SHORTENING VELOCITY OF COLLAGEN AND MUSCLE FIBERS(1)

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SUMMARY: The initial shortening velocity of collagen and glycerinated rabbit psoas fibers were studied as a function of applied force while immersed in media where an isothermal phase transition occurred. Quantitatively similar results were found for both kinds of fibers. In the two-phase region the Hill equation is obeyed with the same constants that have been found for stimulated muscle. It is suggested that a similar underlying mechanism governs contractility in these systems.

The dependence of the initial shortening velocity, v, of stimulated muscle on the applied force, f, can be described by a variety of empirical relations (2)(3). The most popular of these, due to A. V. Hill, (4) is expressed as

$$v = b(f_o - f)/(f+a) \qquad (1)$$

Here f_o is the isometric force and a and b are constants for a given muscle. Expressing Eq. (1) in terms of the maximum velocity, v_m, observed at zero force

$$\frac{v}{v_m} = \frac{k(1 - f/f_o)}{(k + f/f_o)} \qquad (2)$$

The quantity $k = a/f_o$ will be called the Hill constant. For all stimulated muscles k is in the range 0.11 to 0.55 and is found to be 0.25 to 0.33 for striated muscles. The theoretical derivations of Eq. (1) have been either phenomelogical in character (5)(6)(7) or based on the specific structural characteristics of striated muscle (8)(9)(10)(11).

The shortening of collagen, as well as other fibrous proteins, is known to accompany the highly cooperative crystal-liquid phase transition (12)(13)(14) which is also postulated to be involved in muscular contraction (15)(16)(17). Several velocity studies of collagen have been reported (18)(19) but no direct relation to Eq. (1) was apparent. We report here the results of shortening velocity experiments with collagen and glycerinated muscle fibers which can be analyzed in terms of Eq. (2).

The collagen experiments were conducted at 50°C in aqueous KCNS solutions of different concentrations. The relative length (at zero force) depends on the salt concentration as is shown in the insert of Fig. 1. The isothermal melting transition, as mani-

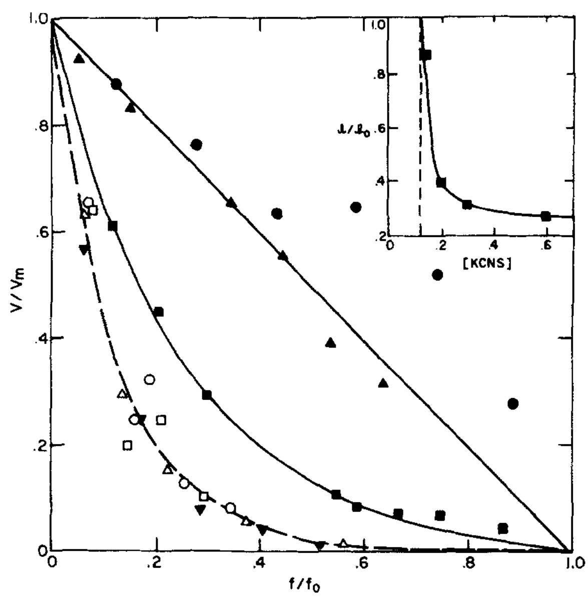

Fig. 1. Plot of ratio of shortening velocity at force f to maximum velocity against relative force for collagen in aqueous KCNS solutions. f_o is the isometric force. Dashed line encompasses data for 0.83M ▼, 0.70M △, 0.50M ○, 0.41M □. Solid curves for 0.30M ■, 0.27M ▲ and 0.20M ●. Insert, plot of relative length as function of KCNS concentration. Temperature 50°C.

fested by a large diminution of length with a small change in concentration, is readily apparent. The transformation is complete at concentrations equal to or greater than 0.4M KCNS. Also in this figure is a plot of the relative shortening velocity against the relative force. At the higher salt concentrations the results are concentration independent. The data in this concentration range cannot be fitted quantitatively to the Hill equation. However, at lower salt concentrations the shortening velocity depends on the applied force in the manner dictated by Eq. (2). The solid curve that is drawn for 0.3M KCNS represents Eq. (2) with k = 0.2. Therefore, under these conditions not only is the functional form of Hill's equation followed but the constant for collagen is about the same as for stimulated muscle. With a further reduction in salt concentration the Hill form is also obeyed but with a much larger constant. We find, therefore, that the Hill relation is not obeyed at salt concentrations where melting is complete at zero force. It is, however, followed when the final state lies in the transition or two-phase region. The value of the Hill constant depends on where in the two-phase region the experiments are conducted. A reexamination of the previous collagen data (18)(19) indicates that complete melting occurred at the salt concentrations used. Therefore, a quantitative identification with Hill's relation could not be made (18).

Shortening velocity studies of glycerinated rabbit psoas yield essentially the same pattern as collagen. A typical set of results obtained by varying the Ca^{++} concentration is shown in Fig. 2. Under these particular conditions the fiber is completely transformed at the highest Ca^{++} concentration shown while at the lowest concentration it does not regain its original length.*

*When the (Ca^{++}) is increased above 10^{-3}M, l/l_o also increases. This behavior results from a minimum in the isotrophic melting temperature similar to that found when the ATP concentration is fixed and the Mg^{++} concentration is varied (20).

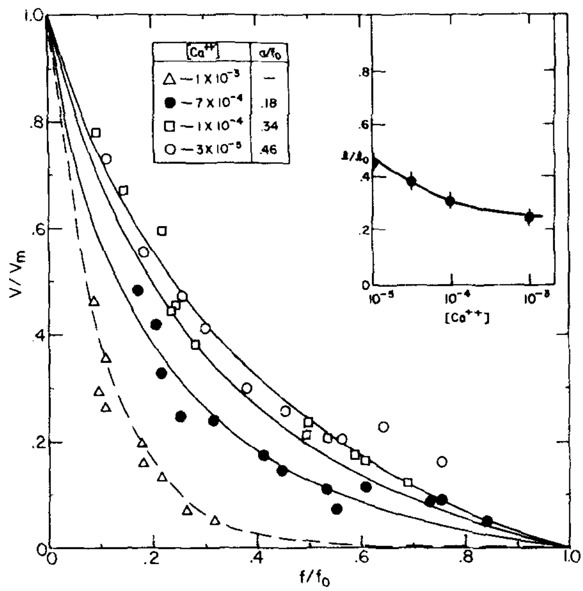

Fig. 2. Plot of ratio of shortening velocity at force f to maximum velocity against relative force for glycerinated rabbit psoas at different concentrations of Ca^{++}. f_o is the isometric force. Supernatant solution 5mM ATP, 10^{-2}M Mg^{++}. Solid line drawn in accordance with Eq. (2) with constants a/f_o indicated in figure. Insert, plot of relative length as function of Ca^{++} concentration. Temperature 25°C.

At the highest Ca^{++} concentration, corresponding to the complete transformation, Hill's relation is not followed but as the concentration is reduced the equation is quantitatively obeyed. Each of the solid lines through the data points are drawn according to Eq. (2). The appropriate constants are also indicated in the figure. The value of the constant increases as the transition region is traversed. Thus the experimental relations between the shortening velocity and applied force are virtually identical for collagen and glycerinated rabbit psoas when comparison is made in the same portions of the transition region.

The Hill constants are found to be similar to those for stimulated muscle.**

Previous reports for muscle models follow the same principles established in Fig. 2. For example, under one set of conditions Ulbrecht, Ulbrecht and Weber (22) found that Hill's equation, with k = 0.13, was valid for glycerinated rabbit psoas. For the same supernatant composition, however, this equation was not followed by the glycerinated adductor muscle of Anodonta (23). In this case the results are very similar to the dashed curve of Fig. 2. Wise, Rondinoni and Briggs (24) found that glycerinated rabbit psoas obeyed Hill's relation for two Ca^{++} concentrations, with constants that changed from 0.3 to 0.6. From their plot of the isometric force against Ca^{++} concentration it is seen that the concentration change corresponds to traversing the transition region in a similar manner to that shown in Fig. 2. Podolsky and Teichholz (25) report that for skinned muscle fibers the Hill constant of 0.23 is independent of $p_{Ca^{++}}$ in the range 5.5 to 6.5. Examination of their force-concentration curve (25)(26) shows that these concentrations correspond to the final portion of the transition region.

The identical shortening velocity-force relations for collagen and glycerinated rabbit psoas and their adherence to Hill's equation with constants similar to stimulated muscle strongly suggests a common contractile mechanism for all three systems. Since the shortening of collagen is the result of a melting transition (12)(13)(14) similar process can be attributed

**An isothermal phase transition can also be induced in glycerinated rabbit psoas by varying the ATP concentration while the Ca^{++} and Mg^{++} concentrations are held fixed (20)(21). The shortening velocity-force relations are very similar to those shown in Fig.2 when compared in terms of the isothermal transition.

to the muscle fibers. The behavior of these fibrous systems is consistent with their common major morphological feature. The thick filaments of striated muscle have all the structural characteristics of a fibrous protein. Therefore, it is not unexpected that they display contractile properties associated with this class of macromolecules.

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