# *Break-shock Reflexes and "Supramaximal" Contraction-response of Mammalian Nerve-muscle to Single Shock Stimuli.*

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The following observations continue some of those reported previously to the Society by Mr. N. B. Dreyer and myself (1) and by Dr. K. Sassa and myself (2). But in the present instance the technique has been considerably modified in the hope of securing finer discrimination between the contraction forms obtained. The speed and intensity of the reactions of mammalian muscle with its blood supply intact rendered desirable greater lightness in the moving parts of the myograph. The free vibration rate of the isometric myograph now used has been more than 900 a second; its damping such that when suddenly released from a torsional deviation, approximately that obtaining in the muscle observations, the vibrations ceased to be visible under tenfold enlargement in about 0·03 sec. The registration of the myograph movement has been by optical projection on a travelling photographic plate, time being recorded on the plate by a rotary shadow-marker of the pattern devised by Mr. Bull, of the Institut Marey, Paris.

The reflex preparation has been *tibialis anticus* muscle in the spinal cat, decerebrated and free from drugs. The stimulus used has been a single break-shock given by an automatic key and applied by platinum electrodes 5 mm. apart to the central stump of the cut and isolated afferent nerve (popliteal, internal saphenous or digital branch of musculocutaneous) or, for the motor control, to the peripheral stump of the cut motor nerve (peroneal), kathode proximally for the former, kathode distally for the latter. The magnification of the muscle movement has been sixty times: that is, for a myogram of 30 mm. height recording a tension of 915 grm., the muscle, *e.g.*, of 12 cm. length, shortened 1/240 of its length; the myograms are thus practically isometric.

The trend of the results obtained can be conveniently indicated by describing briefly the changes observable (Fig. 1) in the reflex myogram under progressive step-by-step increments of strength of the break-shock delivered as stimulus to the afferent nerve, *e.g.*, popliteal. Starting with a break-shock of little above threshold value for reflex stimulation, *e.g.*, the secondary coil at 60 cm. from primary on the inductorium scale, the reflex myogram then obtained is of lower crest-height and less steep ascent than is the maximal-twitch myogram (subsequently obtained by break-shock stimulation of

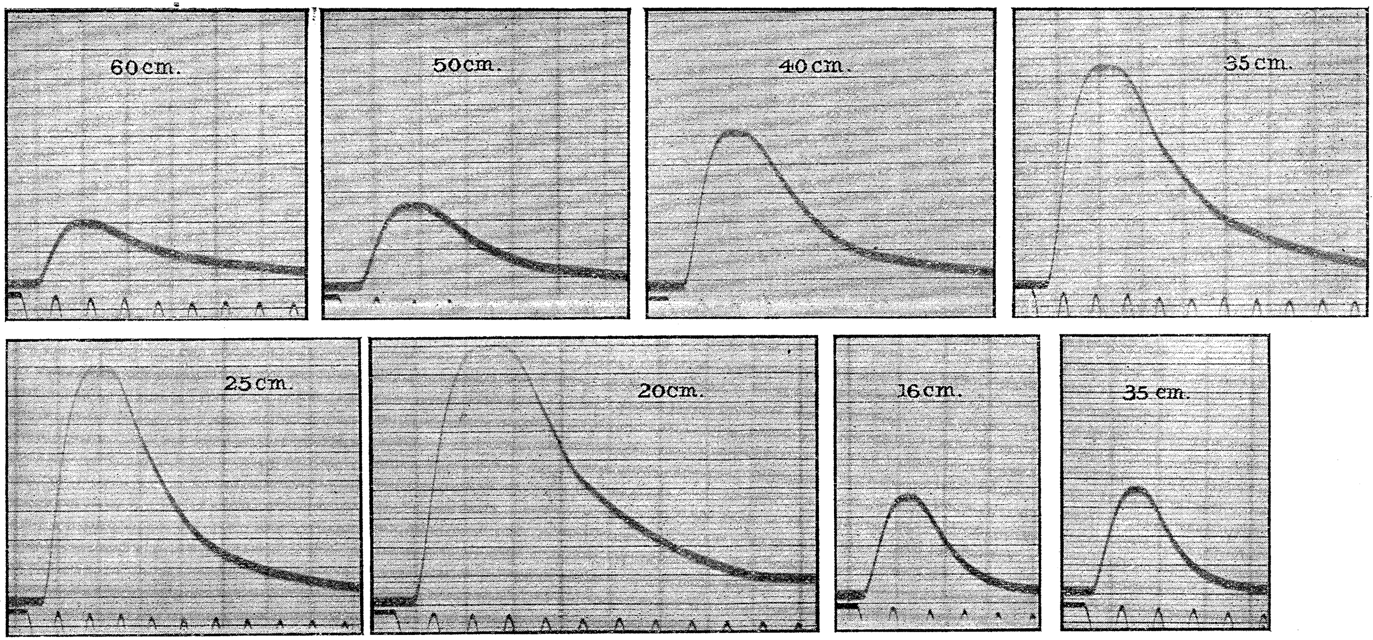


Fig. 1.—Reflex contractions of tibialis anticus (spinal cat), each excited by a single break-shock to central stump of cut popliteal nerve, the coil distance in centimetres on inductorium scale shown by numerals against the corresponding inset in the figure. Lower two insets to right are maximal twitches to single break-shock to cut motor nerve, coil distances similarly indicated. Time ordinates $\frac{1}{25}$ sec. apart each $\frac{1}{5}$ sec. shown by stronger vertical. The horizontals, 1 mm. apart, indicate tensions of the isometric record; value of each 1 mm. interval is approximately 31 grm.* Magnification of muscle-shortening is 60 times. Stimulus-signal below.

* Throughout the figures, except fig. 3, the "shadow myograph" was arranged to give a record 50 mm. in height for a tension of 1500 grm. The tendency of the torsional excursions to become somewhat less relatively with successive equal increments of torsional pull was counteracted by setting the rectilinear shadow's fall upon the camera slit in such a way as to slightly increase the optical magnifications with progressive deviations of the shadow from its zero position. The calibration of the records after this had been done gave the following results: 5 mm. vertical height = 150 grm. tension; 10 mm. v.h. = 300 grm. t.; 15 mm. v.h. = 450 grm. t.; 20 mm. v.h. = 610 grm. t.; 25 mm. v.h. = 765 grm. t.; 30 = 915; 40 = 1210; 50 = 1500.

appropriate strength applied direct to the distal stump of the cut motor nerve). But the crest-height of the reflex contraction is attained later than that of the maximal twitch even when the height of the former is considerably less than that of the latter. The decline of the reflex contraction is considerably longer than that of the twitch. These differences accord with the considerations admirably given by Forbes and Gregg (3) in their discussion of their observations comparing the galvanometer records of the action current of the break-shock flexion-reflex (decerebrate) with that of the directly stimulated motor nerve. They pointed out that such differences as those above are not incompatible with the centrifugal impulses in the reflex, being, as for the motor twitch, not more than one, *i.e.*, not multiple, per nerve-fibre, since the total volley in the reflex may very probably be less nearly synchronous, *i.e.*, may, though single per fibre, be distributed through the constituent motor fibres as a group during a somewhat longer period of time.

Through a certain range of further increase of the break-shock stimulus the same above-mentioned characters of the reflex contraction as compared with maximal twitch continue to hold, but the crest-height of the reflex contraction continually approaches more and more to that of the maximal-twitch and the duration of the reflex contraction continues to be no less and usually still further prolonged. Then, as the stimulus is further augmented, there is reached a strength of stimulus at which the crest-height of the reflex contractions equals and, with strengths of stimulus beyond that, exceeds, the crest-height of the maximal twitch itself, while likewise the total duration of the reflex contraction exceeds, usually very considerably, that of the maximal twitch.

The strength of stimulus at which the reflex contraction thus begins to surpass the maximal twitch's crest-height is not necessarily great. Thus, in the experiment from which fig. 1 is taken, the reflex contraction's crest-height began to exceed that of the maximal motor-nerve twitch when the secondary coil stood at 45 cm. from the primary, the maximal twitch compared with it being sampled at 16 cm. of secondary's distance from primary. The stimulus for the reflex was, therefore, very weak relatively to that used for the maximal twitch, though the contraction evoked by the former was the greater. The reflex contraction evoked by the coil at 40 cm. (fig. 1), still much weaker than that used for the standard maximal twitch, exceeded the maximal twitch yet more. With further increase of the stimulus the tension developed by the reflex contraction may become considerably more than twice as great as that developed by the maximal twitch; and the duration of reflex contraction twice or thrice or even four times that of the twitch. In the final steps of increase of the stimulus, *e.g.*, where the break-shock can be felt when the

electrodes are placed on the tongue, and at closer coil distances still becomes unpleasant (secondary coil at 16 cm. or less), the resulting increments in reflex contraction tend to be increments of duration more than of crest-height

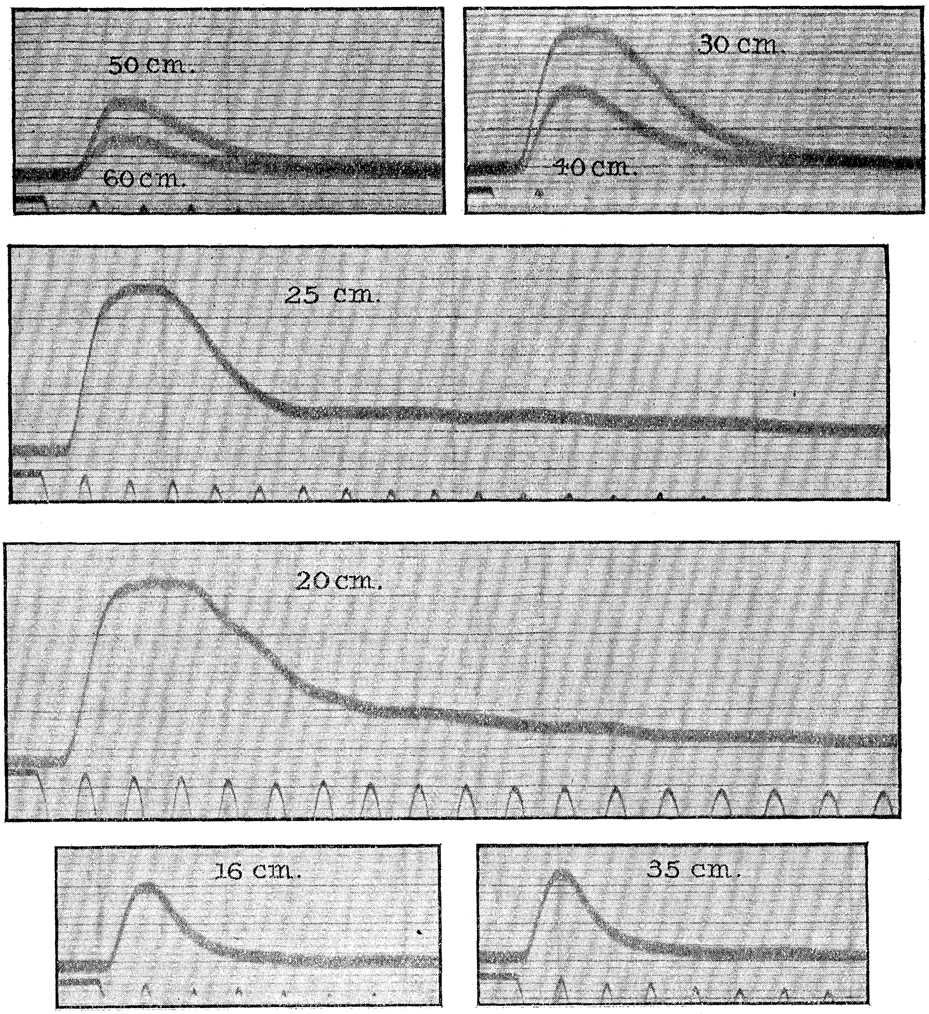


FIG. 2.—Similar to fig. 1, but the break-shock reflexes evoked from internal saphenous nerve instead of popliteal. The numerals at each inset give the coil distances for the break-shock. The two lowest insets show the maximal twitch elicited *viâ* motor nerve direct with the coil distances for the break-shock employed. Time ordinates and tension abscissæ as in fig. 1. Stimulus-signal below.

(figs. 2 and 7). With these strong stimuli the period of declining tension tends to be drawn out and to exhibit irregular undulations.

The above description applies to the spinal preparation as employed in

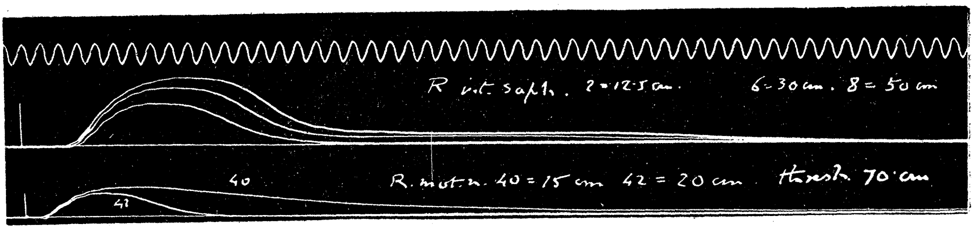


Fig. 3.—Upper curves. Three break-shock reflexes (tibialis anticus, spinal cat) from internal saphenous at coil distances marked on the figure. Lower curves, a maximal twitch by break-shock to motor nerve at 20 cm., and a "supramaximal response" by break-shock at 15 cm. coil distance. Time marked by 100 d.v. fork. Isometric "fall" myograph. Motor-nerve threshold at 70 cm.

these experiments, that is, at times varying from four hours to twenty-eight days after spinal transections at levels between the 9th thoracic and the 2nd lumbar segments of the cord. But, as shown previously (2), (7), (8), the description cannot be carried over with security to the decerebrate preparation. In this latter the reflex threshold is higher (7), (8), the reflex contraction is less strong and runs a different course (2), (7), and the latent period is, in my experience, considerably longer. These differences from the "spinal" reflex are instanced in the records given in fig. 5. The latencies are as long as some of those found by Jolly (11), with action currents, for the contra-lateral

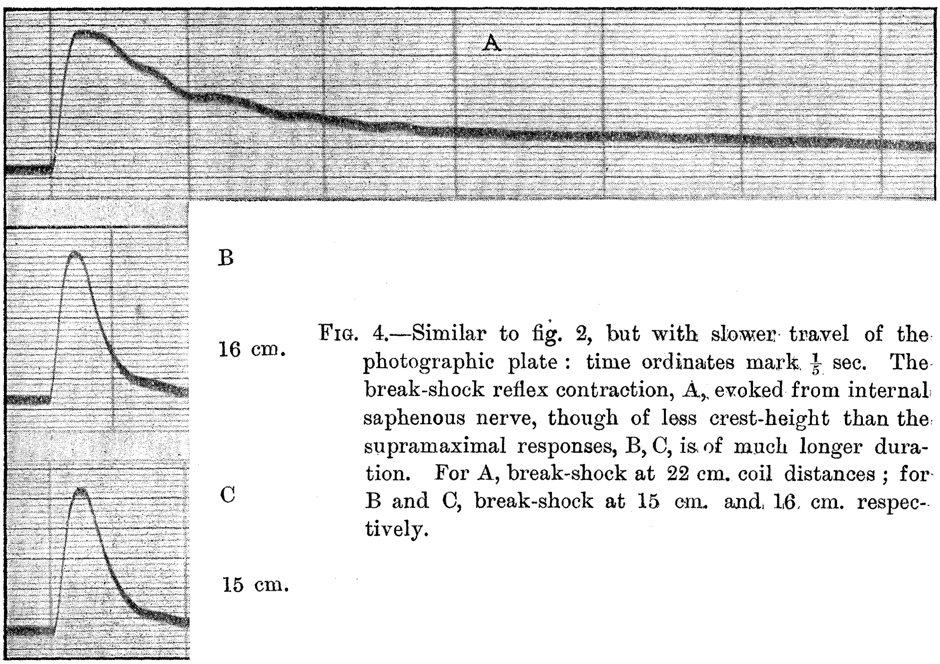


Fig. 4.—Similar to fig. 2, but with slower travel of the photographic plate: time ordinates mark $\frac{1}{5}$ sec. The break-shock reflex contraction, A, evoked from internal saphenous nerve, though of less crest-height than the supramaximal responses, B, C, is of much longer duration. For A, break-shock at 22 cm. coil distances; for B and C, break-shock at 15 cm. and 16 cm. respectively.

reflex. They and the course of the contraction suggest that in the decerebrate preparation the contraction of this ipsilateral reflex is possibly, in some cases, the rebound phase of a diphasic reaction, whose first phase is mainly inhibitory, owing to admixture of concurrent inhibition and contraction, although the inhibition cannot, owing to absence of actual contraction in the muscle at the time when the reflex is initiated, make itself apparent by

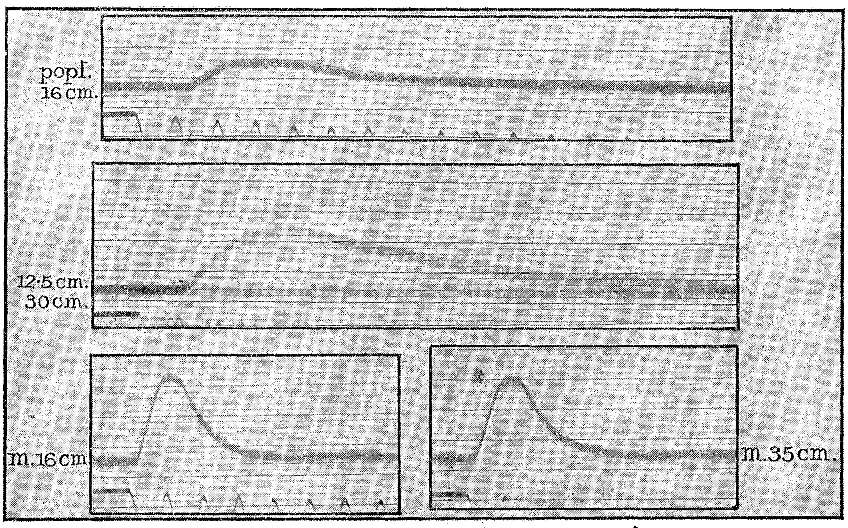


Fig. 5.—Similar to fig. 1, but from a decerebrate preparation instead of a spinal preparation. The upper two insets are reflex contractions (tibialis anticus) evoked by single break-shock to central stump of popliteal nerve; the numerals against each inset indicate the coil distances—the shocks for the reflex contractions are very strong; in the middle inset the break-shock at coil distance of 30 cm. produced no contraction. The lower two insets are maximal twitches evoked by break-shock to motor nerve at 16 cm. and 35 cm. respectively. Time ordinates and tension abscissæ as in fig. 1. Stimulus-signal below.

any relaxation of the muscle, but only by delay and reduction of the ensuing contraction.

The observations, in so far as they cover the ground of those reported in the two previous papers (1 and 2) confirm and amplify them. (1) A single break-shock of moderate intensity, applied to a bared afferent nerve, not rarely evokes a reflex contraction exceeding in tension and duration the "maximal" twitch elicitable by break-shock stimulation of the motor nerve itself. (2) The rise of tension in the reflex contraction very soon after its first onset is not rarely of steeper gradient than is that of maximal twitch. This steeper gradient is observable in some instances even before the termination of the first 0·01″ from commencement of the contraction. (3) The maximal

tension of the reflex contraction is attained later than that of the twitch. (4) The crest of the reflex myogram tends commonly to be more plateau-like than is that of the twitch.* (5) The decline of tension of the reflex contraction is more prolonged than is that of the twitch. (6) The reflex myogram elicited by the break-shock *viâ* each of the afferent nerves used is of more or less characteristic form for each of those nerves severally. Thus, internal saphenous gives a lower and more prolonged crest-plateau (figs. 2, 3) than does popliteal.

These differences observable between break-shock reflex contraction and the maximal twitch evoked from motor nerve suggest that, while in the latter the motor nerve conveys but a single nervous impulse per fibre, in the former the centrifugal nervous impulses are, at least in some of the efferent fibres, repetitive. It was shown by Sassa and myself (2) that this difference persists after the proprioceptive reflex arc of the reacting muscle itself is broken. The responsible difference, therefore, between the nervous preparations compared for reflex and twitch is that while that of the latter consists of motor nerve, muscle, and neuromyal junction, that of the former comprises in addition the reflex (spinal) centre and the central stump of the afferent nerve. The added factor that at once appeals as that most probably responsible for the difference between the reactions of the two preparations is doubtless the spinal centre present in the former and absent from the latter. Prior, however, to accepting this inference, certain contingencies have to be borne in mind.

In the mammalian motor nerve-muscle preparation, as in that of the frog, the muscle response under progressively increasing break-shock stimuli, starting from threshold value upwards, is a twitch contraction, which progressively increases in strength through a certain range of stimulus increments (sub-maximal), and then remains practically without further increase (fig. 6), *i.e.*, is " maximal " throughout a very considerable succeeding range of further increments of stimulus. When, however, this long range of maximal stimuli is followed to its stronger end, there comes a point where, with further increase of the break-shock, the muscular response begins again to increase, and increases rapidly (fig. 6). This point in the inductorium used in these experiments showed considerable variation, but was usually where secondary coil was about 15 cm. on the scale from primary.

* In view of the precautions taken to minimise lag and overthrow in the myograph used in these records, it is noteworthy that the crest of the motor twitch contraction in this mammalian muscle with intact blood circulation appears in the myograms not as a round-curved peak, but rather as a plateau, although the plateau is short, ending slightly more abruptly than it began.

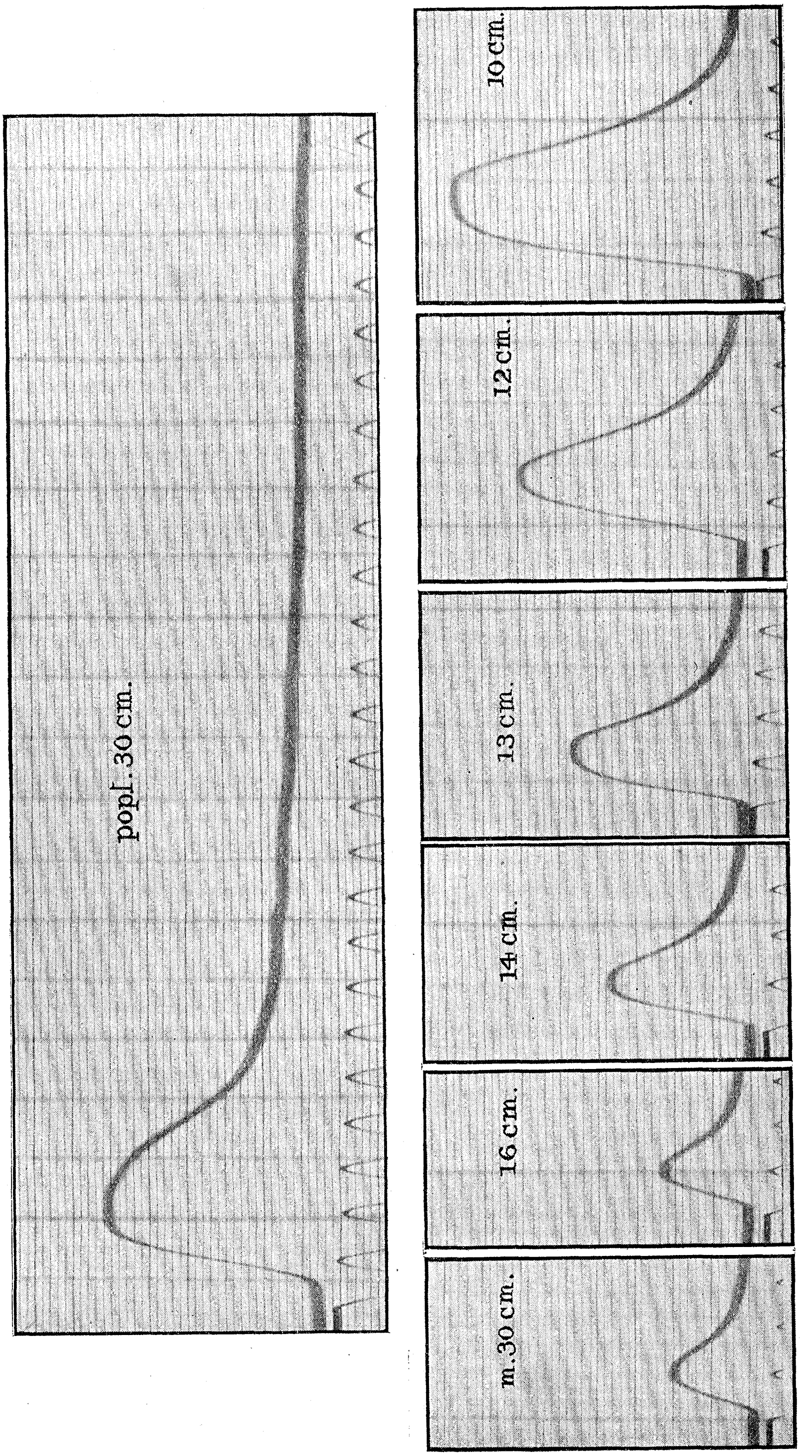


FIG. 6.—Lower row are maximal twitches and supramaximal contraction responses, evoked by single break-shock applied direct to cut motor nerve, for comparison with reflex contraction (upper inset) to single break-shock applied to central stump of popliteal nerve. Numerals against each inset give the coil distances for the break-shocks. The photographic plate was, as shown by the ordinates, travelling rather more quickly for the reflex record than for the other records, the speed for all these latter was the same. Tension abscissæ as usual. Stimulus-signal below.

Sometimes it did not occur even when 10 cm. was reached. These "supra-maximal" contractions thus elicited from motor nerve appear from their myogram features to be tetanic (fig. 6). They differ from the twitch in their greater height and the greater steepness of up-gradient which their ascent soon after its outset assumes, and, from the reflex contractions, in their brief latency, their more peaked, less plateau-topped climax and more rapidly falling, less prolonged, decline. Many of them cannot be explained by mere addition to the kathodal (closing) twitch of a simple opening twitch from anode, even supposing the intervention of the refractory phase of the nerve-fibre did not disallow such an assumption. Their course and character invite further examination, which I purpose to make. Their interest here is for the indications they afford that a single break-shock stimulus can, if of high strength, excite not merely one impulse, but a repetitive series of impulses in fibres of a motor nerve (*cf.* Forbes and Gregg (4)).

The form of the "supra-maximal" responses, as they progressively increase under successive increments of the break-shock stimulus, seems inadmissible of other interpretation. As the secondary coil is by equal steps brought nearer to the primary, the crest-height of the responses increases more and more rapidly, as does, of course, the physical value of the induced current. The development of contraction-tension thus reached by the higher members of the "supra-maximal" response series may amount to more than double that of the ordinary maximal twitch. This seems explicable only by their contraction being tetanic in nature. With the higher members of the series, the latent period between stimulus and commencement of contraction becomes remarkably shorter than that of the ordinary maximal twitch, though the place of the electrodes be retained for both at the same distance up the motor nerve. This led me to suspect at first that the strong current employed might by escape be exciting the muscle itself directly, although the distance between the muscle and the electrode the nearer to it was more than 60 mm. But on ligating, with a thread soaked in normal saline, the nerve 20 mm. distal to the electrodes, *i.e.*, between muscle and the seat of the electrodes on the nerve, all contraction in response to the strongest break-shock given by the electrodes at once ceased. Moreover, strong break-shocks applied to the afferent nerve show similarly no sign of "escape," as evidenced by the latency of reaction being still as great as with the weaker (fig. 5).

It is difficult, in the light of Adrian's demonstration that the "all-or-none" principle obtains in the impulse reaction of motor nerve-fibres, to suppose that these strong stimuli given to the motor nerve can cause it to deliver *stronger* nerve impulses to the neuro-myal junction or the muscle-fibres than

do the moderate or weak. And since break-shock stimuli of lower strength than these strong ones already produce the maximal twitch, *i.e.*, are by definition "maximal" and excite all the motor nerve-fibres to the muscle, these latter strong ones cannot excite a greater number of the motor nerve-fibres than do those former. The seat of the initial causation of the "supra-maximal" response seems, therefore, excluded from being either at the neuro-myal junction or in the muscular fibres proper.

Bearing in mind, however, features of the "local excitatory process," the process recognised by Adrian and Keith Lucas (5), (6), to occur at the seat of stimulation of an excitable tissue, and elucidated by them, there seems no inherent unlikelihood that a single shock applied to a nerve should, if strong, evoke a short series of impulses in individual nerve-fibres. Forbes and Gregg (4) have already called attention to this probability. Persistence of the excited state at the locus of application of the strong stimulus should, if suitably prolonged, result in initiation thence of a succession of propagated disturbances, impulses, along the fibres. This view merely demands that the nerve-fibre reacts essentially similarly to cardiac muscle-fibre. Garten (9) has shown that under continued stimulation by a strong voltaic current the response of the mammalian nerve is a rhythmic series of action-currents.

But if motor nerve-fibres can be excited by a single induction shock so as to react repetitively, so also presumably can afferent nerve-fibres. The evidence of repetitive discharge in the break-shock reflex may, therefore, be referable to repetitive response on the part of the directly stimulated afferent fibres themselves rather than to repetitive response developed in the reflex centre. To this possibility the present observations supply no entirely decisive answer. It is noteworthy, however, that the motor nerve-fibres indicate tetanic response only when the break-shock stimulus is of a far higher strength than are break-shocks fully sufficing to evoke reflex contractions of tetanic character when applied to the afferent nerve. These strong break-shock stimuli are presumably of a strength corresponding with that named by Forbes and Gregg (4), in their work with action-currents, "the maximal limiting value." If the tetanic character of the reflex contraction is attributable to repetitive response in the afferent nerve-fibres themselves, these latter must differ from motor nerve-fibres by reacting repetitively to stimuli sometimes a hundred-fold weaker than those required for making ordinary motor nerve-fibres so react. Again, the differences (figs. 4 and 8A) are striking between the myogram forms of, on the one hand the "supra-maximal responses" produced by break-shock stimulations of motor nerve, and on the other hand the break-shock reflex contractions evoked by stimulation of the afferent nerve. Even in instances wherein

the two crest-heights are approximately equal, the time-relations of the development and subsidence of tension are widely different. In no break-shock reflex have I met decline of tension in relation to crest-height so rapidly precipitous as it is quite commonly in the "supra-maximal" motor-nerve responses. Again, on the view that the tetanic character of the reflex contraction evoked by a break-shock applied to the afferent nerve is referable to repetitive reaction to the break-shock by the stimulated afferent nerve-fibres themselves, the distribution of the repetitive process both in time and among the individual nerve-fibres must be assumed to be considerably different in the internal saphenous nerve from what it is in the popliteal nerve; the low prolonged break-shock reflex from the former contrasts with the higher less plateau-like fountain-topped reflex contraction given by the latter. Again, the fact that the intensity and extent of the break-shock reflex contraction is much greater in the spinal preparation than in the decerebrate, a circumstance which affects the conditions of the spinal centre but cannot be thought to influence that of the afferent nerve-trunk itself at the seat of stimulation, argues for the centre rather than the afferent nerve being responsible for the development of the tetanus of the reflex response.

On the other hand, if the motor nerve-fibres begin to respond repetitively at high strength of the break-shock stimulus, it is prudent to suppose that so also do the afferent fibres under similar strong stimuli. In this the results endorse the opinion reached by Forbes and Gregg (4), who write after their study of the nerve action-current, and their experience of the spread of reflex activity to remote muscles in the decerebrate preparation: "Of the conceivable explanations" . . "that have occurred to us, we incline to regard as the most probable that a second propagated disturbance, or even a series of them, may be evoked in each afferent nerve-fibre by a single shock, if sufficiently strong."

Evidence of this may be looked for, in the present experiments, in some change possibly discernible in the character of the reflex contraction on and after the break-shock reaches about that strength at which it excites "supra-maximal" contractions when applied direct to the motor nerve, *i.e.*, at about 15 cm. on the scale of the inductorium used in these experiments. A change in the form of the reflex myograms is in fact noticeable usually at about this place on the inductorium scale. This change consists, as mentioned earlier in the text, in a considerable further prolongation (fig. 7) in the duration of the reflex contraction to the break-shock, accompanied by little or no further increase in the crest-height, the reflex in its slow subsidence not rarely exhibiting late subsidiary crests (fig. 4), assuming a somewhat dicrotic or even tricrotic character.

That a reflex contraction is sometimes of the nature of a simple twitch, *i.e.*, non-tetanic, seems clearly shown by observations of Jolly (10) and of Wertheim-Salamonsen (12) on the muscular action-current in the knee-jerk. But the probability seems that the tetanic character so commonly observed in

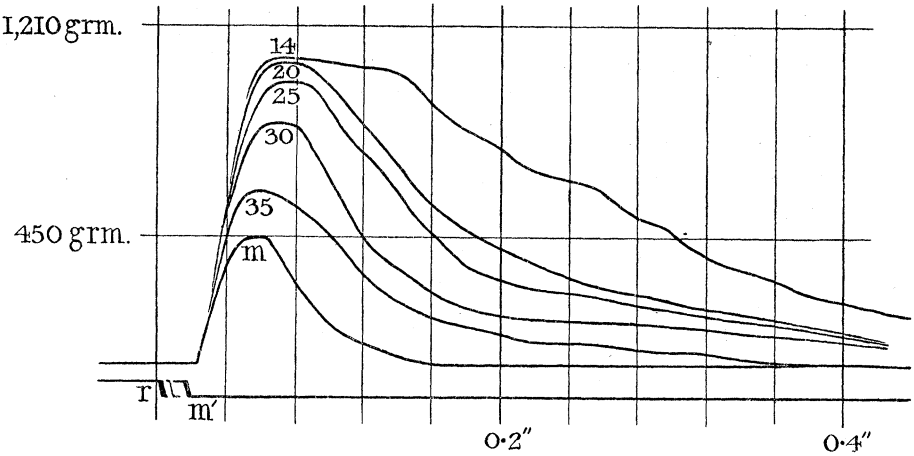


FIG. 7.—Superposed tracings of photographic myograms all from same experiment comparing those of greater crest-height than the maximal twitch, and indicating the change in the height and duration relation when the break stimulation to the afferent nerve (poplit.), is pushed to high strength, *i.e.*, 14 cm. The lowest curve (*m*) is the maximal twitch as given from 35 cm. up to 20 cm. The numerals opposite the other curves give the coil-distance of the break-shock for each ; tibialis anticus, spinal cat. Time ordinates mark $\frac{1}{25}$ sec. : the drop of signal line at *r* shows latency for the weaker reflexes, at *m′* the latency for the motor twitches ; the faint line of drop between these gives latency for the strongest reflexes.

the reflex contractions dealt with in this paper, as evoked by a break-shock applied to the bared afferent nerve, is, when that shock is of weak or moderate intensity, referable to the reaction of the centre itself, and is, even when the break-shock is stronger, still chiefly due to the centre. That is to say, even when initiated by so brief a stimulus as a single induction shock, the reflex action seems to involve some central process whose result is repetitive discharge of impulses. The repetitive discharge of motor impulses is obviously not to be thought of as more than the final outcome of the reaction in the "centre." The relatively prolonged duration of that outcome and the long central latency preliminary to it, together with other more general considerations, suggest that underlying the discharge there is some central process of other kind; this underlying process need not, from the repetitive nature of the discharge, be inferred to be itself repetitive, or if under some circumstances rhythmically maintained, to be itself essentially rhythmic. It finds expression through a mechanism (nerve-fibre) whose only mode of response

to excitation of more than very brief duration is rhythmic (tetanic). If, for the convenience of avoiding periphrasis in referring to it, we speak of the central process underlying and at back of the repetitive centrifugal discharge as the "charge" in contradistinction to the "discharge" it evokes, one feature that we may infer about the "charge" is its relatively long duration, *i.e.*, relatively to the whole cycle of a nervous impulse, and another is that, in response to

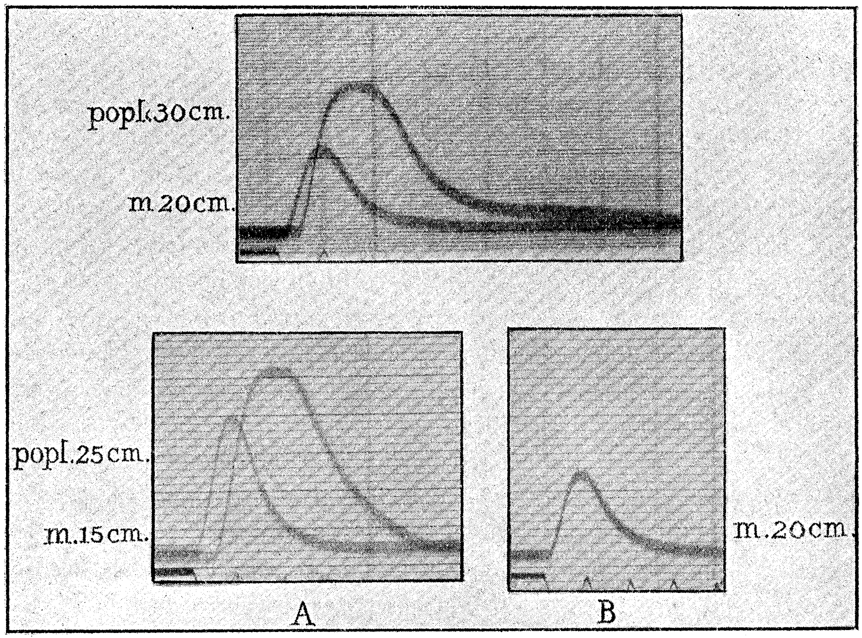


FIG. 8.—Upper record: reflex contraction of tibialis anticus (spinal cat) given by single break-shock at 30 cm. coil distance to central stump of popliteal nerve, followed on the same plate by record of maximal twitch given by single break-shock at 20 cm. coil distance, cut motor nerve; time ordinates at $\frac{1}{25}$ sec. intervals; tension abscissæ 31 grm. per millimetre. Lower record, A, similar to above from another experiment: the reflex by break-shock at 35 cm. coil distance, and the motor response distinctly "supramaximal" by break-shock at 15 cm.; the true maximal twitch, as determined by subsequent trial, is given at B, the instance shown being with break-shock at 20 cm. coil distance. Stimulus-signal below.

stronger break-shock stimuli of the afferent nerve, other conditions remaining the same, it attains a given degree of intensity, or amounts to a given quantity, more rapidly and dies out less soon than when such stimuli are weaker. In searching for a refractory phase for it in the flexion-reflex, Miss Sowton and myself (7) could find no positive evidence of such; that is to say, the period of refractoriness that was indicated for the reflex in our experiments was so brief that it could be accounted for apart from the central

process by the refractory period of the afferent or efferent fibres themselves. In several respects it seems to me that the central "charge" process suggests comparison with the "local excitatory process" of Adrian and Keith Lucas, referred to above. In using for it the term central "charge" there is, of course, no intention of implying to it the electrical attributions of that term.

*Summary.*

The maximal twitch-contraction of tibialis anticus muscle (cat) evoked by a single break-shock applied to the cut motor nerve is compared with the same muscle's contraction as evoked reflexly (spinal preparation) by a single break-shock applied to an afferent nerve. The reflex contraction is found to exceed the former when the break-shock for the former is even considerably weaker than that employed for the latter. Evidence is given that this is due to the reflex response being tetanic in nature. If the break-shock is, however, quite strong (*i.e.*, above the limiting maximal value of Forbes and Gregg) there is evidence that it excites even when applied to the motor nerve a response of tetanic quality. The so-called "over-maximal twitch" is in reality a response of this kind. Such responses are in this paper termed "supra-maximal responses."

Probability is shown that a reaction of like kind obtains in the afferent nerve when the single-shock applied to it is of comparably high value. In this latter case there is added to the tetanic reaction of the spinal centre a tetanic reaction from afferent nerve fibres themselves. But with weak and moderate break-shock stimuli the seat of origination of the tetanic character of the reflex discharge appears to lie mainly, if not wholly, in the centre itself. It is inferred that it arises there from a process, a "charge" process, which is relatively long-lasting in comparison with the cycle of a nerve-impulse, a process which is more intense and of longer duration when the afferent fibres excited are many than when they are fewer.

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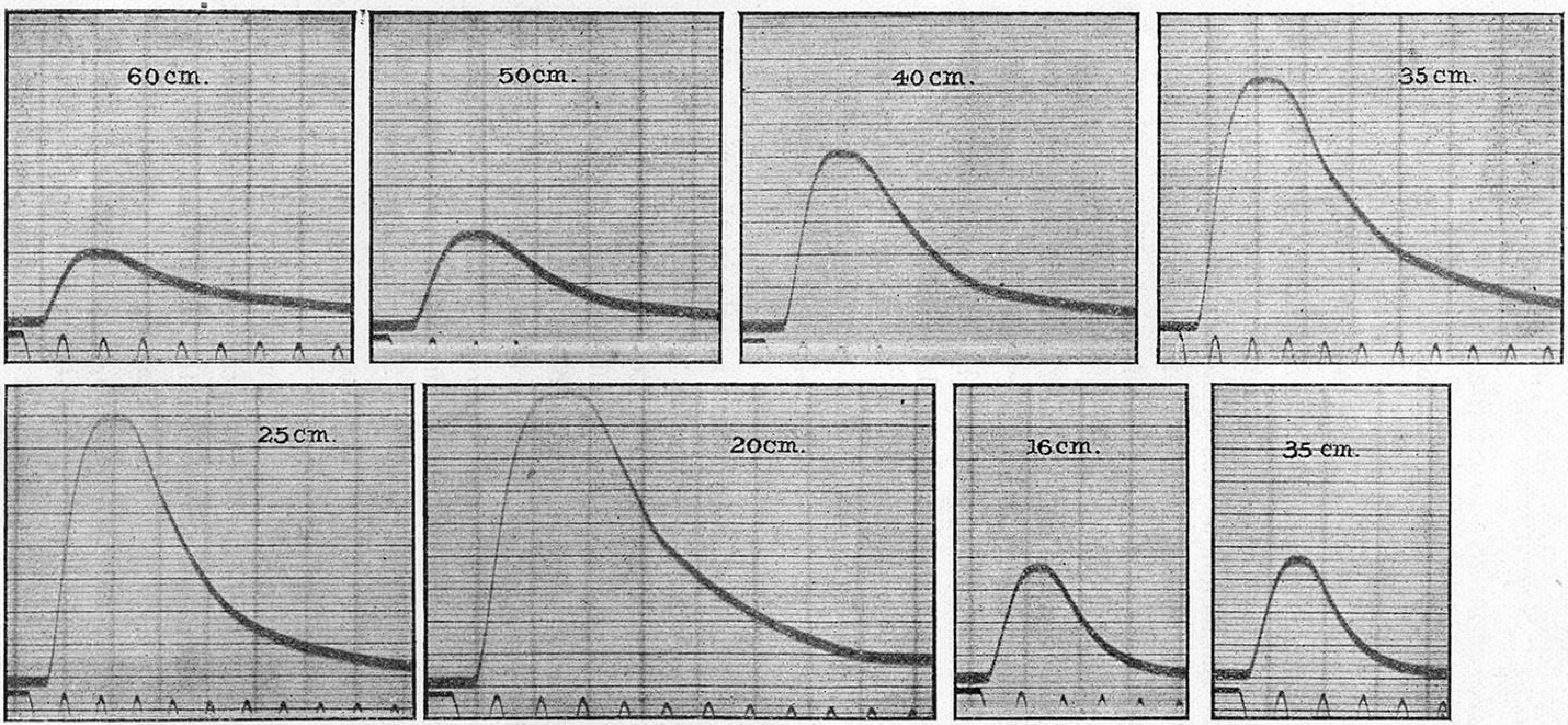


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* Throughout the figures, except fig. 3, the "shadow myograph" was arranged to give a record 50 mm. in height for a tension of 1500 grm. The tendency of the torsional excursions to become somewhat less relatively with successive equal increments of torsional pull was counteracted by setting the rectilinear shadow's fall upon the camera slit in such a way as to slightly increase the optical magnifications with progressive deviations of the shadow from its zero position. The calibration of the records after this had been done gave the following results: 5 mm. vertical height = 150 grm. tension; 10 mm. v.h. = 300 grm. t.; 15 mm. v.h. = 450 grm. t.; 20 mm. v.h. = 610 grm. t.; 25 mm. v.h. = 765 grm. t.; 30 = 915; 40 = 1210; 50 = 1500.

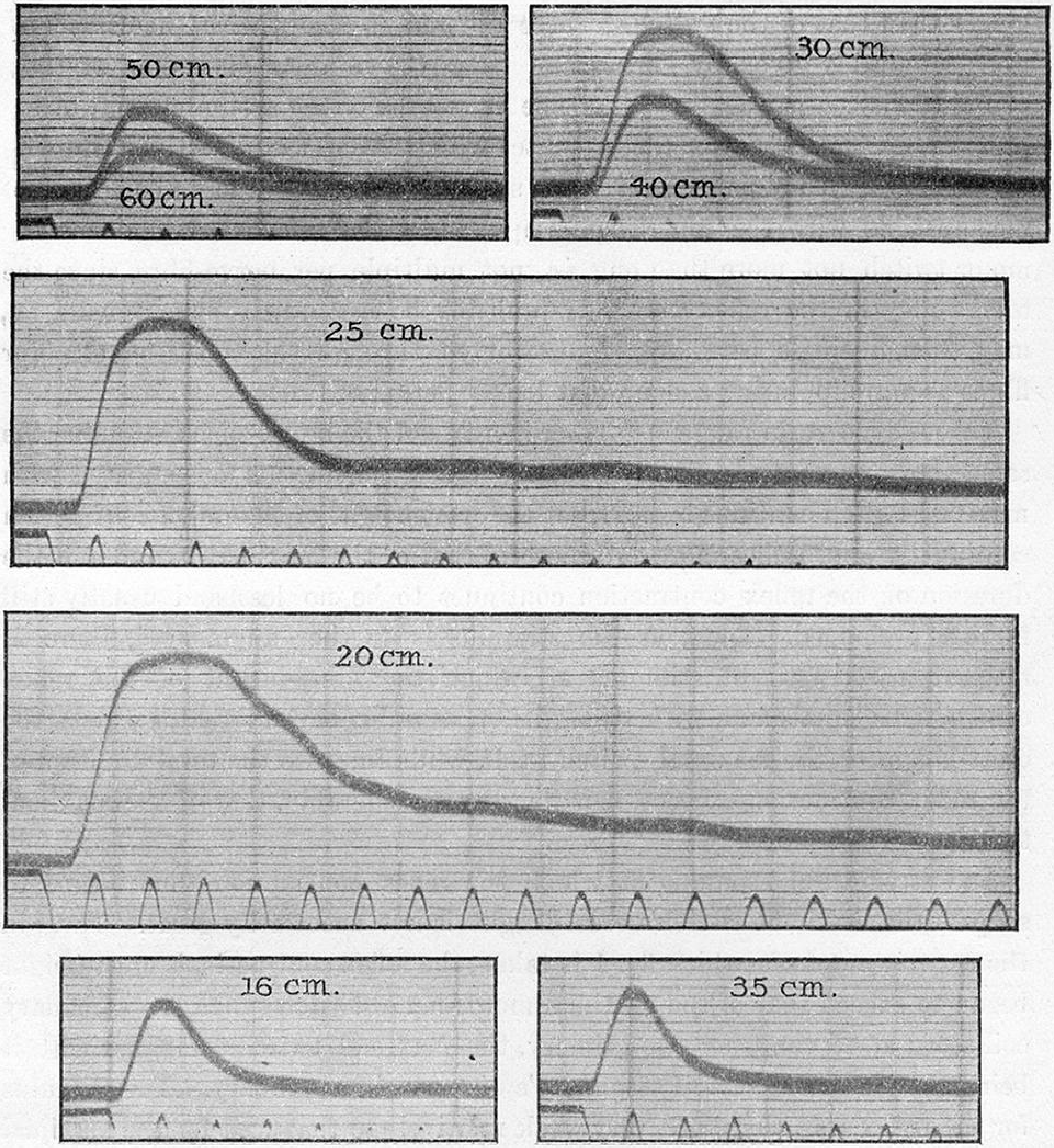
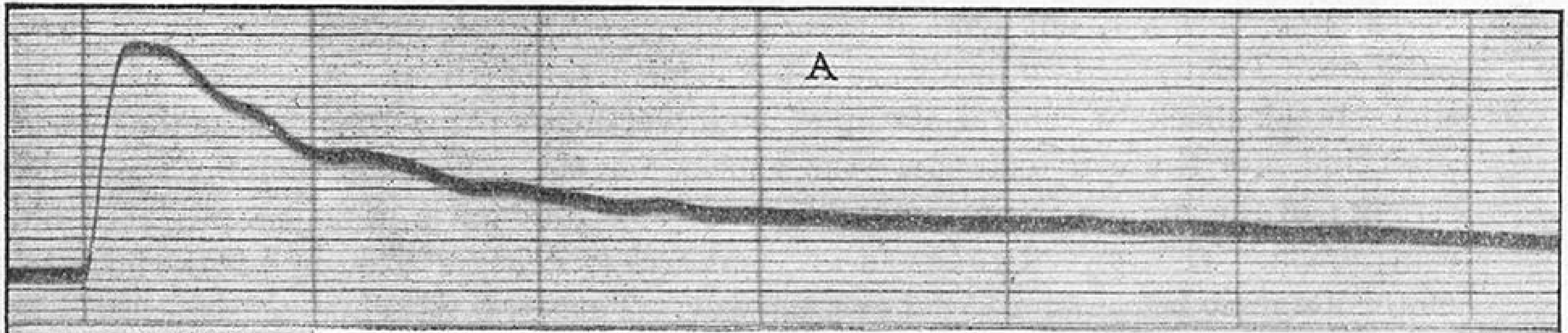
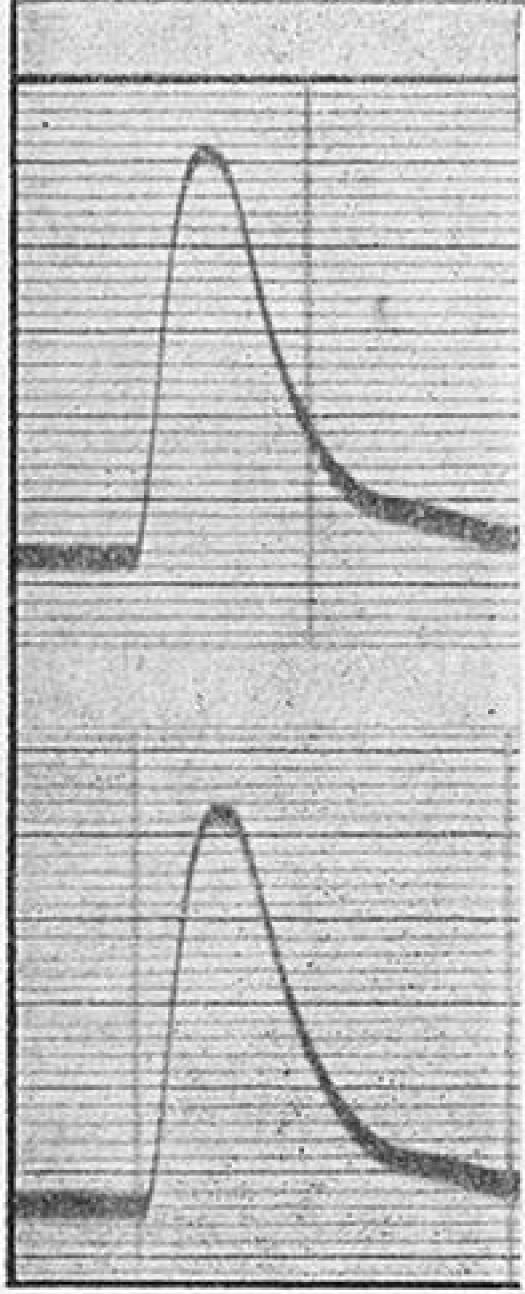



Fig. 2.—Similar to fig. 1, but the break-shock reflexes evoked from internal saphenous nerve instead of popliteal. The numerals at each inset give the coil distances for the break-shock. The two lowest insets show the maximal twitch elicited *viâ* motor nerve direct with the coil distances for the break-shock employed. Time ordinates and tension abscissæ as in fig. 1. Stimulus-signal below.



B

16 cm.

C

15 cm.

Fig. 4.—Similar to fig. 2, but with slower travel of the photographic plate: time ordinates mark $\frac{1}{5}$ sec. The break-shock reflex contraction, A, evoked from internal saphenous nerve, though of less crest-height than the supramaximal responses, B, C, is of much longer duration. For A, break-shock at 22 cm. coil distances; for B and C, break-shock at 15 cm. and 16 cm. respectively.

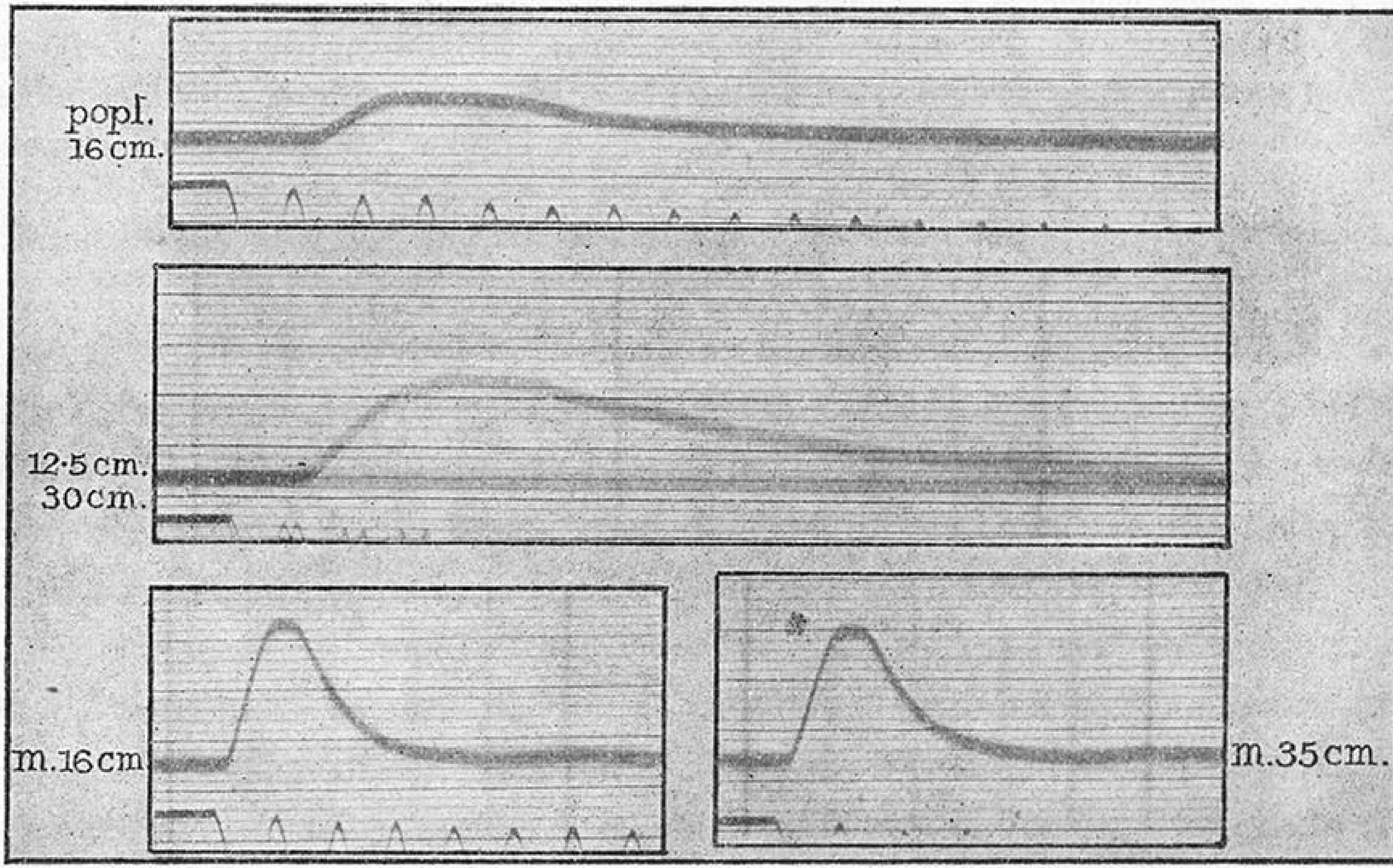



FIG. 5.—Similar to fig. 1, but from a decerebrate preparation instead of a spinal preparation. The upper two insets are reflex contractions (tibialis anticus) evoked by single break-shock to central stump of popliteal nerve; the numerals against each inset indicate the coil distances—the shocks for the reflex contractions are very strong; in the middle inset the break-shock at coil distance of 30 cm. produced no contraction. The lower two insets are maximal twitches evoked by break-shock to motor nerve at 16 cm. and 35 cm. respectively. Time ordinates and tension abscissæ as in fig. 1. Stimulus-signal below.

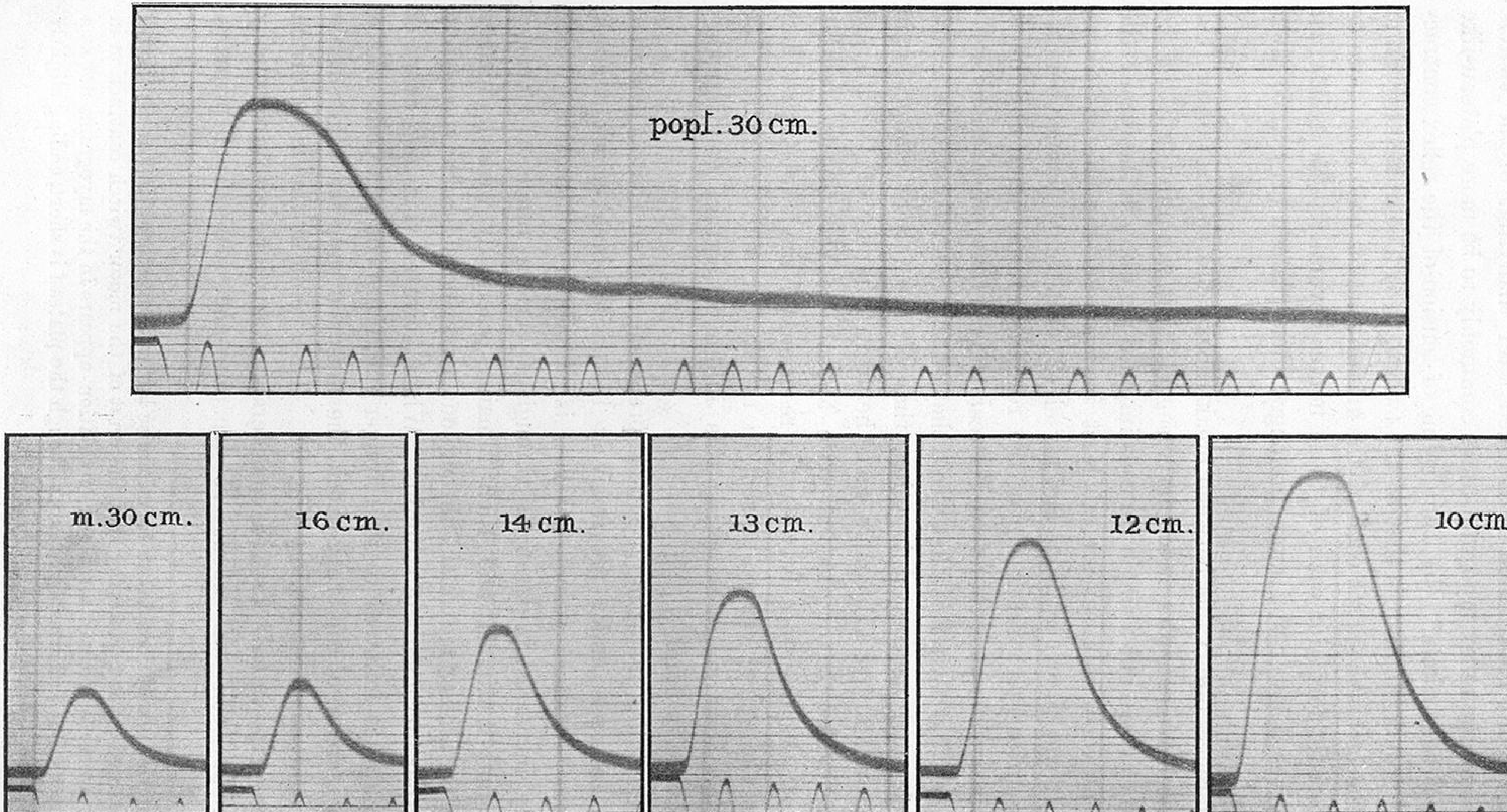



Fig. 6.—Lower row are maximal twitches and supramaximal contraction responses, evoked by single break-shock applied direct to cut motor nerve, for comparison with reflex contraction (upper inset) to single break-shock applied to central stump of popliteal nerve. Numerals against each inset give the coil distances for the break-shocks. The photographic plate was, as shown by the ordinates, travelling rather more quickly for the reflex record than for the other records, the speed for all these latter was the same. Tension abscissæ as usual. Stimulus-signal below.

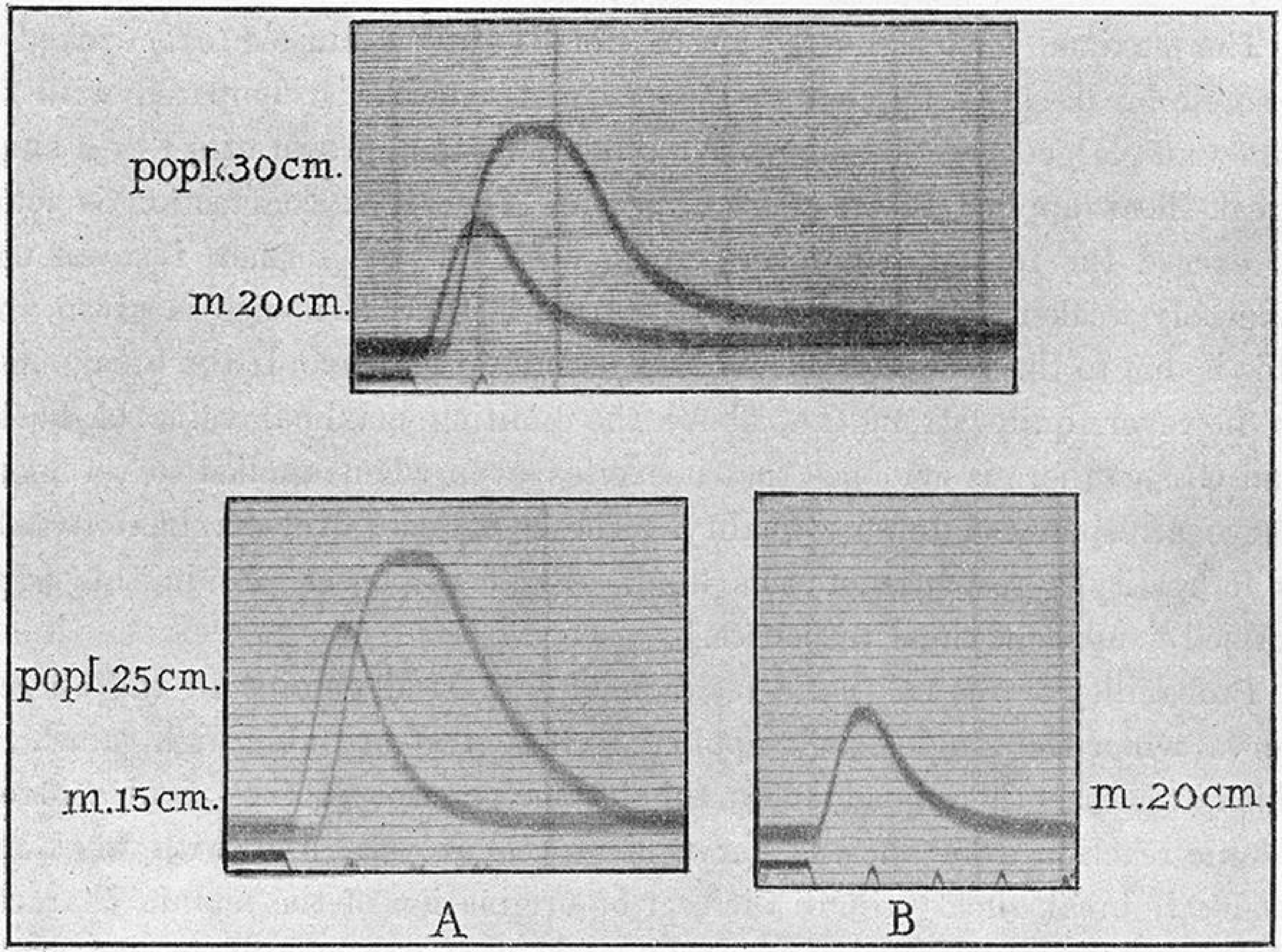



FIG. 8.—Upper record: reflex contraction of tibialis anticus (spinal cat) given by single break-shock at 30 cm. coil distance to central stump of popliteal nerve, followed on the same plate by record of maximal twitch given by single break-shock at 20 cm. coil distance, cut motor nerve; time ordinates at $\frac{1}{25}$ sec. intervals; tension abscissæ 31 grm. per millimetre. Lower record, A, similar to above from another experiment: the reflex by break-shock at 35 cm. coil distance, and the motor response distinctly "supramaximal" by break-shock at 15 cm.; the true maximal twitch, as determined by subsequent trial, is given at B, the instance shown being with break-shock at 20 cm. coil distance. Stimulus-signal below.