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## ERRATUM

P. 143, Fig. 20. *For* 'peroneal' *read* 'popliteal'.

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# THE DISCHARGE OF IMPULSES IN MOTOR NERVE FIBRES. Part II. The frequency of discharge in reflex and voluntary contractions.

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In Part I of the present series(1) we described a method of recording the normal discharge of motor impulses in single fibres of the phrenic nerve. The method consists in cutting through all but one of the active motor fibres of the nerve and recording the action currents from this one fibre by electrodes placed on the nerve trunk below the divided area (cf. Fig. 1 *B*). As a rule at least three or four fibres were left uncut, but in five experiments the impulses recorded during the respiratory discharge formed a single, fairly regular series and were presumably derived from a single source. We found that during normal breathing (in the rabbit anæsthetized with urethane) the frequency of the impulses in each nerve fibre was very low (20–30 a sec.)—so low in fact that the muscle fibre response would be an incompletely fused tetanus. When the force of inspiration was increased the frequency of discharge rose to 50–80 a sec. Since there was no clear evidence that more neurones came into play with the stronger contraction, we concluded that the contraction of the diaphragm is regulated mainly by varying the frequency of the motor impulses over a range which would give a varying degree of fusion and summation of the contractile waves in the muscle fibres.

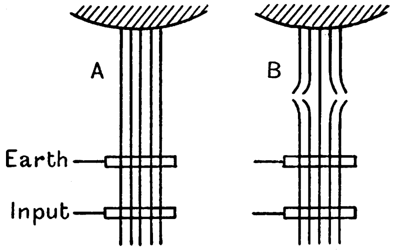


Fig. 1. Arrangement of electrodes for leading from entire nerve trunk, *A*, and single nerve fibre, *B*.

We have now applied the same method to determine the frequency of the motor discharges in various reflexes of the hind limb in the cat. We have found the same very low frequencies with feeble contractions and the same increase when the contraction becomes more forcible, though with certain reflexes there is also a marked increase in the number of fibres in action. The results of this work are given in Section I; in Section II we describe confirmatory experiments in which the action currents of single groups of muscle fibres are recorded during reflex contractions in the cat and voluntary contractions in man.

## SECTION I. IMPULSES IN SINGLE MOTOR NERVE FIBRES IN REFLEX CONTRACTIONS OF THE HIND LIMB.

### *Method.*

All the experiments in this section were made on cats which were deeply anæsthetized and then either decapitated by Sherrington's technique or decerebrated by the trephine method with or without previous spinal transection. One hind limb was fixed by a drill through the lower end of the femur and by clamps in the region of the pelvis and foot. In some experiments the other limb was immobilised by nerve section, but as a rule the innervation of both limbs was interfered with as little as possible in order to secure the greatest possible reflex activity. This is necessary because our method of recording the nerve action currents makes it impossible to use electrical stimulation to elicit the reflexes and mechanical stimulation is usually much less effective. The nerve under investigation was divided as close as possible to its entry into the muscle and dissected for 2–3 cm. proximally. The whole preparation was then placed inside a metal screening box connected to earth and the nerve (irrigated repeatedly with warm Ringer) was slung on two paint brush electrodes, the proximal connected to earth and the distal to the input of the three valve amplifier (Fig. 1 *A*). To avoid electrical artefacts the reflexes were produced by pinching the feet or moving the limbs or head with a pair of forceps made of vulcanite with long handles which extended outside the screening box. Permanent records of the reflex discharge in the nerve were made with the capillary electrometer, but in making these we have been guided more and more by the information obtained by amplifying the action currents still further and leading them to a loud speaker (cf. Part I, Fig. 2). By listening to the nerve discharge throughout the experiment we have been able to save a great deal of time and photographic material and to detect various points which would almost certainly have been missed had we relied entirely on photographic records.

After a few preliminary observations on the reflex discharge from the entire nerve trunk, the preparation was removed from the screening box and the nerve laid across a small glass platform and focussed with a binocular dissecting microscope. The progressive division of the nerve fibres was carried out by the method described in Part I. The final stages of the operation were controlled by repeated observations of the action currents in the nerve distal to the section and eventually, if all had gone well, the stage was reached at which the action currents form a single series. As in the experiments on the phrenic this stage was usually reached when there were still three or four undivided fibres bridging the gap in the nerve, but it is clear that the action currents are due to only one of these fibres, since the impulses form a single series and further division either suppresses the discharge entirely or else leaves it unchanged. When the division of the nerve had been successfully carried out, the preparation was placed once more in the screening box and the reflex discharges were photographed with the electrometer. The intact connective tissue sheath of the nerve preserves the uncut fibres from further damage during manipulation and the character of the discharge remains unchanged for periods of 2–3 hours. There is, of course, a considerable risk of carrying the section of the nerve too far and missing the single fibre stage, but only about one in three of our experiments have failed from this cause.

It will be realised that for this measure of success the nerve must be carefully chosen. The most suitable size appears to be one containing about 150 fibres at the point where the section is to be made, and for ease in manipulation it must be possible to dissect out a length of 2·5 to 3 cm. of the nerve. We have found various small nerves which comply more or less with these conditions. They are the nerve to the peroneus longus, the upper or lower branch to the tibialis anticus, a branch of the anterior crural which runs down on the mesial surface of the vastus lateralis and supplies the lower third of that muscle and another branch of the anterior crural supplying the vastus medialis. Those to the peroneus longus and tibialis anticus have been used for the study of the flexion reflex, and those to the thigh muscles for the extensor reflexes. The former have been studied exclusively in the spinal and the latter in the decerebrate preparation.

### *Results.* (1) *The flexion reflex.*

When the foot of a spinal animal is pinched, the tibialis anticus contracts strongly and flexes the ankle joint: the peroneus longus also contracts but not so strongly, its function being to assist the flexion and to prevent inversion of the foot (cf. Sherrington(2)). Both muscles are supplied from the main peroneal nerve trunk, the arrangement of the terminal branches in the cat being shown in Langley's diagram (3).

*Nerve to peroneus longus.* Our first experiments were made on the nerve to the peroneus longus. This can be secured with a minimum of dissection and freed from the main peroneal trunk for a considerable length (3–4 cm.). A section of the nerve stained in osmic acid contained 129 fibres of $10\mu$ or more in diameter and 55 under $10\mu$. This represents the whole nerve supply to the muscle, and as the nerve must be cut distally to allow of the electric recording, no afferent impulses can pass from the muscle to the spinal cord. The other nerves we have used do not form the entire supply of the muscles they innervate, but here too it must be remembered that some of the afferent supply from the muscle had to be sacrificed. Fortunately the evidence brought forward in Section II shows that the main result is quite unaffected by this factor.

The nerve to the peroneus longus was successfully brought to the single fibre stage in three experiments. A record of the beginning and middle of a reflex discharge is shown in Fig. 2. The stimulus was a gradually increasing pressure on the foot and it will be seen, (*a*) that the frequency of the impulses rises slowly at the beginning of the contraction, (*b*) that at the height of the discharge the frequency is only 16 a sec. and (*c*) that although the impulses evidently form a single series the regularity of the discharge is by no means absolute—in fact the intervals between successive impulses may vary by as much as 30 p.c. from the average value. The record in Fig. 2 is typical of a large number made in the course of the three experiments; in all of them the frequency of discharge remained below 30 a sec. even with the strongest stimulation,

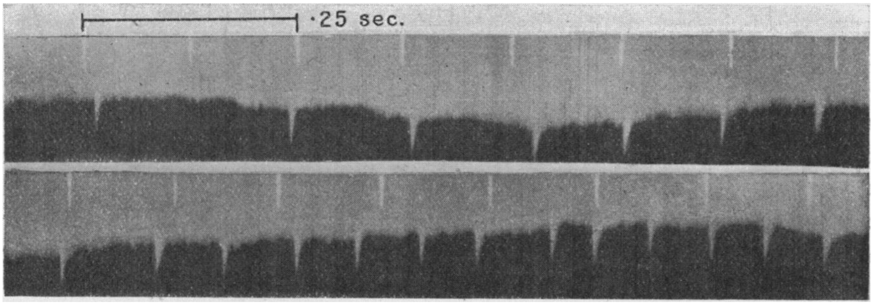


Fig. 2. *Exp.* 2. Decapitate cat. Nerve to peroneus longus, final stage of dissection. Flexion reflex produced by pinching foot. Above, beginning of discharge; below, 1 sec. later. Time marker (white lines at the top of the record) gives 0·125 sec. intervals.

and in all the frequency rose and declined gradually. The evolution of the discharge may be seen in Fig. 3 which gives two curves showing

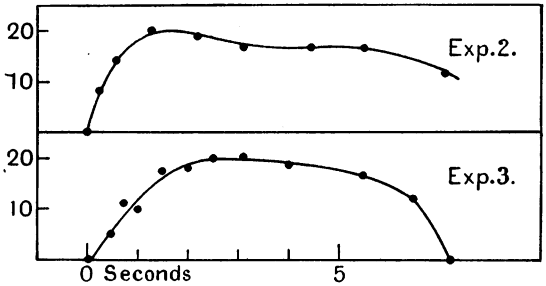


Fig. 3. Curves showing frequency of impulses per sec. in nerve fibre to peroneus longus during flexion reflex. *Exp.* 2. Decapitate preparation. *Exp.* 3. Decerebrate with spinal transection.

the frequency at different times after the beginning of the contraction. As the muscle has lost its nerve supply we cannot compare these curves with those of the tension developed in the contraction, but if all the nerve fibres behave alike the contraction would rise and decline gradually and would never be very powerful. As three nerve fibres selected at random in three different animals were all found to give a low frequency discharge of the same kind it may safely be assumed that all the motor fibres behave alike, and observations of the contraction before the nerves were cut showed that the stimulation we employed did produce a feeble reflex contraction of gradual onset and decline.

The contractions appeared to develop smoothly, but it is clear that in the group of muscle fibres innervated by one nerve fibre the contraction must have been an incomplete tetanus, in fact at the beginning of the response it would be little more than a succession of twitches. The average tension in the whole muscle would rise gradually as the frequency of the discharge increases, at first from the increased frequency of these isolated twitches and later from the summation of the contractile effect in the individual muscle fibres.

*Nerve to tibialis anticus.* Three successful experiments of the same type were made on one or other of the two main nerve twigs to the tibialis anticus. Fig. 4 shows the reflex discharge in the nerve in one of these at different stages of the experiment. In the top record the nerve is intact (though cut distally at its junction with the muscle) and the electrometer is shunted to record the very large fluctuations of potential. The middle record was obtained after about nine-tenths of the fibres had been cut through, and the lowest, which shows a single series of action currents, was made after division of all but three fibres. One of these was only $5\mu$ diam., the other two were over $10\mu$, and one of them was bent irregularly and presumably took no part in the discharge. The three records are not strictly comparable, but they were all obtained at the height of the discharge with a strong stimulus to the foot. It will be seen that the frequency of the impulses in the single fibre is distinctly higher than in the nerve to the peroneus longus, and this is shown more clearly in Fig. 5 which gives the frequency at each moment throughout a reflex contraction lasting 9 secs. The highest frequency reached in this discharge is 40 a sec., not high enough to produce a completely fused tetanus in the muscle fibres, but twice as high as in the nerve to the peroneus longus. In another experiment the maximum rate was 44 a sec.

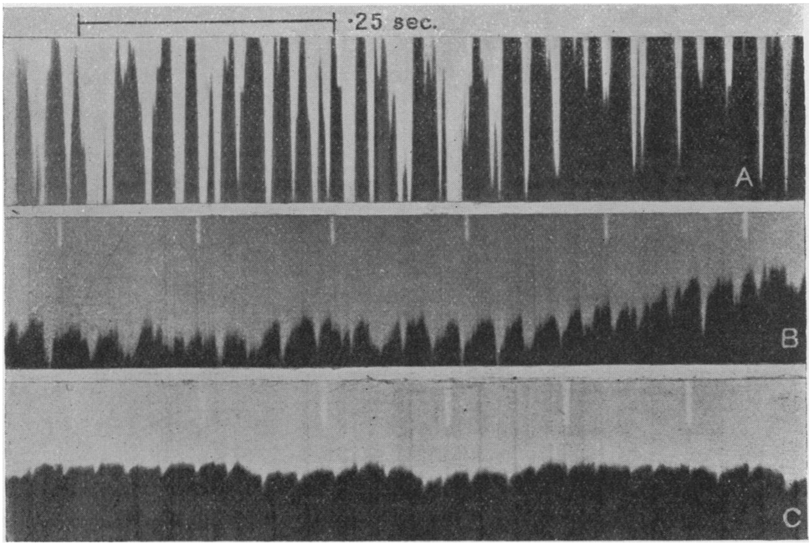


**Fig. 4.** ***Exp.*** **6. Decapitate cat. Nerve branch to tibialis anticus. Records made at height of flexion reflex. *A*, whole nerve; *B*, partially divided; *C*, final stage, three fibres remaining. Single impulse series at 30 a sec.**

The higher values reached with the nerve to the tibialis are evidently related to the fact that we are dealing with a much stronger contraction, the tibialis being a prime mover in the flexion of the ankle and the peroneus longus an accessory. But with weak stimulation the frequency may be just as low as in the nerve to the peroneus longus, and it is possible to vary the frequency of the reflex discharge at will by altering the pressure of the forceps on the foot. After a strong stimulus the after discharge may last for several seconds at a frequency which gradually declines to 10 a sec. or less. In the intervals between stimulation the nerve fibre is usually quiet. On one occasion however we found a persistent discharge at about 15 a sec. (estimated very roughly by ear) and were finally able to trace it to the fact that the foot had become cold. Warming the foot by pads wrung out in hot water abolished the discharge and it returned again whenever the pads were removed and the foot allowed to cool.

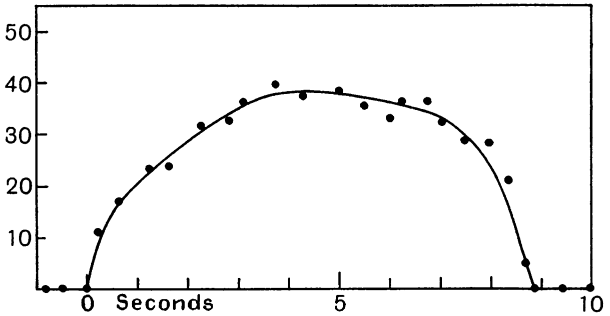


Fig. 5. *Exp.* 6. Curve showing frequency of impulses per sec. in nerve fibre to tibialis anticus during flexion reflex. Decapitate preparation.

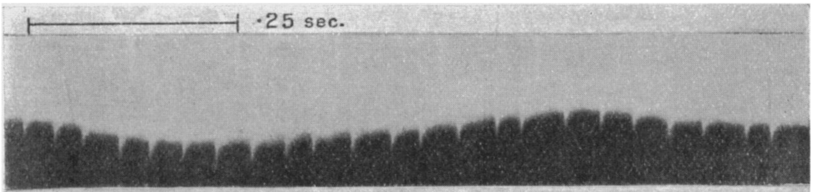
(2) *Extension reflexes, nerves to quadriceps.*

The nerve fibres of the anterior crural supplying the quadriceps were studied in three successful experiments on decerebrate preparations. Two of these gave a strong extension on mechanical stimulation of the contralateral foot; in the third we failed to elicit the crossed extension reflex, but we were able instead to produce a strong extension of both legs by moving the head from the horizontal position to that in which the long axis makes an angle of 45° with the horizontal, the preparation lying on its back. This is the position in which the tonic effect of the labyrinths is at its maximum, and the extension occurring in this experiment is therefore an example of the tonic labyrinthine reflex.

The main features of the discharge in single fibres of the anterior crural nerve are, first, that it may persist at a frequency of 10–25 a sec. for long periods in the absence of external stimulation, and, second, that during a movement of extension the discharge rises fairly rapidly to frequencies as high as 90 a sec.

A record of the persistent discharge is given in Fig. 6 from the preparation showing active labyrinthine reflexes. The nerve was the lowest branch to the vastus lateralis[1], all the other nerves of the leg being

Fig. 6.



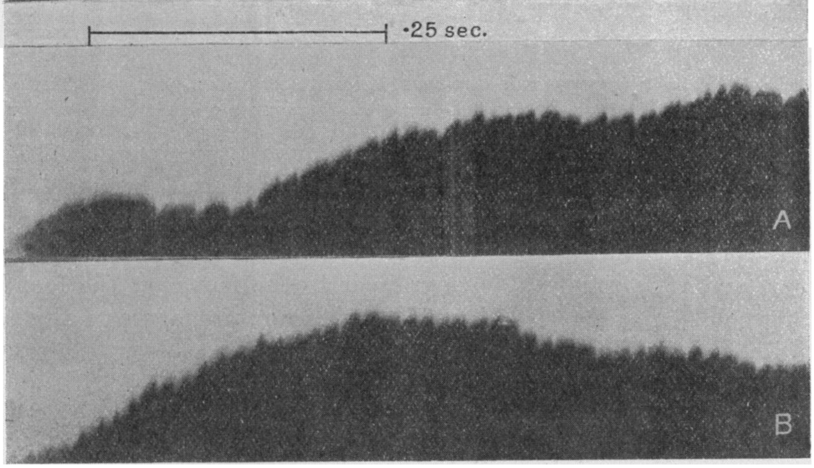


Fig. 7.

Fig. 6. *Exp.* 11. Decerebrate cat. Nerve to vastus lateralis. Several fibres intact. Portion of long record showing persistent "tonic" discharge in one fibre at 25 a sec. Increase of contraction due to stimulating labyrinths brings more fibres into play.

Fig. 7. *Exp.* 10. Decerebrate cat. Nerve to vastus medialis. Final stage. Crossed extension reflex produced by pinching contralateral foot. *A*, beginning of contraction; *B*, height of discharge. Frequency, 65 a sec.

intact. The discharge could be inhibited by pinching the ipsilateral foot but returned again as the extensor tone reasserted itself. Similar discharges were found in the other two experiments, but in these the extensor tone was less and the discharge was sometimes absent for long periods, to return again after manipulation of the leg.

We have no doubt that these persistent low frequency discharges are the cause of the "tonic" contraction of decerebrate rigidity, and

[1] A section of this nerve gave 103 large and 49 small fibres in the region selected for dissection

that the "tone" of the quadriceps is in fact maintained by incompletely fused tetanic contractions in various groups of muscle fibres. But it might be objected that the nerve discharge as it appears in our records may have been changed from its normal character owing to the section of the sensory fibres. This objection applies, of course, to all our records from divided nerves, but it becomes of especial importance in the case of reflexes which may be maintained by the afferent impulses from the muscle. The difficulty can be overcome by experiments of a different kind, but these and the general discussion of "tonic" innervation must be reserved for Section II.

When movements of extension are produced by stimulation of the contralateral foot the frequency of the impulses rises fairly rapidly to values which range from 60 to 90 a sec. Fig. 7 gives two portions of a record from a nerve twig to the vastus medialis, and Fig. 8 shows one made on a rapidly moving plate at the height of a discharge with maximal stimulation. Here the average rate is 82 a sec., and the shortest interval between successive responses gives a rate of 95 a sec.—the most rapid we have found in any experiment. This record is one of many which we have made from time to time to satisfy ourselves that the electrometer excursions are due to single impulses and not to groups

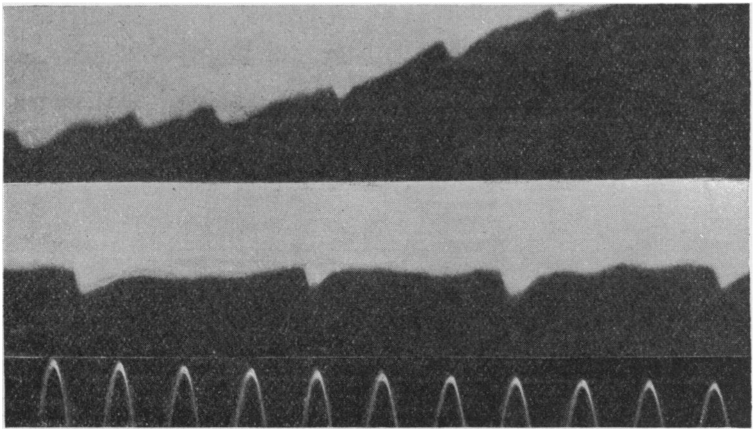


Fig. 8. **Above.** *Exp.* 10. Decerebrate cat. Nerve to vastus medialis. Final stage of dissection. Record at height of crossed extension reflex. Frequency, average 63 a sec. Shortest interval between impulses, 82 a sec.

**Below.** *Exp.* 6. Decapitate cat. Nerve to tibialis anticus. Final stage. Record at height of flexion reflex. Frequency, 31 a sec.

Time marker gives ·01 sec. intervals.

occurring in rapid succession. Inspection of the record shows no evidence of this and the analysis gives a succession of simple monophasic action currents. The lower record is from the nerve to the tibialis anticus during the flexion reflex.

Fig. 9 gives the frequency curves for two discharges in the crossed extension reflex, one starting from the background of a persistent low frequency discharge and one from a quiet nerve. A comparison with Figs. 3 and 5 shows the much greater frequencies which are reached in these extensor reflexes.

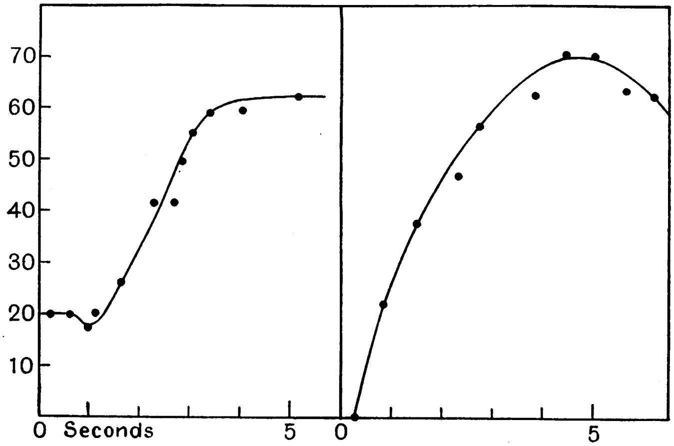


Fig. 9. *Exp.* 10. Frequency of impulses per sec. in nerve fibre to vastus medialis during crossed extension reflex.

We have not examined enough reflexes to say whether the difference in frequency is characteristic of flexor and extensor reflexes or whether it is merely due to the fact that the contractions we were able to elicit were more nearly maximal in decerebrate crossed extension than in spinal flexion. There is however another point of difference which may have more significance, and this concerns the grading of contraction in the various reflexes.

*Grading of contraction.* In the individual nerve fibres of the phrenic we found that the frequency of the impulses varied over a range from about 15 to 90 a sec. Electrical stimulation of the whole nerve at frequencies ranging from 15 a sec. upwards gave a series of contractions of gradually increasing force. With low frequencies the contraction was an incomplete tetanus and the increase in force with higher rates was due to the more and more complete summation of the individual twitches.

The contraction became maximal or nearly so when the rate was 50–60 a sec. Thus the frequency of the reflex discharge varied over just the range required to produce graded contractions in the diaphragm.

In the present experiments we find the reflex frequencies ranging from as low as 5 to as high as 90 a sec. The effect of stimulating the

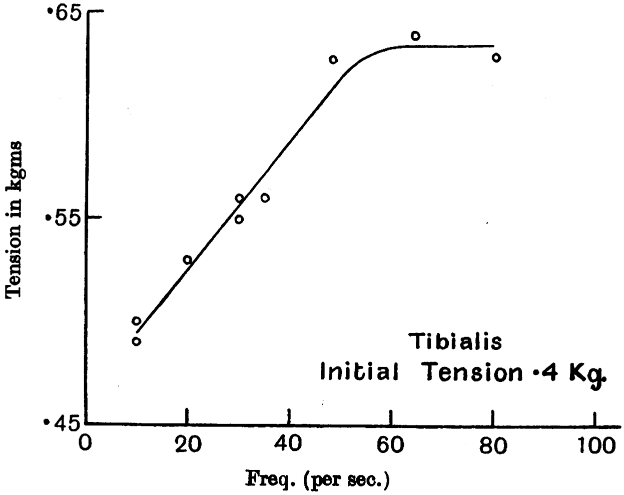


Fig. 10 *A*.

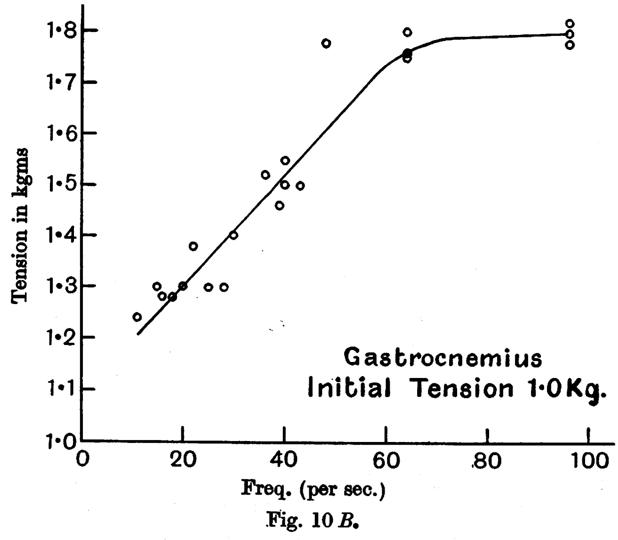


Fig. 10 *B*.

Fig. 10. Tension developed in leg muscles with stimulation of motor nerve at various frequencies. Decerebrate. *A*, tibialis anticus; *B*, gastrocnemius and soleus. Contractions not strictly isometric.

nerve to the tibialis anticus with rhythmic induction shocks at different frequencies is shown in Fig. 10 *A*. The quadriceps gave too powerful a contraction for the very simple myograph arrangement which we used, but we have records made by stimulating the popliteal nerve and measuring the pull of the combined gastrocnemius and soleus (Fig. 10 *B*). The nerves were cut proximally and stimulated by shocks from a rotating contact breaker in the primary circuit of the induction coil. The myograph was a lever moving a pointer over a scale and pulled by the muscle against the resistance of an elastic band. The muscle was able to shorten 5 mm. or more during the contraction and the tensions developed are lower than those usually obtained with strict isometric recording. No attempt was made to reduce the inertia of the lever since we were concerned merely with the average tension developed at different frequencies of stimulation. Both curves are remarkable in showing a linear relation between the tension developed and the frequency of stimulation over a range from about 15 to 40 a sec., but the exact form of the curve would no doubt vary with the initial tension on the muscle. It is clear, however, that the frequencies which we find in the reflex discharge of the individual nerve fibres lie mainly within the range where a change in frequency alters the level of muscular summation and so produces a change in the force of contraction. With more perfect myographic recording Liddell and Sherrington(4) have found small fluctuations in tension corresponding to stimulus rhythms as high as 90 a sec., so that even the highest frequencies we have found in the individual nerve fibres must fall short of producing a completely smooth tetanus. We cannot exclude the possibility that higher rates of discharge may sometimes occur, but an increase above 100 a sec. could have little or no functional value as far as the muscle is concerned.

In the discharge of the phrenic we found no evidence of more motor neurones coming into play with stronger contractions, and we have found no evidence to show that this occurs to any marked extent in the reflex discharges to the peroneus or tibialis[1]. Any sensory stimulus producing a movement of the leg muscles invariably produced a discharge of impulses in the single nerve fibre, and the discharge in this fibre

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[1] Electrical stimulation of afferent nerves in the spinal cat can evidently produce reflex contractions in the tibialis which are graded by the change in number of active fibres. But a stronger electric stimulus excites more afferent fibres without altering the frequency of the impulses in each fibre, whereas pinching the foot more strongly will probably increase the frequency of discharge from the receptors without much increase in the number in action. This may account for our finding only that type of muscular grading which depends on increased frequency of discharge.

appeared to last throughout the period of contraction. To investigate the time relations more closely we made one experiment in which the electric responses of the entire nerve trunk above the damaged region were compared with those of the single nerve fibre below it.

The former were magnified by a separate three valve amplifier followed by a power amplifier which led to a loud speaker movement of the "balanced armature" type. The vibrating reed carried a small glass pointer which projected into the eyepiece of the capillary electrometer. The excursions of the pointer, magnified 40 times on the film, were rarely greater than 1 mm. and considerable distorsion was introduced by the amplifying and recording system, but a comparison with simultaneous electrometer records from the same leads showed that the system was adequate to signal the beginning and end of the discharge in the entire nerve. The loud speaker movement forms a convenient signal for electrical stimulation (see p. 141).

In this experiment the discharge in the single nerve fibre coincided in time with the discharge of the whole nerve, *i.e.* the single fibre, chosen at random, did not come into play any later than the other fibres. Evidence pointing in the same direction was obtained from records made from nerves in the earlier stages of the dissection when several fibres were still active, for these showed little sign of greater complexity in the discharge (*i.e.* more fibres in action) in the middle than at the beginning or end of the discharge, whatever the stimulus. An example of one such record is given in Fig. 11 *A*. The records obtained from the muscle itself and discussed in Section II show that one group of muscle

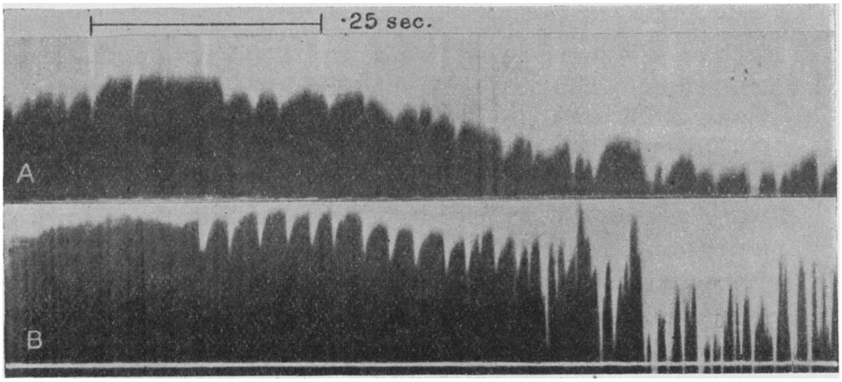

Fig. 11. *A*. *Exp.* 7. Decapitate cat. Nerve to tibialis anticus, several fibres intact. Beginning of flexion reflex.

*B*. *Exp.* 13. Decerebrate cat. Nerve to vastus lateralis, several fibres intact. Beginning of crossed extension reflex. Many fresh fibres come into play ·3 sec. after the first.

fibres may occasionally come into play before the majority, but they support the view that in these reflexes there is very little to change in the number of active neurones after the contraction has begun.

In the case of the quadriceps, however, there is no doubt that the number of fibres in action increases progressively as the contraction develops. This can be seen at once from Fig. 11 *B* which gives a record from the nerve to the vastus lateralis before the final stage of the dissection was reached. A single series of impulses appears at the beginning of the contraction, but at a later stage many more neurones come into play and the action current record becomes increasingly complex. Subsequent dissection gave the usual single fibre discharge without the additional impulses. The fact that some neurones only come into play with strong contractions may explain why we do not always find the persistent "tonic" discharge when we have reached the single fibre stage. All our preparations showed occasional low frequency discharges in the absence of external stimulation, but we have not enough evidence to say whether the same nerve fibre is used at one time for maintaining the tone of the extensors and at another time becomes active only at the height of a powerful contraction. The significance of these results will be discussed later in Section II.

## SECTION II. THE ELECTRIC RESPONSE IN SMALL GROUPS OF MUSCLE FIBRES.

The experiments on the divided nerve are technically difficult and in interpreting their results we have to reckon with the fact that some or all of the sensory impulses from the muscle are prevented from reaching the cord. But it is unlikely that they will produce a radical change in the frequency of the discharge, and this is so low that the muscle fibres should certainly respond to every impulse reaching them from the nerve. Consequently the electric responses in the individual muscle fibres should give just as accurate a measure of the nerve fibre frequency as the record made from the nerve itself. We have not attempted to dissect out individual muscle fibres, or groups supplied by a single nerve fibre, since most of the information we need can be readily obtained by the use of very small electrodes buried in the substance of the intact muscle. The principle involved can be seen in the diagrams in Fig. 12.

If two point electrodes *a* and *a′* are placed in a muscle at a distance apart which is large compared with the diameter of the muscle fibres (as in Fig. 12) they will record the algebraic sum of the potential changes in many fibres besides those in contact with the electrodes, for a potential gradient in a fibre some distance away, as at $x$, will produce a considerable potential difference between the $a$ and $a'$. But if the electrodes are brought very close together ($b$, $b'$, Fig. 12 *B*) their sphere of influence will be reduced proportionately and the potential gradient must now occur at $x'$ if it is to have the same effect as that at $x$ when the electrodes are at $a$ and $a'$. After trials of various types we finally adopted the arrangement shown in Fig. 13. An enamelled copper wire, No. 36 gauge, *i.e.* $193\mu$ diam., is passed up the centre of a small hypodermic steel needle and held in position by a plug. The exposed end of the copper wire projects into the orifice of the needle and forms one electrode. The needle itself forms the other. The gap separating the two electrodes is very small, little more than the thickness of the enamelled covering of the wire, but the wire has a diameter 3–4 times as large as that of a muscle fibre, and if the end is ground off obliquely to fit the end of the needle the exposed area is larger still. Sharper localization is secured by using two smaller wires (No. 44 gauge, *i.e.* $81\mu$ diam.) placed side by side in a hypodermic needle, but this arrangement has certain practical disadvantages which are not present with the concentric type. In the latter the body of the needle is connected to earth and the wire to the grid of the amplifier, and as the needle has a relatively large surface it provides a low resistance path from the animal to the earth. This makes it possible to use electrical stimulation and to work without the careful electrical shielding which is necessary when both leads are of high resistance, but the localization is not sharp enough to distinguish the responses of individual fibres, or fibre groups, in powerful contractions where every fibre is in action, and our records with the concentric type of electrode give most information in relatively feeble contractions

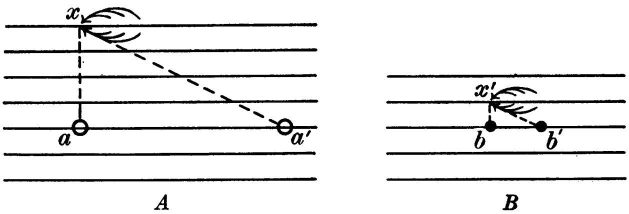

Fig. 12. To show greater localisation due to electrodes of small dimensions. (See text.)

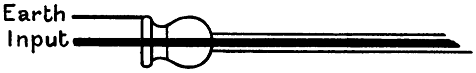

Fig. 13. Concentric needle electrode.

of the type in which the motor neurones do not all come into play at once.

Our observations have been made on man and on spinal and decerebrate animals. Those on man will be described first since they deal with a type of contraction which might be expected to differ considerably from the reflexes investigated by the method of nerve section.

### (1) *Voluntary contraction in man.*

The muscle most commonly employed has been the triceps of the left arm. The needle electrode is thrust into the muscle with the central wire connected to the input of the amplifier. As a rule the electrometer is shunted to one-sixth or less of its normal sensitivity, for the action currents are much larger than those of nerve. When the muscle is completely relaxed the record shows no electric changes. With a slight degree of voluntary contraction sharply isolated action currents appear at a rate which may begin as low as 6 a sec. and rises gradually as the contraction develops. Records of these low frequency discharges are given in Fig. 14. In Fig. 14 *A* the short time relations and the simple contour of each response show that it must be due to a single muscle fibre or to a group of muscle fibres acting in unison and so presumably innervated by a single nerve fibre. In agreement with

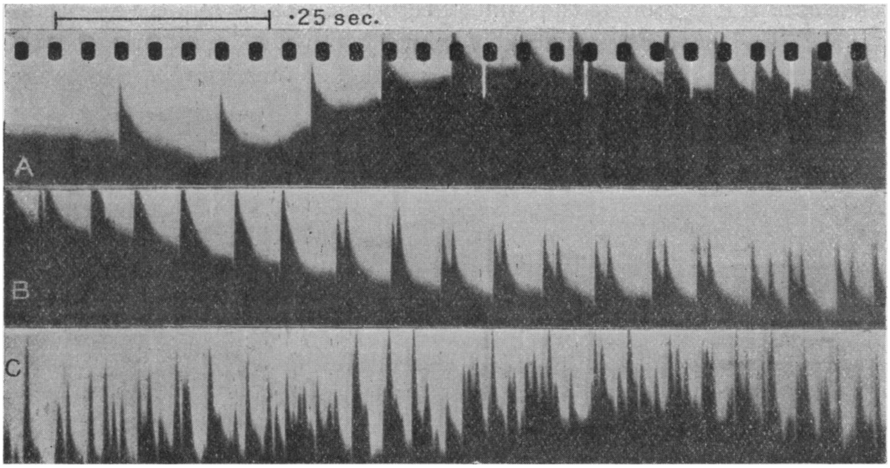

Fig. 14. Action currents in human triceps (E. D. A.) recorded with concentric needle electrodes during gradually increasing voluntary contraction. *A*, beginning of contraction; *B*, follows on *A*; *C*, powerful contraction.

this it will be seen that the responses form a definite series of exactly the same type as those in Fig. 2 (nerve to peroneus longus). At the end of this record, however, a second series of action currents appears and this continues in Fig. 14 *B*: in the later stages of the record, as the contraction becomes more nearly maximal, so many fresh rhythms have appeared that it is impossible to pick out the individual series (Fig. 14 *C*). This can sometimes be done in the photographic records from the fortunate chance that a fresh group of fibres bears a different orientation to the electrode and so produces an action current of a distinct form. Records showing this are given in Fig. 15. In the upper record there is first a single series at a frequency of 14 a sec., and a second series comes in after 0·6 sec. In the lower the tension has risen to 2 kg. and a series of inverted responses now appears beginning like the first two at a low frequency which increases gradually.

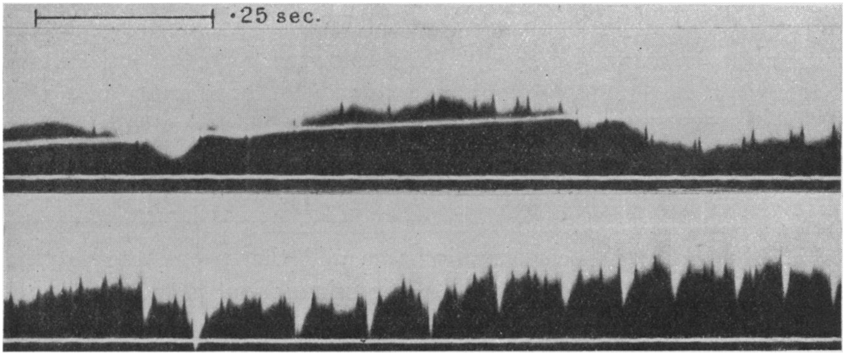

Fig. 15. Voluntary contraction of triceps (E. D. A.). Concentric needle electrodes. Pull recorded by rising line on record (connected with spring balance).

Above. Beginning of contraction.

Below. Pull = 2 kg. A fresh series of action currents appears.

Records of this kind show that in each group of muscle fibres the frequency of excitation may be so low that there can be very little summation of the contractile effect; that the frequency rises as the contraction becomes more powerful, and that at the same time more and more fibre groups come into play. The individual rhythms can often be followed much more easily in the sound records made by leading the amplified action currents into the loud speaker[1], for the ear can pick out each new series by slight differences in intensity and quality which are hard to detect in the complex electrometer record.

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[1] The method was demonstrated to the Physiological Society on October 13th, 1928.

We have been at some pains to satisfy ourselves that no fresh type of electric response enters into our records at any stage in the contraction and that the apparent complexity with strong contractions is merely due to the activity of more and more fibre groups. In view of the results obtained from the single nerve fibres this could scarcely be doubted. But a different suggestion has been put forward by Wachholder(5) and the results on which his view is based make an interesting commentary on the analysis of the electromyogram. Wachholder used two needles 2 cm. apart in the substance of the muscle and recorded the action currents with a string galvanometer. With very feeble contractions he found, as we have done, that the individual responses were separated by long intervals and that they formed a definite series with a frequency increasing gradually from a lower limit of about 5 a sec. But with stronger contractions he observed the appearance of a new type of response made up of a continuous train of rapid oscillations (at 200 a sec. or more) becoming gradually larger and larger and finally obscuring the isolated responses of the first type. As a possible explanation of these two types he suggests that the first may represent the initial rhythm of the cortical discharge and the second the rhythm superimposed on the first owing to the stimulation of the muscle receptors, but he is careful to point out the difficulties involved in this view and the exact significance of the two types is left an open question. Again Richter(6) has recorded the electromyogram in normal subjects and those with various nervous diseases, using a diffuse electrode on the head and a pad placed over the muscle and communicating with it by a small hole made through the skin. His records for feeble contractions show the same features as ours, as they give one or more independent series of responses at a low frequency which increases progressively. But he, like Wachholder, seems inclined to attribute the irregular secondary waves which appear in stronger contractions to some different type of nerve discharge less regular than that producing the primary waves. These modern studies may be compared with the original work of Piper and others in which large pad electrodes lead off from the muscle through the skin. By this method there is little or no indication of any change in frequency as the contraction develops. Small, irregular waves are present throughout and it is only in extreme fatigue that a definite change in frequency can be observed.

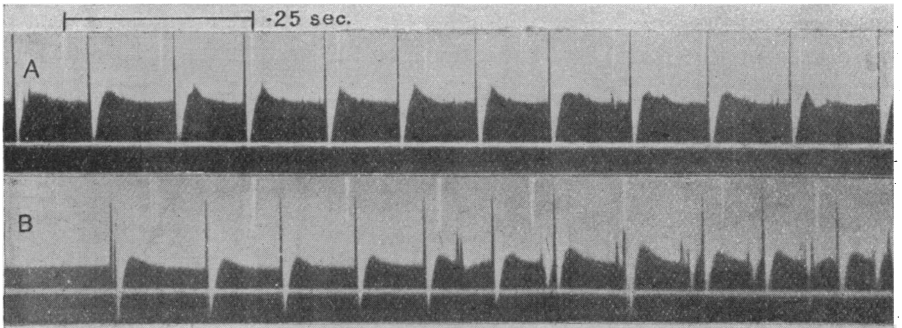
It will be seen that the detailed structure of the electromyogram becomes clearer and clearer as the electrode system has become better and better adapted for recording the electric change in a few fibres instead of the average change in the whole muscle. The needles used by Wachholder were 2 cm. apart and so would naturally pick up the responses of a large number of fibres besides those in the line joining the needles. With Richter's electrodes the puncture through the skin covering the muscle will act as a low resistance path leading from a small area on the surface of the muscle to the pad on the skin, and the electric responses will be due mainly to the fibres just below the puncture. With both systems the electric changes in a restricted number of muscle fibres will have the greatest effect on the record, but many other fibres will affect it in a minor degree. These will produce the small oscillations appearing with a strong contraction and the oscillations will be irregular and of high frequency because they are due to very many fibre groups acting independently. There is nothing new in this explanation of the small irregular waves, for it was put forward by Piper in his original work on the electromyogram. Perhaps the best evidence in favour of this view is given by comparing the sound records made with the concentric and with the double wire type of electrode. With the latter the localisation will be sharper, and with strong contractions there is usually one prominent rhythm of fairly high frequency. At present, however, we have not yet succeeded in making good photographic records with this type of electrode.

We conclude that the voluntary contraction in man is maintained, like the reflex contractions in the cat, by a series of nerve impulses which range from 5 to 50 or more a sec. in each nerve fibre, and that the gradation in force is brought about by changes in the discharge frequency in each fibre and also by changes in the number of fibres in action.

### (2) *Reflex contractions in the cat. Mechanical stimulation.*

Records made by the same method on various reflexes from the hind limb confirm those already obtained by leading from single nerve fibres, and show that the general character of the discharge in those experiments was not affected by the section of some of the afferent nerve fibres from the muscle. But the ability to record from an intact muscle allows us to study also the reflexes which are elicited by stimulation of end organs in the muscle itself. For instance in the persistent (tonic) contraction of the quadriceps in decerebrate rigidity we have always found a persistent succession of action currents at a frequency of 5–25 a sec. (see Fig. 16 *A*). The discharge may last without interruption for many minutes and the persistence and apparent regularity is such that we have often been deceived into thinking it due to an electrical artefact from a motor or contact breaker in some other part of the laboratory. Since the series of responses shows no sign of interruption or change in amplitude over long periods, it is unlikely that we have to deal with two or more fibre groups acting in rotation, though we have made no observations of the total length of time for which the series may persist and it is quite possible that other fibre groups may come into play at intervals of 10 minutes or more. It is clear that the tonic contraction which suffices to keep the leg extended when the animal is on its back is maintained by only a small fraction of the fibres in the quadriceps, for as a rule the records show only one prominent series of action currents and a change in the position of the needle point in the muscle may alter the size of the responses without bringing in a fresh series. It is our impression that the active fibres are more numerous in the deeper parts of the quadriceps (the crureus etc.), and more numerous in the soleus than in the gastrocnemius, but we have not yet collected enough evidence to be sure of this. The increased contraction produced by manipulating the leg etc. leads to an immediate increase

Fig. 16.



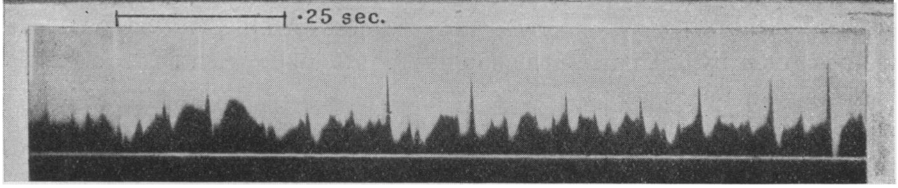


Fig. 17.

Fig. 16. *Exp.* 18. Decerebrate cat. Needle in right quadriceps.

*A*. Persistent "tonic" discharge. Portion of long record. Frequency 9·5 a sec.

*B*. Stretch reflex produced by flexing leg: beginning of response.

Fig. 17. *Exp.* 19. Decapitate cat. Needle in right tibialis anticus. Beginning of flexion reflex produced by pinching foot. Many fibres seem to be in action.

in the frequency of the persistent impulse discharge and to the appearance of other independent rhythms beginning at a low frequency and increasing rapidly until the record may become completely confused. Records made during the stretch reflex in the quadriceps or gastrocnemius show the same features and are often quite indistinguishable from those made from the human triceps during a progressive voluntary contraction (Fig. 16 *B*).

These records taken in conjunction with those from the divided nerves leave us in no doubt that the persistent contractions of the extensor muscles in decerebrate rigidity are due to low frequency impulse discharges in a fraction of the motor nerve fibres. As regards the frequency range, it is satisfactory to find that our figures agree with those recently obtained by Denny-Brown (7) by an entirely different method[1].

One other point deserves mention for it confirms the observations made in Section I on the changes in the number of fibres in action. In these we found little evidence of an accession of fresh neurones in stronger contractions when we were dealing with the tibialis anticus and peroneus longus in the spinal animal, but definite evidence in the case of the quadriceps in the decerebrate animal. The observations on the muscle action currents agree with this, for the records from the leg muscles in the spinal flexion reflex produced by pinching the foot are quite unlike those from the extensors in the decerebrate animal. Instead of each impulse series standing out sharply with more and more appearing as the contraction develops, we find a much less regular succession of action currents which vary in size and duration and appear to be due to a number of fibre groups responding more or less in phase but at slightly different times. An example of this type of discharge is given in Fig. 17. Since the action currents are nearly always composite in the records from the ankle flexors (spinal) we cannot say how many neurones are in action from moment to moment, but at least there is nothing like the progressive addition of more and more fibre groups which appears in the quadriceps. The differences pointed out by Liddell and Sherrington (9) between the spinal "d'emblée" type of reflex and the recruitment type characteristic of the extensor reflexes are well known and the difference in the character of our records is clearly related to these, but in the hamstring muscles in the spinal animal we have usually found an intermediate type of discharge, beginning with isolated action

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[1] The complete account of Denny-Brown's valuable work on the postural reflexes did not appear early enough to allow us to refer to it in detail. In general our conclusions agree so closely with his that we find we have stated them in almost identical terms.

currents and going on very soon to the confused responses due to the simultaneous activity of many fibres near the point of the needle. In man the voluntary contraction of the tibialis anticus gives records showing individual rhythms and the accession of fresh fibres just as clearly as do the extensor muscles in the cat's thigh.

On such questions as the maximum frequency of discharge, the possibility of a rotation of activity, etc. we must reserve judgment until we have more perfect electrodes which can be trusted to pick out the action currents of single fibre groups at the height of a contraction. The concentric type of electrode, however, has one advantage which is not likely to be possessed by systems giving sharper localisation in that it allows us to use electrical stimulation to elicit the reflex contractions. So much of our knowledge of the motor centres has been obtained by this method of stimulation, that we were disappointed to find it impossible to eliminate the stimulus artefact when we were leading from the nerve fibre and correspondingly glad that it could be done without difficulty by leading from the muscle with electrodes of the unipolar type.

### (3) *Reflex contractions. Electrical stimulation.*

Records of the action currents in various muscles in response to rhythmic stimulation of afferent nerves were published by Cooper and Adrian(8) in 1924 and a distinction was drawn between the flexion reflex (spinal animal) where the stimulus rhythm is reproduced in the action current record and the crossed extension reflex (decerebrate) where it is usually absent. These differences were found to agree with those shown previously in the muscle tension records by Liddell and Sherrington(9) and subsequent work has confirmed the distinction(10). Hitherto the action currents have been led from an entire muscle, and with this arrangement the electromyogram of the quadriceps in the crossed extension reflex is usually made up of a rapid and irregular series of oscillations of much the same appearance whatever the frequency of the stimuli to the afferent nerve. In some preparations there are larger waves at the same frequency as the stimuli, but throughout the record the rapid irregular discharge is the main feature of the response. On the other hand, in the flexion reflex (spinal animal) the response may consist entirely of large "primary" waves recurring with the frequency of stimulation, though there is sometimes a background of irregular "secondary" waves of high frequency. Each primary wave is obviously due to a more or less synchronous volley of impulses in many motor fibres evoked by the corresponding volley of impulses in the afferent nerve. The nature of the discharges which produce the rapid irregular waves was more uncertain, but it can be made out by recording from single fibre groups instead of from the entire muscle.

In these experiments the popliteal branch of the sciatic was cut through distally and stimulated by shielded electrodes with break shocks from a coreless coil coupled to a rotating contact breaker of the type described by Cooper and Adrian. The frequency of stimulation was read on an electric speed indicator and was marked on the record by the loud speaker movement carrying a pointer in the eyepiece of the electrometer (see p. 131). The movement was driven by a battery through a circuit interrupted by an independent set of contacts revolving on the same shaft as those in the primary circuit of the induction coil. This arrangement is capable of signalling the stimulation rate up to 200 a sec. or more.

### *Crossed extension reflex (decerebrate).*

As before we were unable to analyse the rhythms of individual fibre groups at the height of the discharge, but the records throughout weak contractions and at the beginning and end of powerful contractions are clear enough. They show one or more rhythms ranging between 10 and 20 a sec., varying with the strength of the stimulus and the period for which it has been in action and usually bearing no relation to the frequency of stimulation. Our clearest records were made from the gastrocnemius and soleus group, probably because these muscles contract less forcibly and the fibre groups which are in action are further apart. A selection from one experiment is given in Fig. 18. Here the stimuli were near threshold value and there was a long latent period. The records show the moment at which the stimulation ends and the beginning of the after discharge. With stimuli at 3, 88 and 228 a sec. the response frequencies are 16, 14 and 18 a sec. With weaker stimuli at 228 a sec. the response frequency is only 11 a sec. There is no break in the rhythm when the stimulus ceases and the degree of regularity throughout the contraction is of the same order as in all the motor discharges already described. Fig. 19 *A* is from another experiment of the same kind made at the end of the after discharge and showing the progressive decline in frequency.

Thus with electrical stimulation of afferent nerves the irregular response of an extensor muscle is built up out of responses in the individual fibre groups which appear not to differ in any way from those produced

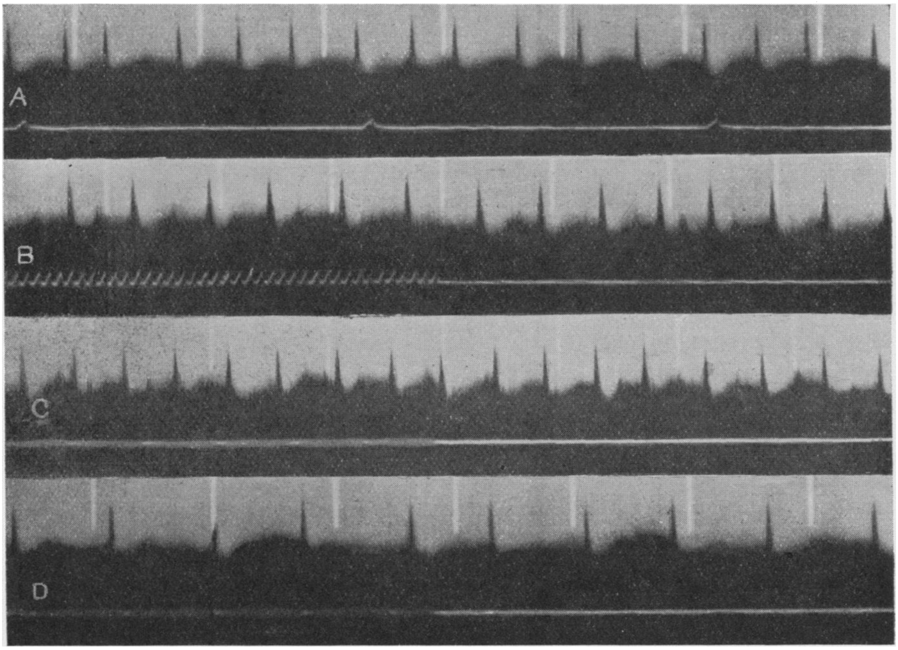

Fig. 18. *Exp.* 20. Decerebrate cat. Needle in right gastrocnemius or soleus. Stimulation to left peroneal nerve at various frequencies. Stimuli near threshold strength. In *B*, *C* and *D* the records show the end of stimulation and the beginning of the after discharge.

| | | | | |
|---|---|---|---|---|
| *A*. | Stimuli | 3 a sec. | Frequency | 16 a sec. |
| *B*. | ,, | 88 ,, | ,, | 14 ,, |
| *C*. | ,, | 228 ,, | ,, | 18 ,, |
| *D*. | ,, | 228 (weaker). | ,, | 11 ,, |

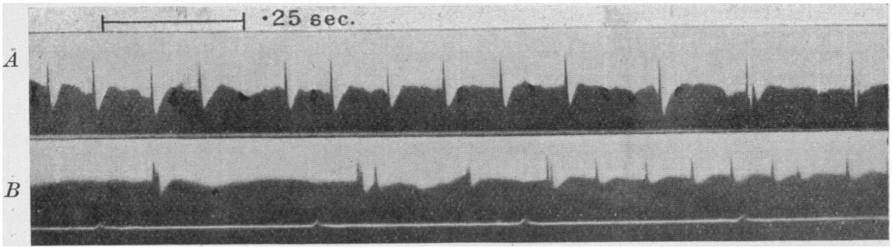

Fig. 19. *A*. *Exp.* 18. Decerebrate cat. Needle in right quadriceps. End of after discharge of crossed extension reflex produced by stimulating left sciatic at 80 a sec.

*B*. *Exp.* 20. Decerebrate cat. Needle in right gastrocnemius or soleus. Stimuli at 3 a sec. to left peroneal. Beginning of response, showing double action currents occurring after each stimulus with a shorter and shorter latency. After the third stimulus the usual type of discharge appears.

by the normal stimulation of the sense organs. With weak stimulation the frequency in each fibre group may never exceed 15–20 a sec. There is usually a sharp initial rise to a fixed rate which is maintained during the stimulation period and followed by a more gradual decline. Such changes in rate will naturally alter the force of contraction, but in these reflexes, as in voluntary contractions, the grading must depend mainly on the number of fibres in action.

Except at the beginning of the discharge there has been no indication of the stimulus frequency in these records, but in Exp. 20 with rates of stimulation up to 10 a sec. there is a definite grouping of impulses at the beginning of the response to fairly strong stimuli. An example of this is given in the lower half of Fig. 19. The stimulation is at 3 a sec. and two action currents in rapid succession follow each of the first three stimuli, the interval between the stimulus and the double response becoming shorter and shorter (0·081, 0·056 and 0·029 secs.). After the second of these double responses the usual low frequency discharge develops in the usual way and no further double responses are seen after the third. If all the muscle fibre groups behave alike, the contraction would evidently show some indication of the stimulus rhythm during the first second and would then cease to do so. The record is particularly interesting when taken in conjunction with that in Fig. 20 where we see how prominently the stimulus rhythm is represented in the spinal flexion reflex.

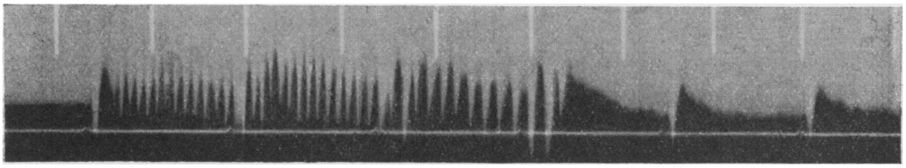

Fig. 20. *Exp.* 19. Decapitate cat. Needle in right tibialis anticus. Stimuli to right peroneal at 6 a sec. Beginning of discharge. The record shows the "primary" response to each stimulus and "secondary" responses after the first three stimuli.

| | | | | |
|---|---|---|---|---|
| Frequency of secondary | discharge after | first | stimulus | 85 a sec. |
| ,, | ,, | second | ,, | 75 ,, |
| ,, | ,, | third | ,, | 60 ,, |

### *Flexion reflex* (*spinal*).

The response of the entire muscle in the flexion reflex is often a single series of large action currents which recur with the frequency of stimulation and can scarcely be distinguished from the action currents produced by stimulating the motor instead of the sensory nerve. We should naturally expect that the records made with the needle electrode in responses of this type would differ very little, except in the sharpness of the action currents, from those made from the entire muscle, and many of our records from the ankle flexors show nothing more than a series of action currents at the same frequency as the stimulus.

In many preparations, however, the response of the entire muscle shows the rapid, irregular secondary waves as well as the large primary waves, and we were anxious to analyse these into the single fibre discharges. Unfortunately we failed to detect anything but the simple primary wave discharge in all but one preparation, probably because the majority of the neurones discharge at the same rate as the stimuli and only a few contribute to the secondary waves. In one preparation however the response was of unusual type, beginning with a very powerful flexion reverting almost at once to a weaker sustained contraction. This may have been due to a concurrent inhibition set up by the proprioceptors in the leg, for the limb was not fixed and there was no resistance to the movement.

A record of the beginning of the discharge in this experiment is given in Fig. 20. The stimuli occur at 6 a sec. It will be seen that each stimulus is followed by a distinct action current occurring after a brief interval, and that during the first half second there is also a rapid succession of action currents beginning at a frequency of 80 a sec. These are much the same size as the "primary" action currents which follow the stimulus rhythm, and so are probably due to the same fibre group. The rhythm of the rapid discharge is thrown out by each stimulus; in the third period it has fallen to 60 a sec. and it then ceases abruptly, though the small notches on the base line show that much the same thing may be going on for a longer period in other fibre groups. Fig. 20 is typical of many records made from the same preparation and, although the contraction did not follow the usual course, the discharge probably gives a fair representation of the make up of the secondary waves. It appears, then, that each volley of afferent impulses in addition to causing the corresponding volley of motor impulses which make the primary wave, sets up in some of the motor neurones a rhythmic discharge of the same type as that developed in voluntary contractions, and in the reflexes to mechanical stimuli, *i.e.* a discharge which varies in frequency according to the general level of excitation in the motor centres.

## DISCUSSION.

The most remarkable point which arises from this paper is that the discharge of a motor nerve cell can scarcely be distinguished from the discharge of a sense organ. In both the frequency of the discharge controls the intensity of the effect which the message produces and is itself controlled by the intensity of excitation. The sense organ may give a series of impulses with a nearer approach to a completely regular rhythm, but in both the frequency varies over much the same range under average conditions of excitation. It must be admitted that the data for the frequencies of the sensory discharge have been obtained partly from cold-blooded and partly from warm-blooded animals, and in only a few cases have we exact information as to the frequency in each nerve fibre. But there is little doubt that a range of 5 to 100 a sec. would cover the frequencies found in a large number of sense organs subjected to a stimulus of normal intensity, just as it covers the normal frequencies of the motor discharge. That the range of frequency should be so much alike is all the more striking when we consider the different structures involved. The only structural factors common to the sense organ and the motor nerve cell appear to be the terminal arborisation which links the axon of the sensory fibre with the cells of the sense organ, and that which invests the nerve cell or forms the junctional zone between its dendrites and the axons of other neurones. The suggestion that we are dealing with some fundamental property of synapses in general is strengthened by the fact that the discharge in the eel's optic nerve fibres seems to be of the same character (11), for in this case the discharge must be generated in the synaptic regions of the retina rather than in the rod and cone layer. Clearly more work must be done before we can accept the view that all nervous messages are of the same general type, but some of the consequences of this view may be pointed out. In the first place it would mean that we must abandon the idea that central inhibition can be explained on the lines suggested by Lucas (12), Forbes (13) and Adrian (14), *i.e.* by the depressant effects produced by high frequency impulse discharge. Various heroic assumptions might overcome the difficulties which would arise, but they are scarcely worth making[1]. We must therefore

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[1] Objections to this view have been raised on the score of the lasting inhibitory effect which may follow a single stimulus (15). These objections can be met by the fact that in any case the inhibitory discharge must be produced by a "central process" of the same kind as that which gives the excitatory effect and that this may certainly outlast the stimulus. But on any scheme based on the interference of trains of impulses

revert to the view that two qualitatively different processes can occur in the synapses to account for the inhibitory and the excitatory effect. A scheme on these lines has been worked out in detail by Sherrington (16), and it is there suggested that excitation of the motor neurones by the afferent impulses is due to the liberation of a specific exciting substance in the synaptic regions. The work of Lewis (17) on the control of the skin vessels by impulses reaching them through the collaterals of sensory fibres, and that of Dale and Gasser (18) on the contractions produced in denervated muscle by stimulation of the sensory nerve and by drugs of the acetyl choline class, suggest very strongly that the terminations of sensory fibres may produce substances which have a stimulating effect on certain tissues, and the production of $NH_3$ during the activity of medullated nerve shows that the passage of an impulse into the spreading central terminations of an afferent fibre might liberate substances of considerable activity. It is, however, quite possible that all the discharges of the motor neurones are not brought about by the same mechanism. In the spinal flexion reflex, for instance, each volley of afferent impulses seems to be directly transmitted to the motor neurones, and there is little reason to suppose that we have to deal with a process differing greatly from that involved in the conduction of an impulse from one section of a nerve fibre to the next. But the production of the secondary waves (Fig. 20) demands a mechanism of the type operating in the crossed extension reflex where direct transmission does not occur, and here the cause of the discharge may well be a more lasting excitatory state produced in the synaptic region as a result of the passage of each impulse. Sherrington has pointed out how the latent period, rate of rise and length of after discharge in the crossed extension reflex depend on the strength of stimulation, *i.e.* on the concentration of impulses arriving at the synaptic regions. Again, in the optic nerve discharge the latent period depends on the number of receptors in action as well as on the intensity of the stimulus, and it seems as though each impulse which enters the synaptic zone within a given time adds its quota to the excitatory effect—as we should expect it to do if the effect depends on the presence of something liberated by the impulse and not immediately destroyed.

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we have to face the difficulty that in an intense excitation, where the central paths are discharging at fairly high frequencies, inhibition should be brought about much more easily than in a feeble excitation where the frequency is lower. In fact if intensity of excitatory effect depends on frequency, the greater the excitation the smaller will be the degree of inhibition needed to extinguish it.

Whatever the excitatory process may be, we can visualise its operation in the motor centres by the diagram given in Fig. 21. This is intended to represent the development of a contraction such as the crossed extension reflex in the quadriceps. The motor neurones are indicated by the vertical lines and the numbers on these lines represent the frequency of discharge from the neurone when the excitation reaches a particular level. At the beginning of the contraction there are a few isolated centres of excitation producing a low frequency discharge in a few neurones; as more sensory impulses arrive the level of excitation rises and spreads over the motor centre, giving a high frequency discharge in many nerve fibres. This diagram applies only to the recruitment type of reflex where the connection between afferent and efferent neurones is indirect. As we have seen, in the spinal flexion reflexes a given afferent nerve or group of receptors is much more closely linked with a given group of motor neurones. When an afferent nerve is stimulated rhythmically the motor neurones discharge with the same rhythm: when receptors are stimulated the frequency of the motor discharge varies with the strength of the stimulus, *i.e.* with the frequency in the afferent fibres, but a high frequency discharge from a given group of receptors shows no tendency to activate more motor neurones than one of low frequency. With the mechanical stimuli which we have used only a fraction of the muscle can have been active; that fraction remained constant and the contractions were graded entirely by the frequency, because we varied the

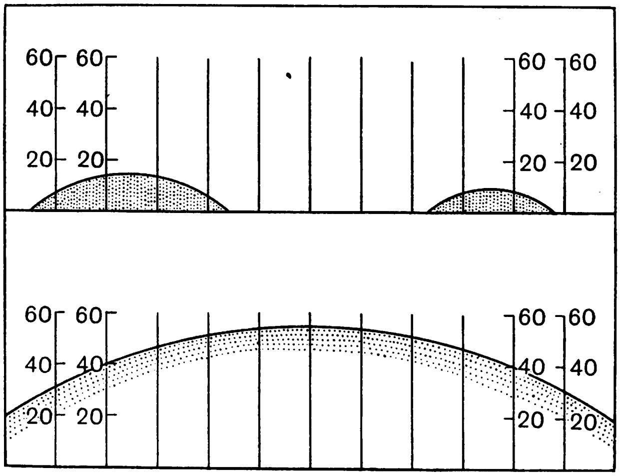

**Fig. 21.** Development of excitation process in a group of neurones (see text).

intensity of the stimulus rather than the area covered by it. Graded electrical stimulation of an afferent nerve must produce just the reverse of this, for here (if we neglect the secondary waves) the frequency of the motor discharge is fixed by the frequency of stimulation, but an increase in the stimulus will excite more afferent fibres and so will activate more motor neurones. It will be seen, therefore, that our results do not conflict with the evidence brought forward by Cooper, Denny-Brown and Sherrington(19) as to the "fractional activation" of muscles, and they confirm the distinction drawn by Liddell and Sherrington(9) between the "recruitment" and the "d'emblée" type of response.

We have made no attempt to deal with the arguments which have appeared in support of the view that the motor nerve fibre may discharge at frequencies so high that the muscle is unable to respond to each nerve impulse. The records of single nerve fibre discharges show that in fact the frequency is often so low that the muscle fibres must fail to give a smooth contraction, but we cannot say that maximal sensory stimulation may not produce reflex discharges of higher frequency than those we have recorded. Certainly in the spinal flexion reflex the frequency of the primary waves may be brought well above 100 a sec. by rhythmic stimulation. But the fact that the average frequency with a fairly strong contraction is round about 50 a sec. in our nerve fibre records makes it difficult to accept the most plausible line of evidence in favour of very high frequencies as a normal occurrence in certain reflexes. This evidence is derived from the alcohol block method used by Forbes and Olmsted(20) and Liddell and Olmsted(21) and based on the view that alcohol will block or at least diminish the frequency of a train of high frequency impulses whilst leaving a lower frequency untouched. The fact that alcohol applied to the motor nerve causes an extinction of certain reflexes although the nerve can still conduct when stimulated electrically is held to indicate that the reflex discharge must have been extinguished in virtue of its high frequency, and for this to occur the impulses must follow one another at intervals which Forbes and Olmsted reckon as certainly no more than 3·5 and probably no more than $3\sigma$. But it is clear that an alcohol block which only comes into action when the frequency of the discharge exceeds 300 a sec. would not have the least effect on any of the discharges recorded in our experiments on single nerve fibres, where the frequency has never risen above 100. The failure of the reflexes under the alcohol block must be due to some other cause than the high frequency of the discharge, and if this be admitted it becomes doubtful if the method can really furnish reliable information about the reflex frequency.

An important point which must be left untouched concerns the degree of synchronous activity in the neurones carrying out a particular reflex. This was discussed in Part I, and for the present we have little to add, as we have been mainly concerned with the individual neurone.

All these questions relate to the mechanism of the neurone, but there are several points of interest relating to the muscular contraction and arising from the fact that, except in powerful contractions, the response of the individual fibres will be an incomplete tetanus or often little more than a succession of twitches. A contraction sustained in this way may need a greater expenditure of energy than one due to a complete tetanus in fewer fibres, but it may have the great advantage of preventing the accumulation of metabolites which causes the early fatigue of a complete tetanus. This would be due in part to the long time elapsing between each excitation, but the removal of waste products might also be favoured by the improved blood supply. It is at least probable that the flow of blood through a steadily contracted muscle will be much smaller than through one where the different fibre groups are in continual movement owing to the intermittent contractile waves set up by a low frequency discharge. Thus the type of discharge which we find in the postural reflexes seems excellently adapted for maintaining a moderate degree of contraction for long periods without fatigue.

## SUMMARY.

Records have been made of the reflex impulse discharges in individual nerve fibres supplying various muscles in the hind limb of the cat. The method was that previously used for recording discharges in the nerve fibres of the phrenic. The reflexes (spinal flexion and decerebrate crossed extension) were produced by mechanical stimulation (pinching the foot), and the discharges were recorded in nerve fibres supplying the peroneus longus and tibialis anticus (flexion) and the vastus medialis and lateralis (extension). Confirmatory experiments were made by leading from restricted groups of muscle fibres by electrodes of very small dimensions. The action currents were recorded by a three valve amplifier and capillary electrometer, and much information was gained by converting the action currents into sound waves by means of a second power amplifier and a loud speaker. The main results are as follows:

(1) Flexion reflex (spinal). In the nerve fibres to the peroneus longus the discharge has been a series of impulses recurring fairly regularly

at a frequency which varies from 5 to 25 a sec. The frequency increases as the contraction develops. In the fibres to the tibialis anticus the discharge is of the same type but the frequency may reach 45 a sec. With mechanical stimulation of the foot the grading of the contraction appears to be due mainly to this change in frequency, for there is little evidence of changes in the number of neurones in action.

(2) Extension reflexes (decerebrate). In the nerve fibres to the quadriceps there are often persistent discharges ranging from 10 or less to 25 a sec., when the postural tone of the muscle is well marked. During a crossed extension or an extension due to stimulation of the labyrinths the discharge rises to frequencies which may be as high as 90 a sec., and there is evidence that many fresh neurones come into play as the contraction develops.

(3) Records of muscle action currents made by concentric needle electrodes show the discharge of groups of muscle fibres innervated by single neurones, and these agree with the discharges recorded in the single nerve fibres. At present the method can only be used with certainty during weak contractions where the active fibre groups are some distance apart, but in those we find the same low frequency discharges and the same increase in frequency and in the number of fibres in action as the contraction increases.

(4) During voluntary contraction of the triceps in man the impulse discharges are of the same type as those in the cat's quadriceps. The electromyogram of the entire muscle is compounded of the rhythmic discharges in the different groups of muscle fibres. These vary in frequency with the strength of the contraction, and the irregular high frequency oscillations in the electromyogram are due to fibre groups responding out of phase with one another.

(5) The persistent tonic contraction of the quadriceps in decerebrate rigidity is maintained by discharges at a frequency of about 5–25 a sec. from some of the neurones. During the stretch reflex the frequency increases and more neurones come into play.

(6) When the crossed extension reflex is elicited by rhythmic electrical stimulation to a sensory nerve, the frequency of the discharge usually bears no relation to the frequency of the stimuli, but increases with the contraction from a lower limit of 5–10 a sec.

(7) In the spinal flexion reflex with electrical stimulation each volley of afferent impulses produces a corresponding response in the motor neurone. In the intervals between these responses there may be a rhythmic discharge of varying frequency.

(8) The likeness between the impulse discharge from a sense organ and that from a motor nerve cell suggests that both are due to some property common to axon or dendrite terminations in general.

(9) The low frequency of discharge in the motor nerve fibres during weak contractions may be of importance in preventing the accumulation of metabolites within the muscle fibres and in assisting the blood flow through the muscle.

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