Mechanical behavior of skeletal muscle during intermittent voluntary isometric contractions in humans

N. K. Vøllestad, I. Sejersted, and E. Saugen. Mechanical behavior of skeletal muscle during intermittent voluntary isometric contractions in humans. J. Appl. Physiol. 83(5): 1557–1565, 1997.—Changes in contractile speed and force-fusion properties were examined during repetitive isometric contractions with the knee extensors at three different target force levels. Seven healthy subjects were studied at target force levels of 30, 45, and 60% of their maximal voluntary contraction (MVC) force. Repeated 6-s contractions followed by 4-s rest were continued until exhaustion. Contractile speed was determined for contractions elicited by electrical stimulation at 1–50 Hz given during exercise and a subsequent 27-min recovery period. Contraction time remained unchanged during exercise and recovery, except for an initial rapid shift in the twitch properties. Half relaxation time (RT50) decreased gradually by 20–40% during exercise at 30 and 45% of MVC. In the recovery period, RT50 values were not fully restored to preexerciser levels. During exercise at 60% MVC, the RT50 decreased for twitches and increased for the 50-Hz stimulation. In the recovery period after 60% MVC, RT50 values declined toward those seen after the 30 and 45% MVC exercise. The force oscillation amplitude in unfused tetani relative to the mean force increased during exercise at 30 and 45% MVC but remained unaltered during the 60% MVC exercise. This altered force-fusion was closely associated with the changes in RT50. The faster relaxation may at least partly explain the increased energy cost of contraction reported previously for the same type of exercise.

MUSCLE FATIGUE is often associated with slowing of contractile speed (see Refs. 16, 37 for review). This has been demonstrated by reduced rates of force generation and relaxation following intense sustained voluntary contractions and tetanic stimulation of animal muscle in vitro (5, 9, 12). Much less is known about the changes in contractile speed during more normal activation patterns of human skeletal muscle. It is well documented that submaximal voluntary contractions are generated by only a fraction of the motor units and that they are often activated by subtetanic excitation rates (2, 14, 25). Other studies demonstrate a temporal rise in the myoelectrical activity as assessed by the integrated electromyogram amplitude (2, 23). This increase is probably caused in part by a gradual recruitment of fresh motor units, but an increased rate of excitation in units already active could probably also contribute (2). Studies of physiological responses during fatigue from low-force voluntary isometric activity thus introduce additional degrees of freedom not present in other studies. Nevertheless, the interpretation of changes seen during this type of exercise is important to understand the physiological responses to prolonged voluntary muscle activity.

During exercise consisting of voluntary low-force repetitive contractions, Vøllestad and co-workers (35) demonstrated a gradual decline in force-generating capacity, without the concomitant chemical changes seen during sustained ischemic contractions (12, 18). Repetitive isometric contractions also induce a progressive rise in energy cost of contraction, demonstrated by an increased oxygen uptake in the muscle (27, 36) and a higher rate of metabolic heat production during contraction (29). Contractile speed is closely associated with the metabolic heat production and energy cost of contraction (16, 39, 41), suggesting that the rate of force generation and relaxation may increase with fatigue from repetitive isometric exercise. Thus the exercise-induced changes in muscle energetics and activation pattern occur in a direction opposite to that seen during sustained voluntary or electrically stimulated contractions (4, 5, 12, 18).

Prolonged submaximal exercise is associated with a fatigue-induced recruitment of the faster type II muscle fibers, which have a higher energy cost of contraction compared with type I (6, 7). To what extent this increased activation of type II fibers causes a temporal rise in energy turnover can be examined by comparing the responses during repetitive isometric exercise at different target force levels. With an increased target force, a larger proportion of type II fibers will be activated from start, and the rise in energy cost of contraction and, consequently, contractile speed is expected to be smaller.

The aim of the present study was to investigate the changes in muscle contractile speed during and after voluntary repetitive isometric contractions carried out until exhaustion and to compare the changes at different contraction levels. This was accomplished by examining time to peak force and half relaxation time (RT50), together with the maximum rate of force change, when the muscle was stimulated electrically at stimulation frequencies from 1 to 50 Hz. Furthermore, we wanted to examine the effects of fatigue and altered contractile speed on the force-fusion properties during submaximal tetanic activation. The relative force oscillation amplitude was examined when the muscle was stimulated at rates similar to those recorded during voluntary contractions at submaximal force levels, i.e., 10–20 Hz (2, 25). Preliminary reports have been given elsewhere (31, 34).

METHODS

Subjects. Five healthy men and two healthy women (age 22–30 yr, height 170–182 cm; weight 59–83 kg) volunteered...
to participate in the present experiments. They were all physically active students but not particularly trained for any sports activity. After a routine medical examination, an informed consent to participate was obtained. During the last 14 days before the experiment, the subjects were familiarized with the experimental setup and the exercise protocol. The study was approved by the Regional Ethics Committee for Medical Studies, Norway.

Protocol. All subjects participated in three separate experiments, with repetitive isometric contractions at target forces of 30, 45, and 60% of maximal voluntary contraction (MVC). The experiments were carried out on separate days with at least 1-wk interval. All subjects carried out the 30% MVC experiments first. The order of the experiments at the two highest force levels was randomized. The exercise was carried out while the subjects were sitting with the knee flexed at an angle of −80° and with the back inclined backward at a hip angle of −110°. The subjects’ hips were strapped to the seat to ensure minimal movement. The force generated with each of the knee extensors was measured with a strain gauge connected to a padded loop around the ankle. Voluntary contractions were each carried out while the subjects were sitting with the knee flexed at an angle of −80° and with the back inclined backward at a hip angle of −110°. The subjects’ hips were strapped to the seat to ensure minimal movement. The force generated with each of the knee extensors was measured with a strain gauge connected to a padded loop around the ankle. Voluntary contractions were each carried out while the subjects were sitting with the knee flexed at an angle of −80° and with the back inclined backward at a hip angle of −110°. The subjects’ hips were strapped to the seat to ensure minimal movement. The force generated with each of the knee extensors was measured with a strain gauge connected to a padded loop around the ankle. Voluntary contractions were each carried out while the subjects were sitting with the knee flexed at an angle of −80° and with the back inclined backward at a hip angle of −110°. The subjects’ hips were strapped to the seat to ensure minimal movement. The force generated with each of the knee extensors was measured with a strain gauge connected to a padded loop around the ankle. Voluntary contractions were each carried out while the subjects were sitting with the knee flexed at an angle of −80° and with the back inclined backward at a hip angle of −110°. The subjects’ hips were strapped to the seat to ensure minimal movement. The force generated with each of the knee extensors was measured with a strain gauge connected to a padded loop around the ankle. Voluntary contractions were each carried out while the subjects were sitting with the knee flexed at an angle of −80° and with the back inclined backward at a hip angle of −110°. The subjects’ hips were strapped to the seat to ensure minimal movement. The force generated with each of the knee extensors was measured with a strain gauge connected to a padded loop around the ankle. Voluntary contractions were each carried out while the subjects were sitting with the knee flexed at an angle of −80° and with the back inclined backward at a hip angle of −110°. The subjects’ hips were strapped to the seat to ensure minimal movement. The force generated with each of the knee extensors was measured with a strain gauge connected to a padded loop around the ankle. Voluntary contractions were each carried out while the subjects were sitting with the knee flexed at an angle of −80° and with the back inclined backward at a hip angle of −110°. The subjects’ hips were strapped to the seat to ensure minimal movement. The force generated with each of the knee extensors was measured with a strain gauge connected to a padded loop around the ankle. Voluntary contractions were each carried out while the subjects were sitting with the knee flexed at an angle of −80° and with the back inclined backward at a hip angle of −110°. The subjects’ hips were strapped to the seat to ensure minimal movement. The force generated with each of the knee extensors was measured with a strain gauge connected to a padded loop around the ankle. Voluntary contractions were each carried out while the subjects were sitting with the knee flexed at an angle of −80° and with the back inclined backward at a hip angle of −110°. The subjects’ hips were strapped to the seat to ensure minimal movement. The force generated with each of the knee extensors was measured with a strain gauge connected to a padded loop around the ankle. Voluntary contractions were each carried out while the subjects were sitting with the knee flexed at an angle of −80° and with the back inclined backward at a hip angle of −110°. The subjects’ hips were strapped to the seat to ensure minimal movement. The force generated with each of the knee extensors was measured with a strain gauge connected to a padded loop around the ankle. Voluntary contractions were each carried out while the subjects were sitting with the knee flexed at an angle of −80° and with the back inclined backward at a hip angle of −110°. The subjects’ hips were straps...
was continuously analog-to-digital converted (Metrabyte Das-16, Keithley, Cleveland, OH) and stored on a hard disk. The data-sampling frequency was 1 kHz during the electrically evoked test contractions and 50 Hz in the other periods.

Calculations. Contraction time (CT) was calculated as the time elapsed for force to increase from 10 to 90% of peak force. The maximal rate of force generation (MCR) was calculated as the peak value of \( \frac{dF}{dt} \) divided by peak force, where F is force and t is time (3, 5, 40). Peak force in unfused tetanic contractions elicited by 10- to 20-Hz stimulation appeared after a variable number of pulses (cf. Fig. 4). Hence, reliable assessment of CT could only be obtained from the twitch and the 50-Hz contractions that displayed smooth force increments until peak force was reached. RT\(_{1/2}\) was calculated as the time elapsed for force to fall by 50% from peak force after the last stimulation pulse. The corresponding maximal relaxation rate (MRR) was calculated as the nadir value of \( \frac{dF}{dt} \) divided by peak force.

Contractions generated by stimulation frequencies of 10 and 15 Hz were unfused and showed clear oscillations. The average amplitude of these oscillations \( (\Delta F) \) was determined after the initial rapid rise in tension had subsided (cf. Fig. 4). The mean force \( (F_m) \) in the same period was also determined. Any changes in contractile speed would be expected to affect \( \Delta F \). In addition, fatigue will influence both \( \Delta F \) and \( F_m \). The combined effect of repetitive isometric exercise on force-fusion properties and force-generating capacity was monitored as the the change in the relative force oscillation amplitude \( (\Delta F/F_m) \).

Statistics. Values are means \pm SE, unless otherwise stated. One-way analysis of variance for repeated measures was performed to evaluate the temporal changes, except for the changes in \( \Delta F/F_m \), which were tested by paired t-tests.

RESULTS

Force and endurance. The endurance times were 45 \pm 5, 15 \pm 1, and 5.6 \pm 0.3 min for the repetitive exercise at 30, 45, and 60% MVC, respectively. The MVC force decreased gradually by \~35\%-40\% during exercise in all experiments (Table 2). Over the 27-min postexercise recovery period, MVC force increased to 86--88% of preexercise levels in all three protocols. The final values were significantly lower than preexercise control values (\( P < 0.04 \)).

The force response to all stimulation frequencies declined during the exercise period in all experiments, as illustrated in Fig. 2 for twitches and 15- and 50-Hz stimulation (F\(_{tw}\), F\(_{15}\), and F\(_{50}\) respectively). The reductions (relative to the preexercise values) were similar to, or larger than, those observed for MVC (Fig. 2, Table 2). The rate of force loss increased with increasing target force. A notable exception from the steady decline in force during exercise was the F\(_{tw}\), which increased initially, before a gradual decline was seen. This initial rise probably reflected the degree of post-tetanic potentiation that occurs predominantly in type II fibers (11). With increasing target force, a larger initial rise in F\(_{tw}\) was observed.

In the postexercise recovery period, the time course of force recovery varied, but none of the force responses was fully restored after 27 min (Table 2 and Fig. 2). After the 30% MVC exercise, F\(_{tw}\) remained stable, whereas a consistent increase in the peak force of the trains at 15--50 Hz was observed (\( P < 0.007 \)). In the first 3 min, F\(_{50}\) increased rapidly before it leveled off at 80--85% of control values. A similar rapid initial increase was observed after the 45% MVC exercise for twitch force and contractions elicited by 15 Hz or more (Fig. 2). In contrast, F\(_{10}\) remained unchanged in the recovery period (\( P = 0.88 \)). After exhaustion from exercise at 60% MVC, peak force at all stimulation frequencies recovered rapidly before it declined again during the remaining recovery period (\( P < 0.0001 \)).

CT and MCR. CT determined from the 50-Hz stimulation remained unaltered during both exercise and recovery at all three intensities (\( P > 0.23 \); Fig. 3). Twitch CT decreased in all experiments by \~20\% after the first 6-s target force contraction. Thereafter, no further changes were seen in the fatiguing exercise or in recovery (\( P > 0.5 \)). The initial decline in CT was associated with an increased MCR (Table 3). For all experiments, both CT and MCR remained virtually unchanged during the entire exercise and recovery period.

RT\(_{1/2}\) and MRR. RT\(_{1/2}\) values for all stimulation frequencies decreased gradually during exercise at 30 and 45% MVC (\( P < 0.05 \)). During the 30% MVC exercise, RT\(_{1/2}\) determined from contractions elicited by 10-Hz stimulation declined most rapidly and reached 34 \pm 3\% of the preexercise control value at exhaustion. RT\(_{1/2}\) from the other stimulation patterns declined to

Table 2. Force responses determined at exhaustion and after 27 min of recovery

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<th>Exhaustion</th>
<th>27-min Recovery</th>
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<td>30% MVC</td>
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<td>Force, %</td>
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<td>MVC</td>
<td>66 \pm 5</td>
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<td>10 Hz</td>
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<td>20 Hz</td>
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Values are means \pm SE; \( n = 7 \) subjects. Data given as %preexercise control in experiments consisting of repetitive isometric contractions at 30, 45, and 60% maximal voluntary contraction (MVC).
other frequencies caused temporal changes in RT\textsubscript{1/2} similar to, but less pronounced than, the responses from 50-Hz stimulation.

In the recovery period after the exercise at 30% MVC, small but significant increases in RT\textsubscript{1/2} were observed for all contractions (P < 0.04; Fig. 3), except for the 10-Hz stimulation, which remained low. After the exercise at 45% MVC, RT\textsubscript{1/2} values for all stimulations remained at the levels attained at exhaustion (P > 0.07). In contrast, after exercise at 60% MVC, a decline in RT\textsubscript{1/2} was seen in contractions generated by all frequencies (P < 0.001), although RT\textsubscript{1/2} from twitches increased initially (Fig. 3). The final recovery values of RT\textsubscript{1/2} after repeated isometric exercise at the three different target force levels were thus almost the same, despite an 8- to 10-fold variation in endurance times. MRR changed as a mirror image of the RT\textsubscript{1/2} for all stimulation frequencies and exercise runs (Table 3). Close and inverse relationships were observed between RT\textsubscript{1/2} and MRR throughout the entire exercise and recovery period. The mean correlation coefficients ranged from \( \pm 0.84 \) to \( -0.93 \) for the different stimulation paradigms.

Mechanical response to low-frequency stimulation.

Stimulation at 10 and 15 Hz always generated unfused tetani, which showed clear oscillations in force (Fig. 4). In the 30 and 45% MVC experiments, the amplitude of these oscillations \( \Delta F \) increased slightly while the \( F_m \) decreased, as illustrated for 10-Hz contractions in Fig. 4. However, \( \Delta F \) decreased during exercise at 60% MVC but increased again in the recovery period. Furthermore, during exercise at 30 and 45% MVC, \( \Delta F/F_m \) remained elevated in the postexercise recovery period (Fig. 5). In contrast, \( \Delta F/F_m \) remained unchanged during 60% MVC exercise (P = 0.106) but increased in the postexercise period (P = 0.001) to a value similar to those seen after exercise at the two lower force levels.

Figure 6 shows that there was a close and inverse relationship between RT\textsubscript{1/2} and the \( \Delta F/F_m \) during 10-Hz stimulation. Individual data from resting control muscle, exhaustion, and 27-min recovery all display the same relationship, irrespective of the target force level. The largest effects of changes in RT\textsubscript{1/2} values were seen at the lowest values of RT\textsubscript{1/2}, whereas almost negligible oscillations were found at the longest RT\textsubscript{1/2} values (above 80 ms).

Control experiments.

For the three subjects who carried out control experiments, in which the test contraction program (MVCs and electrical stimulation) was employed without any voluntary activity, force and contractile speed remained unaltered. After 60 min, the range of RT\textsubscript{1/2} for the different stimulation regimens was 96–105%, compared with the control value. Similar small changes were seen for MRR, CT, MCR, and force.

DISCUSSION

The major finding of the present experiments was a gradual fall in RT\textsubscript{1/2} during fatigue from repetitive isometric exercise at 30 and 45% MVC target force while the CT remained unchanged. Furthermore, RT\textsubscript{1/2}
values changed consistently in twitches and trains of stimuli from low to high frequency and always inversely to the MRR. These changes are in sharp contrast to those frequently observed during sustained voluntary contractions or tetanic stimulation (5, 9, 12) but in keeping with a small decline in twitch time recorded during repeated maximal contractions at low duty cycles (22). The amplitude of force oscillations during tetani elicited by low-frequency stimulation (10 and 15 Hz) increased as the \( F_m \) declined. These changes were maintained in the recovery period. During exercise at 60% MVC, the changes in RT\(_{1/2}\) values were more variable and depended on the stimulation frequency. Furthermore, repetitive isometric exercise at this highest target force induced a parallel decline in the \( D_F \) in unfused tetanic contractions and \( F_m \). In the postexercise recovery period, however, the oscillation amplitude increased to values comparable to those seen after the exercise at 30 and 45% MVC.

The RT\(_{1/2}\) either remained shorter than control (30 and 45% MVC exercise) in the postexercise recovery period or
shifted from values longer than preexercise control values to shorter values (e.g., 50-Hz stimulation after 60% MVC exercise). The end points for RT1/2 were thus remarkably similar among the three target force levels. A similar convergence in the recovery period was also observed for the ΔF/Fm ratio. There was a close and inverse relationship between ΔF/Fm and RT1/2 under all conditions.

The methods used in this study to determine the contractile speed have been validated in numerous other studies that showed contractile slowing with fatigue of both human and animal muscle (5, 8, 12, 19). Here consistent measurements were made of both time measurements (RT1/2 and CT) as well as rate measurements (MRR and MCR) in response to a wide range of stimulus frequencies. All seven subjects showed a gradual decline in RT1/2 in response to five different stimulation regimes in each of two experiments carried out on separate days at different target force levels (30 and 45% MVC). Similar values were obtained from unfatigued muscle of each subject in three separate experiments on different days (Table 1), and when the subjects sat resting in the chair for 60–90 min. It is, therefore, reasonable to assume that both the constancy of CT as well as the marked changes in RT1/2 values reflect the real mechanical properties of the muscle-tendon unit.

Mechanical responses in relation to muscle chemistry. Fatigue in human muscle in vivo is mostly studied by experimental protocols allowing a precise determination of the excitation pattern (electrical stimulation) or in situations where the excitation pattern is well known (MVCs). The results from these studies, together with data extrapolated from fatigue induced by electrical stimulation in vitro, almost unequivocally associate fatigue with a slowing of relaxation [see review by Fitts (16)]. This slowing is usually attributed to the large changes in high-energy substrate and metabolite concentrations (5, 9, 12, 18).

It was previously demonstrated that only moderate initial changes in high-energy Pi, lactate, and H+ levels occur during repetitive isometric exercise at 30% MVC (27, 35). Furthermore, we have previously estimated...
that the rate of ATP turnover during this type of exercise is well below the limits for aerobic metabolism (29, 36). The low amounts of lactate production support the opinion that the ATP demand during this type of exercise is adequately met by oxidative ATP resynthesis (27, 36). The absence of large changes in substrate and metabolite levels may explain why contractile slowing was not found during repetitive isometric exercise at the two lowest force levels. Even though we have no direct evidence of changes in metabolites in the present study, it is reasonable to assume that the 60% MVC repetitive isometric exercise may have induced larger changes in high-energy P, and other metabolites compared with the 30 and 45% MVC exercise. These chemical changes may have caused the slowing of relaxation demonstrated for the tetanic contractions during the 60% MVC exercise. The slowing of relaxation was reversed with a time course similar to recovery of metabolite changes after exercise (17, 30). However, no known metabolic factors can explain why RT_{1/2} values decreased during the low-force contractions or in the recovery period.

A recent paper by Ferrington and co-workers (15) demonstrated that prolonged exercise in rats induced an increased proportion of functional Ca^{2+} pumps at the sarcoplasmic reticulum (SR) membrane. If this response occurs also in our human model involving isometric contractions, faster relaxation is predicted. Analysis of functional Ca^{2+} pumps during repetitive isometric exercise may thus be an important step toward understanding the mechanisms behind the increased contractile speed.

Changes in muscle fiber activation pattern. The sequence in which motor units are recruited may influence the contractile properties of muscle during voluntary contractions executed at different intensities (25, 40). It has previously been shown that low-force contractions involve only a fraction of the motor-unit pool and that these are predominantly type I fibers (2, 24). As exercise progresses, these fibers fatigue and thus produce less force when a given electrical stimulation is applied. Thus an increasing fraction of the force response elicited by external stimulation will be generated by the faster type II fibers. The muscle as a whole will thus appear with faster contractile properties, even in the absence of changes at the cellular level.

At higher target forces, the initially recruited fraction of type II fibers increases. The greater twitch potentiation after the first 45% compared with the first 30% contraction indicates that a substantially larger number of type II fibers were recruited initially during this more intense exercise regime (11). Thus, at the higher target force, fatigue will develop simultaneously in both type I and in the active type II fibers, and the dominance of unfatigued type II fibers on contractile speed will be decreased. In consequence, the temporal changes in muscle activation pattern would predict a lesser decline in RT_{1/2} during exercise at higher target force. We did not observe this. Furthermore, one would expect that RT_{1/2} and CT would be altered in a similar manner, as they are both heavily dependent on the fiber type (1, 20, 40). The lack of changes in CT, apart from an initial change, indicates that the changes in contractile speed observed in these experiments were not primarily due to selective fatigue of type I fibers. This interpretation is in keeping with a small decline in twitch time recorded when 10-s maximal contractions with the elbow flexors were repeated every 100 or 200 s (22). Therefore, we conclude that the gradual fall in RT_{1/2} reflects a change in mechanical properties at the cellular level.

Muscle temperature. The contractile speed of skeletal muscle is sensitive to temperature, exhibiting a Q_{10} of~2 above 25°C (33, 39). We have recently reported a 3–4°C increase in muscle temperature during 30% MVC repetitive isometric exercise to exhaustion (29), and a similar increase has been seen during 60% MVC repetitive isometric exercise (unpublished observations). The expected increase in contractile speed due to increasing muscle temperature would then be~30%. The relaxation rates increased by 50–170% (cf. Table 3), and, hence, part of this rise could possibly be a temperature effect. However, temperature changes are shown to affect CT and RT_{1/2} equally (5, 33). In addition, muscle temperature falls linearly in the recovery period (29), predicting a linear rise in RT_{1/2}. Therefore, the constancy of CT presently observed while RT_{1/2} decreased markedly during exercise, with only little normalization in the postexercise recovery period, does not indicate that the changes in RT_{1/2} primarily are a consequence of the changes in muscle temperature.

Contractile changes and muscle energetics. At the cellular level, the relaxation process is regulated by enzymes controlling the rate of Ca^{2+} reuptake in the SR and, possibly, also the rate of cross-bridge detachment (12, 16). Hence, the decline in RT_{1/2} during the 30 and 45% MVC exercise is expected to coincide with an increase in the rate of ATP utilization. This contention agrees well with the observed increase in energy cost during 30% MVC repetitive isometric exercise, seen as a twofold increase in oxygen uptake in the working muscle (27, 36), and a 75% increase in metabolic heat production during contraction (29). Furthermore, the decrease in RT_{1/2} and increase in energy turnover follow similar time courses during exercise and show a similar slow return toward control values during postexercise recovery. The present data, therefore, strongly indicate that the decline in RT_{1/2} seen during the 30 and 45% MVC exercise is caused by a higher rate of ATP utilization either at the cross bridges or at the membrane of the SR.

The changes in RT_{1/2} during the 60% MVC exercise clearly differ from those seen at the lower exercise intensities in the respect that RT_{1/2} increased initially from all stimulation regimes and remained elevated for the higher frequencies throughout the exercise. At exhaustion, the change in RT_{1/2} seemed to be “dose” dependent, with the slowest relaxation seen from the 50-Hz stimulation. The short endurance may indicate that the energy turnover during the 60% MVC exercise is at or beyond the limit for aerobic ATP replenishment during the hyperaemic rest period between contrac-
ations. If this is true, the test contractions may perturb
the balance between ATP demand and resynthesis even
further. Because RT_{1/2} from twitch contraction became
shorter and CT did not increase, it is likely that the
slowing of RT_{1/2} from 50-Hz stimulation was a specific
effect of this regime. Therefore, we believe that this
slowing of relaxation may reflect a transient larger rise
in P_i and H^+ levels due to a disturbance of the aerobic
recovery by the high-frequency pulse train.

After cessation of the 60% MVC exercise, rapid shifts
in RT_{1/2} values were seen. Values for RT_{1/2} from 50-Hz
trains declined throughout recovery from ~40% above
control to a level ~20% below. The time course of the
initial rapid decline is similar to that for the recovery of
phosphocreatine and P_i, after sustained ischemic con-
traction (17). These final values converged with those
recorded after 30 and 45% MVC exercise. Thus all three
types of exercise lead to a generally faster muscle once
substrate and metabolite changes had been reversed.

Consequences of faster relaxation. Relaxation rate is
an important factor in determining the contractile
response of the muscle fibers during isometric contrac-
tion. It was previously documented that the motor unit
discharge rate is in the order of 10–15 Hz during
submaximal voluntary contractions in humans (2, 25).
As shown in Fig. 4 for unfused tetanic contraction of the
whole muscle during electrical stimulation, these low
excitation rates result in large oscillations of the force
output. The ΔF, together with F_{mv}, is expected to be
influenced by any changes in relaxation rate, as shown
for the ΔF/F_m ratio and RT_{1/2} in Fig. 6. The same
relationship between these indicators of mechanical
behavior was observed independent of fatigue and
target force level, despite quite different changes in
RT_{1/2} and ΔF/F_m ratio during repetitive isometric ex-
ercise at 60% MVC compared with 30 and 45% MVC (cf.
Figs. 3 and 5).

Oscillation of isometric tension is associated with a
higher cross-bridge cycling rate than during a fully
fused isometric contraction, in which cross-bridge turn-
over is relatively slow (41). The energy cost of contrac-
tion, expressed as the ratio between the rate of ATP
demand and resynthesis of ATP, is thus expected to be higher in
unfused compared with fully fused isometric contrac-
tions. In keeping with this, Wiles and Edwards (38)
found that when the unfatigued human adductor polli-
cis muscle was stimulated at a wide range of frequen-
cies, the energy cost of contraction was linearly and
closely correlated to the ΔF/F_m ratio. In fact, at the
lowest stimulation frequencies in which the highest
values for both energy cost and ΔF/F_m were found, the
energy cost of contractions was six times higher than
that observed during maximal stimulation. We have
recently reported a similar sixfold difference in energy
cost between submaximal (10% MVC) and MVC in the
vastus lateralis muscle (28). The increase in energy
cost during and after the repetitive isometric contrac-
tions may thus involve a two-step process. An enhanced
rate of ATP turnover at the Ca^{2+}-adenosinetriphospha-
tase (ATPase) causes a faster relaxation. Consequently,
larger tension and possibly also length adjustments
consequent to the faster contractile speed occur, and
this altered mechanical behavior causes a larger rate of
ATP turnover at the myosin ATPase.

This hypothesis may also explain why the relation-
ship between a change in contractile properties and
energetics seems to depend on the type of contractile
activity. When exhaustive 30% MVC repetitive isomet-
ric exercise was performed between two bouts of sub-
maximal bicycling, the oxygen uptake during bicycling
remained unaltered, even though a 70% rise in energy
cost during repetitive isometric exercise was observed
(27). We have observed similar results with dynamic
knee extension exercise before and after repetitive
isometric exercise (unpublished observations). An expla-
nation for the coupling between type of contraction and
the effect of fatigue on contraction efficiency may be
found in the different patterns of motor unit excitation.
During repetitive isometric exercise, as in the present
study, each contraction is held for several seconds, so
that the energy utilized over a given time period
depends primarily on the force-fusion properties of the
active motor units and is less dependent on the initial
force generation. Because the motor unit firing rate
during repetitive isometric exercise at 30% MVC is low
(2), an altered ΔF/F_m ratio will have a large impact on
the total energy utilization. In contrast, during dy-
namic exercise such as bicycling, each contraction is
short (a fraction of a second), but the motor units are
activated at high frequencies (10). Under these condi-
tions, the ΔF/F_m ratio is small and the overall energy
turnover is dominated by that associated with the
initial force generation. In addition, the shape of the
force-frequency relationship predicts that changes in
RT_{1/2} will have minor effect on ΔF/F_m during high-
intensity stimulation. These reasons are in keeping
with the observation of higher energy cost for
isometric twitch and short intermittent tetani than for
tetanic contractions of longer duration (21, 26). Other
experiments showing that the slowing of relaxation
often seen during sustained contraction is associated
with a decreased energy cost (13, 32) is in keeping with
a close connection between changes in mechanical and
metabolic properties.

In conclusion, our results indicate that repetitive
low-force isometric contractions induce a gradual fall in
the RT_{1/2} while the CT is unaltered. With higher target
force levels, the faster relaxation may be masked
during exercise, probably by the slowing effect of anaero-
bic metabolites. Our data further suggest that the
reduced RT_{1/2} occurs at the cellular level and is not
primarily caused by temperature rise or selective muscle
fiber recruitment and fatigue. The most likely cause is
an increased turnover rate of the SR Ca^{2+}-ATPase or
the myosin ATPase. We argue that voluntary submax-
imal isometric contractions are associated with low
motor-unit excitation rates and corresponding oscilla-
tions in force output. The faster relaxation may thus
induce increased amplitudes of force oscillations in the
active motor units and thereby increase the energy cost
of contraction.
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