THE FREQUENCY OF DISCHARGE FROM THE SPINAL CORD IN THE FROG.

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DURING a voluntary or reflex movement the contracting muscle gives rise to a rapidly oscillating action current. The larger oscillations sometimes show a fairly definite rhythm of about 50 per sec., but if every oscillation is counted the frequency is usually nearer 120–150 per sec. and there is no true regularity in the series. Since the electromyogram was first studied by Piper and Buchanan the interpretation of these waves has been a source of controversy. According to one view each wave which appears in the muscle is due to a corresponding volley of impulses in the motor nerve fibres, so that the frequency of the electromyogram is an exact reproduction of the frequency of discharge from the motor cells of the cord. According to the other, the frequency in the muscle is usually determined by the muscle alone and represents a vain attempt to follow a much more rapid succession of impulses, or even some continuous state of excitation, arising in the spinal centres.

Without attempting a complete survey of previous work (which has been given by Forbes(1), Trendelenburg(2) and others) it may be said that the former view is strongly supported by the observations of the action currents in the phrenic nerve during respiration, first made by Dittler(3) and confirmed and extended by Gasser and Newcomer(4). Here the electrical oscillations in the nerve synchronise exactly with those in the muscle which it supplies, the frequency being about 90 per sec. It is also supported by the recent work of Bass and Trendelenburg which shows synchronous irregularities in the response taken from different regions in a large muscle. On the other hand the view that the frequency of nervous discharge is greater than the frequency of oscillations in the electromyogram gains considerable weight from the fact, shown by Buchanan(5), Forbes and Rappleye(6), and Fahrenkamp(7), that the frequency of the electromyogram can be altered by changing the temperature of the muscle. Buchanan worked on the reflex contractions of strychninised frogs where the electric responses occur in a succession of short groups. She found that the frequency of the action currents in each group depended only on the temperature of the muscle and not on that of the spinal cord and concluded that the electromyogram could not represent the frequency of discharge from the spinal cord. Forbes and Rappleye found that in human muscles the frequency of the voluntary electromyogram could be changed by heating or cooling the limb, and showed that this result might be explained on the supposition that the spinal centres discharge at a rate of 300–1000 per sec., a rate too rapid to be followed by the muscle. The same conclusion has been reached by Athanasiu(8) on evidence which will be discussed later.

Our interest in these conflicting results arose from an attempt made by Adrian and Olmsted(9) to determine the refractory period of the arc for the flexion reflex in the cat. Quantitative data of the rates of recovery of reflex paths seemed essential to the analysis of central conduction and we tried to obtain these by stimulating an afferent nerve with double or repeated shocks and observing the electric responses in the reflexly contracting muscle. It was found that the muscle would not respond more rapidly than 160–200 times per sec. when the afferent nerve was stimulated although it could be made to respond up to 400 times per sec. by stimulating the motor nerve. We concluded that the limiting frequency of 160 per sec. was imposed by the central part of the arc, since the muscle and the peripheral nerves would all respond more rapidly. This conclusion is quite incompatible with the view that the spinal centres normally discharge at a rate too rapid for the muscle to follow. It is conceivable that the path for the flexion reflex differs radically from that of the other reflexes, or that the use of rhythmic electric stimuli imposes an abnormally slow rate of discharge, but neither explanation seemed very likely. As a first step, therefore, we have re-examined some of the evidence which favours the higher rate of discharge from the cord.

The central fact is that in a reflex or a voluntary movement a change of temperature in the contracting muscle is found to alter the frequency of the electromyogram. We have repeated Forbes' observations on the electromyogram of human muscles in voluntary contraction before and after cooling the forearm with ice and we have found the change in frequency which he describes, but it did not seem to us that this result was conclusive evidence in favour of a very rapid rate of discharge from the central nervous system. Weizsäcker(10) and Dusser de Barenne(11) have shown recently that the frequency of the electromyogram depends on the integrity of the proprioceptor nerves from the muscle. If these are interfered with, as by disease or by injecting novocaine into the muscle, the frequency of the oscillations is reduced. This result agrees with Hoffmann's view that the voluntary contraction is made up partly of a series of tendon reflexes reinforced from higher centres, and it suggests that cooling the muscle may affect the frequency of the electromyogram because the sensory side of the arc is impaired and not because the muscle cannot respond as rapidly as it did before. An increase in frequency on warming is not so readily explained, but here too the change in the state of the proprioceptors cannot be excluded. This objection does not apply to Buchanan's experiments on frogs, for in some of these the proprioceptor arc was destroyed by cutting the dorsal roots. These experiments we deal with below.

Method. We used spinal frogs, the brain being destroyed from 1 to 24 hours before the records were made. When the spinal cord was to be maintained at a constant temperature the body of the frog was surrounded by coils of lead tubing through which water could be circulated. When the temperature of the cord was to be changed it was cooled by placing ice in a metal container over the lower vertebræ or warmed by concentrating the rays of a "pointolite" lamp (500 C.P.) over the same area. The amount of heating could be readily controlled by an iris diaphragm in front of the condenser lens. An approximate idea of the temperature of the cord was given by a small thermometer thrust down the œsophagus into the stomach. As the heating or cooling was greatest on the surface of the back the change of temperature of the spinal cord would be greater than that in the stomach, but a comparison of the actual temperature in the vertebral canal measured with a thermo-junction and the temperature given by a thermometer in the stomach showed a difference of not more than two degrees when a steady state had been reached.

The temperature of the muscle was controlled by fixing the legs of the frog in two double walled metal troughs through which water could be circulated. The troughs were open at the top to admit the non-polarisable electrodes connecting the muscle to the galvanometer. The surface of the trough was insulated with shellac and the limb was kept just out of contact with it. With this arrangement the temperature of the muscle became very nearly constant when water at a given temperature had been circulating for 20 minutes; it was measured by a thermometer with a small bulb pressed against the surface of the muscle: in control observations this was found to give a reading identical with that obtained from a thermo-junction thrust into the substance of the muscle.

The contractions whose action currents were to be recorded were produced either by pinching the fore-limbs or the opposite hind limb or by electrical stimuli to an afferent nerve, usually the opposite sciatic or one of the dorsal roots of the same side. The stimuli were break induction shocks from a coreless coil delivered by a rotating contact breaker previously described (12). The muscles used were the gastrocnemius or the hamstrings or adductors of the thigh. The gastrocnemius was isolated except at its origin and the electrodes (Lapicque type) were applied to the middle of the muscle and to the tendon. When the thigh muscles were used they were not isolated and the electrodes were merely fixed to the surface of the muscle. With such an arrangement the action currents might have been derived from more than one muscle, but it was found that the contraction of muscles other than that under the electrodes produced little or no effect on the record. The action currents were recorded with the string galvanometer on cinematograph film moving at a speed of about 15 cm. per sec. The usual tests were made to detect the presence of artefacts in the record due to the spread of the stimulating current.

We had two main difficulties to contend with. The first was that the state of reflex excitability did not remain constant during the lengthy periods needed to pass from one temperature to another. This applies more especially to the reflexes produced by stimulating an afferent nerve, but the variation was serious only during the breeding season. The other difficulty arose in counting the oscillations in the electromyogram. These vary greatly in size and it is often difficult to decide whether a large wave does not mask one or more smaller ones near it. In stating our results we have given (*a*) the total number of oscillations per sec., counting every rapid excursion of the string, however small, as a wave, and (*b*) the number of "large waves" per sec. For the latter we have counted every wave which is more than half the size of the largest wave in the record. The choice of this standard is quite arbitrary but the significance of these figures will appear later. The interval between successive oscillations is extremely variable and in the frog we have never seen anything approaching the almost regular 50 per sec. rhythm which is sometimes present in the human electromyogram. At the same time the total number of waves counted in successive tenths of a second does not usually vary by more than 20 p.c. Fig. 1 shows a typical electromyogram of the adductors of the thigh in a spinal frog at 15·5° C. stimulated by pinching the fore-limbs, and this gives a good idea of the degree of irregularity usually present.

Effect of altering the temperature of muscle. In this series of experiments the temperature of the spinal cord remained constant and that of the muscles was changed. In some, a single muscle was brought successively to different temperatures, in others one leg was cooled and the other was warmed and the action current was led from them alternately. In the first experiments the muscles were examined at two temperatures, one above and the other below that of the cord and in these there was generally a decided difference in the frequencies of the electromyograms. As Buchanan had previously shown, this difference was present after the dorsal roots from the muscle had been cut. For example in a frog with the 8, 9 and 10 dorsal roots cut on both sides and the action currents led from the two gastrocnemii, one warmed to 22° and the other cooled to 10°, the body being at 15°, the reflex contractions obtained by pinching the fore-limbs gave an electromyogram of 100–120 oscillations per sec. for the warm muscle and 70–90 for the cold. The differences were evident but they were not very great and in some experiments it was by no means certain that they existed at all. A survey of the records and a comparison with Buchanan's results suggested that the difference in frequency was greatest when the muscle was cooled to a temperature much below that of the spinal cord. This had been anticipated on theoretical grounds. Beritoff(13) in his analysis of the frog's electromyogram has pointed out that the limiting frequency of response in the reflex arc will be determined by that part of the arc in which the refractory period is longest; the muscle might become the slowest component of the arc if it were cooled although it was not so when the whole arc was at one temperature. He finds that in the summer frog the maximum frequency which the muscle can follow when the motor nerve is stimulated is about 200 per sec. The average frequency in the reflex electromyogram is 100 to 120 per sec. If this represents the rate of discharge from the spinal centres a change in the temperature of the muscle will not affect the frequency of the electromyogram unless the muscle is cooled down to a temperature at which it will no longer respond to 120 impulses per sec. As soon as this temperature is reached the frequency of the electromyogram will be determined by the ability of the muscle to respond, and not by the rate of discharge from the cord.

If the change in frequency recorded in Buchanan's and our experiments is to be explained in this way we ought to find (*a*) that warming the muscle above the temperature of the spinal cord should not alter the frequency, and (*b*) that cooling it should not do so until the temperature of the muscle is such that it would no longer be able to respond to impulses reaching it with this frequency from the motor nerve. It would be difficult to obtain direct evidence on the latter point as it would involve bringing the muscle to many different temperatures, but it can be shown that a small reduction of temperature is quite enough to make the muscle unable to follow the discharge from the cord although the frequency of this is no greater than that of the normal electromyogram. In Table I we have compared the frequency of the reflex electromyogram in the gastrocnemius with the maximum frequency of response of which the muscle was capable when the motor nerve was stimulated. The data are taken from five frogs all at a uniform temperature throughout.

TABLE I.

Exp.	Temp. ° C.	Frequency of reflex electromyogram per sec.	Maximum frequency of response in muscle per sec.
1	10	80– 90	120
2	10	80–100	120
3	14	100–120	160
4	14	120	160
5	13·5	100–130	160

Exps. made in November; reflex contraction produced by pinching; dorsal roots not cut. Motor nerve afterwards stimulated *in situ* to give column 4.

It will be seen that the muscle is normally responding at a rate which is fairly close to its maximum capacity. How much this maximum rate is reduced by cooling may be seen from another experiment in which a gastrocnemius-sciatic preparation was maintained at various temperatures in a water-jacketed chamber and stimulated with rhythmic induction shocks.

Exp. 6. (Sept.) Gastrocnemius-sciatic preparation, stimulus to sciatic.

Temp. ° C.	Maximum frequency of electric response in muscle per sec.
7	80
13	160
20	240

The maximum frequency is more than doubled for a rise of 10° C., so that a fall of 5° should reduce the maximum frequency by at least 50 p.c. A reference to Table I shows that a reduction of this extent would be quite enough to make the muscle unable to respond as rapidly as it did in the reflex contraction before it was cooled. Thus we should expect a change in the frequency of the electromyogram on cooling the muscle through 5°, even though the frequency at normal temperatures is determined by the cord alone. At the same time the experiments bring no evidence against the alternative view that the frequency of discharge from the cord is too rapid for the muscle to follow even at normal temperatures.

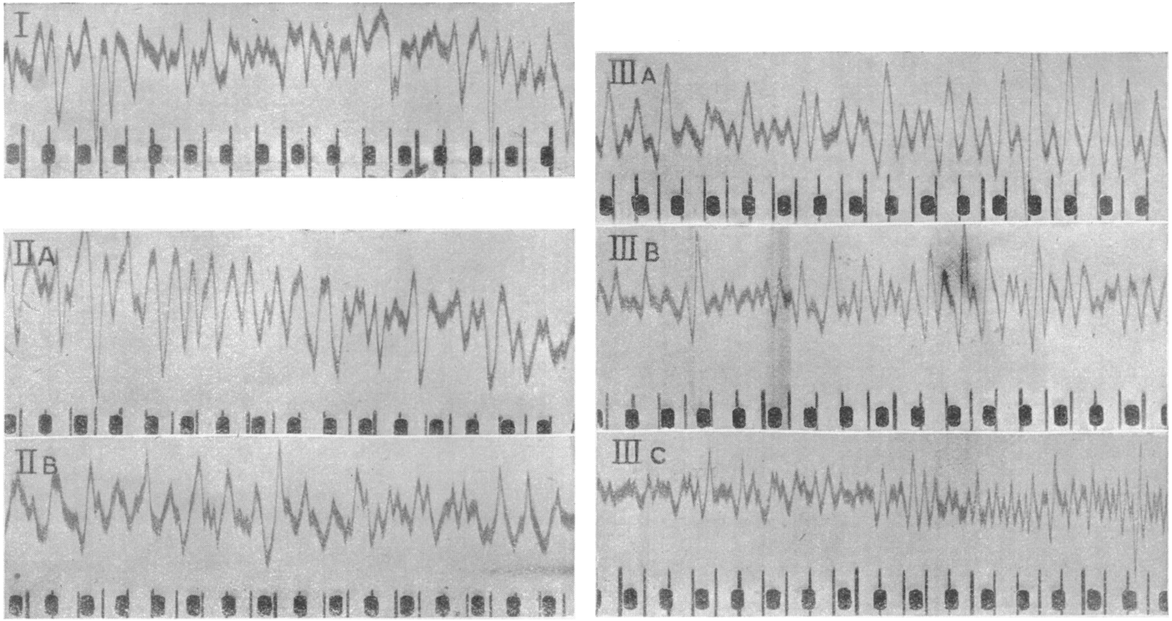
Much more decisive evidence is likely to be gained by warming the muscle instead of cooling it. If the discharge from the cord is normally too rapid for the muscle to follow, warming the muscle should increase the frequency of the electromyogram and the increase should continue with rising temperature as long as there is any difference between the frequency of discharge from the cord and the frequency of response in the muscle. To test this point we have made three complete experiments (Table II) in which the body of the frog was kept at a temperature of about 10° C. and the muscle was examined at temperatures ranging between 10° and 25° C. The leads were taken from the hamstring muscles and reflex struggling movements were produced by pinching the fore-limbs.

TABLE II. Reflex contraction of hamstring muscles.

	Temperature		Reflex electric response Frequency per sec.	
Exp.	Cord ° C.	Muscle ° C.	Counting all waves	Large waves only
7	9	13	130, 120, 150, 150, 140	80, 80, 50, 50, 80
	—	19	110, 100, 120, 120, 110	40, 30, 40, 50
	11	20	140, 150, 140, 130, 110	60, 40, 60, 50, 40
	9	11·5	100, 120, 110, 100, 120	50, 50, 50, 60, 60
8	10	11	130, 120, 120, 120, 110	50, 60, 40, 60, 40
	—	22	140, 130, 150, 110, 130	40, 60, 50, 40, 60
	—	12	100, 110, 110, 90, 90	40, 50, 40, 40, 50
	—	18	130, 120, 140, 140, 150	60, 40, 40, 50, 40
9	9	20	130, 100, 120, 90, 110	30, 40, 30, 30, 30
	—	12	110, 130, 90, 110, 80	30, 20, 30, 40, 30
	11	19	140, 110, 120, 130	30, 40, 50, 30, 30
	—	25	110, 140, 150, 120, 100	40, 30, 50, 40, 60
	—	11·5	120, 130, 130, 110, 130	30, 50, 40, 50, 40

Exps. made in May. Dorsal roots not cut. Oscillations counted in periods of one-tenth sec. taken at random from different parts of the record.

Table II shows that on the whole the frequency of the reflex electromyogram is slightly increased by a ten degree rise of temperature when all the waves are counted, but the difference is rarely greater than 20 p.c. and during a good deal of the records it cannot be detected at all. The average increase in frequency for a 10° rise works out at 7 p.c. There is no evidence of any change in frequency when only the large waves are counted. Typical records of these experiments are given in



Figs. 1–3.

Fig. 1. Normal reflex electromyogram. Contraction of hamstrings on pinching fore-limb. $T = 15{\cdot}5°$ C.

Fig. 2. Reflex response in thigh muscles (Exp. 7). (*a*) Cord 9° C., Muscle 11·5° C., Frequency 120. (*b*) Cord 11° C., Muscle 20° C., Frequency 120–130.

Fig. 3. Sciatic-gastrocnemius preparation. 640 stim. per sec. to nerve. Electric response of muscle (Exp. 10). (*a*) 7° C., Frequency 80 per sec. (*b*) 10° C., Frequency 110 per sec. (*c*) 20° C., Frequency 170 per sec. Time marker gives ·02 sec. in all records.

Fig. 2 (*a*) and (*b*.) In (*a*) the muscle was at 11·5°, in (*b*) at 20°, the spinal cord being at 9–11°. The frequency is about 120 per sec. in both. It will be noticed, however, that the peaks of the waves are inclined to be sharper at the higher temperature. This distinction makes the very small waves easier to count at the higher temperatures and it may therefore in part explain the slight increase in total frequency observed in some records.

It is difficult to reconcile these results with the view that the frequency of the electromyogram is determined by the muscle, the discharge from the cord being too rapid for it to follow. If this were correct, we should expect a much greater change in frequency for a 10° rise of temperature. The "specific muscular rhythm," *i.e.* the frequency of the electric response in the muscle to continuous or very rapid stimulation by way of the nerve, presumably depends on the refractory period of the muscle, and this changes in the ratio 3 : 1 for a 10° rise. Garten(14) has recorded the "specific muscular rhythm" in a rabbit's muscle at different temperatures and finds it two to three times as rapid at 35° as at 25°. Buchanan found an average frequency of 172 per sec. in frog's muscle at 23–25° and of 56 at 9–11°. We have recorded the action currents of the frog's gastrocnemius at different temperatures in response to stimulation of the sciatic nerve with strong induction shocks at the rate of 600–800 per sec. and we find a slightly lower value for the temperature coefficient. The figures for three such experiments are shown in Table III. According to these experiments a rise of 10° should increase the frequency of the specific muscular rhythm by at least 70 p.c. whereas the frequency of the reflex electromyogram increases by less than 10 p.c. The great difference in the two cases may be seen by comparing Fig. 3 (*a*), (*b*) and (*c*) with Fig. 2. Fig. 2 shows the reflex electromyogram and warming the muscle has very little effect on it; Fig. 3 shows the electric response of a muscle to 640 stimuli per sec. in

TABLE III. Gastrocnemius-sciatic preparation in constant temperature chamber. Break shocks 600–800 per sec. to the sciatic.

Exp.	Temp. ° C.	Frequency of electric response in muscle (counting all waves)
10	7	80
	13	110–120
	20	150–170
11	11	60–100
	20	150–200
12	8	70–90
	23	170–200

the motor nerve. At 7° C. the frequency is 80 per sec., at 10° it is 110 and at 20° it is 170. Figs. 2 and 3 are not strictly comparable as regards the actual rates of discharge for the reflex experiment was made in April and the other in August, but they show that a rise of temperature has a much greater effect when the responses are produced by stimulating the motor nerve at such a rate that the muscle is unable to respond to all the impulses reaching it.

These experiments make it highly probable that the frequency of discharge from the spinal cord is not as a rule too great for the muscle to follow. The slight increase which appears in parts of the record when the muscle is warmed may show that the cord sometimes discharges at a greater frequency than the muscle can follow when it is at normal temperature, but this cannot be much more than 20 p.c. above the frequency of the normal electromyogram and such a rate is evidently not constant.

The conclusion to be drawn from these experiments is that the maximum rate of discharge from the cord in the frog at room temperature is 120–150 per sec., and that the frequency of the oscillations in the electromyogram is usually identical with the frequency of discharge from the cord.

Comparison of natural with artificial stimuli. Before going further we may enquire how far the maximum rate of discharge from the cord depends on the nature of the stimulus, whether a natural stimulus such as pinching the foot may lead to a greater frequency than is given by rhythmic stimulation of an afferent nerve trunk. In a number of experiments we have used rhythmic stimuli at various rates and our results agree closely with those published by Beritoff. In winter frogs at 14° C. with stimuli up to about 50 per sec. the frequency of response in the muscle is usually greater than that of the stimulus, each stimulus corresponding to a group of 2 or 3 action current oscillations. With frequencies of stimulation between 50 and 120 per sec. the muscle response is regular and has the same frequency as the stimulus; with stimuli above 120 per sec. the response becomes irregular and the frequency remains about 120 per sec. An irregular response of this kind is quite indistinguishable from that produced by pinching. This may be seen from the records in Fig. 4 where (*a*) is the response to pinching, and (*b*) the response of the same muscle to 80 stimuli per sec. applied to an afferent nerve trunk. In this experiment the cord had been cooled to 9° so that a frequency of 80 was enough to give an irregular response.

Evidently there is no essential difference in the response to natural and artificial stimuli as long as the frequency of the latter is great enough.

In three experiments in which the response became irregular with rates of stimulation above 120 per sec., the muscle was afterwards stimulated by its motor nerve and found to be capable of a regular response with a frequency of 160 per sec. Its failure to follow reflex stimulation above 120 per sec. is therefore an added argument for the view that this limit is imposed by the conducting paths in the cord and not by the muscle itself.

Effect of altering the temperature of the spinal cord. So far the evidence is in favour of the view that the reflex electromyogram gives a fairly accurate rendering of the frequency of discharge from the spinal cord. There is however a very serious objection to this view. Buchanan showed that cooling the spinal cord in a frog did not alter the frequency of the "wavelets" of a strychnine convulsion although cooling the muscle did so. She pointed out the difficulty of reconciling this with the view stated above and so far as we are aware the objection has never been met. A reduction in the temperature of the cord would be almost certain to increase the refractory period of the central conducting paths and to lower the maximum frequency of discharge from the cord. Such a reduction has been shown by Garten(15) in the discharge of the nerve cell which activates the electric organ of Malapterurus. Here a fall of 10° C. reduces the frequency of discharge from the cell to a third of its former value. Since there is no such change in the reflex (strychnine) response of the frog's muscle when the cord is cooled, the most likely explanation is to suppose that the frequency of discharge from the cord is too rapid to be followed by the muscle even though the cord is at a low temperature. This conclusion is in flat contradiction to the results given in the preceding section. We have repeated the experiment of warming and cooling the spinal cord and our results agree on the whole with Buchanan's. The contractions were provoked by pinching; strychnine was given in a few experiments to increase the excitability of the cord but as a rule good reflex contractions were obtained without it. The muscle was kept at a temperature equal to or slightly above that of the cord when warmed; so that, according to our previous results, the muscle should be able to respond to all the impulses reaching it. The results of five of these experiments are given below in Table IV. It is true that in most cases there is a small increase in total frequency when the cord is warmed; in some it is considerable (*e.g.* Exp. 15), in some it is present in parts of the record only (Exps. 13 and 14); but the

TABLE IV.

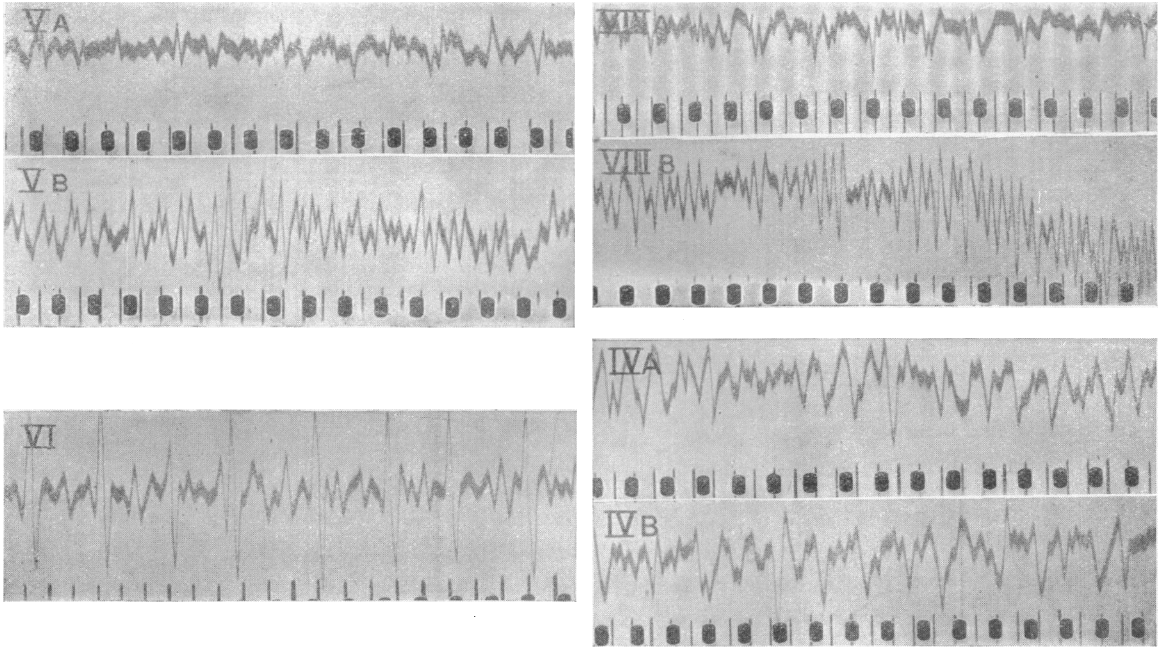
	Temperature		Reflex electric response Frequency per sec.		
Exp.	Cord °C.	Muscle °C.	Total	Large waves only	Remarks
13	20	21	120, 170, 160, 180	70, 90, 70, 50	Dorsal roots intact
	6·5	21·5	130, 130	20, 20	
14	20	18	130, 90, 120, 100, 150	40, 60, 50, 50, 70	Dorsal roots cut
	7	21	120, 130, 110, 120, 110	40, 40, 30, 20, 30	
15	6	22	80, 90, 70, 100	10, 20, 15, 20	Dorsal roots intact
	22	23	150, 160, 120, 130, 140	100, 100, 80, 90, 70	
	5	19·5	110, 80, 100	20, 15, 30	
16	14	20	120, 130, 140, 110, 130	40, 50, 60, 60, 40	Dorsal roots intact
	6	21	100, 80, 120	30, 20, 20	
17	9	21	100, 130, 125	40, 30, 40, 30	Dorsal roots intact
	20	20	150, 150, 200, 150	60, 40, 40, 50, 30	

Exps. 13 to 16 made in March–May; Exp. 17 in November. Temperature of cord measured approximately by thermometer in œsophagus. Actual temperatures about 2° higher when cord is warm and 2° lower when cold (see p. 211). Strychnine was not used in these experiments.

temperature of the cord was usually altered by 15° C. and we should therefore expect a change in the frequency of discharge from the cord much greater than is shown in these electromyograms. In fact a comparison of Tables II and IV shows the paradoxical result that if all waves are counted the frequency of the electromyogram is little affected by changing the temperature either of the muscle or of the central nervous system!

The paradox becomes less startling when we consider the amplitude as well as the frequency of the action current oscillations, for cooling and warming the cord produces a considerable change in the appearance of the record although the frequency does not alter much. This is shown in Figs. 5 (*a*) and (*b*) and Fig. 6 taken from Exps. 14 and 22. When the cord is at the higher temperature the record shows an almost regular succession of large waves with very few small. At the lower temperature the record is much more irregular and consists of occasional large waves separated by groups of many smaller ones. This is shown very well in Fig. 6, where the cord was at 4° C. The change in character was evident in all our experiments and it is shown by the change in frequency of the large waves recorded in column 4 of Table IV.

Now in a record such as that of Fig. 6 where the cord is at a low temperature it is unlikely that all the fibres of the muscle are in action during each of the small electric oscillations. The sudden intrusion of much larger waves shows that the small size of the wave preceding can scarcely be due to incomplete recovery on the part of all the muscle



Figs 4–6, 8.

Fig. 4. Cord at 9° C., Muscle at 15° C., Reflex response (*a*) to pinching of fore-limb; (*b*) to rhythmic stimulation of afferent nerve at 80 per sec.

Fig. 5. Reflex response to pinching (Exp. 14). (*a*) Cord 7° C., Muscle 21° C. (*b*) Cord 20° C., Muscle 18° C.

Fig. 6. Reflex response to pinching (Exp. 22). Cord 4·5° C., Muscle 11° C.

Fig. 8. Reflex response to rhythmic stimulation of afferent nerve at 80 stim. per sec. (*a*) Cord 4° C., Muscle 19° C., Irregular response. (*b*) Cord 19° C., Muscle 20° C., Regular response.

fibres. The simplest explanation is that the small waves are due to the activity of a few only of the muscle fibres and that the greater part of the muscle only comes into play during the larger waves. When the cord is warm (Fig. 5 (*b*)) the greater part of the muscle is activated much more frequently since the large waves are much closer together. It follows that when the cord is warm the spinal centres send out volleys of impulses in rapid succession, each volley being a discharge from the greater part of the motor centre and occupying most of the fibres in the motor nerve. When the cord is cooled the main volleys are separated by much longer intervals and in between the centre keeps up a straggling, independent fire from a few units at a time. This straggling fire may be produced by some of the arcs in the spinal centre which have very much shorter time relations than the majority, or it may mean that the cooling has interfered with the unity of action of the centre so that its different parts no longer discharge synchronously. The small waves would then be due to a discharge from nerve cells which were too late to take part in the main volley, either because of a longer latency or because they were out of touch with the other units. In any case it is clear that the effect of cooling the cord is to produce a great reduction in the frequency of the large waves.

The results of cooling the cord (if our explanation is correct) can be shown diagrammatically as in Fig. 7. The tracings above the diagram are copied from a record of the electromyogram with the cord hot and cold (Exp. 18), and the diagram gives the suggested analysis of these records. The lower lines represent the discharges occurring in each motor neurone, or in each group of muscle fibres innervated by a single neurone, and the line above shows how these would add together to give the electric response of the whole muscle. When the cord is cold four neurones are represented as responding synchronously and three more at the same frequency but out of phase with the rest. When the cord is warm five neurones respond synchronously at one and a half times the frequency and two are out of phase. The resulting electromyograms have the same number of oscillations per sec. in either case, but when the cord is warm the large waves are one and a half times as frequent as they are when it is cold.

The foregoing experiments have shown that cooling the cord does cause an appreciable change in the character of the electromyogram. This change can be explained without assuming that the cord discharges too rapidly for the muscle to follow and it is extremely difficult to see how it could arise if this view were correct.

There is, however, another test which may be applied; the reflex contractions may be produced by rhythmic stimulation of an afferent nerve instead of by pinching the skin. With the cord at a normal temperature, if an afferent nerve is stimulated with 120 shocks per sec. the reflex electromyogram will show a regular series of action currents with a frequency of 120 per sec. If the stimulation is more rapid the response becomes irregular but does not increase in frequency. We have supposed that this limiting frequency of regular response is imposed by the spinal centres and not by the muscle; if so, the limiting frequency should be very much reduced when the cord is cooled. If the cord can really respond much more rapidly than 120 per sec. and the frequency of the electromyogram is due to the muscle, then there is no reason why it should be reduced when the cord is cooled.

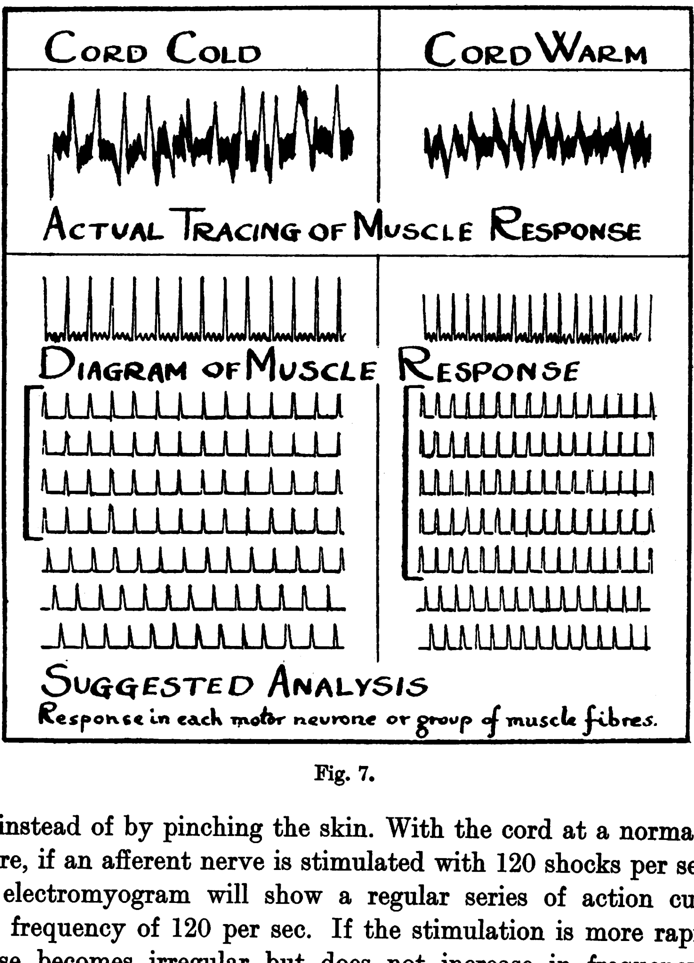


Fig. 7.

We have made three experiments on the same lines as those in Table IV with the difference that the reflex contractions were produced by rhythmic stimulation of an afferent nerve (usually the opposite sciatic) at various rates from 32 to 320 per sec. A typical result is shown in Fig. 8. In Fig. 8 (*b*) the muscle is at 20° and the cord at 19°; the opposite sciatic was stimulated 80 times per sec. and the muscle gives a regular series of responses at the same frequency. In Fig. 8 (*a*) the muscle is at 19° and the cord has been cooled to 4°. The response to 80 stimuli per sec. is now an irregular medley of small waves with a few much larger, in fact it closely resembles the electromyograms in Figs. 5 and 6 where the cord was cooled. The total number of waves per sec. is actually greater in Fig. 8 (*a*) than in (*b*), but it is clear that the cord at 4° is no longer able to give a regular series of discharges at 80 per sec. At this temperature stimuli at 32 per sec. to the afferent nerve gave a regular series of responses at 32 per sec. in the muscle, but higher rates of stimulation were not followed.

Table V shows the maximum frequency of stimulation which will give a regular series of responses at different temperatures of the spinal cord. In all the experiments the response is counted as regular as long as it exhibits the rhythm of the stimulus; at low frequencies of stimulation the response to each shock may be multiple, but the record shows a definite rhythm and is quite unlike the irregular response given by more rapid stimulation. The table shows also the "Irregular frequency," *i.e.* the total number of waves per sec. in the electromyogram when the response is no longer regular. Like Table IV it confirms Buchanan's observation that the frequency of the electromyogram does not change

TABLE V. Spinal frog: rhythmic stimulation to afferent nerve at different frequencies.

	Temperature		Reflex electric response	
Exp.	Cord °C.	Muscle °C.	Maximum regular frequency per sec.	"Irregular frequency" per sec.
19	19	20	120	100–120
	8	19	48	110
	20	19	160	120–150
	4	20	32	100
	20	19	160	120–150
20	11·5	20	96	100
	7	20	doubtful	100–120
	16	20	128	120–140
	21	20	160	130–150
	7	20	48	100–120
21	13	21	80	100–120
	19	21	120	100–130

The following stimulation frequencies were used for testing: 32, (40), 48, 64, 80, 96, 120, (128), (144), 160 and various higher values. The figures in the third column are accurate only as between these values. The frequencies enclosed in brackets were often omitted from the series.

to any great extent when the cord is cooled, but it also confirms the suggestion that there is a great decrease in the frequency with which the centre can respond as a whole. If the figures in this table are compared with those in Table IV it will be seen that there is a very good agreement between the maximum frequency of regular response on rhythmic stimulation (Table V, column 3) and the frequency of the large waves in the response to pinching (Table IV, column 4) with the cord at different temperatures.

We conclude, as before, that the frequency of the electromyogram is determined by the spinal centres and not by the muscle, and we may add that the spinal centre is so constituted that it cannot discharge as a whole more often than 120 times per sec. at 15° C. or 32 times at 7° C., presumably on account of the refractory phase of some part of the conducting structures.

In one other respect this hypothesis is open to experimental verification. When the cord is cooled to 6° the frequency of the electromyogram may be as high as 120 per sec. when every wave is counted, but we have supposed that the individual motor nerve fibres and the groups of muscle fibres which they innervate are for the most part responding at a much slower frequency. If they are, then cooling the muscle down to the temperature of the cord will not reduce the frequency of the electromyogram even though a temperature is reached at which the individual muscle fibres would be unable to respond as rapidly as 120 times per sec. We have made three experiments in which the cord was cooled and the temperature of the muscle was varied. These are recorded in Table VI.

TABLE VI.

	Temperature		Reflex response to pinching Frequency per sec.	
Exp.	Cord ° C.	Muscle ° C.	All waves	Large waves only
22	4·5	11	110, 120, 110, 120, 120	40, 40, 20, 40, 30
	4	24	110, 140, 120, 110, 130	40, 30, 30, 30, 40
23	7	10	130, 130, 130, 150, 140	40, 40, 50, 50, 30
	6·5	15	150, 120, 140, 140, 130	30, 50, 40, 30, 40
	8·5	18	140, 140, 130, 150, 120	40, 30, 50, 40, 50
24	5·5	7·5	80, 70, 80, 60, 60	30, 30, 30, 10, 20
	* 5	7	90, 80, 100, 80, 70	30, 40, 30, 30, 20

* In this experiment the muscle was the gastrocnemius; in all the others the hamstrings were used.

Unfortunately the method of cooling the muscle by circulating cold water through the double walled trough did not allow very low temperatures to be reached. Nevertheless in Exp. 23 it will be seen that the muscle at 10° gave a reflex response with a frequency as high as 150 per sec., and in Exp. 24 the muscle at 7° gave a frequency of 100 per sec. Both these values are well above the average for the maximum frequency of response of a muscle at that temperature when the motor nerve is stimulated and every fibre is brought into play by each stimulus, though they are not outside the extreme limits which are sometimes found. The experiments are therefore scarcely conclusive, though the high frequencies obtained in the reflex contraction do suggest very strongly that the whole muscle is not in action during each wave of the electromyogram. Incidentally the figures in this table agree with those in Table II in that the frequency does not alter when the temperature of the muscle is raised.

Remarks. The experiments just described are of interest in connection with the recent work of Athanasiu(8). From a study of the electromyogram of different muscles (mammalian as a rule) he concludes that every record is made up of oscillations of two different origins, large waves of frequency from 70 to 150 per sec. due to the activity of the muscle and small waves of frequency from 300 to 500 per sec. due to the passage of impulses in the motor nerve fibres. Our own records of the normal electromyogram (of the frog, the cat, and man) show occasional clusters of very small waves of high frequency, but we have never been able to make out any clear separation of two such types of wave as Athanasiu describes, since there are always many of intermediate size. It should be added, however, that we have not made any detailed statistical examination of our records. But it is noteworthy that the records in which two such groups of waves are most evident are those in which the spinal cord was cooled (*e.g.* Figs. 5 and 6). Here the large waves are less frequent and are separated by groups of very much smaller ones. We have suggested above that these small waves are due to the activity of only a small part of the muscle and that they are produced by a discharge of impulses from a few of the neurones in the spinal centre, which can only discharge as a whole at a much lower frequency. According to Athanasiu's explanation the small waves should be caused by impulses in the nerves and the large waves by the muscle, which is unable to respond to every impulse that reaches it. But the results given in Tables IV and V show that it is cooling the cord and not the muscle which reduces the frequency of the large waves in the electromyogram; it is very difficult to see how this result could be achieved if Athanasiu's explanation is correct. Cooling the cord should reduce the frequency of impulses in the nerve, but if this is still too rapid for the muscle to follow, the effect would be either to leave the muscular response unchanged or else to make its frequency increase. This follows from the fact that if a nerve is stimulated at a frequency too great to be followed by the muscle, the only effect of an increase in the frequency of stimulation is to cause a reduction in that of the muscle response, presumably because there is a greater interference between successive impulses at the nerve ending. This result is shown very clearly in an experiment of Athanasiu's (16), and we have observed it repeatedly. Thus, if the small waves are due to the nervous impulses and the large waves to the muscle we should expect to find that cooling the spinal cord would reduce the frequency of the former and increase or leave unchanged that of the large waves. The fact that the frequency of the large waves is greatly reduced by cooling the cord is therefore definitely opposed to Athanasiu's conception of the electromyogram if we have understood it correctly. It is indeed difficult to imagine any explanation for the reduced frequency of the large waves as long as we suppose that this is not identical with the frequency of discharge of the spinal centres.

The conception of the electromyogram to which we have been led has some important consequences. We have supposed that the centre usually responds as a whole, sending out repeated volleys of impulses from most or all of the motor neurones which are included in it, but that in certain conditions (*e.g.* when the cord is cooled) small groups of neurones may discharge independently of the main volleys. A possibility of this kind was first suggested in 1877 by Brücke to account for the very small electrical effects observed in voluntarily contracting muscles as compared with those given by an artificial tetanus. It is, however, fairly clear that under normal conditions the responses in the centre must be more or less synchronous. Unless they were we should be most unlikely to find electromyograms showing the least approach to a definite frequency. But if the small waves in the electromyogram are due to the activity of only a few neurones when the cord is cooled, the same thing may occur to some extent at a normal temperature also. Piper considered that the spinal centres in man tended always to respond at a definite frequency which varied to some extent with the muscle concerned and was in the neighbourhood of 50 per sec., and he supposed that any departure from this rhythm was due to neurones out of phase with the main body. This view has been generally abandoned, since a large number of electromyograms show no trace of a dominant rhythm of 50 per sec.; but it may still be true, as Piper supposed, that the more irregular the record the greater the lack of coordination between the different neurones which supply the muscle. If so a study of the electromyogram in different conditions may lead to valuable information about the general make-up of a reflex "centre" in the cord.

Further discussion of the mammalian electromyogram would be premature. The experiments we have described have been confined to frogs and they do not prove that the mammalian spinal cord cannot discharge impulses at a frequency too rapid for the muscle to follow. In the frog the maximum frequency of discharge from the cord is not far off the maximum frequency of response in the muscle and it may perhaps surpass it in other animals. At the same time the view that it does so has been based partly at least on the temperature effects in frogs and we have found that these are in reality best explained on the view that the discharge from the cord has the same frequency as the electromyogram.

SUMMARY.

The theory that in reflex or voluntary contraction the nerve centres send out impulses at a greater frequency than that shown in the electromyogram has been submitted to examination. This view has been based on the effects of local alterations of temperature which suggest that the frequency of the electromyogram is determined by the muscle rather than the cord. On the other hand a serious objection arises from the fact that a muscle stimulated reflexly will not give a regular response at a frequency greater than 160–200 per sec. (in a mammal), whereas it will respond regularly at 300–400 per sec. when the motor nerve is stimulated.

We have examined the effects of temperature alterations in spinal frogs and we find that they do not support the view that the discharge from the cord is too rapid for the muscle to follow. If a frog's muscle is warmed through 10° C., the average increase in the frequency of the reflex electromyogram is less than 10 p.c., whereas if the muscle is responding to a very rapid series of stimuli to the motor nerve (600–800 per sec.) a rise of 10° will increase the frequency of response by 70 p.c. Cooling the muscle may reduce the frequency of the reflex electromyogram, but this, in the frog, is the inevitable result of the prolongation of the refractory period of the muscle.

It was shown by Buchanan that altering the temperature of the spinal cord did not alter the frequency of the "wavelets" in a strychnine

contraction. In general agreement with this we find that cooling or warming the cord usually causes but a slight change in the frequency of the reflex electromyogram. But there is a considerable change in the form of the response, for the number of large waves per sec. varies very clearly with the temperature of the cord though the frequency may be unaltered when waves of every size are counted. The explanation we take to be that the large waves represent the simultaneous discharge of impulses from the majority of the nerve cells and consequent contraction of the majority of the muscle fibres, and that the small waves represent the discharge from a small number of nerve cells out of phase with the rest. On this view the frequency with which the centre discharges as a whole is represented by the number of large waves, and this varies with the temperature of the spinal cord and not with that of the muscle. This view agrees more or less with Piper's original interpretation of the electromyogram. It is supported by the results of rhythmic stimulation of afferent nerves, etc.

We conclude that in the frog the nerve cells in the spinal cord do not discharge impulses at a frequency greater than about 120 per sec. at 15° C.

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