ON THE RELATION BETWEEN FORCE AND SHORTENING DURING MUSCLE TWITCH

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During the contraction phase of isotonic twitch there must be the change of muscle force. When initial acceleration was augmented by using heavy load or inertia lever\(^1,2,3\), the muscle tension developed far bigger than the load and the condition of twitch was not ‘isotonic’ in real meaning. As far as a single twitch was concerned, the change of force should not be neglected. In the previous study\(^1\), it was concluded that the initial shortening, which means the shortening performed during the initial acceleration, was independent of inertia or equivalent mass of the lever system within a considerably wide range. On the contrary, the secondary shortening (or excess shortening), which means the shortening performed during the slowing phase of contraction, was decreased with the increase of equivalent mass. In the present paper further investigations on the initial and secondary shortenings especially under after-load condition or under the control of shortening velocity were carried out.

METHODS

The material used was the sartorius muscle of the frog (Rana nigromaculata) or the toad (Bufo vulgaris). Three types of lever system are shown in Fig. 1. The inertia lever was made of light wood (40×1×0.3 cm) and the moment of inertia was controlled by changing the weight of counter rider (Fig. 1, O) or the distance between the rider and the center of the lever. The isotonic lever was made of straw as light as possible. In type B, the inertia lever is connected with small thread to the isotonic lever, so as to slacken when the former moves quicker than the latter. One end of the muscle was fixed to the hook of the lever and the other end was connected to the mechano-electronic transducer (RCA 5734) with thread and insulator. The displacement of the lever was recorded by photo-tube mechanograph, namely the light-sector attached on the lever cut the light streaming through the slit towards the phototube. Tension and displacement were recorded simultaneously by using Yokogawa’s magnetic oscillograph.

In order to control the velocity of contraction, the speed-controller, originally deviced by BUCHTHAL\(^4\), detailld in Fig. 2, was used. The upward movement of

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Received for publication May 8, 1960.

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FIG. 1. Three types of lever system.

Type A: inertia lever,
Type B: isotonic lever with inertia lever,
Type C: isotonic lever with velocity controller,

L: load,
M: muscle,
O: counter balance,
P: velocity controller,
R: mechano-electronic transducer
S: stimulating electrode,
St₁, St₂: stopper,
T: light screening paper

FIG. 2. Diagram of the velocity controller.

Circulating liquid is glycerol and water (1:1). Arrows show the direction of flow. The velocity of flow is adjusted by the revolution number of motor.
piston (Fig. 2) was released through electric relay after some time-delay from the opening of camera shutter. This delay was adjusted so as to synchronize the starting of piston movement with that of the lever which was pulled up by the muscle. The tip of piston was shaped in hook and the piston did not push the lever, but it could limit the maximum velocity of contraction. Stimulus was the supra-maximal square pulse with duration of 5 msec and cathode was applied to the pelvic end of the muscle.

RESULTS

1. The initial shortening in the twitch of constant velocity; At first, the maximum velocity of contraction was limited by the piston of velocity controller (Fig. 1, C). In Fig. 3, four pairs of tension and shortening curves are shown. Each pair was recorded simultaneously. The maximum velocity of shortening was 7.2 cm/sec (Fig. 3, A), 5.0 cm/sec (Fig. 3, B), 3.8 cm/sec (Fig. 3, C) and 2.5 cm/sec (Fig. 3, D) respectively. And the amount of initial shortening is marked with arrow in each figure. Under the condition of constant velocity, no inflecting point was observed in the shortening curve, but the initial shortening was defined as the amount of shortening at the moment when the initial development of tension decreased to the level of resting tension (i.e. load level). The amount of initial shortening (Si) was usually 10-12% of initial length of the muscle. The initial development of tension becomes higher and longer when the velocity of shortening is limited slower, but the amount of initial shortening is almost unchanged independently of the time course of tension development (Fig. 3, A, B and C). When the velocity of contraction was limited too slow for muscle to shorten as much as Si in normal twitch, the tension curve did not fall back to the resting level or did not cross it at least within the contraction time (Fig. 3, D). The contraction time of the frog muscle was about 9/100 sec at 20°C and Si in normal twitch was about 3 mm. Therefore, the lower limit of the velocity for completion of initial shortening should be 3.5 cm/sec. Virtually when the velocity was depressed slower than 3.5 cm/sec, the total shortening became less than Si in normal twitch and the tension curve did not cross the level of resting tension (Fig. 3, D).

The similar result is shown in Fig. 4, in which four pairs of records are traced on the same figure. The amount of initial shortening is independent of the velocity of contraction, provided that the shortening was finished within the contraction time. In this experiment the piston was fixed to the end of the lever and the lever was pushed upwards after the initial shortening. This method has an advantage to be able to decide the crossing point of the tension curve and the level of resting tension precisely, because the tension curve falls down to zero after the initial shortening. In this case the shortening curve after the initial shortening shows the movement of piston and does not mean the excess shorten-
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Fig. 3. Tension and shortening in constant velocity twitch.
frog sartorius muscle, 21°C, load 0.5g, top: tension, middle: shortening, bottom: stimulus. Shortening velocity was 7.2 cm/sec (A), 5.0 cm/sec (B), 3.8 cm/sec (C) and 2.5 cm/sec (D). Si: initial shortening, time: 1/100 sec. (see text)

ing of the muscle. The amount of initial shortening decreased also in this case when the velocity of contraction was limited under 3.5 cm/sec.

2. Preceded starting of the velocity controller; If the time delay (i.e. latency) for piston movement was little less than that for muscle movement, the lever pursued the piston and collided with it in the half way of contraction and continued to contract thereafter with the velocity limited by the piston (Fig. 5, B). When the piston began to move much earlier, the lever did not collide with the piston until the contraction was almost over (Fig. 5, A). It is striking that in both cases the amount of initial shortening (the length indicated with arrows in Fig. 5) does not alter, in spite of the great difference of the time course of tension development. It is not necessary, therefore, to adjust the time delay of the piston strictly to the start of the twitch movement.

3. After-load experiment; The inertia lever as shown in Fig. 1, A was used. The stop (Fig. 1, St1) under the lever hindered the muscle to be lengthened by heavy load so as to keep the initial length of the muscle unchanged throughout a series of experiment. One of the results is shown in Fig. 6. A pair of curves 1 and 1' in Fig. 6 are the traces of tension and shortening curve loaded with 4 g. When the load increased, the tension development became greater and the shortening became slower (Fig. 6, 1-1', 2-2', 3-3'). The amount of initial short-
Fig. 4. Tension and shortening in constant velocity twitch.

frog sartorius muscle, 17°C, load 1 g, RT: resting tension, S: stimulus, Si: initial shortening. A pair of curves 1 and 1' and so on were recorded simultaneously. Shortening velocity was 7.6 cm/sec (1'), 7.1 cm/sec (2'), 4.9 cm/sec (3') and 2.8 cm/sec (4'). time: 1/100 sec. (see text)

Fig. 5. Tension and shortening in constant velocity twitch.

frog sartorius muscle, 21°C, load 0.5 g, top: tension, middle: shortening, bottom: stimulus. The amount of initial shortening is shown by arrow. time: 1/100 sec. (see text)

Fig. 6. Tension and shortening in after-load twitch.

toad sartorius muscle, 14°C, RT: resting tension (2 g), Si: initial shortening. A pair of curves 1 and 1' and so on were recorded simultaneously. Load was 4 g (1), 8 g (2), 20 g (3) and 25 g (4). Equivalent mass of inertia lever was 100 g. time: 1/100 sec. (see text)
enie (Fig. 6, Si), however, remained unchanged. In Fig. 6, 4-4’, the load was 20 g and muscle could not contract as much as Si. In this case the tension curve did not fall back to the level of resting tension during the whole course of the twitch. The amount of initial shortening does not depend on the load, provided with the same initial length of the resting muscle.

4. Arrested twitch and secondary shortening; The isotonic lever with inertia lever as shown in Fig. 1, B was used. In this system the total or secondary shortening in inertia twitch was observed easily, because after initial shortening the thread between two levers slackened. When the shortening was arrested by the stop (St2) at the various height below the maximum twitch height, the new tension development corresponded with the plateau in the shortening curve was observed even at the higher arrest than the level of initial shortening (Fig. 7, Si). Namely the secondary shortening as well as the initial shortening is an active process and not a passive ejection by the lever system.

**Fig. 7.** Tension and shortening in arrested twitch.

*toad sartorius muscle, 13°C, load 2 g, S: stimulus, Si: initial shortening. A pair of curves 1 and 1' and so on were recorded simultaneously. time: 1/100 sec. (see text)*

In Fig. 8 the relation between equivalent mass and initial shortening (white dot) or total shortening (black dot) is shown. The difference of both shortenings is secondary shortening. The amount of initial shortening (Si) is independent of equivalent mass, and where the muscle can not contract more than Si, in other

**Fig. 8.** Equivalent mass and initial shortening or total shortening.

*toad sartorius muscle, 19°C, white dot: initial shortening, black dot: total shortening. The amount of initial shortening (Si) is independent of equivalent mass as far as muscle can contract more than Si.*
words the total shortening is less than $S_i$, tension curve does not return to its resting value until the end of contraction and secondary shortening can not be observed.

**DISCUSSION**

It was concluded in the previous paper\textsuperscript{1} that the amount of initial shortening was a function of the initial length of the muscle and it did not depend on the equivalent mass of the lever system. Furthermore, it was observed in the present study that the amount of initial shortening did not depend on the velocity of contraction or the load, provided that the initial shortening finished its whole process within the contraction time of a twitch. At the instant when the initial tension development fell back to the level of resting tension, the length of the elastic element\textsuperscript{3} should be the same as the length in resting state before stimulation. Consequently, the amount of shortening at that instant, (i.e. the initial shortening), means real active shortening of the contractile element. The independency of the initial shortening from the load, inertia and velocity of contraction would be explained as that the contractile element can shorten as much as certain amount which depends only on the initial length or geometrical arrangement of atoms of contractile protein in resting state and does not depend on the external resistance for shortening.

The initial shortening is not due to the passive pulling of elastic element stretched by the contractile element which shortens previously by certain amount. Because the velocity of initial shortening is much larger than the estimated value of elastic pulling especially under heavy inertia\textsuperscript{1}. Recently SANDOW\textsuperscript{5} suggested that there might be two different active states in contraction of skeletal muscle because the hump was observed in differentiated tension curve of twitch or tetanus. Then it is plausible that there are two different contractile elements in muscle, one is stronger than the other and takes its part in the initial shortening and does shorten by a constant amount despite the external resistance. It would be suggestive that there are two kinds of theory about the contractile mechanism of skeletal muscle; one is folding of actomyosin or the transmutation theory\textsuperscript{4} and the other is sliding model\textsuperscript{6,7}.

Another explanation is also possible that during the initial shortening almost all contractile units are in active state and only little or no units are relaxing, but during the secondary shortening the number of relaxing units are gradually increasing. Four this explanation, however, the relaxation of contractile units must be postulated to be initiated by a spatial factor of the completion of the initial shortening and not by a time factor from the stimulus.
SUMMARY

1. The relation between tension and shortening during twitch of frog's or toad's sartorius muscle were investigated.
2. When the velocity of contraction was controlled by the velocity controller or the inertia lever, the amount of initial shortening (Si) did not change in spite of the change in time course of tension development, as far as the velocity was not so slow that the initial shortening could not be finished within the contraction time.
3. In the after-load experiment under the same initial length, the amount of Si did not depend on the weight of load as far as the initial shortening was finished within the contraction time.
4. The secondary shortening is also active one, because when the twitch was arrested during the secondary shortening, new active tension developed.
5. When the velocity of contraction was too slow to shorten as much as Si within the contraction time, no secondary shortening was observed.

This study was supported in part by research grant GA BMR-5934 from the Rockefeller Foundation.

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