

THE FORCE EXERTED BY ACTIVE STRIATED MUSCLE DURING AND AFTER CHANGE OF LENGTH

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The tension exerted by a fully active muscle during shortening is less, during lengthening greater, than in an isometric contraction. The tension-length relation under isometric conditions is well known, while the relation between speed of movement and tension has been investigated by many authors by the use of two principal techniques: the *constant load* (or isotonic) and the *constant speed* (Levin & Wyman, 1927) methods. For shortening it has been found to follow the simple characteristic equation described by Hill (1938), but during forcible extension it appears to be more complicated. Thus Katz (1939) found, with moderate loads (up to about 1.7 times the isometric tension), that the speed of isotonic lengthening diminished progressively during the stretch. With still larger loads, the speed was high as though the tension had reached a limiting value.

In the present experiments, the constant speed method has been applied to frog, toad and dogfish muscle, with special attention paid to the course of tension after the end of the movement. The dogfish muscle was studied because the experiments of Levin & Wyman (1927) appeared to indicate that it could exert larger tension without 'give' and that its behaviour during lengthening might be similar to, and as simple as, that during shortening.

In the course of these experiments we obtained further evidence that the events during stretch are not merely the inverse of those during shortening: over a wide range of speed, the rise of tension during lengthening appeared to depend only upon the distance and not the speed, quite unlike the fall of tension during shortening. A much greater symmetry, however, characterizes the events after the change of length: when stretching ceases, the excess of tension immediately begins to decay, but if stimulation is continued the final value attained after several seconds is usually appreciably above the tension developed in an isometric contraction at the same length. In the same manner, after a shortening, the redevelopment of tension towards isometric is often incomplete, as already observed by Buchthal (1942) in the case of single fibres.

METHODS

Stretches at constant speed were applied to muscles from dogfish (*Scyllium canicula*), toad (*Bufo bufo*) and frog (*Rana temporaria*) by means of a Levin-Wyman ergometer; the tension was recorded throughout the movement. The muscles were kept at 0° C. in oxygenated salt solution: Pantin's (1946) solution was used for coracomandibulars of small dogfish (45 cm.), and Ringer's solution buffered at pH 7.0 with phosphate buffer containing 6 mg. P/100 ml. for sartorii of toads and frogs. A light jeweller's chain linked the muscle to the tension lever on the ergometer; tension was recorded directly on a smoked drum in the case of dogfish muscles and displayed on a cathode-ray tube through a photo-cell amplifier in the case of toad and frog muscles. Stimulation consisted of condenser discharges with a repetition frequency up to 10/sec. In certain cases the frequency was increased above that needed to get a fused tetanus in order to study the effect of frequency.

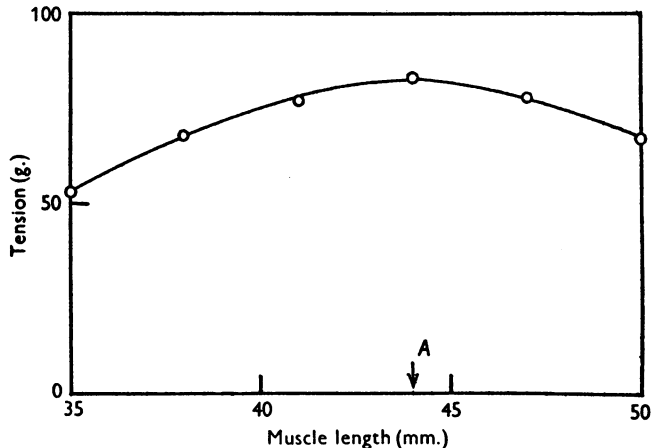


Fig. 1. Maximum tension developed at different lengths in isometric contraction of dogfish jaw muscle (standard length, 37 mm.; weight 600 mg.). In temperature 0° C. Stimulus frequency 5/sec.

The muscle was kept isometric until its full tension had developed (1-3 sec. according to the muscle). A stretch of 4-5 mm. was then applied at a constant speed between 0.5 and 30 mm./sec. The total duration of stimulus was conditioned by the type of experiment. Stimulation was stopped immediately after the stretch when only the rise of tension was being studied, but was sometimes prolonged for about 30 sec. in order to follow the later slow fall of tension.

In certain cases the events associated with shortening were studied in a similar manner.

Isometric contractions at the final length were imposed before and after each record of stretch or shortening; sets of measurements were accepted only if no significant change was found.

The isometric tension of a muscle varies with the length at which it is measured. The effect is a large one and has been described by many authors (e.g. Hill, 1925; Fenn & Latchford, 1933). An example for dogfish muscle is given in Fig. 1. Stretches or shortenings were applied between various lengths on both sides of the length at which the tension developed is maximum.

RESULTS

The rise of tension during a stretch

The general features of the tension changes during a stretch are well illustrated in the typical experiment of Fig. 2 on a toad sartorius. Stretches of 4 mm. at speeds of 1.9, 5.0 and 8.0 mm./sec. were applied to a tetanized muscle begin-

ning at 1.5 sec., by which time the full isometric tension had been developed. It is clear that the maximum tension reached during the stretch is almost the same in the three cases. The speed being uniform during each stretch, a tension-time curve can be transformed into the dynamic tension-length relation. The similarity of the three events is then still more evident; indeed in this experiment the dynamic tension-length diagrams are identical (first experiment of Table 1). Only at very low speeds is the difference in tension during stretch appreciable, as indicated in the experiment of 4 May (Table 1): even in that case the difference both in tension and work hardly exceeds 10 %.

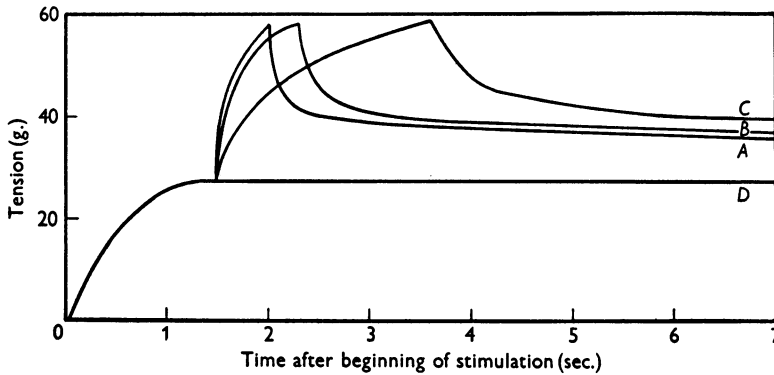


Fig. 2. Tension during and after stretch of toad sartorius at 0° C. (standard length 28 mm.; weight 134 mg.). Stretch from 21.5 to 25.5 mm. began after 1.5 sec. of stimulation: curve A at 8 mm./sec., B at 5 mm./sec., C at 1.9 mm./sec. D isometric at final length 25.5 mm. Stimulus frequency 3/sec.

The same general results were obtained with the dogfish muscle (Table 1). For speeds above 1 mm./sec. both increase of tension and work done in stretch remain almost independent of speed.

The contrast to shortening becomes evident when the two kinds of experiment are made on a given muscle, as in the following example for dogfish muscle: the final values of tension are given as percentages of the isometric tension at the terminal length for both shortening and stretching at two different speeds, the range and the final length being the same in all cases.

	Speed (0.9 mm./sec.)	Speed (7.4 mm./sec.)
Stretch	202	210
Shortening	70	52

The effect of speed of movement on the final tension is obviously quite different in the two cases: it is negligible in stretch but large in shortening. On the other hand, when the movement is very slow the rise of tension in the stretch is much larger than the corresponding decrease of tension which accompanies shortening. That, of course, might be expected from an extra-

polation of the characteristic relation for shortening (Hill, 1938) and the fact that the tension does not increase much with speed of stretch might be through 'give', due to some irreversible change of internal state of the muscle.

TABLE 1. Muscle tensions during stretches at constant speed

	Speed of stretch (mm./sec.)	Tension at beginning of stretch (g.)	Tension at middle of stretch (g.)	Tension at end of stretch (g.)	Work (g.cm.)
Toad					
26 Apr.	1.9	28	52	58	20.0
	5.0	28	53	57	20.7
	8.0	28	52	57	19.6
4 May	0.9	100	149	163	57.5
	2.0	100	160	178	61.0
	3.6	100	164	184	63.4
	6.2	100	167	183	64.5
Dogfish					
5 Aug.	0.9	37	—	115	—
	3.3	36	—	120	—
	7.4	37	—	118	—
	17.0	37	—	116	—
8 Aug.	0.5	110	—	178	64.0
	6.0	110	—	195	72.0
	30.0	110	—	207	74.5
9 Aug. A	0.9	110	—	232	90.0
	7.4	110	—	241	96.0
B	0.9	—	—	244	94.0
	7.4	—	—	256	99.0

A, stretch from length less than that for maximum isometric tension. B, stretch from length greater than that for maximum isometric tension. Temp. 0° C.

The readjustment of tension after stretch and shortening

As soon as a stretch finishes, and provided the stimulation is continued, the tension falls back towards the new isometric level; but for the toad muscle of Fig. 2 it has not reached that level even after a further 3 sec. The figure shows further that the tension falls the more quickly as the stretch has been more rapid, despite the fact that the tension at the end of the stretch is about the same. Moreover, the quicker the stretch the less is the final excess of tension above isometric.

These observations have been extended in the case of dogfish muscle to stimulus durations up to 30 sec. after the end of the stretch. The tension rise after constant speed shortenings has also been studied to see if any corresponding difference from the ordinary isometric tension occurs. The evidence of Fig. 3 shows that such deviations do arise in both cases. A muscle was brought to length 34 mm. both by stretching it from 29 to 34 mm. (curve *A*) and by shortening at the same speed, 0.6 mm./sec., from 39 to 34 mm. (curve *B*). The tension developed at a constant length 34 mm. is given for comparison in curve *C*. After the end of movement the tension immediately begins to readjust itself towards, but eventually settles at a value different

from, the isometric: about 20 g. above isometric after stretch and the same amount below after shortening. The level reached is quite steady at about 7 sec. after the movement ends, but is approached rather more rapidly with shortening than with stretch. The muscles have to be in good condition to stand such long tetani, otherwise fatigue is likely to interfere with the results. For this reason isometric tetani were regularly interposed and the series discontinued at the first sign of important change.

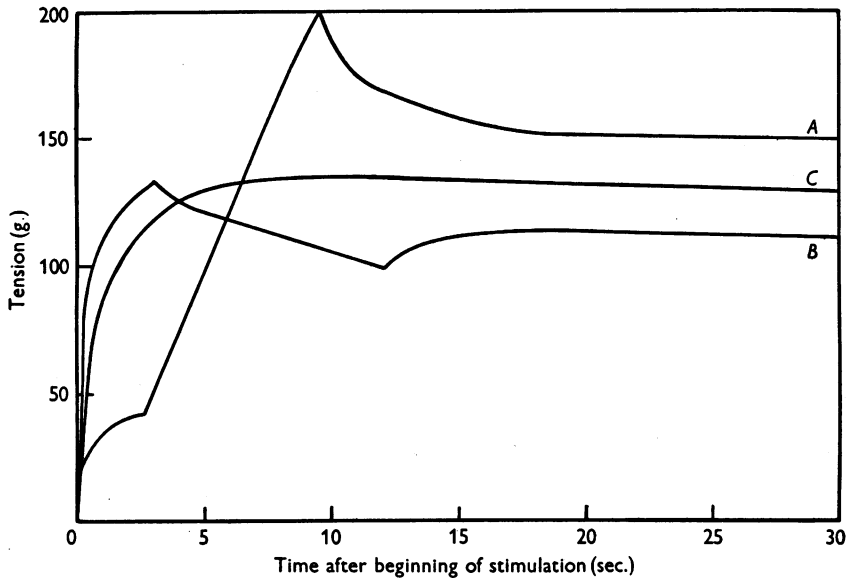


Fig. 3. Tension changes during and after movement in dogfish muscle (standard length 35 mm.; weight 740 mg.). Curve *A*, stretch 29–34 mm., *B* shortening 39–34 mm. Movement began after 3 sec. of stimulation. Curve *C*, isometric 34 mm., with identical traces before, between and after curves *A* and *B*. Temperature 0° C. Stimulus frequency 5/sec.

Two factors were found which influenced the readjustment of tension after movement. The effect of speed has already been mentioned in respect of stretch of toad muscle (Fig. 2): the quicker the stretch the less the final excess above the isometric tension. The same rule applies to shortening as illustrated for dogfish muscle in Fig. 4, where after the same amount of shortening at speeds of 0.5 and 8 mm./sec. the tension settled respectively at 24 and 6 % below the isometric tension for the same length. After a very sudden release the tension rises to the isometric value at the final length (Gasser & Hill, 1924).

The other factor affecting recovery of tension was the length at the end of movement. The isometric tension during a tetanus goes through a maximum at a length just greater than that in the body, and the stretches were applied either on the rising limb of the tension length curve (Fig. 1), or around the peak of the curve, or on the falling limb. Table 2 shows that the residue of

tension above isometric is greater when the stretch had been applied around the peak or on the falling limb of the tension length curve. Even in the region to the right of the maximum of Fig. 1, where the isometric tension is less the greater the length, the rise of tension with stretch is as large as that on the other side of the maximum; and it is in that same region that the residual tension is higher.

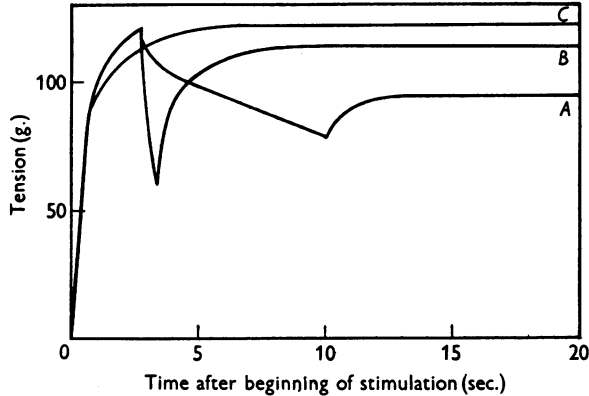


Fig. 4. Recovery of tension after shortening at different speeds. Dogfish jaw muscle, 0° C. (standard length 33 mm., weight 540 mg.). Stimulus frequency 5/sec. Shortening 42–37 mm., curves *A* at 0.5 mm./sec., *B* at 8 mm./sec., *C*, isometric 37 mm.

TABLE 2. Residue of tension above isometric during 'after-stretch', following stretches at constant speed over various parts of the isometric tension-length curve

Date (Aug.)	Rising limb	Top	Falling limb
2	2	—	24
3	2	—	13
4	11	—	20
5	16	—	52
6	11	19	—
7	0	22	—
10	—	20	—
11	—	17	—

Dogfish muscle, with residual tensions expressed as percentages of the full isometric value. Stretches of 5 mm. were applied either on the rising limb, or at the top, or on the falling limb of the tension-length curve (see Fig. 1).

In some experiments after a slow shortening at constant speed, and when tension had readjusted itself to about 80 % of the normal isometric tension, the stimulus was stopped for varying lengths of time and then restarted. If it was stopped long enough to allow the tension to fall to zero, the tension which redeveloped reached the full isometric value at that length; if the interval was shorter the tension redeveloped was less (Fig. 5). The lower value of final tension after shortening may be related, as mentioned in the following discussion, to some genuine internal change of structure: a fall of the tension

to zero gives the different elements of the muscle the opportunity to return to their normal arrangement. In the case of a stretch, the tension never rises again above isometric after the interruption.

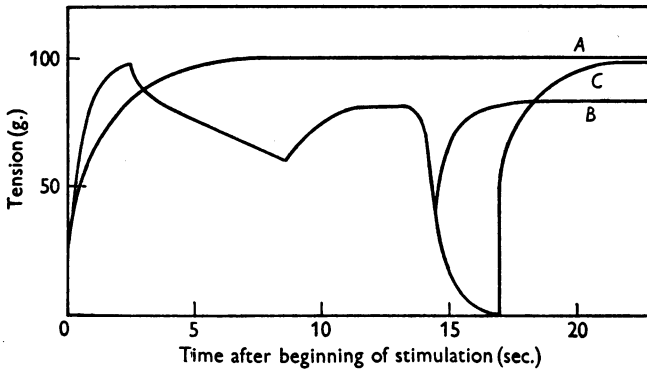


Fig. 5. Dogfish muscle 0°C . (standard length 33 mm., weight 380 mg.). Stimulus frequency 5/sec. Effect of break in stimulation during recovery of tension after 5 mm. shortening at 1.1 mm./sec. Curve A, isometric tension; B, stimulus stopped for 0.7 sec. during tension readjustment after shortening; C, stimulus stopped for 3 sec.

DISCUSSION

The response of dogfish muscle to stretch disagrees in some respects with the results of Levin & Wyman (1927), inasmuch as they found a much greater symmetry in the changes of tension during stretch and shortening. The present experiments, however, were performed at 0°C ., while it is probable that Levin & Wyman were working at room temperature. Since the jaw muscle of dogfish is quite thick (at least 3 mm.) only the outer layers of an isolated muscle can get sufficient oxygen supply at room temperature: consequently during the longer time of a slower stretch the muscle might contract less actively than during the shorter time of a quicker stretch and the work would be less. This biases the results in favour of quick stretches and exaggerates the true influence of speed. This suggestion is supported by the effect of frequency of stimulation. High frequencies also depress muscular response and it was, in fact, possible to reproduce Levin & Wyman's results in that way: dogfish muscles at 0°C . were stretched at two speeds (0.9 and 8.4 mm./sec.) and the work done during each stretch was measured. This was repeated at three different frequencies of stimulation. The work done at the higher speed of stretch was always greater than at the lower speed, but the difference between the two increased with stimulus frequency; with 7, 12 and 25 shocks/sec., the values of the work done in the fast stretches were respectively 7, 22 and 70 % greater than in the slow stretches and were associated with lower tensions as the frequency of stimulation increased.

Another explanation might have been suggested; according to Levin & Wyman themselves, the work done in stretch becomes constant at high speeds: could not all the speeds used in the present experiments lie within this region owing to the temperature difference? This is disproved by reference to the shortening experiment mentioned above, where the effect of speed on work done is large. The symmetry of the curve in Fig. 3 of Levin & Wyman's paper shows that, for the range of speeds where large changes occur during shortening, similar changes should occur during stretches at the same speeds: no such variation was present, and it may thus be concluded that dogfish muscle responds to stretch in a manner similar to frog and toad.

The tension after the end of movement settles to a steady level different from the isometric value at the final length attained. Might not friction, either external or internal, be the cause of the difference? External friction can readily be discarded: the muscle was kept in fluid during the experiments, the electrodes offered negligible resistance and the tension-recording system was practically frictionless—especially when using photocells. The extra heat production which accompanies shortening might be related to internal friction, but then a similar heat increment would be expected in lengthening. On the contrary, Abbott & Aubert (1952) could detect a slightly decreased rate of heat production during the fall of tension after stretch had ended but while stimulation was continued, comparable to the 'negative heat of lengthening' observed in a slow isotonic stretch. During this process the series elastic elements of the muscle-lever system, placed under stress during the imposed movement, expend some of their elastic energy in slowly stretching the contractile material; far from being dissipated as heat, that work entirely disappears together with a certain amount of heat.

Fig. 1 suggests another possibility. A muscle cannot be regarded as a single contractile element uniform throughout its length. Hill (1949) has pointed out that it is very improbable that a muscle fibre, with a length hundreds of times its diameter, should have a constant strength throughout. During shortening against a constant load the stronger portions may be expected to stretch the weaker ones; during a stretch to be stretched less than the weaker ones. It is doubtful whether isolated single fibres really present the mechanical homogeneity sometimes assumed. In a whole muscle, with a large number of fibres acting in parallel, an average value is obtained, and even in the presence of a certain amount of connective tissue the average cross-section must be relatively more constant than in a single fibre. Since a given muscle can develop the same tension at different lengths the possibility arises that various regions along a muscle fibre may be brought to work on opposite sides of the tension maximum. Different tensions might then be developed at the same length, depending on the way of arriving at the length. The continued depression of tension after shortening at constant speed could be

explained in this way, but it is not so easy to imagine after a stretch a final tension above isometric—especially a value higher than the maximum of the isometric tension-length curve. The constant occurrence of the decrease in heat production during a slow ‘after-stretch’ points rather to some genuine internal change of structure. Some support for this idea is provided when a muscle is slowly lengthened isotonicly. Katz (1939) demonstrated a continuous drop in the speed of lengthening, the speed being less than would be expected from extrapolation of the characteristic equation. Almost the whole of a very slow stretch and not merely the later parts seem to be ‘reversible’ (Abbott & Aubert, 1952), and is associated with a constant negative heat of lengthening. It seems, therefore, as though some progressive internal reorganization has occurred with perhaps an accompanying increase of maximum isometric tension P_0 .

A corresponding change may occur during shortening. If the muscle of Fig. 1 is stimulated at length A and allowed to contract isotonicly under an afterload of 53 g., it will shorten until its length is 35 mm. where the isometric tension is 53 g. If, however, the muscle is stimulated isometrically at length A until the full tension has been established and then suddenly allowed to shorten under the same 53 g. load, the amount of shortening is always appreciably less than in the first case with no preliminary isometric contraction.

This effect has been verified on frog muscle (Aubert & Nuyts, 1952) and suggests that a large tension developed during activity is linked with an increased rigidity of the muscle. The hysteresis-like effect apparent in tension after slow movement may thus be due to some change within the molecular framework of the muscle: during isometric contraction a sort of crystalline pattern seems to be produced which is distorted when movement occurs. Interruption of stimulation long enough for the tension to fall to zero breaks the distorted pattern so that the normal isometric tension can develop when the stimulus is restarted. It is not surprising that forced stretch may bring temporary damage to such a crystalline network, repairable as the framework is rebuilt in the course of the next stimulation. These are the characteristics of ‘give’ in muscles.

SUMMARY

1. The events when an active muscle is stretched are not merely the converse of those during shortening.

2. The tension rise which accompanies an imposed stretch at constant speed depends on the distance moved and hardly at all on the speed of movement: this is in contrast to changes observed during shortening (except at very low speeds).

3. After the end of a stretch at constant speed, and provided that stimulation is continued, the tension falls back towards but remains considerably above the isometric tension at the terminal length.

4. Similarly, after a slow shortening at constant speed, the tension remains considerably below the isometric value.

5. When such an excess or deficit of tension is being manifested, if excitation is interrupted long enough for the tension to drop to zero, the full isometric value is re-established when excitation is resumed.

6. The possibility that previous shortenings or lengthening influence the internal structure, and so affect the final tension at a given length, is discussed.

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