d*, stimulus strength = 10 × alpha-maximum; *e*, alpha-maximum stimulus after 25 μg succinylcholine; *f*, 1·1 alpha-maximum stimulus after 25 μg succinylcholine. The slowly conducting receptor fibre was activated at 2·5 times the alpha-maximum voltage. Lower traces are tension records (increase signalled downwards); upper traces are receptor discharges.
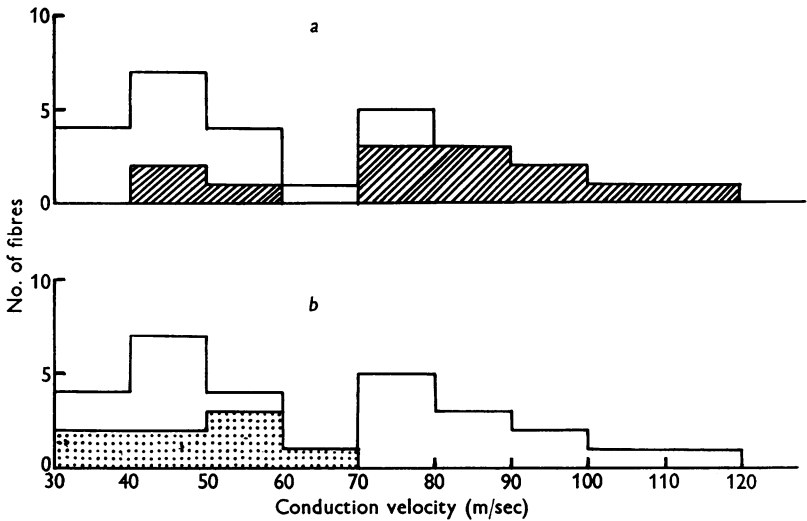
Fig. 3. Spindle receptor fibres activated by single shocks or by tetanic stimulation. □ All fibres. ▨ Fibres activated by single shock to muscle nerve with or without succinylcholine. ⊞ Fibres activated only by repetitive stimulation with or without succinylcholine.
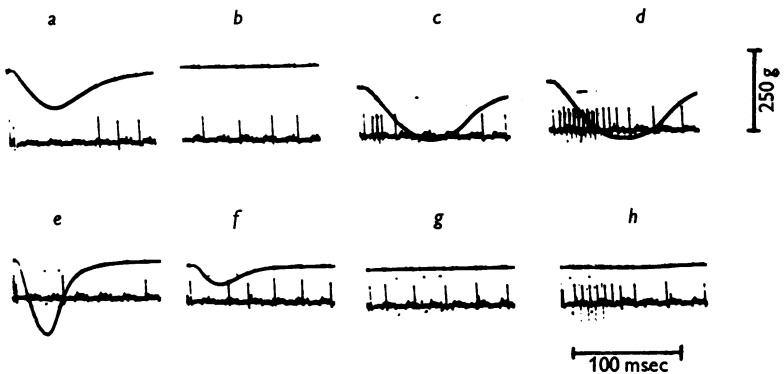

Fig. 4. Activation of a muscle spindle receptor (16) (fibre conduction velocity = 56 m/sec) by tetanic stimulation of the muscle nerve. Plantaris receptor; spinal rabbit under urethane anaesthesia. Records a–d form part of records taken at 5 sec intervals 7·5 min after 500 μg succinylcholine stimulating at 5·8 times alpha-maximum voltage: a, single stimulus; b, no stimulus; c, 4 stimuli, one response; d, 10 stimuli, three responses. Note the effect of increasing the number of stimuli. e–h form part of records taken at 5 sec intervals about 22 min after a, stimulating at 8·3 times alpha-maximum voltage synchronous with the injection of 300 μg succinylcholine: e–g, single shocks, h, tetanic stimulation.

Fibres which were not activated. Seven receptors were not activated by single or tetanic stimulation of the muscle nerve by stimuli up to ten times the alpha-maximum voltage. In all seven fibres extrafusal contraction was maximal; in no instances were the extra fusal muscle fibres paralysed by means of succinylcholine or gallamine. Six of these receptors were investigated before the technique of selective block of the extrafusal muscle fibres was fully developed (11, 21, 22, 24, 25, 28); the remaining fibre (12) died after the first dose of succinylcholine. If the selective block technique has been used, the receptors might have been activated by single shocks or repetitive stimuli to the muscle nerve, but this suggestion can only remain conjectural in the present circumstances.

The 'early discharge'. The early discharge of mammalian muscle spindles (Hunt & Kuffler, 1951) was seen in only five spindle receptor fibres (Table 1). It was easiest to demonstrate when the muscle was slack. The receptor fibres in which it occurred were all of high conduction velocity (70, 74, 74, 106, 112 m/sec). This is in agreement with the observations of Granit, Pompeiano & Waltman (1959), who found the early discharge almost exclusively in spindle receptor fibres of high conduction velocity.

The nature of the motor fibres to the muscle spindle

Since the increase in the frequency of discharge of muscle spindle receptors in the present work results from contraction of intrafusal muscle fibres, the threshold at which activation of a particular spindle receptor occurred was taken to be identical with the threshold of the spindle motor fibres. Of twenty-one spindle receptors which were activated by stimulation of the muscle nerve, in only two was activation obtained below the alpha-maximum voltage. The effect occurred at the alpha-maximum voltage in three fibres, at just above the alpha-maximum voltage in three others (1·1; 1·1; 1·3). In thirteen fibres the threshold at which the spindle response could be driven was at, or more than twice, the alpha-maximum voltage.

An idea of the conduction velocity of spindle motor fibres was obtained by comparing these figures with those of Leksell (1945). Leksell determined the relative thresholds of gamma and alpha motor fibres (identified by measurement of conduction velocity) of hind-limb muscles of the cat. He found that the gamma fibres were activated after the stimulus strength was raised above the value which activated the least sensitive of the alpha motor fibres. Hence it seems that the two fibres (16 and 26), which were activated at 0·13 and 0·42 times the alpha-maximum voltage, were supplied by spindle motor fibres probably conducting in the alpha range of velocities: the receptors which were activated at stimulus strengths above

twice the alpha-maximum voltage were probably conducting at gamma velocity.

Spontaneous discharge of mammalian muscle spindles

Many spontaneously active receptors, which discharged when the muscle was slack, were encountered. The majority of these had receptor fibres of the slowly conducting type (Table 1). In nine animals under urethane anaesthesia only one fibre conducting impulses faster than 70 m/sec was spontaneously active. In contrast, twelve out of fourteen muscle spindles with fibres conducting impulses below 70 m/sec were spontaneously active. These spontaneous discharges were in all instances noted before the injection of succinylcholine or gallamine.

DISCUSSION

The results indicate that both types of spindle receptors can be activated by repetitive stimulation of the muscle nerve (cf. Hunt, 1954; Harvey & Matthews, 1960). In addition, they indicate that although all spindle receptor fibres can probably be activated by repetitive stimulation of the muscle nerve, only a limited number also respond to single shocks to the muscle nerve, and these mostly lie in the upper range of conduction velocities. It seems, therefore, that the spindle receptors investigated in the present work fall into two groups. One group consists of receptors which are usually silent in slack muscle, possess receptor fibres of high conduction velocity and are activated by single shocks to the muscle nerve. They may also show an early discharge. The other group comprises receptors which are usually active spontaneously, are connected to receptor fibres of lower conduction velocity and are usually activated only by repetitive stimulation of the muscle nerve. They do not show an early discharge.

In many fibres, activation only occurred after complete or partial paralysis of the extrafusal muscle fibres with succinylcholine chloride. It is suggested that the effect obtained after succinylcholine is due to the absence of the unloading effect of extrafusal contraction when the intrafusal muscle fibres act unhindered on adequate stimulation of spindle motor fibres. One source of doubt as to the validity of this interpretation is the fact that succinylcholine causes marked excitation of the spindle receptors in addition to paralysing the extrafusal muscle fibres. It might be argued that succinylcholine, which blocks by depolarization, lowers the threshold of the receptors and pre-disposes them to repetitive discharges on stimulation of the muscle nerve. However, activation of a receptor has been obtained in the absence of the drug, the effects not differing qualitatively or quantitatively when repeated in its presence. Furthermore, the

effect has been obtained by blocking extrafusal contraction by the use of gallamine, which blocks the neuromuscular junction of skeletal muscle without exciting the spindle receptors. Gallamine does not block transmission across intrafusal end-plates after it has blocked extrafusal end-plates completely (Granit, Homma & Matthews, 1959).

Can the present findings be correlated with the histology of the muscle spindle? Considering first the intrafusal muscle fibres, it is suggested that the receptors which are activated by single muscle nerve shocks are influenced by a different type of intrafusal muscle from the receptors which are activated by tetanic stimulation alone. This suggestion is entertained because of evidence from three different sources, which indicates that both twitch and tonic intrafusal muscle fibres exist. First, Kuffler, Hunt & Quilliam (1951) recorded slow intrafusal potentials from the tenuissimus muscle of the cat. Secondly, Boyd (1958), using histological techniques, demonstrated the presence of two types of muscle fibres, large and small, in the muscle spindles of the cat's tenuissimus muscle. He later stated that the large intrafusal muscle fibres contracted in an all-or-nothing fashion, whereas the small intrafusal muscle fibres were capable of graded responses (Boyd, 1959). Thirdly, Eyzaguirre (1960) recorded propagated potentials from the muscle spindles of the cat's tenuissimus muscle. He maintained, on account of the absence of slow intrafusal potentials, that the intrafusal muscle fibres were twitch fibres. It is doubtful, however, if the recording of potential changes in this manner will exclude the existence of slow intrafusal muscle fibres, for Ginsborg has shown that slow muscle fibres of the chick are capable of propagated responses (Ginsborg, 1959).

Returning to the present results, the receptors of the first group, that is, those activated by single nerve shocks, possibly lie on twitch intrafusal muscle fibres, whereas the receptors in the second group (activated only by tetanic stimulation of the muscle nerve) lie on tonic intrafusal muscle fibres.

Whether these two groups of receptor fibres come from primary and secondary endings respectively cannot be answered definitely, because of lack of figures of the conduction velocities and fibre sizes of primary and secondary spindle receptor fibres from the gastrocnemius medialis and plantaris muscles of the rabbit. In the vastus muscle of the rabbit the primary and secondary receptor fibres measured $8–12\mu$ and $6–9\mu$ respectively inside the muscle (Barker, 1948). Hagbarth & Wohlfart (1952) found that the spindle receptor fibres measured $8–15\mu$ but did not divide them into two groups, primary and secondary (cat's gastrocnemius medialis, soleus, and tibialis anterior muscles). Both these figures, which were obtained by direct measurement in fixed and stained preparations, are

unsuitable for comparing with the conduction velocities of the fibres studied in the present work. This is because the maximum expected conduction velocities from the studies in the two papers cited above would be 72 and 90 m/sec respectively (using a conversion factor of six) whereas fibres conducting at over 100 m/sec were encountered in the present work. Two other pieces of evidence, less direct than those quoted above, point to 70 m/sec as a reasonable figure which could be used in dividing spindle receptor fibres into primary and secondary. Hagbarth & Wohlfart (1952) showed that receptor fibres from certain hind-limb muscles of the cat occurred in three different diameter groupings, viz. 1–5μ, 5–11μ, 11μ and over (see also Lloyd & Chang, 1948). Secondly, Hunt (1954) found that spindle receptor fibres of the cat's gastrocnemius medialis and soleus muscles fell into two definite groups conducting at 24–72 m/sec and 72–120 m/sec respectively. A reasonable way of dividing the twenty-eight spindle receptor fibres studied in this work is to regard fibres conducting at 70 m/sec and above as coming from primary endings and those conducting impulses below 70 m/sec as originating from secondary endings.

This would imply that the great majority of primary endings lie on twitch intrafusal muscle fibres, since they can be activated by single shocks to the muscle nerve, and the majority of secondary endings on tonic intrafusal muscle fibres, needing a short tetanus for activation. However, the series is not large enough to say how many exceptions there may be to this postulate.

SUMMARY

1. A study has been made of the responses of twenty-eight spindle receptor fibres from the gastrocnemius medialis and plantaris muscles of anaesthetized rabbits under conditions of maximal and minimal extrafusal contraction.

2. A technique by which intrafusal muscle fibres can be activated selectively is described. It consists of paralysing the extrafusal muscle fibres partially or completely by retrograde injection of succinylcholine, coupled with adequate stimulation of the muscle nerve by single shocks or brief tetani.

3. The spindle receptor fibres of high conduction velocity (> 70 m/sec) were activated by single shocks to the muscle nerve. The majority of spindle receptor fibres of lower conduction (70 m/sec or less) were activated only by repetitive stimulation of the muscle nerves.

4. The voltage at which activation of the spindle receptors occurred was at or above the voltage which evoked a maximal twitch of the extrafusal muscle fibres. However, two endings were activated by stimuli which were only a fraction of the voltage which was needed to produce a maximal extrafusal twitch.

5. An attempt is made to correlate the findings with the types of receptor ending and with the nature of intrafusal muscle fibres.

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