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## Twitch potentiation is greater after a fatiguing submaximal isometric contraction performed at short vs. long quadriceps muscle length

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**Place, Nicolas, Nicola A. Maffiuletti, Yves Ballay, and Romuald Lepers.** Twitch potentiation is greater after a fatiguing submaximal isometric contraction performed at short vs. long quadriceps muscle length. *J Appl Physiol* 98: 429–436, 2005. First published October 8, 2004; doi:10.1152/jappphysiol.00664.2004.—Endurance time of a submaximal sustained contraction is longer when the muscle is fatigued in a shortened position. The aim of the present study was to compare central and peripheral mechanisms of fatigue after an isometric contraction of the knee extensor muscles performed at 20% maximal voluntary contraction (MVC) at two knee angles (35°, short length vs. 75°, long length; 0° = full extension) until exhaustion. Eleven men (24 ± 4 yr) attended two experimental randomized sessions. Endurance time was greater at 35° compared with 75° (974 ± 457 vs. 398 ± 144 s;  $P < 0.001$ ) despite a similar reduction in knee extensor MVC (−28.4 ± 16.0%,  $P < 0.001$  vs. −27.6 ± 18.8%,  $P < 0.001$ , respectively). Voluntary activation level was similarly depressed after the fatiguing contraction performed at the two muscle lengths (−19 ± 16.7% at 35°,  $P < 0.01$  vs. −13.7 ± 14.5% at 75°,  $P < 0.01$ ). After the fatiguing contraction, peak twitch potentiation was observed only at the short length (+31.8 ± 17.6% at 35°,  $P < 0.01$  vs. +6.4 ± 21.3% at 75°,  $P > 0.05$ ), whereas M-wave properties were similarly altered for the two angles. These results suggest that 1) central fatigue at task failure for a sustained isometric contraction was not dependent on the muscle length, and 2) the longer endurance time of a sustained isometric contraction performed at a shortened length is related to potentiation. It is suggested that the greater endurance time of a sustained isometric contraction observed at 35° is related to the occurrence of potentiation at this short length, because central fatigue is similar at task failure for both tasks.

sustained contraction; central activation; muscular twitch; M wave

THE TIME TO TASK FAILURE (endurance time) for a submaximal contraction is dependent on the details of the task (13, 21, 22, 24), including the joint angle or muscle length. For example, muscle fatigability of the elbow flexor, ankle dorsiflexor and quadriceps muscles is less in a shortened length compared with the length at the optimal joint angle (11, 30, 32), with the optimal joint angle being that angle at which subjects exhibited the greater maximal voluntary contraction (MVC) force.

Several muscular (peripheral) mechanisms may explain the advantage of short muscle length compared with a long or optimal muscle length during submaximal contractions. These mechanisms may include the following: 1) increased cross-bridge activity at longer muscle lengths leading to a rise in intramuscular pressure (30) and a larger ATP turnover (11) or differences in intracellular  $P_i$  concentration (3); 2) increased internal muscle force at longer muscle lengths (32), and 3)

differences in failure of sarcolemmal action potential propagation in the transverse tubules (37). These proposed mechanisms originate at sites peripheral to the neuromuscular junction. However, central neural mechanisms also contribute to the reduction in force during sustained contractions (14, 26, 38), but the contribution of such neural mechanisms to the differences in endurance time during a submaximal task at varying muscle lengths is not defined.

No known study has examined the central and peripheral mechanisms contributing to task failure for a submaximal isometric contraction performed at different muscle lengths. Therefore, the purpose of this study was to compare central and peripheral mechanisms of muscle fatigue by using voluntary and evoked contractions performed before and after a fatiguing isometric contraction of the knee extensor muscles performed at the 20% MVC at two different knee joint angles (35 vs. 75°). It was hypothesized that the greater endurance time at a short muscle length for a sustained fatiguing contraction is associated with less peripheral fatigue.

### METHODS

#### Subjects

Eleven physically active men [age, 24 ± 4 (SD) yr; body mass, 67 ± 7 kg; height, 177 ± 6 cm] volunteered to participate in the study after they were informed of the experimental procedures and possible risks. Before participation, each subject gave written consent, and the local ethical committee approved the study protocol.

#### Experimental Protocol

Each subject was required to perform the same protocol with the right knee extensor muscles at two different lengths during two experimental randomized sessions separated by at least 48 h. The two knee angles tested were 35° (short length) and 75° (long length) (0° = full extension) according to the study of Babault et al. (2). The two experiments were performed for each subject at the same time of the day.

Before the experimental protocol, the subjects performed a standardized warm-up that included 5 min of cycling on a cycle ergometer (Excalibur, Lode, Groningen, The Netherlands) at a power output equivalent to 2 W/kg. The experimental protocol comprised the following: 1) three electrically evoked twitches separated by 4 s, 2) three paired stimuli (doublets) separated by 4 s, 3) knee extensor MVC force assessment with doublets delivered over the isometric plateau (superimposed doublet) and 1.5 s after each MVC (potentiated doublet) to assess voluntary activation level according to the twitch interpolation technique (1), 4) an isometric contraction of the knee extensor muscles sustained at 20% of the corresponding MVC force

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until failure, and 5) steps 1-3 were repeated immediately after the end of the sustained contraction.

**MVC force.** Each subject performed 3 MVCs of the knee extensor muscles before the fatiguing contraction and 2 MVCs after the fatiguing contraction. Each MVC was ~5 s in duration with a 60-s rest period between each trial. Strong verbal encouragement was given to the subjects during each MVC. The greatest level of force achieved by the subjects before the fatiguing exercise was taken as the MVC force and used for calculation of the submaximal target force.

**Fatiguing contraction.** Each subject performed an isometric fatiguing contraction at a target value of 20% of MVC force as determined from MVC performed on that day. This intensity was chosen to compare these data with those from a previous study conducted in our laboratory (36). Visual feedback of the force exerted was displayed on an oscilloscope; the gain of the visual feedback was kept constant between the two sessions for each subject. Force fluctuations were quantified during the sustained contraction, and the fatiguing contraction was terminated when the force fell below the required target force for a 3-s period despite strong verbal encouragement by the investigators.

An index of perceived effort, the rating of perceived exertion (RPE), was assessed according to the Borg scale from 6 to 20 (7) every 30 s during the fatiguing exercise.

#### Data Collection

**Evoked contractions.** Transcutaneous electrically evoked contractions were induced by using a high-voltage (maximal voltage 400 V) constant-current stimulator (model DS7, Digitimer, Hertfordshire, UK). The femoral nerve was stimulated using a monopolar cathode ball electrode (0.5-cm diameter) pressed into the femoral triangle by the experimenter. The site of stimulation was marked on the skin so that it could be repeated after the sustained contraction and between the two sessions. The anode was a 50-cm<sup>2</sup> (10 × 5 cm) rectangular electrode (Compex, Ecublens, Switzerland) located in the gluteal fold opposite the cathode. The optimal intensity of stimulation (i.e., that which recruited all knee extensor motor units) was considered to be reached when an increase in the stimulation intensity did not induce a further increase in the amplitude of the twitch force and the peak-to-peak amplitude of the vastus lateralis (VL) compound muscle action potential (M wave, see *Electrical recordings*). The stimulus duration was 1 ms, and the interval of the stimuli in the doublet was 10 ms. Once the optimal intensity was found, it was kept constant throughout the session for each subject.

**Mechanical recordings.** Maximal isometric force and mechanical responses from the electrical stimulation of the right knee extensors were recorded using an isometric ergometer that comprised a chair (Multi-form, la Roque d'Anthéron, France) connected to a strain gauge (sensitivity: 1.993 mV/V and 0.0049 V/N; SBB 200 kg, Tempo Technologies, Taipei, Taiwan). Subjects were seated with the trunk-thigh angle at 90°, and the strain gauge was securely strapped between the ankle and the machine. Extraneous movement of the upper body was limited by two crossover shoulder harnesses and a belt across the abdomen. Both experiments were performed on the right leg at a knee angle of 35° or 75°, and these were performed in randomized order.

**Electrical recordings.** Electromyographic (EMG) activity of the VL, vastus medialis (VM), and rectus femoris (RF) muscles was recorded with pairs of silver chloride circular (recording diameter of 10 mm) surface electrodes (Controle Graphique Medical, Brie-Comte-Robert, France) positioned lengthwise over the middle of the muscle belly with an interelectrode (center-to-center) distance of 20 mm. These recording sites were determined in pilot testing by eliciting the greatest M-wave amplitude for each muscle via femoral nerve stimulation at the beginning of each test (36). This method enabled the comparison of surface EMG signals between the two muscle lengths. The reference electrode was attached to the left wrist. Low resistance between the two electrodes (<5 kΩ) was obtained by abrading the

skin, and oil and dirt were removed from the skin using alcohol. Myoelectrical signals were amplified with a bandwidth frequency ranging from 15 Hz to 2 kHz (common mode rejection ratio = 90 dB; impedance input = 100 MΩ; gain = 1,000), digitized online at a sampling frequency 2 kHz using a computer (IPC 486) and stored for analysis with commercially available software (Tida, Heka Elektronik, Lambrecht/Pfalz, Germany).

#### Data Analysis

**Mechanical recordings.** Mechanical parameters for single or paired stimuli were analyzed, and the average of three trials was used for further analysis. MVC was considered as the peak force attained during the contraction, and maximal voluntary activation level was estimated according to the following formula: voluntary activation level = [1 - (superimposed doublet amplitude/potentiated doublet amplitude)] × 100. Peak force was the only parameter analyzed using doublet stimulation. The following variables were analyzed from the twitch response: peak twitch, time to peak twitch, maximal rate of tension development, one-half relaxation time, and maximal rate of tension relaxation.

**EMG activity.** M-wave peak-to-peak amplitude and duration were analyzed for VL, VM, and RF muscles with the average of the three trials used for analysis, because M-wave parameters are highly reproducible (33). A representative recording of M waves for the three muscles investigated is presented in Fig. 1. EMG for the MVC of the VL, VM, and RF muscles were quantified as the root mean square (RMS) for a 0.5-s interval at peak force (250 ms-interval either side of the peak force). Maximal RMS EMG values were then normalized to the amplitude of the M wave for the respective muscles so as to obtain the RMS/M ratio. This normalization procedure accounted for peripheral influences (neuromuscular propagation failure and/or changes in impedance) from the EMG recordings. The RMS activity was also quantified for VL, VM, and RF muscles during the first and the last 15 s of the sustained contraction.

**Force fluctuations.** The amplitude of the force fluctuations was quantified as the coefficient of variation (= SD/mean × 100) for a 15-s epoch at the beginning and at the end of the fatiguing task.

#### Statistical Analysis

One-way factor ANOVA was used to compare the time to task failure at the two muscle lengths. Separate two-factor (time × angle) ANOVAs with repeated measures on time were performed to compare

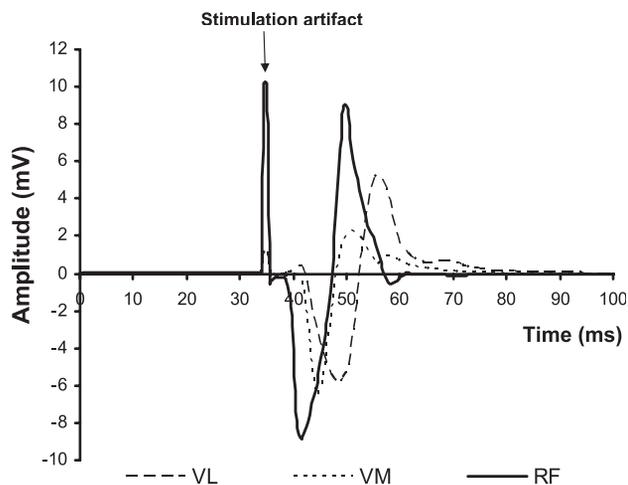


Fig. 1. Representative recording of averaged M wave evoked by electrically transcutaneous motor nerve stimulation on vastus lateralis (VL), vastus medialis (VM), and rectus femoris (RF) muscles. Note that the M wave is easy to distinguish from the artifact.

dependent variables measured before and after the fatiguing protocol, force fluctuations, and RPE measured during the sustained contraction. Three-factor ANOVA (angle  $\times$  time  $\times$  muscle) with repeated measures on time was used to compare RMS during the fatiguing contraction. One-way ANOVA was consistently adopted to compare preexercise to postexercise changes in dependent variables between the two knee angles ( $\Delta 35^\circ$  vs.  $\Delta 75^\circ$ ). Post hoc analyses (Newman-Keuls) were used to test for differences among pairs of means when appropriate. A significance level of  $P < 0.05$  was used to identify statistical significance. The statistical analyses were performed by using Statistica software for Windows (Statsoft, version 6.1, Statistica, Tulsa, OK). Data are reported as means  $\pm$  SD within the text and the table and displayed as means  $\pm$  SE in the figures.

## RESULTS

### Knee Extensor MVC Force and Endurance Time

The MVC performed before the sustained contraction at  $35^\circ$  ( $294 \pm 48$  N) was 27% less ( $P = 0.001$ ) than that performed at  $75^\circ$  ( $411 \pm 73$  N at  $75^\circ$ ; Fig. 2A). However, MVC RMS values before the sustained contraction were not significantly different ( $P > 0.25$ ) between the two joint angles for any muscles (VL:  $0.46 \pm 0.18$  mV at  $35^\circ$  vs.  $0.40 \pm 0.20$  mV at  $75^\circ$ ; VM:  $0.48 \pm 0.18$  mV at  $35^\circ$  vs.  $0.48 \pm 0.16$  mV at  $75^\circ$ ; RF:  $1.0 \pm 0.37$  mV at  $35^\circ$  vs.  $0.82 \pm 0.35$  mV at  $75^\circ$ ).

The endurance time of the sustained contraction performed at 20% of MVC was twice as long for the knee joint angle of  $35^\circ$  ( $974 \pm 457$  s) compared with the endurance time performed at  $75^\circ$  ( $398 \pm 144$  s;  $P < 0.001$ ; Fig. 2B). There was a significant linear correlation between endurance time and MVC at  $75^\circ$  [Pearson correlation coefficient ( $r = 0.54$ ,  $n = 11$ ,  $P < 0.05$ ; Fig. 2C)] but not at  $35^\circ$  ( $r = 0.28$ ,  $n = 11$ ,  $P > 0.05$ ; Fig. 2C). Despite a substantial difference in the endurance time between the two knee joint angles, the reduction in MVC force ( $P < 0.001$ ) was similar at exhaustion for the two conditions ( $P = 0.91$ ) ( $-28.4 \pm 16.0\%$  at  $35^\circ$  vs.  $-27.6 \pm 18.8\%$  at  $75^\circ$ ; Fig. 3A).

### Central Fatigue

Maximal voluntary activation level, which was estimated during the performance of the MVC, was similar for the two muscle lengths ( $P = 0.77$ ) before ( $81.2 \pm 9.8\%$ ) and after the fatiguing contraction. The reduction in maximal voluntary activation level was significant after the fatiguing contractions ( $P < 0.001$ ), and this reduction was similar ( $P = 0.44$ ) for both tasks ( $-19 \pm 16.7\%$  at  $35^\circ$  vs.  $-13.7 \pm 14.5\%$  at  $75^\circ$ ; Fig. 3B). RMS/M during MVC diminished significantly after exercise for VL and VM muscles for both muscle lengths ( $P < 0.01$  for both muscles; see Fig. 3C), with a trend toward significance for RF muscle ( $P = 0.09$ ). The reduction in RMS/M was similar for the two knee joint angles ( $P > 0.48$ ).

There was a linear correlation between MVC loss and voluntary activation level loss at the two muscle lengths ( $35^\circ$ :  $r = 0.74$ ,  $n = 11$ ,  $P < 0.01$ ;  $75^\circ$ :  $r = 0.63$ ,  $n = 11$ ,  $P < 0.05$ ; see Fig. 4), indicating that those subjects who had the greatest reduction in MVC force also had the greatest decline in voluntary activation at the end of both tasks.

RPE increased during the fatiguing contractions for both knee joint angles. RPE ranged from  $8.3 \pm 2.1$  and  $8.3 \pm 1.3$  for 35 and  $75^\circ$ , respectively, at the beginning of the contraction to  $20 \pm 0$  at the end of the fatiguing contraction; these data were not statistically different between the two angles ( $P = 0.40$ ).

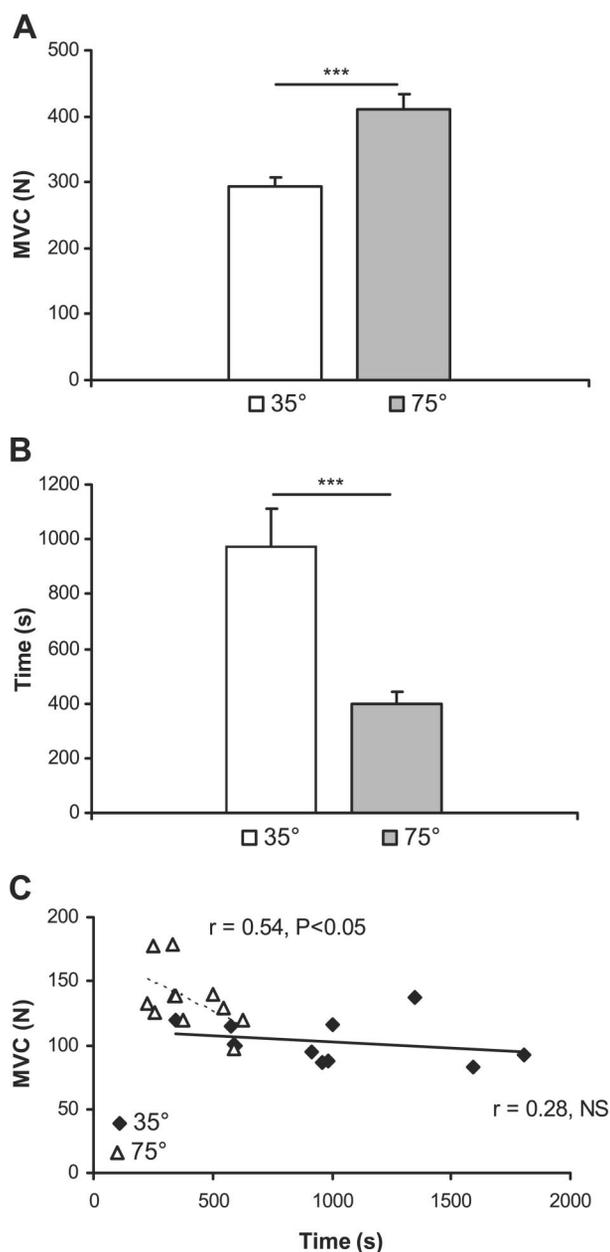


Fig. 2. A: mean ( $\pm$  SE) maximal voluntary force was greater for the  $75^\circ$  compared with the  $35^\circ$  ( $***P < 0.001$ ). B: mean ( $\pm$  SE) endurance time for the sustained contraction was longer ( $***P < 0.001$ ) at  $35^\circ$  (short quadriceps length) than at  $75^\circ$  (long muscle length). C: there was a linear correlation between the maximal voluntary contraction (MVC) and the endurance time at  $75^\circ$  [Pearson correlation coefficient ( $r = 0.54$ ,  $n = 11$ ,  $P < 0.05$ )]. No significant relation was found at  $35^\circ$  ( $r = 0.28$ ;  $n = 11$ ; NS, nonsignificant).

Force fluctuations increased ( $P < 0.001$ ) throughout the sustained contractions. The relative increase was similar ( $P = 0.12$ ) for knee joint angle of  $35^\circ$  ( $+300 \pm 272\%$ ) and  $75^\circ$  ( $+248 \pm 178\%$ ).

### EMG Activity During the Sustained Contraction

Knee extensor muscle RMS activity started at the same relative level ( $P > 0.05$ ) and increased significantly ( $P < 0.05$ ) during the fatiguing task for both angles. The RMS values (% MVC RMS) at the end of the fatiguing contractions were

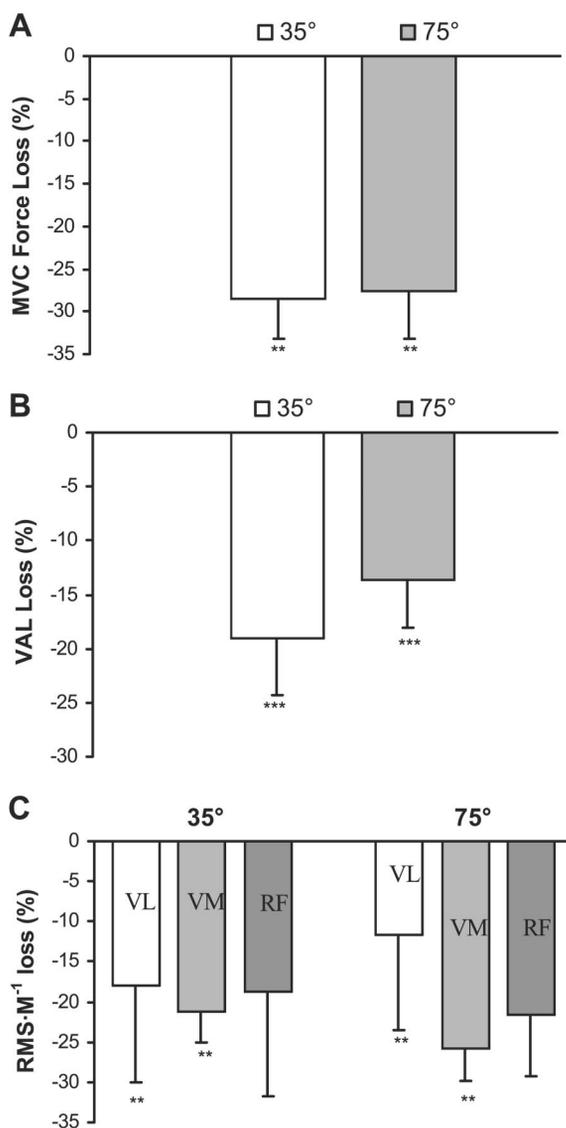


Fig. 3. A: mean ( $\pm$  SE) maximal voluntary isometric contraction force losses were similar for both muscle lengths immediately after the sustained contraction. B: mean ( $\pm$  SE) voluntary activation level (VAL) losses were equivalent across knee angles immediately after the sustained contraction. C: mean ( $\pm$  SE) maximal root mean square electromyograph values normalized to the amplitude of the M wave (RMS/M) losses for VL, VM, and RF muscle at each muscle length. Significantly different from preexercise values: \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . No difference was found between the 2 angles.

$45.3 \pm 15.6\%$  at  $35^\circ$  vs.  $49.7 \pm 17.3\%$  at  $75^\circ$  for VL,  $41.3 \pm 12.7$  at  $35^\circ$  vs.  $48.5 \pm 15.8\%$  at  $75^\circ$  for VM and  $28.8 \pm 10.6\%$  at  $35^\circ$  vs.  $31.0 \pm 9.7\%$  at  $75^\circ$  for RF muscle (Fig. 5). No statistical difference was found between the two joint angles for any of the muscles. At exhaustion, RF RMS activity was lower than RMS of VL and VM muscles at both angles ( $P < 0.05$  at  $35^\circ$  and  $P < 0.01$  at  $75^\circ$ ).

#### Peripheral Fatigue

Peak twitch was greater at  $75^\circ$  than at  $35^\circ$  before exercise ( $77.7 \pm 14$  vs.  $46.5 \pm 11.2$  N, respectively;  $P < 0.01$ ). Maximal rate of tension development was also greater at  $75^\circ$  ( $P < 0.001$ ) before and after the fatiguing contractions. For example, maximal rate of tension development was  $1.47 \pm$

$0.88$  N/ms at  $35^\circ$  vs.  $2.36 \pm 0.77$  N/ms at  $75^\circ$  before fatigue. However, at the end of the exercise, peak twitch potentiation occurred at  $35^\circ$  but not at  $75^\circ$  ( $+31.8 \pm 17.6\%$ ,  $P < 0.01$  vs.  $+6.4 \pm 21.3\%$ ,  $P = 0.40$ , respectively; Fig. 6A) and the relative increase in peak twitch was different between the two angles ( $P < 0.01$ ; Fig. 6A). Peak doublet force was also greater at  $75^\circ$  compared with that at  $35^\circ$  before the sustained contraction ( $168.1 \pm 35.4$  vs.  $109.2 \pm 24.6$  N, respectively;  $P < 0.05$ ). Similar to the twitch amplitude, the potentiation of the doublet was significant at  $35^\circ$  but not at  $75^\circ$  ( $+19.3 \pm 10\%$ ,  $P < 0.01$  vs.  $+1.9 \pm 13.7\%$ ,  $P = 0.69$ ; Fig. 6B), and the relative increase was different across the two joint angles ( $P < 0.05$ ; Fig. 6B). The large intersubject variability in peak twitch and peak doublet after the exercise at  $75^\circ$  may contribute to the high standard deviation values, compared with the lower variability at  $35^\circ$ .

A significant correlation ( $r = 0.72$ ,  $P < 0.01$ ) was observed between doublet potentiation and endurance time at  $35^\circ$  (Fig. 7) but not for the  $75^\circ$  knee joint angle ( $r = 0.21$ ,  $P > 0.05$ ; Fig. 7).

Time to peak twitch force significantly decreased after the sustained fatiguing contraction ( $P < 0.001$ ) for both knee joint angles (from  $73.4 \pm 12.8$  to  $59.9 \pm 9$  ms at  $35^\circ$  and from  $60.1 \pm 4.6$  to  $54.9 \pm 5.5$  ms at  $75^\circ$ ). Furthermore, the maximal rate of tension development significantly ( $P < 0.05$ ) increased (from  $1.47 \pm 0.88$  to  $2.27 \pm 1.27$  N/ms at  $35^\circ$  and from  $2.36 \pm 0.77$  to  $2.52 \pm 1.22$  N/ms at  $75^\circ$ ). The one-half relaxation time did not change after the sustained contraction ( $P = 0.1$ ), for either knee joint angle ( $P = 0.25$ ) (from  $59.4 \pm 20.7$  to  $58.5 \pm 19.1$  ms at  $35^\circ$  and from  $74.2 \pm 18.8$  to  $65 \pm 22.2$  ms at  $75^\circ$ ). However, the maximal rate of tension relaxation increased ( $P < 0.01$ ) for both knee joint angles (from  $1.42 \pm 0.89$  to  $2.15 \pm 1.40$  N/ms for  $35^\circ$  and from  $1.78 \pm 1.19$  to  $2.29 \pm 1.04$  N/ms for  $75^\circ$ ). Except for the greater decrease in time to peak twitch at  $35^\circ$  ( $P = 0.044$ ), other changes in twitch properties were not statistically different between the two knee joint angles.

Knee angle did not affect M-wave amplitude and duration of VL, VM, and RF muscles differently after the sustained contraction ( $P > 0.05$ ). However, the fatiguing contraction significantly reduced VL amplitude ( $P = 0.013$ ), VL and VM durations ( $P = 0.018$  and  $P = 0.011$ , respectively) similarly for each knee joint angle after the fatiguing contraction (see Table 1).

#### DISCUSSION

The aim of the present study was to compare central and peripheral mechanisms contributing to the difference in time to task failure for a submaximal fatiguing contraction when performed at two knee joint angles. Our results showed 1) a greater endurance time at a knee joint angle of  $35^\circ$  (shortened) than at  $75^\circ$  despite a similar MVC loss for the two conditions, 2) similar central fatigue for the two joint angles, and 3) different magnitudes of change in the behavior of contractile properties between  $35^\circ$  and  $75^\circ$  after the sustained contraction.

#### Endurance Time Differed at Two Muscle Lengths

Our results confirmed that time to exhaustion is length dependent; the greater the length of the quadriceps muscle, the briefer the endurance time (16, 32). Furthermore, these results

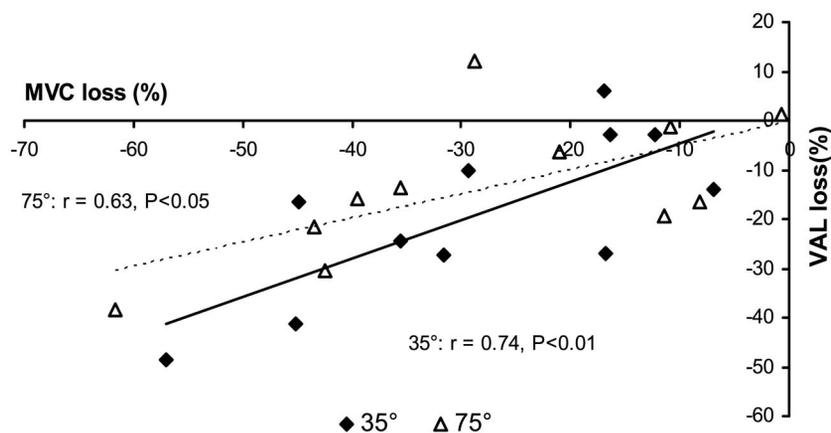


Fig. 4. There was a linear correlation between the maximal voluntary contraction (MVC) loss and the voluntary activation loss (VAL) after the fatiguing exercise for both knee angles (35°:  $r = 0.74, n = 11, P < 0.01$ ; 75°:  $r = 0.63, n = 11, P < 0.05$ ).

are consistent with findings from a previous study in our laboratory (36) that reported a shorter endurance time at a knee angle of 90° (291 s) compared with the present study at shorter muscle lengths (974 s at 35° and 398 s at 75°). However, Rochette et al. (36) showed similar endurance times in seated and supine position, despite a change in the RF length between the two conditions. Visser et al. (40) also reported a lesser influence on RF length when changing hip angle compared with the length changes of the quadriceps muscle when knee angle is altered, and this may explain the discrepancy between the results of Rochette et al. (36) and that of the present study.

The length dependence of endurance time could be explained, at least in part, by the difference in maximal absolute force between the two angles and thus by the different absolute target force for the sustained contraction (82 N at 75° vs. 59 N at 35°). We found a significant correlation between MVC and endurance time at 75°; i.e., the stronger the subject was, the lesser the endurance time at this angle. However, the small sample size of this study may have influenced the lack of correlation for the 35° knee joint angle. An exponential relation between target force and endurance time has previously been found for the elbow flexor muscles (22), and this was likely due to a reduced pressor response during the fatiguing task (18). In the present study, the lack of correlation between endurance time and the target force exerted at 35° indicates that other mechanisms may determine task failure in the shortened

position. A rise in internal force due to an increased number of active cross bridges when lengthening the muscle (16, 32) could be the major cause of the mechanical disadvantage of the shortened compared with the lengthened quadriceps (2). In the present study, the longer quadriceps length (75°) was very close to its optimal joint angle, which has been previously estimated at 70–80° of knee flexion (5, 25). Furthermore, there was a significant association between target force and endurance

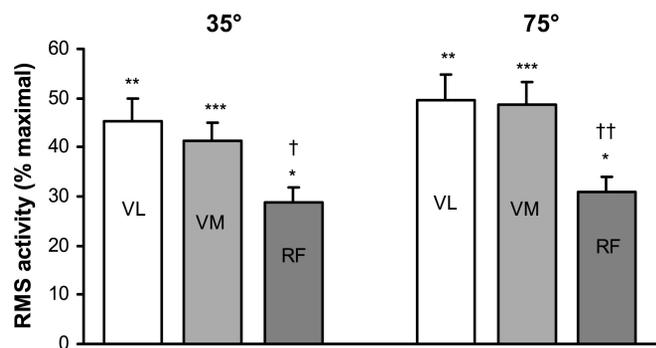


Fig. 5. Mean ( $\pm$  SE) RMS activity of VL, VM, and RF muscles attained during the last 15 s of the sustained contraction and expressed in percentage of the MVC RMS before exercise. Significantly different from the RMS measured during the first 15 s of the sustained contraction at the same angle: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . Significantly different from VL and VM at the same angle: † $P < 0.05$ , †† $P < 0.01$ .

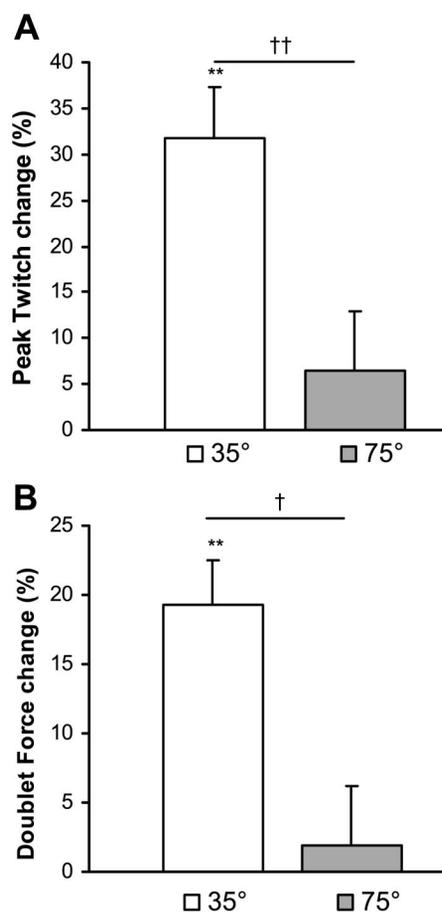
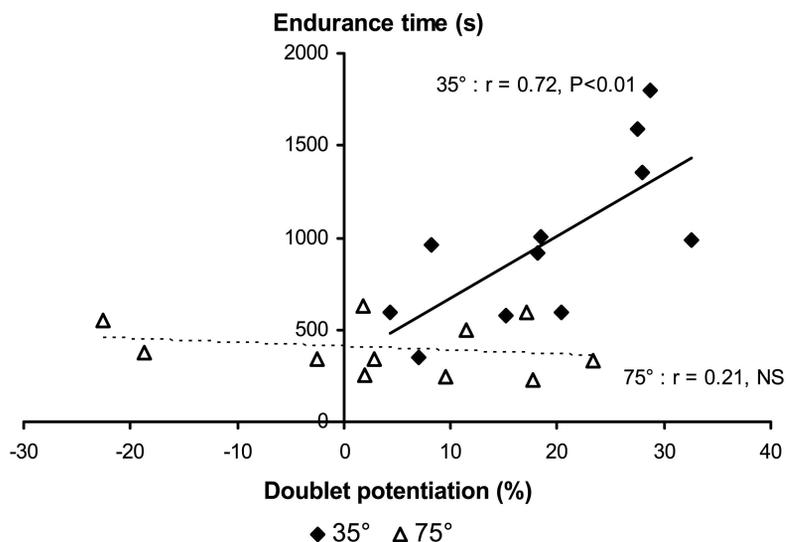


Fig. 6. Mean ( $\pm$  SE) peak force changes for twitch (A) and doublet (B) evoked after the sustained contraction. \*\*Significantly different from preexercise values,  $P < 0.01$ . Significantly different between the 2 muscle lengths: † $P < 0.05$ , †† $P < 0.01$ .

Fig. 7. There was a linear correlation between doublet potentiation (%) and the endurance time at 35° ( $r = 0.72$ ,  $n = 11$ ,  $P < 0.01$ ). No relation was found at 75° ( $r = 0.21$ ,  $n = 11$ ,  $P > 0.05$ ).



ance time at this joint angle. Consequently, the optimal cross-bridge interaction at this greater joint angle (75°) length may have led to an increased intramuscular pressure (30) compared with 35°, which could explain at least partly the briefer endurance time at 75° compared with the 35° joint angle.

Force fluctuations are mediated by descending drive and peripheral afferent feedback (8, 29). In the present study, the similar increase in force fluctuations at the two knee angles would indicate that the rate of increase in the descending drive and/or peripheral feedback during the contraction was similar and thus did not contribute to the different endurance times at the two muscle lengths.

#### Similar Level of Fatigue

MVC reduction in the present study was similar across joint angles. The magnitude of loss (~28%) is consistent with previous studies performed at the same relative intensity on the knee extensor muscles (36) and elbow flexor muscles (19, 20). Nevertheless, the similar reduction in MVC force for both knee joint angles was surprising; although the voluntary activation level reduction was similar after the sustained contraction at the two angles, potentiation of the twitch occurred only at the shortest length. Thus the MVC was expected to be better preserved at 35° due to the increased contractility. One issue could be a premature termination of the exercise at 35°, due perhaps to a loss of motivation or to excessive pain near the

end of the contraction. This premature termination could have led to an underestimation of the voluntary activation level loss at this length.

#### Central Mechanisms of Fatigue

The same magnitude of central fatigue for the two muscle lengths was indicated by 1) a similar level of RMS activity in the latter stages of the sustained contraction, 2) the same voluntary activation level loss (significantly correlated with MVC reduction), and 3) comparable RMS/M alterations at both joint angles. These results indicate that a decreased descending command from supraspinal and/or spinal centers was the major cause of MVC loss. A failure from the central nervous system to achieve full voluntary activation has already been found toward the endurance limit of a sustained plantar flexion performed at 30% of MVC (27) and for elderly people at the end of a 35% MVC elbow flexion (6). In contrast, Klass et al. (23) did not report any changes either in voluntary activation level or in RMS/M after repeated dynamic plantar flexions at 50% of MVC. Consequently, it appears that the extent of central fatigue depends on the type of task (continuous vs. intermittent, duration, muscle group) performed to induce fatigue.

In the present study, we observed a similar voluntary activation level loss between the two angles despite different contraction durations and a lesser rate of increase of RMS activity during the fatiguing contraction performed at the shortest length. Indeed, no difference was found in RMS activity of the knee extensor muscles either at the beginning nor at the end of the sustained contraction between the two joint angles. Moreover, the lack of significant alterations in RMS/M loss for RF might be explained by the lesser utilization of this muscle during the exercise, as was previously shown in dynamic conditions (17).

Consequently, we can speculate on a slower development of central fatigue during the sustained contraction at 35°, which may explain in part the greater endurance time observed at this position. Nevertheless, this assertion seems to be limited by the recent studies of Farina et al. (10), which showed that the increase in EMG activity during such tasks provided limited

Table 1. Peak-to-peak amplitude and duration of the maximal M wave associated with the single twitch before and immediately after the sustained contraction

	Amplitude, mV		Duration, ms	
	Pre	Post	Pre	Post
VL	11.93±3.57	11.31±3.58*	7.60±2.18	6.71±1.87*
VM	10.04±2.44	9.85±2.52	9.03±3.49	8.09±3.42*
RF	10.59±3.42	10.67±3.91	7.62±3.10	7.76±3.57

Values are means ± SD. Data of the two muscle lengths were similar and were thus averaged for each muscle. VL, vastus lateralis; VM, vastus medialis; RF, rectus femoris; Pre, before sustained contraction; Post, immediately after sustained contraction. \*Significantly different from Pre value,  $P < 0.05$ .

information about motor unit activity. The surface EMG underestimates the activation signal sent from the spinal cord to muscle as a result of the cancellation of positive and negative phases of motor unit action potentials (9). We assume that signal cancellation occurred similarly during the two tasks.

### Contractile Properties

Contractile properties were influenced differently by the fatiguing contraction at different muscle lengths. As previously shown, contractile properties before exercise were potentiated when muscle length was increased (2, 28). It is commonly accepted that this phenomenon is principally caused by several mechanisms such as greater number of active cross bridges due to an optimal actin-myosin overlap (5) or increased sensitivity of the myofilaments for intracellular  $Ca^{2+}$  concentration (4). Maffiuletti and Lepers (28) showed potentiated MVC and contractile properties when lengthening RF muscle from seated to supine position. So a change in one synergist length could modify contractile and thus fatigability properties of the whole muscle group. In the present study, we induced a change in the length of three quadriceps synergists that influenced the fatigability of the knee extensors.

Consequently, peak twitch and peak doublet force were significantly potentiated at 35° but not at 75° when recorded after the fatiguing contractions. This indicates that excitation-contraction coupling potentiation occurred after a fatiguing contraction performed at 35°. Because the M-wave characteristics were altered to a similar magnitude for the two muscle lengths, the differences in potentiation was not due to neuromuscular propagation. Thus processes located distal to the muscle cell membrane must have played a dominant role in the longer endurance time at the shortened muscle length. Myosin regulatory light chain phosphorylation level has been found to be correlated with the magnitude of twitch potentiation (39). Indeed, phosphorylated myosin regulatory light chains are in optimal position to interact with actin (41), which increase  $Ca^{2+}$  sensitivity and force generation during unfused muscle stimulation, as is the case for twitch or doublet. We hypothesize that the fatiguing exercise considered here caused myosin regulatory light chain phosphorylation and thus potentiation of contractile properties at 35°, as was the case after long duration exercise such as running (31, 33).

Interestingly, we found a significant correlation between the magnitude of doublet potentiation and the endurance time at 35°, although the sample size was small. Potentiation mediated by myosin regulatory light chain phosphorylation may compensate for the reduced release of  $Ca^{2+}$  during the exercise, which could help to maintain the submaximal target force at 35° (12). Thus the mechanisms causing the potentiation of the doublet might be responsible for the longer endurance time at the shortened muscle length. Alternatively, the endurance time may have determined the magnitude of potentiation. The lack of potentiation observed at 75° might be simply because the duration for the submaximal contraction was too brief for potentiation to develop. However, with the present data we cannot determine whether muscle length or contraction duration (endurance time) is the cause or the effect.

In contrast to 35°, greater peak twitch or peak doublet potentiation was not observed after fatigue at 75°. However, the briefer time to peak twitch and greater maximal rates of

tension development and relaxation reported after the exercise indicate an enhancement of the contractile properties at this length. In a previous study, Rassier et al. (35) found a similar level of myosin regulatory light chain phosphorylation at different muscle lengths despite a length-dependence of staircase potentiation in mammalian skeletal muscle. Rassier et al. explained this discrepancy by claiming that there is a ceiling effect and that the room for activity-induced potentiation may be smaller at a long length because twitch amplitude at rest is higher than at shorter length. At a joint angle of 75°, VL, VM, and RF (at a hip joint angle of 90°) muscles have theoretically been shown to be within the ascending limb or plateau phase of their own force-length relations (15). Thus we can assume that these muscles are already potentiated due to an increased  $Ca^{2+}$  sensitivity, and the effects of myosin regulatory light chain phosphorylation are likely to be smaller. It appears therefore that the mechanical disadvantage observed at rest at 35° is attenuated when quadriceps muscle is fatigued.

In conclusion, the endurance time of a submaximal fatiguing isometric contraction of the knee extensor muscles was briefer when performed at a greater muscle length (knee joint angle of 75°) compared with a shorter muscle length (knee joint angle of 35°). At task failure, the reduction in MVC force and central fatigue were similar. In contrast, at task failure, the twitch and doublet were potentiated at the shortened position but not at the lengthened position, indicating that excitation-contraction coupling was differently affected at the two muscle lengths. These data suggest a relation between postactivation potentiation and the duration of the sustained contraction but further studies are needed to clarify this finding.

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### REFERENCES

1. Allen GM, Gandevia SC, and McKenzie DK. Reliability of measurements of muscle strength and voluntary activation using twitch interpolation. *Muscle Nerve* 18: 593–600, 1995.
2. Babault N, Pousson M, Michaut A, and Van Hoecke J. Effect of quadriceps femoris muscle length on neural activation during isometric and concentric contractions. *J Appl Physiol* 94: 983–990, 2003.
3. Baker AJ, Carson PJ, Green AT, Miller RG, and Weiner MW. Influence of human muscle length on energy transduction studied by  $^{31}P$ -NMR. *J Appl Physiol* 73: 160–165, 1992.
4. Balnave CD and Allen DG. The effect of muscle length on intracellular calcium and force in single fibres from mouse skeletal muscle. *J Physiol* 492: 705–713, 1996.
5. Becker R and Awiszus F. Physiological alterations of maximal voluntary quadriceps activation by changes of knee joint angle. *Muscle Nerve* 24: 667–672, 2001.
6. Bilodeau M, Henderson TK, Nolte BE, Pursley PJ, and Sandfort GL. Effect of aging on fatigue characteristics of elbow flexor muscles during sustained submaximal contraction. *J Appl Physiol* 91: 2654–2664, 2001.
7. Borg G. Perceived exertion as an indicator of somatic stress. *Scand J Rehabil Med* 2: 92–98, 1970.
8. Cresswell AG and Loscher WN. Significance of peripheral afferent input to the alpha-motoneurone pool for enhancement of tremor during an isometric fatiguing contraction. *Eur J Appl Physiol* 82: 129–136, 2000.
9. Day SJ and Hulliger M. Experimental simulation of cat electromyogram: evidence for algebraic summation of motor-unit action-potential trains. *J Neurophysiol* 86: 2144–2158, 2001.
10. Farina D, Merletti R, and Enoka RM. The extraction of neural strategies from the surface EMG. *J Appl Physiol* 96: 1486–1495, 2004.
11. Fitch S and McComas A. Influence of human muscle length on fatigue. *J Physiol* 362: 205–213, 1985.

12. **Fowles JR and Green HJ.** Coexistence of potentiation and low-frequency fatigue during voluntary exercise in human skeletal muscle. *Can J Physiol Pharmacol* 81: 1092–1100, 2003.
13. **Fuglevand AJ, Zackowski KM, Huey KA, and Enoka RM.** Impairment of neuromuscular propagation during human fatiguing contractions at submaximal forces. *J Physiol* 460: 549–572, 1993.
14. **Gandevia SC.** Spinal and supraspinal factors in human muscle fatigue. *Physiol Rev* 81: 1725–1789, 2001.
15. **Herzog W, Abrahamse SK, and ter Keurs HE.** Theoretical determination of force-length relations of intact human skeletal muscles using the cross-bridge model. *Pflügers Arch* 416: 113–119, 1990.
16. **Hisaeda HO, Shinohara M, Kouzaki M, and Fukunaga T.** Effect of local blood circulation and absolute torque on muscle endurance at two different knee-joint angles in humans. *Eur J Appl Physiol* 86: 17–23, 2001.
17. **Housh TJ, deVries HA, Johnson GO, Evans SA, Housh DJ, Stout JR, Bradway RM, and Evetovich TK.** Neuromuscular fatigue thresholds of the vastus lateralis, vastus medialis and rectus femoris muscles. *Electromyogr Clin Neurophysiol* 36: 247–255, 1996.
18. **Hunter SK, Critchlow A, Shin IS, and Enoka RM.** Fatigability of the elbow flexor muscles for a sustained submaximal contraction is similar in men and women matched for strength. *J Appl Physiol* 96: 195–202, 2004.
19. **Hunter SK and Enoka RM.** Sex differences in the fatigability of arm muscles depends on absolute force during isometric contractions. *J Appl Physiol* 91: 2686–2694, 2001.
20. **Hunter SK and Enoka RM.** Changes in muscle activation can prolong the endurance time of a submaximal isometric contraction in humans. *J Appl Physiol* 94: 108–118, 2003.
21. **Hunter SK, Lepers R, MacGillis CJ, and Enoka RM.** Activation among the elbow flexor muscles differs when maintaining arm position during a fatiguing contraction. *J Appl Physiol* 94: 2439–2447, 2003.
22. **Hunter SK, Ryan DL, Ortega JD, and Enoka RM.** Task differences with the same load torque alter the endurance time of submaximal fatiguing contractions in humans. *J Neurophysiol* 88: 3087–3096, 2002.
23. **Klass M, Guissard N, and Duchateau J.** Limiting mechanisms of force production after repetitive dynamic contractions in human triceps surae. *J Appl Physiol* 96: 1516–1521, 2004.
24. **Kouzaki M, Shinohara M, Masani K, Kanehisa H, and Fukunaga T.** Alternate muscle activity observed between knee extensor synergists during low-level sustained contractions. *J Appl Physiol* 93: 675–684, 2002.
25. **Kubo K, Tsunoda N, Kanehisa H, and Fukunaga T.** Activation of agonist and antagonist muscles at different joint angles during maximal isometric efforts. *Eur J Appl Physiol* 91: 349–352, 2004.
26. **Loscher WN, Cresswell AG, and Thorstensson A.** Excitatory drive to the alpha-motoneuron pool during a fatiguing submaximal contraction in man. *J Physiol* 491: 271–280, 1996.
27. **Loscher WN, Cresswell AG, and Thorstensson A.** Central fatigue during a long-lasting submaximal contraction of the triceps surae. *Exp Brain Res* 108: 305–314, 1996.
28. **Maffiuletti NA and Lepers R.** Quadriceps femoris torque and EMG activity in seated versus supine position. *Med Sci Sports Exerc* 35: 1511–1516, 2003.
29. **McAuley JH and Marsden CD.** Physiological and pathological tremors and rhythmic central motor control. *Brain* 123: 1545–1567, 2000.
30. **McKenzie DK and Gandevia SC.** Influence of muscle length on human inspiratory and limb muscle endurance. *Respir Physiol* 67: 171–182, 1987.
31. **Millet GY, Lepers R, Maffiuletti NA, Babault N, Martin V, and Lattier G.** Alterations of neuromuscular function after an ultramarathon. *J Appl Physiol* 92: 486–492, 2002.
32. **Ng AV, Agre JC, Hanson P, Harrington MS, and Nagle FJ.** Influence of muscle length and force on endurance and pressor responses to isometric exercise. *J Appl Physiol* 76: 2561–2569, 1994.
33. **Place N, Lepers R, Deley G, and Millet GY.** Time course of neuromuscular alterations during a prolonged running exercise. *Med Sci Sports Exerc* 36: 1347–1356, 2004.
34. **Rassier DE.** The effects of length on fatigue and twitch potentiation in human skeletal muscle. *Clin Physiol* 20: 474–482, 2000.
35. **Rassier DE, Tubman LA, and MacIntosh BR.** Length-dependent potentiation and myosin light chain phosphorylation in rat gastrocnemius muscle. *Am J Physiol Cell Physiol* 273: C198–C204, 1997.
36. **Rochette L, Hunter SK, Place N, and Lepers R.** Activation varies among the knee extensor muscles during a submaximal fatiguing contraction in the seated and supine postures. *J Appl Physiol* 95: 1515–1522, 2003.
37. **Sacco P, McIntyre DB, and Jones DA.** Effects of length and stimulation frequency on fatigue of the human tibialis anterior muscle. *J Appl Physiol* 77: 1148–1154, 1994.
38. **Sacco P, Thickbroom GW, Byrnes ML, and Mastaglia FL.** Changes in corticomotor excitability after fatiguing muscle contractions. *Muscle Nerve* 23: 1840–1846, 2000.
39. **Sweeney HL, Bowman BF, and Stull JT.** Myosin light chain phosphorylation in vertebrate striated muscle: regulation and function. *Am J Physiol Cell Physiol* 264: C1085–C1095, 1993.
40. **Visser JJ, Hoogkamer JE, Bobbert MF, and Huijing PA.** Length and moment arm of human leg muscles as a function of knee and hip-joint angles. *Eur J Appl Physiol* 61: 453–460, 1990.
41. **Yang Z, Stull JT, Levine RJ, and Sweeney HL.** Changes in interfilament spacing mimic the effects of myosin regulatory light chain phosphorylation in rabbit psoas fibers. *J Struct Biol* 122: 139–148, 1998.