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CHANGE IN STIFFNESS OF MAMMALIAN MUSCLE FIBERS CAUSED BY STRETCH

YOSHIFUSA ITO AND OSAMU OYAMA

2nd Department of Physiology, Nagoya University School of Medicine
(Director: Prof. Ryo Ito)

ABSTRACT

Change in stiffness of mammalian muscle fibers caused by stretch (conditioning stretch) was investigated. The stiffness was defined as initial rise of tension versus time at the beginning of linear stretch (test stretch) of equilibrated muscle. Effects of a sinusoidal conditioning stretch on the stiffness depended on the amplitude of the oscillation but were almost independent of the duration of the conditioning. Against a rapid decrease in stiffness caused by stretch, the recovery of stiffness during maintenance at a constant length was gradual. It has been established that a hump of the muscle tension usually observed at the beginning of linear stretch is caused by the initial great stiffness of muscle fibers and the following rapid decrease of it.

INTRODUCTION

The mechanical properties of muscles have been represented by a simple model consisting of a dashpot and a spring, or of a dashpot and two springs[1)2)3)]. This model can be referred to as a linear model because of the linear properties of their elements and is valid to express qualitatively the relation between tension and length of muscle when it is stretched. Tension development during the dynamic phase of muscle stretch, and tension fall during maintenance at the extended level after the stretch, or tension change during sinusoidal stretch are approximately simulated by the model. Frequency of impulse discharges from a spindle receptor situated in such a muscle can also be analysed on the basis of this model[4)].

However, the actual length-tension relation of muscles differs from that of the linear model. A hump in the tension curve can be often observed at the beginning of linear stretch of muscles. The decay of tension after the end of linear stretch also differs from that of a linear model. During the dynamic phase of muscle stretch, the muscle tension increases acceleratively except at the beginning of the stretch, but a decelerative increase is expected in a linear model. These discrepancies have been discussed in the report on the response of muscle spindle discharges[4)] and on the behavior of glycerinated

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伊藤嘉房, 尾山 修
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muscle fibers[5].

The appearance of the hump mentioned above implies that muscles are stiff when they are sustained at a constant length for a long period and are softened by stretch. The present experiments are designed to analyse the non-linear behavior of muscles, defining the stiffness as initial rise of tension versus time in equilibrated muscle fibers at the beginning of linear stretch (5 mm/sec). Analysis of this nature of muscles is important to study the response of muscle spindles. Another meaning of the analysis exists in the field of physiology of physical excercise. Preliminary movements before game should soften muscles in the whole body.

METHOD

Psoas muscles were excised from ten adult rats anaesthetized with ether, and were torn into bundles of fibers with transverse areas of about 2 mm^2. Each bundle was mounted on the apparatus in such a way that its effective length was 3 cm, and bathed in Ringer solution. The Ringer solution was of the following composition (mM/l): NaCl 154, KCl 5.6, $NaHCO_3$ 2.9, $CaCl_2$ 2.3, NaH_2PO_4 1.9. The experiments were performed at room temperatures of 18–22°C.

The technique and the apparatus were similar to those used by F. Ito[6]. The apparatus is shown in Fig. 1. One end of the bundle was fixed on a perspex hook which was attached to a transducer (T of Fig. 1, vacuum tube RCA 5734). The other end of the bundle was fixed on a stretcher which was a lever (L) of a pen motor (PM). The pen motor was driven by an output current of an analog computer (HITAC 505 T). The movement of the lever was monitored as follows; the middle part of it was blackened with paint and moved over a slit, and its movement was measured by the amount of light passing through the slit with a phototransistor (PT). Length and tension were displayed on beams of a dual cathode ray oscilloscope and recorded on film.

In the present experiments the bundle of muscle fibers was stretched twice in each trial; the first was conditioning stretch and the second was

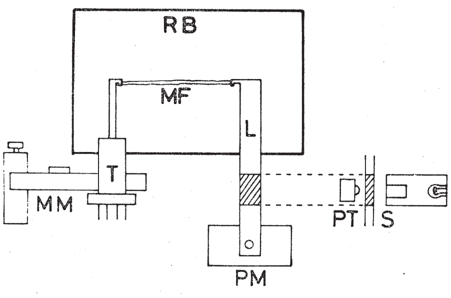

FIG. 1. Experimental arrangement. The muscle fiber bundle (MF) was immersed in Ringer's bath (RB). One end of the bundle was fixed to a hook attached to the anodal pin of RCA 5734 (T) which was mounted on a micrometer (MM). The other end was fixed to a lever (L) of a pen moter (PM). The middle part of the lever which was blackened moved over a slit (S), and its movement was measured by the amount of light passing through the slit with a phototransistor (PT).

test one. The test strech was linear throughout the present experiments. The conditioning stretch was sinusoidal or linear. The sinusoidal stretch was followed by damping so as to equilibrate the intrinsic states of muscle fibers. Duration of sustentation between conditioning and test stretches was changed. Duration and magnitude of conditioning stretch were also changed variously.

RESULTS

I. Sinusoidal conditioning stretch

The effects of sinusoidal conditioning stretch on the stiffness of muscle fiber bundles are illustrated in Figs. 2, 3 and 4. These figures show graphically the stiffness which has been defined in the introduction, where dots are experimental data and solid lines are obtained from empirical formulas (1),

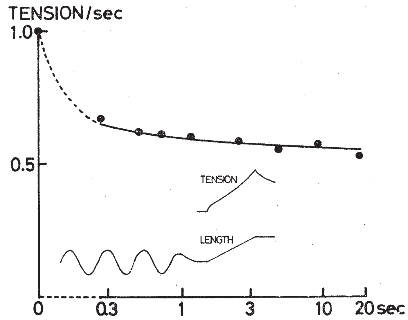

FIG. 2. Effect of change in duration of conditioning sinusoidal stretch upon the stiffness of muscle fibers. The stiffness after a long sustentation at the resting length *in situ* is taken as unity of ordinate. The conditioning stretch was followed bv critical damping. Abscissa shows sum of the duration of sinusoidal stretch and the duration (see text) of damping oscillation. Dots are experimental data and solid line obtained from the empirical formula (1) in the discussion. Dotted line is drawn arbitrarily so as to combine smoothly the solid line and the control. Inset shows patterns of stretch and tension change during test stretch as functions of time. The frequency of conditioning stretch was 5 cycle/sec and the amplitude was 1 mm. The interval between the initiations of the damping and the test stretches was fixed at 0.3 sec.

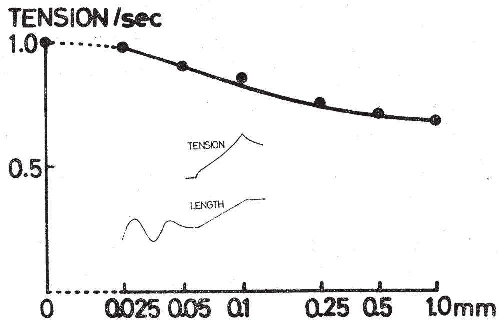

FIG. 3. Effect of change in amplitude of conditioning sinusoidal stretch upon the stiffness of muscle fibers. Unity of ordinate is determined in the same way as in Fig. 2 The conditioning stretch was followed by the critical damping. The residual of the intervals between the initiations of the damping and the test stretch subtracted by the duration of damping oscillation was 0.13 sec. Dots are experimental data and solid line obtained from the empirical formula (2) in discussion. Dotted line is drawn arbitrarily smoothly from the control to the solid line. Inset is the same as in Fig. 2. The frequency of conditioning stretch was 5 cycle/sec and sum of duration of sinusoidal stretch and the converted duration of damping oscillation was 0.4 sec.

(2) and (3) in the discussion. Insets in the figures show patterns of conditioning and test stretches, and of tension change during the test stretch. The bundles were initially extended to the resting length *in situ*. The stiffness after a long maintenance at the resting length *in situ* was taken as unity of ordinate in each graph of these figures.

At first, the effects of change in the duration of conditioning stretch were investigated. One of the experimental results is illustrated in Fig. 2, where the duration of damping oscillation which is added to the duration of sinusoidal stretch is expressed as such that the total value of movement during the damping oscillation is equal to the product of average movement during sinusoidal stretch by the duration of damping and the sum of the durations is taken as the duration of conditioning stretch. Against our expectation that the stiffness of muscle should decay approximately exponentially during conditioning stretch, it decayed more rapidly at the initial part of the conditioning stretch and more slowly during continued stretch. It may be probable to say that the effect of the conditioning sinusoidal stretch of a definite amplitude on muscle tension is somewhat all-or-none in nature.

On the other hand, the decrease in stiffness with increase in amplitude of conditioning stretch was gradual. The effects of change in amplitude of conditioning stretch on the change in stiffness of muscle fibers are shown in Fig. 3. When the amplitude was smaller than 0.02 mm, the decay of stiffness was almost indetectable throughout all trials in this experiment. The gradual decay of stiffness was observed as the amplitude of conditioning stretch was increased beyond 0.03 mm. From the results shown in Figs. 2 and 3, it can be concluded that an essential factor which decides the degree of softening of muscle fibers is not the duration of conditioning stretch but its magnitude.

The time course of recovery of the stiffness during sustentation at resting length *in situ* after conditioning stretch was investigated. The results of a series of trials are shown in Fig. 4, in which the duration of sustentation is converted on the same basis as in Fig. 2; that is, the residual of interval between initiations of the damping and the test stretches subtracted by the duration of the damping osclilation was taken as the duration of sustentation in the figure. As shown in it, the recovery of stiffness of muscle fibers is slower when compared with the rapid decay of that during the conditioning stretch. If the decay of stiffness of muscle fibers may be explained by a sort of destruction of the structure, it can be said that essential features of the stiffness change are the rapid destruction and the slow recovery of the structure.

II. Linear conditioning stretch

The results of a series of trials are shown in Fig. 5. Like as in the case of sinusoidal stretch, the tension rise at the beginning of the test stretch

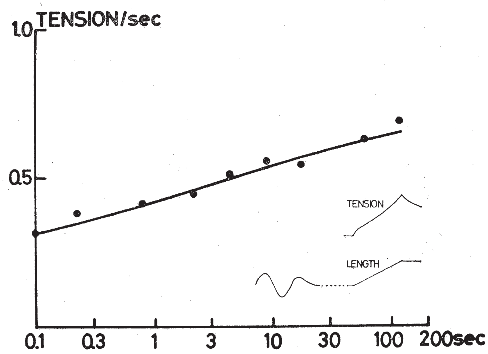

FIG. 4. Effect of change in duration of sustentation after conditioning stretch upon the stiffness of muscle fibers. Unity of ordinate was determined in the same way as in Fig. 2. Conditioning stretch was followed by critical damping. Abscissa shows the residual of the interval between the initiations of the damping and the test stretch subtracted by the duration of the damping oscillation. Dots are experimental data and solid line obtained from the empirical formula (3) in discussion. Inset is the same as in Fig. 2. The amplitude of conditioning stretch was 1 mm, the duration of sinusiodal stretch was 1 sec and the freqency was 5 cycle/sec.

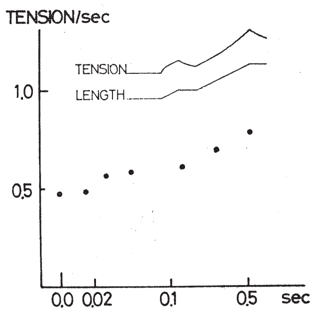

FIG. 5. Effect of change in duration of sustentation at the extended length after linear conditioning stretch on the tension rise at the beginning of test stretch. Unity of ordinate is determined in the same way as in Fig. 2. Abscissa shows the duration of the sustentation. Inset shows patterns of the stretch and the tension change during the stretch as functions of time. In this series of trials, the size and the velocity of the conditioning stretch were 0.5 mm and 5 mm/sec respectively.

increased, as the interval beween conditioning and test stretches increased. It was noticed that the tension of muscle fibers decayed continuously during the maintenance of them at extended level after the conditioning stretch. Therefore, the tension rise at the beginning of the test stretch is not the stiffness defined in the present paper, because the muscle fibers are not equibrated before the test stretch. It seems that non linear viscoelastic properties of muscle fibers may influence complicatedly the increase in the tension rise versus time in this case. Nevertheless, it is possible to conclude from these results that muscle fibers are softened rapidly by linear conditioning stretch and stiffened by maintenance at a constant length, because the changes in the tension rise versus time in this experiment are conspicuous.

DISCUSSION

If the viscoelastic properties of muscles are simulated by a model consisting of viscous and elastic elements, whose coefficients are constant or vary only with velocity or/and size of stretch of the elements and not with time, the rate of tension rise at the beginning of muscle stretch from its arbitrary definite equilibrated state, defined as the stiffness in this report, should not be changed by a preceding stretch. However, the stiffness depends actually on the magnitude of the preceding stretch and the duration of maintenance at a constant length. Consequently, it may be concluded with some degree of confidence that at least one of the viscoelastic coefficients of muscle is a function of velocity or/and size of muscle stretch and time.

In the present experiments, it was observed that conditioning stretch always softened muscle fibers and maintenance at a constant length stiffened them. The time course of decay of the stiffness during the conditioning strech, the dependency of the stiffness on the amplitude of the conditioning stretch and the time course of recovery of the stiffness during maintenance at a constant length can be represented by the following empirical formulas, (1), (2) and (3) respectively,

$$S_T = 0.500 + 0.102(T + 0.0014)^{-0.24} \tag{1}$$

$$S_A = 1 - 0.34 \exp(-0.0022/A) \tag{2}$$

and

$$S_t = 1 - 0.58(t + 0.13)^{-0.106}, \tag{3}$$

where S_T and S_A are the stiffness of muscles expressed as functions of the duration and the amplitude of conditioning stretch respectively, S_t the stiffness of muscles expressed as a function of the duration of sustentation, A the size of stretch taking the resting length *in situ* as unity, and T the duration of conditioning sinusoidal stretch, t the duration of maintaining at a constant length taking one second as unity. In the formular expressions, the stiffness after a long maintenance at the resting length *in situ* was taken as unity. The curves obtained from these formulas are drawn in Figs. (1), (2) and (3).

The formula (1) represents that the effect of conditioning stretch of a definite amplitude is somewhat all-or-none; that is, even a shock of damped oscillation softens muscle fibers remarkably and a long continuation of conditioning stretch produces only a little effect. We get $\left(\frac{\partial S_A}{\partial A}\right)_{A=0} = 0$ from the equation (2). This fact implies that the effect of the conditioning stretch is very small when its amplitude is smaller than a certain value (0.06% of the resting length *in situ*). If the muscle fibers are extended by a slip between the actin filaments and myosin filaments, the slip may be less than 6 Å when the amplitude of conditioning stretch is of such a small value. The value is comparable with the length of a hydrogen bond. These facts seem to suggest that the stiffness of muscle fibers is related to the interactions between actin and myosin filaments.

If the viscoelastic coefficients of muscle fibers do not vary with time, the stiffness of muscle fibers can be clearly separated into two parts, one of which belongs to viscosity and the other to elasticity. However, the coefficients vary with time so that the separation is impossible and the change in stiffness can be expressed as the change in elastic coefficients as well as in viscous coefficients or in both with time. Because of this ambiguity, we do not dare to express the change in stiffness as the change in viscosity or elasticity.

The hump of the muscle tension observed at the begining of muscle stretch after long sustentation at a constant length can be explained conclusively by the initial stiffness of muscle and the following softening during stretch.

SUMMARY

1) Stiffness of muscle fibers after sinusoidal or linear conditioning stretch was detected by the amount of tension development at the begining of linear test stretch, in the psoas muscle fibers of the rat.

2) The stiffness always decayed rapidly during conditioning stretch, and recovered slowly during sustentation of the muscle at a constant length.

3) The stiffness decreased gradually, as the amplitude of conditioning stretch increased over 0.1% of the resting length *in situ*.

4) Experimental formulas to represent these results were derived.

5) It seems that a hump of the muscle tension at the beginning of linear stretch is caused by the initial great stiffness of muscle fibers and the following rapid decrease of it.

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