Brevity, Frequency of Rhythm, and Amount of Reflex Nervous Discharge, as indicated by Reflex Contraction.

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During an enquiry, for Surgeon-General Sir David Bruce's Committee on Tetanus, into the neuro-muscular changes produced by tetanus-toxin, it became desirable to re-examine certain commonly accepted data regarding the reactions of normal reflex-centres.

I.

The first of these that engaged us regarded the reaction of a spinal reflex-centre to a single momentary stimulus applied to a main afferent nerve playing on the centre. Evidence was desired as to whether the reflex nervous discharge in response to the single volley of simultaneous centripetal impulses thus thrown into it consists similarly of a single volley of emitted impulses, or whether it consists of a volley-series, brief but yet repetitive, a series of volleys. The form of the reflex contraction should throw light on this, when compared as to its space and time relations with that of the simple muscle-twitch evoked by a like stimulus applied to the motor nerve of the same muscle as that observed for the reflex.

That in certain cases the reflex response is a single-volley discharge is extremely probable. The proprioceptive reflex of vastocrureus ("knee-jerk")* and of tibialis anticus† appears to be simple twitches commonly though not always. Using the same reflex as we ourselves turned to, Forbes and Gregg‡ find that as evoked by a single break-shock the reflex nervous response, as judged by its electrical effect, is often a single-volley discharge; they point out that dicrotism of the response need not mean that any neurone discharges twice. On the other hand, the fact that,§ when the single break-shock is strong, the reflex contraction may exceed in height the maximal twitch obtainable direct through motor nerve suggests that the reflex discharge is then, although brief, a repetitive volley-series. Beritoff|| notes that in reflex tetani produced in the winter frog by strong faradisation at rates below 40 per second, some of the component shocks used as

* *Cf.* W. A. Jolly, 'Quart. Journ. Exp. Physiol.,' vol. 4, p. 66 (1911).
† C. Asayama, 'Quart. Journ. Exp. Physiol.,' vol. 9, p. 265 (1915).
‡ A. Forbes and A. Gregg, 'Amer. Journ. Physiol.,' vol. 37, p. 175 (1915).
§ Sherrington and Sowton, 'Journ. Physiol.,' vol. 49, p. 331 (1915).
|| J. S. Beritoff, 'Zeitschr. f. Biol.,' vol. 62, p. 125 (1913).

stimuli may be followed by as many as 3–5 muscular action-current waves. The well-known slow subsidence of contraction frequently met as the after effect (T. Graham-Brown's* terminal phenomenon) seems an instance of the same kind, though more pronounced.

For our observations the muscle used was tibialis anticus, the preparation a spinal cat previously decerebrated under chloroform, the afferent nerve the popliteal, and the stimulus a single break-shock obtained by opening the primary circuit by a pendulum key set similarly throughout the whole series of experiments. The muscular contraction was recorded by an isometric myograph whose own vibration period was much shorter than that of the simple muscular twitch and damped to give it some "dead-beat" character. After the samples of reflex contraction had been obtained by stimulation of the popliteal nerve, the peroneal nerve, innervating tibialis anticus, was severed and the stimulus, arranged to be maximal, was applied to the distal stump of this motor nerve itself. The break-shock cathode was placed proximal on the afferent nerve for the reflex, distal on the motor nerve for the "direct" twitch. The preparation and its attachment to the myograph remained unaltered. The interval between the two observations was sometimes only four minutes, the electrodes and interelectrodal distance remained the same for both. Contraction curves showing duration and tension-height concurrently were thus obtained for the same muscle both in its reflex and direct response in the same individual preparation using a single break-shock stimulus delivered by the same key.

The condition of the preparations was usually very good, judging from the lowness of the threshold stimulus, both reflex and peripheral. It is to be regretted that the stimulus value was not obtained by the Martin† method, but the apparatus for that has not been at hand for us. The values taken were readings of the Berne inductorium scale, the primary fed by a 2-volt cell. The threshold readings were often very low indeed, far below 30 Berne units (=27 cm. on the ordinary scale), *e.g.*, 30 units—70° angular turn of the secondary spiral, sometimes 30°–80°. Often the difference between the threshold for the reflex and for the motor-nerve observation was only a few degrees of the angular scale.

Results.—Our graphic records of the reflex contraction to the single break-shock have not rarely been very similar to those of the twitch-contraction to the shock applied to motor nerve itself. This has been so most frequently when the break-shock stimulus for the reflex is near threshold value; it is the case also sometimes when the break-shock

* T. Graham-Brown, 'Quart. Journ. Exp. Physiol.,' vol. 7, p. 199 (1914).

† E. G. Martin, 'Measurement of Induction Shocks,' New York, 1912.

stimulus is much above threshold. More usually, however, the reflex contraction is more prolonged, and commonly also of greater height, which with the isometric torsion myograph means of greater power, than is the maximal twitch evoked by a single break-shock applied to motor nerve. This is sometimes so when the break-shock stimulus used is not far above threshold value; it is almost always so, in our experience, when the stimulus, though still of moderate intensity, is yet considerably above threshold value. The same stimulus, as judged by position of the secondary coil on the inductory

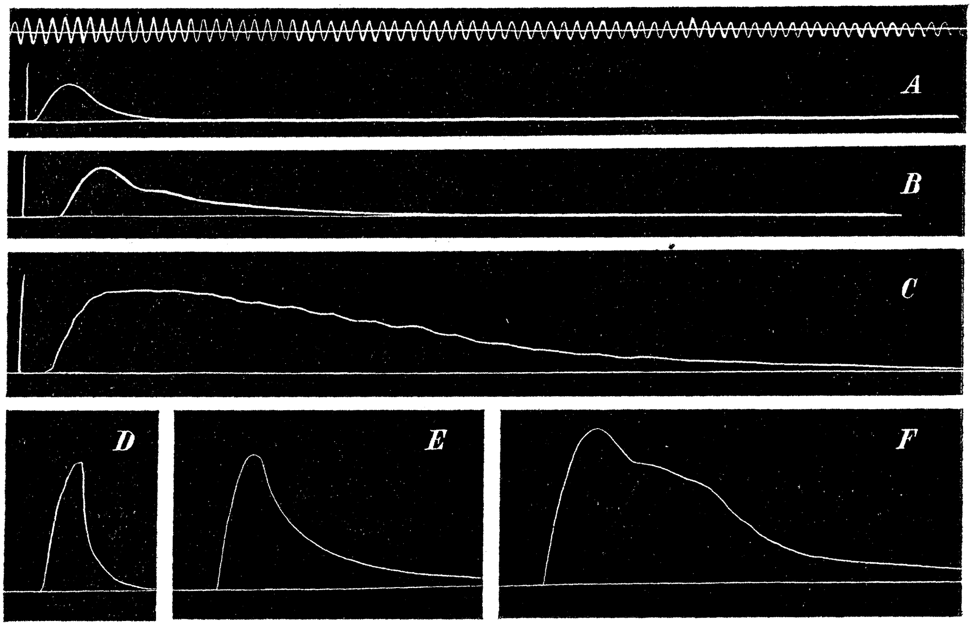

FIG. 1.—Contractions of *tibialis anticus* (spinal cat) in response to a single break-shock stimulus, in B, C, E, F, applied to afferent nerve (popliteal), in A and D applied to motor nerve (peroneal) direct. A, B, C, from one preparation; D, E, F, from another preparation. A and C, break-shock = 1000 units of Berne coil = 14 cm. distance on scale; B, at 500 units = 15·8 cm. on scale; D and F, at 15 cm. on scale = 750 units; E, at 18 cm. on scale = 200 units. Top line, tuning-fork marking 0·01 sec.

scale, gives reflexly a contraction more powerful and more prolonged than it gives when applied to the motor nerve itself. At greater strengths still the single-induction shock produces reflexly a contraction which may have a height thrice as great and a duration seven or eight times as long as the maximal contraction which it produced when applied directly to the motor nerve itself. There can thus be no doubt but that a single momentary stimulus applied to an afferent nerve often evokes a repetitive discharge of impulses from the reflex centre to which that afferent nerve conducts. The

repetitive discharge occurs not unfrequently when the stimulus is not strong. Condition of the reflex centre rather than intensity of stimulus is the decisive factor.

II.

A second point engaging us concerned the frequency of the rate of the impulse-volleys of the reflex discharge in response to rhythmic stimulation of the afferent nerve at various rates of frequency. A conclusion drawn by previous observers* has been that, when the spinal centre receives successive stimuli at rates of frequency greater than 10 a second, the motor centre ceases to follow the rhythm of the stimulation. Its response is said to be then of an independent rhythm rate, a rhythm proper to itself and exhibiting a frequency of about 10 a second. The basis of this conclusion was the observation that, below rates of stimulation of 10 a second, the muscular contraction showed waves synchronous with the rhythm of stimulation of the reflex channel, and that, with stimulations more frequent than 10 a second, the muscular contraction exhibited, instead of undulations synchronous with the stimulus rhythm, undulations, slight and somewhat irregular, recurring at the rate approximately of 10 a second. This observation and conclusion were at variance with some earlier results by François Franck and Pitres† ; they were difficult to harmonise with certain experience of our own in nerve-centres poisoned with tetanus-toxin. Hence the necessity for re-examining the point in normal reflexes in order to confirm or not its normal occurrence. For this our experiments have been with the flexion-reflex of the hind-limb (cat), the preparation being spinal, the popliteal trunk the afferent nerve, and the muscle tibialis anticus, the main flexor of ankle.

(1) The contraction was recorded isometrically, the myograph recorder having a vibration period of about 0·011 second. In the primary circuit of the inductorium was a flat spring, whose vibration frequency, by alteration of the length of the spring, could be varied readily between 10 and 60 a second. The spring was armed with a fine style set close above a mercury pool. We find the myograph of the reflex contraction exhibits clear mechanical rhythm synchronous with the stimulation at rates up to 55 a second, and sometimes beyond that. With rates up to 30 a second the synchronous tremor is so coarse as to be obvious to the unaided eye. This method of synchronous rhythm showed, therefore, in its graphic application, that at frequency-rates up to somewhat above 55 per second, the rhythmic

* V. Horsley and E. A. Schäfer, 'Journ. Physiol.,' vol. 7, p. 111 (1886).

† F. Franck and A. Pitres, 'Archives de Physiol.,' Ser. 3, vol. 5, p. 18 (1885).

discharge of the reflex centre follows the full frequence-rate of the afferent nerve stimulation, the centre emitting successive volleys of centrifugal impulses at the same rate as those evoked in and transmitted to it by the afferent nerve.

(2) The finger, on touching the muscle-tendon, detects a slight thrill at rates of stimulation of the afferent nerve even above 55 per second. To test whether this thrill has the same frequency as the stimulation rate, a

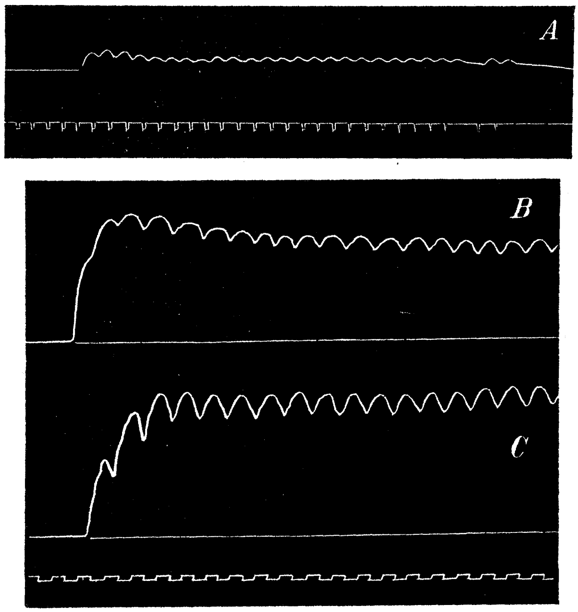

FIG. 2.—A, reflex contraction of *tibialis anticus* (spinal cat) to faradisation of afferent nerve (popliteal), at 15 per sec., as signalled below. The period of unshortcircuiting the second circuit is not shown, but the interrupter in primary circuit lapsed during the time of unshortcircuiting, and just prior to that one of the interruptions missed, and this irregularity the reflex tetanus has followed perfectly. B and C, similar preparation from another experiment; faradisation at 23 per sec.; B, the reflex response; C, response to stimulation of motor nerve; second coil at 18 cm. = 250 Berne units, for both.

myograph recorder was prepared, whose vibration period was 65 per second when attached to the contracted muscle, as tested by suddenly jerking and releasing it. The afferent nerve was then stimulated with a break-shock series of 65 per second. The recording myograph was thus used as a resonator for that pitch of vibration which should obtain in the muscle under the stimulation used if the reflex harmonised with the afferent nerve's stimulation. The result was that the myograph record then exhibited a vibration of 65 per second throughout the duration of each reflex tetanus.

Various strengths of stimulus were used, and various heights of tetanic contraction resulted, and all showed fine tremor of 65-per-second frequency. The same "resonance" method, when applied to tetani similarly provoked, but through the motor nerve direct, instead of through the afferent nerve and reflex centre, similarly gave tremor of 65-per-second rate, somewhat more marked in degree than with the reflex tetani. A resonance method is obviously open to some fallacies. Any movement of the recorder is liable to be accompanied by undulations of the periodicity proper to the recorder. But the continuance of the vibration throughout the long flat top of each tetanus record argues that underlying that there was a muscle vibration with which the lever's own period truly synchronised.

(3) The applicability both of the first mentioned "synchronous rhythm"

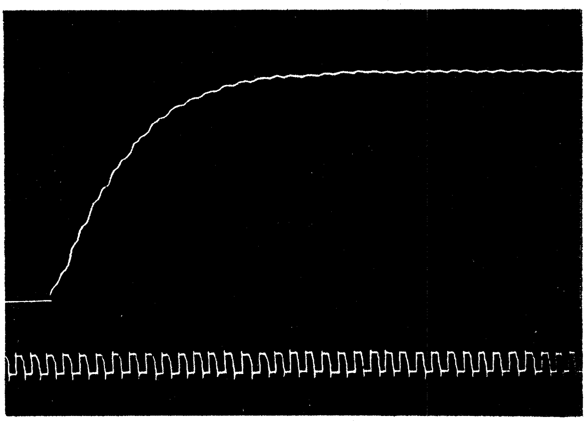

FIG. 3.—Reflex response of *tibialis anticus* (spinal cat) to faradisation of afferent nerve (popliteal) at 60 per sec.

method and the "resonance" method, for the purpose in view, depends obviously on two conditions. The individual centrifugal impulses composing each volley must be very approximately simultaneous; if they are not so, the end of one volley will commingle with the beginning of the next, and, the muscle contraction examined being that of its fibre-complex as a whole, the contraction waves will merge and may become inseparable in the record. Also, even though the successive centrifugal impulse-volleys remain discrete, the sluggishness of the contraction wave itself sets a limit to the separateness of successive waves when they follow at rates higher than a certain number per second, which number may conceivably be much lower than that at which the reflex centre can still discharge discrete impulse volleys. This limitation, due to the relatively prolonged apex-maximum of each contraction wave, can be determined by recording the tetanic contraction of the muscle

in response to repetitive stimulation of the motor nerve at various rates. We have controlled this in the muscle we used for the reflex, tibialis anticus, and in the gastrocnemius (without soleus), and find the limit with our myograph at close to 65 per second. Above that frequency, and sometimes a little below it, the tetanic contraction in response to motor-nerve stimulation exhibits practically no visible undulation.

It was noted, however, by Marey,* a number of years ago (1867), that when the motor nerve is stimulated by rhythmic stimuli of progressively quicker and quicker rate there is, after a frequency has been reached at which the tetanic contraction becomes a smooth non-vibratory line, a still further increase in the contraction height and tension on further increasing the frequency of the rhythmic stimuli. "Après que toute vibration a disparu dans le graphique, on voit la ligne tracée s'élever de plus en plus sous l'influence d'excitations de plus en plus rapprochées."† This further increment of contraction, due to increment in number of nerve-impulses per second in the motor nerve, offered a means of testing whether the reflex centre can respond with increased frequency-rate of discharge even after its afferent nerve's stimulation-rate has reached and passed beyond that pitch at which in the muscle individual contraction waves cease to be visibly distinguishable by the myogram.

Marey's observations, in the description extant of them, may not have been entirely free from objection; using a rotating interrupter, as he did, the individual breaks are more sudden under the quicker rotation, and the individual break-shocks therefore become more powerful as individual stimuli. He was, however, presumably using maximal stimuli throughout, and in that case further increase in their stimulation potency would not account for the increase of contraction observed. In applying the experiment to reflex contraction, where it is less easy to be sure that the individual stimuli are maximal, it would be preferable, when increasing their serial frequence, not to change the speed of the individual acts of breaking of the primary circuit.

To attain this, the following plan was devised (C. S. S.). The current path of the primary circuit was bifurcated for a short distance into two equal branches, each including a Hg pool, the twin pools lying under the ends of a horizontal spar, which was fixed transversely at its middle to a horizontal steel wire stretched between rigid uprights. The wire carried a horizontal armature, which could be acted on by the poles of a small electromagnet, and from one end of the armature a vertical needle on slightly torsing the

* E. J. Marey, 'Du Mouvement dans les Fonctions de la Vie,' p. 376. Paris, 1868.

† *Loc. cit.*, p. 376.

stretched wire dipped into a Hg pool beneath it. An electric circuit, independent of the stimulating circuit, was arranged so that its current passed through the electromagnet when the armature needle entered the Hg pool beneath. The wire therefore continued to vibrate at its own torsional frequency, the rate depending on its length and diameter and on the weight and moment of the armature and cross-spar with which it was loaded. The cross-spar carried, insulated from the torsion-vibrator's circuit, two fine wires re-uniting the short twin paths of the primary circuit of the stimulating inductorium. Each of these wires joined at its one end a fine gilt needle fixed vertically at end of the horizontal spar, the needle point lying close above the corresponding Hg pool. When the steel wire was torsed, one of the twin branches of the primary circuit was made and the other broken, and *vice versâ* in its elastic recoil in the opposite direction. With both of the twin branches of the circuit in use, the current passed therefore alternately by one and the other, the speed of break (and make) being identical in the two. With both of the twin branches in use, the frequency of breaking (and making) of the primary circuit was, of course, the double of the frequency when only one of them was in use. The frequency of the torsion vibration could be readily altered within wide limits by altering the length of the steel wire or by adjusting a screw-weight attached to the armature carried by the wire.

With this interrupter the frequency of the break-shocks applied to the nerve could, by closing a key, be doubled and, by opening it, halved without other change in the stimulation as it progressed; we sought for the degree of frequency beyond which further increase of frequency, *e.g.* doubling, caused no further appreciable increase in the tetanic contraction. Using it on the motor-nerve direct we confirmed Marey's observation that further increase of stimulus frequency beyond that at which the myograph record becomes steady and non-vibratory does produce increase in height and tension of contraction up to a certain point.

Turning then to the reflex preparation, and using similar reflex and similar isometric records to those already mentioned our results have been as follows. When the reflex contraction was in progress under a stimulation of the afferent nerve at 50 per second, increase, namely doubling, the frequency caused immediate marked increase in the height (tension) of the contraction, which fell back to the previous height again at once on returning to the previous slower rate. There was no reason to suspect any difference between the making and breaking of the primary circuit as carried out by the torsional interrupter in the two twin branches respectively. But to control this as a possibility the observations were repeated with alternate priority of one or

other of the interrupted branches. It made no difference to the result which one of the two branches of the circuit preceded in the sequence.

A control of this point lay also in measurement of the threshold stimulus for contraction as evoked by the circuit through each of its twin paths respectively; the threshold was found to be the same for both. A further control was obtained by comparing the height of the reflex tetanus produced (α) by use of both paths, in the way above described, with the tetanus height produced (β) by use of either of the paths alone, *i.e.*, half the frequency rate of α, the secondary coil being set further from the primary coil for obs. α than for obs. β, so that the strength of the individual shocks was less for the doubled frequency-rate than for the single-path frequency-rate. It was found that the strength of the individual shock might be considerably less

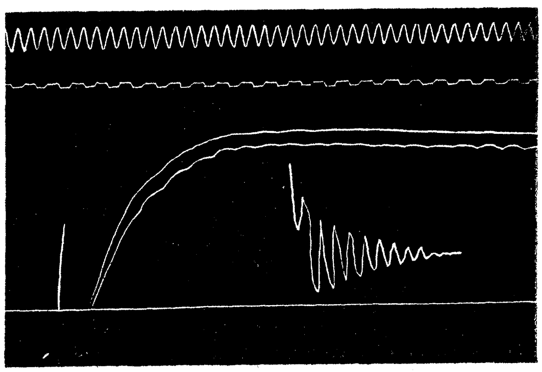

Fig. 4.—Two reflex responses of *tibialis anticus* (spinal cat) obtained in immediate succession, the lower to faradisation (of afferent nerve, popliteal) at 54 per sec., the higher by doubling the frequency (see text); the higher with the coil at 15 cm. = 750 Berne units, the lower with coil at 14·5 cm. = about 850 Berne units. Top line, 100 per sec. fork; second line, signal for 55 per sec. interrupter. Inset: the record of the vibration proper to the recording spring, lever, and attached tendon.

during the doubled-frequency rate than during the undoubled, and the resulting tetanus height yet be greater for the doubled than for the undoubled, although the frequency-rate of the latter was 50 per second or over. Thus, in instance, a shock-series at 110 per second, the secondary coil being at 100 units on the Berne scale (secondary coil 20·3 cm. from primary), gave a tetanus record of 14 mm. height; while in the same preparation the two immediately preceding observations with either of the twin paths singly gave a tetanus of 12 mm. height only, although for them the secondary stood at 150 units on the Berne scale (secondary coil 19·4 cm. from primary), the frequency-rate of each of the twin paths being, of course, 55 per second.

The individual break-shock stimuli being similar throughout and delivered throughout by the same unmoved electrode (cathode for break-shock

proximal to anode on the afferent nerve), the sole stimulation-change accompanying the contraction-increment is the increased number of stimuli per second. This increase of contraction-height on increasing (doubling) the

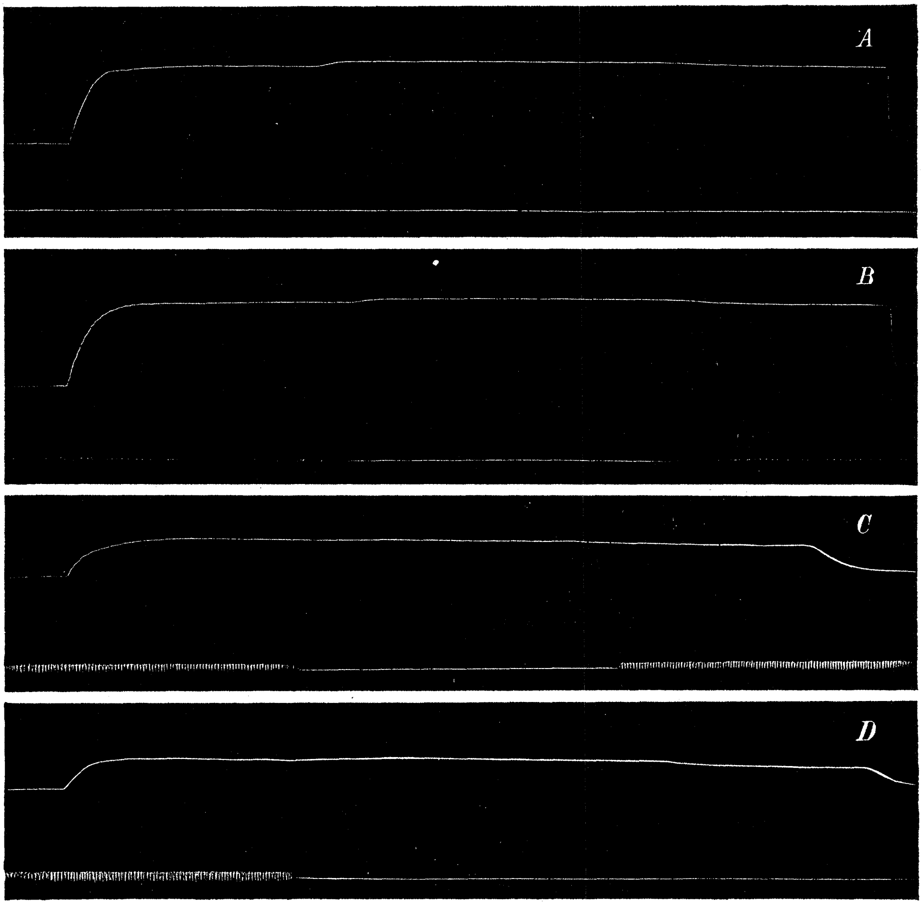

Fig. 5.—Reflex contractions of *tibialis anticus* (spinal cat), showing effect of intercurrent doubling of frequency rate of interrupter in primary. A and B, initial (and terminal) rate of stimulation, 65 per sec.; intermediate period, shown by higher plateau of contraction, at 130 per sec. In B the order of succession of the twin branches of the circuit is reverse of that in A. C and D similar, but with rate of 75 per sec. (doubling to 150 per sec.); the increase of height of the plateau obtained by doubling is still obvious, though less than in A and B. The signal, as set for the slower rate of interruption, has failed to pick up the quicker rate.

stimulation frequence was observed in experiments carrying the initial, *i.e.*, undoubled, frequence of stimulation up to 75 per second. When that rate was reached the increment of contraction-height obtained by further increase (doubling) became quite small, though still quite indubitable. The rate of

reflex discharge must, therefore, with increase of the rate of stimulation of the afferent nerve to beyond 75 per second increase to beyond 75 per second. Whether that rate approaches actually near to the limit of the rate of frequency which the reflex centre's discharge can follow cannot, of course, be answered by this method. There is nothing to show that when in the experiment the stimulation-frequency is changed from 75 per second to 150 per second, the reflex discharge does not, in fact, follow the latter figure, as we may suppose the motor nerve to do in the case of its direct stimulation.

The results by mechanical methods stand therefore no longer in contradic- with those obtained by the galvanometer using oscillations traceable to muscular action currents. C. Foà* followed in the chloralised dog action currents of the contracting femoral quadriceps synchronous with the electrical stimuli up to 20 per second, and in the frog up to 58 per second. Beritoff† concludes from galvanometric records that the discharge-frequency of the flexion-reflex in the winter-frog may approach to 75 per second, and in the summer frog to 150 per second, and P. Hoffmann‡ that in the frog the frequency may follow at first at 100 per second, though soon dropping to half that number. With these our observations by mechanical registration in the "spinal" cat are obviously perfectly compatible.

The datum that the spinal reflex-centre is a mechanism constructed with a recurrent refractory phase of 100σ duration was irreconcilable with observations§ tending to show that the duration of the spinal reflex-centre's refractory phase is of an order not far removed from that of the nerve-muscle preparation itself. The present results greatly relieve that difficulty, for, although their method does not measure the actual duration of the spinal refractory phase, they do show that the extremest length of that phase does not, under ordinary circumstances, extend beyond 12σ.

III.

A third point requiring re-determination was the ratio between the maximal power of the reflex tetanus and that of the peripheral tetanus excited by faradisation of the muscle's motor nerve. The statement based on direct experiment has been that the maximal power of the spinal reflex contraction amounts to less than six-tenths of that developed by the maximal contraction evoked by direct faradisation of the motor nerve.||

* 'Zeitschr. f. allg. Physiol.,' vol. 13, p. 35 (1912).

† 'Zeitschr. f. Biol.,' vol. 62, p. 125 (1913); *ibid.*, vol. 64, p. 161 (1914).

‡ 'Archiv f. Physiol.,' 1911, Suppl., p. 233.

§ Sherrington and S. C. M. Sowton, 'Journ. Physiol.,' vol. 49, p. 342 (1915).

|| V. Horsley, 'Brain,' vol. 21, p. 547 (1898).

For examining this point, we have again used tibialis anticus as muscle, and as our spinal reflex the reflex evoked by faradisation of the popliteal nerve, and then in the same preparation we have registered similarly the maximal tetanus obtainable by direct faradisation of the motor nerve (peroneal) itself. We employed the same frequency-rate of faradisation for both reflex and direct effect, and both observations were obtained with exactly the same registering apparatus, sometimes within four minutes of each other. The myograph resistance was, as in our other observations, a torsion-wire and the record isometric. The upper part of the scale of resistance of the myograph was, within the limits of pull developed by the

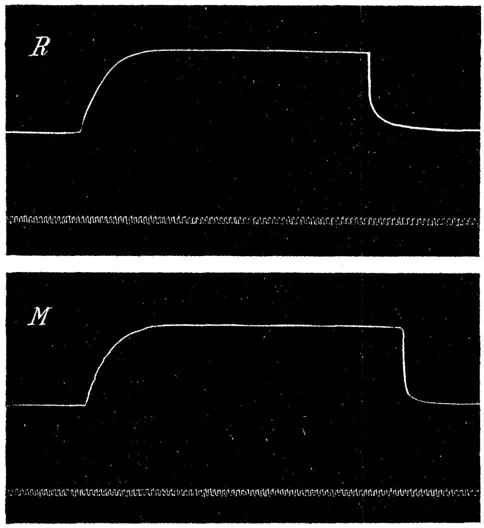

FIG. 6.—Maximal reflex (R) and maximal motor-nerve (M) responses of *tibialis anticus* (spinal cat) obtained from same preparation, rate of faradisation 75 per sec. in each case, and the secondary coil being at 12·8 cm. = 2000 Berne units for both. Under each the signal recording the interruptions in the primary.

muscular contraction, almost as open for the higher limits as for its range near zero. The animals (cat) were young and small, and the maximal tensions in different animals observed varied between 650 and 940 grm.

Our results have been as follows: The ratio between the power of the maximal tetanus of the spinal reflex and that of the maximal tetanus obtainable by faradisation of the motor nerve is often unity, 1/1. In not a few preparations it is somewhat less, *e.g.*, reflex/direct = 9/10; in some preparations it is very markedly less, *e.g.*, 6·5/10.

That the maximal power of tetanic contraction obtainable from a muscle reflex is often equal to the maximal tetanic power obtainable, under the

same frequency-rate of faradisation, by direct faradisation of the motor nerve itself, bears on the question whether any one afferent nerve can set into action the whole of the reflex centre to which it is afferent.*

Summary of Conclusions.

1. A single momentary stimulus of moderate intensity, *e.g.*, a break-shock, even though not far above threshold value of stimulation, applied to the afferent nerve of a spinal reflex centre, evokes from that centre not uncommonly a brief repetitive series of volleys of motor impulses. This it tends to do the more the stimulus, within limits, is increased in intensity, but the state of the reflex centre at the time is also a decisive factor.

2. The rhythm of repetition of volley-discharges from the spinal reflex centre is traced by the mechanical method to be of synchronous rate with that of stimulation of the afferent nerve up to a frequency of 55 per second, and, by a mechanical resonance method, up to a frequency of 65 per second. By a "doubling frequency" method, it is shown further that the frequency-rate of the reflex discharge has not reached its limit under a stimulation of 75 per second, but surpasses that degree, though to what extent the method cannot say.

3. The maximal mechanical power of a muscle contracting under spinal reflex action is sometimes as great as the maximal which can be evoked from it by direct faradisation of the motor nerve itself.

* M. Camis, 'Journ. Physiol.,' vol. 39, p. 228 (1909).