

Durations of Isometric Twitch and After-action of Tetanus. 431

FIG. 3, D.—“Abnormal” twitch of normal muscle after prolonged rest; same preparation as in fig. 2 at 17.0° ; string 40 mm. per amp. Initial tension 40 gms., tension developed 140 (cf. fig. 1, B).

FIG. 5.—Twitch followed by a short tetanus in which the twitch has been placed immediately beneath the corresponding part of the curve of relaxation of tetanic response to show the close coincidence of the two curves. $T = 15^{\circ}$.

REFERENCES.

- (1) Sherrington, C. S. ‘Roy. Soc. Proc.,’ vol. 92, B, pp. 245–258 (1921).
- (2) Liddell, E. G. T., and C. S. Sherrington. *Ibid.*, vol. 95, B, pp. 299–339 (1923).
- (3) Lucas, K. ‘Jour. Physiol.,’ vol. 30, pp. 443–448 (1904).
- (4) Hartree, W., and A. V. Hill. *Ibid.*, vol. 55, pp. 389–411 (1921).
- (5) Forbes, A., L. H. Ray and A. McH. Hopkins. ‘Amer. Jour. Physiol.,’ vol. 65, pp. 300–311 (1923).
- (6) Gasser, H. S., and A. V. Hill. ‘Roy. Soc. Proc.,’ vol. 96, B, pp. 398–437 (1924).

*The Relation between the Durations of the Isometric Twitch
and of the After-action of Tetanus.*

By JOHN FARQUHAR FULTON, B.A., Christopher Welch Scholar, Laboratory
of Physiology, Oxford.

(Communicated by Sir Charles Sherrington, P.R.S.—Received November 13,
1924.)

[PLATES 32–36.]

CONTENTS.

I. Introduction	431
II. Duration of the Mechanical Responses.....	432
1. Twitch and after-action	433
2. Fatigue and the “angle”	434
III. Relaxation and Viscosity.....	436
1. The rate of fall in relaxation.....	437
2. Relaxation and fatigue.....	438
IV. The Relation between Twitch and Tetanus.....	439
V. Summary.....	441
VI. References	442

I. INTRODUCTION.

In skeletal muscle with its circulation intact (1) increase within physiological limits of the initial passive tension of the muscle not only (*a*) increases

the active tension developed by the muscle in tetanic contraction, but (b) also increases the duration of the tetanic plateau after cessation of the exciting stimuli. For convenience, this after-continuance of the tension was termed the "after-action." As Gad and Heymans (2, see their fig. 17A) many years ago suggested—not knowing of the increased duration of the twitch with increasing tension—that the duration of a single response was nearly the same as that of the after-action, the question of the relation between these two phases of muscular activity at once presents itself.

As the method of recording previously employed (1) was not of sufficient delicacy to admit of accurate comparison between these relatively brief intervals, the more precise optical device recently described (3) has been utilised for the present investigation. Since the electrical responses have been in all cases recorded simultaneously with the mechanical, the duration of the twitch has been taken as the interval between the beginning of the electrical change and the "angle" at the end of the twitch plateau (see IV)—two points which can be measured significantly to 0.001 sec. In the previous communication referred to above (1), the after-action was measured from the cessation of the stimuli to half-relaxation. Much more accurate than this, however, for the first point is the beginning of the last electrical change of the tetanus; and since, as will be shown presently, there is at the end of the tetanic response of a fresh preparation an "angle" (fig. 1, Plate 32) comparable to that of the twitch, *the interval between these two points—the beginning of the last electrical response and the plateau "angle"*—has been termed the after-action. The intact gastrocnemius muscles of decerebrate frogs (*R. temporaria*, freshly caught) prepared in the usual way (3, 4) were used throughout. Special precautions were taken to ensure normal circulation in the recording muscle and adequate respiration of the preparation.

II. DURATION OF THE MECHANICAL RESPONSES.

In order to make the records of the twitch and tetanus strictly comparable, it was arranged that the twitch should be recorded on the same photographic plate as the tetanus, preceding the latter by a brief interval varying with the speed of the plate. To examine the effect of initial tension upon the twitch and after-action, successive records were taken from a freshly made preparation at intervals of from four to five minutes. The tension was increased in small increments for each successive response, but to ensure complete recovery between them (as passive tension interferes with the circulation)

Durations of Isometric Twitch and After-action of Tetanus. 433

the tension was removed from the muscle immediately the response had ceased. At the end of the experiment, as a control, a record was taken of a response at a small initial tension corresponding with the first one of the experiment.

1. *Twitch and after-action.*

The general result of such an experiment (of which 15 have been performed successfully) is that the duration of the twitch measured to its "angle" is (at all initial tensions) invariably somewhat greater than the duration of the corresponding after-action of a tetanus, *provided the tetanus be less than 0.2 to 0.3 sec. (i.e., 10 to 15 stimuli at 50 per second)* in duration. Thus, in fig. 1, A, Plate 32, showing a record taken on a relatively "fast" plate (30 cm. per second), the duration of the twitch is 65σ , while the duration of the after-action of the tetanus—in this case composed of seven responses at 50 per second—is 50σ . It is noteworthy that the end of this tetanus is characterised by a particularly sharp terminal angle. Fig. 1, B, shows the next response of the same preparation at slightly higher initial tension, in which the tetanus was composed of 13 responses. The duration of the twitch is 66σ , and the after-action 60σ . In this response, though the tension developed is greater, the subsidence angle is less sharp. On increasing the duration of the tetanus slightly more (0.4 sec.) the duration of the after-action becomes equal, or very nearly so, to the duration of the twitch (see Table I). This fact is useful, since it renders more simple the examination of the relative effect of tension upon the duration of twitch and after-action.

A duration of tetanus was chosen which at relatively small initial tensions was characterised by an after-action of the same duration as that of the twitch. Successive records were then taken at increasing initial tensions. Such experiments have shown that so long as the muscle remains fresh and relatively unfatigued, the duration of the twitch remains equal to that of the after-action at all initial tensions. Thus, in the experiment summarised in Table I.* at 34 gms. initial stretch (23.5°), the duration of twitch and after-action were each 40σ , while at 218 gms. stretch their durations were 48σ . Perhaps the most striking feature of the experiment is the control observation in which returning to 25 gms. stretch after subjecting the muscle to relatively severe tensions the duration of the twitch is again 40σ and of the corresponding after-

* To make the analysis of the electrical responses given in Tables I of the two preceding papers strictly comparable with the results herein tabulated, the measurements have all been taken from the same experiment. The twitches reproduced in fig. 2 of the second paper (Plate 30) are also from this experiment.

action, 41 to 42 σ . With a somewhat more prolonged tetanus (0.5 to 0.6 sec.) even in a fresh preparation, the after-action becomes invariably longer than the twitch, as is shown in the two responses at the bottom of Table I.

Table I.—Showing the relation of the twitch to the tetanus (intact gastrocnemius of 30 gm. decerebrate frog); duration of tetanus, 0.38 sec. in first preparation, and 0.54 sec. in the last).

Preparation at 23.5°.							
Initial tension (gms.).	Twitch.			Tetanus.			Ratio of twitch/tetanus tensions.
	Tension developed above initial.	Duration to "angle" (0.001 sec.).	Rate of proportional fall (to half-relax.).	Tension developed above initial.	Duration of after-action (0.001 sec.).	Rate of proportional fall (to half-relax.).	
5?	113?*	39	11.3 (10)	680	37	34.0 (20)	0.166?
34	150	40	11.5 (13)	1023	40	33.0 (31)	0.147
57	187	42	11.7 (16)	1084	43	32.9 (33)	0.173
110	198	44	11.6 (17)	1094	45	32.0 (33)	0.185
172	186	46	11.7 (16)	983	47	31.0 (32)	0.190
218	178	48	11.1 (16)	872	48	29.1 (30)	0.204
25	165	40	11.7 (14)	1025	41	33.0 (31)	0.161
Same Preparation at 19°.							
5-10	113	49	9.4 (12)	972	50	27.7 (35)	0.116
45	173	57	9.1 (19)	1125	58	27.3 (41)	0.154
110	181	63	8.6 (21)	1067	74	26.6 (40)	0.166
175	170	63	8.5 (20)	953	79	21.2 (45)	0.176
Another Preparation at 25° (Frog same weight).†							
38	162	36	13.4 (12)	1069	38	31.4 (34)	0.151
73	191	40	12.8 (15)	1132	42	31.4 (36)	0.169

* Twitch "abnormal," as described in 4, p. 427; fig. 3 D, Plate 31.

† These two responses are shown in fig. 2, Plate 33, of this paper.

2. Fatigue and the "Angle."

The increase in the duration of the after-action above that of the twitch may be taken as the first sign of fatigue, for it is accompanied by an "angle" at the end of the plateau, which is slightly less precise than those of the preceding responses. With a little experience in analysing such curves, one soon

Durations of Isometric Twitch and After-action of Tetanus. 435

becomes able to tell at a glance the "condition" of the preparation from the configuration of the end of the plateau. The sharp and precise angle characteristic of the first four or five responses of a fresh normal muscle with good circulation may become after excessive stimulation less clear and may even disappear altogether, giving way to a smoothly rounded curve. Under these circumstances the after-action becomes greatly lengthened (see the last two responses at 19°—Table I.), and in severe fatigue cannot be measured at all owing to the complete disappearance of the "angle."

The "angle" of the tetanus plateau, therefore, provides an index of the condition of the preparation even more delicate than the "angle" of the twitch. The factors concerned in the production of a sharp angle at the end of a tetanus are, of course, the same as in the twitch (4, p. 426). For satisfactory observation of the "angle" an accurate myograph and perfect fixation of the preparation are necessary. With these precautions, raising the temperature is found to sharpen the angle and any factor tending to induce fatigue, such as interfering with the circulation or stimulating too long, eventually causes its complete obliteration. To produce slight symptoms of fatigue for purposes of study one has only to vary the length of the tetanus plateau. With but six or seven stimuli composing the tetanus as in fig. 1, A, Plate 32, the "angle" is as precise as in a twitch. With a tetanus of 0.38 sec. (at 50 per sec.) as in fig. 3, A, Plate 34, the "angle" is clear, but less precise; while with a tetanus of 0.58 sec. (fig. 3, B), the "angle," though still recognisable, is much less clear, and the after-action in this case is 6σ longer than the duration of the twitch. In fig. 2A, Plate 33, in which a tetanus of 0.54 sec. is shown in a fresh preparation, the after-action is 2σ longer than the twitch (see Table I.). In general, one may say, therefore, that the shorter the tetanus, the more precise is the angle and the more closely does it resemble the "angle" by the twitch.

Very slight degrees of fatigue may also be observed in successive short tetanic responses with increasing degrees of initial stretch. If for the first response the tension is so slight that 1–2 mm. of shortening of the tendon occurs before appreciable tension is developed (fig. 4, Plate 35), the tension developed is relatively small (as are also the electrical responses) and the terminal angle may be almost as clear-cut as in the twitch (see fig. 7, B, C, and D of previous paper, 3). On increasing the initial tension, the plateau tension becomes greater, and the "angle" though still clearly present as in fig. 2, A and B, Plate 33, is less clear-cut. Also the successive responses become more perfectly fused at high tensions than at low (fig. 7, of 3), and in any given

tetanus, as is well known, they are more perfectly fused toward the end of the plateau than at the beginning. Progressive fusion of the individual mechanical responses, with its associated modifications of the terminal "angle," may accordingly be taken as indicating the progressive development of slight fatigue.

Another most effectual way of inducing fatigue in even the freshest preparation is to stimulate for a brief interval (0.3 to 0.6 sec.) with stimuli too rapid for the muscle to follow mechanically. Thus, 50-60 stimuli per second delivered to a frog's gastrocnemius at 20° is followed by normal relaxation, but on raising the rate to 100 per second (fig. 5, Plate 36), and stimulating for the same period, the relaxation exhibits symptoms of the most severe fatigue, from which 30 to 40 mins. may be required for recovery. One feels that this observation may have an important bearing upon the optimal rhythm of stimulation from the cord, for it seems unlikely that stimuli should arrive from the central nervous system at such a rate as to produce severe fatigue, especially as a rate of 100 per second produces very little more tension than stimuli at 50 per second. Yet the higher rhythm would be necessary if it were to be inhibited by Wedensky interference.

Arresting the circulation gives rise quickly to fatigue. In fig. 5, Plate 36, the response of the gastrocnemius of a 25-gm. frog is shown 25 minutes after excising the heart. Similar results may be obtained by tying the femoral artery. Though there is some recovery on release after ligation for a period of over 20 minutes, the "angle" of the twitch and tetanus has not, in my experience, regained its previous precision. Six to ten hours after the cutting of the nerve (at 20°), even though the circulation remains active, the "angles" also disappear permanently, owing, presumably, to progressive nutritive changes of the muscle substance (and the alterations in the excitability of the nerve?). It would seem, therefore, that these changes are accelerated by stopping the circulation. Such observations warn against the unrestricted acceptance of inferences as to the normal activity of muscle drawn from experiments performed upon excised tissue.

III. RELAXATION AND VISCOSITY.

It has been suggested elsewhere (4) that, in view of the sharpness of the "angle" of the twitch, the curve of relaxation in a normal muscle represents the "viscous return of the muscle." In other words, at the "angle" contractile activity (the flow of H-ions?) ceases completely and abruptly, and the shape of the resulting fall to the base-line is governed by the internal viscosity

Durations of Isometric Twitch and After-action of Tetanus. 437

of the muscle substance. To uphold this inference there is required evidence (1) that the *rate of fall* is the same from every plateau tension either of the twitch or of the tetanus, and (2) that "neutralisation" of the activating ions as they reach the contractile elements is almost instantaneous.

1. *The Rate of Fall in Relaxation.*

To determine the *rate of fall* accurately in the twitch is a matter of some difficulty, as the error in measuring the absolute time of fall may be as great as 10 per cent. However this may be, values of satisfying regularity are obtained by measuring the duration from the "angle" to half-relaxation and the results obtained by independent observers compared. The values thus obtained were now divided into the corresponding plateau tensions (above the initial). The resulting figure may be taken as the "*rate of proportional fall*."* Since the rate of fall is not a linear function of the height of the plateau, the values obtained in this way are not strictly comparable, but they appear to be as nearly comparable as any index which one can obtain.

In column 4, of Table I, the values of the rate of proportional fall are given for the twitch at different initial tensions, and beside them are placed in parenthesis the absolute time intervals from which the proportions were obtained. It will be seen that the values at $23\cdot5^{\circ}$ are almost constant, varying from 11.1 to 11.7. As the tensions may be determined accurately to 2 gm., the chief source of error is in the determination of the absolute time interval. The greatest variation from determinations by other observers is 10.5 to 12.2, which is probably considerably greater than actually exists. The values finally settled upon were obtained three times at different times of the day by the same observer (J. F. F.). From these determinations the conclusion seems warranted that *the rate of fall of the twitch to half-relaxation approaches a constant value for all initial tensions, the temperature remaining constant.*

Turning to the tetanus, it is obvious that here, since the tensions developed are very much greater than in the twitch, one would anticipate the rate of the first half of the fall to be very much more rapid, and one finds this to be true experimentally. Employing the same method of analysis as in the twitch the rate of proportional fall is found to vary at $23\cdot5^{\circ}$ between 34 and 29.1, but as the value decreases regularly with increasing initial passive tensions, and as the modifications of the terminal "angle" explained above, show increasing

* Though similar in principle this figure is determined in a different way from the corresponding figure for the "*maximum rate of proportional fall*" determined by A. V. Hill and Hartree (7, p. 393). They took the angle of most rapid fall and divided that by the tension.

evidence of slight fatigue, one may attribute the falling *rate* in part at least to fatigue, especially as the control observation at the end returns to a value of 33. At 19°, where fatigue is much more obvious, the value falls even more (from 27·7 to 21·2). In the responses shown in fig. 2, Plate 34 (at 25°), an interval of 10 minutes was permitted to elapse between the two responses, with the result that the rate of fall is identical in the two instances (Table I), but as the duration of the tetanus in these two responses (0·54 sec.) is considerably longer than the duration in the experiment tabulated in the first part of Table I (0·38 sec.), the commencement of the fall, being more influenced by fatigue, is less rapid. These observations make it seem quite clear that in the complete absence of fatigue the rate of the first half of the fall of the response at the end of tetanus approaches a constant value—as in the case of the relaxation of the twitch. It would follow from this that the *rate of relaxation from a twitch or from a tetanus in an unfatigued muscle is largely if not entirely independent of the tension developed.*

2. Relaxation and Fatigue.

We are now in a position to consider more in detail the possible nature of fatigue. It has been shown elsewhere (3) that extremely small alterations in the initial tension (0 to 2 gm.)—too minute to be measured with the isometric recording device used—produce large alterations in the contractile energy liberated (as measured by the size of the electrical response), as well as the total tension (3, fig. 7, Table III) developed during the response. The modern theories of muscular contraction introduced largely by the work of Hill and Meyerhof have taught us to think of energy liberated in a contracting muscle in terms of lactic acid production. For convenience let us use as an arbitrary measure of the amount of acid liberated in a given response the size of the galvanometer deflections during the response. As it has been shown that the tension developed is closely parallel to the size of the action current, this is probably as accurate an index as any that one can employ. In Table III of the first paper above (p. 415), it was shown that the tetanus plateau responses at initial tensions varying from 0 to 45 gm. varied progressively from 12 to 15·5 mm., and the first responses of the tetanus varied in size from 7 to 30·5 mm. It follows that in the responses in which the least lactic acid is produced the smallest amount of tension is developed, and it is clearly significant that in these small responses the “angle” of the tetanus approaches the sharpness of the “angle” in the twitch. It would seem, therefore, a justifiable conclusion that in short tetani at small initial tensions the acid ions are disposed of

Durations of Isometric Twitch and After-action of Tetanus. 439

("neutralised") immediately they have acted upon the interface, and that when the H-ions produced by the last stimulus have ceased to flow on to the contractile interface (*i.e.*, when their concentration has fallen below the threshold value) at that instant one observes the "angle" in the mechanical response. When, however, a somewhat prolonged tetanus is given at a higher initial tension the rate of lactic acid production is greater, and under these apparently "unnatural" circumstances the neutralising apparatus in the muscle, being unable to cope with the heightened rate of lactic acid production, temporarily fails, neutralisation ceases to be instantaneous, and H-ions accumulate at the contractile membrane, "lingering" there for a time after their flow has ceased. Though this seems a likely picture of what actually occurs, it is at best but a device to assist the imagination, and whatever the true process is, the end result of an increased rate of lactic acid production is a dulling of the "angle"—and this has been referred to as fatigue.

As the experiments just described appear at present to throw little, if any, light upon the mechanism of neutralisation of the acid ions, one can only draw attention to the ingenious hypothesis recently put forward by Tiegs (6). It is based upon his observation that crawfish muscle (which, like other striated muscle, is believed to be composed of fibres built upon the skeletons of two double-helicoid membranes) is innervated by two types of nerve fibre, one going invariably to one helicoid membrane, the other to the other. The stimulation of one group of nerve fibres, as is well known, results in contraction of the muscle, stimulation of the other inhibits contraction. This has led Tiegs to believe that one membrane, when excited, causes the liberation of acid ions; the other, the liberation of an unknown base which serves to neutralise the acid. As the skeletal muscle of higher animals has two helicoid membranes and but one innervation, this author has concluded that both are stimulated simultaneously by the nerve impulse, but the H-ions, migrating more rapidly than the basic ions, produce their effect before being neutralised by the unknown base. Though attractive, it would be unprofitable to deal further with this interesting suggestion until Tiegs's morphological results have been corroborated.

IV. THE RELATION BETWEEN TWITCH AND TETANUS.

A point of interest bearing upon the problem of the genesis of tetanus is the fact disclosed in the last column of Table I, that the ratio of the twitch tension to the tension developed in the tetanus (above the initial in both cases) increases with the initial passive stretch. The twitch, in other words, becomes

relatively larger than the tetanus at high initial tensions, and the ratio between the two does not pass through a maximum as does the tension itself, but increases steadily, however great the initial stretch becomes. At very severe initial stretches—which probably do considerable damage to the fibres, since the tension is passive, not active—the ratio between the twitch and tetanus approaches unity. The tetanus plateau is, under these conditions, very little higher than the plateau of the twitch, and the ascent of the first response has become in large measure the ascent of the tetanus. But the “plateau” of a response at very severe initial tension tends always to ascend, and this is probably attributable to the greater capacity for shortening possessed by the contractile elements, which have thus been artificially lengthened, since it is not observed at more moderate initial stretches.

The gradually ascending “plateau” which is to be observed, on the other hand, at extremely small initial tensions (such as in fig. 4, Plate 35, in which 3 mm. shortening of the tendon occurred) is clearly to be put down to a different cause, for here shortening is at least 100 times greater than in a response in which the twitch-tetanus ratio approaches unity. It seems evident, therefore, that the ascending plateau under these circumstances is associated with the small degree of tension developed. This together with the observations on the twitch-tetanus ratio leads to the conclusion that the development of *tension per se*, not shortening, causes the formation of the flat plateau in the response of muscle to serial stimuli. The *mechanism* by which the development of tension brings about the formation of a flat plateau is quite another question, and considerable light appears to be thrown upon it by the behaviour of the electrical changes during the ascent (see fig. 3, Plate 34).

To account for the behaviour of the electrical changes during this period it has already been suggested (3, p. 410) that alterations in shape of the muscle associated with the development of tension (rather than with shortening) cause the duration of the successive waves of permeability passing along the polarised (helicoid?) membrane to become more brief, and that the energy liberated becomes, in consequence, much less in amount for each successive response, until a steady condition is achieved in which the energy liberation is only sufficient to maintain tension and not adequate to cause further alterations in shape. This is in agreement with Hartree and Hill's (7) observation that the tetanus is not the mere additive effect of single twitches, but that each successive response becomes more and more modified. In keeping with this also is the fact that, even within very small limits, the greater the altera-

Durations of Isometric Twitch and After-action of Tetanus. 441

tions in shape permitted at constant initial tension (see Table II, 3), the smaller is the tension of the plateau and the greater the diminution in size of the successive electrical responses during the ascent. The effect, therefore, would appear to be upon the initial processes in contraction—the properties of the polarised membrane—and not one upon the contractile elements themselves. The latter appear in almost every circumstance to be mere passive agents but little affected by the mechanical conditions of the muscle (but see 3, p. 413).

The diminution in size of the successive electrical responses during the mechanical ascent of a tetanus suggests an explanation of the twitch being of greater duration than the corresponding after-action of a short tetanus (fig. 1A, Plate 32). It was pointed out in the previous paper (p. 424) that the electrical responses of the twitch became larger as the duration of the twitch becomes greater (as when the initial passive tension is gradually increased), and since greater active tension is developed in these more prolonged twitches it was inferred that more contractile energy is liberated. The diminution in the successive electrical responses during the tetanus ascent would indicate, on the other hand, that the number of acid ions liberated by each stimulus becomes progressively less until the plateau is reached. The effective concentration (or the flow?) of the “contractile” ions would therefore continue for a shorter time after each plateau stimulus than after the twitch stimulus, provided there is no fatigue. In view of this it would seem suggestive that the ratio of the size of the galvanometric deflection in the twitch to that of the last plateau response in fig. 1A, Plate 32, is approximately 1.36, and the ratio of the corresponding durations of twitch and after-action $65\sigma/50\sigma$ is equal to 1.30. This rough degree of parallelism between these two ratios has been observed in all experiments with brief tetani, and is probably, therefore, significant.

V. SUMMARY.

Employing the optical device described above (p. 406), the following observations have been made upon the mechanical responses of twitch and tetanus of the intact gastrocnemius of decerebrate frogs.

1. A sharp “angle” exists at the termination of the tetanus plateau of unfatigued muscle which is comparable to the “angle” previously described for the twitch. The factors involved in the production of a sharp “angle” in a tetanus are the same as those involved in the twitch.

2. The duration of the twitch is always greater than the duration of the corresponding after-action of a brief tetanus. This is in keeping with the

observation that each of the successive electrical responses during the tetanus plateau is smaller than that of the twitch.

3. Any factors tending to produce fatigue cause the "angle" to become obscured, and the after-action to become lengthened.

4. The rate of relaxation is independent of the tension developed in the twitch or in the tetanus; this is in favour of the view that the shape of the curve of relaxation in unfatigued muscle is determined by the viscosity of the muscle substance. With even slight fatigue the shape of the curve of relaxation is greatly modified.

5. In normal muscle with active circulation the H-ions produced in short responses appear to the "neutralised" instantaneously as they reach the contractile surfaces. Fatigue, on this view, results when the neutralisation of the H-ions ceases to be instantaneous.

6. The ratio of the twitch-tetanus tensions approaches unity as the initial passive tension upon the muscle is increased.

7. The mechanism of the production of a flat plateau in the tetanus is discussed, and it is suggested that the changes produced in the polarised membrane by the development of tension (rather than by shortening) are responsible for the production of a plateau. The behaviour of the successive electrical responses during the mechanical ascent of a tetanus lends further evidence for this view.

VI. REFERENCES.

- (1) Fulton, J. F., 'Roy. Soc. Proc.', vol. 96, B, pp. 475-490 (1924).
- (2) Gad and Heymans, 'Arch. f. Anat. u. Physiol., Abt. Physiol.', suppl. 1890, pp. 59-115, Taf. 4-8 (1890).
- (3) Fulton, J. F., 'Roy. Soc. Proc.', this Number, pp. 405-423 (1925).
- (4) Fulton, J. F., 'Roy. Soc. Proc.', this Number, pp. 424-431 (1925).
- (5) Hill, A. V., and W. Hartree, 'Journ. Physiol.', vol. 54, pp. 84-128 (1921).
- (6) Tiegs, O. W., 'Austral. Journ. Exper. Biol. and Med. Sci.', vol. 1, pp. 11-29 (1924).
- (7) Hartree, W., and A. V. Hill, 'Journ. Physiol.', vol. 55, pp. 389-411.

DESCRIPTION OF PLATES.

PLATE 32.

FIG. 1.—Responses of intact gastrocnemius of 30 gm. frog at 15° to short tetani preceded by twitch. String tension 40 mm. per amp. Time above = 0.04 sec. Plate falling at 30 cm. per sec. For other conditions see fig. 2. A.—Initial tension 5-7 gms. Tetanus composed of 7 stimuli. Cessation of stimuli not signalled (done by hand by breaking primary circuit). Note sharp terminal "angle" of tetanus. B.—Initial tension 8-10 gms. Tetanus composed of 13 stimuli. Note modification of the "angle."

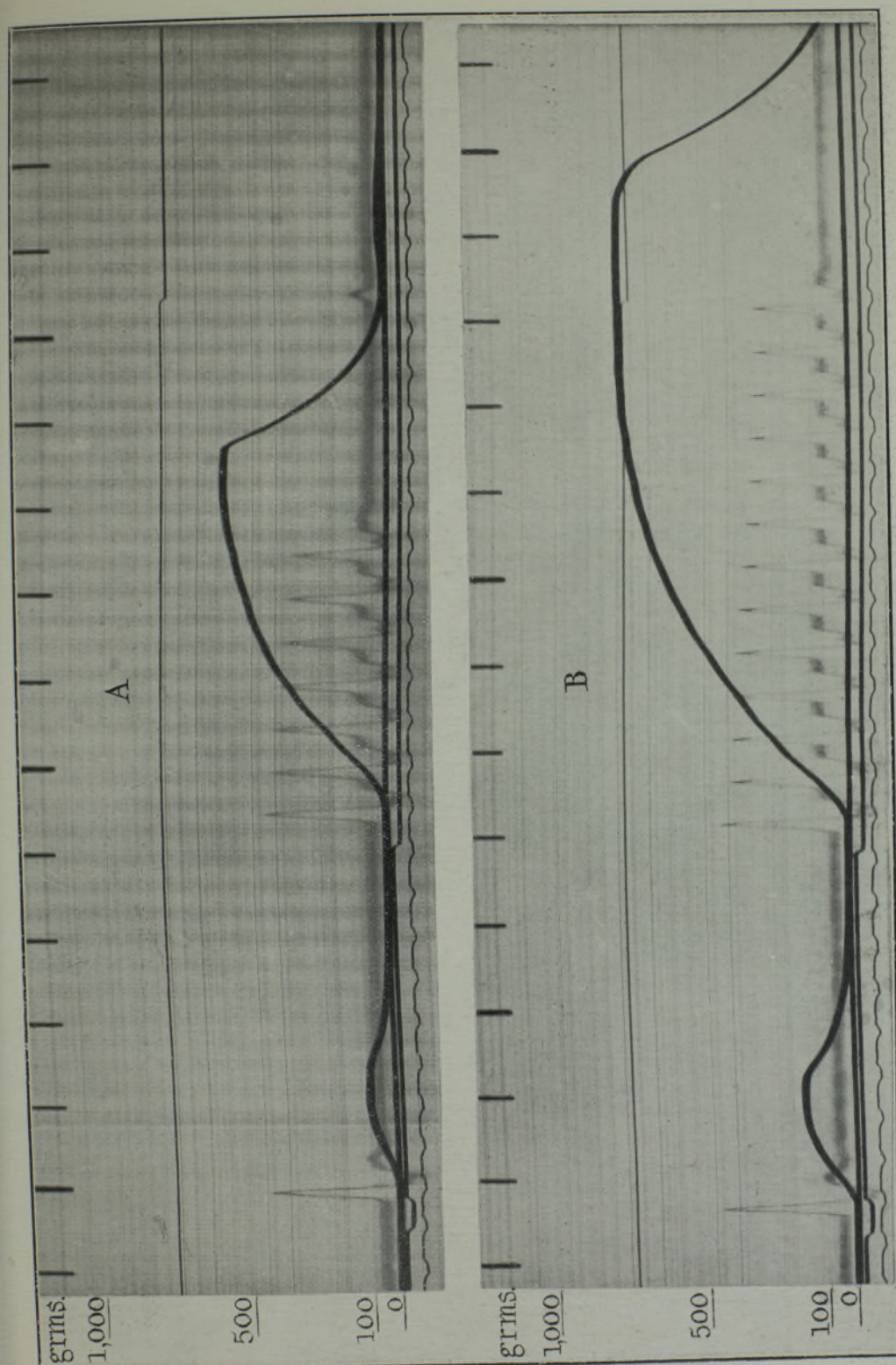


FIG. 1.

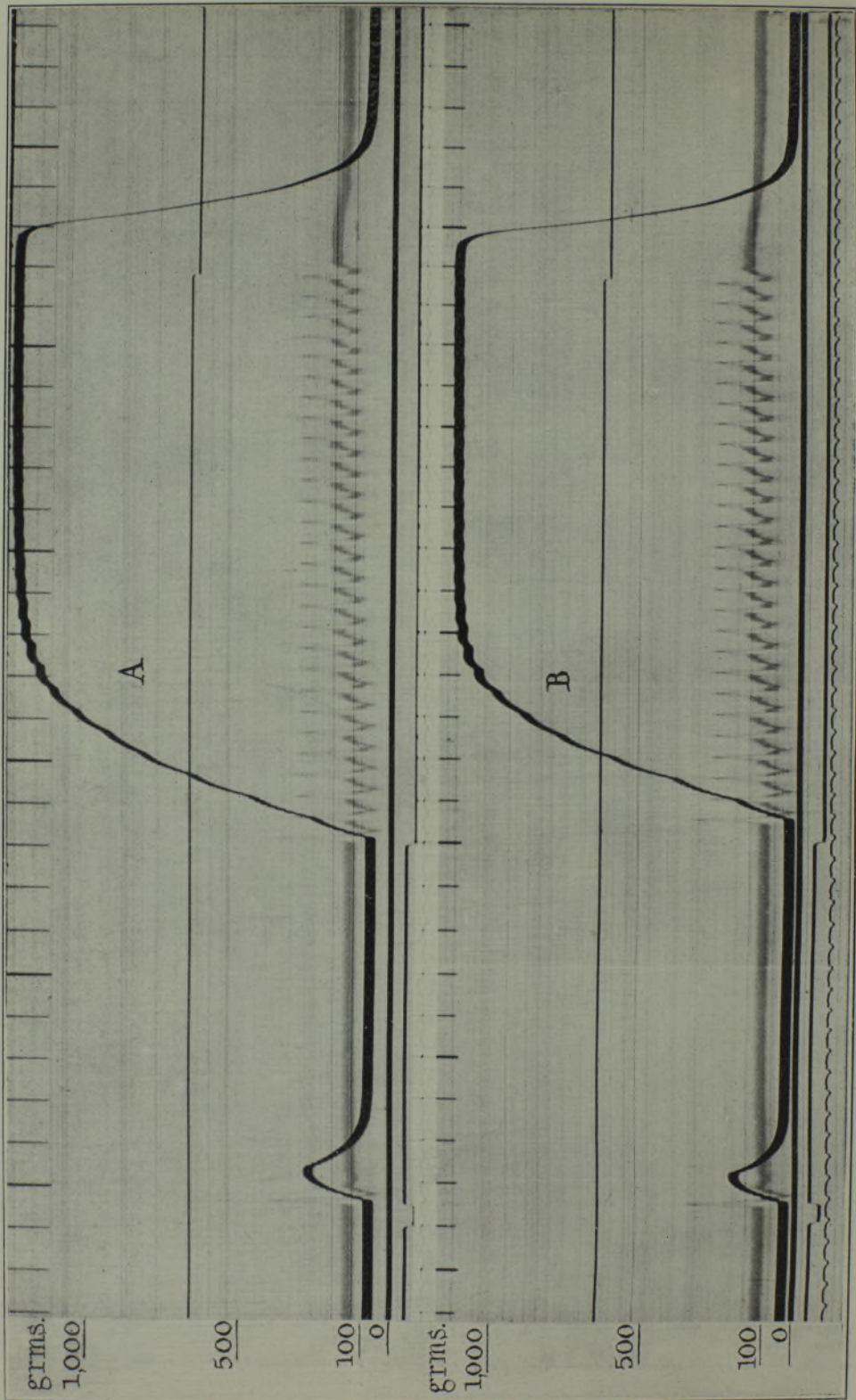


FIG. 2.

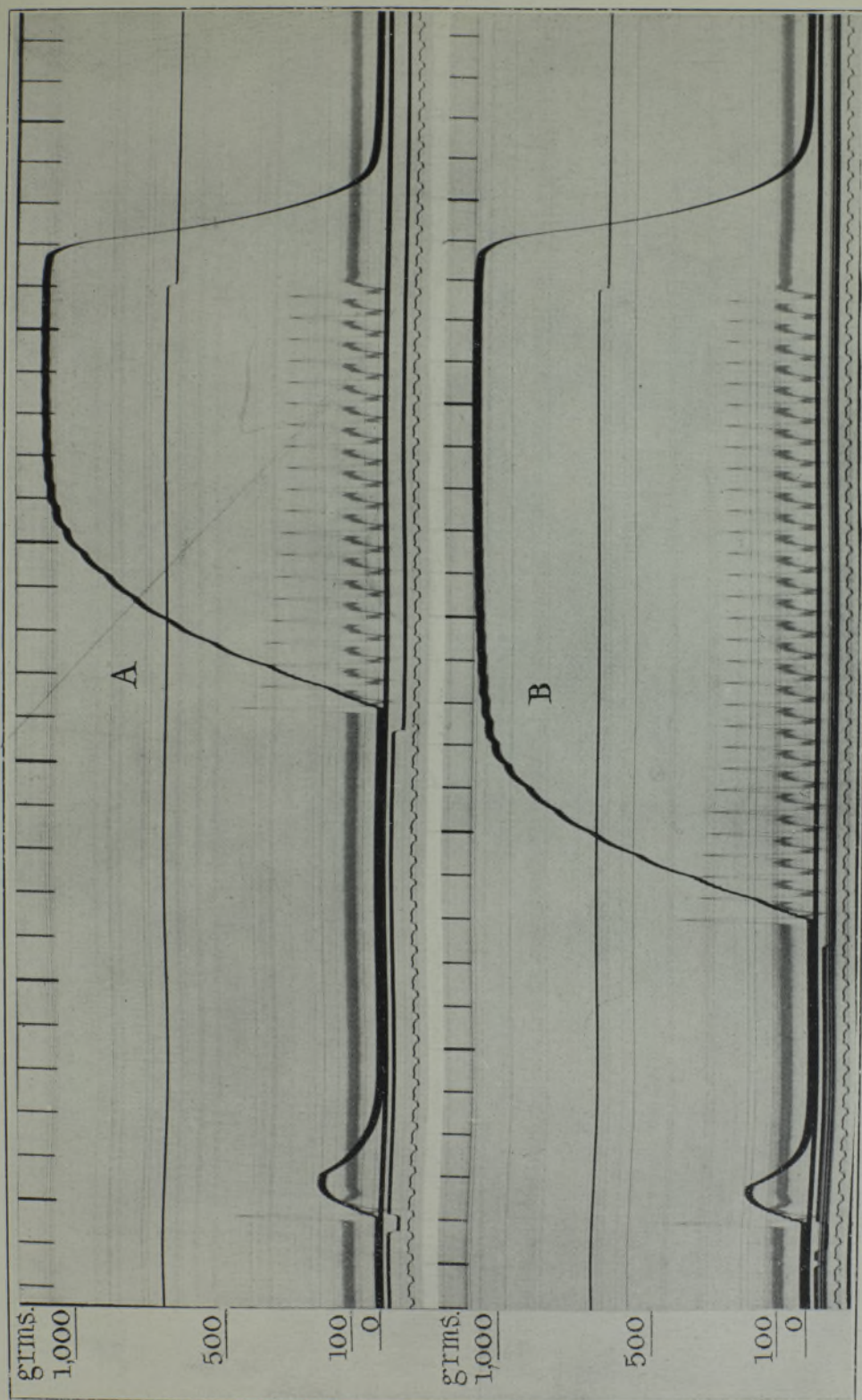


FIG. 3.

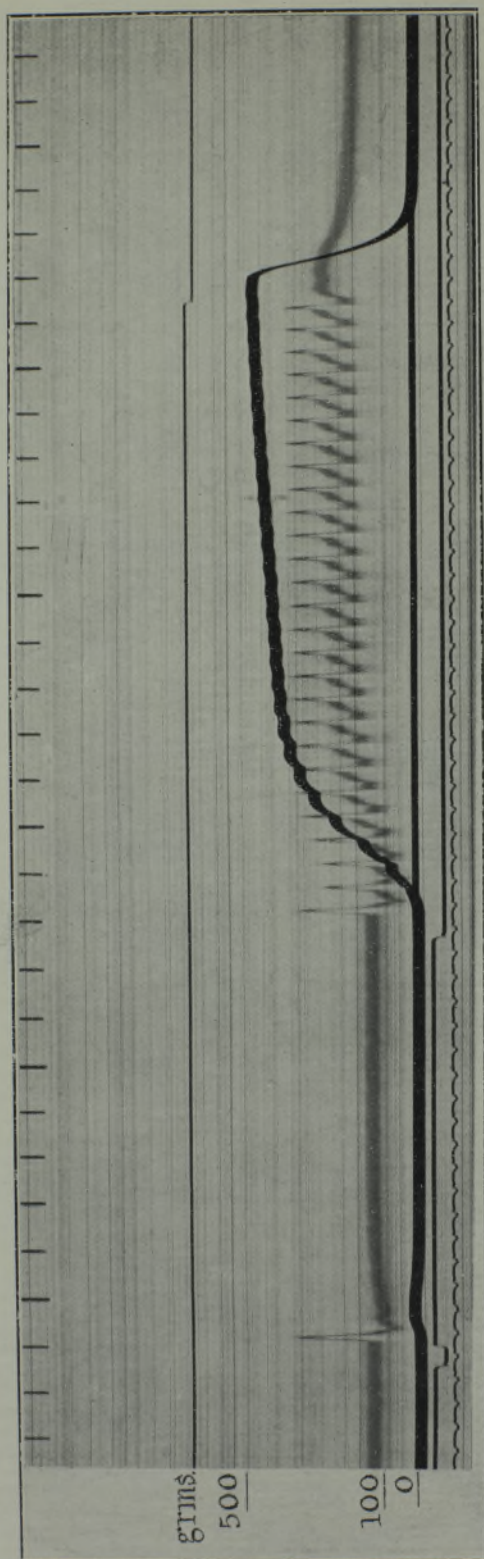


FIG. 4.

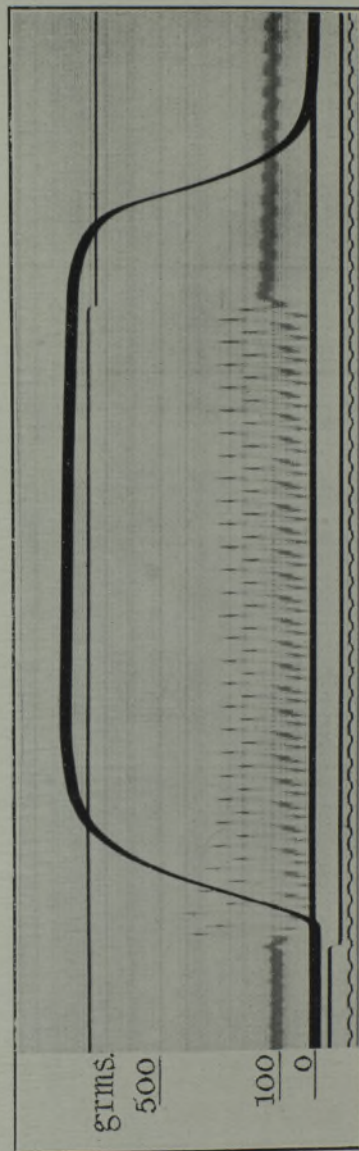


FIG. 5.

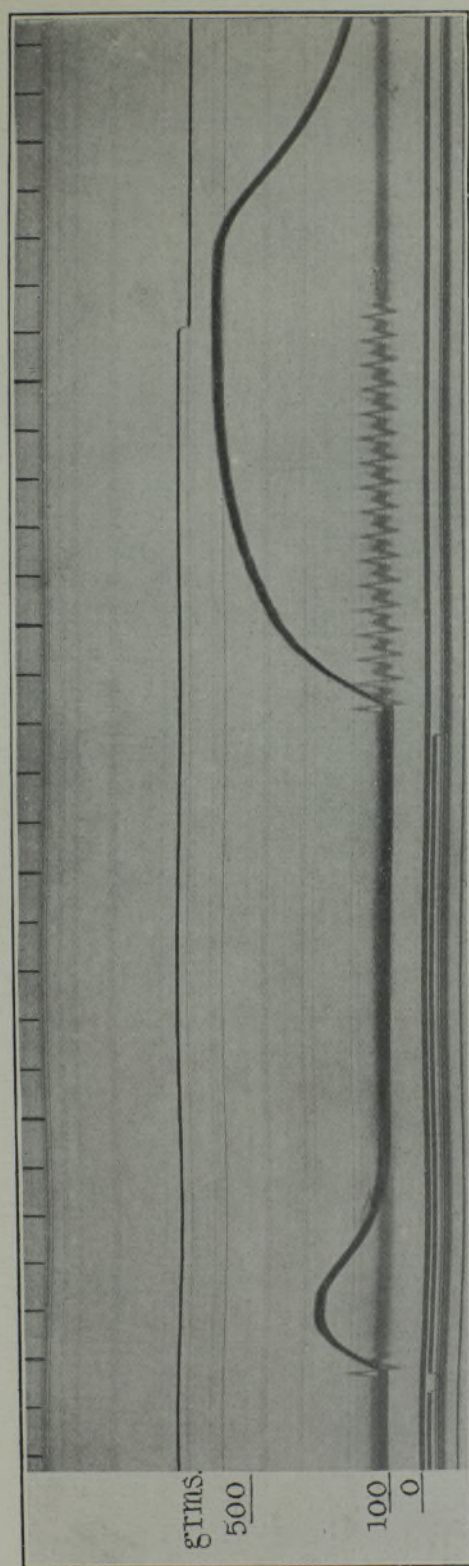


FIG. 6.

Durations of Isometric Twitch and After-action of Tetanus. 443

PLATE 33.

FIG. 2.—Responses of intact gastrocnemius of 30 gm. frog at 25° to a short tetanus (0.54 sec.) preceded by twitch. String tension 42 mm. per amp. at magnification of 285. Time above = 0.04 sec. Plate falling at 15 cm. per sec. A: Initial tension 73 gm. Scale of tensions on left. B: Initial tension 38 gm. For further analysis of curves see the bottom of Table I; further explanation of figures given in legend to fig. 3 in first paper above (p. 422).

PLATE 34.

FIG. 3.—Responses of intact gastrocnemius of frog at 24° , showing the effect on the terminal "angle" of the tetanus of increased duration of the plateau at constant initial tension (25 gm.). String tension 55 mm. per amp. Time above = 0.04 sec. A: Duration of plateau, 0.38 sec. The twitch in this record being the first response of the muscle after a rest is "abnormal," as described in the paper on shape of the twitch (4). B: Duration of plateau, 0.58 sec. Note slight rounding of the terminal angle. Here the twitch is normal (*cf.* with those in figure 2 of previous paper, Plate 30).

PLATE 35.

FIG. 4.—Response of gastrocnemius of 30 gm. frog at 24° , in which 3 mm. shortening was permitted before developing appreciable tension. Note the precise nature of the terminal angle, it being almost completely unmodified by fatigue. (From an unsuccessful experiment in which the difficulty of movement of the leads during contraction was not avoided, as is indicated by the deportment of the string.)

FIG. 5.—Gastrocnemius at 20° stimulated at 100 per sec. Though 2.0 mm. shortening were permitted which in itself would tend to cut down the energy liberated, the relaxation, nevertheless, shows all the characteristic signs of severe fatigue. The previous response of this preparation was at 50 per sec. and exhibited a sharp angle.

PLATE 36.

FIG. 6.—Response of gastrocnemius at 18° , 25 minutes after the circulation had been stopped by excision of the heart. String tension, 33 mm. per amp.