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THE SPINDLE MOTOR NERVES TO THE GASTROCNEMIUS MUSCLE OF THE RABBIT

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It was suggested by Merton (1953) that the length of a muscle is set by means of a follow-up servo mechanism. According to this theory, a reflex contraction of a muscle is brought about by the muscle spindles being made to shorten by the intrafusal muscle fibres. This increases the frequency of discharge of the afferent endings in the nuclear bag of the spindles, which in turn leads to a shortening of the main muscle via the myotatic reflex arc. This shortening then continues until the frequency of discharge of the nuclear bag endings falls to its previous level through the unloading of the spindles. Thus the main muscle is assumed to follow the changes in length of the intrafusal muscle fibres. For stability in such a system the length of the intrafusal muscles must be independent of changes in length of the main muscle, brought about by external forces. Hunt's (1951) finding that lightly stretching a muscle inhibits the spindle motor fibres, allowing the intrafusal muscles to slacken, raises a major objection to the follow-up servo theory. For this reason the behaviour of the spindle motor fibres in response to stretching the main muscle has been reinvestigated. Briefly the question is, does the main muscle follow the spindle muscles or do the spindle muscles follow the main muscle?

Our experiments have shown that the motor fibres in the gastrocnemius nerves fall into three groups in terms of their responses to reflex stimulation, drugs and asphyxia. Two of these groups have properties already familiar and correspond to the extrafusal motor and the gamma intrafusal motor fibres. The third group is new. Throughout the description of experiments it will be provisionally referred to as 'type II spindle motor fibres', a procedure which the Discussion will try to justify.

The gamma intrafusal motor fibres were largely unaffected by muscle stretch whereas the type II were always inhibited. If these results are taken together with the known complexity of structure and innervation, both sensory and motor, of the muscle spindles, then it is clear that the follow-up servo process can at best form only a part of a much more complex mechanism.

For a true understanding of the control of muscles more must be found out about the working and possible integrative action of the muscle spindles.

A preliminary account of this work (Pascoe, 1958) has appeared; the present account differs from that in several respects, because further experience has shown that some fibres were originally wrongly classified.

METHODS

Rabbits were anaesthetized with 5% thiopentone sodium solution given by the marginal ear vein, and anaesthesia was maintained throughout the dissection with the same solution given via a polythene cannula tied into the femoral vein of the right side. Both carotid arteries were tied and the trachea was cannulated. The left leg was denervated except for the nerve supplying the lateral gastrocnemius and soleus muscles, and that to the medial gastrocnemius muscle. The central end of the cut sural nerve was separated from the sciatic nerve for stimulating. The sciatic nerve was approached through a lateral incision in the thigh muscles and during recording the wound was filled with liquid paraffin B.P. which had been previously saturated with water. The tendons of the plantaris and semi-membranosus muscles were separated from the Achilles tendon and cut. The Achilles tendon was ligated near its insertion and freed by cutting off the calcaneal tuberosity. The leg was held by three clamps, two on the femur and one on the lower end of the tibia; the clamps were then fixed rigidly to a myograph stand with the preparation lying on its right side. The Achilles tendon was attached to a myograph whose deflexions were displayed on the cathode ray oscilloscope. The gastrocnemius and soleus muscles were stretched by pulling on the myograph by hand. In some experiments the Achilles tendon was not separated and in these instances the muscles were stretched by dorsi-flexing the foot. With the leg fixed and the denervations completed the animal was decerebrated after receiving 5–10 mg of hexamethonium bromide intravenously. The decerebration was made with a sucker through a large, medially placed hole in the skull, and after removing the forebrain the torn arteries at the base of the brain were permanently clipped. The preparation was then allowed to recover from the anaesthetic and the hexamethonium bromide for about an hour. Nerve filaments from either the medial or lateral gastrocnemius nerves were prepared by slitting the nerve sheath with fine scissors, cutting a strand of nerve fibres and separating it centrally for about 15 mm. This filament was then split until unitary activity could be recorded. The potentials were led off with one platinum-wire electrode on the nerve filament and the other side of the amplifier attached to one of the bone clamps, which was also grounded. The potentials were amplified and displayed on a cathode ray oscilloscope (see note, p. 134).

The discharges we have recorded in this fashion were all from fibres which otherwise would have run to the muscle and hence can be presumed to be motor to it, since sensory discharges from the muscle have never been recorded with this technique.

Stimuli were given through twin platinum-wire electrodes connected through an isolating transformer to a conventional square-wave stimulator. The duration of stimuli was 120 μsec and their amplitude could be read from a meter during the experiment.

Nomenclature. Throughout the paper 'spindle motor' or 'intrafusal motor' is used to describe those nerve fibres which activate muscle fibres in the muscle spindles. 'Extrafusal motor' is used to indicate the nerve fibres going to the main muscle fibres, i.e. those responsible for external tension. The term 'sensory' is used to indicate those fibres carrying information to the central nervous system. Nothing further is implied by this adjective. 'Muscle stretch' refers to stretching the soleus and gastrocnemius muscles; the effects described are thus all autogenetic.

RESULTS

The motoneurones to the gastrocnemius muscles are here divided into three groups. First, the extrafusal motor fibres, whose properties are well known; we shall not discuss them except where it is necessary to point out differences in their behaviour from that of the other two groups. These latter are referred to as spindle motor and for convenience named type I and type II. The reasons for this separation from the extrafusal motor fibres and the division into two types should become apparent later in this section of the paper, and they will be referred to again in the Discussion.

Substantially similar results have been obtained from nerve filaments supplying the lateral head of the gastrocnemius muscle and the soleus muscle, and from the nerve to the medial head of the gastrocnemius muscle. The results apply therefore to the gastrocnemius muscles and possibly also to soleus, but of this we cannot be certain.

Type I spindle motor fibres

Discharge pattern. The characteristic pattern of discharge from fibres in this group was a regular and maintained firing lasting up to several hours when the preparation was undisturbed. A few fibres fired irregularly and many others were silent, but these also could be made to fire regularly, e.g. by electrical stimulation of the ipsilateral sural nerve. A discharge was judged as being irregular by eye from the records or by ear from the loudspeaker. No attempt has been made to measure the intervals between impulses and assess their scatter since the immense amount of work involved appeared not to be justified. A characteristic irregularity in the discharges of extrafusal motoneurones is the double discharge (Eccles & Hoff, 1932) in which the impulse interval is considerably shorter than the mean interval (Fig. 2). Discharges of this sort have not been recorded from any of the fibres of this group. In all instances where double discharges have been recorded, or heard with the loudspeaker from otherwise regularly discharging units, further investigation has shown these to be not spindle motor but extrafusal motor fibres. The frequencies of discharge of fibres in this group recorded from undisturbed preparations has varied from 0 to 90 impulses per second, and the frequency of any one fibre has remained fairly constant for long periods.

Reflexes influencing the pattern of discharge. In all twelve instances where it has been employed, electrical stimulation of the ipsilateral sural nerve caused the fibres to fire at an increased frequency, and fibres which in the undisturbed preparation were silent could most easily be caused to fire by this form of stimulation. The nature of the discharge depended upon the excitability of the preparation. In a highly excitable one a single shock to the sural nerve led to a burst of impulses in the spindle motor fibre, followed by contraction of the triceps surae. The discharges in the fibre would then slow or stop, and this was followed by relaxation of the muscle. Occasionally a single shock to the sural nerve caused bursts of activity in the fibre alternating with periods of silence, and this was accompanied by rhythmical contractions of the muscles. In less excitable preparations only the first stage, excitation of the spindle motor fibre discharge, was seen after a single shock to the ipsilateral sural nerve; the increased frequency of discharge seen after the sural nerve shock then died away progressively till the resting frequency was reached. In the least excitable preparations a single shock to the sural nerve produced no discharge, but when the stimulus was repeated several times at about once a second a repetitive discharge of the fibre was seen, which frequently outlasted the period of stimulation for several seconds.

In addition to electrical stimulation of the ipsilateral sural nerve the effects of 'natural' stimulation have been studied. In active preparations stimulation of the skin by lightly stroking the fur caused a rise in the frequency of discharge. This was most noticeable in those fibres which in the unstimulated preparation were silent or discharged at only a low frequency. This rise in frequency after cutaneous stimulation was thought at first to be absent in those fibres discharging at a higher frequency (Pascoe, 1958), but it has since been observed in fibres firing at frequencies as high as 50 impulses per second. The stimulatory effect of lightly stroking the fur on the discharges of spindle motor fibres appeared not to be restricted to any particular skin area. Paradoxically, however, the skin of the ears was the only region from which a stimulatory effect was not obtained, in contrast with the finding of Granit, Job & Kaada (1952). In no instance was inhibition of a spindle motor fibre discharge produced by stroking the fur.

Pinching the skin usually had a similar but quantitatively greater effect than stroking. In particular, the skin of the paws and contralateral heel was very receptive. In two experiments, where pinching the contralateral heel produced a quickening of the discharge frequency and a rise in tension of the gastrocnemius and soleus muscles, the instantaneous frequency and the tension were plotted against time. In both experiments the rise in frequency of discharge preceded the rise in tension in the muscle, in one experiment by 20–30 msec and in the other by 40–50 msec. In the same way the fall in frequency preceded the fall in tension. A rise in tension in the muscle has always been accompanied by a rise in frequency of the type I spindle motor fibre discharges; however, a rise in frequency of the spindle motor fibre discharge is not always followed by an increased tension of the muscle.

In most instances pinching has led to an increased frequency of discharge from the spindle motor fibres, but on several occasions pinching the forepaw has caused a slowing of the discharge. In one experiment where activity of two spindle motor fibres of type I with easily distinguishable action potentials was recorded simultaneously from the same nerve filament, the discharge of one was slowed by pinching the forepaw whereas the discharge of the other was quickened. Pinching the ipsilateral heel quickened both the fibres.

In a few preparations turning the head has had an excitatory effect on the type I spindle motor fibres. Figure 1 is taken from one such experiment. It is not certain whether the effect of head turning was due to true vestibular or neck reflexes or to skin stimulation; one needed only to grasp the head to elicit an increased frequency of discharge of the spindle motor fibre.

The effect of stretching gastrocnemius and soleus muscles on the discharge frequency was studied for twenty-two out of the total of twenty-nine fibres. In every experiment the stretch was the maximum that could be employed. When the Achilles tendon was left attached, the stretch consisted of maximal flexion of the foot. When the tendon was attached to the myograph the tension used was greater than 2 kg.

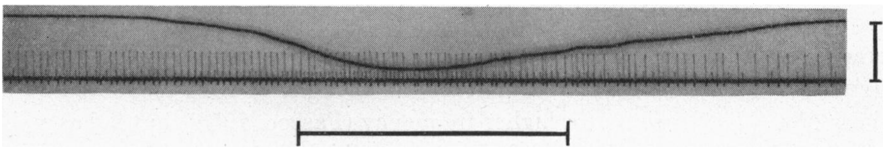

Fig. 1. Discharge of a spindle motor (smaller spike) and an extrafusal motor fibre. The head was turned, jaw towards the left side, producing an increased frequency of discharge of the two fibres and a rise in tension in the muscle. Note a slight tendency for double discharges from the extrafusal motor fibre. Time marker, 1 sec; tension 1 kg; increase in tension signalled downwards.

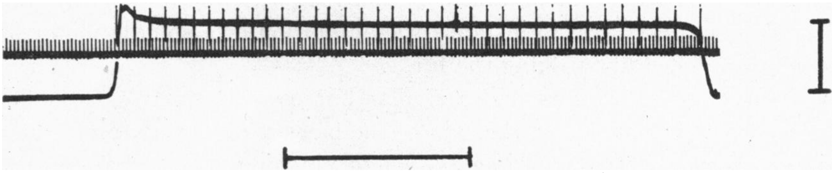

Fig. 2. Effect of stretch of gastrocnemius and soleus muscles on the discharge of a type I spindle motor fibre. Stretch produced no change in the frequency of firing but brought in an extrafusal fibre characterized by its double discharges. Time marker, 1 sec; tension 2 kg; increase in tension signalled by an upward deflexion.

In two fibres the discharge frequency was raised, in each from 13 to 16 impulses per second. The frequency of firing of seven fibres was lowered by stretching the muscles and with the remaining twelve fibres there was no effect (Fig. 2). The discharge frequency of many fibres was raised by muscle stretch, but the effect was not consistently obtained and when it occurred the animal frequently made violent reflex movements, suggesting that the stretch contained a noxious element. The site of this noxious stimulus was not the tendon, since in the three experiments where the tendon was deliberately maltreated by squeezing it with surgical forceps the discharge frequencies were lowered. Moreover, in these instances no reflex movements could be obtained by the most severe crushing of the tendon. It seems likely that the noxious component of the muscle stretch arose from either the skin of the thigh or possibly from the femur. The skin of the upper thigh was definitely not anaesthetic and stretch of the ankle extensors was observed to pull on the cut edges of the skin round the paraffin pool. Attempts to denervate the skin of the upper thigh were not successful. There is no evidence as to the origin of the inhibition by muscle stretch, but the results of tendon stimulation quoted above suggest that the tendon is the likely source.

Discrimination between spindle motor and extrafusal motor fibres. Many of the properties of this group of spindle motor fibres are similar to those of tonic extrafusal motor fibres, and it was necessary to devise a test to decide conclusively in which category to place a tonically firing motor fibre. It was shown by Granit, Pascoe & Steg (1957) and since confirmed by Hunt & Paintal (1958) that the spindle motor fibres are not inhibited by the excitation of anterior horn cells lying in the same segment of the spinal cord (Renshaw, 1941). In the present experiments the ventral roots of the cord were not exposed so that it was not possible to activate the anterior horn cells alone. It was found, however, that by stimulating the whole sciatic nerve in the thigh at a strength just sufficient to cause a twitch of the gastrocnemius muscle, a silent period could be produced in the discharge of extrafusal motor fibres, as is shown in Fig. 3. By the same technique a silent period could not be produced in the discharges of those fibres referred to as spindle motor fibres in the foregoing sections.

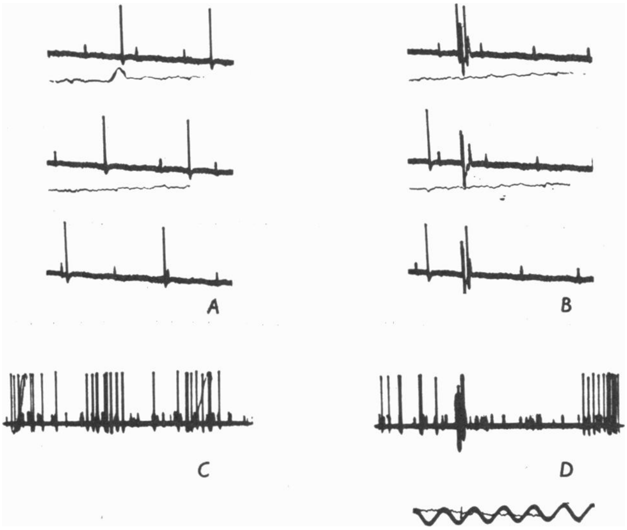

Fig. 3. Discharges of an extrafusal motor and an intrafusal motor fibre. *A*, control, separate sweeps. *C*, control with ten superimposed sweeps. *B*, with stimulation of the ipsilateral sciatic nerve at a strength sufficient to cause a small twitch of the ankle extensors. *D*, as for *B* with ten superimposed sweeps. Note the 80 msec silent period in the discharge of the extrafusal fibre after each stimulus, although the spindle motor fibre discharge was uninfluenced. Time marker, 50 c/s.

A further distinction between the spindle motor and extrafusal motor fibres was that frequently (though not invariably) a single large shock to the ipsilateral sciatic nerve stopped abruptly a tonic discharge in an extrafusal motor fibre, though the same stimulus invariably excited the spindle motor fibres. When a fibre could be stopped in this way it could be restarted by a quick stretch of the triceps surae, confirming that it was an extrafusal motor fibre.

The effects of anaesthetics on the discharge. When ether was administered during a recording from a type I spindle motor fibre a strong stimulatory effect was observed. Fibres already firing steadily were caused to fire at a higher frequency, and fibres which in the undisturbed preparation were silent or fired irregularly now discharged at a regular frequency, as is shown in Fig. 4. In one preparation, ether, ethyl chloride, trichlorethylene and chloroform in turn all caused a quiescent spindle motor fibre to discharge. This effect of volatile anaesthetics is not due to a local stimulatory action on the respiratory tract, since in the few instances where at the start of inhalation there was obvious irritation leading to coughing and sometimes to general movements of the limbs, there was no sustained stimulation of the spindle motor fibre discharge. Thus after a short initial stimulation there was no further effect until usually after one minute of ether inhalation, when a progressive increase in the frequency of discharge developed. That the effect is not due to a noxious stimulation of the respiratory tract is supported by the finding that the stimulatory action is maintained during many minutes of ether inhalation, in such concentration as to abolish all reflexes. It is well known that inhalation of ether stimulates respiration, but it was found impossible to simulate the effect of ether by artificial over-ventilation. It was concluded that the effect of ether was central, and this was confirmed by the finding that urethane had a similar action. Urethane given to a decerebrate preparation was found to increase the frequency of discharge of a spindle motor fibre; successive doses caused increasingly greater effects even when enough was given to stop the respiration.

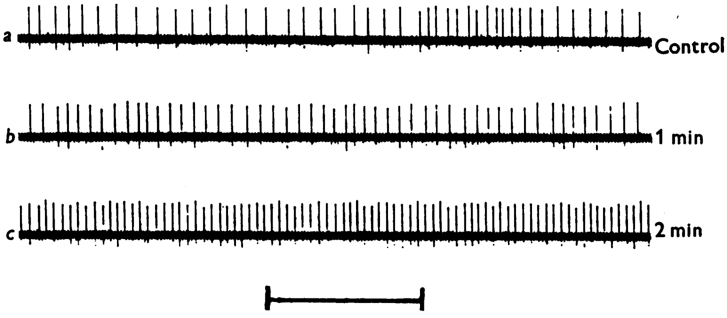

Fig. 4. Discharge of a type I spindle motor fibre. (*a*) control; (*b*) after 1 min; (*c*) after 2 min inhalation of ether; note the increase in the frequency of discharge. Time marker, 1 sec.

In addition to the above anaesthetics, chloralose, hexobarbitone sodium and thiopentone sodium have been tried. These three all caused a lowering in the frequency of discharge of the spindle motor fibres. In the case of chloralose the effect was slow in onset but sustained, whereas the two barbiturates had a rapid action which wore off as was to be expected from the shortlived nature of the anaesthesia produced by these two compounds. An interesting finding was that when thiopentone sodium was given in sufficient quantity to abolish all the reflexes of a decerebrate preparation, the administration of ether had its usual stimulatory action on a spindle motor fibre discharge.

The site of the action of ether has not been determined but it is likely to be supraspinal since the effect of ether on spinal cord reflexes is depressant. Furthermore, in acutely spinalized animals ether produced no stimulation, and the only effect observed was depression of reflex excitability. In two experiments the cerebellum was sucked away without any effect on the ether-maintained discharge. In three experiments the stimulatory action of urethane on spindle motor activity was demonstrated in preparations with intact nervous systems. The animals were anaesthetized with urethane 1·6 g/kg and a filament from a gastrocnemius nerve was prepared in the usual way. A single spindle motor fibre discharge was obtained and then another dose of urethane was given to the preparation. This caused a rise in the frequency of discharge of the fibre similar to that seen in the decerebrate preparations.

Acetylpromazine, 2 mg/kg intravenously rapidly stops this type of fibre discharging, and the effect is maintained for long periods. The reflex excitability of these fibres and of the preparation generally is lowered by this drug (cf. Henatsch & Ingvar, 1956).

The effects of hypertensive drugs. Rise of blood pressure produced by injections of $50\,\mu g$ of adrenaline intravenously or of 5 units of vasopressin had little effect on the frequency of discharge, but in some experiments caused a definite slowing. Excitation has not been seen with these drugs.

Type II spindle motor fibres

In this group have been placed those fibres with discharge characteristics different from those of both the type I spindle motor fibres and the extrafusal motor fibres. There is no direct evidence that the fibres of this group do in fact innervate the intrafusal muscles. All that can be said is that their properties are different from the fibres going to the extrafusal muscle fibres. This point will be raised again in the Discussion.

Discharge pattern. This was irregular, as is shown in Fig. 5. Double or even treble discharges occurred but there was never any sign of a regular discharge frequency. In all, eleven spontaneously discharging fibres come into this group and only in the case of two of them was it possible to influence them reflexly; in both instances stimulation of the ipsilateral sural nerve gave rise to a single discharge with a latency of 10 msec. The two fibres could not be made to fire repetitively no matter how strongly the sural nerve was stimulated. One of these fibres could also be made to give a short burst of impulses by a strong pinch of the ipsilateral forepaw. One other fibre could not normally be made to fire by reflex stimulation, but after 80 sec of artificial over-ventilation a sharp pinch of the ipsilateral forepaw gave rise to a burst of impulses at about 200/sec and lasting approximately 2 sec. This effect was repeated many times, but pinching the forepaw did not invariably cause a discharge even though the animal gave violent reflex movements after each stimulus. To sum up, it can be stated that the majority of the fibres in the group could not be influenced reflexly and that those which could be required strong stimulation.

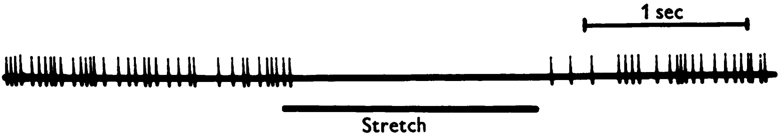

Fig. 5. A type II spindle motor fibre discharge showing its complete inhibition by stretch of gastrocnemius and soleus muscles; note the irregular pattern of firing.

It was seen that a rise in frequency of discharge of a type I spindle motor fibre was often followed after a short delay by a contraction of the ankle extensors. No such relationship between frequency of discharge and reflex tension in the soleus and gastrocnemius muscles has been observed for the type II fibres.

Effect of muscle stretch. Every fibre in this group was inhibited by stretching the ankle extensors (Figs. 5, 6). The tension required might be high or low. In those preparations with an intact Achilles tendon the liminal stretch was obtained when the foot was flexed so that the angle included between it and the shank was a little less than a right angle. The force required to flex the foot to this position varied with the stiffness of the preparation, so that it would seem that the adequate stimulus for inhibition of the spindle motor fibre discharge is elongation of the muscle and not the tension developed in it.

The effect of muscle stretch on this type of fibre is different from that seen with the extrafusal motor fibres. With these, stretch invariably contains an excitatory component, though it is not always obvious since inhibition of an extrafusal motor nerve discharge is not always preceded by a significant excitation. If, however, the extrafusal fibre discharge can be silenced, for example by an ipsilateral noxious stimulus, or by a sustained pull on the tendon (clasp-knife reaction) then the fibre can be restarted by stretching the muscle. Muscle stretch is, however, for the type II fibres, purely inhibitory, and this is true both for jerks and for sustained pulls.

Effect of anaesthetics. In one experiment the effects of thiopentone and urethane on fibres of type I and type II were compared. A filament from the medial gastrocnemius nerve was found to contain an active type I fibre and also a type II. The type II fibre responded with a single discharge to a stimulus applied to the ipsilateral sural nerve, and the type I fibre gave its usual 'burst' response. Thiopentone sodium was then given intravenously. The first effect was to reduce the number of type I fibre discharges to a single ipsilateral sural nerve volley. When more thiopentone sodium was given, the response of the type I fibre to sural nerve stimulation was completely abolished but the type II fibre still responded and with the same latency as before administering the thiopentone. The effects of the thiopentone were allowed to wear off and the responses of the type I fibre to ipsilateral sural nerve stimulation returned. At this stage urethane was given intravenously and it abolished the response of the type II fibre before it had any action on the type I response. The effect of ether on the type II fibres has not been consistent. In two experiments the discharge was depressed and in two a discharge similar to that produced by asphyxia was seen.

Fig. 6. Discharge of a type II spindle motor fibre induced by 85 sec of asphyxia. Note the irregular pattern of discharge and its inhibition by stretch of the gastrocnemius and soleus muscles. Increasing tension signalled as a downward deflexion.

The effect of asphyxia. In six preparations it was observed that a type II fibre discharge could be evoked by tracheal occlusion for 60–90 sec. Sometimes the fibre did not discharge until after the trachea was opened again. In all cases where the effect was seen it was very rapidly progressive, as in Fig. 6. In the early stages of the response, before the frequency had risen too high, it could be abolished or slowed by stretching the ankle extensors; but when the frequency had risen to 200 impulses/sec muscle stretch no longer had any noticeable effect. When the mean frequency lessened towards the end of the discharge stretching the muscle again caused clear-cut inhibition. In preparations which responded in this way to asphyxia the effect could be repeated many times. The effect of asphyxia was due to anoxia, since ventilating the preparation with pure nitrogen from a Starling Ideal pump produced the same effect. The effect of asphyxia was not blocked by previous administration of acetylpromazine 2 mg/kg. The extrafusal motor fibres are also stimulated by asphyxia of the preparation after an initial depression, but the discharge of these fibres cannot be inhibited by stretching the muscle.

The effect of hypertensive drugs. In some instances the fibres have been made to discharge by the administration of large doses of adrenaline, 50–100 μg intravenously. Smaller doses appear to be without effect. Vasopressin 5 i.u. intravenously was usually more effective than adrenaline and the effect, like its hypertensive action, was longer lasting. In no instance was the blood pressure measured, but the rise produced was usually sufficient to cause apnoea. The effect of these drugs on the extrafusal motor fibres was to depress the discharge. No stimulation of the type II spindle motor discharge was obtained by pulling on the carotid arteries.

The relative sizes of the fibres in the two groups

No attempt has yet been made to measure the conduction velocities of the fibres in the two groups, but there is no doubt at all that the type II fibres are larger than the type I. The type I fibres have action potentials very much smaller than those of the extrafusal motor fibres and this finding has been consistent throughout the work. The type II fibres have action potentials of about the same size as the extrafusal motor fibres. The type I fibres without doubt belong to the gamma group of motor fibres and the type II probably to the alpha. In only seven experiments have we seen discharges from the two groups on the same filament, but in all seven the type II discharge has had the larger action potential. In the more recent experiments we have noted that in order to obtain a type II discharge it is best to take a relatively large nerve filament, about a quarter to a half of the medial gastrocnemius nerve. With such a filament the type I discharges are confused in the background noise, though they can be heard in the loudspeaker. To record the potentials from a type I fibre a quite fine filament of nerve is necessary.

It is our opinion that there are probably more of the type I fibres than of the type II, but this may be merely a reflexion of the difficulty of exciting the latter. With a low, mid-collicular, decerebration, the type I fibres are extremely active and it is frequently difficult to split a nerve filament finely enough to see a single fibre discharge. A low decerebration does not seem to increase the activity of the type II fibres, but of this we cannot be certain, since so few of the fibres have shown spontaneous activity.

DISCUSSION

The results show that excluding activity in the motor fibres to extrafusal muscle there can be recorded from the remaining motor nerve fibres to the gastrocnemius muscle two distinct types of discharges. From the differences in amplitude of action potential, the reactions to stretching, anaesthetics and anoxia, it is clear that these two types of discharges come from two separate systems of nerve fibres. The question which immediately arises is, what are the effector organs motivated by these two systems? In the case of the type I fibres there is no doubt that these are the gamma motor fibres studied by Leksell and subsequent workers. The gamma motor neurones are motor to the intrafusal muscle fibres, and their activation leads not to the development of tension in the muscle but to an increased frequency of discharge of the spindle sensory fibres (for a review, see Granit, 1955).

What then is the function of the type II fibres? There is the possibility that they are motor to the extrafusal muscle fibres, since their action potentials are of a comparable amplitude. Against this idea is the fact that the characteristic discharge pattern of the type II fibres has never been recorded with concentric needle electrodes from motor units in the muscle.

Stretching the muscle leads invariably to inhibition of the type II fibre discharge, and it has not been possible to reveal any excitatory effect of stretching whatsoever. This was true for quick stretches as well as for sustained pulls on the muscle, and thus the possibility is eliminated that the type II fibres are identical with the phasic or tonic alpha motor neurones of Granit, Henatsch & Steg (1956). If the type II fibres are motor fibres to extrafusal muscle then we must consider them a distinct group of extrafusal motor fibres unavailable to the myotatic reflex or the tendon jerk, but showing strong autogenetic inhibition. At the moment it seems more profitable to consider the type II fibres as another motor pathway to the intrafusal muscle fibres. Boyd (1958, 1959) has shown histologically and with some physiological support that there are two types of muscle fibres in the muscle spindles of the cat. The one type has discrete end-plates and the other has the 'all over' innervation characteristic of the slow tonic muscles of the frog. The existence of two types of muscle renders a dual motor innervation to the spindle likely. In addition, Barker (1948) noted that one pole of a muscle spindle may receive its motor innervation from several small nerve fibres, whereas the other pole of the same spindle is supplied with only one large fibre (see also Cooper & Daniel, 1956). The diameter of this fibre is twice that of the small fibres and if this ratio is maintained in the motor nerve then the larger fibres could be those of type II.

We have not determined conduction velocities of the type II fibres, so it is not possible to conclude that they are alpha fibres; but it can be stated with certainty that their action potentials are of similar amplitude to those of extrafusal motor fibres when these are recorded from the same nerve filament. Matthews (1933) obtained evidence of intrafusal muscle fibre contraction with stimuli to the motor nerve only 10% greater than that necessary to cause a maximal twitch of the muscle. This was repeated by Hunt & Kuffler (1951) although they interpreted the results differently. Granit, Pompeiano & Waltman (1959) have concluded that some spindles have an alpha motor neurone innervation. They were unable to decide from their results whether this was from collaterals of extrafusal motor fibres as has been shown for amphibia (Katz, 1949), or whether it was a specific motor supply to the spindles. The present results suggest that the latter interpretation is correct.

The most reliable criterion for identifying the type II fibres has been their inhibition by light stretch of the muscle. This raises the question, which receptors in the muscle are responsible for the inhibition? There are three possibilities, nuclear bag or myotube endings on the muscle spindles, and Golgi tendon organs. We are inclined to exclude the latter because the tension required is not high, and it is our impression that the degree of extension of the muscle is the stimulus, and not the tension developed. This is supported by the results of Henatsch & Schulte (1958) who reported that some spindle motor fibres can be inhibited by giving succinylcholine intravenously to the preparation. It is known that succinylcholine stimulates the spindle receptors and not the Golgi tendon organs (Granit, Skoglund & Thesleff, 1953) so it is possible that the inhibition seen by Henatsch & Schulte arose from the spindles. It must be pointed out that in their experiments the succinylcholine was given intravenously and so presumably produced a generalized excitation of spindle receptors all over the body, whereas in our experiments the inhibition of spindle motor discharge was strictly autogenetic.

Before trying to decide which of the spindle receptors are the more likely source of the inhibition, we must first look a little into what is known of the innervation of the spindles. As was stated above, Matthews (1933) was able to activate the nuclear bag receptors by stimuli to the motor nerve as little as 10% above the strength necessary to produce a maximum muscle twitch. In the same paper he reported that he was unable to activate the myotube endings with stimuli at least 30% supramaximal. This remained the position until 1954 when Hunt (1954) showed that the myotube endings could be caused to fire by small-motor-nerve stimulation. This suggests that Matthews failed to excite the myotube endings because the stimuli he used were too weak to excite the small motor fibres. There is thus some evidence that the myotube endings lie on muscle innervated by gamma fibres but not by alpha fibres. The results of Boyd (1959) support this idea. He states, 'secondary sensory innervation occurs on the small muscle fibres almost exclusively'. Thus if we take the results of Matthews (1933), Hunt (1954) and Boyd (1959) it seems likely that in the compound muscle spindles the large muscle fibres are innervated by large motor fibres and the activation of this system leads to a discharge of the nuclear bag endings alone; the small muscle fibres are supplied with small motor fibres and activity in this system leads to the discharge of the myotube endings and probably the nuclear bag endings as well. This is all highly speculative and we must await the results of studies on isolated muscle spindles before it can be decided whether it is an accurate picture of the complex motor and sensory innervation of the muscle spindles.

The results of Hunt & Kuffler (1951) and of Granit *et al.* (1959) show, however, that activation of alpha motor neurones causes a discharge of the nuclear bag endings. One would not expect this sensory discharge to be inhibitory to the same motor neurones; such a high degree of negative feedback would be difficult to interpret. We suggest therefore that the myotube endings are the receptors responsible for the autogenetic inhibition of the type II fibre discharge.

SUMMARY

1. A study has been made of the motor discharges in single units to the gastrocnemius muscles of the decerebrate rabbit. Excluding the discharges of the extrafusal motor fibres there are two types of discharge pattern which we have, for want of a better name, called type I and type II. We have assumed these fibres to be spindle motor fibres.

2. The type I fibres have a regular discharge pattern. This is easily affected, usually increased, by skin stimulation. An increase in the discharge frequency is frequently followed by a rise in the tension of the gastrocnemius muscle. Stretching the gastrocnemius muscle has little effect on the frequency of discharge of these fibres. Ether and urethane increase the frequency of discharge; chloralose, thiopentone, hexobarbitone and acetylpromazine depress the discharge.

3. The type II fibres have an irregular discharge pattern and can only be influenced with great difficulty, if at all, by skin stimulation. Stretch of the gastrocnemius muscle strongly inhibits the discharge. The discharge is powerfully facilitated by asphyxia, by anoxia or by adrenaline or vasopressin in large doses.

4. The type II fibres have larger action potentials than the type I and it is assumed that the type II fibres belong to the alpha group. The action potentials of the type II fibres are of similar amplitude to the extrafusal motor fibres.

5. The results are discussed in relation to what is known of the spindle motor innervation.

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Note added in proof. After this paper was accepted for publication it was discovered that the left leg was not completely denervated, as was stated in Methods. Throughout the work the nerve to the short head of the biceps femoris muscle was intact. We have since done more experiments taking care to cut this nerve and have shown that the inhibition of discharge of the type II fibres produced by pulling on the Achilles tendon is still present. As an additional control it has been shown that the inhibition disappears when the nerves to the gastrocnemius and soleus muscles are cut. There is therefore no doubt that the inhibition of the type II fibres is autogenetic.