Stress relaxation in muscle

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Tension decay following stretch (stress relaxation) has been studied in resting long-fibred smooth and striated muscles. In both types of muscle, tension decays rapidly at first and then more slowly; the decay curve can be resolved into two exponential components, neither of which is significantly affected by changes in temperature or speed of stretch. It is shown that the half-times of fast and slow components of tension decay are related to the intrinsic speed of muscle.

A model is proposed which imitates the properties of preshortened resting muscle at lengths where it shows negligible resting tension.

INTRODUCTION

The tension decay in viscous-elastic materials following stretch is called stress relaxation. This phenomenon has previously been studied in muscle, and complicated analyses were found to be necessary in order to describe the results in terms of combinations of springs and dashpots (Buchthal & Kaiser 1951; Zatzman, Stacy, Randall & Eberstein 1954). In all these studies the muscles were stretched to lengths at which final tension did not decay to zero. The object of the present work was to investigate stress relaxation at muscle lengths where final tension is negligible. Under such conditions only the contractile and series elastic components are involved (Hill 1950a) and analysis of the decay proves to be surprisingly simple.

METHODS

The following muscle preparations have been used: sartorius of toad (*Bufo bufo*), iliofibularis of tortoise, pharynx retractor of the snail *Helix pomatia* and strips from the smooth posterior adductors of *Mytilus edulis*, *Pinna fragilis* (fast part), and from the striated portion of *Pecten's* adductor. All these muscles are long-fibred, the fibres running at least half the length of the muscles. The dissection of the snail muscle has been described by Ramsay (1940) and that of the lamellibranch muscles by Abbott & Lowy (1956a).

The *Helix* muscle was bathed in a solution containing per litre 3·5 g NaCl, 0·15 g KCl, 0·5 g $CaCl_2$, 0·3 g $MgCl_2$ and 5 mg P to bring it to pH 7·5. Sea water was used for the lamellibranch muscles, and Ringer's solution, buffered at pH 7 with phosphate buffer containing 6 mg P/l., for toad and tortoise muscle.

A light jeweller's chain linked the muscle to an isometric lever. Tension was recorded photoelectrically and displayed on a cathode-ray tube.

For each type of muscle the relation was first determined between length and tension developed in response to tetanic stimulation (Abbott & Lowy 1953). The

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muscle was then shortened by stimulation to a length below that at which it develops maximum isometric tetanic tension, i.e. where resting tension is small (Abbott & Lowy 1956*b*). The muscle thus preshortened was stretched at constant speed by about 10 % of the length at which maximum isometric tension is exerted. For this a Levin–Wyman ergometer (Levin & Wyman 1927) was used. The final stretched length was also less than that at which appreciable resting tension appears. Tension was recorded throughout and after movement, and the effects on stress relaxation of variation in speed of stretch and temperature were investigated.

RESULTS

When a muscle preshortened as described is stretched and held at the new length, tension rises during the stretch by an amount depending on the speed and extent of stretch and then falls, at first rapidly, then more slowly. In all the muscles studied this tension decay could be expressed as the sum of two exponential curves. The tension decay, shown on a logarithmic scale, is illustrated in figure 1 for the *Helix* (figure 1*a*) and *Pinna* (figure 1*b*) muscles. An analysis of the time course into two exponential components for *Helix* is given in figure 2. The slow component was obtained from the slope of the linear portion of the decay curve; this was extrapolated back and the tension values subtracted from those in the earlier part of the decay curve to give the time course of the fast component. The
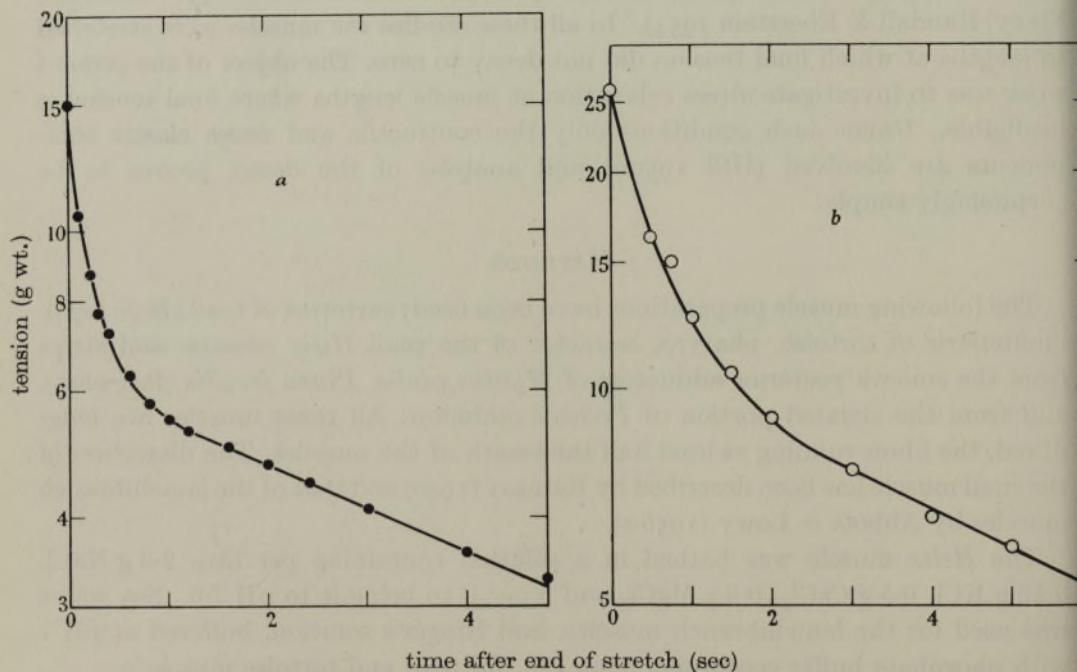

FIGURE 1. *a*, decay of tension in the resting retractor muscle of the snail's pharynx following stretch at constant speed. Tension plotted on a logarithmic scale. (Weight 35 mg; muscle stretched from 25 to 28 mm; temperature 14° C.) *b*, decay of tension in the posterior adductor muscle of *Pinna* (fast part). (Weight 55 mg; muscle stretched from 16 to 19 mm; temperature 14° C.)

two components are obviously exponential with time, and this can be characterized by the time taken for the tension to fall to half-value. Table 1 shows the half-times for the fast and slow components of the tension decay for all the muscles used.

External factors have only a very small effect on the two components. Thus, in *Helix* muscle, varying the speed of stretch over a range of 1 to 20 mm/s does not appreciably alter the time course of the decay curve (figure 3). It will be noted that at the slowest speed of stretch (1·5 mm/s) the rise of tension is considerably smaller
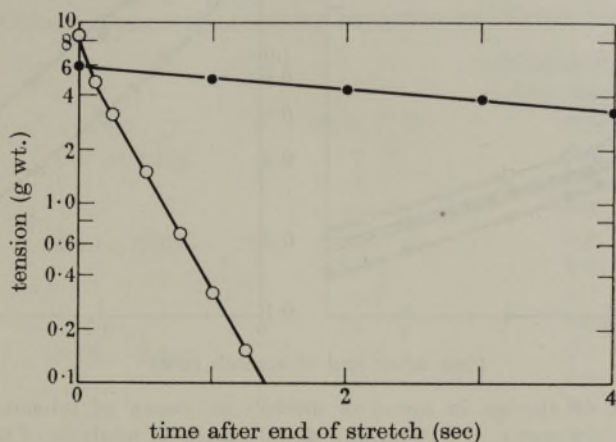

FIGURE 2. Analysis of the curve in figure 1*a* into two exponential components with half-times of 0·25 and 8 s for the fast and slow component respectively.

TABLE 1. VALUES FOR TIME COURSE OF TENSION DECAY FOLLOWING STRETCH OF
RESTING MUSCLE, AND FOR MAXIMUM SPEED OF SHORTENING DURING TETANIC
STIMULATION

| muscle | temperature | half-time of decay components (sec) | | maximum speed of shortening lengths/sec |
		fast	slow	
Mytilus	14° C	5·8	65	0·09*
Helix	14° C	0·3	7·7	0·17*
Pinna	14° C	0·27	6·0	0·3†
tortoise	20° C	0·23	6·2	0·33‡
Pecten	14° C	—	3·0	0·6‡
toad	10° C	0·02	1·5	1·5‡

* Abbott & Lowy (1953).
† Abbott & Lowy (1956*a*).
‡ Abbott & Lowy (unpublished results).

than at 6 mm/s, whereas about the same tension is produced during stretch at 6, 10 and 20 mm/s (figure 3*a*). Apparently the muscle can offer only a limited resistance to stretch. However, figure 3*b* shows that the decay rate of the fast component of tension fall is the same for all speeds of stretch, although the actual tension values differ for the different speeds of stretch. The constancy of the half-times for the slow component is evident from inspection of figure 3*a*.
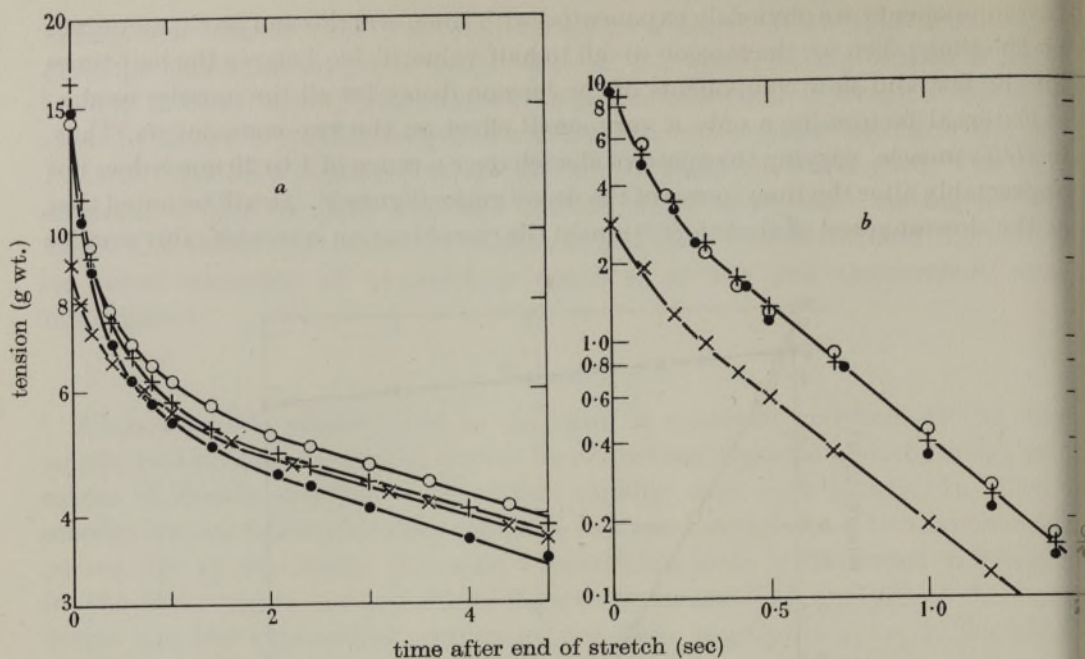
FIGURE 3. *a*, effect of change in speed of stretch on decay of tension in snail muscle. ×, 1·5 mm/s; ○, 6 mm/s; +, 10 mm/s; ●, 20 mm/s. *b*, analysis of the curves in *a* for the fast-tension decay component. Ordinate: difference between recorded tension and extrapolated slow-decay tension. The lower curve is the fast component of tension decay following stretch at the slowest speed.
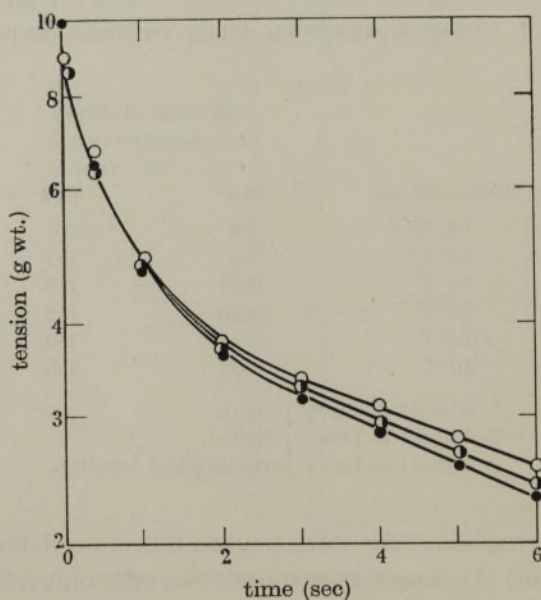

FIGURE 4. Effect of change in temperature on decay of tension in snail muscle following stretch at 10 mm/s. (Muscle weight 37 mg.) ●, 5 and 31° C; ○, 12·5° C; ◐, 18·5° C.

The effect of temperature on the tension decay curve was also found to be small. This agrees with Hill's (1950c) observations on tortoise muscle. In the case of the snail muscle, analysis shows that the decay rate of the fast component is nearly constant. The slow component, however, has a minimum decay rate value between 12 and 15° C (figure 4). Table 2 gives the results of three experiments which show that, though small, this variation with temperature is not negligible.

TABLE 2. THE EFFECT OF TEMPERATURE ON THE SLOW COMPONENT OF
TENSION DECAY FOLLOWING STRETCH OF *HELIX* MUSCLE

date	temp. (° C)	half-time of decay of slow component (sec)
23 Nov. 1954	7	6·3
	12	8·5
	20	7·7
6 Dec. 1954	7	5·8
	11·5	8·4
	18·6	7·7
	31	6·6
13 Dec. 1954	5·8	6·1
	12	6·5
	15·4	9·5
	18	8·9
	22	6·5
	28·4	6·1

It was found that at whatever length the muscles were stretched the fast and slow components of the decay curve are always present. But at lengths where resting tension appears (Abbott & Lowy 1953, 1956b) the amount of the fast-decay component decreases with successive stretches at increasing lengths, and in the smooth muscles a third factor enters: a very slow 'slip' which continues over periods extending for days. At these longer lengths, in both smooth and striated muscles, that tension following stretch does not decay to zero; parallel elastic structures come into play and mask the mechanical response of the contractile elements.

DISCUSSION

Stress relaxation analysis clearly reveals the two-component nature of tension decay in striated and long-fibred smooth muscles—provided they are stretched within lengths where resting tension is negligible. Hill (1950a) has shown that at such lengths it is the resting contractile elements alone which produce the transient rise in tension accompanying stretch. There exists at present no information about the structures responsible for the fast and slow decay. It is of interest to note, however, that in any particular muscle the half-times of the fast and slow components are very different. Comparing the half-times over the whole range of muscles studied, there emerges a relation between the mechanical properties of the contractile elements at rest and the maximum speed at which the muscle can shorten during tetanic stimulation; the quicker the muscle the faster the decay

rates. Table 1 shows the collected values for the slow decay and the relation is illustrated in figure 5. A similar curve is obtained for the fast component. The correlation is reasonable, for the same contractile elements (although in different states) determine shortening speed during activity and rate of tension decay in stress relaxation.

From the decay curves it is also possible to derive a model which imitates the properties of resting muscle. A stress relaxation curve which contains two exponential components will be produced by the stress relaxation of two Maxwell elements in parallel (figure 6).
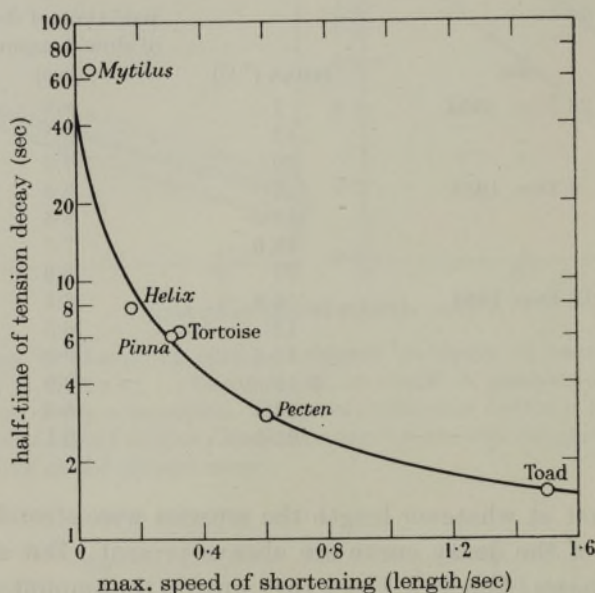

FIGURE 5. Half-times of slow-decay components of stress relaxation plotted against maximum speeds of shortening for a variety of muscles.

With this arrangement the tensions in the two arms summate. The tension P at time t during relaxation will then be given by the expression

$$P = \gamma \left\{ E_1 \exp \frac{(-E_1 t)}{\eta_1} + E_2 \exp \frac{(-E_2 t)}{\eta_2} \right\},$$

where E_1, E_2 are the elasticities of the springs, η_1, η_2 are the viscosities of the dashpots, and γ is the extent of stretch.

The summation of two exponentials with different time characteristics satisfies the stress relaxation curve of the muscles investigated.

The physical characteristics of the model in relation to muscle must be examined. The model necessitates (a) springs which obey Hooke's law, (b) Newtonian viscosity, and (c) the absence of parallel elastic structures, i.e. elements without dashpots. To what extent does muscle fulfil these requirements? Parallel elastic elements can be disregarded as the muscles were studied at lengths where resting tension is negligible. As for constant elasticity, it is well known that the tension-extension relation for muscle is not linear at small tensions. The curves usually shown are

for resting tension produced by parallel elastic structures. But in the present experiments the tension is borne by series elastic elements. Hill (1950b) has measured the tension-extension relation for these elements in vertebrate striated muscle, and the curve in his figure 1 demonstrates that above about 300 g/cm² there is in fact very little deviation from linearity. *Mytilus* smooth muscle gives a very similar tension-extension curve for the series elastic component (Abbott & Lowy, unpublished results). Now the speeds and amount of stretch which have been used in the present experiments were such that the tensions produced were well above those at which extension becomes a linear function of tension. The Hooke's law requirement is therefore satisfied.
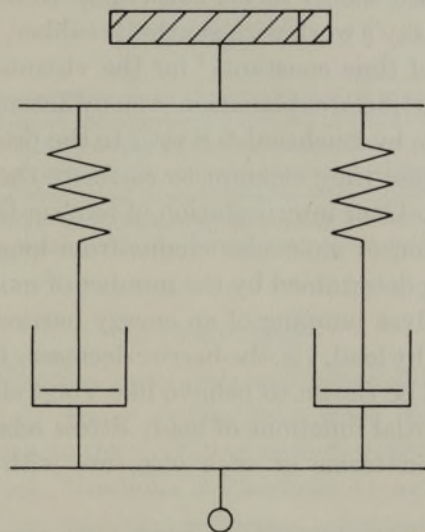

FIGURE 6. Model to illustrate stress relaxation in preshortened resting muscle.

At tensions below those for linearity, the tension increases in *Mytilus* muscle in an approximately exponential manner with increase in length (Abbott & Lowy, unpublished results). Analysis of stress relaxation for a viscous-elastic element under these conditions predicts an inverse relation between tension and time. Assume that tension T is related to length l of the element as $\ln T = k(1+c)$, where k and c are constants. This tension is applied across the dashpot which will begin to lengthen so that

$$T = -\eta \frac{\mathrm{d}l}{\mathrm{d}t}.$$

Therefore

$$T = -\frac{\eta}{kT} \frac{\mathrm{d}T}{\mathrm{d}t}.$$

Integrating,

$$\frac{l}{T} = \frac{k}{\eta} t + c'.$$

When, in muscle, decay of tension is followed for a sufficiently long time until values within the exponential range are reached, we do in fact find an inverse relation between tension and time.

Lastly, there is the requirement of Newtonian viscosity. The small effect of temperature on the tension decay following stretch shows that resting muscle does

not really possess simple, normal viscosity characteristics. No explanation can at present be offered for the broad minimum in decay rate of the slow component of the snail muscle. This may represent a single temperature effect or the inter-action of two opposing changes. In any event, the tension decay must somehow be related to molecular rearrangement within the resting contractile component as a result of flow under stress. It so happens that the characteristics of this phenomenon resemble those of viscous flow and are imitated by the model.

Considering that previous analyses of stress relaxation have used complicated box distributions of viscous-elastic elements (Zatzman *et al.* 1954), or long-short transmutations based on retardation-time spectra (Buchthal & Kaiser 1951), the simplicity of the proposed model seems surprising. Actually the first-mentioned analysis, based on Tobolsky's work with synthetic rubber, required such 'a relative unnatural distribution of time constants' for the viscous-elastic elements that it was considered a rather artificial explanation even by Zatzman and his collaborators.

The contribution made by Buchthal & Kaiser to the problem of stress relaxation is more important, because they attempt to correlate the properties of muscle at rest and during activity. Their interpretation of tension-length relations in muscle is based on transmutation of molecular chains from long to short configuration, length and tension being determined by the number of molecules in the two states. The transmutation involves jumping of an energy barrier, and it is assumed that this barrier is influenced by load, viz. the barrier decreases linearly as load increases. The molecular units can be shown to behave like Voigt elements with retardation times which are exponential functions of load. Stress relaxation in resting muscle can then be analyzed in terms of such elements with a wide distribution of retardation times.

The evidence for the above hypothesis comes from experiments with muscles at lengths where resting tension is appreciable. Buchthal & Kaiser hold that resting tension is mainly due to the contractile material itself and that tension in the parallel elastic structures plays only a small role. This represents a fundamental difference in approach from that adopted here. However, the present experiments show that by working within a range of lengths where resting tension is negligible, stress relaxation follows a simple time course, and this suggests that at the greater lengths the analysis is complicated as a result of resting tension.

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