Similar effects of cooling and fatigue on eccentric and concentric force-velocity relationships in human muscle

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De Ruiter, C. J. and A. De Haan. Similar effects of cooling and fatigue on eccentric and concentric force-velocity relationships in human muscle. J Appl Physiol 90: 2109–2116, 2001.—The purpose of this study was to investigate the effects of muscle temperature and fatigue during stretch (eccentric) and shortening (concentric) contractions of the maximally electrically activated human adductor pollicis muscle. After immersion of the lower arm in water baths of four different temperatures, the calculated muscle temperatures were 36.8, 31.6, 26.6, and 22.3°C. Normalized (isometric force = 100%) eccentric force increased with stretch velocity to maximal values of 136.4 ± 1.6 and 162.1 ± 2.0% at 36.8 and 22.3°C, respectively. After repetitive ischemic concentric contractions, fatigue was less at the lower temperatures, and at all temperatures the loss of eccentric force was smaller than the loss of isometric and concentric force. Consequently, normalized eccentric forces increased during fatigue to 159.7 ± 4.6 and 185.7 ± 7.3% at 36.8 and 22.3°C, respectively. Maximal normalized eccentric force increased exponentially (\( r^2 = 0.95 \)) when \( V_{\text{max}} \) was reduced by cooling and/or fatiguing contractions. This may indicate that a reduction in cross-bridge cycling rate could underlie the significant increases in normalized eccentric force found with cooling and fatigue.

Dynamic contractions; power

In many situations, both in sports and everyday life, skeletal muscles are submitted to eccentric actions, which means that they are lengthened during activation. It has been well established that eccentric muscle force increases with stretch velocity to values significantly (1.2–2 times) higher than maximal isometric force (e.g., Ref. 17). There is, however, considerable variation in the literature regarding the (shape of the) eccentric force-velocity relationship of (human) muscle. This variation partly results from the fact that different muscles have been studied and different methods have been used to activate the muscles (voluntary effort vs. electrical stimulation; e.g., Ref. 13) and/or to calculate eccentric muscle force (e.g., Ref. 10). Of even greater importance may be the fact that muscle temperature varied among studies. Cross-bridge function and, consequently, muscle performance strongly depend on temperature. Important parameters like maximal isometric force production, the rates of force development and relaxation (2, 12, 20, 21), and maximal power production (\( P_{\text{max}} \)) (6, 8, 22, 24) decrease with a decrease in muscle temperature. However, to date, there is no detailed data on how temperature affects eccentric muscle performance. Yet such knowledge is important not only because muscle temperature varies in real life but also because the temperature effects may, at least to an important extent, explain why different eccentric force-velocity relationships have been found under in vitro compared with in vivo conditions. Therefore, the first objective of the present study was to investigate the effect of muscle temperature on the eccentric part of the force-velocity relationship of human muscle.

After fatiguing exercise, concentric muscle force is relatively more depressed than isometric force (7, 11), whereas eccentric force seems to be relatively less affected (5, 8). In addition, there is evidence that there is less fatigue at lower muscle temperatures: the fatigue-induced reductions of isometric and concentric forces are smaller after muscle cooling (8, 12). There are no data on the effect of muscle fatigue on eccentric force production at different temperatures. Therefore, the second objective of the present investigation was to study eccentric force output after fatiguing contractions at different muscle temperatures.

METHODS

Subjects

The study was approved by the local ethics committee, and six healthy subjects (4 women and 2 men) took part after giving their informed consent. The subjects (19–25 yr of age) were all right handed and did not undertake regular exercise of the hand muscles. The subjects visited the laboratory on five different occasions. On their first visit, they were familiarized with the procedures and electrical stimulation. The actual measurements were made during the other four visits.

Force Recording and Stimulation

Methods for stimulating the adductor pollicis and force recording are given in detail elsewhere (9). Briefly, the sub-

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ject sat in an adjustable chair with the left forearm supinated, and the hand was held horizontally and securely fixed with the thumb abducted and in contact with a vertical pin. The pin was attached to a strain gauge mounted below the plane of the hand. The forces reported in the present study are those applied by the thumb at the vertical pin. When the thumb was fully adducted, its length axis was parallel with the length axis of the index finger, and this position was defined as 0° thumb angle. Because the vertical pin of the force transducer was placed between the thumb and the index finger, the smallest thumb angle at which forces could be measured was 36°. It was possible to increase thumb angle up to 74° (maximal abduction) before anatomic limits were approached. Thus, during shortening contractions, the maximal angular displacement was 38°. Timing and duration of stimulation, onset and speed of motor movement, and data-sampling frequency (1,000 Hz) of the force and length signal were computer controlled.

The adductor pollicis muscle was activated by percutaneous electrical stimulation of the ulnar nerve at the wrist with constant-current unidirectional square-wave pulses of 100-μs duration (model DS7, Digitimer, Welwyn Garden City, UK) at different frequencies. The current was set 30% above the stimulus, which produced maximal isometric tonic force.

Temperature

To maintain a constant muscle temperature, the subject’s hand and forearm were immersed in a water bath for 20 min before each of the four tests. During the experiments, an infusion bag was placed over the subject’s lower arm, and this bag was circulated with water from the bath. Bath temperatures were 45.0, 30.5, 22.5, and 17.0°C. Skin temperature was recorded with a thermocouple (diameter 0.25 mm; Thermo Electric International, Warmond, The Netherlands) secured with sporting tape over the adductor pollicis muscle. Muscle temperatures were calculated from the measured skin temperatures by using the recently established linear relationship between skin and muscle temperature [muscle temperature = 1.02(skin temperature) + 0.89; r² = 0.98; Ref. 12]. In the present study, the calculated muscle temperatures at bath temperatures of 45.0, 30.5, 22.5, and 17.0°C were 36.8 ± 0.4 (SE), 31.6 ± 0.4, 26.6 ± 0.5, and 22.3 ± 0.5°C, respectively, which is similar compared with our previous studies (8, 12). Because muscle temperature is the important variable, for clarity the data will be presented in relation to the calculated muscle temperatures.

Experimental Protocol

The eccentric part of the force-velocity relationship. Stretches began from the maximally activated isometric state as described in detail before (10). Because of the slower rate of force development at lower temperatures, the duration of the isometric phase increased with decreasing temperatures and, in the order of decreasing temperature, was 500, 500, 700, and 1,000 ms, respectively (e.g., Fig. 1). Care was taken to prevent activation failure, and stimulation frequency was set to maximize muscle performance at the different temperatures (8, 12). In the order of decreasing temperature, stimulation frequencies were 80, 70, 50, and 40 Hz, respectively. After the isometric phase of the contraction at a thumb angle of 44°, the thumb was abducted by the motor to an angle of 63° at a variety of constant angular velocities (0, 9.6, 19.1, 38.2, 76.4, 152.8, and 229.2°/s) applied in random order. The isometric force before the stretch (Fbefore) was measured immediately before the start of lengthening (Fig. 1). The 19° stretch trajectory was chosen because the angle-force relationship of adductor pollicis muscle was almost (but not completely) flat in the range of 44–63° thumb angle (9, 10). A stretch of 19° (abduction) was large enough, at all velocities, to show the characteristic later part of the stretch response where forces increased linearly with the increase in thumb angle at all temperatures (e.g., Fig. 1). Stimulation was continued for a further 500 ms after the stretch, and isometric force was measured just before the end of stimulation (F_after) (see also Ref. 10). Concentric contractions (see below) were interjected during the sequence of eccentric contractions.

The concentric part of the force-velocity relationship. Concentric force-velocity curves were constructed using short (duration: 1,000–90 ms) isovelocity contractions at six different angular velocities (0, 76.4, 152.8, 229.2, 305.6, and 382.0°/s) applied in random order as described and validated elsewhere (11). With this method, the muscle starts shortening during the rise phase of isometric force development. Therefore, particularly at the highest speeds, it is important that the muscle reach its maximum active state as fast as possible. To achieve this, muscles were stimulated at frequencies known to produce the maximum rate of force development at each temperature, both in the unfatigued and the fatigued muscle (12). At the highest shortening speeds, these stimulation frequencies for 22.3, 26.6, 31.6, and 36.8°C were, respectively, 100, 150, 200, and 300 Hz for the unfatigued muscle.
muscle and 50, 100, 150, and 200 Hz for the fatigued muscle. This procedure guaranteed maximal force (power) production under all circumstances (see also Ref. 8).

The thumb adducted twice at each imposed velocity: once with and once without stimulation of the adductor pollicis (equal to passive shortening). At each velocity, the passive force was subtracted from the total force trace to provide a measure of the active force. Ninety seconds of rest were allowed between contractions.

**Fatigue.** After the force-velocity measurements had been completed in the fresh muscle, inflating a cuff around the upper arm occluded blood supply, and the muscle was fatigued by 56 contractions. To create comparable fatiguing circumstances at all temperatures, the duration of stimulation was kept constant (240 ms) with 760-ms rest between contractions to allow complete force relaxation before the thumb was abducted back for the start of the next contraction.

The stimulation frequency was adjusted to minimize possible failure of electrical activity and was set at the frequency with 70% of the maximum rate of force development (12), which was 50, 40, 30, and 25 Hz, respectively, in order of decreasing temperature. The shortening velocity was set at 90% of the velocity at which the unfatigued muscle is capable of producing its maximal power ($V_{opt}$). With this choice, we anticipated a decrease in $V_{opt}$ during the fatiguing exercise and aimed for about optimum power conditions during the entire series of contractions. In the order of decreasing temperature, the imposed shortening velocities were, respectively, 153, 100, 65, and 42°/s. The constancy of stimulation duration in combination with the decreasing shortening velocity at lower temperatures resulted in a decrease in the shortening trajectory with decreasing temperatures. At 36.8°C, the thumb adducted from 74 to 36°, which is the maximal possible range within the anatomic constraints, whereas at 22.3°C, the thumb adducted from 56 to 45.5°. Because we wanted the fatigue protocol to be similar to the one used in a recent study (10), the 20th and 40th contractions were isovelocity (76.4°/s) lengthening contractions (500-ms isometric phase; e.g., Fig. 1). These were introduced previously (10) to monitor the effect of developing fatigue on eccentric force.

Immediately after the fatiguing protocol, and with the muscle maintained ischemic, a series of 12 contractions, at the same velocities as in the fresh muscle, was carried out to obtain the concentric and the eccentric part of the force-velocity relationship. This series of 12 contractions in the fatigued state took 47 s, after which the cuff around the arm was deflated and the muscle was allowed to recover. Obviously extra fatigue was introduced with every contraction applied in the fatigued state; thus in a way these contractions were part of the fatigue protocol. However, because the 12 contractions were applied in random order, they did not affect our results in a systematic manner. In addition, for each subject, the same order was used at each of the four temperatures.

Isometric recovery was assessed 6 min after deflation of the cuff to check whether there was any indication of muscle damage, although, based on previous results, significant damage was not expected (10).

**Data Analysis**

**Isometric and concentric contractions.** The isometric and concentric characteristics of adductor pollicis muscle at the four temperatures have been studied before (8, 12). Therefore, the results with respect to the temperature dependency of isometric and concentric muscle speed were not analyzed in detail. The concentric force and power-velocity relationships are merely presented to have the complete description of muscle function in the same subjects. For this reason, only one index for relaxation speed was obtained in the present study: the time needed for force to fall from 50 to 25% (late half relaxation time) (see also Ref. 12). All measurements were performed at a thumb angle of 51°, which is the optimum for force production, although the angle-force relationship is very flat over the range (38–74°) of applied thumb angles (9, 10); forces measured at the 51° thumb angle were used to construct the force-velocity relationship. Data points were fitted (least squares) to a hyperbola described by the Hill equation (16). Force values from these curves were multiplied with velocity to obtain power-velocity curves. $V_{opt}$ was defined as the velocity of shortening giving the highest power output ($P_{max}$) on the power-velocity curve. $V_{max}$ was determined as the intercept of the Hill curve with the velocity axis. When power is presented in absolute values, the measured forces were multiplied by the lever arm (70 mm) to obtain muscle torque.

**Eccentric contractions.** The method of analyzing the eccentric force traces has recently been described in detail (10). Briefly, this method divides the stretch-induced force increase into three components based on a model proposed by Noble (19).

The first component (component A in Ref. 10) represents the velocity-dependent increased force production of the cross bridges during stretch. It is present during the stretch and disappears relatively soon (within 500 ms) after the stretch, and, therefore, it is referred to as the transient component of the stretch-induced force increase. The difference between the peak force at the end of the stretch ($F_{peak}$) (Fig. 1) and $F_{after}$ (Fig. 1) was taken to represent the transient (cross-bridge-related) component of the stretch-induced force increase.

The other two components (components B and C in Ref. 10) of the stretch-induced force enhancement are longer lasting. They also develop during the stretch, but they are still present 500 ms after the stretch, provided that muscle activation is continuous. Component B is proposed to be length dependent. The origin of component B is not known, but it has been suggested not to be the cross bridges and could be related to the involvement of passive muscle structures during stretch (15). Component C is the force increase (with a passive and active component) caused by the fact that the muscles are stretched on the ascending limb of the thumb angle-force relationship. The combined effects of components B and C account for the difference between $F_{after}$ and $F_{before}$. Therefore, $F_{after} - F_{before}$ (Fig. 1) was taken as a measure of the long-lasting steady component of the stretch-induced force increase. Recently, it was shown that the steady component was unlikely to be a direct function of active cycling cross bridges, as at 36.8°C neither the velocity of the stretch nor the level of muscle activation (force level) affected it (10). Similarly, in the present study, at all four temperatures the steady component was unaffected by stretch velocity and/or $F_{before}$ (data not shown).

Because the objective of the present study was to investigate the temperature effects on contractile (cross-bridge-related) function, the force enhancement at the end of the stretch ($F_{peak}$) was corrected for the long-lasting steady component; thus eccentric contractile force = $F_{peak} - (F_{after} - F_{before})$. 


Statistics

The results are presented as means ± SE. ANOVA for repeated measures with the within-subjects factors of temperature, fatigue, and velocity was used to test for significant (P < 0.05) differences. Bonferroni post hoc tests were applied to determine significance between individual means.

RESULTS

Unfatigued Muscle

Isometric force was significantly reduced at 26.6°C (56.3 ± 5.1 N) and 22.3°C (46.5 ± 6.0 N) compared with the isometric forces at 31.6 and 36.8°C, which were 65.2 ± 7.8 and 66.5 ± 5.8 N, respectively.

With cooling, the muscle became significantly slower: V\text{max} and V\text{opt} decreased and the late relaxation time increased (Fig. 2, A, C, and D). There was also a marked decrease in P\text{max} with muscle cooling: at 22.3°C only 20.5 ± 2.7% of P\text{max} at 36.8°C was produced (Fig. 2B). Q10 values for P\text{max} increased with each 5°C step decrease of temperature and were 2.0, 3.2, and 4.6. The power reduction was caused by a downward and leftward shift of the concentric force-velocity relationship with decreasing temperature (Fig. 3A).

The eccentric part of the force-velocity relationship was significantly shifted downward at 26.6 and 22.3°C compared with 36.8°C (Fig. 3A). At all temperatures, eccentric force increased significantly with stretch velocity and leveled off at 2°/s (Fig. 3A). However, when forces are normalized to the isometric force obtained at each temperature (Fig. 3B), it becomes clear that the decrease in eccentric force at lower muscle temperatures can be accounted for entirely by the significant decrease in isometric force at 26.6 and 22.3°C. This is also illustrated in Fig. 1, where in a typical example (middle) it is shown that (eccentric) force production (stretches at −76.4°/s) is lower at 22.3°C (trace 2) compared with 36.8°C (trace 1). However, relative to F\text{before}, peak eccentric force is markedly higher in the colder muscle (Fig. 1, bottom). Relative to the isometric force, the eccentric part of the force-velocity relationship was even shifted upward (P < 0.05) with each 5°C step decrease in muscle temperature (Fig. 3B). In contrast, even after normalization for the isometric force, the concentric force-velocity relationship shifted downward and leftward with each 5°C step decrease in temperature (Fig. 3B).

Fatigued Muscle

Figure 4 shows the force during and after repetitive activation without blood flow at each of the four temperatures. Concentric forces (Fig. 4, bottom) significantly declined during repetitive activation, with the greatest force reduction at 36.8°C. There also was a significant temperature effect on the decrease in isometric force (Fig. 4, top), again with the greatest decrease at the highest temperature. Please note that, in the fatigued state (that is between numbers 4 and 5 in Fig. 4), there was a further reduction in isometric force caused by the 12 contractions, which were applied to obtain the force-velocity relationship during fatigue. This force reduction was, however, only significant at 36.8°C. Six minutes after deflation of the cuff (number 6 in Fig. 4), isometric forces had recovered to their prefatigue values at 31.6, 26.6, and
Isometric force remained slightly but significantly depressed at 36.8°C. There were significant interaction effects of temperature and fatigue with respect to force, $V_{\text{max}}$, $P_{\text{max}}$, and $V_{\text{opt}}$, indicating that fatigue was less at lower temperatures (Figs. 2 and 5A). Nevertheless, at all temperatures, there were significant reductions in force (eccentric, isometric, and concentric) in the fatigued state and even at 22.3°C, at which the fatigue level was relatively small; $P_{\text{max}}$ was significantly reduced to 69.5 ± 4.7% (Fig. 5A).

Eccentric force increased significantly with stretch velocity in the fatigued muscles at all temperatures (Fig. 5A). However, in the fatigued muscle at 36.8 and 31.6°C, eccentric force already leveled off at −76.4°/s (instead of −152.8°/s in the unfatigued muscle).

Figure 5A also clearly shows that forces were significantly reduced at all velocities in the fatigued muscles compared with the unfatigued muscle. However, when at each temperature the forces in the fatigued muscles were normalized to the isometric force (equal to 100%), the eccentric forces during fatigue were significantly higher compared with the prefatigue values (Figs. 1 and 5B). In addition, the magnitude of this relative increase in eccentric force during fatigue was significantly greater at 22.3 and 36.8°C compared with the two intermediate temperatures (Fig. 5B). In contrast, even after normalization, concentric forces remained significantly lower compared with their prefatigue values (Fig. 5B). These findings indicate that concentric force reductions were greater than isometric force reductions after repetitive ischemic contractions, whereas eccentric force output was less affected than isometric (and consequently concentric) force production.

In each condition (fatigued and unfatigued muscle at four temperatures), maximal normalized eccentric muscle force was obtained during stretches at −152.8°/s (Fig. 5B). When for each condition the individual $V_{\text{max}}$ values were normalized to the $V_{\text{max}}$ obtained in the unfatigued muscle at 36.8°C (equal to 100%), maximal normalized eccentric force was found to decrease exponentially with an increase in $V_{\text{max}}$: $y = 129.9 e^{-4.7/\left(31.4\right)}$, $r^2 = 0.95$ ($P < 0.05$). This result illustrates that slowing of the muscle, either by decreasing the temperature and/or by fatiguing exercise, leads to an enhancement of eccentric force production relative to the maximal isometric force (see also Fig. 5B).

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Fig. 3. Force-velocity relationship of adductor pollicis muscle at different temperatures. Force-velocity relationships of adductor pollicis muscle were calculated for muscle temperatures of 36.8 (○), 31.6 (●), 26.6 (□), and 22.3°C (■). Values were normalized to the maximal isometric force at 36.8°C (A) or the maximal isometric force at each temperature (B). Values are means ± SE. For reasons of clarity, significant differences are not denoted, but for the concentric and eccentric part of the force-velocity relationship the effects of temperature and velocity were significant.

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Fig. 4. Force changes during and after the ischemic fatigue protocol. Isometric force (top) at the 44° thumb angle and concentric forces during repetitive shortening (bottom) were calculated at muscle temperatures of 36.8 (○), 31.6 (●), 26.6 (□), and 22.3°C (■). Isometric forces, nos. 1, 2, and 3, were obtained from contractions during the fatiguing exercise, and nos. 4, 5, and 6, respectively, are the forces from the first and last contraction applied in the fatigue state and after 6-min recovery. Values are means ± SE. *At 36.8°C, recovered isometric force (at 6) was significantly lower than in the unfatigued muscle (at 1), $P < 0.05$. # At 36.8°C, isometric force of the last contraction applied in the fatigue state (at 5) was significantly lower than of the first contraction in the fatigue state (at 4), $P < 0.05$. For clarity, other significant effects over time and among temperatures are not denoted (see text).
DISCUSSION

This is the first detailed study on the effects of temperature on the complete force-velocity relationship of unfatigued and fatigued human muscle. The relatively small adductor pollicis muscle was investigated because it can be maximally activated with electrical nerve stimulation, thereby excluding influences from the central nervous system. The adductor pollicis...
is also a flat muscle, and its temperature can be easily varied over a broad range. Moreover, during everyday life, the temperature of hand muscles in particular is likely to change substantially because of fluctuations in environmental temperature. The main results show that the declines in muscle performance after fatigue and cooling are very similar. Eccentric force output is relatively less affected by muscle cooling and fatigue compared with isometric force production, whereas cooling and fatigue have the greatest effects on concentric force production.

Unfatigued Muscle

Concentric contractions. The effects of temperature on isometric and concentric muscle properties of adductor pollicis muscle have been described and discussed in detail before (8,12). The decreases in isometric force, $V_{opt}$, $V_{max}$, $P_{max}$, and relaxation rate with muscle cooling (Fig. 2) were very similar compared with our previous study (8). The present finding that $P_{max}$ in particular is very sensitive to temperature changes, especially in the lower temperature range [values of effect of 10°C change on metabolism increased from 2.0 (36.8–31.6°C) to 4.6 (26.6–22.3°C)], also confirms earlier work (8,22).

Eccentric contractions. In the present study, we aimed to obtain the eccentric (and concentric) force-velocity relationships that would directly reflect cross-bridge function; therefore, the total force response ($F_{peak}$) was corrected for by subtraction of the steady component ($F_{after} - F_{before}$), hence, only the transient component is included in the presented eccentric forces (Fig. 1). Please note that, as has been discussed elsewhere (10), the steady component of the stretch response can make a significant contribution to muscle performance when it acts to resist a force. Without this correction for the steady component, all eccentric force-velocity relationships (Figs. 3 and 5) would shift upward, and, because the steady component was independent of velocity, fatigue, and temperature, this upward shift would be relatively greater at low velocities and in the cold and/or in fatigued muscle where isometric forces were low.

At 36.8°C, eccentric force increased with stretch velocity to 136.4 ± 1.6% of the isometric force at a velocity of −152.8°/s, with no further increase at −229.2°/s (Fig. 3B). This finding is very similar to our previous results (137.3 ± 1.5% at −152.8°/s in Ref. 10), but in that study we did not stretch the muscle at −229.2°C, and only now we can conclude that the plateau of the eccentric force-velocity relationship is reached at about −152.8°/s.

A 36.4% additional force during stretch is somewhat lower than the values (50–100%) that have been reported for isolated fiber preparations (5,14,18,26). However, studies on isolated preparations are typically conducted at low temperatures, not only with frog (e.g., in Ref. 5, 1.8°C) but also when mammalian fibers are investigated (e.g., in Ref. 26, 15.1°C). The present results clearly demonstrate that, relative to the isometric force, eccentric force increases not only at higher stretch velocities but also at lower muscle temperatures (Fig. 3B). The greatest relative force increase (62.1 ± 2.0%) was found at 22.3°C when the thumb was abducted at −152.8°/s. With further muscle cooling, normalized eccentric forces probably will continue to increase.

We can only speculate about the mechanism behind the relative preservation of eccentric force with muscle cooling, but it may be related to a slowing of cross-bridge cycling rate at lower temperatures, which may enable the cross bridges to remain attached over a longer distance of movement, thereby increasing the resistance to stretch. Support for a slowing of cross-bridge cycling at lower temperatures comes from the work of Stienen et al. (26). They showed that actomyosin adenosine triphosphatase activity, which is the most important determinant of shortening velocity (1), decreases with temperature reduction. In the present study, the increase in relaxation time and the reductions in $V_{max}$ and $V_{opt}$ after muscle cooling may indicate that cross bridges indeed cycled slower at lower temperatures. Nevertheless, whatever the exact mechanism may be behind the relative preservation of eccentric force with decreasing temperature, clearly it is important to take muscle temperature into account when the results of in vitro and in situ studies are compared with the results of studies carried out in vivo, when muscle temperature is usually higher.

The 36.4% stretch-induced force increase at 36.8°C is higher than those reported for voluntary eccentric contractions in humans (13,27–29), but it is very similar to values found during electrical activation of human muscle (13,29). The lower eccentric forces during voluntary effort have been suggested to arise from the action of a neural inhibitory mechanism during eccentric contractions (28,29). It is unknown how muscle cooling would affect neural inhibition. In addition, it is uncertain whether, during voluntary effort, the central nervous system is capable of adapting muscle activation patterns to temperature-related changes in muscle properties (3). However, in the present study, the central nervous system was bypassed, and, with the knowledge from earlier work (8,11,12), stimulation patterns were chosen to maximize muscle performance at all temperatures.

Fatigued Muscle

Repetitive shortening contractions under ischemic conditions lead to less fatigue at lower temperatures (Figs. 4 and 5). This is in accordance with results from previous studies in which we fatigued the muscle with a series of isometric contractions (8,12). In these and other studies (20,23,25), it was suggested that the slowing of cross-bridge cycling rate at lower temperatures reduces the energy cost of isometric force generation, thereby reducing fatigue. To enhance fatigue in the present study, repetitive shortening instead of isometric contractions were used to increase the metabolic flux. $P_{max}$ at 36.8 and 22.3°C declined to 22.2 ± 4.4 and 69.5 ± 4.7%, respectively, values that indeed were considerably lower than in our previous study with repetitive isometric contractions, where $P_{max}$ was found to decline to 60.0 ± 1.7 and 90.5 ± 1.0% at 37.1
and 22.2°C, respectively (8). Thus fatigue decreased with muscle cooling despite the fact that, at all four temperatures, total activation time was the same and the stimulation frequency and power production were optimized. This finding indicates that not only with isometric exercise (8, 12) but also with dynamic exercise is fatigue reduced after muscle cooling.

During fatigue at 36.8°C, normalized eccentric force increased with stretch velocity to 159.7 ± 4.6% at a velocity of −152.8%/s, which was significantly higher than the 136.4% obtained in the unfatigued muscle (Fig. 5B). Significantly higher normalized values for eccentric force were also found at the other stretch velocities, demonstrating that eccentric muscle force is relatively well preserved during fatigue (Fig. 5B). This finding is in accordance with the limited data on eccentric force production during fatigue (5, 10). Previously, it has been suggested that the relative increase in eccentric force during fatigue could be caused by a slowing of the cross-bridge cycling rate (5, 10), which in the present study was proposed to also underlie the increase in normalized eccentric force with muscle cooling (see above). Indeed, there was a significant negative relationship (r² = 0.95) between Vmax and the relative eccentric force obtained at −152.8%/s. This indicates that, with a reduction in contractile speed (cross-bridge cycling rate), regardless of whether this was due to fatigue and/or cooling, maximal normalized eccentric force increased (see also Fig. 1). Interestingly, not only with respect to eccentric force production but also for other parameters like Pmax, Vmax, and relaxation rate were the effects of muscle cooling and fatigue remarkably similar.

In conclusion, the greatest effects of cooling and fatigue in electrically activated human adductor pollicis muscle were found on the concentric part of the force-velocity relationship, where cooling and fatigue depressed maximal isometric force, Vmax and Pmax. Eccentric force was less affected by muscle cooling and fatigue than were isometric and concentric force production. There was a significant negative relationship between normalized (isometric force = 100%) eccentric force and Vmax of the muscle, suggesting that the improved resistance to stretch after cooling and/or fatigue inducing exercise could be related to a reduction in cross-bridge cycling rate.

**REFERENCES**