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SOME EFFECTS OF STIMULATION OF THE MUSCLE NERVE ON AFFERENT ENDINGS OF MUSCLE SPINDLES, AND THE CLASSIFICATION OF THEIR RESPONSES INTO TYPES A1 AND A2

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The afferent discharge from single sense endings in mammalian muscle was first recorded by B. H. C. Matthews (1933). He was immediately faced with the problem of deducing the nature of any sense ending studied from the patterns of discharge in its afferent fibre. He found two distinct patterns of behaviour during contraction of the muscle elicited by weak stimulation of the mucle nerve, when the rate of discharge of some endings slowed (type A endings), while that of others accelerated (type B endings). Matthews concluded that the A endings were in the muscle spindles, and that the B endings were Golgi tendon organs. This classification has been generally accepted by later workers (Hunt & Kuffler, 1951*b*; Granit, 1955), and has been strengthened by the finding that only the A endings are affected by stimulation of the gamma efferents (Kuffler, Hunt & Quilliam, 1951; Hunt, 1954). Matthews in addition subdivided the A endings into types A 1 and A 2, and suggested that these corresponded to the flower-spray (A 1) and annulo-spiral (A 2) endings of the muscle spindle. The discharge of the A 1 endings slowed during muscle contraction, whether twitch or tetanic, under all the experimental conditions studied. In contrast, the discharge of the A 2 endings, though slowed during a submaximal contraction of the muscle, was dramatically accelerated when the stimulus to the nerve was increased, an effect which was attributed to excitation of the motor nerves to the intrafusal fibres of the muscle spindle. Thus it was suggested that contraction of the intrafusal muscle fibres produced strikingly different effects on the primary (annulo-spiral) and secondary (flower-spray) endings of the muscle spindle, a conclusion which is favoured by the different arrangement of these two types of endings within the muscle spindle.

More recent work, however, has cast doubt on the physiological significance of the subdivision of muscle spindle endings into types A 1 and A 2.

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The classification of an ending as a primary or secondary ending may now be made independently of its classification into type A 1 and A 2, by measuring the conduction velocity of its afferent fibre. For histological observations show that the axons forming the primary ending are of greater diameter, measured near the spindle, than those forming the secondary endings (Ruffini, 1898; Barker, 1948), while electrophysiological experiments show that in the muscle nerve the conduction velocities of the afferent fibres of muscle spindles range from 20 to 120 m/sec (Merton, 1953; Hunt, 1954), and that the reflex connexions of the smaller and larger of these afferent fibres are strikingly different (Eccles, Eccles & Lundberg, 1957; Eccles & Lundberg, 1959). It is therefore widely accepted that afferent fibres with a high conduction velocity come from primary endings and those with a low conduction velocity from secondary endings; but in terms of fibre conduction velocity the precise position and the sharpness of the division between afferents from primary and from secondary endings is not well established, though it is probably about 70 m/sec (Hunt, 1954). On the basis of this classification it has been found that stimulation of single gamma motor fibres, which supply solely the intrafusal fibres, can excite secondary as well as primary endings (Hunt, 1954; Kuffler *et al.* 1951). In addition the A 2 type of discharge is said to have been found both for primary (Hunt & Kuffler, 1951*b*) and for secondary endings (Hunt, 1954) on stimulating only large or alpha motor fibres. From all this work the A 2 type of discharge has been attributed not to activation of intrafusal muscle fibres but to the chance pull of extrafusal muscle fibres upon certain muscle spindles, and the difference between the A 1 and A 2 types of discharge has been considered to be fortuitous (Hunt & Perl, 1960).

There appears, however, to be a difference between the method used by Matthews to classify A 1 and A 2 endings and that used by Hunt and by Kuffler. Hunt & Kuffler (1951*a*, *b*) studied the behaviour of the spindle mainly during twitch contractions or during brief tetanic contractions in which the tension in the muscle barely reached a steady level; and in many cases they stimulated a ventral root filament rather than the muscle nerve. Inequalities in the rate or strength of contraction of different parts of the muscle might then well lead to the mechanical stimulation of some muscle spindles by chance pulls, and in conformity with this it may be noted that they recorded discharges of such varied patterns that they found it difficult to classify the endings into two clear groups. Matthews, on the other hand, stimulated only the whole muscle nerve and apparently relied mainly on the behaviour of the spindle during fairly prolonged tetanic contractions, for he showed that the behaviour of an A 2 ending during a twitch depended greatly upon the initial tension (see his Fig. 14); moreover, he found that almost all endings could be sharply classified. In

any case Matthews stated that he frequently found an increase in the discharge of the A 2 ending on increasing the strength of a stimulus which was already eliciting a maximal tetanic contraction of the muscle (see particularly his Fig. 13), and this cannot readily be attributed to the pull of extrafusal muscle fibres on the spindle. It may be doubted, therefore, whether Hunt & Kuffler were invariably studying the same phenomenon as Matthews. The question then arises as to whether or not the slightly supramaximal stimuli used by Matthews excited the gamma motor fibres, for on the basis of more recent work (Leksell, 1945; Kuffler *et al.* 1951) on the relative thresholds of α and γ motor nerve fibres it might be suggested that his stimuli were too weak to have done so. Matthews's results might then perhaps be attributed to the specific activation of the spindle by some group of nerve fibres which were larger than the γ fibres, for the existence of such a motor supply to the spindle has recently been suggested (Granit, Pompeiano & Waltman, 1959*a*, *b*; Boyd, 1959).

Thus the classification of muscle spindle endings into groups A 1 and A 2 has not been satisfactorily explained, and still presents certain interesting features. Matthews's experiments with tetanic stimulation of the muscle nerve have therefore been repeated to see whether his classification can be confirmed, and in order to compare the thresholds of the stimuli required to elicit A 2 responses with the threshold of the γ motor fibres determined under similar experimental conditions. As described in a preliminary communication (Harvey & Matthews, 1960) it has been found that virtually all muscle spindle endings can give an A 2 response and that this can be attributed to the excitation of γ motor fibres, though in some cases 'α-excitation' of the ending similar to that analysed by Hunt & Kuffler was also observed. Some of the observations are also of interest in relation to current problems of the innervation of the muscle spindle.

METHODS

Preparation. The experiments were performed on twelve cats. Eleven were anaesthetized with pentobarbitone sodium (Nembutal; Abbott Laboratories) given intraperitoneally, and one was decerebrated. The discharge of single muscle spindle endings lying in the soleus muscle was recorded under paraffin from thin dorsal root filaments, exposed by lumbar laminectomy and split under a dissecting microscope. Soleus was completely isolated from the spinal cord by cutting the L 6, L 7, S 1, S 2 dorsal and ventral roots, except in the case of the decerebrate cat in which part of one ventral root unfortunately escaped section (as the behaviour of the six endings then studied was typical the results were included in the series). Isolation of single units was aided by widespread denervation of leg and hip muscles. Muscle spindle afferents were identified by the slowing of their discharge occurring during a submaximal twitch of soleus elicited by stimulating its nerve. The conduction distance was determined at the end of the experiment by dissecting out the sciatic nerve with its attached dorsal roots. In calculating the velocity no correction was made for any possible utilization time intervening between the beginning of the 0·1 msec stimulating pulse and the

initiation of the action potential. One possible source of error in this determination was observed for smaller afferent fibres with relative high thresholds to electrical stimulation. These were sometimes excited ephaptically by the muscle action potential (Lloyd, 1942; Granit *et al.* 1959*b*) when the stimulus was too small to excite them directly, and thus appeared to have an unduly long conduction time (cf. Lundberg & Winsbury, 1960). This artifact was readily recognizable, as on progressive increase of the stimulus strength the conduction time suddenly shortened to its true value.

Altogether 105 endings were studied, but they were not all studied under a full range of experimental conditions. The series probably contains too many primary endings in relation to their frequency of occurrence in the muscle, even though particular care was taken to obtain endings with slowly-conducting afferent fibres; but the series undoubtedly contains muscle spindle afferent endings of all kinds as the conduction velocities of the afferent fibres studied were well scattered between 23 and 116 m/sec (see Fig. 3, and Hunt, 1954). Following Hunt (1954), and in order to facilitate description of the results, a conduction velocity of 72 m/sec has been arbitrarily taken as the dividing line between afferents from primary and afferents from secondary endings.

Myography. The leg of the cat was held rigidly by pins in each end of the tibia. The pelvis was steadied by pins in the iliac crests. The tendon of the soleus muscle was dissected free from that of gastrocnemius and was connected by a rigid link to an isometric myograph. The myograph utilized a mechano-electric transducer valve (RCA 5734) the output of which was amplified and displayed on a cathode-ray tube. The soleus was separated from the lower part of gastrocnemius, which was denervated, and the skin was sewn back over the muscles, leaving the tendon protruding. The temperatures of the muscle, of the paraffin pools and of the cat were usually in the range 36–38° C.

Stimulation. The nerve to soleus was dissected out of the lateral head of gastrocnemius through which it runs and was covered by liquid paraffin contained by flaps of skin and muscle. The stimulating electrodes were applied to the nerve 1–2 cm away from its point of entry into the soleus, and with the cathode closer to the muscle than the anode. The electrodes consisted of a pair of silver wires separated by about 5 mm. The stimuli were square pulses of 0·1 msec duration and were isolated from earth by being delivered through a transformer. The intensity of the stimuli was controlled and determined by means of a calibrated potentiometer. Probably because of the presence of stray connective tissue it was sometimes found that small movements of the nerve on the electrodes produced appreciable changes in the effectiveness of the stimulus. To circumvent this difficulty frequent determinations were made of the threshold of the α motor fibres to single stimuli (by observing the contraction of the muscle), so that comparisons of the strength of stimuli delivered at different times could be made in terms of their relation to the α threshold rather than in absolute units. The absolute value of the threshold of the α motor fibres was always appropriately low and varied from 35 to 160 mV in different experiments. The strength of stimulus required to produce a maximal contraction of the muscle was also frequently checked.

Recording. The action potential of the afferent fibre studied was amplified by conventional means and, in order to facilitate its observation during a tetanic contraction, was displayed on two separate cathode-ray tubes. One tube had a sweep lasting 2–3 sec and the tension developed by the muscle was displayed on its second beam. This record gave a general picture of the time relations between the discharge of the ending and the contraction of the muscle. The second tube had a sweep lasting about 50 msec and allowed the time relations between the stimulating pulses and the action potentials to be determined. This tube received triggering pulses from the stimulator, arranged so that during and only during the period that the nerve was being stimulated the beam was sweeping repetitively with the stimulus artifacts occurring at constant points on the tube face. During a 0·8 sec period of tetanic stimulation 10–15 of these repetitive traces were superimposed in a single photo-

graphic record, alongside a record of the cathode-ray tube with the slow sweep. This method of display was used largely because it was economical of recording paper. When necessary the cathode-ray tube sweeps were stopped and records were taken on photographic paper moving at 18 cm/sec, using about ten times more recording paper. During observations on any one ending a 0·8 sec train of stimulating pulses was delivered every 10 sec. Between consecutive records either the intensity or the frequency of the stimulus could be altered while the camera moved on. This pattern of stimulation was continued for periods of 1–2 min without any significant signs of fatigue of the muscle or of the ending. The natural stimulus artifact was usually very small and so an artificial stimulus artifact was frequently introduced into the action potential records on one or both cathode-ray tubes. Most endings were studied both with the muscle just taut (tension under 50 g) and with the muscle extended to within a few mm of its physiological full extension (tension up to 500 g), except for some secondary endings with high thresholds for tension, which were only studied under appreciable tension. Stimulus frequencies of 1, 30, 50, 70, 100/sec were regularly used at three different intensities of the stimulus. The intensities used were first, sufficient to produce a half to three-quarters maximal contraction of soleus; secondly, about 120–140 % of that required to produce a maximal contraction; and thirdly, about ten times that required to produce a threshold contraction of the muscle (about seven times maximal). Lower frequencies of stimulation and intermediate values of stimulus intensity were also employed on many occasions.

RESULTS

Response to tetanic stimulation

In all but two of the ninety muscle spindle endings studied in this respect tetanic stimulation of the muscle nerve with shocks strong enough to excite the γ motor fibres elicited an A 2 type of response, provided that the initial tension and the frequency of stimulation were appropriately adjusted. The afferent fibres studied had conduction velocities ranging from 23 to 116 m/sec, and it may therefore be concluded that the A 2 response is given both by the primary and by the secondary endings of the muscle spindle (Hunt, 1954). Figure 1 shows a typical A 2 response from a primary ending. The top traces (*a*) show the tension developed in soleus on stimulating its nerve with shocks slightly supramaximal for eliciting a contraction. Immediately beneath the myographic traces, and recorded on the same sweep speed, lie the records of the responses of the single muscle spindle afferent fibre, recorded from a dorsal root filament. During the twitch contraction the discharge of the muscle spindle ending ceased. During the tetanic contraction, though nerve impulses were still recorded, they were not set up at the ending but were due solely to the direct electrical stimulation of the afferent fibre studied. This is shown by the superimposed traces *c*, which record the discharge of the afferent fibre during the period of stimulation with a high-velocity sweep locked to the stimulus. It can be seen in this record that all the spikes follow the stimulus artifacts with a short constant latency. Traces *d*, *e*, and *f* were recorded similarly to *a*, *b*, and *c*, but were taken when the stimulus strength was considerably supramaximal. In this case, during the tetanic contrac-

tions, there are numerous impulses in addition to those set up by the direct electrical stimulation of the afferent fibre, and these must have been initiated at the nerve ending within the muscle spindle. Figure 2 shows a similar response from a secondary ending on increasing the strength of the stimulus.

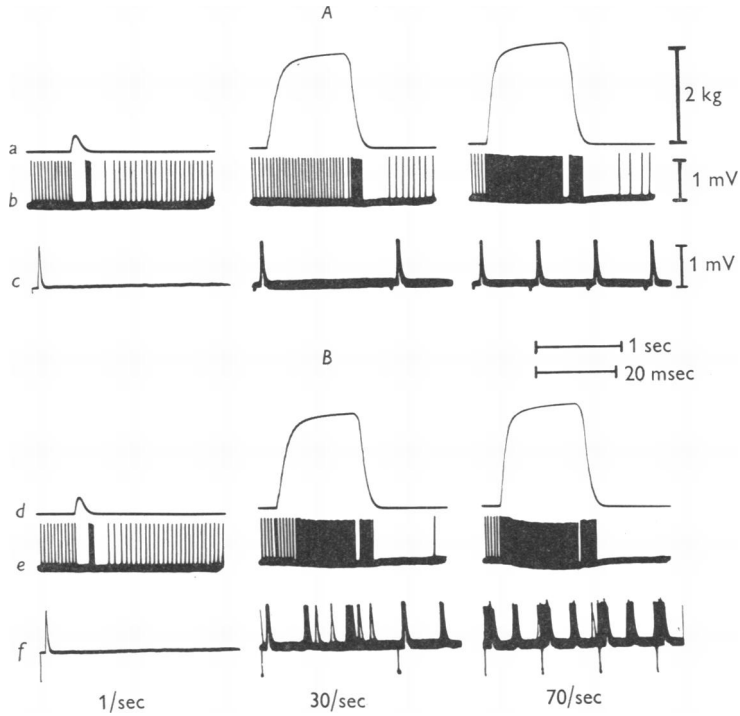

Fig. 1. An A 2 response given by a primary ending (afferent fibre conduction velocity 103 m/sec). *A*, absence of A 2 response on slightly supra-maximal stimulation of muscle nerve (stimulus 1·5 times α threshold). *B*, presence of A 2 response on greatly supramaximal stimulation (stimulus 10 times α threshold). *a*, *d*, myographic records of tension in soleus; *b*, *e*, action potentials of single afferent fibre; these four traces are all on the same slow sweep speed (see upper time scale). *c*, *f*, superimposed traces showing the action potentials of the single afferent fibre occurring during the period of stimulation, but recorded at a high sweep speed (see lower time scale) and with the sweep locked to the stimulus. Stimulus artifacts were introduced artificially into the high-speed records, where they form the downward deflexion; the upward deflexions are action potentials in all records. (Initial tension approximately 10 g. Records retouched.)

Such results were typical and were found for every one of the 55 primary endings and for all but two of the 35 secondary endings studied with tetanic stimulation. The only acceptable interpretation of such a result is that the stronger stimuli excited fusimotor nerve fibres, with a consequent stimulation of the afferent endings of the muscle spindle. The findings thus

confirm previous work showing, by means of stimulation of single γ motor fibres, that both the primary and the secondary endings of the muscle spindle may be so excited (Kuffler *et al.* 1951; Hunt, 1954).

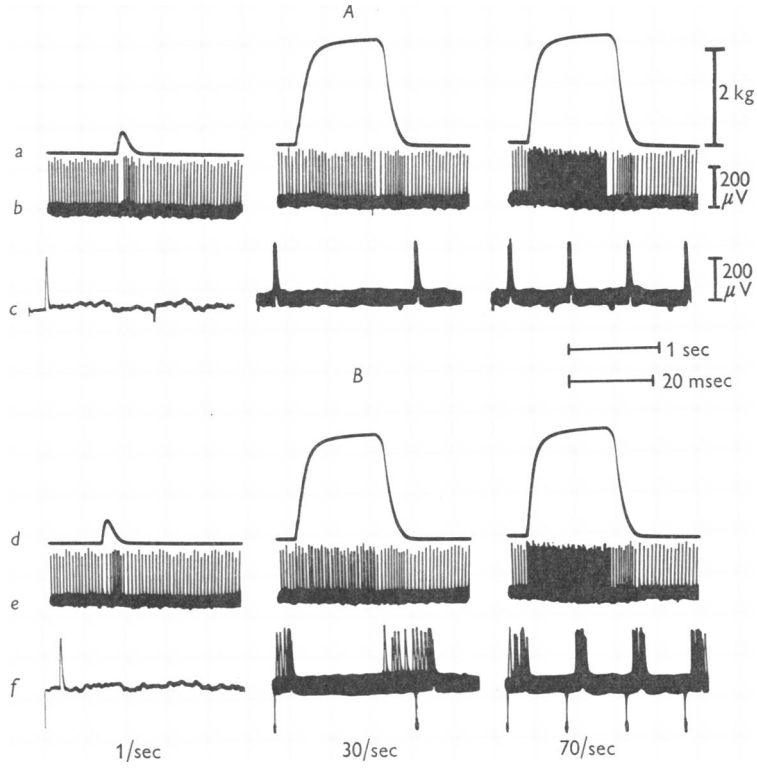

Fig. 2. An A 2 response given by a secondary ending (afferent fibre conduction velocity 45 m/sec). *A*, absence of A 2 response on moderately supramaximal stimulation of muscle nerve (stimulus 2·5 times α threshold). *B*, presence of A 2 response on greatly supra-maximal stimulation (stimulus 12·5 times α threshold). *a*, *d*, myographic records of tension; *b*, *e*, action potentials recorded on same slow sweep speed as myographic records; *c*, *f*, superimposed traces on a high sweep speed of the action potentials occurring during the period of stimulation. Stimulus artifacts present only in the high speed records, where they form the downward deflexions. Initial tension 150 g. (Records retouched.)

In many cases, however, it proved more difficult to produce the A 2 response from secondary than from primary endings. Also the A 2 response of the secondary endings was in general rather weaker than that of the primary endings. For example, in Figs. 1 and 2 it can be seen that the time interval between the direct spike elicited by the stimulus and the subsequent spike initiated at the ending was appreciably longer for the secondary ending, and such a difference was common. In addition,

whereas primary endings usually gave an A 2 response at initial tensions of under 50 g, secondary usually only gave an A 2 response if the initial tension on the muscle was 50–300 g, and in six cases tensions of 300–900 g were required. (For example, the ending of Fig. 2 did not show an A 2 response when the initial tension was 30 g.) For both primary and secondary endings the A 2 responses usually became more marked on increasing the initial tension. In both cases, also, increasing the frequency of stimulation increased the intensity of the excitation of the ending, as judged by a decrease in the time interval from the direct spikes to those evoked at the ending (Figs. 1 and 2); and in the case of a few secondary endings an A 2 response was only found on stimulation at 50/sec or above.

On stimulation at frequencies below 20/sec weak excitation of the ending was sometimes observed, but its detection was hindered by the mechanical effects of the unfused tetanic contraction of the extrafusal fibres. Frequencies of stimulation above 100/sec were only employed occasionally, as the consequent increase in the number of spikes elicited directly by the stimulus tended to mask the A 2 response. Most of the endings studied showed an A 2 response with all the frequencies of stimulation used (usually 30, 50, 70 and 100/sec, often also 20/sec), but two secondary endings only gave an A 2 response on stimulation at 70 and 100/sec and two others gave an A 2 response at 50, 70 and 100/sec, but not at 30/sec. In these four cases only one initial tension was studied. Three other secondary endings and two endings just falling in the primary group (afferent fibre conduction velocity 73 m/sec in each case) behaved similarly at one initial tension, but also gave an A 2 response at 30/sec stimulation when the tension was increased.

The fact that the A 2 response was not detected under some conditions of initial tension and frequency of stimulation, even when using strong stimuli, suggests that the excitatory effect of the intrafusal contraction was too weak to be detected in the face of simultaneous direct electrical stimulation of the afferent fibre studied. Each one of the impulses thereby excited would travel antidromically to the ending and reset its rhythm (Matthews, 1933) so that the discharge of the ending could only be detected when it was of higher frequency than that of the electrical stimulus (except for a few cases of secondary endings with axons conducting at about 30 m/sec whose A 2 threshold was slightly below that of the afferent fibre). In addition, before producing any excitatory action the intrafusal contraction must cause sufficient shortening to overcome the unloading of the spindle due to the contraction of the extrafusal muscle fibres.

Thus the finding of two secondary endings which did not show the A 2 response under any of the conditions studied cannot be taken to mean that no intrafusal effect was present. Indeed, the occurrence of some weak γ excitation was strongly suggested in one of these cases by the finding that on increasing the stimulus strength to considerably above α maximum the ending fired more rapidly at the beginning of the relaxation of the tetanic contraction than it did with weaker stimuli (cf. Matthews, 1933). Other endings with axons of similar conduction velocity (34 and 42 m/sec) did show an A 2 response.

Values of the threshold strength of the stimuli required to produce the A 2 response

On progressive increase of the strength of the tetanic stimulus to the muscle nerve the A 2 response appeared at a definite and repeatable threshold. This presumably corresponded to that of some particular motor nerve fibre supplying the intrafusal muscle fibres of the ending studied. The value of the thresholds of the motor fibres exciting different muscle

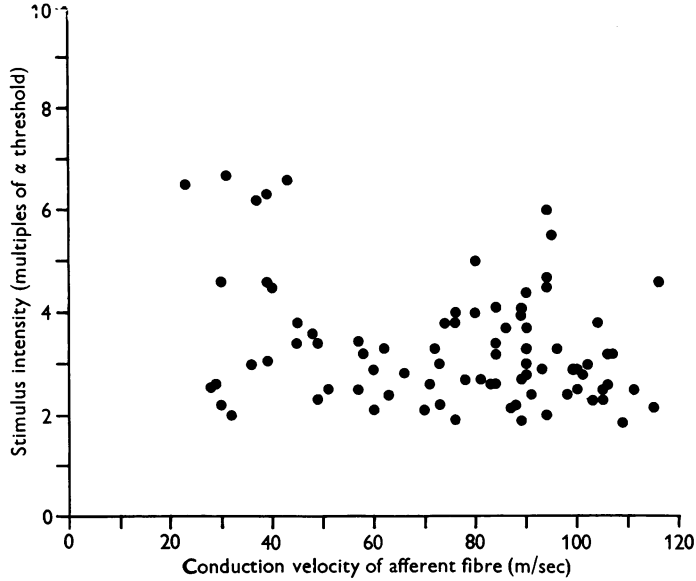

Fig. 3. The distribution of the A 2 thresholds of 84 endings. Abscissa, conduction velocity of the afferent fibre of the ending; ordinate, threshold strength of stimulus required to elicit an A 2 response for the ending. The stimulus strength is expressed in terms of the threshold of the most excitable α motor fibres of the same preparation. A stimulus of 1·6 times α threshold sufficed in all cases to produce a maximal contraction of the muscle.

spindle endings is of interest in relation to current suggestions, based on histological observations, that there are different kinds of intrafusal muscle fibres, with different relations to the primary and the secondary afferent endings, and with motor endings of different types (Barker & Ip, 1960; Boyd, 1959; Cooper, 1960; Cooper & Daniel, 1956). The threshold was expressed in terms of the threshold of the α motor fibres determined at the same time (by observation of the muscle contraction) so that the results of different experiments could be compared. The determination was made with a frequency of stimulation of 70/sec (rarely 50 or 100/sec), as at this frequency the occasional weak excitatory effect of stimulating

α fibres (see later) was masked by the impulses directly excited by the electrical stimulus, while this frequency also favoured the γ excitation of the ending. The initial tension was not closely controlled for this determination; for primary endings it was usually 50–150 g, while for secondary endings rather higher tensions were sometimes necessary (*vide supra*). The distribution of the A 2 thresholds of 84 endings (54 primary, 30 secondary) is shown in Fig. 3, where the strength of the stimulus required to produce an A 2 response is plotted against the conduction velocity of the afferent fibre concerned. A maximal contraction of the muscle was produced by stimuli varying in different preparations from 1·2 to 1·55 times α threshold (maximal response was gauged by size of twitch). The lowest threshold found for an A 2 response was 1·7 times α threshold, and there were only four values below 2·0, so that all the A 2 thresholds plotted can be attributed to excitation of motor fibres with a higher threshold to electrical stimulation than the α fibres. At the end of eight of the twelve experiments the relative thresholds of the different sized motor fibres were sought under existing experimental conditions by recording monophasically their compound action potential from the peripheral end of an appropriate cut ventral root (L 7 or S 1) on stimulating the nerve to soleus. The stimulating electrodes remained undisturbed in the position used when studying the single afferent fibres, but the nerve was crushed at its point of entry into the muscle in order to eliminate the 'back-response' (Leksell, 1945; Brown & Matthews, 1960). The threshold of the least detectable γ wave was 2·1–2·4 times α threshold in five experiments, 1·8 and 1·6 times α threshold in two other experiments; in one experiment the γ wave was so small that it could not be detected with certainty and its threshold could not be determined. These low-threshold γ fibres had conduction velocities, calculated from the shock-response interval and the conduction distance, of 40–45 m/sec. It may be concluded that all the A 2 responses can be attributed to excitation of γ motor fibres.

The γ wave was identified by its occurrence after the α wave (though it sometimes fell in the after-potential of the α wave), and by its requiring a stronger stimulus than that required to produce an α wave of maximum amplitude (Leksell, 1945). The detection of the threshold of the γ wave was facilitated by recording it at five to ten times the amplification used for the simultaneously recorded α wave, and also by superimposing the traces of several sweeps photographically. The determination of the γ threshold was usually made with a stimulus frequency of 2 or 5/sec, but no difference in threshold was found on the one occasion on which the frequency was increased to 70/sec. The form of the α wave was not carefully studied, and the sweep speed used was not high enough to enable small changes in its falling phase to be detected on increasing the stimulus strength.

Crushing the nerve to eliminate the 'back-response' sometimes produced a temporary lowering of the threshold of the α fibres, presumably because of the flow of injury current, but observations on threshold were usually made when the threshold had returned to roughly its previous value. A single observation suggested that slight changes might occur

in the relative thresholds of α and γ fibres as a result of crushing, but because of the difficulty of studying the γ wave in the presence of the back-response no systematic observations were made of its threshold in the intact nerve. In another experiment the effect of the proximity of the stimulating electrode to the crushed end was investigated by determining the relative thresholds of the α and γ fibres, both before and after moving the electrodes 0·5 cm. This procedure made little difference to the relative thresholds and a similar result was obtained when several positions of the stimulating electrode were studied in an experiment on the nerve to the medial head of the gastrocnemius. It is felt, therefore, that the effect of

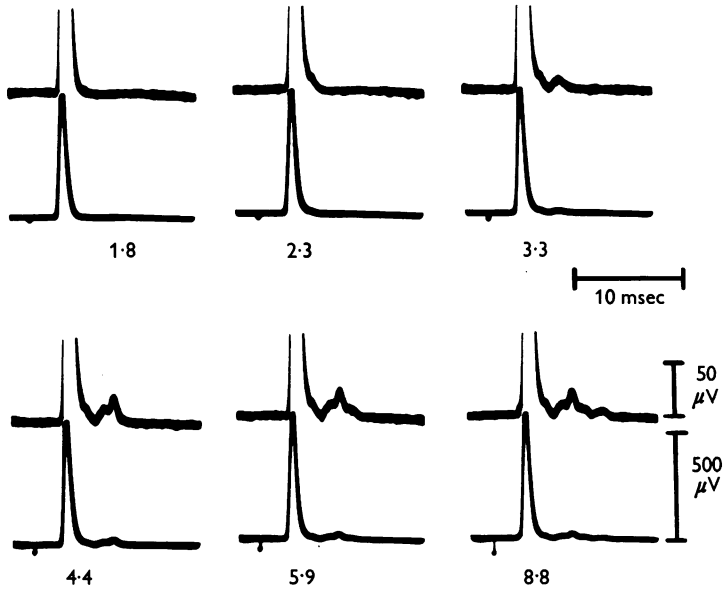

Fig. 4. Records showing the progressive prolongation of the γ wave on increasing the stimulus strength. The compound action potential of the soleus motor fibres was recorded monophasically from the L 7 ventral root on stimulating the soleus nerve. Records were taken simultaneously at two different amplifications in order to favour the display of either the γ wave (above) or the α wave (below). The stimulus strength, in terms of α threshold, is given below each pair of records. (Each record consists of about 15 superimposed traces. Stimulus artifacts introduced into low-gain traces, but not into high-gain traces. Records retouched.)

crushing is unlikely to have invalidated the results, but that no great significance should be attached to the precise value of the γ threshold relative to the α threshold or to the difference of the γ threshold found in the different experiments.

The values, relative to α threshold, of the stimuli required to give a maximal α wave or a threshold γ wave are both rather lower than those found by Leksell (1945). This difference is probably partly due to the fact that Leksell did not study the soleus nerve. This nerve differs from many other motor nerves in that the α motor fibres are smaller than usual, while the γ motor fibres are not (Eccles & Sherrington, 1930). Such an explanation is favoured by our finding in five experiments on the nerve to the medial head of gastrocnemius that the values of γ threshold and of α maximum tended to be higher relative to the α threshold than in soleus nerve (γ threshold 1·8, 2·5, 2·6, 2·8, and 3·3 times α threshold; α maximum 1·2, 1·8, 1·8, 1·8 and 2·0 times α threshold); but the values obtained were lower than that found

by Leksell for a single experiment on this nerve (γ threshold 4·0; α maximum 3·3). There were probably, however, differences in the stimulating arrangements used in the two sets of experiments.

Figure 3 shows that the A 2 thresholds of different endings differed considerably, but that there was no sharp discontinuity between the distribution of the A 2 thresholds of the primary and secondary endings. In both cases many endings gave an A 2 response with stimuli at or below three times α threshold, showing that they were excited by low-threshold

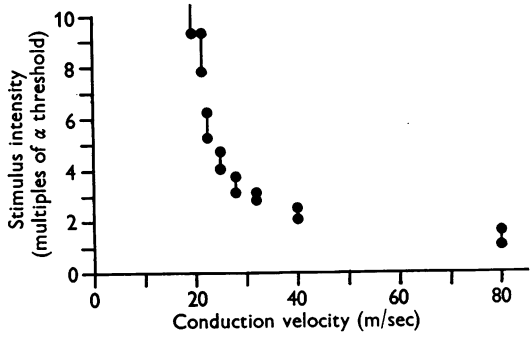

Fig. 5. The strengths of stimuli needed to excite γ motor fibres of different conduction velocities in the experiment of Fig. 4. Abscissa, conduction velocity of various parts of the γ wave; ordinate, strength of stimulus, in terms of α threshold, required to excite different parts of the γ wave. The two points at each conduction velocity correspond to the stimulus required to excite the least detectable γ wave and that required to excite a maximal γ wave of that velocity. (The records used for measurement were taken at a higher sweep speed than those illustrated in Fig. 4.)

γ fibres. In both cases also a few endings had A 2 thresholds above five times α threshold, showing that they were excited by high-threshold γ fibres. Leksell (1945) showed that the more slowly conducting γ fibres had a higher threshold to electrical stimulation than did the more rapidly conducting γ fibres. This was confirmed for the present conditions of stimulation and Figs. 4 and 5 show the relation between the electrical threshold and conduction velocity of various parts of the γ wave found in one experiment. Six other experiments gave similar results, though in only one of them was this wide range of stimulus strengths employed, either because in these cases the strong stimuli 'spread' so as to excite the cut nerve fibres from the lateral head of gastrocnemius, or because the tail of the γ wave was not clearly detectable. In order to discuss the significance of the A 2 thresholds the results expressed in Fig. 5 have been taken to apply approximately to all the experiments. Thus stimuli of three times α threshold excited γ fibres with conduction velocities of 30–48 m/sec, corresponding to fibre diameters of 5–8 μ (Hursh, 1939).

Stimuli above five times α threshold excited γ fibres with conduction velocities below 25 m/sec, corresponding to fibre diameters of less than 4 μ.

It is known, of course, that a single ending can usually be excited by several different γ fibres (Hunt & Kuffler, 1951*a*; Whitteridge, 1959).

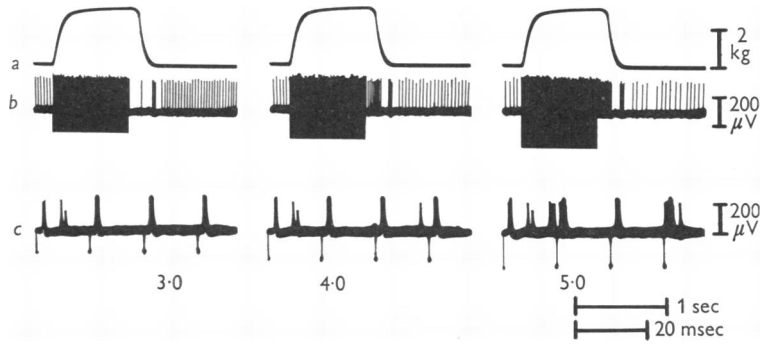

Fig. 6. An example of γ excitation which was subthreshold for the production of an A 2 response (primary ending, afferent fibre conduction velocity 94 m/sec). *a*, myographic records of tension in soleus; *b*, action potentials of afferent fibre recorded on same slow sweep speed as myographic records; *c*, superimposed traces on a high sweep speed of the action potentials occurring during the period of stimulation. Frequency of stimulation 70/sec in all cases. Intensity of stimulation, in terms of α threshold, marked below each set of records, and appreciably supramaximal for the contraction in all cases. The weakest stimuli (left) directly excited the afferent fibre of the ending, and after the last spike so excited only one impulse occurred on the falling phase of the contraction. In addition, the first stimulus of the train excited an 'early discharge' of two impulses, the second being smaller than the first because it followed it so closely, and this was also seen with the stronger stimuli. The intermediate strength stimuli (centre) were followed by a burst of impulses on the falling phase of the contraction, thereby demonstrating γ excitation of the ending; but there was no A 2 response during the period of stimulation. The strongest stimuli (right) caused a typical A 2 response followed by a greater burst of impulses on the falling phase of the contraction. (Stimulus artifacts downward and present in all records. Initial tension, 70 g. Records retouched.)

The γ fibre whose recruitment on increasing the stimulus just suffices to produce an A 2 response from a particular ending need not be the lowest-threshold γ fibre affecting that ending, for weak excitatory effects on an ending might pass undetected, as already discussed. In a few cases it was clearly apparent, on subsequent inspection of the records, that the ending had indeed been excited by a γ fibre of lower threshold than that whose excitation produced the overt A 2 response. For increasing the strength of stimulus already supramaximal for the α fibres caused the ending to fire for a short time after the last of a train of stimuli, while there was no such discharge with weaker stimuli. A striking example is illustrated in Fig. 6. (Such effects were usually less prominent, as most endings

discharged on the falling phase of the contraction with all strengths of stimulation.) In addition, in a few experiments when the initial tension on the muscle was increased the A 2 threshold of the ending fell to a new, lower value, possibly because the excitatory effect of a lower-threshold γ fibre was then sufficiently facilitated by the stretch to cause an A 2 response without the assistance of the higher-threshold γ fibre. Thus it is probable that many of the endings which gave an A 2 response only on stimulation of small γ fibres were also excited by larger γ fibres.

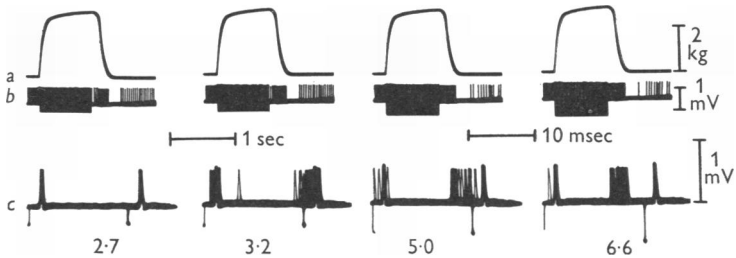

Fig. 7. An example of an increasing excitatory effect on an ending on increasing the strength of the stimulus above the A 2 threshold. (Primary ending, afferent fibre conduction velocity 100 m/sec.) *a*, myographic records; *b*, action potentials at same slow sweep speed as myographic records; *c*, superimposed traces on a high sweep speed of the action potentials occurring during the period of stimulation. Frequency of stimulation 70/sec in all cases. All stimuli were appreciably supramaximal for contraction; their strength, in terms of α threshold, is shown below each set of records. The weakest stimuli (left) were below the A 2 threshold and only excited spikes by direct stimulation of the afferent fibre. All the stronger stimuli excited an A 2 response, but increasing the strength of the stimuli shortened the interval at which impulses initiated at the ending followed the direct spikes. (Stimulus artifacts downward in all records. Initial tension, 45 g. Records retouched.)

It was also observed that many of the endings which gave an A 2 response on stimulation of large γ fibres were further excited by smaller γ fibres, for on increasing the stimulus strength beyond the A 2 threshold a more marked A 2 response was produced, and the latency between the direct spikes and those initiated at the ending decreased. An example of this is shown in Fig. 7, where in each case the increased effect occurred at a definite threshold strength of stimulus and so may be attributed to the recruitment of an additional γ fibre. For one ending the cumulative excitatory effects of four different γ fibres were so distinguished and four different 'incremental thresholds' determined. In no case was the A 2 response found to become less marked on increasing the stimulus strength.

For a number of endings care was taken to determine the value of one of these 'incremental thresholds', because it seemed important to demon-

strate unequivocally that primary endings are regularly influenced by smaller γ fibres. (Only 3 of the 54 primary endings in Fig. 3 have A2 thresholds above 5 times α threshold, and these were all studied in a single experiment.) The results are shown in Fig. 8, where again the A2 thresholds of the 84 units of Fig. 3 have been plotted, but when an 'incremental threshold' of 4·0 or over was observed (29 cases) its value has been plotted in place of the threshold intensity for the A2 response. From this graph

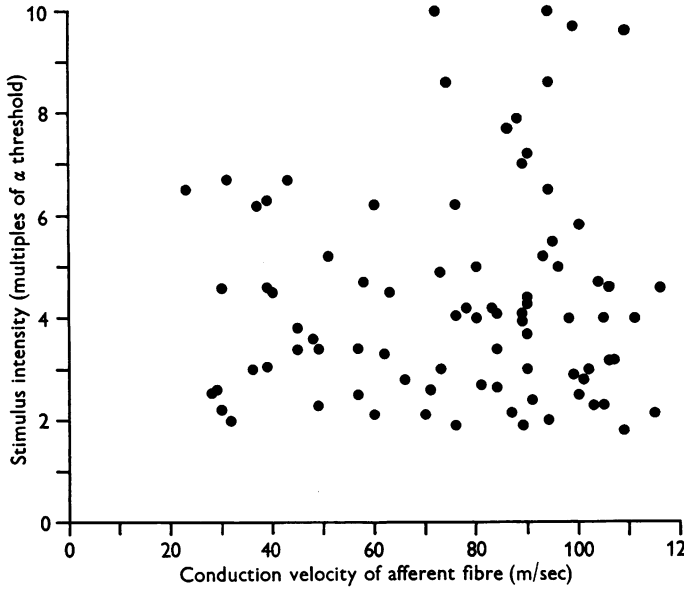

Fig. 8. The distribution for 84 endings of the threshold strengths of the stimuli producing either an A2 response, or a definite increase in the magnitude of the A2 response (29 cases). Only one point has been plotted for each ending, and that was the highest value obtained. Abscissa, conduction velocity of the afferent fibre of the ending; ordinate, stimulus strength in terms of the α threshold. (The two values plotted as 10·0 times α threshold were actually slightly higher. Fig. 3 shows all the A2 thresholds of these 84 endings.)

it may be concluded that both primary and secondary endings may be excited by γ fibres of a wide range of thresholds corresponding to diameters from 4 to 8 μ, or practically the whole of the γ range. (Incremental thresholds of over 10 times α threshold were not sought, partly because, with the present recording arrangement, we were not able reliably to detect small increases in the degree of spindle excitation when they were superimposed on an already large excitatory effect.) Thus the present experiments provide evidence against any suggestion that the γ fibres can be divided into two groups differing both in size and in their action on primary and secondary endings, and the question of the innervation of the

histologically distinct types of intrafusal fibres remains for more direct experimental study.

Response to supramaximal stimulation with single shocks

In the first seven of the twelve cats studied rather little attention was paid to the behaviour of the endings during twitch contractions, though the twitch contractions were regularly recorded on a slow sweep speed, as illustrated in Figs. 1 and 2. Such records showed that the discharge of most endings ceased on the rising phase of the twitch, even though a marked A2 response occurred at the same initial tension and the same strength of stimulus on repetitive stimulation (Fig. 1). (During the falling phase of the twitch some endings fired a burst of impulses with all strengths of stimuli, other endings were silent.) Such behaviour on the rising phase was described by Matthews (1933) and is not surprising in view of the slow rate of contraction of intrafusal muscle fibres and of their relative unresponsiveness to single-shock stimulation of γ motor fibres (Kuffler *et al.* 1951; Eyzaguirre, 1960). Matthews also sometimes found that on increasing the initial tension supramaximal stimulation caused the silence of the A2 endings on the rising phase of the twitch to be replaced by an acceleration of the discharge. Such an acceleration may, however, apparently be produced by stimulating α fibres alone (Hunt & Kuffler, 1951*b*; Hunt, 1954; also observed in the present experiments); and in addition α fibre stimulation may excite an 'early discharge' of the spindle afferent at the foot of the contraction (Hunt & Kuffler, 1951*b*; Granit *et al.* 1959*b*). In view of these complications, and as Matthews's classification had been based primarily on the behaviour of the ending during tetanic stimulation, we did not initially feel that it was profitable to attempt to make endings fire on the rising phase of the twitch, and thereby to confirm the results obtained with tetanic stimulation. Very recently, however, Diete-Spiff (1960) in preliminary experiments on the rabbit found that while, with the aid of partial neuromuscular block with succinylcholine, all primary endings could be made to fire on the rising phase of a twitch, secondary endings could never be made to do so, though after giving succinylcholine they could be excited by tetanic stimulation to give responses of an A2 type. He related this to the histological work of Boyd (1959) suggesting that secondary endings lie almost exclusively on small intrafusal muscle fibres which were presumed to give only non-propagated contractions. In the last five experiments we therefore studied more carefully the behaviour of both secondary and primary endings during the twitch.

Secondary endings. By using strong stimuli and an appreciable initial tension we found that 11 out of 24 secondary endings studied in this manner

could be excited to fire one or two impulses on the rising phase of the twitch. A typical example of such excitation is shown in Fig. 9. The effect has a threshold in the γ range and can be attributed to excitation of γ motor fibres; it cannot be attributed to repetitive firing of the afferent fibre induced by the electrical stimulus for the duration of this was 0·1 msec. The threshold was not regularly determined, but it tended to be higher than the A 2 threshold determined with repetitive stimulation, though it was not always as high as that for the ending of Fig. 9. The demonstration of excitation of the ending on the rising phase of the twitch was favoured by increasing the initial tension. Six secondary endings were excited at initial tensions of less than 300 g, while five other endings

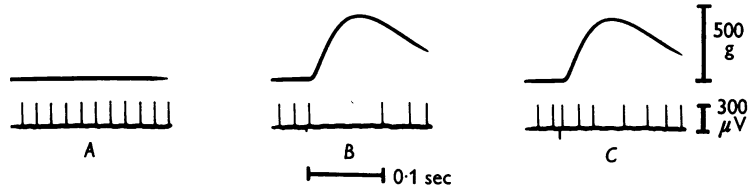

Fig. 9. The response during twitch contractions of a secondary ending (afferent fibre conduction velocity 53 m/sec) which discharged on the rising phase of the contraction when the stimulus was strong. Above, myographic records; below, action potentials recorded on the same sweep speed. *A*, resting discharge at the initial tension of 350 g; *B*, stimulus 4 times α threshold; *C*, stimulus 13 times α threshold. (Records retouched.)

required initial tensions ranging from 350 to 830 g. The remaining 13 secondary endings studied did not show the effect even with strong stimuli when tested with initial tensions of between 300 and 800 g. The effect was best shown when the stimulus was regularly repeated at a rate of 1 or 2/sec, and was often absent from the first of a train of twitches. The conduction velocity of the afferent fibres of the secondary endings which fired on the rising phase ranged from 23 to 65 m/sec, while for those which were silent it ranged from 34 to 66 m/sec.

Primary endings. In contrast with the above results not one of 18 primary endings studied under similar conditions produced any γ-evoked impulses on the rising phase of the twitch with stimuli of 14 times α threshold and initial tensions of about 300 g, approximately corresponding to full physiological extension. (Some had 'early discharges' occurring at the foot of the contraction, and one fired a single spike on the rising phase, but both these effects were produced by stimuli too weak to have excited γ fibres.) For 15 of these endings it was confirmed that they gave normal A 2 responses on repetitive stimulation; moreover it was apparent for 9 of them that the single shock stimulation of the γ fibres had produced

a slight excitatory effect, for the first impulse to be fired on the falling phase of the twitch occurred just perceptibly earlier (about 5 msec) when the stimulus was greatly supramaximal. A number of these endings were tested at initial tensions of up to 500 g without firing on the rising phase. When two were tested at an initial tension of 1 kg one ending fired on the rising phase but the other did not. No doubt more primary endings could have been induced to fire on the rising phase of the twitch by using such large tensions, but this seemed of little value and might have damaged the muscle. (A tension of 1 kg approximately halved the twitch tension, and stretched the muscle well beyond its physiological range.) The interesting finding is that the primary endings of soleus are, in comparison with the secondary endings, extremely reluctant to fire on the rising phase of the twitch; while with tetanic stimulation it is generally easier to demonstrate the excitatory effect of γ fibre stimulation upon primary than upon secondary endings.

Additional results relating to the possible existence of 'α-innervation' of muscle spindles

The question whether or not some muscle spindles are innervated by motor nerve fibres of α diameter is at present controversial. While it is generally agreed that stimulation of α fibres without γ fibres may excite some spindles, the significance of this observation is in doubt. Hunt & Kuffler (1951*b*) and Hunt (1954) distinguished two types of 'α-excitation' of both primary and secondary endings. The first consisted of very varied patterns of discharge of the ending during the rising phase of twitch or brief tetanic contractions. Such discharges were found only when the muscle was under high initial tension, and were attributed to 'tension changes on the spindle produced by the contraction of extrafusal muscle fibres'. Secondly, they described the 'early discharge' occurring at the foot of the contraction and attributed it to the stimulating effect on some spindles of 'early tension changes within the muscle', and not to any specific innervation to the spindles. More recently Granit *et al.* (1959*b*) suggested that the early discharge might consist of two separate components, an initial spike of short latency attributable to ephaptic excitation of the ending (or its afferent fibre) by the muscle action potential, and later spikes attributable to stimulation of the ending by a specific α motor supply to the spindle. In the present experiments both types of 'α-excitation' have been periodically observed for both primary and secondary endings on stimulating the nerve with shocks too weak to have excited γ motor fibres. We do not feel that experiments such as ours can resolve the problem of their interpretation, but certain findings are of interest in this respect.

Early discharges. The 'early discharge' was seen in slightly under half the endings studied. It consisted of 1–4 impulses, was maximally developed with stimuli just maximal for α fibres, and did not increase further on increasing the stimulus so as to excite γ motor fibres. Secondary endings with axons conducting at below 45 m/sec only occasionally had an 'early discharge', and this never consisted of more than one impulse. Otherwise an 'early discharge' was about equally common for primary and for secondary endings. The 'early discharge' was much better shown on stimulation with single shocks, than on repetitive stimulation. On stimulation at 30/sec only two cases were observed in which more than the

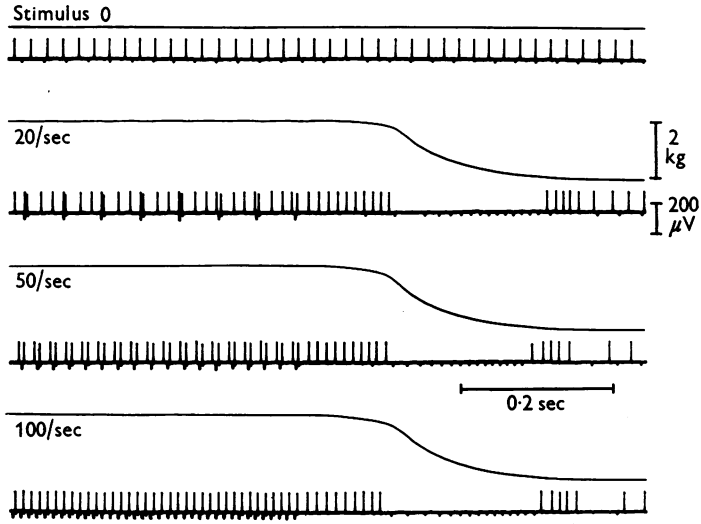

Fig. 10. Four pairs of records showing the typical slight effect, on the intensity of 'α-excitation' of an ending, of altering the frequency of stimulation (primary ending, afferent fibre conduction velocity 98 m/sec). The records show the resting discharge (top), and the last part of tetanic contractions elicited by three different frequencies of stimulation. In each case the myograph record is above, and the action potential record below; they were recorded simultaneously on moving paper. The stimulus intensity was in all cases 1·6 times α threshold, which was slightly supramaximal for contraction but below the threshold of any γ fibres. (In the action potential records the large downward deflexions are the stimulus artifacts; the small downward deflexions are spikes from another ending. Initial tension, 190 g. Records retouched.)

first spike of the early discharge persisted after the first few stimuli (cf. Granit *et al.* 1959*b*), and often the first spike did not persist either (for example see Fig. 6). Any spike of the early discharge which persisted on repetitive stimulation occurred with an almost constant latency just after the spike directly set up by the stimulus. In this it differed from the spikes evoked by γ fibre stimulation, for these appeared rather later with a variable latency, and the two responses could therefore be clearly distinguished. The first spike of the early discharge is probably due to ephaptic stimulation by the muscle action potential (Granit *et al.* 1959*b*), as certainly occurs in the case of motor fibres (Lloyd, 1942; Leksell, 1945; Brown & Matthews, 1960). The failure of the later spikes of the early discharge to persist during tetanic stimulation shows that if these should be due to a true α innervation of the spindle, and not to 'early tension changes' or further ephaptic stimulation, then the excitatory effect of this α innervation is weak in comparison to that of γ innervation.

Occasional 'α-excitation' on low-frequency stimulation. Another pattern of 'α-excitation', prominent only on low-frequency stimulation, was seen in 12 endings (8 primary, 4 secondary) of the 75 which were studied with the full range of stimulus frequencies (most of these also had an early discharge, though this was not maintained on stimulation of 30/sec). This is illustrated in Fig. 10, which shows the response of a primary ending at the end of tetanic contractions elicited by stimuli slightly above maximal for the contraction, but below the γ threshold. The ending fired at a slightly higher rate during the stimulation than at the initial length, and this discharge continued for approximately 100 msec after the last stimulus while the tension in the muscle was still maintained. The interesting and typical feature of this response is that it was barely increased in rate by increasing the frequency of stimulation. This is most clearly shown by comparing the frequencies of discharge in the periods after the last stimuli, but is also shown during the period of stimulation. Comparable insensitivity to increasing the frequency of stimulation above 20/sec was found in all but one of the 12 cases of α excitation and contrasts with the marked effect of increasing the frequency of stimulation of γ efferents. It suggests that the α excitation of the ending results from the contraction of muscle fibres with a low tetanic fusion frequency, in the same range as that of the extrafusal muscle fibres of soleus.

In one exceptional case, that of an ending with an afferent fibre conducting at 49 m/sec, an effect typical of γ excitation, favoured by increasing the frequency of stimulation, was produced by a submaximal stimulus 1·3 times α threshold. The α excitation of this ending was so great that superadded γ excitation could not be detected (it has been included in the series as giving an A 2 response, though its A 2 threshold was not included in Figs. 3 and 8). If such behaviour were at all usual it would have been more frequently observed in the present experiments, for 90 endings were tested with tetanic stimulation just above α maximum (15 were only tested at 70/sec, but the rest were tested with a range of frequencies). We can only suppose that in this case a nerve fibre with an ending on the intrafusal muscle fibres was of α diameter; alternatively it seems possible that a γ efferent fibre had a low threshold for some unknown reason. We do not feel that this exceptional case provides evidence for the existence of α innervation of the spindle on a physiologically significant scale.

Otherwise, the intensity of α excitation of any ending was weaker than γ excitation of the same ending, and was usually weaker than that shown in Fig. 10; in addition, α excitation did not usually produce a discharge continuing so long after the last stimulus as that in Fig. 10. On stimulating at 70/sec it was usually masked by the directly excited spikes, and so did not then interfere with the detection of γ excitation of the same ending. The threshold of the stimulus required to elicit α excitation varied for different endings and was not always sharp, possibly because submaximal stimulation did not always give a steady tetanic contraction and this confused the picture. Precise determination of the threshold was not usually attempted, but it was noted usually to be well below α maximum, and sometimes close to α threshold. In a few cases α excitation was produced by submaximal but not by maximal stimuli. Some other endings, on stimulation of α fibres alone, fired a few impulses on the rising phase of a twitch or of a tetanic contraction, but this discharge did not persist during a maintained tetanic contraction. All these α effects were very dependent upon the initial tension, and were often absent at low tensions.

The certain absence of 'α-excitation' of some secondary endings. It might be suggested that weak α excitation of the endings occurred invariably but was concealed by the antidromic impulses set up by the direct electrical stimulation of the afferent fibres of the endings. For the primary endings such a suggestion cannot be excluded, since their afferent fibres had low thresholds to electrical stimulation, and a maximal muscle contraction could not be produced without exciting them. The threshold to electrical stimulation of the afferent fibres of many secondary endings was, however, rather higher, and it was usually possible to produce a maximal contraction without exciting those conducting at less than 60 m/sec. In this case an excitatory α innervation should be detectable, for if of physiological

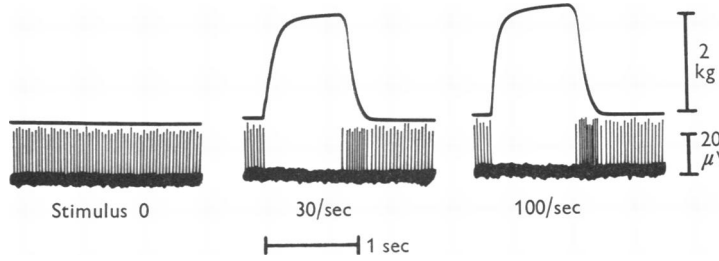

Fig. 11. The response of a secondary ending (afferent fibre conduction velocity 45 m/sec) showing no sign of 'α-excitation' on supramaximal stimulation, even though its afferent fibre was not excited directly. Above, myographic record; below, action potentials on same sweep speed. Stimulus intensity 2·1 times α threshold; a maximal contraction was produced by stimuli 1·3 times α threshold. (The afferent fibre had a threshold to electrical stimulation of 2·3 times α threshold. The A2 response of the same ending, on much stronger stimulation, is shown in Fig. 2. Initial tension 150 g. No stimulus artifacts present, but the period of stimulation can be judged from the tension records. Records retouched.)

importance it would be expected to overcome the unloading effect of the extrafusal contraction sufficiently to cause the ending to fire during a relatively prolonged isometric tetanic contraction. In 14 out of 27 secondary endings tested the discharge at all initial tensions tested ceased completely during a just-supramaximal tetanic contraction. A typical example is shown in Fig. 11. In 6 other endings the discharge always slowed very markedly and in some of these cases ceased when the initial tension was low. In four endings slowing was only slight, while in three, the discharge accelerated (these were among the 12 endings already discussed). The occurrence of slowing, rather than cessation, of the discharge is no evidence for the existence of α innervation of an ending, for the continued response of the ending during contraction might merely indicate that its resting discharge continued in spite of the small rapid release due to the contraction of the muscle. The only objection to accepting this as the sole explanation was the finding that for two of these endings stimula-

tion at 100/sec caused a slightly greater discharge during the contraction than did stimulation at 50/sec. Such an alteration in stimulation frequency causes only a small increase in the extrafusal contraction (Cooper & Eccles, 1930; Buller, Eccles & Eccles, 1960; Matthews, 1959), but this might be different for different parts of the muscle and thereby cause some muscle spindles to be stretched. The main conclusion is, however, that half of the secondary endings with axons less than 10μ in diameter are not excited at all by α motor fibres, and no definite evidence was found for a specific α innervation of the remainder.

DISCUSSION

The principal finding of the present investigation is that virtually all muscle spindle afferent endings will give an A 2 response during tetanic contraction of the muscle, provided that the intensity and frequency of stimulation and the initial tension of the muscle are appropriately adjusted. In Matthews's (1933) experiments only a third of the A endings gave an A 2 response, but most of the other A endings could presumably have been induced to do so if a wider range of stimulating conditions had been used. It may be noted that the modern practice of recording the afferent discharge of the ending from a dorsal root filament, rather than from the muscle nerve as Matthews did, largely eliminates the stimulus artifact which otherwise both hinders the detection of weak A 2 responses and discourages the use of any but the lowest frequencies of stimulation. It remains true, however, that under Matthews's particular experimental conditions some endings did and some endings did not give the A 2 response (see also Cooper, 1959). In the present experiments a greater initial tension was required to elicit an A 2 response from secondary endings than from primary endings, and the resulting response was less marked; in addition, A 2 responses could sometimes only be elicited from secondary endings on using moderately high frequencies of stimulation. The significance of these differences between the two kinds of endings is hard to assess, but they are perhaps related to the relatively high threshold of the secondary endings to stretch of the muscle (Hunt, 1954). Since increasing the frequency of stimulation favoured the production of A 2 responses from both types of ending, there is nothing to suggest that they are excited by the contraction of different types of intrafusal muscle fibres with different contractile properties. In any case, the absence of an A 2 response under some particular set of conditions is no guarantee for the absence of an excitatory effect on the ending. For on stimulating the muscle nerve excitation can only be detected when it is great enough to overcome the artificial threshold created both by the unloading effect of the extrafusal

contraction and by the effect on the ending of the antidromic impulses set up by the electrical stimulation of its afferent fibre.

It might be suggested, however, that a crucial feature of Matthews's A 2 responses was that they were set up by stimuli which were only slightly supramaximal for the contraction, while far stronger stimuli were frequently required in the present experiments. Indeed, Hunt & Kuffler (1951*b*) apparently considered that Matthews could not have excited γ fibres with stimuli of this strength, and consequently attributed his A 2 responses entirely to stimulation of ordinary α motor fibres. The question, however, cannot be decided so definitely, since various reasons can be suggested to explain how Matthews's apparently weak stimuli might have excited γ fibres. In the first place, Matthews gave no information about the relative strengths of the stimuli required to elicit threshold contractions and maximal contractions of the muscle; and it is possible that, while the threshold of the most excitable α fibres was normally low the threshold of the least excitable α fibres approached or even overlapped that of the most excitable γ fibres. This could happen if some fibres in the nerve were slightly damaged under the stimulating electrodes, or might be found in a completely normal nerve if the stimulating electrodes were placed very close to the muscle where some α motor fibres would have subdivided into relatively fine branches (Eccles & Sherrington, 1930). In addition, the stimuli used by Matthews were probably of longer duration than those now in common use, and this might have influenced the relative thresholds of α and γ fibres. It is also possible that he placed the stimulating electrodes on or near a region of nerve which had been partly desheathed, for this was a necessary part of his procedure in isolating single fibres. We found, in three preliminary experiments, that desheathing may markedly lower the threshold of the γ fibres relative to that of the α fibres, particularly for stimuli of long duration. Thus it seems reasonable to suggest that Matthews did excite γ fibres with stimuli which were only slightly supramaximal for contraction, because no other explanation is really acceptable for his production of A 2 responses on increasing the strength of stimuli which were already maximal. This interpretation is favoured by the fact that he found sharp thresholds for the production of the A 2 response. We consider, therefore, that most of Matthews's A 2 responses must have been produced by stimulation of γ motor fibres, and demonstrated the excitatory effect on muscle spindle endings of stimulating the motor supply to the intrafusal muscle fibres.

On the other hand it is possible that those of Matthews's A 2 responses which were obtained with stimuli below maximum for the contraction were due to stimulation of α motor fibres. This was observed in a sixth of the present cases on using low-frequency stimulation, and was previously

described by Hunt & Kuffler (1951*b*) using tetanic contractions of shorter duration. We found these effects to be relatively weak and to behave as if mediated by a system with a low 'tetanic fusion frequency', but this would not have prevented their detection in Matthews's experiments, as he usually employed low frequencies of stimulation. They were, however, often absent at low initial tensions and might not have been prominent in his experiments, particularly as his myograph may not have been as rigid as those now in common use. In any case, such excitation is found for both primary and secondary endings and is adequately explained by supposing that some muscle spindles were stretched by the contraction of extrafusal muscle fibres. Any of Matthews's A 2 responses which were due to this type of excitation are, therefore, probably of little importance (Hunt & Kuffler, 1951*b*; Hunt, 1954), but it cannot be accepted that all his A 2 responses were produced in this way. Moreover, his A 2 responses cannot be equated with the 'early discharge' (caused by stimulation of α fibres), as this consists of a very different pattern of firing, and in the one case in which Matthews observed an early discharge he clearly distinguished it from the A 2 response.

During twitch contractions it proved easier to demonstrate for secondary than for primary endings an excitatory effect of using stimuli strong enough to excite γ fibres. This finding is perhaps related to the magnitude of the decrease of the excitability of the ending produced by the release of the muscle spindle occurring during the extrafusal contraction, which might be expected to be greater for the primary ending. For on slowly releasing a stretched muscle the discharge of the primary ending stops immediately, while that of the secondary ending may continue (Cooper, 1959; Harvey & Matthews, unpublished). The difference in behaviour of primary and secondary endings during the twitch might perhaps be explained by their being differently affected by the contractions of different kinds of intrafusal fibres. In view of the complications introduced by the concomitant extrafusal contraction no conclusion on this point can be drawn from the present experiments; but in the cat it seems very improbable that only primary endings can be excited by intrafusal fibres capable of twitches, as has been suggested for the rabbit (Diete-Spiff, 1960). We are uncertain whether the A 2 responses which Matthews described during twitch contractions depended upon γ excitation of the ending, for in the responses illustrated by him the effect is greater than we have seen. They are similar to those described by Hunt & Kuffler (1951*b*) for α excitation, and moreover were produced by increasing the strength of a submaximal rather than of a maximal stimulus. Matthews's classification, however, was apparently based on the behaviour of the endings during tetanic contraction (1933, p. 21), and twitch contraction may not have been

studied sufficiently systematically to see whether complete agreement with the classification could be obtained by these means. The failure of other workers to obtain a clear distinction between A 1 and A 2 responses with twitch contractions would not then be surprising.

It does not now seem possible to decide upon the distribution of primary and secondary endings between Matthews's two groups (cf. Cooper, 1959, 1960). It certainly seems probable that his A 2 group consisted mainly of primary endings, for these give marked A 2 responses on tetanic stimulation; but his A 1 group probably contained some primary endings as well as secondary endings, for he used relatively weak stimuli ('at least' 30% supramaximal for contraction). Against this view is Matthews's finding that the A 1 endings had a very low threshold to stretch and fired with the least tension on the tendon, while the A 2 endings often had a considerably higher threshold, though never over 10 g (Matthews, 1933, p. 29). The reverse would be expected, as Hunt (1954) found that the threshold to stretch of secondary endings was often much higher than that of the primary endings. Matthews had a few results, based on the relative sizes of action potentials, suggesting that the afferent fibres of A 1 endings were smaller than those of A 2 endings; but his observations were not sufficiently numerous to be applicable to the whole of the series. It may even be questioned whether he studied an appreciable number of secondary endings, as these, unlike the primary endings, are rather insensitive to the rate of application of a stretch (Cooper, 1959), while Matthews's A 1 and A 2 endings were both very sensitive to the rate of stretch. At any rate it seems unlikely that Matthews's division of endings by their A 1 and A 2 behaviour corresponded closely to a division into primary and secondary endings based on measurements of the conduction velocity of the afferent fibres of endings. The classification of muscle spindle endings by their A 1 and A 2 responses therefore seems best discontinued, a view which has already been widely adopted on the basis of the experiments of Hunt & Kuffler (1951*b*).

The fact that all muscle spindle afferent endings may be excited by γ fibre stimulation should not be taken to mean that the γ excitation and control of primary and secondary endings is necessarily identical. The two kinds of endings occupy different positions on the intrafusal muscle fibres, and in initiating the present study we had hoped to confirm a functional difference in the motor control of the endings. We found the A 2 responses of secondary endings weaker and harder to demonstrate than those of primary endings; but both types of endings were excited by stimulation of γ fibres of a wide range of thresholds, and therefore presumably of diameter, and for both primary and secondary endings the excitation appeared to be mediated by a contractile system with a considerably

higher 'fusion frequency' than that of the extrafusal muscle fibres of soleus. Both types of ending were excited on occasion by stimulating α motor fibres alone, and in both cases this could be explained without postulating the existence of a specific α-innervation of the spindle. Thus, though from histological evidence it seems probable that there must be some difference, more fundamental than one of sensitivity, between the responses of primary and secondary endings to intrafusal fibre contraction, it has yet to be demonstrated experimentally.

SUMMARY

1. By recording their discharge from dorsal root filaments the behaviour of de-efferented muscle spindle endings in the soleus muscle of the cat has been studied during tetanic contraction of the muscle elicited by stimulation of the muscle nerve. This was done in order to reinvestigate the classification of muscle spindle afferent endings into two types (Matthews, 1933), according to whether their discharge accelerated (A 2) or slowed (A 1) during supramaximal stimulation.

2. 88 out of 90 endings studied with tetanic stimulation gave an A 2 response when the intensity and frequency of stimulation, and the initial tension of the muscle, were appropriately adjusted. This response was given both by primary and by secondary endings, for the conduction velocities of the afferent fibres studied ranged from 23 to 116 m/sec. If the dividing line of afferent fibre conduction velocity is taken as 72 m/sec (Hunt, 1954), 55 of the endings were primary endings and 35 were secondary endings.

3. A 2 responses could not usually be elicited from secondary endings unless the initial tension was over 50 g, and the tension sometimes had to be considerably higher. Primary endings responded at initial tensions below about 50 g. For both types of endings the A 2 response was favoured by increasing the frequency of stimulation to 70–100/sec, but except for a few secondary endings it was also found on stimulation at 30/sec.

4. The threshold stimulus required to produce an A 2 response was above that required to produce a maximal contraction of the muscle. It was also above the threshold of the most excitable γ motor fibres, which was determined later in the same experiments by recording their compound action potential from a ventral root on stimulating the muscle nerve. The A 2 thresholds of different endings varied considerably, and from a comparison of these values with the thresholds of γ fibres of different conduction velocity it is concluded that both primary and secondary endings may be excited by γ motor fibres of a wide range of diameter.

5. With an initial tension of about 300 g some secondary endings fired

one or two impulses during the rising phase of a twitch, if the stimulus was considerably supramaximal for contraction. At a similar initial tension primary endings did not fire on the rising phase of the twitch contraction, except occasionally when they were so excited by stimulation of α motor fibres.

6. Stimulation of α motor fibres alone (by using weak stimuli) caused, on occasion, two different patterns of excitation of both primary and secondary endings. One was the high-frequency 'early discharge' immediately after the stimulus, while the other discharge was of low frequency. The latter was relatively weak and behaved as if it were mediated by a contractile system with a low 'tetanic fusion frequency'; on stimulation at 70/sec it was masked by the impulses set up by the direct electrical stimulation of the afferent fibre studied and did not interfere with the detection of the A 2 response due to γ excitation of the same ending. The occurrence of such effects does not show whether or not a specific α innervation of the spindle exists for they can be explained otherwise; in any case they were not found for all endings.

7. It is concluded, in agreement with Hunt & Kuffler (1951*b*), that the classification of muscle spindle responses into types A 1 and A 2 lacks simple physiological significance and is best discontinued. It is, however, probable that Matthews's A 2 responses were due to stimulation of γ motor fibres, and demonstrated the effect on muscle spindle endings of the contraction of the intrafusal muscle fibres.

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