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EARLY TENSION RELAXATION DURING A MUSCLE TWITCH

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Information concerning the mechanism of contraction is supplied by the order of the appearance of thermal and mechanical activity following the stimulation of a muscle (Hill, 1950*a*). In a frog's sartorius at 0° C. heat production has begun by 10 msec. after the stimulus (Hill, 1949*a*). In the present experiments, mechanical latency at 0° C. was measured and a piezo-electric method was used to register tension changes during isometric twitches (Abbott & Ritchie, 1948). This method provided the high sensitivity and speed needed to determine the precise form of the earliest phases of the contraction at the point stimulated: it has been used extensively by Sandow (1944, etc.) at higher temperatures to study the early tension relaxation in an isometric twitch.

Sartorius muscles of frogs (*Rana temporaria*) and toads (*Bufo bufo*), and single coraco-hyoid muscles of medium-sized dogfish (*Scyllium canicula*) were used.

METHOD

A Rochelle salt crystal of the bender type was secured at both ends. A force of 1000 dynes applied suddenly to the middle of the crystal produced an output of 0·23 V. for a movement of only 2·2 μ. Delays in the recording system had to be minimized. In all early experiments the muscle (frog or toad sartorius) was looped through a triangular ring of silver. The pelvic and tibial ends were brought together and fixed to a clamp (Fig. 1): the ring was then used for cathodal stimulation and was also the point from which tension was recorded. A light inextensible chain connected the recording ring to the crystal. A chain was chosen because an extensible thread might introduce an appreciable delay in transmission of the tension wave along the thread. The transmission time along the chain was negligible, and the inextensibility of the chain ensured the accurate reproduction of changes in tension. The mass of the chain was 0·64 g., and the force required to move it at the moment of maximum acceleration in the early stages of tension development was less than 0·3 dyne. This was negligible compared with the other forces involved.

The output from the crystal was fed into a cathode follower of input impedance 100 MΩ. connected to an electronic amplifier with a maximum gain of 7000. The time constant of the whole recording system was about 220 msec., which was sufficiently long to transform without distortion the early changes in tension into a voltage output from the amplifier. The output was displayed on a cathode-ray tube, and brightness modulation of the beam provided $\frac{1}{2}$ msec. time marks on the trace. The muscle assembly was mounted in a chamber filled with oxygenated Ringer's solution and the chamber immersed in an ice-water mixture. The muscle was under a resting tension of about 3 g. weight. Before measurements began the Ringer was removed. Tension changes were

recorded during the first 20 msec. of single isometric twitches: super-maximal stimulation by condenser discharges was used.

The same procedure was used during a series of experiments on dogfish muscle carried out at Plymouth during August 1948, but at 18° C. The muscle was looped through the stimulating ring and both ends tied to a clamp. In later experiments with frog muscle a different system was used. The muscle was mounted on a multielectrode assembly described by Hill (1949*b*) and stimulated simultaneously all over. The pelvic end of the muscle was clamped and the tibial end was joined by a short light thread to the crystal. The muscle was stimulated while in Ringer's solution. The latency was exactly the same whichever system was used.

If the early tension drop is not due to an active lengthening of the muscle, its value would be expected to drop to zero when the muscle tension becomes small. The time at which the tension recrosses its baseline might alter progressively as testing tension decreases. The early tension changes in frog muscle at 0° C. were therefore measured at a series of resting tensions. The muscle was mounted on the multielectrode assembly. Each series started from a length about 6 mm. greater than the muscle length in the body. The length was decreased by 1 mm. steps to about 8 mm. below body length; and was increased again with the same steps. Before each record was made, three stimuli were applied to the muscle to make sure that any slack had been taken up.

While one of us, J. M. Ritchie, was working with M. Goffart, the opportunity incidentally arose to examine the early phases of contraction in two types of mammalian muscle: cat tenuissimus and rat diaphragm. A strip of muscle was mounted on the multielectrode assembly. It was soaked in oxygenated Tyrode's solution at 37° C. and maximal 'all-over' stimulation applied at a series of initial lengths.

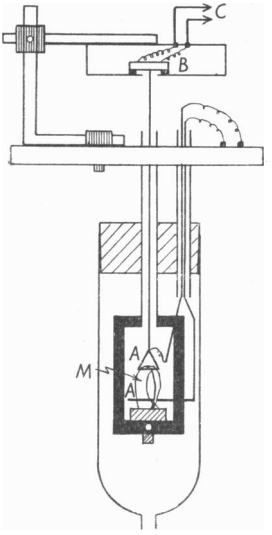

Fig. 1.

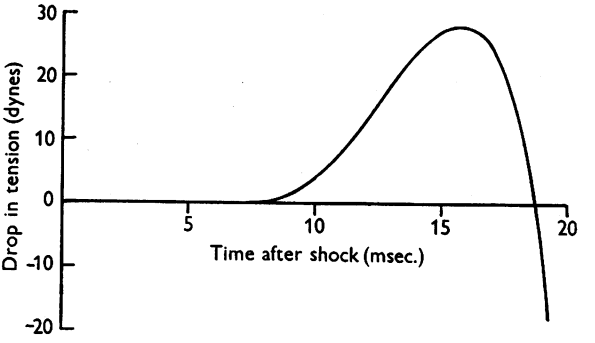

Fig. 2.

Fig. 1. Apparatus for recording the mechanical latent period. *A*, *A*: electrodes; *B*: crystal pick-up; *M*: muscle; *C*: output to amplifier.

Fig. 2. Tension change in frog's sartorius muscle at 0° C. during early stages of isometric twitch.

RESULTS

The exact time when the curve left the baseline was uncertain owing to the gradual onset of the change, so the mechanical latent period was taken as the time from the stimulus to a tension drop of 0·15 dyne. Fig. 2 shows a typical

record for frog muscle at 0° C. under a resting tension of 3 g. weight. The tension decreased initially by about 20 dynes before the main increase in tension which reached 20 kdynes. It began to fall at about 7 msec. and did not increase beyond its resting value until between 15 and 20 msec. after the stimulus.

Table 1 gives the latent periods obtained in the earlier experiments with frog and toad muscle at 0° C., and dogfish muscle at 18° C. Each of the times in the table is the mean of at least four observations taken in quick succession. For frog muscle all the results lay in the range from 6·5 to 7·9 msec. The latent periods were consistent for a given muscle at a given time, but varied for different muscles or for the same muscle if several determinations were made at intervals of a half or a whole day.

TABLE 1. Average latent periods.

Date	No. of traces	Mean latency (msec.)	Time at which base-line is recrossed (msec.)
		Frog, 0° C.	
3.viii.47	5	6·7	15·0
31.viii.47	6	7·1	15·0
31.viii.47	6	7·0	14·7
2.ix.47	6	7·0	14·7
24.ix.47	3	7·4	14·8
2.x.47	4	7·2	13·4
2.x.47	5	7·9	17·4
3.x.47	4	6·5	—
3.x.47	4	6·9	15·0
3.x.47	4	7·6	15·6
4.x.47	4	7·3	14·0
		Toad, 0° C.	
11.v.48	10	9·3	20·5
13.v.48	18	9·2	19·0
14.v.48	6	10·0	21·0
		Dogfish, 18° C.	
3.ix.48	6	1·54	2·9
4.ix.48	5	1·6	3·3
6.ix.48	4	1·8	3·5

In the later experiments the initial decrease in tension was found to be greatest (for frog muscle) when the muscle was about 6 mm. longer than its greatest length in the body (usually about 30 mm.). As the muscle length was diminished in steps of 1 mm. the amount of early tension drop became progressively smaller and the moment at which the tension curve recrossed its baseline became progressively earlier (Fig. 3). Somewhere between curves (*a*) and (*b*) of Fig. 3, at about 1 mm. below its length in the body, the early tension decrease was just visible and the tension began to increase at about 10 msec. after the stimulus. There was no early tension decrease at any muscle length below this, but the time at which a positive tension developed remained constant at about 10 msec. after the stimulus, until at about 6 mm. below the

length in the body the onset of tension was delayed and its rise slowed because the contractile portion of the muscle did not remain sufficiently short at rest to avoid initial slack.

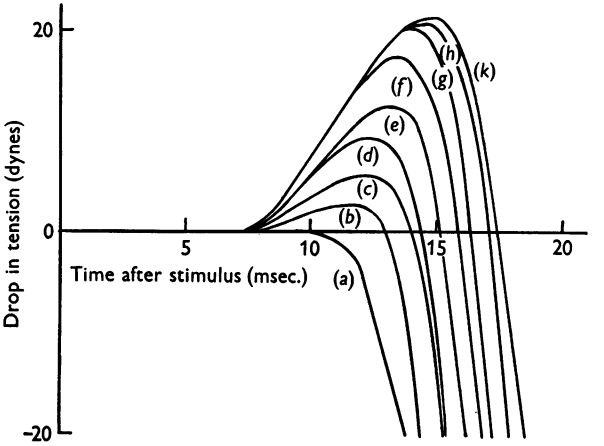

Fig. 3. Early tension changes during isometric twitches of frog sartorius at 0° C. at various muscle lengths, in mm.: (*a*) 27, (*b*) 30, (*c*) 31, (*d*) 32, (*e*) 33, (*f*) 34, (*g*) 35, (*h*) 36, (*k*) 37. Length in body 30·5 mm., weight 75 mg.

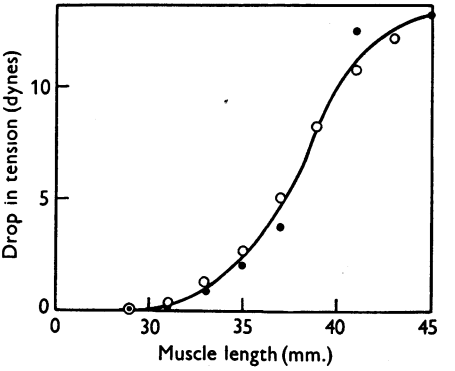

Fig. 4. Total tension fall in a cat tenuissimus muscle during the early phases of isometric twitches. Records were made at a series of increasing lengths (circles) followed by a set at decreasing lengths (dots). Length in body about 40 mm.

Early relaxation of tension occurred also in mammalian muscle. The latent period was about 1 msec. for both cat tenuissimus and for rat diaphragm muscle at 37° C. Fig. 4 shows the extent of the early tension fall in cat muscle at a series of initial lengths.

DISCUSSION

The initial relaxation of tension of a muscle is about 1/1000 of the maximum tension in later contraction. Although it was first noticed by Rauh (1922) and confirmed by other authors, little attention was paid to it. Sandow (1944),

however, using the piezo-electric technique, has further studied this phenomenon and developed a theory to explain it.

This relaxation appears to be a genuine physiological effect, but too little is known about events in the early stage of contraction to permit any definite explanation of it in biophysical or biochemical terms. The present experiments repeat some of those by Sandow on frog muscle but at a lower temperature, 0° C., and extend them to a variety of other muscles. They confirm Sandow (1946, 1947) and lend no support to the theory of Schoepfle & Gilson (1945) that the early relaxation is an artefact produced in the propagation of a tension wave through a viscous elastic medium, since the early relaxation was still visible when the tension was recorded at the point of stimulation.

The sequence of events following a stimulus is discussed in two new papers by Hill: one of these deals with the heat production (Hill, 1950*a*), and the other with the rigidity changes (Hill, 1950*b*). In frog muscle at 0° C. activation heat and rigidity changes are evident by 10 msec., halfway through the latent period as measured by the usual tension lever method. At room temperature the early relaxation appears at the same time as the first change in transparency (Hill, D. K., 1949).

Hill has suggested that the heat of activation is a by-product of the chemical reactions accompanying the sudden change from rest to activity. Probably the early relaxation also has the same origin. Sandow (1945*a*, *b*) relates the phenomenon to the hypothetical formation of a myosin-adenosinetriphosphate complex occurring before the contraction of myosin and the formation of adenosinediphosphate. The form of the tension-time curve is then assumed by him to be the sum of two or more exponential curves. Sandow's hypothesis may be correct, but there is no specific evidence either for or against it, and it is probably better at present to keep to the facts.

The possibility that the relaxation occurs through the expansion of the muscle fibres by heating can be dismissed, even if the heating were not far too small. Water at 0° C.—and this is by far the greatest constituent of muscle—does not expand but shrinks when heated, so this could not explain the relaxation.

SUMMARY

1. Tension changes were measured with a piezo-electric crystal during the early phases of isometric twitches.

2. Early relaxation of tension occurred in frog and toad sartorius at 0° C., in dogfish muscle at 18° C., and in cat tenuissimus and rat diaphragm at 37° C.

3. The latent period for tension change was 7 msec. for frog and 9·5 msec. for toad muscle, both at 0° C.; 1·6 msec. for dogfish muscle at 18° C.; and about 1 msec. for cat tenuissimus and rat diaphragm at 37° C.

4. Muscle length was reduced in steps of 1 mm. The early relaxation diminished progressively to zero, and the moment at which the tension curve recrossed its baseline became progressively earlier up to a limiting value of 10 msec. for frog muscle at 0° C.

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