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THE RESPONSE OF A MUSCLE SPINDLE DURING ACTIVE CONTRACTION OF A MUSCLE.

By BRYAN H. C. MATTHEWS (*Beit Memorial Fellow*), *Fellow of King's College, Cambridge.*

(*From the Physiological Laboratory, Cambridge.*)

A previous paper [Matthews, 1931] described a series of experiments on the behaviour of a single stretch receptor in a frog's muscle: in these experiments the response of the end organ during passive stretching was investigated by observing the action potentials in the nerve supplying this muscle. The present paper describes a further series of experiments made to determine how these end organs respond when the muscle contracts actively.

Method.

The single end organ preparation from the frog's toe, described in detail in the previous paper, was used in the majority of the present experiments. It has been shown that the stretch receptors in these preparations are muscle spindles; and this was confirmed by methods already described [see Matthews, 1931] in several of the preparations used in the present work.

An amplifier and oscillograph which have been described in previous papers [Matthews, 1929] were used to record the action potentials from the nerve, but the system had to be modified to deal with special difficulties which arise when an attempt is made to record sensory action potentials while the tissue is also being stimulated electrically.

The action potential at the electrodes when a single fibre in the nerve of this preparation conducts an impulse amounts to about 20–30 microvolts. If the nerve is stimulated electrically all its fibres are active and produce 10–20 millivolts at the electrodes: the recording system must be used at full sensitivity to record the sensory action potentials, but yet must not be disturbed by the potential 1000 times as great which occurs when the nerve is stimulated. The recording instrument is unbreakable and there is no risk of damage from the 1000 times overload, but this overload is so great that the later valves in the amplifier have

such large potential changes impressed on their grids that a considerable grid current flows for a few thousandths of a second during the overload: as a result the grids become charged, and for a fraction of a second the later valves in the amplifier are out of their working range, and during this time the sensory action potentials cannot be recorded.

It is impossible to avoid this large potential occurring at the recording electrodes whenever the nerve is stimulated electrically: hence the only solution is to make the valves of the amplifier incapable of holding any grid charge that they may acquire. This can be done either by reducing the capacity in the grid circuit or by increasing the leakage to earth: for a number of reasons the former is the better course to adopt. In the present work very small coupling condensers were used throughout the amplifier, various values were tried, but in most of the experiments capacities of 0·001 mfd. were used. The result is that however great the potential occurring at the input may be, the instrument cannot be driven off its working range for more than a few thousandths of a second. The sensory action currents are somewhat distorted by the use of these small condensers and often appear polyphasic as a result: but these distortions do not in any way affect the present work as no attention is paid to the shape of the action potential waves, which are merely required to show when the sensory impulses travel past the electrodes.

Gasser and Erlanger [1930] have also used an amplifier in recording very small electrical variations immediately after much larger ones have occurred; they do not mention the above difficulty although excessive grid swings probably occurred in their amplifier; their calibrations show, however, that their system returned immediately to the same zero after a large deflection. Presumably the first valve in their amplifier to get overloaded swings negative, and the change in anode current is limited, for it can only fall to zero; this would prevent later stages from getting overloaded. Alternatively the valves they use may be able to stand a large overload without giving serious grid current, though this seems less probable.

Adrian [1931] has also used an amplifier with which zero is not upset by an overload; he has used the system of battery coupling. With this the grid circuit capacity is very small indeed, and each grid is connected to earth through a fairly low (100,000 ohm) resistance in the anode circuit of the previous valve; hence the grids are unable to retain any grid charge they may acquire if an overload causes grid current to flow.

Fig. 1 shows the general arrangement of the preparation electrodes and recording myograph. The muscle was immersed in about 5 c.c. of Ringer's fluid, which was always changed every 5 minutes throughout the experiment, for it has been found that if the preparation is left in the same small quantity of Ringer for some time the end organ response is modified [Matthews, 1931]. The thread from the tendon was attached to a torsion spring myograph made from watch spring. On the

spring slid a small stirrup which carried a mirror, and the sensitivity could be varied by moving the stirrup nearer or farther from the anchorage of the spring. A spot of light reflected from the mirror was directed into the camera to record along with the beam from the oscillograph.

For isometric recording the thread from the muscle was attached to an arm on the myograph spring about 2 mm. from the spring (see Fig. 1). The deflections recorded on the film were less than 2 cm. high, and as the beam of light was 6 m. long this represents a movement of the point of attachment on the myograph of under 1/200 mm. A much larger deviation from true isometric contraction will be introduced by the

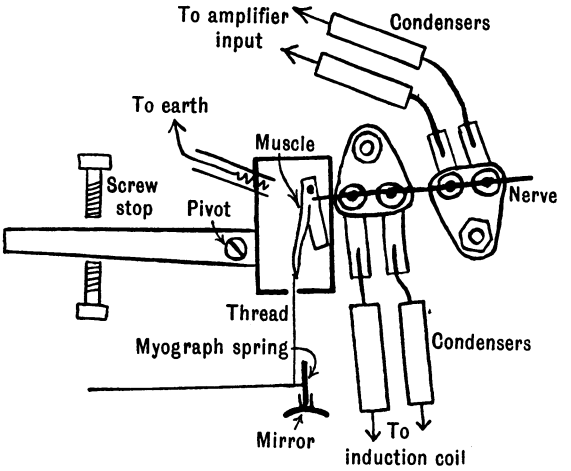

Fig. 1. Sketch plan to show the disposition of the muscle, nerve, myograph, electrodes, etc.

elasticity of the thread when under only slight tension. It is difficult to assess the magnitude of this effect accurately; to avoid it the thread was made as short as possible, and in some experiments fine fishing gut was used in its stead.

For isotonic recording the thread was attached to the arm 8 cm. from the spring. With the amount of shortening that occurred the tension only increased by about 5 p.c. during a contraction, and as the inertia was very small the contraction may be regarded as very nearly isotonic.

The initial tension could be set to any desired value by moving the position of the muscle chamber relative to the myograph; the chamber was fastened to an arm moving between adjustable screw stops. The natural period of the myograph was of the order of 300 vibrations per

second; thus the instrument can be trusted to give accurate records of the mechanical response.

A clock time marker interrupting a separate beam of light marked 1/5 sec. intervals at the side of the record.

The nerve was slung over four non-polarizable Ag, AgCl electrodes; sometimes the proximal pair were used to record and the distal to stimulate, sometimes the connections were reversed: all electrodes were connected to 0·01 mfd. condensers, so that there was no possibility of any steady current being passed through the nerve. A coreless induction coil was used to stimulate. Its coils were coupled tightly by sliding the primary over the secondary, and the strength of shock was regulated by varying the current through the primary, a 2-volt cell, rheostat, and milliammeter being included in the circuit. To produce tetanizing shocks contact was made by a platinum wire on a vibrating steel strip arranged to dip into a mercury cup, and the vibration was maintained electrically when necessary. With this arrangement clean equally spaced make and break shocks of any desired frequency could be obtained by varying the point at which the spring was clamped.

General features of the sensory response during a twitch.

In the experiments described in this section the strength of the primary current was adjusted to that which just gave the maximum mechanical response of the muscle. Experiments cited later seem to show that under these conditions the intra-fusal muscle fibre does not contract, while with stronger stimuli it may do so. In Fig. 2 A and B are shown typical records of the sensory response to a twitch. These were taken with very slight initial tension some time after that tension had been applied, so that the sensory response had died out owing to adaptation of the end organ. The records were taken at an interval of 10 minutes and illustrate the extraordinarily regular behaviour of these end organs, for the records agree not only in general features, but are almost identical impulse for impulse. It will be seen that during shortening one or two impulses are set up, but during relaxation there is a regular rhythmic discharge of declining frequency: in some preparations one impulse was set up as or before the muscle began to shorten as in Fig. 2 A and E, but often this was absent (see Fig. 2 C). If the thread to the tendon was completely slack there was usually no response at all when the muscle twitched, though occasionally one impulse appeared as in Fig. 2 F. There is therefore no evidence that the muscle spindle is excited by the action current of the muscle. The response of the end

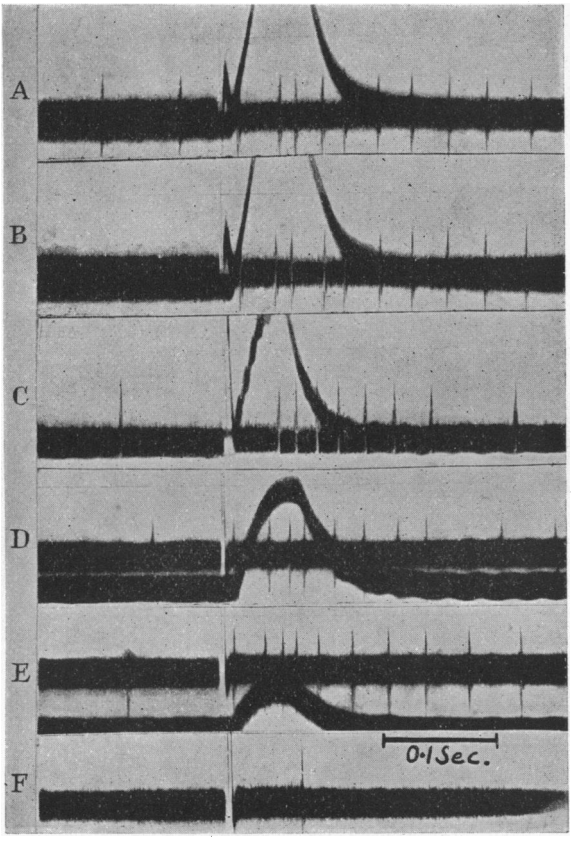

Fig. 2. This and all subsequent figures read left to right. Response in the nerve when the muscle twitches. In records A–E the initial tension is about half a gram, so that the thread is just taut; occasional impulses are set up by this tension, and cause the random deflections on the left of the records. The mechanical record was taken simultaneously with the electrical record. The large excursion just before the muscle contracts is due to the action current of the whole nerve trunk evoked by stimulation. A. Isotonic. Temperature 15° C. B. Isotonic taken 10 minutes later to show the close agreement of the positions of the impulses. Temperature 15° C. C. Same preparation isometric. Temperature 15° C. D and E. Another preparation. Isotonic and isometric contractions. Temperature 16·5° C. F. Same preparation as D and E, thread to the tendon quite slack. Temperature 16·5° C.

The line in F represents 0·1 sec. for all.

organ was much the same whether the muscle was allowed to shorten or not (see Fig. 2 B and C, D and E), but it must be borne in mind that if these tiny muscles are under only slight initial tension, it is impossible to arrange matters so that absolutely no shortening occurs. In several

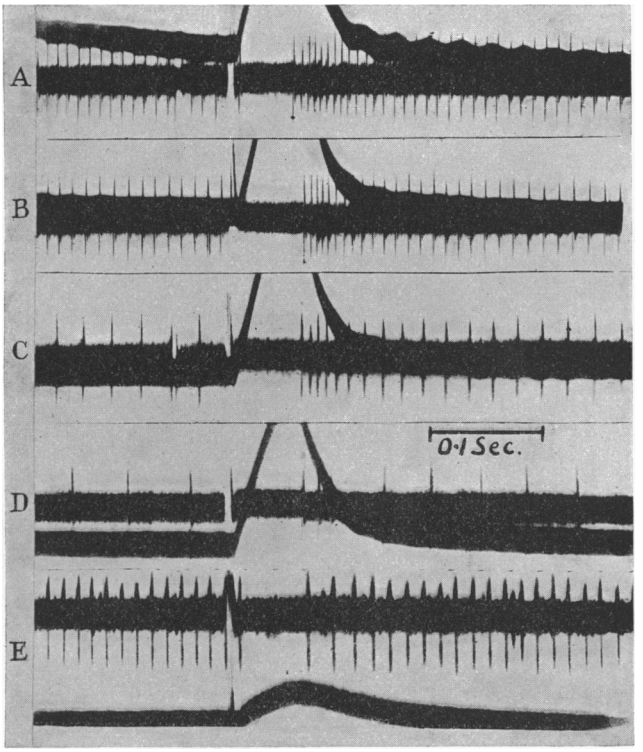

Fig. 3. Twitch superimposed on a steady tension. Temperature 17° C. A–D. Isotonic, tension 2 g. approx. A. 0·5 sec. after loading. B. 1 sec. after loading. C. 5 sec. after loading. D. 15 sec. after loading. E. Another preparation, isometric twitch 2 sec. after a steady extension.

The line in D represents 0·1 sec. for all.

experiments, however, a pin was passed through the knot where the thread was tied to the tendon and inserted in the floor of the muscle chamber. Under these conditions no shortening was possible, but the response was exactly the same as that recorded when the thread was anchored to the myograph.

Thus it is clear that the end organ does not respond much during

shortening or rise of contraction tension in the muscle generally, but during relaxation gives a considerable discharge.

Twitch superimposed on steady tension.

To investigate this failure of the end organ to respond during the rising phase of the mechanical response experiments were performed in which the muscle was first loaded so that the end organ gave a rhythmic discharge and then stimulated to contract.

The results were extremely striking (Fig. 3). It will be seen that the discharge already in progress stops completely during the rising phase of the mechanical response, and restarts at a higher frequency as the muscle relaxes. This occurred in just the same way if the muscle was not allowed to shorten (Fig. 3 E), though the duration of the pause in the discharge was sometimes briefer. The pause has occurred in this way in every preparation that has been examined, when the contraction is produced by just maximal stimuli; in a few preparations the behaviour has been somewhat different with stronger stimuli, and these are discussed in a later section.

To see whether this behaviour is a general property of the frog's stretch receptors the response from other muscles was examined in the same way. In the flex. digitorum muscle there are a considerable number of end organs, and so the response to stretch does not consist of only a single rhythmic series of impulses. Nevertheless, when the muscle twitches the whole response stops until the muscle begins to relax, when the discharge reappears with renewed vigour (Fig. 4 A, B and D). With a gastrocnemius sciatic preparation the pause also occurs, but is broken by a few random impulses.

The pause in the response.

With all the preparations that have been examined a distinct pause occurs: if the initial tension is very great it is broken by random impulses, but with an initial tension of the same order as that which the muscle can produce when stimulated the pause is always absolute provided that the stimulus is only just maximal. To what may the pause be due?

It was thought possible that the action current of the intra-fusal muscle fibre or other fibres in the immediate vicinity of the end organ might prevent it from responding, or that the impulse sent down the sensory fibre when the whole nerve is stimulated produced a long refractory period in the end organ. Further experiments have shown that

neither of these suggested causes is responsible for the pause, which is associated only with the mechanical response in the muscle.

If the muscle is stimulated repeatedly fatigue causes the mechanical

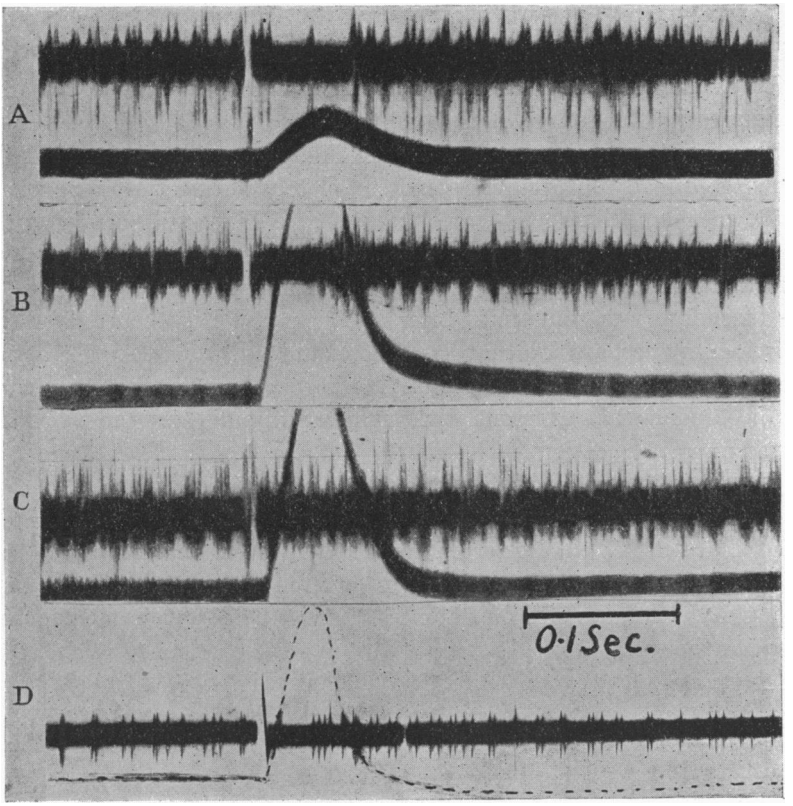

Fig. 4. Records from flex. digitorum muscle preparation containing a number of end organs. A. Isotonic twitch from barely maximal shock, initial tension 5 g. approx. Temperature 16° C. B and C. Isotonic twitches superimposed on a steady tension of 10 g. In B the shock is barely maximal, while in C it is strongly supramaximal. Temperature 16° C. D. Another preparation. Isometric twitch, initial tensions 5 g., shock just maximal. (The mechanical response has been retouched, as it was very faint.) Temperature 16° C.

The line in D represents 0·1 sec. for all.

response to become prolonged, but there is no reason to suppose that a refractory period produced by descending impulses should get longer, for the end organ responds to stretch in just the same way as before the muscle is fatigued. The pause, however, becomes prolonged with the

mechanical response (Fig. 5). When the muscle is so fatigued that there is practically no mechanical response the pause does not occur, although descending impulses should still be able to reach the end organ; also no comparable pause is produced by stimulation if the muscle is curarized. Thus descending impulses cannot be responsible for the pause, although, as will appear later, they are not without effect on the end organ.

Thus the pause appears to be due only to the mechanical response,

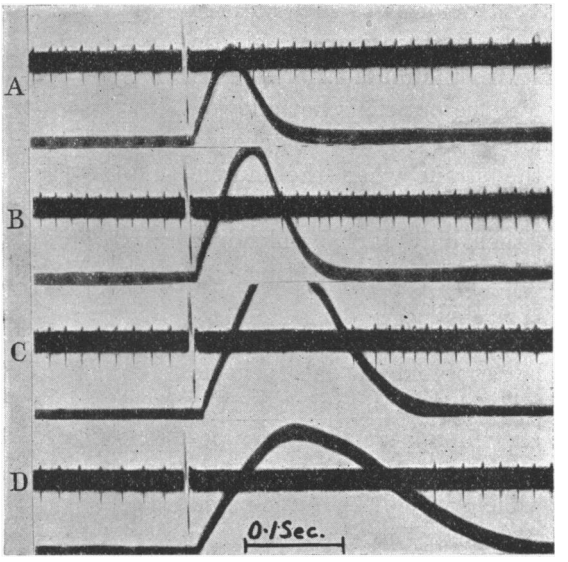

Fig. 5. The effect of fatigue on the pause in the response. Isotonic twitch superimposed on a steady tension of 1 g.; each record was taken between 1 and 2 sec. after the muscle was loaded. Temperature 14° C. A. Muscle rested. B. After 50 twitches. C. After 100 twitches. D. After 200 twitches.
The line in D represent 0·1 sec. for all.

and this conclusion is strongly supported by experiments described below in which the muscle is tetanized.

We will here consider what mechanical arrangements in the muscle might lead to the behaviour which has been described above. All these observations suggest the sort of arrangement that Fulton [1928] postulated to account for the "silent period" in mammalian reflexes. Fulton has pointed out that mammalian muscle spindles are arranged "in parallel" with the muscle fibres, which is also the case in these muscles from the frog.

Fulton's suggested scheme is shown in Fig. 6 A, and in Fig. 6 B is shown a slightly modified version of it which seems to account for all the observed behaviour of these end organs.

In the scheme of Fig. 6 B when the muscle contracts, supposing that the intra-fusal muscle fibre itself does not contract, the strain on the end organ will be removed and so it will cease to respond; as the muscle relaxes the strain on the end organ returns and deforms it so that it is again stimulated. If there is some elastic tissue in series with the muscle fibres (E in Fig. 6 B), even if the muscle is not allowed to shorten, the end organ will be relieved of most of the strain when the muscle contracts unless the initial strain is considerable, and then only partial unloading of the end organ will occur and some impulses might be anticipated.

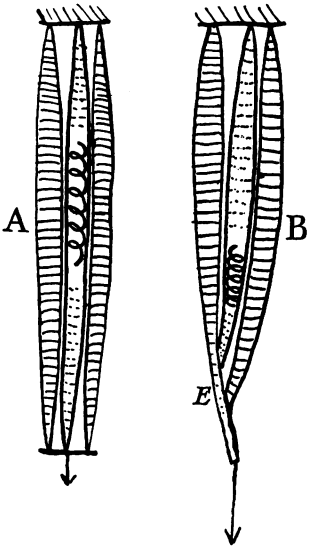

Fig. 6. Sketches to show possible arrangement of the muscle spindle in the muscle. A. Fulton's suggested arrangement. B. Arrangement suggested to account for the observation that the pause still appears if the muscle is not allowed to shorten.

Thus the behaviour observed is exactly what is to be expected if this scheme represents the actual arrangement in the muscle, and as will appear later the behaviour when the muscle is tetanized is exactly that which would be anticipated from this mechanism. The explanation is supported by the fact that the sensory discharge due to steady tension is affected in the same way by a twitch and by a brief period in which the tension is removed (see Fig. 7). In both cases the frequency immediately after the pause is greater than that before it owing no doubt to the brief rest. The pause appears to be due to the longitudinal strain being taken off the end organ by the muscle fibres when they contract.

Tetanization.

With slight initial tension there is no response from the end organ during tetanization. When tetanization ceases there is a brief response. If the initial tension is considerable, the vigorous discharge already in progress stops completely during tetanic contraction, but restarts as the muscle relaxes (see Fig. 8 A). If the muscle has been loaded for some 30 seconds until the response has dropped to a low frequency, after a

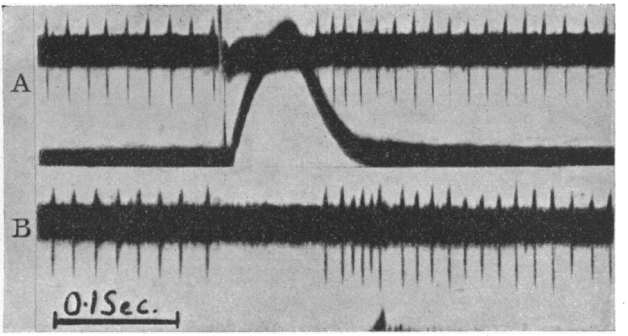

Fig. 7. Comparison between the effect on the response, of the muscle twitching isotonically (A), and the muscle being unloaded completely for an equal period (B). Temperature 15·5° C.

The line in B represents 0·1 sec. for both.

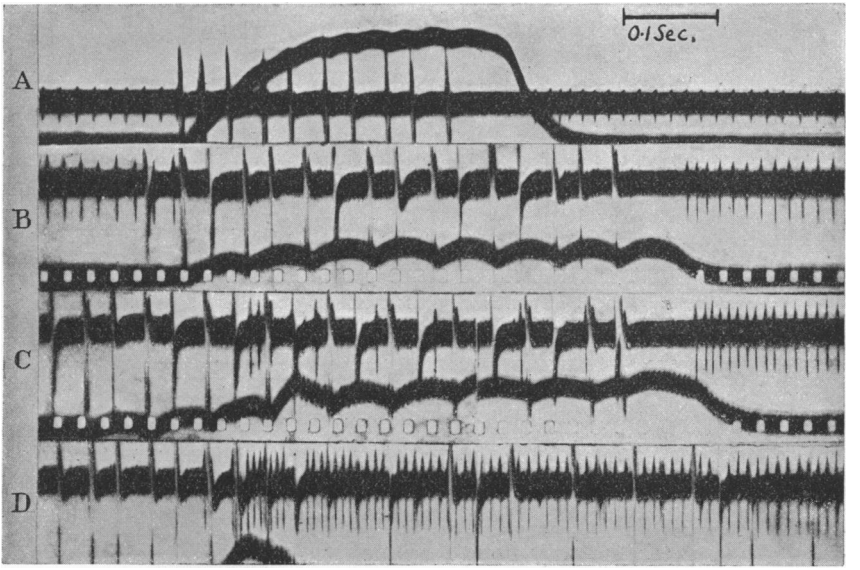

Fig. 8. Effect of tetanic contraction on the response to steady tension. A. Muscle tetanized 2 sec. after loading, isometric response. Temperature 16° C. B. Muscle tetanized 2 sec. after loading, isometric contraction. Temperature 16° C. C. Muscle tetanized and then pulled out to the same extension as that in B. Temperature 16° C. D. Muscle tetanized and then violently extended. Temperature 16° C.

The line in A represents 0·1 sec. for all.

short period of tetanization the frequency of response is higher (Fig. 8 B); evidently the adaptation is reduced after the contraction as it is after a short period of unloading. This lessening of adaptation agrees with the view that the stimulus to the end organ is reduced during tetanic contraction of the muscle.

The results are identical if the muscle is not allowed to shorten, unless the extension of the muscle is so great that the initial tension is considerable (*e.g.* equal to half that produced on tetanization), in which case some random impulses appear. If, however, the muscle is forcibly extended while in tetanic contraction a considerable regular discharge does appear (see Fig. 8 D), but does not increase much if the tetanization ceases. But if during tetanic contraction the muscle be subject to a tension less than the greatest which it can produce when tetanized, little or no response appears (see Fig. 8 C).

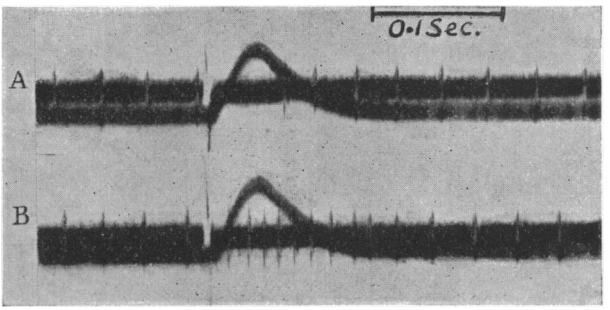

Fig. 9. Isotonic twitch superimposed on a steady tension of 1 g. 2 sec. after loading. Temperature 14·8° C. A. Stimulus only just maximal (4 m.a. in primary). B. Stimulus three times maximal (12 m.a. in primary).
The line in A represents 0·1 sec. for both.

Strength of stimulus and the pause.

It has been pointed out above that in all the experiments so far described the stimulus was adjusted to a strength just great enough to give a maximal mechanical response. In most preparations the pause occurred in the same way however much the stimulus was increased, but in a few preparations (5) when the just maximal stimulus was doubled the pause vanished and was replaced by a characteristic response (Fig. 9 A and B), the frequency rising to a maximum with the tension and falling off again as the muscle relaxed.

An explanation of this anomalous behaviour is suggested by the histology of these muscle spindles. The terminal portions of the muscle

fibre in which the sensory fibre ends are cross striated and are said [Cajal, 1899] to be supplied by a separate motor nerve fibre and are thus like mammalian muscle spindles in which the intra-fusal fibres are cross striated except for the portions immediately under the sensory nerve ending, and are supplied by distinct motor fibres [Sherrington, 1894; Boeke, 1927; Hinsley, 1927]. This was confirmed in two preparations used in the present work. If the twice maximal shock throws the intra-fusal muscle fibre into action and the just maximal shock does not, the experimental results are readily explained. When this muscle fibre did not contract the shortening of the other fibres would unload the end organ during contraction in the way suggested above, and so cause the end organ response to cease until the muscle began to relax: if, on the other hand, the intra-fusal muscle fibres do contract, the stimulus to the end organ will rise as the tension rises and fall again as it falls. Why all preparations do not behave alike in this respect is not clear. It was thought possible that the intra-fusal muscle fibres might in some preparations be inaccessible to stimulation *via* the nerve, but direct stimulation of the muscle through the fluid in the chamber still produced the pause even if the muscle was curarized; presumably under these conditions the shock would take effect on the intra-fusal muscle fibres if the latter were able to respond to direct stimulation. We must conclude that the complete pause which occurs in many preparations, however strong the shock applied directly to the muscle or indirectly through the nerve, indicates that in these preparations the terminal portions of the sensory structure either fail to respond, or respond so feebly that they do not affect the sensory response. In those preparations in which increasing the strength of the shock applied to the nerve obliterated the pause, this occurred also with direct stimulation, though one preparation did not give the pause at all when stimulated directly, whatever the strength of the stimulus.

These experiments point to the conclusion that in some only of the preparations are the intra-fusal muscle fibres capable of contraction, and that both they and the motor fibres which supply them have a rather higher threshold than the other nerve and muscle fibres.

In preparations containing a number of end organs if the stimulus was supramaximal the pause was always obliterated (see Fig. 4 B and C), so that if the above explanation is correct a number of the muscle spindles are situated on structures whose terminal portions are capable of active contraction.

Effect on the end organ of descending impulses.

In all the above experiments when the nerve is stimulated electrically, impulses descend into the sensory structure: it was pointed out above that these could not be held responsible for the pause in the end organ response, and experiments have shown that it is unlikely that they in any way affect the results already discussed: nevertheless, these impulses do reach the end organ and produce observable effects.

Firstly the descending impulse is found to set up a refractory period in the end organ. To observe this the muscle is curarized to prevent the appearance of any mechanical response; it is found that 0·01 p.c. curare is quite without effect on the end organ's response to stretch, although this strength rapidly blocks nerve-muscle conduction (in some experiments 0·001 p.c. was used, but this takes about an hour to abolish this conduction): the response to a given load does not alter at all when the muscle is irrigated for some hours with curare in these concentrations, so it seems safe to regard the stretch receptor as being in normal working condition.

If the muscle is stretched and the nerve stimulated with single shocks, the effect of descending impulses on the rhythmic response can be observed. It is found that after each descending impulse the response follows on from that impulse at the same rate as before. This is most easily explained by reference to Fig. 10, which illustrates the response when descending impulses are superimposed on the rhythm at varying intervals after an ascending impulse; it will be seen that the rhythm is "reset" by the descending impulse but continues at the same rate as before. This resetting of the response makes it clear that the descending impulses are able to reach and make refractory that part of the end organ whence the impulses originate. There is no evident compensatory pause, the interval between the start of the descending impulse and the arrival of the next ascending one is about 15 p.c. longer than the normal spacing of the rhythm (at a temperature of 8° C., and mean rate of response of 30 per sec.). This interval includes the time for conduction of the descending impulse down to the end organ and of the ascending impulse up to the electrodes as well as the interval occupied by the recovery of the region that determines the rhythm. This conduction distance is 4–6 cm., and at this temperature (8° C.) the 15 p.c. excess of the interval between the recording of the descending and succeeding ascending impulse over the interval between successive ascending impulses is accounted for by this conduction time; so if a compensatory

pause does occur it can only be at most 105 p.c. of the normal impulse spacing. This is true if the descending impulse occurs at any point in the rhythm except just before the moment of arrival of an ascending impulse. If it occurs just before an ascending impulse is due, the rhythm is not reset, presumably because the ascending and descending impulses

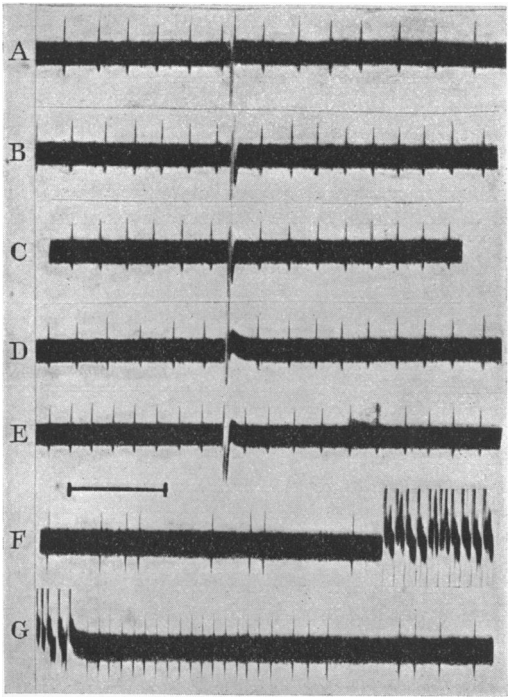

Fig. 10. A–E. Setting up refractory periods in the end organ by descending impulses sent in at various points in the rhythm to steady loading, muscle in 0·01 p.c. curare Ringer. Temperature 16° C. F, G. Apparent reduction of the adaptation of the end organ by descending impulses. Muscle curarized. F. One min. after loading discharge quite irregular and nearly ceased. Start of tetanization of the nerve at 100 per sec. G. Tetanization stopped after 0·6 sec. Vigorous rhythmic response.
The line in F represents 0·1 sec. for A–E, and 0·2 sec. for F and G.

meet somewhere between the electrodes and the end organ and are obliterated. We must conclude that one extra impulse does not change the conditions very greatly in the region that is determining the rhythm.

It is clear that although in the experiment of Fig. 10 the ending takes some 1/30 sec. to recover sufficiently to set up an impulse in response to the steady stimulus, nevertheless its absolute refractory

period is very much shorter. In Fig. 10 A it will be seen that if an impulse is sent into the end organ 1/100 of a sec. after an impulse has arrived at the electrodes the rhythm is reset, therefore this impulse is able to reach the region in which the rhythm is determined, and to produce there a new refractory period; so presumably the absolute refractory period of its predecessor is over. Whether the rhythm is reset in Fig. 10 E is not certain; it appears not to be, which would indicate that the absolute refractory period is not yet over. It should be pointed out that the difficulty in these determinations is due to the fact that the interruption of rhythm is most easily observed when the rhythm has dropped to a fairly slow rate, but then the discharge is not nearly as regular as it is at higher rates, and uncertainties are introduced. However, these difficulties can be reduced by cooling the preparation; this makes it possible to observe these effects with much greater accuracy.

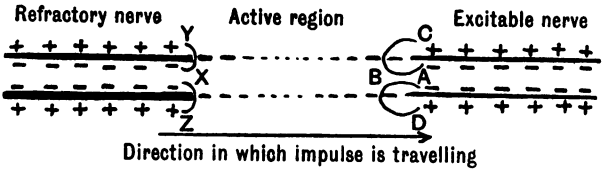

Fig. 11. Sketch to illustrate suggested movements of ions in a nerve fibre.

Descending impulses and adaptation.

The effects of descending impulses on adaptation are extremely interesting but have not as yet been fully worked out. It is found for instance that if descending impulses are set up at a frequency of 20 or less per sec. little effect is produced on the state of adaptation of the end organ: such rates were used in tetanizing the muscle in the experiments described earlier in this paper, so that it is clear that the cessation of response observed during tetanic contraction of the muscle was not dependent on the descending impulses. If descending impulses are set up at a rate of 100 or more per sec. the adaptation is distinctly modified. It was anticipated that descending impulses would increase the adaptation of the end organ, but instead of this it is found in many preparations that the adaptation appears to be diminished. In a number of preparations it has been found that if the nerve is stimulated at 100 per sec. for one minute before loading, when loaded, though the initial frequency of response is much the same as that when it is loaded without having been stimulated, it adapts more slowly; this is evidenced by the fact that the total number

of impulses set up in the 20 sec. following loading may be increased by as much as 30 p.c. In some preparations it has been found that if a load is hung on the muscle for a minute or more until the response has nearly ceased, after stimulation of the nerve for 1 sec. or less at 100 per sec. a renewed outburst of impulses occurs (Fig. 10 F and G).

Thus in some preparations descending impulses apparently diminish the adaptation of the end organ. It is interesting to speculate whether this indicates that the impulse has directional properties. It has been suggested [Matthews, 1931] that adaptation is due to a loss of some ionic active substance by the nerve ending, and this loss might be due in part at least to a movement of ions up the nerve fibre. Such a movement of ions along the nerve fibre does not appear at all contrary to the membrane theory of nerve action, in fact it might rather be expected from it. On this theory the nerve impulse is a wave of depolarization passing along a polarized membrane. At the front of the active region it is supposed that local currents flow depolarizing the membrane ahead and making it active (see Fig. 11 ABC, ABD). These currents must consist of movements of ions and some of the shift of ions will occur parallel to the membrane (A to B). Ionic movements may also occur in the wake of the impulse (XY, XZ), but it seems improbable that these should exactly neutralize those in the forefront of the region of activity, for the nerve impulse is an unsymmetrical process. The action current does not rise and fall symmetrically (see Gasser and Erlanger, 1930], and certainly the conditions at the membrane in the wake of the impulse must be very different from those in front of it, for in the wake is the refractory period and its attendant phenomena. Thus we might expect each impulse to shift the ions slightly along the membrane, and so a stream of impulses passing along in the same direction might cause longitudinal movements of ions in a nerve fibre; these would be in evidence at a nerve ending as alterations in ionic concentrations, though such alterations would not occur in the centre of a symmetrical stretch of nerve fibre.

Clearly if impulses are able to produce any such drift of the ions towards or away from a nerve ending, the drifts produced by ascending and descending impulses will be in reverse directions, for these drifts will be due to the asymmetry of the nerve impulse.

It does not seem impossible that the loss of ions by the nerve ending during adaptation might occur in this way up the nerve fibre. Descending impulses would tend to drift the ions back to the nerve ending, and so cause the apparent reversal of adaptation that has been observed.

It is clearly unsafe to develop this idea further until more experimental evidence has accumulated, for it should be pointed out that the favouring effect of stimulation has not been found in every preparation though it is definitely present in roughly 60 p.c. of those examined.

The favouring effect of stimulation might be taken to indicate that the descending impulses had carried active material to the nerve ending, so that when loaded it was able to maintain a greater response than it could when no descending impulses reached it. It is clear that if this interpretation is correct, and if descending impulses really produce reversal of adaptation in this way, the same effect should occur in other types of end organ. At present there is no evidence of this, but the point clearly merits further consideration.

Discussion.

It must be admitted that mammalian muscle spindles may not function in the same way as do those of the frog, but nevertheless it is interesting that the observed behaviour of the frog's spindle is just that which would be required to regulate automatically the postural contraction of a muscle. As Sherrington has shown, postural tonus is a reflex from the sensory endings in muscle; if the afferent impulses concerned come from the muscle spindles, they would set up impulses until the reflex contraction evoked was sufficient partly to unload them and then a balance would be reached between the loading and reflex unloading, so that the muscle would be kept just taut; with the muscle spindles studied above this would occur over a considerable range of initial extension. The response during contractions of central origin would depend on whether the terminal portions of the sensory structure contract, and at present we have no direct knowledge of when this might occur. The motor fibre to the mammalian muscle spindle is very much smaller than the ordinary motor fibres to muscle fibres [Ruffini, 1898], and small fibres are less excitable than large ones [Erlanger and Gasser, 1924]; whether these differences of excitability extend also to the motor nerve cells from which such fibres originate we do not know, but if the threshold of the motor cell is high as is that of the motor fibre which innervates the muscle spindle then it would only come into action during strong excitation. If this were the case the muscle spindle would subserve the purpose of a self-regulating tonus control mechanism, and also be available during strong contraction to signal information of the mechanical events in the muscle.

The curare experiments described above show that the intra-fusal muscle fibres also always have a higher threshold than the other fibres of the muscle. In the mammalian spindle the intra-fusal fibres are smaller than the other muscle fibres and do not waste after section of the motor nerve as do the other fibres [Sherrington, 1894]; a difference in threshold certainly harmonizes with these other differences.

The pause that occurs in the response to steady tension when the muscle contracts bears a striking resemblance to the "silent period" in mammalian reflexes, and suggests that the two may be related. As

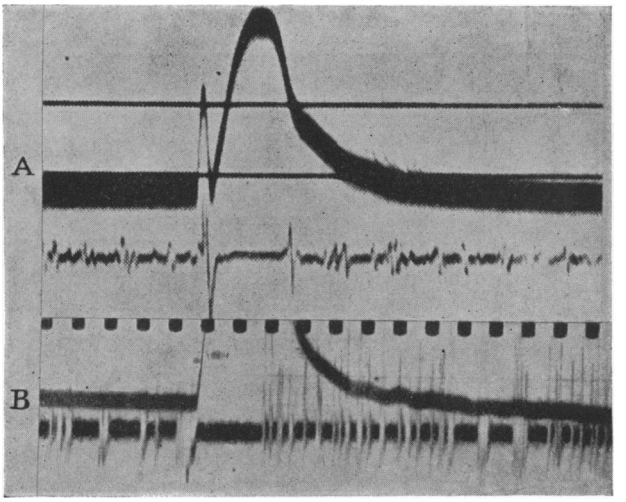

Fig. 12. Comparison of the silent period with the pause in the response to a steady tension from a muscle containing a number of end organs when that muscle twitches. A. Silent period after knee jerk [from Denny Brown, 1928]. B. Pause after a twitch. Temperature 15° C.

Hoffman [1919] originally showed, after a reflex tendon jerk there is a complete absence of action currents in a muscle for about 1/20 sec. This phenomenon has since been studied in some detail by Fulton and Pi-Suner [1928] and Denny Brown [1928]. As the muscle relaxes the action currents appear again and a hump occurs in the mechanical relaxation (see Fig. 12 A). If the mammalian muscle spindle behaves like those in the frog these effects can be explained very simply. As the muscle contracts the muscle spindles cease to be stimulated, and hence the stretch reflex ceases; as the muscle relaxes the spindle is stimulated again and sets up a slightly higher frequency of impulses

than before (see Fig. 3), thus giving rise to more reflex excitation and causing the "hump." As this subsides a balance is once more reached between stimulation of the end organ by mechanical strain and the reflex removal of that strain which results from reflex tonus.

On this hypothesis the "silent period" in reflexes is a direct result of the pause in the end organ response when a muscle contracts. It can be illustrated by comparing a record showing the silent period with one of the responses from the muscle spindles of a frog's muscle when it contracts under some initial tension. It must be admitted that the receptors in mammalian muscle may behave differently from those in the frog, but the general resemblance between the pause and the silent period is so striking that it is difficult to believe that the two are not related.

Denny Brown [1928] has criticized Fulton's explanation of the silent period which agrees with that given above, his most direct objection being that if the silent period were due to unloading of the spindle, in Fulton's scheme (Fig. 6 A) this should only occur if shortening of the muscle took place. Denny Brown showed that this was not the case, and that the silent period still occurred when the muscle contracted isometrically, though it only lasted about a third as long if the muscle was under an initial tension nearly as great as the greatest the muscle could produce in a maximal twitch. It has been found, however, with the frog's muscle spindle that the response to stretch ceases during a twitch even if shortening is not allowed to occur (Fig. 3 E), and for this reason the modified form of Fulton's scheme (Fig. 6 B) was suggested. This observation that the pause does occur even if shortening is avoided removes Denny Brown's main objection to the view that the silent period is due to a cessation of response on the part of the end organ. The alternative hypothesis put forward by Denny Brown, namely that during contraction the spindle sets up impulses which produce central inhibition, is therefore unnecessary, and indeed so far as the frog is concerned no impulses differing in either form or fibre location from those set up by stretch appear during active contraction. In fact, it appears that the phenomena of the silent period could be entirely accounted for if the mammalian muscle spindle behaves like that of the frog.

SUMMARY.

1. A method of observing the sensory response of a single muscle spindle during contraction of a muscle is described.

2. If the muscle is under slight initial tension and twitches either isometrically or isotonically there is little sensory response during the rising phase of the mechanical response, but as relaxation occurs there is a considerable discharge of impulses.

3. There is little or no sensory response if the muscle is slack. It therefore appears that the action current of the muscle does not stimulate the muscle spindle.

4. If the muscle is under some initial tension, when it contracts either isometrically or isotonically, the sensory response to that tension ceases during the rising phase of the mechanical response, and restarts at a higher frequency during relaxation.

5. The pause in the sensory response to stretch, which occurs when the muscle contracts, lengthens *pari passu* with the mechanical response when the muscle is fatigued; it seems to be connected only with the mechanical events in the muscle.

6. During tetanization there is no response from the muscle spindle; if the initial tension is considerable the sensory response to that tension ceases during tetanic contraction of the muscle, and restarts, often at a higher frequency, when the muscle relaxes.

7. The pause also occurs in the sensory response from muscles containing a number of stretch receptors.

8. In some preparations increasing the strength of the shock applied to the nerve obliterates the pause. It is suggested that this is due to contraction of the terminal cross striated portions of the muscle spindle. These have a separate motor fibre, and this motor fibre seems to have a higher threshold than the ordinary motor fibres to the muscle. The intra-fusal fibres also seem to have a higher threshold than the other muscle fibres.

9. Impulses descending the nerve to the muscle spindle evoked by electrical stimulation set up a refractory period in the nerve ending. There is no evidence of a compensatory pause; if such exists it must be less than 105 p.c. of the interval between successive impulses set up by stretch.

10. Descending impulses at a frequency of 100 per sec. reaching the nerve ending appear to reduce its adaptation.

11. A theoretical explanation of this is suggested.

12. The pause in the response of the muscle spindle to steady tension when the muscle contracts is compared to the silent period in mammalian reflexes. It is suggested that the silent period is due to the pause in the response from the muscle spindles.

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