THE EFFERENT REGULATION OF THE MUSCLE SPINDLE IN THE FROG

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(With Eleven Text-figures)

Matthews's experiments (1931a, b) have established that the muscle spindle of the frog contains a sense organ which responds to stretch and ceases to respond when the surrounding muscle fibres shorten. In addition, the spindle is known to possess a motor supply of its own, a bundle of small striated 'intrafusal' muscle fibres. These fibres run through the spindle capsule (Barker, 1948; Katz, 1949, fig. 1) where they establish intimate contact with the sensory nerve, while being separated by a lymphatic space from the 'extrafusal' tissue. These muscle fibres are said to lose their striations at the region of contact with the sensory terminals. The anatomical arrangement suggests that the intrafusal muscle bundle pulls directly on the stretch receptor, in contrast with the ordinary muscle fibres which will release the tension on the sense organ if they shorten. A contraction of the intrafusal muscle fibres, therefore, must affect the response of the stretch receptor in a manner very different from that of the surrounding mass of 'extrafusal' fibres. The function of the intrafusal muscle fibres is believed to be a regulation of mechanical 'bias' on the sense organ, but little is known concerning their motor innervation and the physiological conditions under which they are thrown into activity.

Matthews (1931b) obtained evidence in a few experiments which suggested that the intrafusal muscle fibres are innervated by separate motor axons of high threshold and small diameter. More recently, Tasaki & Mizutani (1944), Tasaki & Tsukagoshi (1944) and Kuffler & Gerard (1947) have investigated the properties of small motor nerve fibres which supply many frog muscles and observed that these axons produce a slow local potential change in the muscle which is wholly different in character from the usual propagated muscle spike, and which is accompanied by a slower type of contraction. Kuffler, Laporte & Ransmeier (1947) found that the maximum tetanus tension evoked by the small axons was about 10–15% of the normal twitch tension, and they suggest that the small axon system may be used for the maintenance of peripheral 'tonus'. In view of Matthews's (1931b) work, however, there is an alternative possibility, namely that the atypical muscle responses described by Kuffler and his colleagues arose in the intrafusal motor system, and that their function was to regulate the response of the stretch receptor.

To decide between these two propositions, it is necessary to record the activity of nerve and muscle fibres simultaneously and to study the effect on the afferent discharge of the different types of motor axons. If it be true that the small, high-
threshold axons supply the intrafusal muscle fibres, and the large, low-threshold motor axons innervate the rest of the muscle, then one should expect the pattern of response shown in Table 1.

**Table 1**

<table>
<thead>
<tr>
<th>Motor axon spike</th>
<th>Stimulation of large motor axon</th>
<th>Stimulation of small motor axon</th>
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<tbody>
<tr>
<td>Muscle action potential</td>
<td>Large size, high speed</td>
<td>Small size, low speed</td>
</tr>
<tr>
<td>Propagated, diphasic spike, large and brief</td>
<td>Non-propagated, mono-phasic, potential, small and long-lasting</td>
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<tr>
<td>Large twitch</td>
<td>Weak and relatively slow contraction</td>
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<tr>
<td>Silent period during rise of twitch (i.e. for about 40 msec. at 20° C.)</td>
<td>No silent period but numerous impulses during rise of contraction</td>
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<td>Afferent discharge from stretch receptor</td>
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Thus, stimulation of the small axons should result in an outburst of sensory impulses, while stimulation of the ordinary motor fibres should be followed by absence of, or a 'gap' in, the afferent discharge (Matthews, 1931b).

The results of the present study were contrary to these expectations: the 'silent period' of Matthews was confirmed if the muscle was allowed to shorten freely, but under isometric conditions the ordinary motor impulse was followed by an immediate sensory discharge, and evidence will be presented to show that this was due to the excitation of intrafusal muscle fibres by branches of the large motor axons. On the other hand, small motor axons were found in many cases which elicited the peculiar local responses described by Kuffler & Gerard (1947) without producing sensory discharges. This made it impossible to regard the small axon system as an integral part of the spindle apparatus, although there was evidence in some experiments that branches of the small motor axons may provide an additional nerve supply to the intrafusal muscle fibres.

The conclusions arrived at in this paper are based on physiological evidence. By fine gradation of electric stimuli and of blocking currents applied to the nerve trunk, different types as well as individual motor axons can be separated, and by a simultaneous recording of the electric responses of nerve and muscle, it is possible to trace the intramuscular pathways of the various axons and to analyse their functional connexions. Such an analysis requires verification by histological methods: the anatomical relationship of the nerve endings is being studied by Prof. J. Z. Young and will be described separately.

**METHOD**

The method of stimulating and recording is shown in Fig. 1. The amplifier was used with condenser coupling, the deflexion to a rectangular input declining to one-half in 0.5 sec. The stimuli consisted of single or double thyatron discharges of short duration (time constant less than 50 μsec.) applied to the sciatic nerve or to the roots of n.spin. IX or X. A constant current was applied through a more distal pair of Ag-AgCl electrodes to block the large axons. The possibility of separating nerve fibres of different size by their different thresholds to stimulating and blocking currents is well known and has been used successfully by others (see Kuffler
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By controlling the intensities of both currents, it was often possible not only to separate the large and small axon groups, but to select individual fibres within each group (see for example Figs. 5, 9, 11 below). In the following the terms ‘large’ and ‘small’ motor axons will be used to distinguish between the groups of nerve fibres which are responsible, respectively, for the classical muscle spike and the slow non-propagated response described by Kuffler & Gerard (1947). The distinction between the two types of muscle response is much more striking than that between the size of the nerve fibres concerned, but for convenience the terms ‘large’ and ‘small axon effects’ will be retained.

The present method of recording (Fig. 1) allows nerve and muscle action potentials to be seen side by side. There was no ambiguity about the nature of any individual action potential: whether it was a muscle spike or an end-plate potential, an afferent or efferent nerve impulse could be decided from the electric sign of the oscillograph deflexion, from its latency and time course, and when necessary was verified by further checks, for example, by placing both recording leads on nerve or muscle only, or reducing the nerve supply, or stimulating, and recording from, spinal roots. The method of simultaneous nerve and muscle recording was so satisfactory that additional registration of the mechanical response became unnecessary. The weak contraction which followed a single impulse in a small motor axon was observed with a binocular microscope.

The preparation was the M. extensor longus dig. IV of English *Rana temporaria*. The muscle is approximately 15 mm. long and consists of parallel fibres running from end to end. It contains two or three intrafusal bundles, each composed of a number of small fibres along which several spindles are distributed in series (Young, 1949). These structures occupy only a small percentage of the total cross-sectional area of the muscle, most of which is taken up by 50–60 fibres, of diameters varying between 10 and 100 μ (Katz, 1948). The muscle is supplied by about a dozen nerve fibres of which three or four are sensory axons, each contacting one or
several muscle spindles. The nerve is a branch of N. peron. lat. which approaches the proximal half of the muscle and divides into two or three twigs before entering it. Occasionally, a sensory twig containing one to three axons leaves the N. peron. lat. at a point a few millimetres proximal to the departure of the main muscle nerve. In some frogs, there was evidence of a few motor axons running in the N. peron. med. and joining the muscle via a connecting branch. In the later experiments, therefore, care was taken to preserve the peroneal nerve plexus, but the results did not differ from those obtained after removal of the medial branch. The preparations were fixed and stained with osmic acid after the experiment, and it was checked whether any nerve fibres had been accidentally cut during the dissection. In some preparations, the nerve supply was intentionally reduced by severing branches until one or two motor and one or two sensory axons remained. In a number of experiments, ventral and dorsal roots of N. spin. IX and X were stimulated separately, and on one occasion, the roots were also used for recording the discharge of afferent impulses from the muscle.

The preparation was mounted in paraffin oil, the tendons of the isolated muscle being gripped by a pair of screw-controlled forceps. In some experiments, one end of the muscle was connected to a light spring so that shortening was permitted with only a slight rise of tension.

When it was desired to apply a curarine solution, a watch-glass was mounted below the muscle, and the preparation was lowered into the solution and soaked until nerve stimuli failed to elicit visible contractions.

The results are based on thirty-eight experiments made during February–September 1948, at temperatures of 13–22°C.

RESULTS

A. The influence of the large motor axons on the muscle spindle

(1) Normal muscle

If two recording electrodes are placed on the muscle, at the region of the nerve entry and the end respectively, and the nerve is stimulated with shocks of increasing intensity, a threshold is reached at which a large muscle spike is recorded. With further increase of the stimulus strength, the spike remains unaltered until the threshold of another motor unit is reached and a step-like increase in the response occurs. There are usually three or four of these threshold 'steps', all within a twofold to threefold range of shock intensities. If one recording electrode is placed on the nerve, as in Fig. 1, the same muscle spikes are seen, but they are preceded by a brief nerve volley travelling into the muscle, and followed by afferent nerve impulses coming from the muscle. The direction of travel is evident from the sign of the deflexion, the large first phase of the spike being always due to a potential drop at the electrode which is first approached by the impulse.

Fig. 2 illustrates an experiment, at 20°C, in which the muscle was under slight resting tension (about 0.1 g.), its ends being immobilized by pairs of holding forceps. The background discharge of several stretch receptors is seen in the second and
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third record. When a shock was applied to the nerve, just strong enough to produce a twitch, the shock artifact (S) was followed by: (i) a descending nerve volley (N₁, downward spike); (ii) a large diphasic muscle spike (M, only partly visible); and (iii) a burst of afferent impulses (Nₛ) beginning at about 7 msec. after the muscle spike. The latency and time course of the twitch which is associated with the spike is well known; according to Sandow (1947), the rising phase lasts about 35 msec. and the total twitch about 150 msec. in a frog's sartorius at 25°C. It is clear,

![Fig. 2. Electric response of nerve and muscle. In (a), a threshold stimulus has been applied to the motor nerve fibres. In (b), the afferent discharge from the resting muscle is seen. For further explanation see text. Note. The records in all figures of this paper read from left to right, but the direction of the spike deflexion varies in different illustrations.](image)

therefore, that the afferent discharge in the experiment of Fig. 2 commenced quite early during the rise of tension, and this appears to contrast with the 'silent period' observed by Matthews (1931b). This discrepancy vanishes if the muscle is allowed to shorten. In Fig. 3 the discharge during an isometric twitch is compared with that during free shortening, the resting tension being about 0.1 g. in the latter, and even less in the isometric case. The lower part of the figures shows the initial portion of the response on an expanded time scale. The muscle spike was so large and steep
that only its slow tail can be seen in the reproduction. During the isometric twitch, there is an afferent discharge commencing at 20 msec. after the muscle spike and lasting 70–80 msec. During the 'isotonic' twitch, there is a distinct silent period lasting about 50 msec. and followed by a burst of impulses during the period of mechanical relaxation (possibly accentuated by an overshoot of the lever). This behaviour is the same as described by Matthews (19316), except that he observed the silent period even if the ends of the muscle had been immobilized. Presumably, this residual difference is due to the choice, in the present experiments, of a parallel-fibred muscle in which isometric conditions with a minimum amount of 'internal shortening' can be more nearly obtained than in the pennate muscles previously used. This agrees, in fact, with Matthews's own explanation (19316, p. 162).

It will be noted that the 'silent period' in Fig. 3 B is preceded by a few afferent nerve impulses which started as early as 7–8 msec. after the muscle spike. The latency of these impulses is shorter than in Fig. 3 A, the difference being attributable to the slightly higher resting tension in Fig. 3 B (see following paragraphs).

When the nerve supply had been cut down, an even clearer picture was obtained. In Fig. 4 A the preparation contained one motor and two sensory axons. A threshold stimulus to the motor nerve invariably resulted in an afferent volley, 9 msec. after the electric muscle response. Similar observations were made in every experiment; as soon as the stimulus exceeded the threshold of one of the motor units, a muscle spike was set up followed within 7–20 msec. by the firing of afferent impulses. There were considerable variations in the latency and number of these afferent spikes. If the muscle was slack and background activity of the stretch receptors completely absent, the motor impulse sometimes failed to excite them, or only a single afferent impulse might be produced. But in these cases, a slight increase of resting tension
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sufficed to make the afferent discharges appear after each muscle spike with great regularity. The latency and number of impulses which followed the muscle spike depended evidently upon the background level of excitation at the stretch receptor and could be varied by slight alterations in the resting tension.

These observations make it seem likely that the afferent firing arises from an activation of the muscle spindle by the motor nerve impulse. The mechanism of this process, however, is still obscure, and even the nature of the afferent spikes is still open to question.

First, it must be proved that the afferent discharges are sensory impulses and originate in the muscle spindles. That they are not repetitive motor impulses coming from the nerve endings is shown: (i) by the absence of repetitive muscle responses; (ii) by the fact that they can be recorded from the dorsal roots of N. spin. IX and X, but not from the ventral roots; and (iii) by their dependence upon resting tension and upon the amount of shortening permitted during contraction. The last two observations (Fig. 3) indicate that the afferent impulses arise in the stretch receptors of the muscle. There are three reasons for classifying these receptors as spindles and not as tendon organs: (i) because crushing the muscle near its tendinous ends did not affect the afferent response; (ii) because several spindles but no tendon end-organ could be demonstrated histologically; and (iii) because the discharge stopped during the period of shortening (Fig. 3 B) which is characteristic of a spindle but contrasts with the behaviour of a tendon receptor (Matthews, 1931 a, b; 1933).

The second question is whether the discharge might have been initiated or influenced by the antidromic impulse which was set up in the sensory axon when the whole nerve was stimulated. In some experiments when a differential block was used, the antidromic impulse did not reach the sense organ so that the present question did not arise. In several experiments, the nerve supply was reduced to one or two sensory axons only, and in these cases stimulation of the sciatic nerve produced a single descending impulse, but no afferent discharge. Finally, in four experiments, the spinal roots were dissected and stimulated separately. In all these experiments, stimulation of the dorsal roots produced one antidromic volley but no afferent firing, while stimulation of the ventral roots produced the same sensory discharge as obtained when the stimulus was applied to the sciatic nerve.

Thus, it is safe to conclude that the afferent impulses from the muscle originate in the spindles and that these are activated in some way by the low-threshold motor axons. The next step was to investigate more closely the relationship between motor nerve impulse and spindle activity.

While the sensory firing was always associated with the excitation of a motor unit, not every motor axon produced the effect. In Fig. 5 A, for instance, the sensory nerve supply had been reduced to a single fibre, while the motor supply consisted of four units which could be identified by separate thresholds, spike sizes and velocities and which could be isolated by differential blocking (see Method). The first motor unit produced a large muscle response but no afferent firing until quite late, during the relaxation of the twitch (80 msec. after the muscle spike). This motor axon ($N_1$) was then blocked and the stimulus increased until the threshold of the
next motor unit ($N_2$) was reached. This unit gave a smaller spike response, but led to an immediate burst of sensory impulses. This is an interesting observation because it shows at once that the afferent firing was not the result of muscle activity as such—the response of the muscle to $N_1$ was, in fact, stronger than to $N_2$—but that there are definite relations between the spindles and certain motor axons.

Fig. 5. Afferent response to impulses in discrete motor axons. The preparation contained axons of well-separated thresholds and conduction velocities, illustrated in C. (Descending nerve spikes give upward, ascending spikes give downward deflexion.) A: a burst of afferent discharges follows an impulse in motor axon $N_4$, but not in motor axon $N_1$. B: the same effect after curarization. ($N_1$ is followed occasionally by a small diphasic muscle spike, but not by afferent discharges.)

(2) Curarized muscle

In an attempt to probe further into the nature of this functional connexion, some unexpected evidence was obtained when nerve-muscle transmission was blocked by curarine or fatigue. The important result was that the electrical and mechanical response of the muscle could be drastically reduced without diminishing the afferent discharge.

When the muscle is curarized sufficiently, the descending nerve volley fails to
elicit any response, motor or sensory. But in order to obtain this condition, about
twice the dose necessary for abolition of a visible twitch is required. With an inter-
mediate dose, the descending impulse still stimulates the muscle spindle, although
all visible contractions have disappeared. In the experiment of Fig. 3, for instance, the
muscle remained attached to the light ‘isotonic’ lever while it was immersed in
a curarine/Ringer solution. After the twitch had been abolished, the solution was re-
placed by paraffin oil, and instead of a large diphasic muscle spike of 30 mV., a small
monophasic end-plate potential (e.p.p.) of about 0.35 mV. was now recorded. There
may have been a small residual muscle spike superimposed on the e.p.p., but its am-
plitude was certainly not greater than 100 μV. Thus, although the muscle spike had
been reduced to less than 0.5 % and the contraction apparently had vanished, the
sensory response was undiminished (Fig. 3C). In fact, it was greater than in Fig. 3 B, for
the pause in the response associated with the ‘extrafusal’ shortening had now been
filled in with sensory impulses. Even in the curarized preparation it could be shown,
by the sudden appearance of an e.p.p., that the sensory discharge occurred when the
threshold of a large motor nerve fibre was exceeded.

These observations were confirmed in twenty out of twenty-one experiments in
which neuro-muscular transmission was blocked until no mechanical response could
be detected. The sensory discharge was sometimes reduced (Fig. 5 B), but in other
cases remained unaltered.

Fig. 4 B shows a similar experiment on a 3-axon preparation in which trans-
mision failed because of progressive ‘fatigue’. The response in records 2–4 was
a propagated muscle spike associated with a twitch, while a little later (records 5–8)
the large spike had vanished and only a small potential change remained accompanied
by a minute, apparently local, contraction. Yet the afferent discharge persisted
without change.

If the dose of curarine was slightly increased a stage of block was attained in
which a single motor impulse was ineffective, while two impulses at a short interval
succeeded in firing the spindle, still without producing any visible motor response.
This is illustrated in Fig. 6: at this critical stage, the response of the sense organ
consisted of a whole burst of impulses—or none at all. This in itself is of interest
because it indicates that between the arrival of the motor and the discharge of the
sensory nerve impulses, there is an intermediary event of an all-or-none character
and of a time course much longer than that of the individual nerve spikes.

Some idea of the time course of this event can be obtained by plotting the
frequency of the sensory impulses against time, as in Fig. 7, the start of the e.p.p.
being taken as the time of origin. The rate of the sensory discharge builds up to
a maximum in about 30–50 msec. (19° C.). A similar effect was seen in several other
experiments, in some of which the ventral roots were stimulated so as to avoid any
influence of the ‘anti-dromic’ sensory spike. The possible significance of this
delayed maximum will be discussed below.

It is clear that impulses in large motor axons can elicit a sensory discharge from
the spindle without the intervention of a visible contraction, but it is quite possible
that the contraction of one or a few small intrafusal fibres would be concealed by the
Fig. 6. Facilitation of afferent discharges in curarized muscle. Intervals between nerve stimuli shown in the figure. Note the 'all-or-none' effect at 9.2 and 12 msec.

Fig. 7. The 'building-up' effect of the afferent discharge in a critically curarized preparation (same experiment as in Fig. 6). The frequency of the discharge has been plotted against time, taking the start of the second e.p.p. as 'zero time'. The reciprocal of the interval between two impulses has been taken as a measure of the instantaneous rate half-way between them. Out of eight successive records, three followed curve A, one followed curve B and four showed no response (C).
mass of inactive muscle around them, and yet a minute intrafusal twitch would be a very effective stimulus to the spindle receptors. In spite of their apparent complexity all the results would be satisfactorily explained if branches of the ordinary motor axons supplied the intrafusal muscle fibres, and if the intrafusal motor junctions were a little more resistant to blocking than the rest of the muscle.

It is impossible to predict whether or not the mechanical response of the intrafusal fibres should be noticeable. That they can contract there is no reason to doubt, for occasional spontaneous twitches were observed in preparations in which the sensory apparatus and a portion of the intrafusal muscle fibres had been isolated (Katz, 1949). It is possible that the intrafusal bundle is surrounded by a lymphatic space and an extension of the spindle capsule which would allow the fibres to shorten without mechanically interfering with, nor being hindered by, the surrounding muscle. An arrangement of this kind must be postulated if the intrafusal fibres are to pull freely on the sense organ, but it would also make it more difficult to observe a mechanical effect on the whole muscle.

While the mechanical conditions are not clear, it is fairly easy to estimate the electrical response which the intrafusal muscle fibres can give. There are two or three intrafusal bundles in the muscle, each containing several fibres; the diameter of these fibres is of the order of 10 μ, as compared with 50 μ for the whole muscle (with variations between 10 and 100 μ (Mayeda, 1890; Katz, 1948)). The total cross-sectional area of the muscle fibres, not including extracellular spaces, is about 10^{-4} cm² (average of twelve muscles), the intrafusal fibres taking up less than 3% of this area. The size of the spike would vary approximately with the cross-section of the active bundle, hence the aggregate spike of the intrafusal fibres would be less than 3% of the maximum muscle spike. In a fairly synchronous maximum volley, the spike of the extensor dig. IV is about 40–50 mV, hence the electric response of all the intrafusal fibres would be less than 3% of the maximum muscle spike. In a fairly synchronous maximum volley, the spike of the extensor dig. IV is about 40–50 mV, hence the electric response of all the intrafusal fibres would be less than 3% of the maximum muscle spike. In a fairly synchronous maximum volley, the spike of the extensor dig. IV is about 40–50 mV, hence the electric response of all the intrafusal fibres would be less than 3% of the maximum muscle spike. In a fairly synchronous maximum volley, the spike of the extensor dig. IV is about 40–50 mV, hence the electric response of all the intrafusal fibres would be less than 3% of the maximum muscle spike.
(b) a small muscle spike ($m \cdot 0.45 \text{ mV}$.) followed by a few sensory nerve impulses ($N_a$), (c) a large muscle spike ($M \cdot 1.8 \text{ mV}$.) without sensory discharge, (d) a sum of (b) and (c). Thus, there was a small muscle spike inseparable from a subsequent firing of the spindle, while the large muscle spike had apparently no connexion with the spindle at all. The small spike may well have arisen in intrafusal muscle fibres, and the large spike in ordinary muscle fibres. The amplitude in this case, viz. 0.45 mV., was greater than in other experiments where an amplitude of 0.1 mV. or less was observed, but it is still compatible with the predicted spike of an intrafusal bundle, assuming that a few adjacent fibres may have fired synchronously. In another experiment, a spike of about 60 $\mu$V., which was invariably associated with sensory impulses, was traced in its course along the muscle, and its conduction velocity was found to be 0.64 m./sec. at 17° C. This is about one-third of the highest speed recorded in this muscle (Katz, 1948). According to Offner, Weinberg & Young (1940), conduction velocity in non-medullated fibres, such as muscle, should vary approximately as the square root of the diameter; a ratio of 3:1 for impulse velocities corresponds fairly well to the ratio of diameters found for large ordinary (100 $\mu$) and intrafusal (10 $\mu$) fibres.

Thus, all the evidence is compatible with the suggestion that the afferent firing is due to a contraction of the intrafusal muscle fibres. The evidence is indirect, but it is strengthened by the fact that the afferent impulses, in critically curarized muscle, occur in groups of an all-or-none character, and that the response builds up to a peak in 30-40 msec. which is approximately the time required for the rise of tension in a twitch (Sandow, 1947).

It was also suggested that the intrafusal fibres are supplied by branches of the ordinary motor axons. This was based on the fact that the afferent firing occurred only when a motor unit was thrown into action and that the two responses to a motor nerve impulse, i.e. muscle and spindle response, while not separable by graded stimuli, could be differentiated by progressive curarization. Now, it has frequently

![Fig. 8. Evidence of a residual muscle spike (m) which is inseparable from a sensory discharge ($N_a$). For full description see text.](image-url)
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been stated that the spindles receive an entirely separate motor nerve supply, and this appears to be borne out by observations on mammalian muscle (Matthews, 1933; Barker, 1948). The situation in frog muscle seems to be a special case, and it is important for a full understanding of the spindle function to obtain definite evidence on this point. It might still be argued that the intrafusal and extrafusal nerve supply, even in the frog, is separate and that (a) the motor responses in normal muscle which are associated with a sensory discharge are entirely intrafusal, or (b) that separate motor axons of identical threshold supply intrafusal and extrafusal fibres.

The first objection is answered by the fact that in the non-curarized preparation, the size of the muscle responses, which preceded the sensory firing, was usually much too large (spikes of many millivolts and large twitches) to be accounted for by the intrafusal bundles.

The second possibility is more difficult to eliminate, but it could only have been a chance occurrence, and it is impossible to believe that such a coincidence of thresholds could have happened invariably, in more than thirty experiments.

Moreover, in several preparations the nerve supply had been reduced to two or three axons. In these cases it was easy to count the physiological units of response, both motor and sensory, and compare them with the histological count of nerve fibres. In an experiment like that of Fig. 4, where one motor and two sensory axons had been counted on the oscilloscope, histological examination confirmed that there were only three residual medullated axons, and the possibility of separate large motor axons supplying the intrafusal fibres was, therefore, ruled out.

B. The relation of the small motor axons to the muscle spindle

The previous experiments dealt only with low-threshold large motor axons which produce in the muscle the classical type of propagated response. There is strong evidence for the suggestion that the intrafusal muscle fibres form part of ordinary motor units, but a part which is relatively resistant to junctional fatigue and curarization. This throws some light on the distribution of motor nerves in frog's muscle, but it is also relevant to the original question concerning the relation between the small motor axons (Tasaki & Mizutani, 1944; Kuffler & Gerard, 1947) and the intrafusal muscle fibres. The small axons might provide an accessory innervation, but they are certainly not the sole supply for the motor apparatus of the spindle. Moreover, the small axons produce weak but visible local contractions in the muscle, and it appears from the experiments described in Section A(2), that even fully propagated activity of intrafusal fibres does not cause a visible movement of the whole muscle.

The question, however, can be tested further by studying the motor and sensory response to stimulation of the small nerve fibres.

By increasing the strength of the stimulus to more than three times the threshold of the ordinary motor axons, the local responses described by Kuffler & Gerard (1947) were obtained. With the help of the constant current block or by micro-dissection, the small motor axons could be isolated and their effects on the muscle
studied in detail. Examples are shown in Figs. 9–10. The results confirm those of Kuffler & Gerard (1947); the potential change in the muscle produced by the high-threshold axons resembles the e.p.p. in its slow monophasic shape and its spatial decrement within a length of a few millimetres. Like the e.p.p. in ordinary curarized motor units, it can sum during successive nerve impulses, is reduced by addition of curarine, and is not lengthened by veratrine. It differs from the e.p.p. in other respects; thus, it gives rise to local contractions but usually not to propagated spikes (cf. Kuffler & Gerard, 1947); its duration is rather larger than that of the e.p.p. (60 msec. as compared with 20 msec., at 20° C.), and the potential recorded at a 'focal' point often shows a very slight positive phase which is not seen with the ordinary e.p.p.

There were frequently three or four small axons of separate threshold, each producing a slow potential change in the muscle. The threshold of these axons varied

![Fig. 9. Separation of small axon responses and afferent nerve spikes. In all three cases, the electric response to a small axon impulse (n) consists only of a slow potential change in the muscle, while the response to a large axon (N) consists of a rapid muscle spike and afferent firing.](image)

between 2.5 and 10 times that of the most excitable motor nerve fibre, and the latency of the response, which is largely due to conduction time in the nerve (Kuffler & Gerard, 1947), increased with the threshold.

The size of the muscle response was usually somewhat larger than previously described; with a single nerve impulse the potential change was as much as 3–4 mV., and a weak, rather slow, contraction could be seen provided the muscle was slack. This in itself indicates that more than the intrafusal portions of the muscles are involved, for the combined spike of all the intrafusal fibres would have been less than 1 mV.

When the influence of the small motor axons on the spindles was examined, it was found that approximately 50% of the small axon units did not produce any afferent
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bring, while other units had an effect similar to that previously described (Section A(i)). In eleven out of twenty-one cases, impulses in small axons produced typical local muscle responses without stimulating the stretch receptors. Examples are shown in Fig. 9 which illustrates the sensory background response, the activation of spindles by a large motor fibre, the lack of any additional effect when large and small motor axons were stimulated together, and the absence of any spindle response, in excess of background activity, when the small axon was stimulated alone. Fig. 10 shows an example of a unit which did produce afferent firing. Finally, Fig. 11 illustrates an experiment in which three small axons were identified, of which the first two initiated spindle discharges while the third one did not.

The negative results make it almost certain that the small axon system cannot be a specific part of the spindle mechanism. The original suggestion, viz. that the response to small nerve stimulation might be entirely intrafusal may, therefore, be discarded. The presence of sensory discharges in some cases suggests that branches of small, as well as of large, motor axons can supply the intrafusal muscle fibres, and this would agree with Matthews's (1931b) finding, that in a few preparations the 'silent period' of the spindle was obliterated when the stimulus to the nerve was made very strong.
The real function of the small axon system, and its histological connexions remain uncertain. The present experiments merely eliminate one possible, and a priori quite plausible, role of this system.

DISCUSSION

The main result of these experiments is to show that during active contraction the spindle is subjected to two antagonistic forces: (i) an additional pull exerted by intrafusal fibres which form part of the active motor units; and (ii) a release of tension due to contraction of the 'extrafusal' portions of the muscle. Whether the muscle activity is accompanied by an increase or decrease in the afferent discharge depends upon the balance of these two factors, and this would depend not only upon the external load, but upon the arrangement of the muscle fibres and their physiological condition, fresh or fatigued. It is probable that the type of innervation found in the extensor dig. IV exists in many other frog muscles, in spite of the different pattern of afferent response (Matthews, 1931). It has been suggested that such differences, during 'isometric' contractions, could be due to a different anatomical arrangement of the tendon and a greater or lesser degree of elastic 'compliance' in the active muscle. Preliminary experiments on sartorius muscles and on a strip of M. iliofibularis showed the same sequence of responses as in the extensor dig. IV, i.e. a threshold muscle spike which was followed by an immediate burst of afferent impulses, and there was also evidence in several of Matthews's (1931) experiments that the 'pause' in the spindle discharge is preceded by sensory impulses quite early during the rise of tension, similar to the behaviour illustrated in Fig. 3B. In the present experiments, the spindle response during activity in most of the motor units followed a simple pattern: when there was a mechanical obstacle which the muscle could not move, the afferent discharge was boosted. On the other hand, when the muscle was able to shorten, the sensory discharge stopped. One would expect that any reflex initiated by the proprioceptors of this type of muscle would be enhanced during the ensuing motor action until the mechanical obstacle is overcome. According to Kato (1934, p. 116) the sensory impulses from frog muscle inhibit the excitation of antagonists. Thus, when an extended muscle of the frog is thrown into action, the simultaneous response of its intrafusal fibres would ensure that any excessive resistance of its antagonists is overcome. If the spindle of the frog, like its mammalian counterpart, served the more general purpose of eliciting stretch reflexes, then it will not only start, but maintain the reflex discharge until shortening occurs. Even in the shortened muscle, the spindle tension would not fall very much below the firing level, because the intrafusal bundle has also been thrown into activity.

It is difficult to see why intrafusal motor junctions should be more resistant to fatigue and curarization than the other nerve-muscle junctions. Yet, the striking observations in Section A(2) can hardly be explained in any other way. The matter may depend upon the relative sizes of nerve ending and muscle fibre: perhaps the safety margin in neuro-muscular transmission is greater the smaller the muscle fibre?
SUMMARY

The motor innervation of the muscle spindle of the frog is investigated by recording simultaneously the responses of muscle and nerve when individual axons are stimulated.

There is evidence that intrafusal and ordinary muscle fibres receive a common innervation and that, as a result, the discharge from the spindle is intensified during isometric contraction, but is stopped when shortening occurs.

When the muscle is curarized progressively, a state is reached in which all visible contractions are abolished, yet the spindle continues to respond to a motor nerve impulse with a train of afferent spikes. When the block is intensified, all indirect responses to nerve stimulation fail. Closer study of this effect suggests that the spindle response arises from a twitch of the intrafusal muscle fibres, and that the intrafusal motor junctions are more resistant to curarine than the ordinary junctions.

The existence of an accessory motor system in frog muscle, which is supplied by small axons and characterized by a slow non-propagated response, is confirmed. There is no evidence for any specific connexion between the small motor axons and the muscle spindles, although frequently branches of these axons appear to innervate intrafusal as well as other parts of the muscle.

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