Residual Force Enhancement after Stretch of Contracting Frog Single Muscle Fibers

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ABSTRACT Single fibers from the tibialis anterior muscle of Rana temporaria at 0.8-3.8°C were subjected to long tetani lasting up to 8 s. Stretch of the fiber early in the tetanus caused an enhancement of force above the isometric control level which decayed only slowly and stayed higher throughout the contraction. This residual enhancement was uninfluenced by velocity of stretch and occurred only on the descending limb of the length-tension curve. The absolute magnitude of the effect increased with sarcomere length to a maximum at ~2.9 μm and then declined. The phenomenon was further characterized by its dependence on the amplitude of stretch. The final force level reached after stretch was usually higher than the isometric force level corresponding to the starting length of the stretch. The possibility that the phenomenon was caused by nonuniformity of sarcomere length along the fiber was examined by (a) laser diffraction studies that showed sarcomere stretch at all locations and (b) studies of 9-10 segment lengths of ~0.6-0.7 mm along the entire fiber, which all elongated during stretch. Length-clamped segments showed residual force enhancement after stretch when compared with the tetanus produced by the same segment held at the short length as well as at the long length. It is concluded that residual force enhancement after stretch is a property shown by all individual segments along the fiber.

INTRODUCTION

Contractile tension in skeletal muscle is well known to increase above the isometric level during and after stretch (Fenn, 1923; Abbott and Aubert, 1951; Hill and Howarth, 1959; Deleze, 1961; Sugi, 1972; Cavagna and Citterio, 1974; Flitney and Hirst, 1978a, b; Curtin and Woledge, 1979; Sugi and Tsuchiya, 1981). This was also shown to be the case in single muscle fibers (Hill, 1977; Edman et al., 1978; Julian and Morgan, 1979).

Further investigation of the detailed features of this response suggested that there might be three components: (a) a velocity-dependent component present only during stretch; (b) a component with a nonlinear force-length relationship present during stretch and decaying after stretch within a few seconds; and...
a component that persisted to the end of long tetani (Edman et al., 1979). The second of these components was the subject of detailed examination in a previous study (Edman et al., 1981). The present study consists of a detailed examination of the third, long-lasting component, which we have called “residual force enhancement after stretch.”

METHODS

Experiments were performed on 33 single muscle fibers from the semitendinosus and the tibialis anterior muscles of Rana temporaria. The fibers were mounted in a muscle chamber (volume 1.2 ml) between an electromagnetic puller and a tension transducer (RCA 5734; RCA Corporation, New York; or AE 801; Aksjeselskapet Mikroelektronikk, Horten, Norway). The temperature of the solution (115.5 mM NaCl, 2.0 mM KCl, 1.8 mM CaCl, 2.0 mM Na phosphate buffer, pH 7.0) in the bath varied between experiments from 0.8 to 3.8°C. During the experiments the temperature was maintained within 0.2°C. Temperature control was obtained by circulating a water glycol solution through the jacket of the muscle chamber from a Colora Ultrathermostat (Colora Messtechnik, GmbH, Lorch, Federal Republic of Germany). The solution in the chamber was either exchanged at least every 2 h or renewed continuously with precooled Ringer by a pump at a flow rate of 5 ml/min. For stimulation, rectangular pulses of 0.2 ms duration were delivered between two platinum plate electrodes placed symmetrically on either side of the fiber, ~1 mm from it. Fused tetani lasting up to 8 s were produced by a train of pulses (frequency 8–22 Hz) at 5-min intervals. Satisfactory fibers could be subjected to over 40 such tetani in an experiment lasting 5–6 h.

Sarcomere length was measured by the laser diffraction technique described by Cleworth and Edman (1972). A 1.5-mm-diam light beam from a 20-mW He-Ne laser was shone through the fiber and the diffraction pattern was displayed on a ground glass screen. Position changes of the first-order beam were recorded on continuously moving 35-mm film (Gevapan 36; Agfa-Gevaert) at 50 or 100 mm/s.

Segment length changes were measured with the technique described by Edman and Hoglund (1981). Opaque markers of black dog’s hair were attached on the upper surface of the fiber 0.5–0.8 mm apart. The fiber was illuminated by an expanded beam of a He-Ne laser. An image of the fiber was projected through a microscope onto a photodiode array (Reticon CCPD 1024, Sunnyvale, CA; scanning rate 2 kHz), which was mounted above the eyepiece of the microscope. The position of two markers was monitored by displaying selected scans of the CCPD 1024 as staggered sweeps on the oscilloscope. A continuous signal of the percent length change of the segment was obtained by analogue computation.

Tension, length, and segment length changes were displayed on a storage oscilloscope (5113 N; Tektronix, Inc., Beaverton, OR). A second similar oscilloscope was used to display the scans of the photodiode array.

Tension fiber length or segment length could be clamped to the desired value by means of feedback control.

Measurements from the film (oscilloscope and laser diffraction recordings) were made on a Nikon comparator (model 6c; Nippon Kogaku K.K., Tokyo) at 10X magnification. The light-intensity distribution of the diffraction pattern was measured on the screen of the Nikon by a light-sensitive diode covered by a circular aperture (0.1 mm diameter). The light-intensity signal and transverse position in the photographic trace were displayed on an x-y recorder.

Statistical analysis was carried out according to Snedecor and Cochran (1967).
Comparison between stretch and control isometric measurements was made with the paired sign test.

**RESULTS**

In a previous study (Edman et al., 1978) we showed for 1-s twitch that the increase in force during stretch of a contracting muscle fiber depended on stretch velocity. However, when the same amplitudes of stretch were used at different velocities, ending at the same time, force decayed along a common path. This phenomenon was also found in the present experiments, where tetani of longer duration were studied. In these experiments, stretch velocity varied between 0.06 and 2.60 lengths/s.

The difference between force found after stretch and that generated isometrically at the corresponding (stretched) fiber length disappeared within ~3 s at sarcomere lengths up to 2.25 μm. At longer lengths, i.e., on the descending limb of the length-tension relationship, a difference in force remained that usually attained a stable level after ~3 s. This long-lasting remainder of the stretch effect is hereafter referred to as “residual force enhancement after stretch.”

The time course of the decay of force enhancement after stretch is shown in Fig. 1. The two different panels pertain to two different amplitudes of stretch (42 and 93 nm per half-sarcomere, respectively). The four symbols correspond to the four sarcomere lengths at which the stretch started. Three of the eight curves approach the baseline after 2.5 s. In these cases, the final length of the muscle fiber corresponded to sarcomere lengths below 2.25 μm. The remaining five curves show different degrees of residual force enhancement depending on sarcomere length and amplitude of stretch. The results shown in Fig. 1 have been confirmed in another 22 fibers. The probability of the increase in force after stretch occurring by chance was <0.005 (n = 22, paired sign test). In 18 fibers studied at sarcomere lengths of 2.3–2.7 μm at the beginning of the stretch (Table I), the mean residual force enhancement after stretch was 0.167% ± 0.091 (SD) of the isometric control force per nanometers per half-sarcomere of applied stretch.

When the stretch was followed by a small release, the gradual decay of force enhancement was interrupted by a steep drop in force (Fig. 2). Tension then redeveloped to the level found with stretch without release. This implies that the residual force enhancement after stretch is present immediately after the stretch, i.e., it does not require time to develop. The same observation was made when, immediately after stretch, the load was clamped at a level where no fiber lengthening or shortening occurred (Edman et al., 1981). With either method, eight fibers were studied with the same result. The force after such stretches followed by critical release was significantly higher than in control isometric tetani (P < 0.005, n = 8).

From Fig. 1 it was concluded that residual force enhancement after stretch depends on sarcomere length and amplitude of stretch. This relationship between stretch amplitude, sarcomere length, and force enhancement was studied by comparing the length-tension relationship after stretch with that obtained from isometric contractions without stretch. Such a relationship is
Figure 1. Changes of force enhancement after stretch with time. Two different amplitudes of stretch were studied: A: 42 nm/half-sarcomere; B: 93 nm/half-sarcomere. The key for symbols indicates sarcomere lengths prior to stretch. Isometric fiber length at 2.25 μm was 0.265 N/mm². Fiber cross-sectional area: 3.4 × 10⁻⁵ mm²; temperature: 3.4°C.
### Table I
SUMMARIZED DATA FOR LONG-LASTING FORCE ENHANCEMENT AFTER STRETCH

| Date      | Date Amplitude of stretch | Residual force enhancement | SL at start of stretch | Ratio of percent force enhancement to stretch amplitude |
|-----------|---------------------------|----------------------------|------------------------|-------------------------------------------------------|
|           | nm per half-sarcomere     | % of control force         | µm                     | % per nm per half-sarcomere                           |
| 17-6-76   | 42                        | 4.7                        | 2.46                   | 0.112                                                 |
| 20-6-76   | 68                        | 6.7                        | 2.66                   | 0.099                                                 |
| 21-6-76   | 28                        | 12.5                       | 2.70                   | 0.446                                                 |
| 22-6-76   | 23                        | 4.5                        | 2.50                   | 0.200                                                 |
| 5-7-77 (I)| 35                        | 3.9                        | 2.45                   | 0.111                                                 |
| 5-7-77 (II)| 42                        | 5.9                        | 2.51                   | 0.140                                                 |
| 6-6-78    | 65                        | 14.2                       | 2.45                   | 0.218                                                 |
| 8-6-78    | 137                       | 23.3                       | 2.50                   | 0.170                                                 |
| 13-6-78 (I)| 275                       | 34.5                       | 2.30                   | 0.125                                                 |
| 13-6-78 (II)| 75                        | 8.5                        | 2.40                   | 0.118                                                 |
| 15-6-78   | 139                       | 16.1                       | 2.55                   | 0.116                                                 |
| 19-6-78   | 74                        | 8.8                        | 2.60                   | 0.119                                                 |
| 29-5-79   | 69                        | 11.9                       | 2.51                   | 0.172                                                 |
| 30-5-79   | 70                        | 8.6                        | 2.53                   | 0.123                                                 |
| 31-5-79   | 50                        | 2.5                        | 2.50                   | 0.050                                                 |
| 7-6-79    | 74                        | 10.5                       | 2.70                   | 0.142                                                 |
| 18-1-80   | 150                       | 37.0                       | 2.50                   | 0.247                                                 |
| 21-1-80   | 150                       | 44.0                       | 2.60                   | 0.293                                                 |

mean 0.167  
SD 0.091, n = 18

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**Figure 2.** Oscilloscope records of three tetani superimposed. Top: lever position calibrated as sarcomere length in the active fiber. Bottom: force. The three tracings are from a stretch (highest force after stretch), a stretch followed by a shortening step (middle force after stretch), and an isometric control at the final length (lowest force after stretch). Fiber length at 2.25 µm sarcomere length: 7.7 mm; cross-sectional area: 18.0 × 10⁻³ mm²; temperature: 2.5°C.
shown in Fig. 3A. In this example the residual force enhancement was measured 4.2 s after stretch (cf. Fig. 1). At a given starting length the force 4.2 s after stretch increased with amplitude of stretch. The probability of the relationship between residual force enhancement after stretch and stretch amplitude occurring by chance was <0.005 (n = 9). Residual force enhancement was much greater when expressed as a percentage of isometric force at longer sarcomere lengths.

Early after the end of stretch, the muscle fiber was capable of carrying considerably higher force than was found during an isometric contraction at the plateau of the length-tension relationship. The possibility was investigated whether the stable force after stretch also could exceed the isometric force at the plateau of the length-tension curve. With the stretches used in this study, forces clearly above the plateau of the isometric length-tension curve were not found. In Fig. 3B the results of an experiment are shown where the muscle fiber was stretched from a sarcomere length of 2.10 μm using three different stretch amplitudes. Force was measured 6 s after the end of stretch. The two values showing the presence of residual force enhancement after stretch were
slightly lower than the forces found at the plateau of the length-tension relationship. Also, with stretches starting at longer lengths, residual force enhancement after stretch was not clearly higher than isometric force on the plateau of the length-tension curve (Fig. 3A). However, the total forces obtained in this case were well above the isometric values found at the starting length; this behavior occurred both in the absence (Fig. 4A) and in the presence (Fig. 4B) of resting force. There was considerable variability between fibers in the magnitude of residual force enhancement after stretch, as suggested by Table I. In nine of the fibers described in Table I, the final tension after stretch was higher than that of the control isometric tetanus at the initial sarcomere length. In a further eight fibers these two tensions were similar, and in one the final tension was lower (experiment of 31-5-79). Fig. 5
illustrates in more detail the length dependence of the residual force enhancement after stretch. An optimum in the relationship was found at \( \sim 3.00 \mu m \) sarcomere length. At longer lengths, residual force enhancement after stretch became smaller. These various aspects of the relationship between stretch amplitude, sarcomere length, and residual force enhancement were confirmed in a total of nine fibers. The optimum sarcomere length was found to vary from 2.70 to 3.15 \( \mu m \) in different fibers.

The dependence of residual force enhancement after stretch on the amplitude of stretch (Fig. 5) suggests the presence of a parallel elastic element carrying the extra force. The parallel elastic element found in the passive fiber cannot be held responsible because it does not contribute to the residual force enhancement after stretch by definition. To test whether a parallel elastic element is formed at the onset of activation, a comparison has been made between a contraction during which the fiber was stretched and a contraction, at the same final length, where stretch was preceded by shortening. This was done in five fibers. The representative result of one such experiment is shown in Fig. 6. The two contractions are compared in this case with the force generated during an isometric contraction at the short length. As can been seen, the force enhancement was almost identical after the stretch and after shortening followed by stretch. This comparison in the group as a whole showed no significant difference \( (P > 0.05, n = 5) \).

We have paid particular attention to the possibility that the residual force
enhancement after stretch results from sarcomere length nonuniformity along the fiber. The length and tension generating capacity of sarcomeres that do not lengthen during stretch, presumably located at the ends of the fiber, may determine the force after stretch. To study the changes in length of the various parts along the fiber during and after stretch, we monitored in five fibers the changes in position of the first-order beam of the diffraction pattern by streak photography. The film was analyzed by densitometry. Results of such an experiment are shown in Fig. 7. Five locations along the length of the fiber were studied. All five sarcomere populations lengthened during the stretch of the fiber. No indication of unstretched or shortening populations could be detected. However, the amount of lengthening differed at the different locations. After the end of stretch light intensity distribution of the first-order beam remained quite stable. The lengthening of the sarcomeres was associated with increased force in all fibers \((P = 0.05, n = 5)\).

In nine fibers, markers were placed along the length of the fiber to study changes in length of the various fiber segments. Segment length varied between 500 and 1,000 \(\mu m\). It was found that all segments lengthened during the stretch (Fig. 8). After the end of stretch, some of the segments shortened gradually, whereas others slowly became longer. The percentage change in
Segment length over 5 s after stretch was 0.54 ± 0.35 (mean of 41 segments in 6 fibers ± 1 SD) compared with 1.74 ± 1.13 during the corresponding time in the control isometric tetani, i.e., the fibers were significantly more stable after stretch \((P < 0.005)\). The increased segment length produced by stretch was associated with increased force in all fibers \((P < 0.005, n = 9)\).

Some segments, such as that shown in Fig. 9, follow the lever movement very accurately after the initial shortening. In such segments we can confidently ascribe the force differences to the properties of the segment. Ideally, the segment should be clamped to follow the required movement. This was done before, during, and after a ramp in five fibers. Fig. 10 shows that residual force enhancement is still found under these circumstances on the descending
Figure 8. Segment length changes at different locations along a muscle fiber during a tetanic contraction lasting 7 s. Top: lever movement calibrated as sarcomere length in the active fiber and force, for stretch during activity and an isometric contraction at the final length. Left: subdivision of the fiber into segments with markers; all individual segment lengths indicated. Right: segment length tracings for each segment along the fiber; the calibration indicates percentage change in segment length. All segment length tracings begin at the same point although the control isometric tetani were all carried out at the final (long) length of the stretch. Fiber length: 8.1 mm at 2.50 μm sarcomere length; cross-sectional area: 13.4 × 10⁻³ mm²; temperature: 2.5°C.
limb of the length-tension relationship. This was consistently so in all segments studied. With this servo control system there are lever movements which, although very small (~0.1% segment length), produce an unstable force record, particularly in the isometric control tetani. The preparation was much more stable after stretch (Fig. 10). In the examples shown in Figs. 9 and 10A, the initial segment length was used for the control isometric tetanus. The force after stretch was higher than the control force ($P = 0.05, n = 5$).

**DISCUSSION**

This study shows that during long tetani in skeletal muscle fibers, a long-lasting force enhancement is produced by stretch; this property is displayed by individual clamped segments of the fiber and by sarcomere populations stretched within a laser beam.

![Graph](image)

**FIGURE 9.** Force (left-hand scale), lever movement calibrated as sarcomere length in the active fiber (right-hand scale), and segment length percent change (middle, more noisy traces). The isometric control tetanus was performed at the starting (short) length of the stretch. Fiber length at 2.57 μm sarcomere length: 9.05 mm; cross-sectional area: 23.8 $\times$ 10$^{-3}$ mm$^2$.

The confirmation of the presence of this property is important because of the suggestion that it resulted from gross nonuniformity of the fiber (Julian and Morgan, 1979). In our own previous work (Edman et al., 1978), we mostly used short tetani in which other components of the response to stretch were dominant. Thus, during stretch, very high forces are attained which increase with velocity of stretch; this is the well-known "negative" part of the force-velocity curve (Aubert, 1956; Katz, 1939). Immediately after the end of stretch, there is a rapid fall of force followed by a more gradual decay lasting ~3 s. The presence of this second component is well accepted (Hill, 1977; Flitney and Hirst, 1978a, b; Julian and Morgan, 1979; Curtin and Woledge, 1979) and has been studied in some detail (Edman et al., 1981).

The separation of the longer-lasting component from these earlier phenomena has been made easier with the accumulation of data concerning the effects of stretch on contracting single fibers (Edman et al., 1978). It is readily
apparent (Figs. 1 and 3) that long-lasting force enhancement does not occur on the plateau of the length-tension curve. Phenomena elicited by stretch that occur on the descending limb of the length-tension curve but not on the plateau may therefore be attributed to residual force enhancement after stretch. The most important of these is the shift to the right of the force-velocity curve (Fig. 5 of Edman et al., 1978; Sugi and Tsuchiya, 1981). Thus, residual force enhancement after stretch is also an enhancement of the ability of muscle to shorten at greater speed (and therefore greater power) at any finite load (Cavagna and Citterio, 1974).

**Figure 10.** Segment length clamp. A. The isometric control contraction was performed at the starting (short) segment length of the stretch. Traces from top on left-hand side: segment length, lever movement, and force. Fiber length at 2.25 μm: 9.5 mm. Resting sarcomere length before stimulation: 2.5 μm. B. Segment length clamp with isometric control at the final (long) segment length of the stretch fiber length at 2.5 μm: 8.1 mm; cross-sectional area: 13.43 × 10^{-3} mm²; temperature: 2.5°C. The dynamic changes in force in the resting fiber subjected to stretch under segment-length clamp conditions are recorded in both panels.
Separation of residual force enhancement from the earlier decaying component was most dramatically demonstrated by applying a small shortening step (Fig. 2) that removed the decaying component (Edman et al., 1981). These two components also have very different force-length characteristics; the decaying component has an angle at a critical amplitude of stretch above which little further increase in force occurs, whereas the residual force enhancement after stretch has an almost linear force-stretch relationship (Figs. 3 and 5).

It has been suggested that residual force enhancement after stretch is a property of some sarcomeres within the fiber that remain at the original length (Julian and Morgan, 1979). This is somewhat contrary to the evidence of Hill (1977), who only found lengthening of the sarcomeres by direct microscopy. Further evidence of sarcomere lengthening is given by our studies of the movements of the first-order laser diffraction pattern (Fig. 7). These show that wherever one directs the beam along the fibers, the first order moves towards the zero order during stretch. There are two difficulties about this evidence: (a) there may be sarcomeres hidden by the tendon that do not lengthen; these sarcomeres cannot be studied because the tendon interferes with the laser beam; (b) because of translation of the fiber through the laser beam, different populations of sarcomeres are analyzed before, during, and after stretch. We have therefore studied the behavior of individual segments along the fiber. Placement of markers at 0.5–1.0-mm intervals along the fiber allowed it to be divided up into about 10 different segments. Analysis of the movements of these segments showed that all segments were elongated by stretch, i.e., we were unable to confirm the postulate of Julian and Morgan (1979) that some segments remained unstretched. Further evidence on residual force enhancement by stretch was obtained in segments that did not show internal movement (Fig. 9). This was also achieved by clamping segment length to a stretch ramp and comparing the resulting force with that obtained in isometric tetani with the segment clamped at the short and long segment lengths. In such a clamped single segment, shortening and lengthening during contraction were prevented apart from the applied stretch. Residual force enhancement after stretch was always obtained, the final force being higher than that with an isometric clamp at the initial length (Fig. 10A). Further pursuance of the hypothesis of nonuniformity therefore requires the postulate that such nonuniformity occur within a segment.

If the hypothesis of Julian and Morgan (1979) is applied on a single segment, it predicts that the force is determined by the unstretched sarcomeres, i.e., it will be the force obtained in isometric tetani at the short length. This is denied by the finding that the final force after stretch is usually higher than in the isometric tetanus at the short length (Figs. 3A, 4, 6, and 9). This finding was obtained in a clamped segment as well as in fiber length control recordings (Figs. 9 and 10A). Our results show that before stretch, some segments lengthen and some shorten (Fig. 8). During stretch, however, all segments were found to elongate (Fig. 8). A most important finding in the analysis is that the change in the fiber responsible for residual force enhancement after
stretch is set immediately at the end of stretch, because it is revealed by a release at this time (Fig. 2). This result excludes the possibility that residual force enhancement after stretch is produced by a slowly developing process after the end of the stretch. This is in line with the fact that there is significantly less redistribution of segment length (Fig. 8) after the end of stretch compared with isometric control tetani. The first-order laser diffraction pattern was also more stable after stretch (Fig. 7).

In our previous study (Edman et al., 1978), we thought that residual force enhancement after stretch was compatible with recruitment of a passive elastic element in parallel with the contractile system. This idea is compatible with the characteristics of the response, i.e., dependence on amplitude of stretch (Fig. 5) and the shift to the right of the force-velocity curve (Edman et al., 1978). The possibility was considered that this parallel elastic element might be formed within the myofibrillar system during activation. In that case, shortening followed by stretch back to the starting length would have no effect. However, this procedure does produce residual force enhancement after stretch (Fig. 6). Therefore, if the element is formed during activation, it is not slackened by shortening but must realign itself in accordance with the short length.

The absence of residual force enhancement after stretch at the plateau of the length tension curve where filament overlap is optimal suggests that this is not a property of the cross-bridges as suggested by Sugi and Tsuchiya (1981). However, the phenomenon resides within a small, 0.5–1.0-mm segment. It is also necessary to explain the fact that total force never exceeds the isometric force on the plateau of the length tension curve (Fig. 3B), which suggests that this is not a recruitment of additional contractile potential. The myofibrillar or intermyofibrillar architecture may be subjected to strains during activity causing extra force to be recruited by stretch, but the presence of this extra force following a prior shortening (Fig. 6) would have to be explained on this basis.

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