THE RELATION OF LENGTH TO TENSION DEVELOPMENT AND HEAT PRODUCTION ON CONTRACTION IN MUSCLE. By C. L. EVANS and A. V. HILL.

(*From the Physiological Laboratory, Cambridge.*)

THE experiments of which the results are described here were undertaken at the suggestion of Professor Starling, with the view to testing the theory put forward by Blix that the variable factor among the mechanical conditions which determines the mechanical performance and the heat production of muscle is the initial length of the muscle and to find what relation, if any, exists between the length of the muscle and the tension and heat which it produces on isometric contraction.

According to Blix(1) the total tension sustained by a contracted muscle alters according to the initial length of the muscle, the relation between total tension and length being often expressed by an S-shaped curve. The heat production, according to him(2), increases progressively with increasing initial length of muscle, to attain a maximum only when the muscle is incapable of further extension. Essentially the same question was investigated by Heidenhain(3), but he arrived at different results, for his figures show first an increase and then a diminution of the heat production with increasing initial length (initial tension was what he actually measured) when isometric contractions were executed by the muscle.

It was thought that with the improved apparatus now available for myothermal experiments, some direct information might easily be gained on this point.

Methods.—The muscle employed in these experiments was in most cases the double sartorius preparation of large *R. esculenta*; in one or two cases the semimembranosi were used, but these had the disadvantage of lying less uniformly on the junctions, and moreover their cross sectional area was less uniform at different parts of their length than that of the sartorii. The muscles were left attached to the ischium, which was held firmly in a clamp, the muscles being arranged one on each side of the thermoelectric junctions of a straight thermopile of the type figured by Hill(4), and the ends of the muscle being tied together and attached by an inextensible (shellacked) thread to the tension lever designed by Hill(5); by means of a fine adjustment the lever apparatus could be moved as a whole either up or down, and thus the initial length of the muscle, and its initial tension, could be altered at will. The pitch of the adjusting screw being known, the alteration in initial length of the muscle was also exactly known from the number of turns given to the fine adjustment screw. The initial tension of the muscle, and also the tension produced on contraction, were found by measurements of the record of the tension lever on a stationary smoked drum. The lever magnified about 47 times, and the spring was a strong one, and therefore movement of the lever on its axis was not attended with any marked alteration in the length of the muscle. Thus a tension of 50 grams weight acting at the point of attachment of the muscle and causing a displacement of 7·3 mm. at the writing point of the lever, only moved the point of application about 0·16 mm. The small error which was introduced into the measurement of the increment of length of the muscle by such a displacement of the tension lever could therefore be neglected, since at extensions of the muscle to even a quarter more than its original length (about 35 mm.) it would amount to less than 0·5 mm.

The thermopile with the muscle was protected from stray draughts and radiations, either by the use of the myothermal chamber described by Hill(6), or by being placed inside a Dewar vessel in air or saline. Although temperature equilibrium was reached sooner in the Dewar vessel, the myothermal chamber was found to be more suitable, since the connection of the muscle to the lever could be more conveniently arranged.

As stimuli maximal opening shocks were in most cases employed, though in a few cases tetani of about ·04 sec. duration were tried, and found to give similar results. Constancy of stimulus was ensured by the use of a Lucas' spring key for opening the primary circuit in the case where single shocks were employed. The duration of the short tetani was also obtained constant by means of this apparatus.

It is scarcely necessary to mention that in all the experiments especial care was taken to avoid movement of the muscle over the junctions on contraction; any cases which occurred were readily detected, and experiments in which any of the readings showed that movement had taken place were rejected.

The results of a typical experiment are given below, to illustrate the alterations of tension development and heat formation when isometric contractions are executed at different lengths of muscle. The results are also given graphically in Fig. 1 (upper pair of curves).

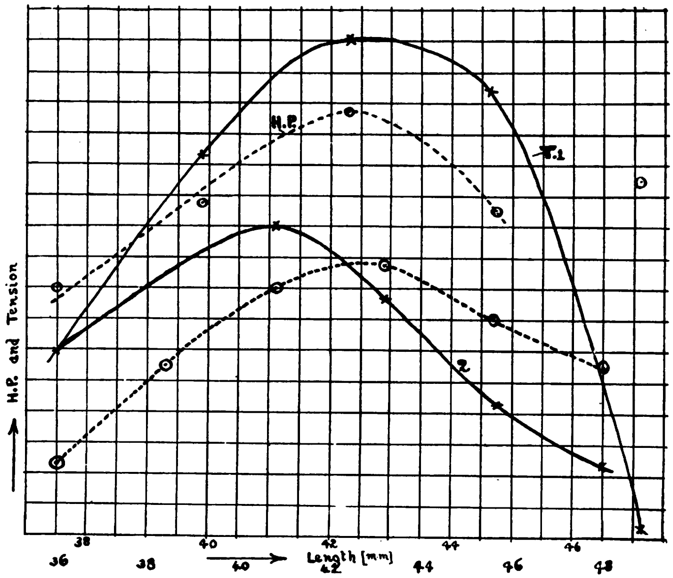

Fig. 1.

Exp. 1. Two sartorii muscles in myothermal chamber. Maximal opening shocks with 4 ohms resistance in primary circuit.

L=initial length of muscle mm.	t=initial tension on muscle grms.	T=increase of tension on contraction grms.	H=heat production (deflection of galvanometer in mm.)	$\frac{T}{H}$	$\frac{H}{L}$	$\frac{T}{L}$
37·5	0·0	41·8	54·0	·77	1·44	1·12
39·9	2·7	54·7	61·5	·89	1·54	1·37
42·3	13·7	62·3	67·5	·92	1·60	1·47
44·7	37·7	59·0	61·0	·96	1·36	1·32
47·1	81·0	30·7	63·0	·49	1·34	0·65

The figures given in the table represent the mean results obtained in an experiment in which the length of the muscle was first increased and then diminished again. The ratios of heat produced and of tension developed to the initial length of the muscle, as given in the respective columns, show that these increase to a maximum with increasing length of muscle, and then diminish again (Fig. 1). With the exception of the first and last figures of the column, the values of T/H are fairly uniform. The low values for the extreme conditions of the muscle are due to the fact that the tension rises to a maximum and then declines from it again rather more rapidly than the heat production does, so that the efficiency of the muscle is less when under very small or very great initial tensions than when under moderate ones. The low value of T/H at the top of the column where there was no initial tension is also no doubt due, to some extent, to the difficulty in ensuring that the muscle was without initial tension, but yet not slack. If there were any slack to be taken in, the tension development would suffer. The arbitrary decision of what is to be regarded as the natural length of an excised muscle is a matter of considerable difficulty.

Other experiments have given similar results; the following is typical.

Exp. 2. Two sartorii under same conditions as Exp. 1.

L=initial length mm.	t=initial tension grms.	T=tension developed grms.	H=deflection mm.	$\frac{T}{H}$	$\frac{H}{L}$	$\frac{T}{L}$
36·0	0·0	29·5	44·5	·67	1·23	·82
38·4	1·4	42·5	51·0	·83	1·32	1·10
40·8	8·2	50·0	56·0	·89	1·37	1·22
43·2	32·0	38·5	57·5	·67	1·33	0·89
45·6	82·0	21·3	54·0	·39	1·18	·47
48·0	126·0	11·7	51·0	·23	1·06	·24

This experiment illustrates a fact which was observed in several cases, namely that the maximum heat production is obtained at a greater length of muscle than the maximal tension development; this is best seen in Fig. 1 (lower pair of curves). Although this was the case, the tension development and heat production per unit length both reached a maximum at the same initial length, in other words, beyond this length at which the maximal tension was produced the increase in length necessary to cause a certain further increase in heat production increased rapidly.

In Exp. 1 the maxima both of tension production and of heat production were reached at the same length of muscle, but the result shown in the second pair of curves of Fig. 1 was the more usual one. The average of ten experiments for instance showed that the maximal tension developed resulted when the muscle had been extended by about 12 % of its original "unloaded" length, while the maximum heat production resulted after about 17 % increase in length. It is interesting to compare these data with some others relative to the length of the muscle in its natural position in the body, and when removed from the body. Some measurements were made of the length of the sartorius muscle of the frog under these two conditions, and it was found that the muscle *in situ*, with the leg flexed to a right angle and abducted, was about 20% longer than when measured after excision and allowed to hang quite free without load (the minimum difference was 14% and the maximum 26%). Bearing in mind that in our measurements of tension development and heat production, the "unloaded" muscle with which we started was in reality subjected to a slight tension sufficient to prevent the thread hanging slack, it is not unlikely that the maximal heat production was reached at a total extension of roughly 20%, or about the natural length of the muscle *in situ*, while the maximum tension was attained at a somewhat shorter length, such as would obtain after the contraction in the body had already commenced.

In most of the experiments the ratio T/H was found to be constant over a limited range, which included somewhat considerable amounts of stretching, though the value diminishes rapidly when the initial tension exceeds a certain limit. Within the limits of extension likely to occur frequently in the body (*i.e.* up to 20% or 30%), the ratio is often very constant, as in the following experiment where the extension reached 30% of the original length.

Exp. 3. Double sartorius preparation in oxygenated Ringer's solution in Dewar vessel. Maximal opening shocks.

Initial length mm.	Initial tension grms.	Tension development grms.	Heat production mm.	$\frac{T}{H}$
23·0	0	50·6	103	0·49
25·4	13·7	54·0	110	0·49
27·8	37·7	61·0	126·5	0·48
30·2	58·3	52·8	114·5	0·46

In the following experiment also, in which the muscle was less extended, the value of T/H was fairly constant up to 20% extension. In this particular case the sectional area of the muscle was 13 sq. mm., so that the tension was equal to 300 grms. per sq. cm. at the maximal initial length and about 770 grms. per sq. cm. in the contracted state. (The muscles often broke across when the tension at rest exceeded 1000 grms. per sq. cm.)

Exp. 4. Double sartorius preparation in myothermal chamber.

Initial length mm.	Initial tension grms.	Tension development grms.	Heat production	$\frac{T}{H}$
37·5	0	61	59·5	1·02
39·9	1·4	83·5	76·5	1·09
42·3	13·7	75·5	80·5	0·94
44·7	38·5	63·0	73·0	0·86

The constancy of T/H implies a constancy in the mechanical efficiency of the muscle; this latter only falls away rapidly when the muscle is extended far beyond its natural length—perhaps a safeguard against rupture of the muscle. In those cases where the ratio only sustains a maximal value for a short time, as in Exp. 1 and 2, it is interesting to note that this maximum is reached at a length which does not differ greatly from that of the muscle *in situ* (19 and 12°/₀).

In Fig. 2 the results of Exp. 4 are shown. Three tension curves are there reproduced; firstly (*A*) the tension to which the resting

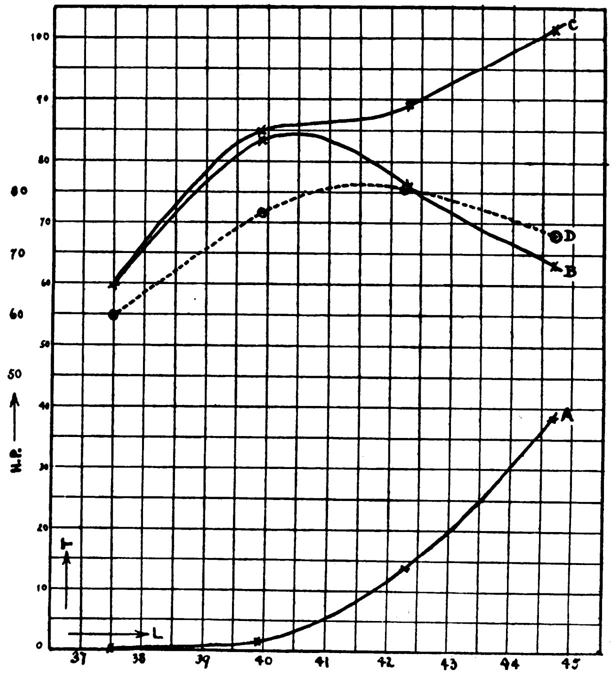

Fig. 2.

muscle was subjected; second (*B*) the curve of tension developed on contraction; lastly (*C*) the curve showing the total tension which the contracted muscle was sustaining, *i.e.* the sum of the other two curves. The only curve to which the curve of heat production (*D*) seems to correspond is that of tension developed. Although the curve of total tension sustained bears a certain resemblance to the curves figured by Blix, yet the results of the thermal measurements which we have obtained are rather in agreement with those of Heidenhain than with those of Blix.

CONCLUSIONS.

1. With increasing length the heat production of isometric twitches or short tetani increases to a maximum, and with further increase of length diminishes again. The maximal heat production was obtained at an average increment of 17 % of the initial unextended length, or at about the same length as the resting muscle has when *in situ* in the body.

2. The tension developed by the isometric contraction follows a similar curve to that of the heat production, although there is a tendency for the maximal tension to be set up at a smaller length than the maximal heat production, namely, when the length of the muscle has been increased by 12 % of the original unloaded length.

3. From the form of the curves of tension and heat production and from the position of their maxima, it follows that the ratio T/H is only constant for a certain range of extensions of the muscle; for very high extensions it rapidly diminishes. The maximal values of T/H are reached at about the natural length of the muscle *in situ*, and the range of constancy of T/H usually obtains at lengths either less, or not much greater, than this length.

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