EXPERIMENTS ON THE CHARACTER OF THE MUSCULAR CONTRACTIONS WHICH ARE EVOKED BY EXCITATION OF THE VARIOUS PARTS OF THE MOTOR TRACT. By VICTOR HORSLEY, M.B., B.S., *Professor Superintendent of the Brown Institution,* AND E. A. SCHÄFER, F.R.S., *Jodrell Professor of Physiology.* Pl. V.

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I. METHODS OF EXPERIMENT.

THE experiments which we record in this paper have been performed by the following method,—the subjects of experiment being dogs, cats, rabbits, and monkeys:—The animal having been brought under the influence of chloroform or other anæsthetic, the surface of the brain over the motor region is freely exposed and its electrical excitability tested. The button of a receiving tambour, such as those which are employed for obtaining cardiographic tracings, is then applied to the muscle whose contraction it is wished to record, the tambour itself being either firmly strapped to the limb, or fixed securely by an iron clamp independently of the limb (in the latter case the limb must be rigidly fastened down to the board or table). In either case the receiving tambour is connected by indiarubber tubing to a recording tambour, the lever of which writes upon a moving surface of smoked glazed paper on which the time in seconds and the duration of the excitation are also simultaneously marked. By this method the bulging of the muscle during its contraction is registered. In some experiments, however, we have recorded the shortening of the muscle by attaching its tendon to the receiving tambour, extension being effected by an elastic band, in the manner described by Franck and Pitres[1], and in others we have connected the tendon by a thread directly to a bell-crank myographic lever without the intervention of tambours and tubing, the extension being effected in this case also by means of an

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[1] François-Franck et Pitres, Travaux du laboratoire de M. Marey, IV. 1878—79.

elastic band. All these methods have yielded in our hands similar results, but we have found the first one to be on the whole the most convenient, and it is therefore the one which we have generally adopted[1].

The excitation which we have employed has been that caused by a series of induction shocks produced by varying the current of one or two Daniell elements sent through the primary coil of a Du Bois sliding inductorium. The variations are brought about by the short-circuiting of the current by a vibrating metallic reed which is kept in motion by an electromagnet and the point of which dips in and out of a cup of mercury (Plate V., Fig. 1 A and B). The reed-vibrator is so constructed that its rate can be varied by means of a sliding clamp from 5 to 100 double vibrations a second, the lengths corresponding to 10, 20, 30, 40 and 50 per second being also marked upon it. By employing an instrument of this description in which the battery current is varied but never broken, the effect of the extra-current in producing too great a disproportion in the intensity of the make- and break-shocks is eliminated. The reed was generally so set that with each vibration the point—a vertical piece of platinum wire—was only just permitted to dip into and out of the mercury, so that the closing and opening effect were so close as to cause their corresponding induction shocks to produce practically only a single excitation[2]. Electrodes of platinum wire with their points about 3 mm. apart were used for applying the excitation to the nervous substance, except in the case of the spinal cord, into which were inserted steel needles coated with shellac except at one spot a short distance from the point.

For the purposes of our experiments it was convenient to consider the motor tract as consisting of 4 parts, viz.: (1) Its origin in the grey matter of the cortex cerebri. (2) The fibres passing down from this in the corona radiata. (3) Its continuation in the spinal cord (pyramidal tract, and nerve-cells of anterior cornu). (4) Its peripheral continuation in the anterior roots and motor nerve-fibres. We find all these parts to be directly excitable by electricity, such excitation always evoking contractions of the skeletal muscles, provided the degree of anæsthesia be not too intense.

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[1] A similar method was employed by Marey and Mendelssohn to register the bulging of contracting muscles in man (Marey, Travaux, IV. p. 144, fig. 29).

[2] Of this, however, we could not always be sure, especially when employing the more rapid rates of vibration, which may not improbably have yielded twice as many excitations as the rate of vibration, a circumstance which as will be seen can only serve to strengthen our general conclusions.

In all of our experiments we have commenced by recording the contractions which result from excitation of the cerebral cortex, and the epileptoid contractions by which in many cases they are succeeded. We have usually begun by employing excitations of a rapid rate (50 per second), and have then taken tracings at gradually decreasing rates (40, 30, 20 and 10). The paper—one of Hering's long blackened sheets—was generally moving throughout the greater part of each experiment, and we thus occasionally obtained a record of spontaneous and reflex contractions.

After taking a sufficient number of tracings resulting from excitation of the cerebral cortex, we have then proceeded to remove the cortex over the part excited, and have stimulated the corona radiata in the same manner and at the same series of rates as before. Next we have exposed and cut the spinal cord in the dorsal region, and have repeated the excitations upon the distal cut end. Finally, in a few instances, we have completed the series of observations by cutting and stimulating the peripheral end of the motor nerve.

II. EXCITATION OF THE CEREBRAL CORTEX.

Electrical excitation.—It is stated by Franck and Pitres[1], and the statement has been generally accepted by subsequent writers[2], that so far as the rate or frequency of the muscular response producing tetanus is concerned, excitation of any part of the motor tract, the grey matter of the cerebral cortex not excluded, is responded to by a succession of twitches (secousses) corresponding with the frequency of the excitation exactly as in the case of the excitation of a motor nerve. In other words, if the cerebral cortex in the motor region be stimulated 5, 10, 20 up to 40 times in a second, the muscles affected will respond by contractions compounded of 5, 10, 20 up to 40 twitches per second, whilst above this rate the individual twitches become fused so as to form a complete tetanic contraction[3].

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[1] Travaux du lab. de Marey, IV.

[2] As for instance by Landois, *Text-book of Human Physiology*, English Translation by Stirling, p. 916.

[3] It is right here to state that although this is the conclusion that might naturally be drawn from the description which MM. Franck and Pitres give of the results which they have obtained by the application to the cerebral cortex of a series of efficacious and rapidly succeeding excitations (30, 50, 100 interruptions per second) and from the figure which

The results of most of our experiments are in direct contradiction to this general statement, so far at least as concerns the more rapid rate of excitation. We have found in nearly all cases that whatever the rate of excitation employed, provided it was not allowed to fall below a certain limit, the frequency of muscular response to stimulation of the cortex, as indicated by the undulations described by the myograph lever, does not vary with the rate of excitation, but maintains a nearly uniform rate of about 10 per second (see Plate V., Figs. 3 A, 4 A, 4 B, 5 A, 5 B and 6 A).

From 9 to 11 undulations per second are by far the most frequently met with, but they are occasionally as slow as 8 or as frequent as 13 or more per second. These extremes however are usually only found here and there in the course of a tracing. The rate of muscular response appears to be tolerably constant in the different kinds of animals experimented upon, indeed the variations in different individuals of the same species may be as great or greater than those met with in animals of entirely different species. Thus while in one dog the average rate of muscular response to frequently interrupted electrical excitation of the cerebral cortex was 9·29 per second, in another it was 10·64, in a cat 10·00, in another cat 11·26 and in a monkey 11·00.

Occasionally there is a tendency shown to an increased acceleration of the rate of muscular response with increased rate of excitation of the cortex, but by no means in proportion. Thus it is sometimes seen that while excitations at the rate of 20 per second produce 10 or at the most 11 muscular responses, an excitation at the rate of 30, 40 or 50 per second will here and there shew 12 and 13 responses in a second; and in very rare instances as many as 18 or 20 can be counted (but this higher rate of response is seldom maintained for more than one or two seconds).

When the excitations are applied at the rate of 10 or less than 10 per second the muscular responses occur with almost mathematical

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they give in illustration of that description (*loc. cit.* and *Arch. de phys.* 1885, fig. 6, p. 18) in which figure an excitation of 30 per second is represented as producing an incomplete tetanus, the curve of which shows undulations of a corresponding rate and an excitation of 50 per second is represented as producing a complete tetanus, in which the undulations are fused, the authors subsequently make the following remark (p. 19) which somewhat modifies the absoluteness of that conclusion:—

"En général on peut dire que le tétanos provoqué par la faradisation de l'écorce n'est "pas aussi régulièrement en rapport avec le nombre et l'intensité des excitations "provocatrices que l'est le tétanos, provoqué par la stimulation directe du muscle ou du "nerf moteur. Dans le tétanos cortico-musculaire, la ligne d'ascension est souvent brisée "et la fusion n'est pas toujours complète alors que les secousses électriques se succèdent "avec une rapidité qui serait suffisante pour la produire si les mêmes excitations étaient "appliquées au muscle ou au nerf moteur."

accuracy at the same rate. It is with the higher rates of excitation that the greatest amount of variation occurs, but even here, as above remarked, it is very small in amount.

In three instances, and in three only, out of a large number of experiments, have we obtained, when using rates of excitation higher than about 10 per second, any indication of a rate of muscular response coinciding with the rate of excitation. In two of these cases (dog and cat) the waves which were most evident upon the tracing were of the normal rate of about 10 or 11 per second, but upon these waves it was possible, especially with the aid of a lens, to make out the existence of very minute undulations which corresponded with the rate of excitation.

In the third case (rabbit) these rapid undulations were sufficiently prominent to obscure the slower waves of normal rate, although signs of the existence of these could here and there be detected.

It may further be mentioned that in all three cases the rapid undulations appeared equally in the tracings obtained by excitation of the cortex cerebri, corona radiata, and medulla spinalis.

Epileptoid contractions succeeding electrical excitation of the cortex. The contractions of a more or less epileptoid character which succeed the electrical excitation of the cortex cerebri also show, and in a well marked manner, small waves upon the tracing (Plate V., Fig. 4, A). These waves have a very uniform rate of 8 to 10 per second, being rarely as many as 12 or 13. Usually, however, a sort of rhythmic summation occurs, resulting in the production of larger contractions 2 or 4 in the second, the well known clonic contractions of epilepsy (Figs. 3 A and 4 A), but upon the curves of these larger contractions the smaller waves are in many parts distinctly apparent, and it is not uncommon to find the summation incomplete so that a well marked clonus having a rhythm of 8 to 10 per second is recorded (Fig. 5 A)[1].

Rate of muscular response in spontaneous (voluntary) and reflex contractions in animals. It has been stated that occasionally we have obtained tracings of spontaneous or voluntary and reflex contractions of the same muscle which has been prepared for recording the response to electrical excitation. The tracings of these spontaneous contractions and also of contractions resulting from reflex excitation show in all cases more or less regular waves, which are seen very distinctly both at the

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[1] A further discussion of these epileptoid contractions resulting from electrical excitation, and a comparison between them and similar movements produced in cases of disease or injury in man and animals, will be deferred to a future paper.

commencement, i.e. upon the rise of the curve, and also throughout the course of the contraction. The rate of the undulations so recorded is almost exactly the same as those caused by electrical excitation of the cortex, and as the smaller waves of the subsequent epileptoid period, and they show the average rate of muscular response in the case of voluntary or spontaneous contractions to be also about 9 or 10 per second, exhibiting however as in the other cases variations of from 8 to 12 or 13[1].

For example in one monkey experimented upon in which the average rate of muscular response to rapid electrical excitation of the cortex cerebri was 11 per second, the average rate in response to a voluntary stimulus was also 11 per second; and the waves visible upon the tracing of the epileptoid contractions averaged as nearly as possible the same rate. Moreover there is not only this correspondence in rate but also in the form of the curve which is obtained.

This fact is exceedingly well illustrated in the accompanying figure (fig. 2 A and B) in which the tracing of a spontaneous contraction is shown at B, and one of a contraction resulting from electrical excitation at A. The curves were taken upon a cylinder revolving rapidly at the same rate in both cases, and are seen to be practically identical, both in the rhythm of the undulations which compose the curve and in the general form of the whole curve. In this case the electrical excitation (60 per second) was much more rapid than the rhythm of the undulations, which succeed one another in both curves at the rate of about 12 per second.

III. Result of exciting the Corona Radiata.

Excitation of the corona radiata after removal of the corresponding portion of the cortex has in our hands given results, which so far as regards the rhythm of muscular response, are practically identical with those got from previous excitation of the cortex (Plate V., Figs. 3 B, 4 C, 5 C). Thus in a dog in which excitation of the cortex produced waves averaging 10·44 per second

Excitation of the corona radiata gave 10·77 per second.

In another dog	in which	excitation of the	cortex	gave	10·64	per sec.
„	„	„	corona	„	10·30	„
In a cat	„	„	cortex	„	11·26	„
„	„	„	corona	„	11·57	„

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[1] Almost exactly the same results are obtained from the record of voluntary muscular contractions in man (see the succeeding paper).

With low rates of excitation (10, 20, 30) the muscular response is almost exactly 10 per second in most of the animals we have experimented on. With higher rates there is sometimes a distinct tendency to acceleration of rate of response which is rather more marked than in the case of the cortex. Thus, in a cat, in which the muscular response to a cortical excitation produced by a reed vibrating 40 times in the second was almost uniformly 10 per second, the response to excitation of the corona at the same rate was 18: and in a monkey in which a cortical excitation of 40 was responded to by about 11 muscular twitches, the excitation of the corona at the same rate was responded to by 20 per second or more.

Excitation of the corona is very rarely followed by epileptoid after-contractions, especially if the whole of the corresponding cortical area has been completely removed[1]. In those instances in our own experiments in which epilepsy has followed excitation of the corona, the tracings of the spasms have been similar to those obtained after cortical excitation, exhibiting large waves of 1 to 4 per second with small undulations upon them of from 8 to 10 per second.

IV. Result of excitation of the Spinal Cord.

The usual result of exciting the peripheral cut end of the spinal cord, at rates varying from 10 to 50 per second, is to produce contractions in the muscles of the limbs which are almost exactly identical as regards rate of response with those obtained by excitation of the cortex cerebri and corona radiata (Plate V., Fig. 3 *c*.). As a general rule it may be stated positively that for higher rates of excitation the response does not coincide with the rate of excitation, but that for all rates of excitation there is a uniform rate of response averaging about 10 per second. Thus to take instances from some of the experiments before quoted from:—in a dog, in which the average rate of response to rapid cortical faradization was 10·64 per sec. and that to coronal excitation 10·30; the waves upon the muscle curves produced by faradization of the cord show

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[1] Franck and Pitres state (" Recherches sur les convulsions épileptiformes d'origine corticale," *Arch. de physiol.* III série t. II. pp. 14—20), positively that epilepsy never follows excitation of the corona radiata alone but that, to set it going, excitation of the cortex is absolutely necessary. In this point they differ from Albertoni and others. We shall show immediately however that excitation of the cut spinal cord is sometimes followed by epileptoid spasms.

a rate of 10·5 per second; in another dog the numbers are 10·44, 10·77 and 10·70, and in a cat 11·26, 11·57 and 11·00. This is the result obtained in by far the majority of our experiments, but in some as in the case of excitation of the corona radiata, there is a distinct tendency to acceleration of rate of response with the higher rates of excitation. For instance, in a monkey in which the response to cortical faradization was 11 per second, and the response to coronal excitation with reed of 40 rate was about 20, the response to excitation of the cord by the same rate of reed was also about 20. In this last case, although with the high rate of excitation, acceleration of the response rhythm was marked, yet with a reed of 10 per second giving make- and break-shocks the response averaged almost exactly 10 per second.

The acceleration however very seldom attains the rate of the excitation if the latter is higher than 10 per second, indeed in only two of our experiments (one rabbit and one dog) has it done so.

In the majority of the experiments we have found the muscular responses caused by excitation of the cord to be even more regular than those caused by excitation of the higher parts of the central nervous system[1].

In two cases (cat and rabbit) in which the spinal cord was strongly faradized, the continuous contraction with small undulations, which was at first produced as usual by the faradization, passed into a remarkable rhythmic condition characterized by large clonic contractions. The myographic curve of these contractions (Fig. 6 B) shows distinctly a frequency of from 8 to 10 per second.

In the case which is here illustrated this rate of clonus lasted for several seconds, after which the contractions gradually became less accentuated as exhaustion began to supervene, and took on a somewhat greater frequency (15 or more in the second). Towards the end, as the exhaustion became more complete, the contractions again became slower and were occasionally interrupted, response to the excitation of the cord eventually failing altogether.

Contractions prolonged after cessation of electrical excitation of the spinal cord. The cessation of strong excitation of the spinal cord is sometimes not immediately succeeded by muscular relaxation. It occasionally happens in mammals but almost constantly in the frog, that the condition of contraction only slowly passes off. During this after-action the tracings exhibit undulations similar to those which

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[1] Kronecker and Hall (*Arch. f.* (*Anat. u.*) *Phys.* 1879, *Supplement-Heft.*) obtained as the result of excitation of the spinal cord in a rabbit 40 times per second, a muscular response of about half that rate.

occur during the excitation and having a rhythm of 8 to 10 per second. This continued contraction can only be ascribed to the continued activity of the grey matter of the cord, and the rhythm of these undulations must afford a probably correct indication of the rhythm of discharge of nervous impulses from the motor cells when these are acting independently. These spontaneous undulations never succeed one another more rapidly than about 10 per second, even if the previous rapid electrical excitation of the cord has produced an accelerated rhythm of muscular response, but they may as in the case of the impulses resulting from after-activity of the cerebral cortex become summated to produce larger epileptiform contractions of slower rate.

This epileptiform summation we have obtained in two or three instances, and its occurrence no doubt affords prima facie evidence not only of the possibility of setting up epileptoid spasms without the participation of the motor cerebral cortex (see note on a previous page) but also with regard to the seat of the summation of rapidly recurring nervous impulses which are passing down the motor tract.

It is interesting to remark that the so-termed "ankle-clonus", which is certainly dependent in some way or another upon the integrity and activity of the grey matter of the cord, exhibits a rhythm of from 6 or 10 contractions per second[1]. It may also be pointed out that the rhythm of muscular response to the reflex excitation of the cord in a frog or toad poisoned by strychnine has very nearly the same rate[2].

V. EXCITATION OF THE MOTOR NERVE.

Excitation of the motor nerve has given in our hands results in no respect different from those which are well known. The muscular response has followed exactly in all cases the rate of excitation. Up to a rate of excitation of 20 per second the waves upon the ascent of the curve, and for some distance along its course, are distinct and easily to be counted; excitations produced by a reed of 30 or more vibrations per second give a tetanus with the waves completely fused (Plate V., Fig. 4 D)[3].

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[1] Gowers, *Diagnosis of diseases of the spinal cord*, 2nd Edition, 1881, p. 23.

[2] This was first shown by Lovén with the capillary electrometer (*Nord. Med. Ark.* 1879; *Centralbl. f. d. med. Wiss.* 1881), and he also succeeded in recording the undulations by the aid of a myographic lever.

[3] Franck and Pitres (*Arch. de Physiol.* 1885, p. 18,) give 45 excitations per second as the minimum necessary to produce complete tetanus in the muscles whether applied direct or to the motor nerve or to any part of the motor tract.

The chief value of this stage of the experiments is to show that the undulations obtained on excitation of the nerve-centres were not due to any defect in the method of recording the contractions, or produced by any instrumental error, since otherwise they would be exhibited upon the curves obtained as the result of excitation of the motor nerve.

VI. SUMMARY AND CONCLUSIONS.

The general results of our experiments may be summarized as follows:—

1. The rhythm of muscular response to electrical excitation of the nerve-centres is the same whether the excitation be applied to the grey matter of the cerebral cortex in the motor region, or to the fibres of the corona radiata emanating from that region, or to the spinal cord (but not to the peripheral motor nerves). The rate of the rhythm is not the same as that of the excitation except when the frequency of excitation is 10 per second or less. With all higher rates of excitation the rhythm of muscular response is maintained at a fairly uniform rate of about 10 per second.
2. The rhythm of muscular response in the case of voluntary and reflex contractions is essentially the same as that which results from electrical excitation of the nerve-centres.
3. The rhythm of muscular response in all cases of after-excitation (whether distinctly epileptoid in their nature or not) is fundamentally the same as that of voluntary and reflex contractions, and of contractions immediately produced by a rapidly recurring electrical excitation, but the response, in the case of epilepsy, may present a secondary rhythmic summation which produces a clonus of slower rate.

The principal conclusion to be drawn from these results, which have been supplemented by numerous observations on voluntary and epileptoid contractions in man[1], seems to be this—that every prolonged contraction of the skeletal muscles which is provoked by excitation, whether natural or not, of any part of the nerve-centres, is a tetanic contraction which has been produced by a series of impulses generated in the nerve-centres and passing along the motor nerves at an average rate of about 10 per second.

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[1] For the observations upon voluntary contractions see succeeding paper.

As to the place of generation of the rhythm it is certain that in some cases it occurs in the lower nerve-centres (i.e. in the motor nerve-cells of the spinal cord, medulla oblongata, pons and mesencephalon). At least this conclusion appears to follow from the fact that when we excite the motor tract above those centres by a rapidly interrupted electrical stimulation the excitation manifests itself by a muscular response which has a rhythm of only 10 per second, whereas it is certain that the rapid excitation of the nerve-fibres of the motor tract must have caused equally frequent nervous impulses to pass along those fibres. It is clear, therefore, that these rapidly succeeding impulses have not been transmitted unaltered through the motor nerve-cells, but have become summated within them and converted into a smaller number of impulses, which are then forwarded with a constant slower rhythm by the peripheral motor nerve fibres to the muscles.

This hypothesis will also explain why it is that in some cases there is seen a rhythm of muscular response which is the same as that of the electrical excitation (even when the latter is rapidly interrupted), or if not quite equal to the rate of excitation, yet considerably exceeding the normal rhythm. For in these instances we have merely to suppose that for some reason or another the usual summation of impulses within the nerve-cells has either altogether failed to take place, or has occurred imperfectly, with the result that the rapidly succeeding nervous impulses are transmitted to the motor nerve fibres, either with unaltered rhythm or with a relatively slight amount of diminution in rate.

We cannot claim either to have proved or disproved that, in the case of nervous impulses originating naturally, or as the result of rapid electrical excitation in the grey matter of the cerebral cortex, the rhythmic summation may occur in the nerve-cells of the cortex. But although in no way disproved by our experiments the supposition is at least unnecessary, for, as we have shown, the rhythm is usually exactly the same whether the cortical nerve-cells are or are not included in the path of the nervous impulses. There is in short nothing in the results of the experiments to indicate that the discharge of nervous impulses from the cortical nerve cells has a rhythmic character at all, although there are strong *à priori* considerations in favour of such a hypothesis[1].

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[1] The fact that in some individuals the automatic action of the cortical cells may occasionally produce a muscular response having a rhythm of 12 or 13 or even more per second, whereas the automatic action of the nerve-cells of the spinal cord appears to be never capable of originating a rhythm of greater frequency than 10 per second, lends probability to this hypothesis.

We have not entered into an account of the literature of this subject, because it has lately been treated of at great length by the accomplished authors to whose articles we have so frequently had occasion to make reference. With regard to the very different conclusions we have been led from our experiments to draw regarding the rhythm of muscular response to rapid excitation of the nerve-centres, we would here remark that most of the tracings which are given by Franck and Pitres in illustration of the results obtained by them from electrical excitation of the cortex cerebri and corona exhibit with great distinctness and regularity the rhythmic undulations which we have described in this paper. These authors seem however not to have attached any importance to the undulations in question, or at least, to have entirely failed to appreciate their true significance. It is moreover obvious in many cases that the rhythm of the undulations they have thus recorded is by no means coincident with the rate of excitation. Unfortunately a time tracing is in most instances omitted, so that the exact rhythm cannot be determined, but the general similarity of the curves represented by them to those obtained by ourselves renders it sufficiently clear that, as regards matter of fact, there is no actual contradiction in our respective results.

Similar small rhythmic undulations are also very distinct on many of the tracings of epileptoid spasms which they have put on record.

DESCRIPTION OF THE FIGURES. PLATE V.

FIG. 1. *A*. Reed vibrator with sliding clamp, capable of causing variations in the battery current through a Du Bois coil (as in Helmholtz's modification of Neef's hammer) and thus producing closing and opening shocks in the secondary coil of about equal intensity. By moving the clamp the rate of vibration of the reed can be varied from 5 to 100 double vibrations per second.

B shows the vibrator arranged in connexion with the battery and coil.

FIG. 2. A. Tracing obtained from one of the hamstring muscles of a monkey during rapid electrical excitation (with 60 reed) of the cerebral cortex close to the upper end of the furrow of Rolando.

B. A similar tracing from the same muscle contracting under the influence of the will.

In both tracings the undulations exhibit a frequency of about 12 per second.

FIG. 3. Tracings obtained from the extensor longus digitorum muscle of

the fore-arm of a dog as the result of rapid electrical excitation of the several parts of the motor tract.

A. Excitation of cerebral cortex with 30 reed (followed by epilepsy).

B. Excitation of corona radiata with 40 reed after removal of cortex.

C. Excitation of distal end of cut spinal cord (cervical region) with 30 reed.

D. Excitation of musculospiral nerve with 30 reed.

FIG. 4. Tracings from the muscle of a dog during excitation of the cortex cerebri and corona radiata.

A. Excitation of the cortex with 10 reed (followed by epilepsy).

B. Excitation of the cortex with 20 reed.

A and B both exhibit summation.

C. Excitation of the corona with 40 reed.

FIG. 5. Tracing from a dog during excitation of cortex cerebri and corona radiata.

A. Excitation of cortex with 30 reed (followed by epilepsy).

B. Excitation of cortex with 20 reed (followed by epilepsy).

C. Excitation of corona with 20 reed.

FIG. 6. Tracings from a rabbit.

A. Excitation of cortex cerebri with 50 reed.

B. Excitation of spinal cord with 50 reed.

In Fig. 6 B, there is just visible during the first four seconds, besides the undulations of slower rhythm (about 10 or 11 per second), a faint indication of responses coinciding with the rate of excitation. This is not afterwards seen although the same rate of excitation is continued throughout the whole time of the tracing.

In all the tracings shown in Figs. 3, 4, 5 and 6 the time in seconds is marked by vertical lines upon the curve.

The tracings shown in Fig. 2, are taken at a much more rapid rate than the others.

All the tracings are to be read from left to right with the exception of fig. 2 B, which has been inadvertently copied so as to read from right to left.

Fig. 1A.

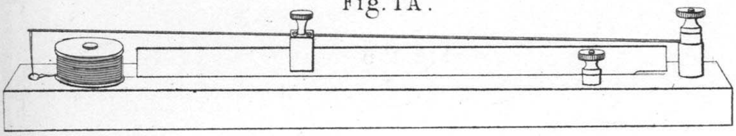


Fig. 1B.

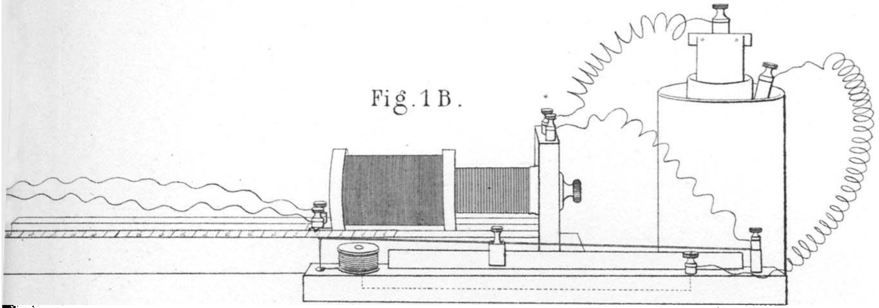


Fig. 3A.

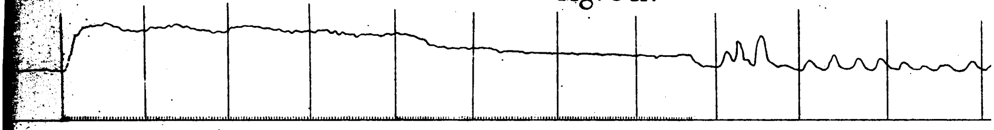


Fig. 3B.

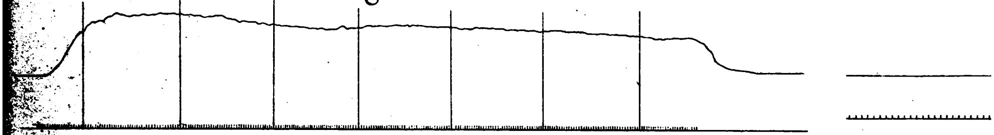


Fig. 3C.

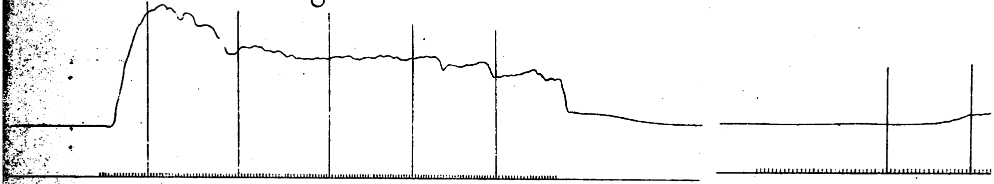
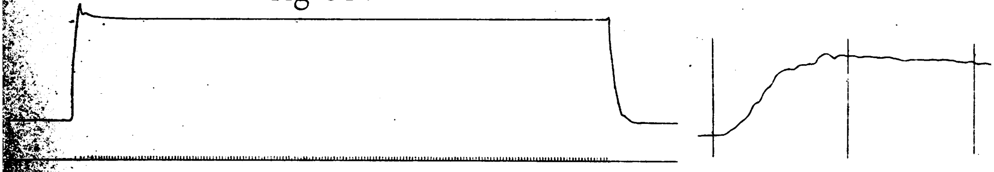


Fig. 3D.



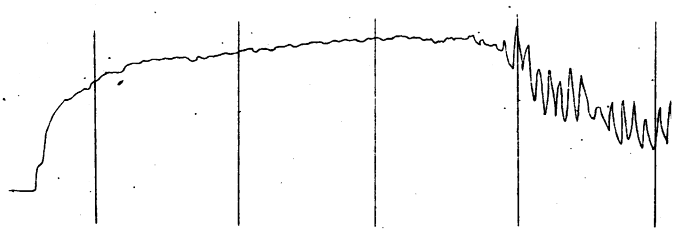


Fig. 2 B.

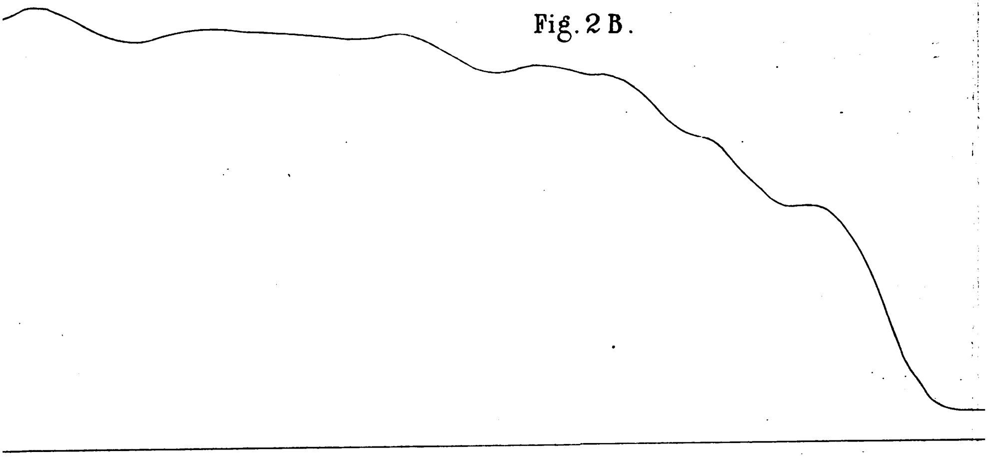


Fig. 4 A.

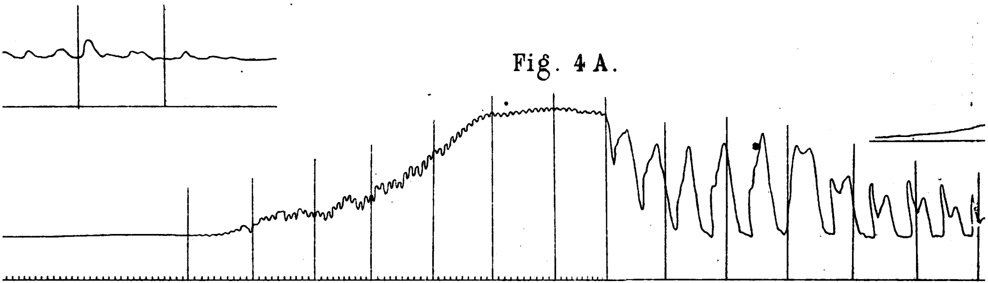


Fig. 4 B.

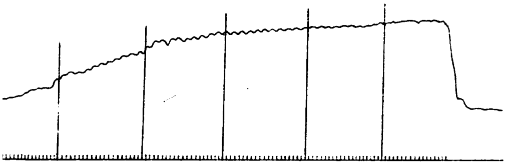


Fig. 5 A.

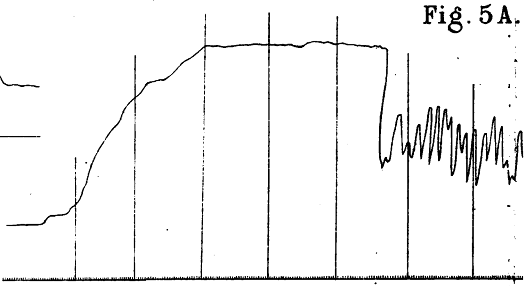


Fig. 6 A.

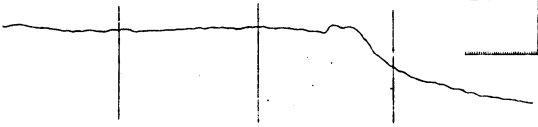
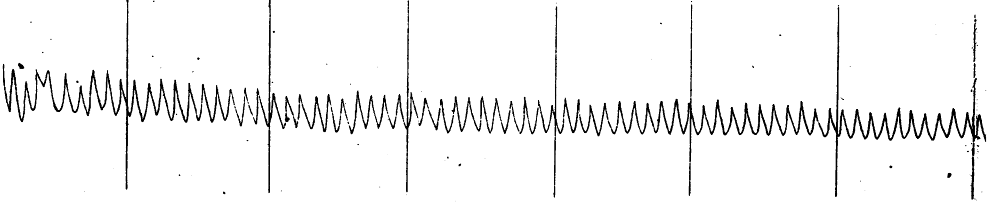
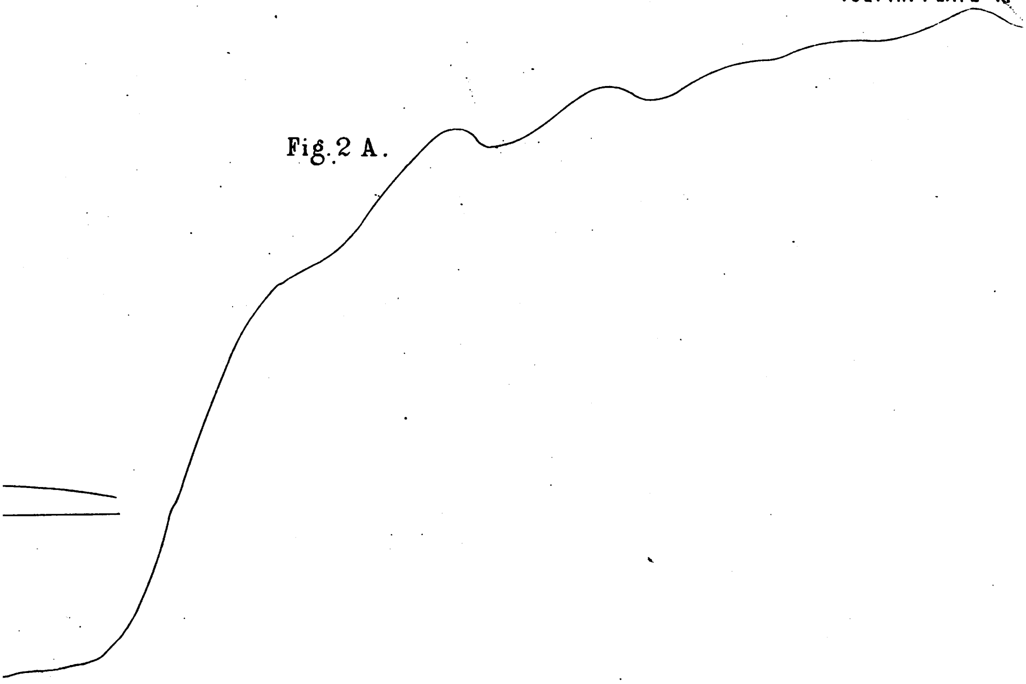


Fig. 6 B.



THE CAMBRIDGE SCIENTIFIC INSTRUMENT COMPANY.

Fig. 2 A.



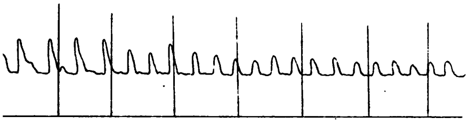
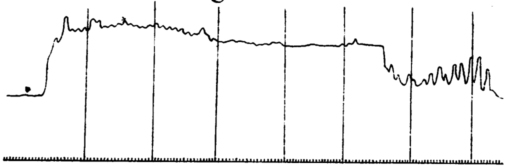


Fig. 4 C.

Fig. 5 B.



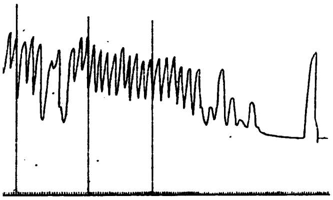
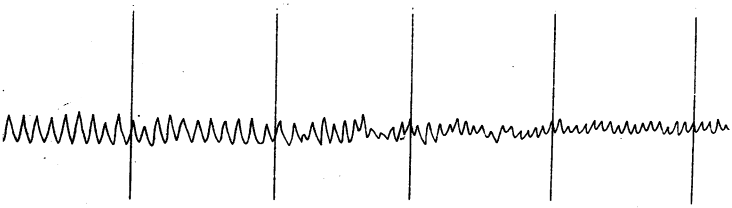


Fig. 5 C.



APPENDIX.

The following table exhibits the details of one of our experiments. We give it in order to show the method by which the preceding results have been obtained.

Dog. Mongrel, about 6 lbs. weight. The dashes indicate seconds in which the undulations were too indistinct to be exactly computed.

Position of secondary coil in mm.	Rate of excitation-reed	Part excited.	Undulations per sec.	Position of secondary coil.	Rate of excitation-reed	Part excited	Undulations per sec.
70	50	cortex faradization for 7″	—	70	50	cortex faradization for 7″	10
			11				—
			12				11
			—				10
			—				—
			10				9
			11				11
		epileptoid contractions for 7″	9				
			—			epileptoid contractions for 6″	10
			9				10
			8				—
			—				—
			—				—
			—				—
70	50	cortex faradization for 5″	11				
			10	60	30	cortex faradization for 6″	—
			10				11
			10				10
			10				11
		epileptoid contractions for 4″	8				11
			8				—
			—				
			—				

60	30	cortex	faradization for 8"	— 10 10 10 9·5 10 — —
			epilepsy for 6"	— 4 4 3 3 —
50	40	corona	faradization for 4"	— — 10 10
50	40	corona	faradization for 6"	— 12 12 11 11 11
50	30	corona	faradization for 6"	— — — — 10 10
50	30	spinal cord	faradization for 8"	— 13 12 12 — — — —
50	30	spinal cord	faradization for 7"	— — 11 11 — 12 —
70	30	spinal cord	faradization for 6"	— 10 11 8 8 —
70	30	spinal cord	faradization for 12"	— 12 9 9 11 9 10 9 — — — —
70	30	spinal cord	faradization for 12"	— 12 10 10 11 12 10·5 — — — — —
70	50	spinal cord	faradization for 8"	— 12 13 13 — — — —