

# Activation varies among the knee extensor muscles during a submaximal fatiguing contraction in the seated and supine postures

L. Rochette,<sup>1</sup> S. K. Hunter,<sup>2</sup> N. Place,<sup>1</sup> and R. Lepers<sup>1</sup>

<sup>1</sup>Institut National de la Santé et de la Recherche Médicale/Equipe de Recherche et d'Innovation Technologique 0207, Motricité-Plasticité, Unité de Formation et de Recherche Sciences et Techniques des Activités Physiques et Sportive, Université de Bourgogne, 21078 Dijon, France; and <sup>2</sup>Department of Integrative Physiology University of Colorado at Boulder, Boulder, Colorado 80309-0354

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## Rochette, L., S. K. Hunter, N. Place, and R. Lepers.

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; 10.1152/jappphysiol.00334.2003.—Ten young men sustained an isometric contraction of the knee extensor muscles at 20% of the maximum voluntary contraction (MVC) torque on three separate occasions in a seated posture. Subjects performed an isometric knee extension contraction on a fourth occasion in a supine posture. The time to task failure for the seated posture was similar across sessions ( $291 \pm 84$  s;  $P > 0.05$ ), and the MVC torque was similarly reduced across sessions after the fatiguing contraction ( $42 \pm 12\%$ ). The rate of increase in electromyograph (EMG) activity (%MVC) and torque fluctuations during the fatiguing contractions were similar across sessions. However, the rate of increase in EMG differed among the knee extensor muscles: the rectus femoris began at a greater amplitude ( $31.5 \pm 11.0\%$ ) compared with the vastus lateralis and vastus medialis muscles ( $18.8 \pm 5.3\%$ ), but it ended at a similar value ( $45.4 \pm 3.1\%$ ). The time to task failure and increase in EMG activity were similar for the seated and supine tasks; however, the reduction in MVC torque was greater for the seated posture. These findings indicate that the time to task failure for the knee extensor muscles that have a common tendon insertion did not alter over repeat sessions as had been observed for the elbow flexor muscles (Hunter SK and Enoka RM. *J Appl Physiol* 94: 108–118, 2003).

electromyograph; force fluctuations; task failure; muscle length

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TIME TO TASK FAILURE OF A submaximal sustained contraction can be modulated by changes within the nervous system and reflected in the patterns and rate of increase in the electromyograph (EMG) within a muscle and across synergist muscles (1, 24, 39, 42). For example, the increase in EMG activity during a submaximal fatiguing contraction primarily represents a recruitment of additional motor units with some modulation of discharge rate as the muscle fibers of the active motor units become progressively fatigued (4, 5,

11, 16), although the contribution of signal cancellation of the EMG signal (7, 44) is not known for a sustained contraction. Consequently, a deviation from the rate of increase of the averaged EMG for a muscle suggests a change in the motor unit recruitment pattern.

Adjustments of EMG activity during fatiguing contractions when maintaining a submaximal force can be modified by chronic interventions such as immobilization (39, 40) and practice over repeat sessions (19). For example, some subjects who performed a contraction of the elbow flexor muscles while maintaining a force at 20% of maximal voluntary contraction (MVC) force increased their time to task failure across three sessions, and this was associated with alterations in the level and patterns of EMG activity (19). The adjustments included changes in the rate of increase in the force fluctuations, the rate of increase in bursting activity of the EMG signal, and the rate of increase in the averaged EMG among the synergists of the elbow flexor muscles. In contrast, there was no change in time to task failure over repeated session for a submaximal fatiguing contraction of a small muscle of the hand, the first dorsal interosseous (13). Differences between these muscle groups include the number of muscles that contribute to the primary action, the motor unit recruitment range (25), and the various tendon insertions of the elbow flexor muscles compared with a common insertion for the first dorsal interosseous muscle. Alternatively, the quadriceps that contribute to knee extension comprise multiple muscles with three of the muscles sharing a common insertion into the patella tendon, limiting the force modulation of the individual muscles. These observations raised the question of whether the time to task failure for a submaximal contraction maintained for force with the knee extensor muscles would alter with repeat performances of the task. The purpose of the study was to compare the time to task failure and pattern of EMG activity of the knee extensor muscles across three performances while maintaining a submaximal force.

Adjustments in the joint angle and muscle length will influence the torque, maximization of activation

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Address for reprint requests and other correspondence: L. Rochette, Institut National de la Santé et de la Recherche Médicale/Equipe de Recherche et d'Innovation Technologique 0207, Unité de formation et de Recherche Sciences et Techniques des Activités Physiques et Sportive, Université de Bourgogne, 21078 Dijon, France.

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(27, 29), activity of a single motor unit (5), EMG activity (2), and the fatigability of a muscle group (12, 18, 32). For example, maximal torque of the knee extensor muscles was reduced when subjects maintained a supine posture vs. a seated posture (27). The length of the rectus femoris (RF), a biarticulate muscle contributing to knee extension, is shortened when a subject is seated vs. in a supine posture. The reduced maximal torque in the supine posture included less EMG activity and decreased ability of the subject to maximally activate the quadriceps (27). The time to task failure for a submaximal contraction can be limited by the neural activation of a muscle (19); however, the influence of changes in posture on the pattern of EMG activity among the knee extensor muscles and the subsequent time to task failure is not understood. Therefore, a secondary purpose was to compare the time to task failure and EMG activity of the knee extensor muscles in a seated posture vs. supine posture. Preliminary results from this study have been presented in abstract form (37).

## METHODS

### *Subjects*

Ten physically active men volunteered to participate in the study. The mean ( $\pm$  SD) values for the age, height, and body mass of the subjects were  $26 \pm 5$  yr,  $178 \pm 7$  cm, and  $73 \pm 7$  kg, respectively. Before participation, each subject was informed of the purpose and potential risks of the study and gave their written voluntary consent. The local Ethical Committee approved the study protocol.

### *Experimental Protocol*

Each subject attended four experimental sessions: three separate sessions to perform a fatiguing contraction with the knee extensor muscles for a seated posture and an additional session to perform the fatiguing contraction in a supine posture.

*Seated task across three sessions.* Each subject was required to perform the same protocol with the knee extensor muscles on three occasions, with 1 wk separating each session. The experiments for each subject were performed on the right leg and at the same time of the day on each occasion. This protocol was performed with the subject in a seated posture, a trunk-thigh angle of  $90^\circ$  and a knee joint angle of  $90^\circ$ . The protocol comprised the following: 1) a 5-min warm-up that included several low-force submaximal isometric contractions of the knee flexor and knee extensor muscles; 2) assessment of MVC torque with the knee extensor and knee flexor muscles; 3) submaximal isometric contractions sustained for 5 s at target torques of 20, 50, and 80% MVC with the knee extensor muscles so as to evaluate the reliability of the EMG-force relation across sessions; 4) performance of an isometric fatiguing contraction with the knee extensor muscles sustained at 20% MVC torque until task failure; and 5) assessment of MVC torque of the knee extensor and knee flexor muscles immediately after termination of the fatiguing contraction.

*Supine task.* Each subject performed the same experimental protocol outlined above but with the trunk-hip angle at  $180^\circ$  (supine task). This was performed so as to evaluate the influence of the hip joint angle on EMG activity and time to task failure of knee extensor muscles for a fatiguing contrac-

tion. The experiment was performed at least 2 wk after the third session of *experiment 1* and on one occasion.

*MVC FORCE.* Each subject performed three maximal 3-s isometric contractions with the knee extensor muscles, followed by a 30-s rest period. The MVC task consisted of a gradual increase in force from zero to maximum over 3 s, with the maximal force held for 2–3 s. Verbal encouragement was given to the subjects during each maximal voluntary contraction. Subjects were also provided with visual feedback of the knee extensor muscle torque on a monitor that was placed 1 m in front of the subject. The gain of the visual feedback was changed between each trial (15). If the peak torques from two of the three trials were not within 5% of each other, additional trials were performed until this was accomplished. The greatest torque achieved by the subject was taken as the MVC torque and for calculation of submaximal target torques. The same procedure was followed for assessment of the MVC torque of the knee flexor muscles so as to obtain the peak EMG from the biceps femoris (BF) muscle and assess coactivation during the fatiguing contraction.

*FATIGUING CONTRACTION.* Each subject performed an isometric fatiguing contraction with the knee extensor muscles maintained at 20% of MVC torque as determined from the MVC performed on that day. Visual feedback of the torque exerted was displayed on the monitor. The fatiguing contraction was terminated when torque fell below the target level for a 5-s period despite strong verbal encouragement from the investigators.

### *Data Collection*

*Strength measurement.* Instantaneous isometric torque at the knee joint was recorded by using a Biodex isokinetic dynamometer (Shirley, NY). The subjects were placed in a seated posture with the trunk-thigh angle at  $90^\circ$  for the seated task. Each subject was securely strapped to the test chair with two crossover-shoulder harnesses and a belt across the abdomen. During the supine task, each subject was with a trunk-thigh angle of  $180^\circ$ . Extraneous movement of the upper body while in the supine position was also minimized with the crossover-shoulder harnesses and a belt across the abdomen. The axis of the dynamometer was aligned with the knee-extension axis, and the lever arm was attached to the shank with a strap. To allow the recording of the BF EMG, a board was placed underneath the subject with a hole where the electrodes were placed so as to avoid any compression of the surface electrodes and wires. Both experiments were performed on the right leg and with a knee joint angle of  $90^\circ$  of flexion ( $0^\circ$  = knee fully extended).

*EMG recording.* Muscle electrical activity (EMG) of the vastus lateralis (VL), vastus medialis (VM), RF, and BF muscles was recorded with pairs of silver chloride circular (diameter 20 mm) surface electrodes (Controle Graphique Medical, Brie-Comte-Robert, France). The skin was carefully prepared to obtain a low resistance between the two electrodes ( $<5$  k $\Omega$ ) by light abrasion and removal of oil and dirt with an alcohol swab. Electrodes were coated with electrode gel and fixed lengthwise on the skin over the middle of the VL, VM, RF, and BF muscles and with an interelectrode distance of 20 mm. The electrodes were placed at  $\frac{2}{3}$  on the line from the anterior spina iliaca superior to the lateral side of the patella for the VL, at  $\frac{4}{5}$  on the line between the anterior spina iliaca superior and the joint space in front of the anterior border of the medial ligament for the VM, at  $\frac{1}{2}$  on the line from the anterior spina iliaca superior to the superior part of the patella for the RF, and at 50% on the line between the ischial tuberosity and the lateral epicondyle of

the tibia for the BF. These sites were determined in pilot testing by eliciting the greatest M wave amplitude that was able to be evoked for each muscle via femoral nerve stimulation (model DS7, Digimeter, Hertfordshire, UK). These procedures were performed so as to avoid the innervation zone and therefore obtain the optimal amplitude of the EMG response (30). The reference electrode was placed on a bony prominence on the right wrist. Myoelectric signals were amplified with a bandwidth frequency ranging from 1.5 to 500 Hz (common mode rejection ratio = 100 M $\Omega$ ; gain = 1,000). Torque and EMG signals were digitized on-line (sampling frequency 2,000 Hz) by using a digital computer (IPC 486). EMG recordings of the knee extensor muscles are reliable across repeat sessions of the knee extensor muscles (36).

#### Data Analysis

**EMG activity.** EMG signals of VL, VM, RF, and BF muscles were collected on-line and quantified as the root mean square (RMS). For the MVC and submaximal isometric contractions at target torques of 20, 50 and 80% MVC, EMG signals were quantified as the RMS over a 0.5-s period after the torque had reached a plateau. EMG amplitude was calculated for consecutive sampling intervals that were 10% duration of the time to task failure for the VL, VM, RF, and BF muscles. The RMS of the EMG signal was normalized to that determined during the MVC performed before the fatiguing contraction.

**Coefficient of variation.** The amplitude of the torque fluctuations was quantified as the coefficient of variation (CV = SD/mean) for consecutive 10% windows of the time to task failure.

#### Statistical Analysis

All variables were statistically examined for normality and allowed for the appropriate use of parametric statistics. The time to task failure was compared across the sessions for the seated task by using a one-way, repeated-measures ANOVA. The EMG RMS amplitude of the knee extensor and knee flexor muscles, calculated during the fatiguing task, was analyzed using a three-factor, repeated-measures ANOVA [session  $\times$  muscle  $\times$  time (10, 20, 30, 40, 50, 60, 70, 80, 90, 100%)] with repeated measures on time and session. The amplitude of the torque fluctuations (CV of torque) was analyzed using a two-factor, repeated-measures ANOVA [session  $\times$  muscle  $\times$  time (10, 20, 30, 40, 50, 60, 70, 80, 90, and 100%)] with repeated measures on time and session. The MVC torque and the EMG RMS were analyzed by using a two-factor, repeated-measures ANOVA [session  $\times$  exercise (pre, post)] with repeated measures on exercise and session. The EMG-torque relation was analyzed by using with a two-factor, repeated-measures ANOVA (session  $\times$  muscle) with repeated measures on session. Separate repeated-measures ANOVAs were used to compare the dependent variables in the supine and seated postures. When significant main effects were found, the post hoc analysis (Tukey) was performed. Significance was accepted when  $P < 0.05$ . The statistical analyses were undertaken by using Statistica software for Windows (StatSoft, version 5.1, Statistica, Tulsa, OK). All data are expressed as means  $\pm$  SD within the text and displayed as means  $\pm$  SE in the figures.

## RESULTS

### Seated Posture Task Across Sessions

This study examined the time to task failure and pattern of EMG activity of the knee extensor muscles

for a fatiguing contraction sustained at 20% of MVC torque over three repeat sessions with the subject in a seated posture. Time to task failure for the fatiguing contractions did not change significantly from session 1 to session 3. The time to task failure for sessions 1, 2, and 3 were  $289 \pm 79$ ,  $314 \pm 94$ , and  $309 \pm 87$  s respectively (Fig. 1A). The intraclass correlation for the three sessions was  $r = 0.68$ .

**MVC torque.** AGONIST: KNEE EXTENSOR MUSCLES. The MVC torque recorded before the fatiguing contraction was similar across the three sessions. After the fatiguing contraction, the MVC torque of the knee extensor muscles (mean of 3 sessions) declined by  $42 \pm 12\%$  from  $314 \pm 64$  to  $186 \pm 69$  N $\cdot$ m ( $P < 0.001$ ). The reduction in MVC torque was also similar across sessions ( $P > 0.05$ ) (Fig. 1B).

ANTAGONIST: KNEE FLEXOR MUSCLES. The MVC torque of the knee flexor muscles performed before the fatiguing contraction was similar for sessions 1, 2, and 3. Furthermore, there was no difference in MVC torque before and after the fatiguing contraction of the knee flexor muscle group ( $104 \pm 5$  vs.  $98 \pm 4$  N $\cdot$ m;  $P < 0.17$ ). The EMG amplitude during the performance of the MVC of the BF muscle was not different before and after the fatiguing contraction ( $7.3 \pm 1.8$  vs.  $7.0 \pm 1.1\%$ ).

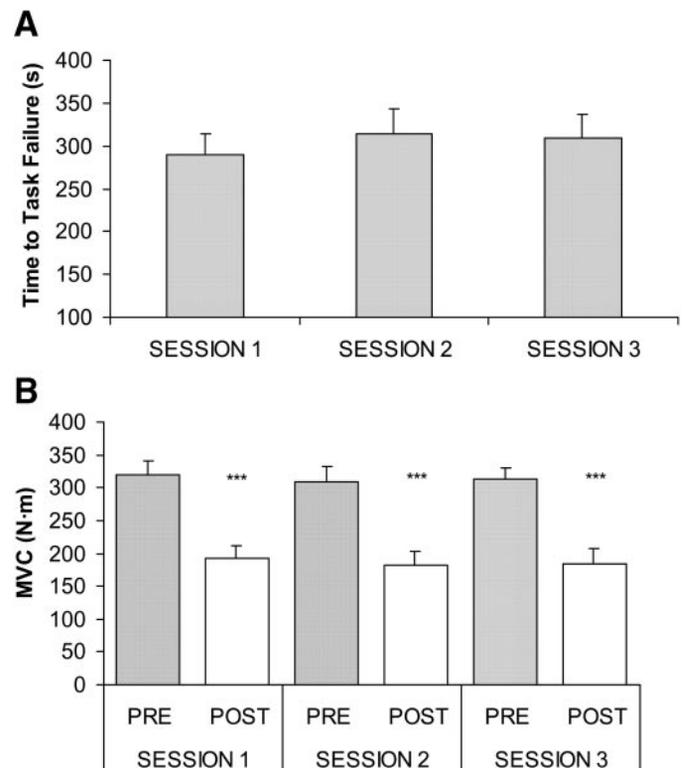


Fig. 1. Time to task failure and maximal voluntary contraction (MVC) torque across the 3 sessions for the seated task. A: time to task failure (mean  $\pm$  SE) was similar across the 3 sessions ( $P > 0.05$ ). B: MVC torque (mean  $\pm$  SE) of the knee extensor muscles, before (pre) and immediately after (post) the fatiguing contraction was similar across the 3 sessions ( $P > 0.05$ ). Reduction in MVC torque was  $42 \pm 12\%$ . \*\*\*Significantly different from pre value,  $P < 0.001$ .

**EMG-torque relation.** The average amplitude of the RMS of the EMG (normalized to MVC value) for the knee extensor muscles was determined for brief isometric contractions held at 20, 50, and 80% of MVC torque. EMG increased with contraction intensity for all the knee extensor muscles ( $P < 0.05$ ) and was similar across sessions ( $P > 0.05$ ). There was no interaction for intensity and session ( $P > 0.05$ ), indicating that the increase in EMG was consistent across the three sessions. The EMG for the RF muscle was greater at 20% than the VM and VL muscles but similar at the higher intensities of contraction as indicated by an interaction of muscle and intensity ( $P < 0.05$ ) (Fig. 2). There was no interaction of muscle and session, indicating that across sessions the increase in EMG was consistent for each of the knee extensor muscles.

**EMG activity.** AGONISTS: KNEE EXTENSOR MUSCLES. The RMS EMG (%peak MVC) for each knee extensor muscle during the fatiguing contractions was similar across the three sessions ( $P > 0.05$ ). The EMG of the knee extensor muscles (VL, VM, and RF) progressively increased throughout the fatiguing contraction ( $P < 0.001$ ). At the beginning of the contraction (first 10% of time to task failure) the EMG was  $21.7 \pm 1.2\%$  and increased to  $45.4 \pm 3.1\%$  at the end of the fatiguing contraction (last 10% of time to task failure). Furthermore, there was no interaction for time and session ( $P > 0.05$ ), indicating that the increase in EMG during the fatiguing contraction was similar across sessions for the knee extensor muscles.

However, the rate of increase among the knee extensor muscles differed during the fatiguing contraction ( $P < 0.05$ ). The average rates of increase in EMG of the monoarticular muscles, VL and VM, were greater than the biarticular muscle, the RF muscle. The RF EMG began at a greater value ( $29.7 \pm 2.5\%$ ) compared with the VL and VM muscles ( $18.5 \pm 2.7\%$ ) and ended at a similar value ( $45.4 \pm 3.0\%$ ). Therefore, the RF increased at lower average rate compared with the VL and VM ( $P < 0.001$ ) (Fig. 3A).

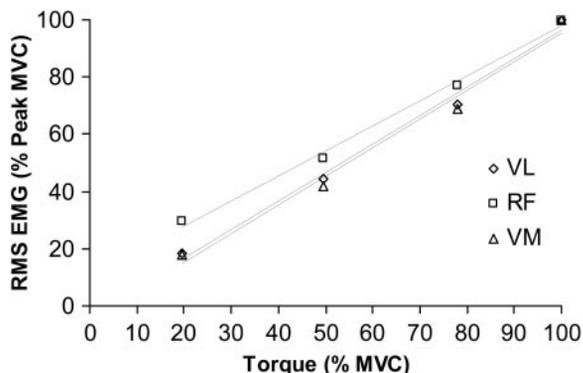


Fig. 2. Relation between root mean square (RMS) electromyograph (EMG, %peak value during the MVC) and the net torque (%MVC torque) of the knee extensor muscles. EMG values of the 3 sessions are averaged because there was no difference across sessions ( $P > 0.05$ ). The EMG increased with the target torque, but the EMG for rectus femoris (RF) muscle was greater at the lower intensities of contraction compared with vastus lateralis (VL) and vastus medialis (VM) muscles ( $P < 0.05$ ).

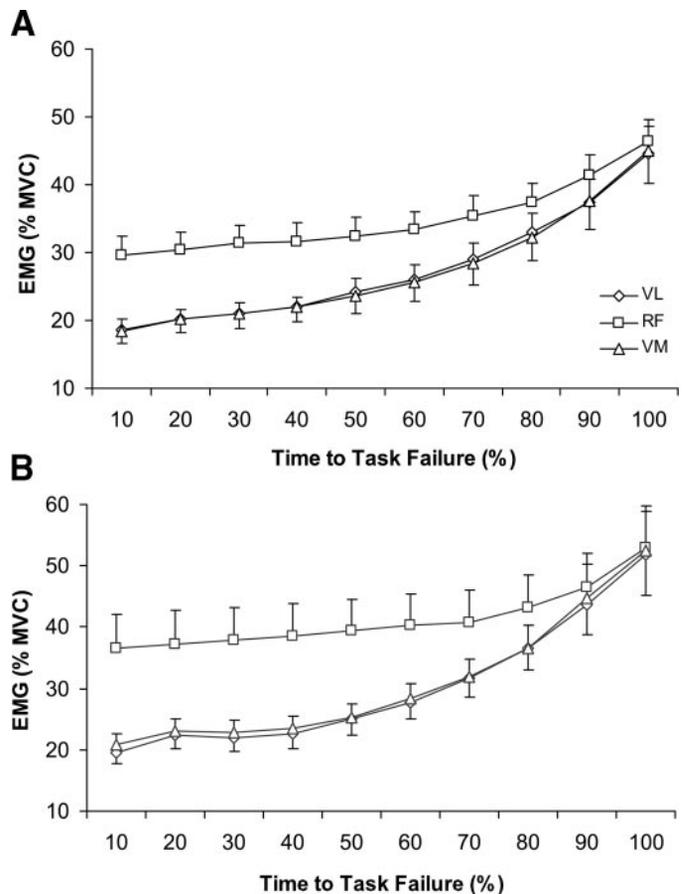


Fig. 3. Mean RMS EMG (normalized to the maximum RMS EMG obtained during the MVC) during the fatiguing contraction in the seated (A) and the supine (B) postures for the VL, RF, and VM muscles. Values are means  $\pm$  SE. Each data point represents the mean RMS EMG for 10% of the time to task failure. A: RMS EMG was averaged across sessions because there was no main effect of sessions. B: increase in EMG activity for all the knee extensor muscles was similar for the supine and seated tasks ( $P > 0.05$ ). The EMG for the RF was greater at the beginning of the fatiguing contraction ( $P < 0.05$ ) compared with the VL and VM muscles but ended at a similar value ( $P > 0.05$ ) for the seated and supine tasks.

ANTAGONIST: BF MUSCLE. EMG activity of the BF increased significantly throughout the fatiguing contraction ( $P < 0.001$ ) (Fig. 4). However, the rate of increase of the BF EMG during the fatiguing contraction performed over the three sessions differed between sessions 1 and 3 and between sessions 2 and 3 ( $P < 0.05$ ). At the end of fatiguing contraction, the BF RMS for the sessions 1, 2, and 3 was  $4.5 \pm 0.9$ ,  $4.3 \pm 0.9$ , and  $3.8 \pm 0.7\%$  respectively. Consequently, the rate of increase in EMG of the BF muscle was reduced across sessions.

**Torque fluctuations.** The amplitude of the normalized torque fluctuations, which was characterized by the CV for torque, increased significantly during the fatiguing contractions ( $P < 0.001$ ). However, the CV remained similar until 60% of time to task failure ( $P < 0.05$ ), after which the CV increased significantly (Fig. 5). Consistent with the EMG results, the average rate of increase in CV did not differ across the sessions.

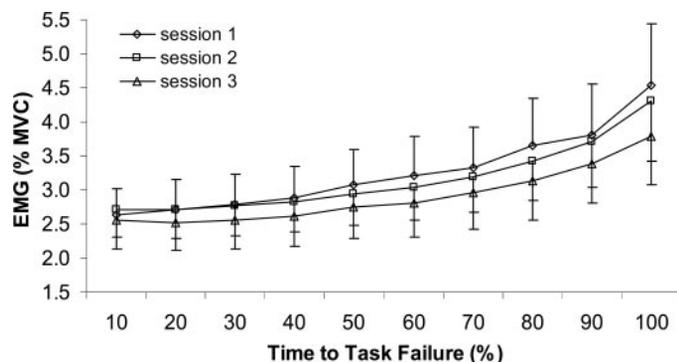


Fig. 4. Mean RMS EMG (normalized to the maximum EMG obtained during the MVC) of the antagonistic biceps femoris muscle during the fatiguing contraction for *sessions 1, 2, and 3*. Values are means  $\pm$  SE. Each data point represents the mean EMG for 10% of the time to task failure. The EMG increases significantly during the fatiguing contraction ( $P < 0.001$ ) for all sessions. The average rate of increase in EMG decreased significantly from *session 1* to *session 3* ( $P < 0.05$ ).

#### Seated vs. Supine Posture

**MVC and time to task failure.** The MVC torque recorded before the fatiguing contraction was greater for the seated task compared with that performed in the supine posture ( $314 \pm 62$  vs.  $272 \pm 49$  N·m;  $P < 0.05$ ). The decline in MVC torque after the fatiguing contraction was greater for the seated task vs. the supine task ( $42 \pm 12$  vs.  $35 \pm 12\%$ , respectively;  $P < 0.05$ ). Despite the greater reduction in maximal torque, the time to task failure for the fatiguing contraction (performed at 20% of the MVC value recorded for that posture) did not differ between the seated task ( $304 \pm 77$  s) and the supine task ( $272 \pm 82$  s;  $P > 0.05$ ). Furthermore, there was no difference in time to task failure for the seated and supine tasks when an analysis of covariance was performed, covarying for the reduction in MVC torque ( $P > 0.05$ ) (Fig. 6). This indicates that the greater reduction in MVC torque after the seated task was independent of the time to task failure.

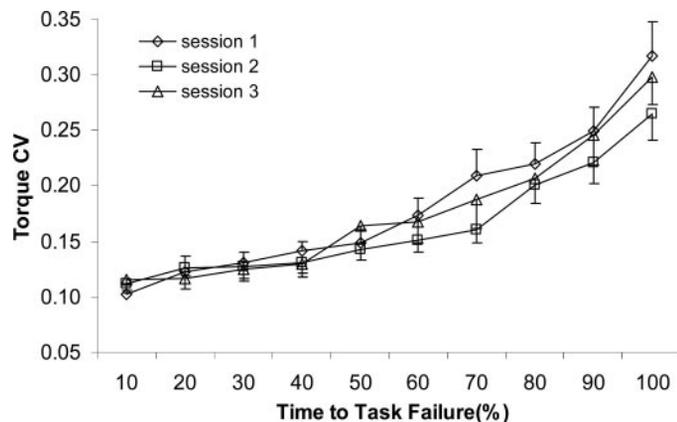


Fig. 5. Coefficient of variation (CV) for torque (mean  $\pm$  SE) during the fatiguing contraction. The CV was similar across sessions ( $P > 0.05$ ). The CV is presented for each session, and each data point represents the mean CV for 10% of the time to task failure. The CV increased significantly during the 3 fatiguing contractions ( $P < 0.001$ ).

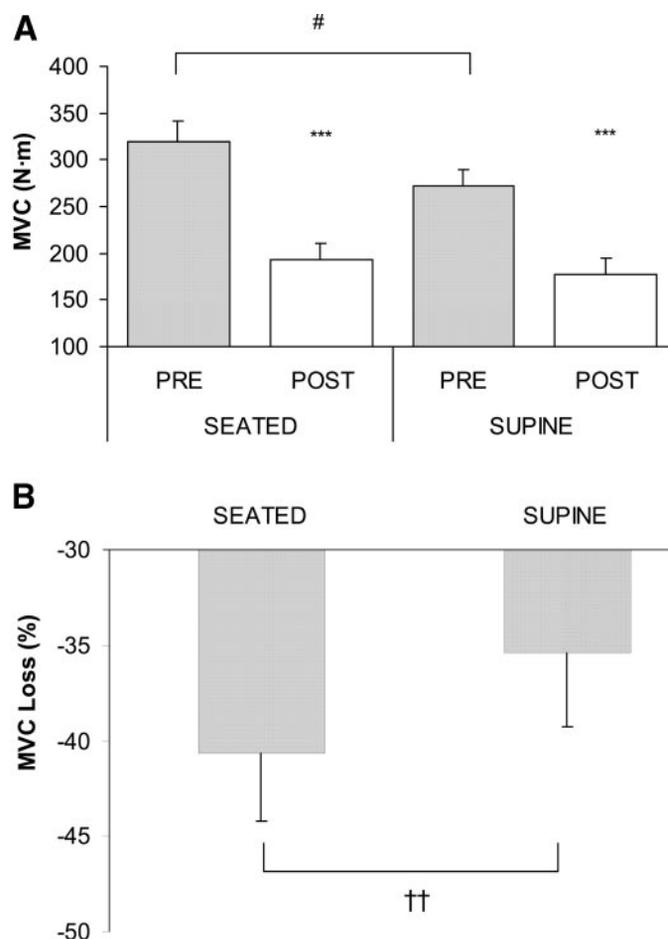


Fig. 6. A: MVC (mean  $\pm$  SE) before and immediately after the fatiguing contraction for the seated task (average value of the 3 sessions) and the supine task. The MVC torque performed before the fatiguing contraction was greater for the seated task compared with the supine task ( $P < 0.05$ ). B: reduction in MVC torque (mean  $\pm$  SE) after the fatiguing contraction was greater for the seated task compared with the supine task ( $41 \pm 11$  vs.  $35 \pm 12\%$ , respectively;  $P < 0.01$ ). \*\*\*Significantly different from pre value,  $P < 0.001$ . #Significant difference in MVC torque performed before the fatiguing contraction between the 2 tasks,  $P < 0.05$ . ††Significantly greater decrease in MVC torque for the seated task,  $P < 0.01$ .

**EMG activity.** The EMG activity of all the knee extensor muscles increased throughout the fatiguing contraction for the supine task ( $P < 0.001$ ). Furthermore, the rate of increase in EMG for all the knee extensor muscles was similar for the supine and seated tasks ( $P > 0.05$ ). As was observed for the seated posture, the RF had a greater EMG amplitude at the beginning of the contraction compared with the VL and VM muscles for the supine posture but a similar EMG value at the end of the contraction (Fig. 3B). Therefore, the pattern of EMG activity of the knee extensor muscles, and in particular the RF muscle, was not influenced by the change in hip-trunk angle.

**Torque fluctuations.** The CV for torque increased during the fatiguing contractions ( $P < 0.001$ ). Consistent with the EMG results, the average rate of increase in CV did not differ between the seated and the supine postures ( $P > 0.05$ ).

## DISCUSSION

The primary purpose of the study was to compare the time to task failure and the pattern of EMG activity of the knee extensor muscles across three performances while maintaining a submaximal torque. A secondary purpose was to compare the time to task failure and EMG activity of the knee extensor muscles in a seated posture vs. a supine posture. The major findings were that 1) the time to task failure and pattern of the EMG activity did not change across repeat performances of a submaximal contraction of the knee extensor muscles; 2) the time to task failure performed at the same relative target torque was not influenced by the change in posture, but the reduction in maximal torque after the fatiguing contraction was greater for the seated task compared with the supine task; and 3) the pattern of EMG activity differed among knee extensor muscles during the submaximal fatiguing contraction for both the seated and supine tasks. The EMG activity for the RF was greater at the beginning of the contractions compared with the VL and VM muscles but at termination of the task had similar values. These findings indicate that the rate of increase in EMG activity among the knee extensor muscles and the subsequent time to task failure did not alter over repeat sessions as had been observed for the elbow flexor muscles (19).

### *Time to Task Failure Was Similar Across Sessions for the Knee Extensor Muscles*

Time to task failure for a submaximal isometric contraction performed with the knee extensor muscles while in the seated posture was similar across sessions. The reduction in MVC torque after the fatiguing contraction did not change across the three sessions, indicating a similar magnitude of fatigue at the end of the seated task. In contrast, when subjects maintained a force at 20% of MVC force across three sessions with the elbow flexor muscles (19), the time to task failure increased over the three sessions by an average of 60% of time to task failure for 9 of the 16 subjects. The improvement in performance was independent of the target force exerted but was associated with alterations in the rate of increase in the averaged EMG between sessions and among the synergists, the rate of bursting of the EMG signal, and the rate of increase in force fluctuations. This provided evidence that the time to task failure for a low-force contraction of the elbow flexor muscles can be limited by neural activation of the muscles (19). The elbow flexor muscle group consists of four major agonists that have different origins, insertions, and moment arms, each independently exerting a torque at the elbow joint (31, 43). In contrast, the knee extensor muscle group comprises four agonists, three that have a common insertion onto the patella and act together to exert a torque at the knee, possibly limiting independent alterations of activation and torque of each muscle. Accordingly, practice of a task in which subjects were required to maintain a force of the knee extensors muscles did not involve alterations in the activation of the individual muscles

nor the time to task failure. Consistent with these findings, there was no change in time to task failure over repeated session for a submaximal fatiguing contraction of a small muscle of the hand, the first dorsal interosseous (13), which has a single tendon insertion. In contrast, the time to task failure and EMG activity did not adapt across sessions for the elbow flexor muscles when the task was to control for the position of the limb while supporting an inertial load (20). Taken together, these results suggest the capacity of the nervous system to modulate synergist muscles and the duration of a low-intensity contraction specific to controlling for force is related to the structural organization of a muscle group.

Consistent with the EMG results was the similar rate of increase in torque fluctuations during the contractions across the sessions for the knee extensor muscles. The increase in torque fluctuations during a fatiguing contraction is mediated by descending drive and peripheral afferent feedback (6, 28). These results indicate that the rate of increase in the descending drive and peripheral feedback during the fatiguing contractions were similar across the sessions for the knee extensor muscles. In contrast, torque fluctuations changed during a fatiguing contraction across repeat sessions for the elbow flexor muscles and in parallel with the changes in EMG activity for those subjects who improved their time to task failure (19). These results underscore that the different capacity to change the activation of synergist muscles and the duration of a low-force contraction is related to the muscle group.

To investigate the role of activation by an antagonistic muscle during the fatiguing contraction of the knee extensor muscles, the EMG activity of the BF muscle was measured across the three sessions. The magnitude of activation by the BF muscle was small but increased throughout the fatiguing contraction and this is similar to findings from another study (9). However, we found the EMG activity of this antagonist muscle decreased across the sessions. This is consistent with studies investigating adaptations of antagonist muscles after a period of isometric training (35, 38). Despite the reduction in activation by the BF muscle, there was no increase in time to task failure across sessions, probably because the magnitude of muscle activity of the BF muscle was small.

### *Increase in EMG Activity Differed Between Synergist Muscles*

The EMG activity of a muscle will progressively increase when an individual is asked to maintain a submaximal force until exhaustion (10, 13, 41). The increase in EMG activity is influenced primarily by an increase in the recruitment of additional motor units (4, 5, 14, 16), and possibly motor unit synchronization (23) and signal cancellation (7). We found the knee extensor muscles exhibited the characteristic increase in EMG activity toward exhaustion, which was 45% of the level achieved during the MVC performed before

the fatiguing contraction. We also normalized the EMG achieved at the end of the fatiguing contraction to the peak EMG achieved during a MVC performed immediately after termination of the task. The reduction in EMG activity was substantial, at 60% of post-MVC value. The mechanism for the deficit in EMG activity despite maximal effort by the subjects is not clear but may involve inhibition of spinal and supraspinal centers, which is more prominent for low-force contractions (13, 14). However, the contribution during a sustained fatiguing contraction of signal cancellation of the interference EMG from overlapping positive and negative phases of action potentials (7, 44) is not known, although it is unlikely that signal cancellation differed across sessions because of the similar electrode placement and similar rate of increase in EMG activity during the repeated contractions.

The rate of increase in EMG activity was similar across sessions but differed among the knee extensor muscles. The EMG activity of the RF at the beginning of the contractions was larger (30% of maximum) compared with the VL and VM (19%) but similar at termination of the contraction (45%). Consequently, the rate of increase of EMG activity was less for the RF muscle compared with the VL and VM. We also observed a nonparallel EMG-force relation among the quadriceps muscles when subjects were asked to exert torque at increasing intensities (Fig. 2), which is similar to other findings (34). This difference in EMG activity among the knee extensor muscles during the sustained contractions may be due to the specific functions of the monoarticular muscles (VL and VM) compared with biarticular muscles (RF) (9, 22). The biarticular muscles provide regulation of the distribution of the net moments about the hip and the knee joint, whereas the monoarticular muscles regulate that about the knee joint (21). Alternatively, signal cancellation may have been greater at the beginning of the contraction for the RF compared with the VL and VM muscles, but this is unlikely because the measurement parameters were similar across muscles. Nevertheless, the results of this study indicate that a synergist muscle is not representative of the activation pattern of the muscle group during an isometric fatiguing contraction.

#### *Time to Task Failure and Activation Patterns Were Similar for Seated and Supine Postures*

A secondary purpose of the study was to compare the time to task failure and EMG activity of the knee extensor muscles in a seated posture vs. a supine posture. By altering posture, we examined the influence of the length of the RF muscle on the EMG activity and time to task failure. When subjects were in a seated posture, the RF muscle was shortened. Other studies show that muscle length can influence the fatigability of the muscle (12, 18, 31, 32). However, we observed no differences in the time to task failure between the seated and supine postures. Furthermore, the rate of increase in the EMG activity of the RF, VL, and VM muscles and the increase in torque fluctua-

tions of the knee extensor muscles were not different across the two tasks. Consequently, the change in length of the RF muscle did not significantly influence the time to sustain a low-force contraction of the knee extensor muscles.

Related to these findings was the magnitude of the MVC torque exerted before and after the fatiguing contraction. The MVC of the knee extensor muscles was less in the seated posture by 10% and consistent with other studies when performed before the fatiguing tasks (27). This difference was attributed to less activation of the knee extensor muscles in the supine posture (27), possibly with little influence of the shortened RF muscle (33). However, the loss of MVC torque was less for the supine task compared with the seated task despite a similar time to task failure for two postures. All the subjects were highly motivated with a similar rise in torque fluctuations and increase in EMG during the two tasks. Furthermore, the criteria for terminating the tasks were similar, and therefore the supine task was not terminated prematurely, which may have explained the reduced loss of MVC torque. Consequently, these results suggest that those factors resulting in task failure for the two postures were likely to be different to the mechanisms for the reduction in MVC that was performed after the fatiguing contraction. Accordingly, decreases in the force exerted during sustained maximal contractions appear to be primarily attributable to impairment in processes that are distal to the neuromuscular junction (3, 15). Alternatively, the reduction in force associated with contractions at low forces appears to involve both neural and peripheral mechanisms (8, 26). These results underscore that those mechanisms responsible for reduction in force depend on the details of the task.

In summary, practice of a sustained submaximal isometric contraction at a low force with the knee extensor muscles that share a common tendon insertion did not alter the EMG activity, torque fluctuations, or time to task failure as had been observed for the elbow flexor muscles (19). These results indicate that the capacity to modulate activation of synergist muscles during a low-intensity contraction controlled for force is related to the structural organization of a muscle group. However, the amplitude and rate of increase in EMG activity varied among the knee extensor muscles during the fatiguing contraction, indicating that a synergist is not representative of the activation pattern of a muscle group. The greater EMG activity of the RF muscle was not due to alterations in muscle length, which was manipulated by performing the fatiguing contraction in the seated and supine posture. Although the time to task failure was similar with alterations in posture, the reduction in maximal torque was greater for the seated task. These results suggest that the mechanisms that contribute to task failure of a low-intensity sustained contraction are different from those that contribute to loss of torque for a maximal contraction.

## REFERENCES

1. Akima H, Foley JM, Prior BM, Dudley GA, and Meyer RA. Vastus lateralis fatigue alters recruitment of musculus quadriceps femoris in humans. *J Appl Physiol* 92: 679–684, 2002.
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. Bigland-Ritchie B, Cafarelli E, and Vollestad NK. Fatigue of submaximal static contractions. *Acta Physiol Scand Suppl* 556: 137–148, 1986.
4. Carpentier A, Duchateau J, and Hainaut K. Motor unit behaviour and contractile changes during fatigue in the human first dorsal interosseus. *J Physiol* 534: 903–912, 2001.
5. Christova P, Kossev A, and Radicheva N. Discharge rate of selected motor units in human biceps brachii at different muscle lengths. *J Electromyogr Kinesiol* 8: 287–294, 1998.
6. 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.
7. 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.
8. Duchateau J, Balestra C, Carpentier A, and Hainaut K. Reflex regulation during sustained and intermittent submaximal contractions in humans. *J Physiol* 541: 959–967, 2002.
9. Ebenbichler GR, Kollmitzer J, Glockler L, Bochdanský T, Kopf A, and Fialka V. The role of the biarticular agonist and cocontracting antagonist pair in isometric muscle fatigue. *Muscle Nerve* 21: 1706–1713, 1998.
10. Ebenbichler G, Kollmitzer J, Quittan M, Uhl F, Kirtley C, and Fialka V. EMG fatigue patterns accompanying isometric fatiguing knee-extensions are different in mono- and bi-articular muscles. *Electroencephalogr Clin Neurophysiol* 109: 256–262, 1998.
11. Fallentin N, Jorgensen K, and Simonsen EB. Motor unit recruitment during prolonged isometric contractions. *Eur J Appl Physiol Occup Physiol* 67: 335–341, 1993.
12. Fitch S and McComas A. Influence of human muscle length on fatigue. *J Physiol* 362: 205–213, 1985.
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. Gandevia SC, Allen GM, Butler JE, and Taylor JL. Supraspinal factors in human muscle fatigue: evidence for suboptimal output from the motor cortex. *J Physiol* 490: 529–536, 1996.
16. Garland SJ, Enoka RM, Serrano LP, and Robinson GA. Behavior of motor units in human biceps brachii during a submaximal fatiguing contraction. *J Appl Physiol* 76: 2411–2419, 1994.
17. Garland SJ, Griffin L, and Ivanova T. Motor unit discharge rate is not associated with muscle relaxation time in sustained submaximal contractions in humans. *Neurosci Lett* 239: 25–28, 1997.
18. 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.
19. 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.
20. Hunter SK, Lepers R, MacGilliss 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.
21. Jacobs R and van Ingen Schenau GJ. Control of an external force in leg extensions in humans. *J Physiol* 457: 611–626, 1992.
22. Kamo M. Discharge behavior of motor units in knee extensors during the initial stage of constant-force isometric contraction at low force level. *Eur J Appl Physiol* 86: 375–381, 2002.
23. Kleine BU, Stegeman DF, Mund D, and Anders C. Influence of motoneuron firing synchronization on SEMG characteristics in dependence of electrode position. *J Appl Physiol* 91: 1588–1599, 2001.
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. Kukulka CG and Clamann HP. Comparison of the recruitment and discharge properties of motor units in human brachial biceps and adductor pollicis during isometric contractions. *Brain Res* 219: 45–55, 1981.
26. Löscher 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. Maffioletti NA and Lepers R. Knee extensors voluntary and electrically evoked torque and EMG activity in seated vs. supine position. *Am J Sports Med*. In press.
28. McAuley JH and Marsden CD. Physiological and pathological tremors and rhythmic central motor control. *Brain* 123: 1545–1567, 2000.
29. McKenzie DK and Gandevia SC. Influence of muscle length on human inspiratory and limb muscle endurance. *Respir Physiol* 67: 171–182, 1987.
30. Merletti R, Rainoldi A, and Farina D. Surface electromyography for noninvasive characterization of muscle. *Exerc Sport Sci Rev* 29: 20–25, 2001.
31. Murray WM, Buchanan TS, and Delp SL. The isometric functional capacity of muscles that cross the elbow. *J Biomech* 33: 943–952, 2000.
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. Pavol MJ and Grabiner MD. Knee strength variability between individuals across ranges of motion and hip angles. *Med Sci Sports Exerc* 32: 985–992, 2000.
34. Pincivero DM and Coelho AJ. Activation linearity and parallelism of the superficial quadriceps across the isometric intensity spectrum. *Muscle Nerve* 23: 393–398, 2000.
35. Psek JA and Cafarelli E. Behavior of coactive muscles during fatigue. *J Appl Physiol* 74: 170–175, 1993.
36. Rainoldi A, Bullock-Saxton JE, Cavarretta F, and Hogan N. Repeatability of maximal voluntary force and of surface EMG variables during voluntary isometric contraction of quadriceps muscles in healthy subjects. *J Electromyogr Kinesiol* 11: 425–438, 2001.
37. Rochette L, Place N, Lepers R, Hunter SK, MacGilliss CJ, and Enoka RM. Activation differs among the knee extensor muscles during a submaximal isometric fatiguing contraction (Abstract). *Arch Physiol Biochem* 110: 25, 2002.
38. Rothmuller C and Cafarelli E. Effect of vibration on antagonist muscle coactivation during progressive fatigue in humans. *J Physiol* 485: 857–864, 1995.
39. Semmler JG, Kutzscher DV, and Enoka RM. Gender differences in the fatigability of human skeletal muscle. *J Neurophysiol* 82: 3590–3593, 1999.
40. Semmler JG, Kutzscher DV, and Enoka RM. Limb immobilization alters muscle activation patterns during a fatiguing isometric contraction. *Muscle Nerve* 23: 1381–1392, 2000.
41. Stephens JA and Taylor A. Fatigue of maintained voluntary muscle contraction in man. *J Physiol* 220: 1–18, 1972.
42. Tamaki H, Kitada K, Akamine T, Murata F, Sakou T, and Kurata H. Alternate activity in the synergistic muscles during prolonged low-level contractions. *J Appl Physiol* 84: 1943–1951, 1998.
43. Van Zuylen EJ, Gielen CC, and Denier van der Gon JJ. Coordination and inhomogeneous activation of human arm muscles during isometric torques. *J Neurophysiol* 60: 1523–1548, 1988.
44. Yao W, Fuglevand RJ, and Enoka RM. Motor-unit synchronization increases EMG amplitude and decreases force steadiness of simulated contractions. *J Neurophysiol* 83: 441–452, 2000.