SCANDINAVIAN JOURNAL OF
MEDICINE & SCIENCE
IN SPORTS

Neuromuscular fatigue differs following unilateral vs bilateral sustained submaximal contractions

B. Matkowski[1], N. Place[2], A. Martin[1], R. Lepers[1]

[1]INSERM U887, Université de Bourgogne, Dijon, France, [2]Institut des Sciences du Mouvement et de la Médecine du Sport, Université de Genève, Genève, Switzerland
Corresponding author: Boris Matkowski, INSERM U887, Faculté des Sciences du Sport, Université de Bourgogne, BP 27 877 21 078 Dijon Cedex, France. Tel: +33 3 80 39 67 61, Fax: +33 3 80 39 67 49, E-mail: boris.matkowski@u-bourgogne.fr

The purpose of the present study was to compare the mechanisms of fatigue induced by a unilateral vs a bilateral submaximal isometric knee extension. Ten physically active men completed two experimental sessions, randomly presented. They were asked to maintain an isometric knee extension force corresponding to 20% of the maximal voluntary contraction (MVC) until task failure with one leg (unilateral) vs two legs (bilateral). MVCs were performed before and after the sustained contraction. Transcutaneous electrical stimuli were used to examine central (voluntary activation) and peripheral (peak doublet force at rest) fatigue on the exercised leg. Time to task failure was significantly shorter ($P < 0.05$) for the bilateral (245 ± 76 s) compared with the unilateral task (295 ± 85 s). Unilateral MVC force and maximal voluntary activation losses were significantly greater ($P < 0.05$) after the unilateral task than after the bilateral task. Peak doublet force was significantly reduced ($P < 0.01$) after the unilateral task, but not after the bilateral task. The present results demonstrated that time to task failure of a submaximal fatiguing contraction may depend on the number of limbs involved in the task. The greater time to task failure with one leg may have induced greater contractile alterations and a larger MVC loss following the unilateral task.

Sustaining a submaximal isometric contraction for as long as possible leads inevitably to muscle fatigue, which can be characterized by a reduction in the maximal voluntary contraction (MVC) force. Fatigue is task dependent, as task failure appears more or less prematurely according to the characteristics of the task (Enoka & Stuart, 1992; Place et al., 2005; Gondin et al., 2006). Indeed, fatigue (i.e. MVC force reduction) begins long before task failure occurs during submaximal contractions (Søgaard et al., 2006).

There is evidence that task to failure of a submaximal isometric contraction depends on the absolute level of force to be maintained, and generally, stronger subjects have a briefer time to task failure (Hunter & Enoka, 2001; Hunter et al., 2002, 2004). This phenomenon is generally explained by the greater muscle mass involved in stronger subjects, causing an increase in intramuscular pressure, occlusion of blood flow, accumulation of metabolites, heightened metaboreflex responses and impairment of oxygen delivery to the muscle (Hunter et al., 2004). However, this has been evidenced by comparing different populations – with different metabolic properties – according to criteria such as gender (Hunter et al., 2003, 2005b), age (Hunter et al., 2005a) or both (Hunter & Enoka, 2001; Hunter et al., 2002), by using unilateral tasks of the dominant (Place et al., 2005; Gondin et al., 2006) or the non-dominant limb (Hunter et al., 2002, 2004). To override these latter comparisons, bilateral vs unilateral tasks realized by the same subject and at the same relative level of force should be investigated. However, comparison of the neuromuscular alterations when sustaining isometric submaximal contractions until task failure with one vs two segments at the same relative level of force has, to our knowledge, never been examined.

Therefore, the purpose of the present study was to compare the time to task failure and the associated MVC force loss for unilateral vs bilateral fatiguing contractions performed at the same relative level of force on the knee extensor muscles. We hypothesized that endurance time would be longer for the submaximal isometric unilateral contraction compared with bilateral contraction because of the lower level of absolute force maintained by the subjects. To distinguish between central and peripheral adaptations to fatigue, evoked and voluntary contractions were used.

Materials and methods
Subjects

The experiments were performed on 10 physically active men (age: 25.8 ± 5.9 years; height: 179.6 ± 5.6 cm; mass: 74.1 ± 6.6 kg; means $\pm$ standard deviation (SD)) who volun-

teered to participate in the study after they were informed of the experimental procedures and possible risks. None of the subjects had any known neurological and neuromuscular disorder. To determine footedness, the dominant foot (or leg) was defined as the ''effector foot'' (Maupas et al., 2002), i.e. the leg with which subjects spontaneously kick a ball. Before participation, each subject gave a written consent and the University of Burgundy committee on Human Research approved the protocol. The study was conducted according to the Declaration of Helsinki.

Overview

Subjects reported to the laboratory on two occasions, separated by at least 72 h, to perform a protocol that focused on a fatiguing contraction with the knee extensor muscles during a unilateral or a bilateral session. In both sessions, the task was to maintain a force equal to 20% of the MVC force until task failure. In one session, the fatiguing contraction involved the non-dominant leg (left leg for all subjects); this was referred to as the unilateral task. In the other session, the fatiguing contraction involved both legs; this was referred to as the bilateral task. The order of the two tasks was randomized for each subject across experimental days. The two experiments were performed for each subject at the same time of the day to avoid the effect of circadian rhythms (Martin et al., 1999; Guette et al., 2005). All neuromuscular testings were only performed on the non-dominant leg before and immediately after task failure.

Experimental protocol

Before the experimental protocol, subjects performed a standardized warm-up that included several (~ 10) submaximal voluntary contractions between ~ 20% and 80% of the estimated MVC force on both legs. This warm-up was followed by a 2-min resting period without any contraction. The experimental protocol was the same for the two sessions and was performed in the following way (Fig. 1): (1) Two 5-s unilateral left knee extensors MVC force assessments (with a recovery period of 60 s between trials) with doublet delivered 1.5 s before the MVC (resting peak doublet), over the isometric plateau (superimposed doublet) and 1.5 s after each MVC (potentiated peak doublet), to assess the maximal voluntary activation level (VAL) according to the interpolated twitch technique (Place et al., 2007). The greatest level of force achieved by the subject before the fatiguing exercise was taken as the MVC force and used for calculation of the submaximal target force. (2) Two 5-s unilateral right knee extensor MVC force assessments. (3) Two 5-s bilateral (left+right) knee extensor MVC force assessments. (4) Performance of the unilateral or the bilateral task until failure (time to task failure) at 20% of MVC. (5) One MVC with the left knee extensor muscles with doublet delivered over the isometric plateau and 1.5 s after the MVC. (6) One MVC with the right knee extensor muscles. (7) One bilateral MVC.

A subsequent trial was performed if the difference in the peak force between the two MVCs was > 5%. Strong verbal encouragement was given to the subjects during each MVC and during the time to task failure. For the unilateral task, MVC of the left knee extensor muscles was used to determine the submaximal intensity of the sustained contraction, i.e. 20% of MVC. For the bilateral task, MVC of both (left+right) knee extensor muscles was used to determine the submaximal intensity of the sustained contraction. Procedures (1), (2), (3) and (5), (6), (7) were performed in a randomized order before and after time to task failure during both sessions.

Fatiguing contraction

Each subject performed an isometric fatiguing contraction at a target force value of 20% of MVC force as determined from MVC performed on that day. Visual feedback of the force exerted during the sustained contraction was displayed on a screen located 1 m in front of the subject; the gain of the visual feedback (1 N/cm) was kept constant between the two tasks for each subject. Force feedback was displayed as a horizontal line and the subjects were required to reach an upper target line fixed at the target level. The contraction was terminated when the subject deviated from the target force by -5% for a 3-s period, despite strong verbal encouragement by the investigators. This time was recorded as the time to task failure. Subjects were not informed of the time to task failure until completion of the second session.

The rating of perceived exertion (RPE) was assessed according to the Borg scale from 6 to 20 (Borg, 1970) at regular intervals during the fatiguing exercise.

Data collection

Evoked contractions

In order to assess the central and peripheral components of fatigue, transcutaneous electrically evoked contractions were
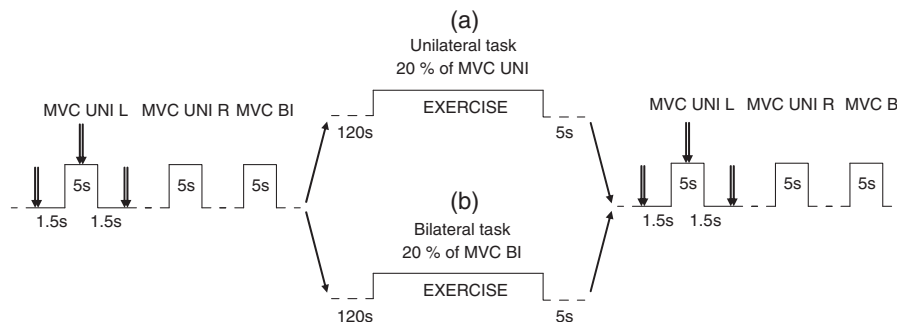

Fig. 1. Graphical overview of the protocol. (a) Unilateral (UNI) session, with a resting doublet (double arrow), superimposed doublet during the maximal unilateral voluntary contraction (MVC) of the left (L) knee extensor muscles, and potentiated doublet, MVC of the right (R) knee extensor muscles, and MVC of both (bilateral) knee extensor muscles before and immediately after the fatiguing isometric unilateral contractions (20% MVC unilateral). (b) Bilateral (BI) session, similar protocol with the fatiguing isometric contractions performed with both legs (20% MVC bilateral). Subject performed the left, right and bilateral MVCs in a random order before and after the fatiguing tasks.

induced using a high-voltage (maximal voltage 400 V) constant-current stimulator (model DS7, Digitimer, Hertfordshire, UK) (Place et al., 2007). The femoral nerve was stimulated using a monopolar cathode ball electrode (0.5 cm diameter) pressed into the femoral triangle by the same experimenter during all testing sessions. The site of stimulation was marked on the skin by indelible ink so that it could be repeated after the sustained contraction. The anode was a $50 \, cm^2$ (10 cm × 5 cm) rectangular electrode (Compex SA, Ecublens, Switzerland) located in the gluteal fold opposite the cathode. The optimal intensity of stimulation 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 knee extensors compound muscle action potentials (M-wave). This intensity was further increased by 25% (to ensure that it was supramaximal) and was kept constant throughout the session for each subject. The stimulus duration was 1 ms and the interval of the stimuli in the paired stimulations (doublet) was 13 ms, i.e. ∼ 77 Hz. This stimulation frequency was chosen to enable the study of M-wave characteristics (Loscher et al., 1996). The second M-wave of the doublet was analyzed for vastus lateralis (VL) and rectus femoris (RF) muscles. Resting peak doublet amplitude was used rather than the peak twitch amplitude because it is a better index of fatigue-induced contractile alterations than peak twitch (Kufel et al., 2002; Place et al., 2007).

Mechanical recordings

Maximal isometric force and mechanical responses from the electrical stimulation of the knee extensor muscle were recorded using an isometric ergometer that includes a chair (Multi-form, la Roque d'Anthéron, France) connected to a strain gauge (sensitivity: 1.993 mV/V and 0.0049 V/N; Allegro, Sallanches, France). Subjects were seated with a 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. For the two sessions, the knee angle tested was 80° (0° was fully extended), i.e. close to the optimal length for maximal force production (Becker & Awiszus, 2001; Kubo et al., 2004).

Electrical recordings

Electromyographic activity (EMG) of VL and RF muscles was recorded with pairs of silver chloride circular surface electrodes (recording diameter of 10 mm, Controle Graphique Medical, Brie-Comte-Robert, France) with an interelectrode distance of 20 mm (center to center). The electrodes were placed at 2/3 on the line from the anterior spina iliaca superior to the lateral side of the patella for the VL and at 1/2 on the line from the anterior spina iliaca superior to the superior part of the patella for the RF (Rochette et al., 2003). These recording sites were adjusted in pilot testing by eliciting the greatest M-wave amplitude at a given intensity for each knee extensor muscle via femoral nerve stimulation at the beginning of the experiments and marked on the skin by indelible ink so that they could be repeated for the second session (Place et al., 2005). The reference electrode was attached to the patella of the right knee. Low resistance between the two electrodes ($< 5 \, k\Omega$) 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 = 1000). Mechanical and electrical signals were digitized on-line at a sampling frequency of 2 kHz using a computer (IPC 486; Newton PC, Dijon, France) and stored for analysis with commercially available software (Tida, Heka Elektronik, Lambrecht/Pfalz, Germany).

Data analysis

Mechanical recordings

MVC force was considered as the peak force attained during the contraction. Maximal VAL was calculated using the following formula, i.e., Maximal VAL = [1 − (superimposed doublet amplitude/potentiated doublet amplitude)] × 100 (Allen et al., 1995). In five cases, in which the doublet was applied when the torque level was slightly below the real maximal voluntary force, a correction was applied in the original equation, as suggested by Strojnik and Komi (1998). In these few cases, maximal VAL was calculated as follows: [1 − (superimposed doublet amplitude × voluntary torque level just before the superimposed doublet/maximal voluntary torque)/potentiated doublet amplitude] × 100.

Peak force was analyzed for the doublet before and after the MVC force.

EMG activity

M-wave peak-to-peak amplitude and duration were analyzed for VL and RF muscles. EMG of the VL and RF muscles measured during the MVC was 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.

RMS activity was also quantified for VL and RF muscles during consecutive sampling intervals that were 10% of the time to task failure on the left leg for the unilateral task and on the left and right legs for bilateral tasks. RMS of the EMG signal was normalized to that determined during the MVC performed before the fatiguing contraction, i.e. by left unilateral knee extensors MVC during the unilateral task and by bilateral knee extensors MVC during the bilateral task. In addition to this normalization, the last 10% of the time to task failure was also normalized with the MVC performed after the fatiguing contraction.

Statistical analysis

A paired *t*-test was used to compare the time to task failure between the two sessions. Separated two-factor analysis of variance (ANOVA) (task [unilateral vs bilateral] × time [Pre vs Post]) with repeated measures were used to compare MVC force, maximal VAL and peak force doublet (only on the left leg). Separated three-factor ANOVA (task [unilateral vs bilateral] × time [Pre vs Post] × muscle [VL vs RF]) with repeated measures were used to compare the M-wave amplitude and duration for each muscle on a left leg.

Separated three-factor ANOVA (leg [Right vs Left] × muscle [VL vs RF] × time [10% vs 20% vs . . . vs 100%]) with repeated measures were used to compare EMG activity during time to task failure in the bilateral exercise. Separated three-factor ANOVA (task [unilateral vs bilateral] × muscle [VL vs RF] × time [10% vs 20% vs . . . vs 100%]) with repeated measures were used to compare EMG activity on the left leg during time to task failure between both tasks. *Post hoc*

analyses (Tukey) were used to test for differences among pairs of means when appropriate. Pearson's correlation coefficients (*R*) were used to assess the association between various selected variables. A significance level of *P*<0.05 was used to identify statistical significance. The statistical analyses were performed using Statistica software for Windows (Statsoft, version 6.1, Statistica, Tulsa, Oklahoma, USA). Data are reported as mean ± SD within the text and displayed as means ± standard error in the figures.

Results
Knee extensors MVC force loss and time to task failure

MVCs performed before the sustained contraction were similar across sessions (195 ± 34 vs 190 ± 28 N, 189 ± 29 vs 181 ± 26 N and 418 ± 78 vs 396 ± 82 N for the left, right and both legs, during the unilateral and the bilateral session, respectively; *P*>0.05). Time to task failure of the sustained contraction performed at 20% of MVC was significantly longer (+14%; *P*<0.05) for the unilateral task (295 ± 90 s) than for the bilateral task (245 ± 80 s) [Fig. 2(a)].

During the unilateral task, time to task failure was performed with the left leg. For this task, the right knee extensors' MVC force was not different (*P*>0.05) before and after exercise (189 ± 29 vs 184 ± 27 N, respectively). For the bilateral session, the right knee extensors' MVC force was significantly lower after the fatiguing exercise (−15.2 ± 9.3%; 181 ± 26 vs 154 ± 33 N, respectively; *P*<0.01). After the bilateral session, MVC reduction was similar for both the left and the right leg. The reduction observed post-exercise in the left knee extensors MVC force was significant (*P*<0.01) for both tasks, and was significantly greater (*P*<0.01) for the unilateral than for the bilateral task [−36.6 ± 8.4% vs −22.2 ± 8.5%, respectively; Fig. 4(a)]. The reduction in the bilateral MVC force was significant after the fatiguing exercise for the unilateral session (−22.1 ± 7.8%; 418 ± 78.1 vs 329 ± 81 N, respectively; *P*<0.01) and for the bilateral session (−25.8 ± 10.2%; 396 ± 80 vs 295 ± 79 N, respectively; *P*<0.01), and was not different between the two sessions. There was a significant negative linear
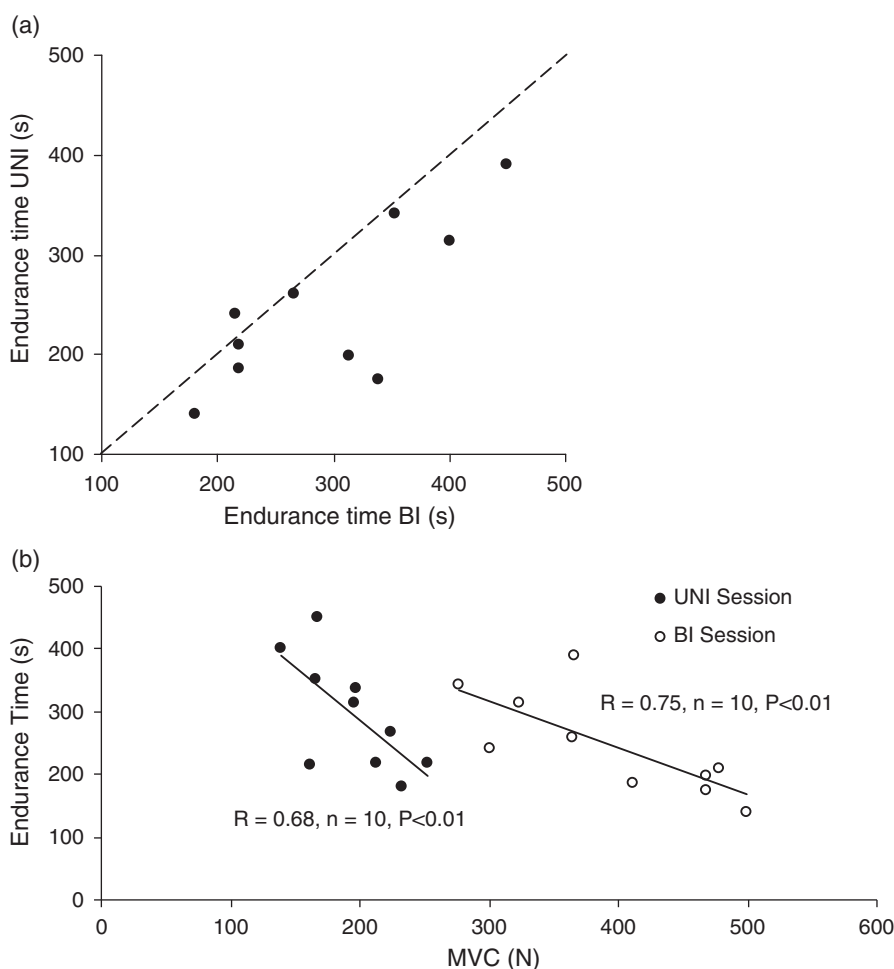

Fig. 2. (a) Time to task failure (*n* = 10) for both tasks. Data points below the line of identity indicate that the time to task failure for the bilateral task was shorter than for the unilateral (UNI) task. (b) There were significant correlations between the maximal voluntary contraction (MVC) and the time to task failure for unilateral and bilateral (BI) sessions.

correlation between time to task failure and MVC for the unilateral ($P<0.01$) and the bilateral ($P<0.01$) task [Fig. 2(b)].

RPE

RPE increased during the fatiguing contraction for both exercises. RPE ranged from 7.9 ± 0.9 to 8.4 ± 1.8 for the unilateral and bilateral exercises, respectively, at the beginning of the contraction and reached 20 ± 0 at the end of the fatiguing contractions. The rate of increase in the RPE was the same during both exercises (Fig. 3).

Central fatigue

Maximal VAL was similar for both sessions before exercise ($97.4 \pm 2.3\%$ vs $95.8 \pm 3.0\%$, for the unilateral and the bilateral session, respectively; $P>0.05$). The reduction in maximal VAL was significant ($P<0.01$) after both fatiguing contractions, but more pronounced for the unilateral exercise than for the bilateral exercise [$-12.9 \pm 7.4\%$ vs $-6.8 \pm 8.1\%$, for the unilateral and bilateral session, respectively; $P<0.01$; Fig. 4(b)]. Maximal RMS/M during unilateral MVC significantly ($P<0.05$) decreased for both RF and VL muscles after both unilateral and bilateral sessions, but the losses were not different between the two sessions.

Peripheral fatigue

Resting peak doublet force was similar before exercise for both sessions (80.1 ± 9.3 vs 76.4 ± 14.3 N for the unilateral and the bilateral task, respectively; $P>0.05$). However, at the end of the exercise, the resting peak doublet force loss was significant ($P<0.01$) after the unilateral fatiguing contraction [$-24.0 \pm 8.8\%$; Fig. 4(c)], but it was not altered after the bilateral task.

Peak-to-peak M-wave amplitude and duration of the VL muscle were similar before and after both fatiguing exercises (6.0 ± 3.7–6.3 ± 4.3 mV for amplitude and 5.4 ± 1.7–5.6 ± 0.9 ms for duration, average values for unilateral and bilateral tasks,
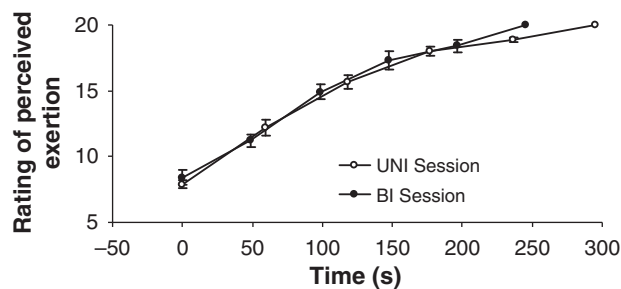

Fig 3. Time course of the rating of perceived exertion (RPE) collected during both sessions. UNI, unilateral; BI, bilateral.
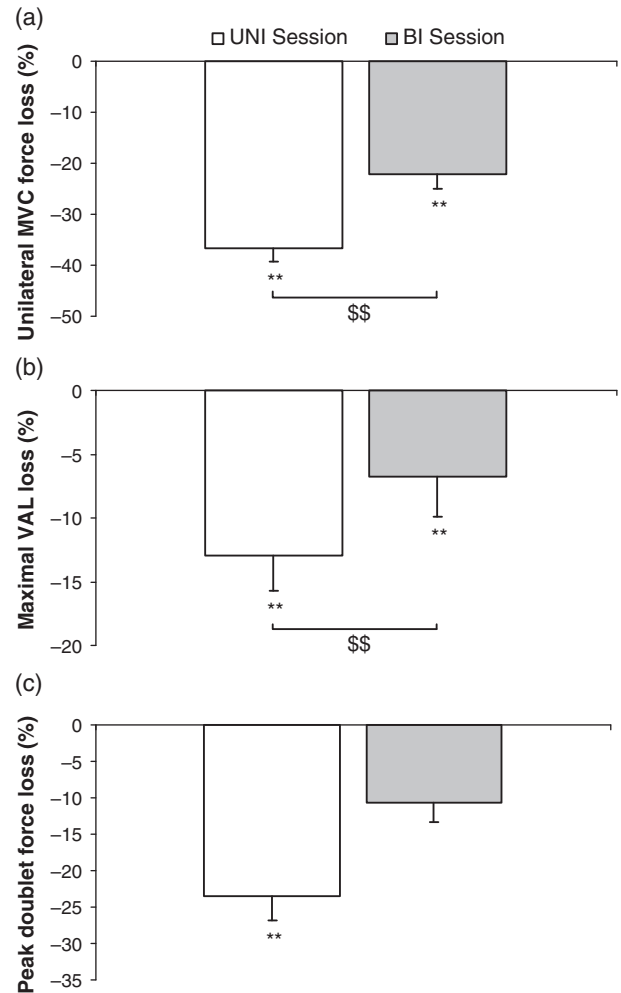
Fig. 4. (a) The unilateral left leg maximal voluntary contraction (MVC) force loss was significantly greater after the unilateral task than after the bilateral task. (b) Maximal voluntary activation level (VAL) loss after the fatiguing contraction was significantly greater for the unilateral than for the bilateral task. (c) Resting peak doublet force loss was significant for the unilateral session only. **Significant loss after the sustained contraction, $P<0.01$. $^{\$\$}$Significant difference between the two sessions, $P<0.01$. UNI, one-leg left fatiguing exercise; BI, two-leg fatiguing exercise.

respectively). Peak-to-peak M-wave amplitude of the RF muscle was similar before and after both fatiguing exercises (3.8 ± 1.7 vs 3.8 ± 2.3 mV for the unilateral and for the bilateral task, respectively, pooled data). However, the peak-to-peak M-wave duration of the RF muscle significantly increased ($P<0.05$) after the unilateral task (4.8 ± 1.0 vs 5.7 ± 1.2 ms), but was not altered after the bilateral task (4.6 ± 0.8 vs 4.7 ± 1.0 ms).

EMG activity during the sustained contraction

For each muscle, EMG RMS started at the same relative level ($P>0.05$) and increased significantly ($P<0.05$) during the fatiguing contraction for both

exercises (Fig. 5). For the bilateral task, the increase in VL and RF EMG activity was not different between the two legs. Therefore, EMG RMS of VL and RF muscles of the two legs were averaged during bilateral fatiguing contraction. The EMG RMS values of VL muscle at the end of the fatiguing contractions were $46.0 \pm 18.3\%$ MVC EMG RMS for the unilateral task and $37.3 \pm 8.6\%$ MVC EMG RMS for the bilateral task, respectively. The RMS values (% MVC RMS) of RF muscle at the end of the fatiguing contractions were $29.2 \pm 11.5\%$ for the unilateral task and $24.3 \pm 9.3\%$ for the bilateral task, respectively.

In addition, for the last 10% of the time to task failure, RMS EMG was also normalized to the RMS MVC performed after the fatiguing contraction [Fig. 6(a) and (b)]. For the first 10%, RMS EMG of VL and RF muscles were not different between the two fatiguing exercise. However, for the last 10%, EMG of VL and RF muscles were significantly greater for the unilateral task ($P < 0.05$) than for the bilateral task.

Discussion

The aim of the present study was to compare the time to task failure and the associated MVC force loss for unilateral vs bilateral fatiguing contractions performed on the knee extensor muscles. The two tasks examined in the protocol required each subject to exert the same relative muscle torque for as long as possible. We hypothesized that the endurance time would be longer for the submaximal isometric unilateral contraction compared with bilateral contraction because of the lower level of absolute force maintained by the subjects. The main results are (i) a greater time to task failure for the unilateral

exercise than for the bilateral exercise, (ii) a greater reduction in the unilateral MVC force and maximal VAL of the knee extensor muscles after the unilateral task compared with the bilateral task and (iii) a decrease in the peak doublet force after the unilateral task, but not after the bilateral task.

Time to task failure differed between the unilateral and the bilateral task

The time to task failure of the unilateral task observed in this study was in accordance with a previous study conducted at a similar relative intensity (Place et al., 2005). Moreover, we observed a relationship between MVC force and time to task failure. It has already been shown that time to task failure depends on the subject's MVC force during a submaximal isometric sustained contraction performed with one limb; indeed, the stronger the subjects, the shorter the time to task failure (Hunter & Enoka, 2001; Hunter et al., 2004; Place et al., 2005). The present results are in accordance with this observation and extend the findings to bilateral tasks. Besides, the original finding of this study is a shorter time to task failure for the bilateral task compared with the unilateral task. The difference observed in the time to task failure while both exercises were performed at the same relative level of force may be due to differences in the activation pattern, in muscle perfusion and/or in the muscle mass involved.

Time to task failure of a submaximal isometric continuous contraction may be influenced by the activation pattern of synergistic muscles (Fallentin et al., 1993; Semmler et al., 2000). The increased EMG activity consistently observed during sustained submaximal contraction is attributable to an increased motor unit recruitment and/or discharge
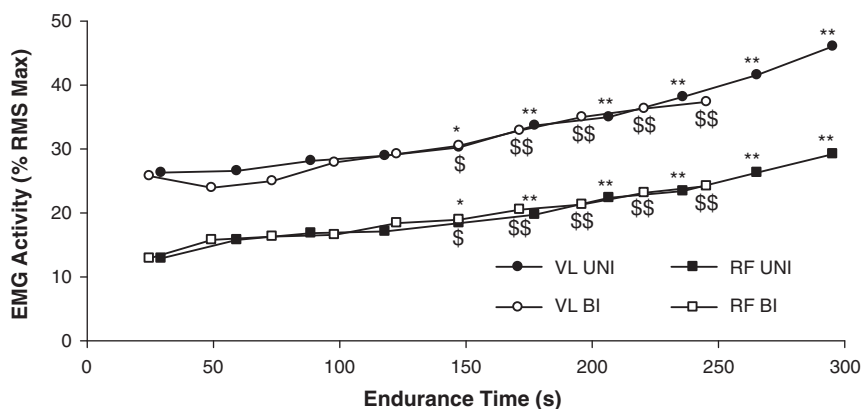

Fig. 5. Electromyographic activity (EMG) activity during the fatiguing isometric contractions for vastus lateralis (VL) and rectus femoris (RF) muscles, sustained at 20% of the maximum until task failure for unilateral and bilateral tasks. The rate of increase was similar for the two tasks. *Significantly different from the first 10% value for the unilateral session, $P < 0.05$. **Significantly different from the first 10% value for the unilateral session, $P < 0.01$. $^{\$}$Significantly different from the first 10% value for the bilateral session, $P < 0.05$. $^{\$\$}$Significantly different from the first 10% value for the bilateral session, $P < 0.01$. UNI, one-leg fatiguing exercise; BI, two-leg fatiguing exercise.
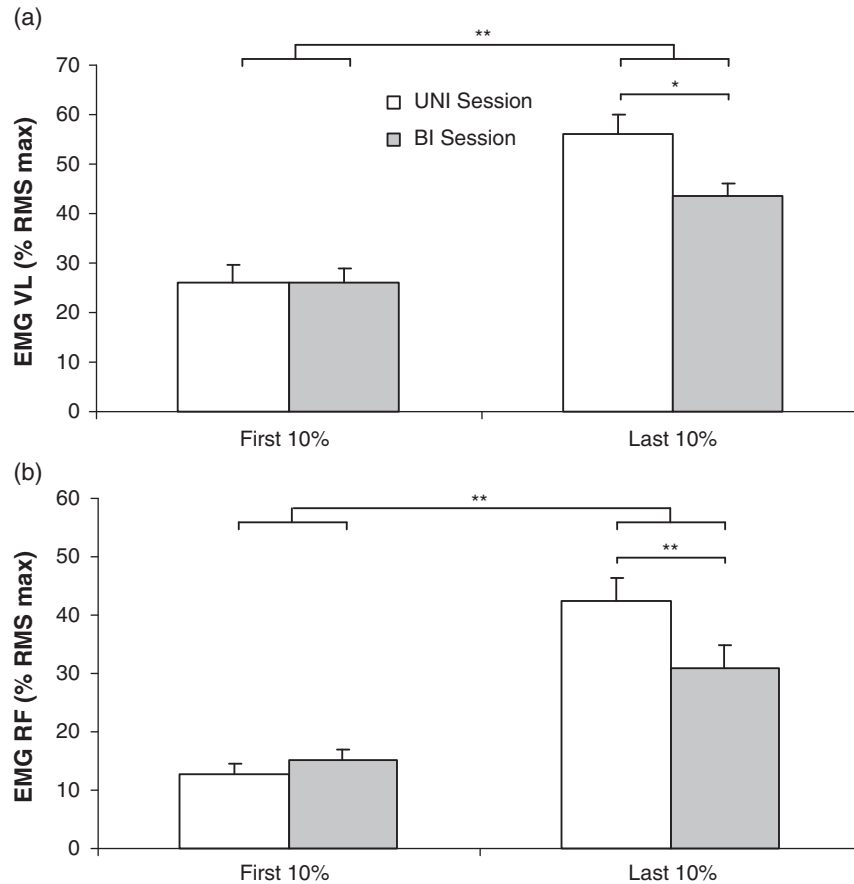
(a)

(b)

Fig. 6. Root mean square (RMS) electromyographic activity (EMG) of (a) the vastus lateralis (VL) and (b) the rectus femoris (RF) muscle in the last 10% of time to task failure (normalized to maximal RMS post-exercise) was significantly lower for the bilateral than the unilateral session. *Significantly different, $P < 0.05$. **Significantly different, $P < 0.01$. UNI, one-leg fatiguing exercise; BI, two-leg fatiguing exercise.

rate (Denny-Brown, 1949; Edwards & Lippold, 1956; Lloyd, 1971) although it has recently been found that discharge rates could decline during the course of a submaximal contraction (Mottram et al., 2005). In our study, the EMG activity of VL and RF muscles started at the same relative level for both conditions, suggesting that initial knee extensor muscle activation was similar during one- or two-leg contractions. EMG activity increased at the same rate for both tasks, but reached a lesser level at the termination of the bilateral task compared with the unilateral task. We observed a similar rate of increase in EMG activity for the two tasks; such results have already been reported while comparing a force task (maintaining a constant force while pushing against a force transducer) with a position task (supporting an equivalent inertial load while maintaining a constant joint angle) (Mottram et al., 2005). Despite this similar increase in surface EMG, Mottram et al. (2005) observed a greater level of motor unit recruitment during the position task compared with the force task. Therefore, the briefer time to task failure

during the bilateral task could be due, at least partly, to an earlier recruitment of the motor unit pool. It has been suggested that small muscles allow contractions for a long time, have a better perfusion during exercise, as intramuscular pressure generated is less than that in larger muscular groups (Nagle et al., 1988; Williams, 1991; Seals, 1993; Smolander et al., 1998). In addition to these studies, a previous study by Seals (1989) compared blood pressure during an isometric handgrip exercise performed with the left, the right or both arms. Subjects had to sustain 30% of MVC for 2.5 min. Before exercise, the blood pressure was the same in each condition. After the 2.5-min exercise, the blood pressure increased in each condition but was significantly greater for exercise performed with both arms. In the present study, similar mechanisms involving a decrease in muscle perfusion by an increase in the active muscle mass could explain the shorter time to task failure for the bilateral task compared with the unilateral task.

RPE increased similarly for both fatiguing exercises. RPE is a measure of the individual's sense of

the relative intensity of sustained physical activity and is probably based on the descending voluntary command (Carson et al., 2002). Maximal RPE (i.e. task failure) was attained on average ~ 1 min earlier during the bilateral task, suggesting that sustaining an ~ 2-fold higher load during the bilateral task required a slightly greater effort for our subjects. This idea is in accordance with the hypothesis of a premature fatigue in the bilateral condition due to a greater muscle mass solicited.

Mechanisms of fatigue differed between the unilateral and the bilateral task

The longer time to task failure for the unilateral task was associated with a greater unilateral MVC loss. MVC loss of knee extensor muscles for the unilateral task was in the same range as that of previous studies examining one-leg contractions (Rochette et al., 2003; Place et al., 2005).

A similar RMS/M decrease following fatiguing contractions for both unilateral and bilateral tasks was found, suggesting that central fatigue occurred, although this index should be interpreted cautiously (Place et al., 2007). However, maximal VAL loss was greater for the unilateral task, suggesting a greater amount of central fatigue in this condition. It has recently been shown that maximal VAL is more discriminating than RMS/M to appreciate the level of central fatigue (Place et al., 2007). Therefore, this difference in the magnitude of central fatigue between the unilateral and the bilateral task could be partly a result of increased metabolites concentrations, as suggested by Hunter and Enoka (2001). This increasing metabolite concentration may be due to increased activation of III and IV afferents, which are sensitive at the metabolic modifications, and probably contributes to neural adjustments during sustained contractions (Duchateau et al., 2002). In addition, we found a significant correlation ($r = 0.87$ for the unilateral task and $r = 0.90$ for the bilateral task, $P < 0.01$) between EMG activity and RPE during both tasks, suggesting that greater levels of inhibition during bilateral contraction are unlikely to explain our results.

The amplitude of the mechanical response evoked by electrical stimulation of motor nerve allows to apprehend a possible alteration in the excitation–contraction coupling process. We noted that the decrease in the peak doublet force was greater after the unilateral task; therefore, contractile failure could also explain the greater MVC loss following the unilateral task compared with the bilateral task. As M-wave properties were relatively well preserved, our data indicate that alterations located beyond the sarcolemma may have occurred (for a review, see Allen et al., 2008).

Perspectives

The originality of the present study was to compare neuromuscular fatigue when sustaining isometric submaximal contractions until task failure with one (non-dominant) vs two segments at the same relative level of force. Our study showed that time to task failure was greater when performing submaximal isometric contraction with one leg compared with two legs. This finding suggests that time to task failure of a submaximal fatiguing contraction of the knee extensor muscles depends on the muscle mass involved (Hunter et al., 2004). The greater time to task failure with one leg may have induced greater contractile alterations and a larger MVC loss following the unilateral task. Overall, these findings indicated that neuromuscular alterations differ when a task is performed with one or two legs but further studies are needed to clarify the exact origin of this difference concerning fatigue mechanisms.

Key words: electromyography, muscle activation, evoked contraction, task failure, knee extensor muscles.

Acknowledgements

References

Allen GM, Gandevia SC, McKenzie DK. Reliability of measurements of muscle strength and voluntary activation using twitch interpolation. Muscle Nerve 1995: 18: 593–600.

Allen DG, Lamb GD, Westerblad H. Skeletal muscle fatigue: cellular mechanisms. Physiol Rev 2008: 88: 287–332.

Becker R, Awiszus F. Physiological alterations of maximal voluntary quadriceps activation by changes of knee joint angle. Muscle Nerve 2001: 24: 667–672.

Borg G. Perceived exertion as an indicator of somatic stress. Scand J Rehabil Med 1970: 2: 92–98.

Carson RG, Riek S, Shahbazpour N. Central and peripheral mediation of human force sensation following eccentric or concentric contractions. J Physiol 2002: 539: 913–925.

Denny-Brown D. Interpretation of the electromyogram. Arch Neurol Psychiatry 1949: 61: 99–128.

Duchateau J, Balestra C, Carpentier A, Hainaut K. Reflex regulation during sustained and intermittent submaximal contractions in humans. J Physiol 2002: 541: 959–967.

Edwards RG, Lippold OC. The relation between force and integrated electrical

activity in fatigued muscle. J Physiol 1956: 132: 677–681.

Enoka RM, Stuart DG. Neurobiology of muscle fatigue. J Appl Physiol 1992: 72: 1631–1648.

Fallentin N, Jorgensen K, Simonsen EB. Motor unit recruitment during prolonged isometric contractions. Eur J Appl Physiol Occup Physiol 1993: 67: 335–341.

Gondin J, Guette M, Jubeau M, Ballay Y, Martin A. Central and peripheral contributions to fatigue after electrostimulation training. Med Sci Sports Exerc 2006: 38: 1147–1156.

Guette M, Gondin J, Martin A. Time-of-day effect on the torque and neuro-muscular properties of dominant and non-dominant quadriceps femoris. Chronobiol Int 2005: 22: 541–558.

Hunter SK, Critchlow A, Enoka RM. Influence of aging on sex differences in muscle fatigability. J Appl Physiol 2004: 97: 1723–1732.

Hunter SK, Critchlow A, Enoka RM. Muscle endurance is greater for old men compared with strength-matched young men. J Appl Physiol 2005a: 99: 890–897.

Hunter SK, Enoka RM. Sex differences in the fatigability of arm muscles depends on absolute force during isometric contractions. J Appl Physiol 2001: 91: 2686–2694.

Hunter SK, Lepers R, MacGillis CJ, Enoka RM. Activation among the elbow flexor muscles differs when maintaining arm position during a fatiguing contraction. J Appl Physiol 2003: 94: 2439–2447.

Hunter SK, Rochette L, Critchlow A, Enoka RM. Time to task failure differs with load type when old adults perform a submaximal fatiguing contraction. Muscle Nerve 2005b: 31: 730–740.

Hunter SK, Ryan DL, Ortega JD, Enoka RM. Task differences with the same load torque alter the endurance time of submaximal fatiguing contractions in

humans. J Neurophysiol 2002: 88: 3087–3096.

Kubo K, Tsunoda N, Kanehisa H, Fukunaga T. Activation of agonist and antagonist muscles at different joint angles during maximal isometric efforts. Eur J Appl Physiol 2004: 91: 349–352.

Kufel TJ, Pineda LA, Mador MJ. Comparison of potentiated and unpotentiated twitches as an index of muscle fatigue. Muscle Nerve 2002: 25: 438–444.

Lloyd AJ. Surface electromyography during sustained isometric contractions. J Appl Physiol 1971: 30: 713–719.

Loscher WN, Cresswell AG, Thorstensson A. Excitatory drive to the alpha-motoneuron pool during a fatiguing submaximal contraction in man. J Physiol 1996: 491(Part 1): 271–280.

Martin A, Carpentier A, Guissard N, van Hoecke J, Duchateau J. Effect of time of day on force variation in a human muscle. Muscle Nerve 1999: 22: 1380–1387.

Maupas E, Paysant J, Datie AM, Martinet N, Andre JM. Functional asymmetries of the lower limbs. A comparison between clinical assessment of laterality, isokinetic evaluation and electrogoniometric monitoring of knees during walking. Gait Posture 2002: 16: 304–312.

Mottram CJ, Jakobi JM, Semmler JG, Enoka RM. Motor-unit activity differs with load type during a fatiguing contraction. J Neurophysiol 2005: 93: 1381–1392.

Nagle FJ, Seals DR, Hanson P. Time to fatigue during isometric exercise using different muscle masses. Int J Sports Med 1988: 9: 313–315.

Place N, Maffiuletti NA, Ballay Y, Lepers R. Twitch potentiation is greater after a fatiguing submaximal isometric contraction performed at short vs long

quadriceps muscle length. J Appl Physiol 2005: 98: 429–436.

Place N, Maffiuletti NA, Martin A, Lepers R. Assessment of the reliability of central and peripheral fatigue after sustained maximal voluntary contraction of the quadriceps muscle. Muscle Nerve 2007: 35: 486–495.

Rochette L, Hunter SK, Place N, Lepers R. Activation varies among the knee extensor muscles during a submaximal fatiguing contraction in the seated and supine postures. J Appl Physiol 2003: 95: 1515–1522.

Seals DR. Influence of muscle mass on sympathetic neural activation during isometric exercise. J Appl Physiol 1989: 67: 1801–1806.

Seals DR. Influence of active muscle size on sympathetic nerve discharge during isometric contractions in humans. J Appl Physiol 1993: 75: 1426–1431.

Semmler JG, Kutzscher DV, Enoka RM. Limb immobilization alters muscle activation patterns during a fatiguing isometric contraction. Muscle Nerve 2000: 23: 1381–1392.

Smolander J, Aminoff T, Korhonen I, Tervo M, Shen N, Korhonen O, Louhevaara V. Heart rate and blood pressure responses to isometric exercise in young and older men. Eur J Appl Physiol Occup Physiol 1998: 77: 439–444.

Søgaard K, Gandevia SC, Todd G, Petersen NT, Taylor JL. The effect of sustained low-intensity contractions on supraspinal fatigue in human elbow flexor muscles. J Physiol 2006: 573: 511–523.

Strojnik V, Komi PV. Neuromuscular fatigue after maximal stretch-shortening cycle exercise. J Appl Physiol 1998: 84: 344–350.

Williams CA. Effect of muscle mass on the pressor response in man during isometric contractions. J Physiol 1991: 435: 573–584.