Neuromuscular fatigue development during maximal concentric and isometric knee extensions

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Babault, Nicolas, Kevin Desbrosses, Marie-Sophie Fabre, Anne Michaut, and Michel Pousson. Neuromuscular fatigue development during maximal concentric and isometric knee extensions. J Appl Physiol 100: 780–785, 2006. First published November 10, 2005; doi:10.1152/japplphysiol.00737.2005.—This study aimed to investigate mechanisms of neuromuscular fatigue during maximal concentric and isometric leg extensions inducing similar torque decrements. Nine physically active men performed two separate fatigue sessions maintained until similar torque decreases were obtained. The first session, only conducted under isokinetic concentric conditions (CON), consisted of three series of 30 maximal voluntary concentric knee extensions (60°/s). The second session, exclusively isometric (ISO), mimicked the torque decreases registered during the CON session while performing three long-lasting ISO contractions. Maximal voluntary torque, activation level (twitch interpolation technique), electromyographic activity (root mean square and median frequency) of the vastus lateralis muscle, and electrically evoked doublet-twitch mechanical properties were measured before and at the end of each of the three series. After the three series, similar torque decrements were obtained for both fatiguing procedures. The total fatigue induction contraction durations were not different among procedures. With equivalent voluntary torque decrements, the doublet-twitch amplitude reduction was significantly greater (P < 0.01) during the two first series of the CON procedure compared with ISO. No difference was observed for the third series. Although no difference was recorded with fatigue for median frequency changes between CON and ISO, activation levels and root mean square values demonstrated greater reductions (P < 0.05) for all three series during the ISO procedure compared with CON. Performing CON or ISO fatiguing exercises demonstrated different fatigue origins. With CON exercises, peripheral fatigue developed first, followed by central fatigue, whereas with ISO exercises the fatigue pattern was inverted. The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

electromyography; evoked contractions; twitch interpolation

THE ABILITY OF HUMAN SUBJECTS to generate maximal voluntary torque varies greatly when considering various muscular contrac-tile actions. More particularly, isometric and concentric actions are distinct regarding muscular mechanical properties and motor unit activation by the central nervous system. Broadly speaking, maximal torque, whether voluntary or electrically evoked, is higher during isometric contractions compared with concentric contractions, with the concentric torque declining with increasing angular velocity (38). Likewise, maximal motor unit activation capacity appears to differ between these two muscular action modes. Studies estimating motor unit activation from electromyographic (EMG) activity (41) or twitch interpolation (3) have demonstrated the presence of an inhibitory mechanism at slow concentric velocities. Such motor unit inhibition would limit the development of maximal tension during contractions performed at slow concentric velocities (31) but also during isometric actions, depending on joint angle (4).

Neuromuscular fatigue also appears to develop differently, depending on the muscular action modes. Defined as the decline in muscle performance during and after repetitive contractions, fatigue has been shown to be task dependent (see Ref. 9) and is generally considered to arise via two main mechanisms. Central fatigue arises proximal to the motor axons and leads to reductions of motor unit activation. Peripheral fatigue is located within the muscle itself, with components also related to the neuromuscular junction or terminal branches of the motor axons. From the literature, it appeared that fatigue origins depend on the muscular action mode (e.g., Ref. 18) and movement angular velocity (e.g., Ref. 23). For example, using the twitch interpolation technique, Gandevia et al. (12) argued that 30°/s concentric exercise-induced fatigue might primarily be peripheral in origin, whereas Pasquet et al. (30) obtained central fatigue (EMG activity decreases) during faster concentric contractions.

According to Kay et al. (18), distinct fatigue origins may be incriminated after long-lasting concentric and isometric contractions, the latter resulting in a more pronounced central fatigue than the former. However, most studies dealing with the comparison of the different contraction modes on neuromuscular fatigue have used quite similar fatiguing procedures that produced different torque decrements (18, 32, 37). Therefore, it can be questioned whether the mechanisms implied in exercise-induced fatigue are still different with various contraction modes but similar torque decays. Accordingly, the aim of the present study was to investigate mechanisms of neuromuscular fatigue when a similar relative fatigue level (i.e., similar torque decreases) is induced under maximal isometric and concentric contractions of the right leg extensors.
METHODS

Subjects. The experiments were performed with nine physically active men who gave their written, informed consent before participation. Their mean age (±SD), height, and body mass were 21.2 ± 1.1 yr, 170.0 ± 7.0 cm, and 71.0 ± 6.5 kg, respectively. All subjects were informed about the purpose and procedures of the tests. The study was conducted according to the declaration of Helsinki and was approved by the local ethics committee.

Data collection. Tests were carried out on a Biodex 3 isokinetic dynamometer (Biodex, Shirley, NY). Subjects were seated upright with a 100° hip angle on the dynamometer chair. Velcro straps were applied tightly across the thorax and pelvis with the distal right leg fixed to the dynamometer lever arm. The axis of rotation of the dynamometer was aligned to the lateral femoral condyle, indicating the anatomical joint axis of the knee. Torque was then measured and recorded instantaneously. Concentric contractions were conducted using a 60°/s angular velocity within a 75° range of motion, from 95 to 20° knee flexion (0°: full leg extension). No preactivation was permitted before all concentric contractions. Isometric contractions were performed with the knee flexed at a 55° joint angle. This angle corresponded to the middle of the concentric range of motion.

The EMG signal was recorded during all contractions using one pair of silver-chloride electrodes positioned on the middle portion of the belly of vastus lateralis muscle. This muscle was chosen because it is considered to be representative of the whole knee extensor muscle group (1). Low impedance (<2 kΩ) was obtained by shaving, abrad- ing, and cleaning the skin. The interelectrode distance was 2 cm (center to center). The reference electrode was fixed to the patella of the opposite leg. EMG signals were amplified with a bandwidth frequency ranging from 10 to 2,000 Hz (common mode rejection ratio = 90 dB; impedance input = 100 MΩ; gain = 1,000). Then, both the root mean square (RMS) amplitude and median frequency (MF) were calculated. During isometric contractions, the RMS amplitude was calculated over a 500-ms period preceding the electrical stimulation (described below). For 60°/s concentric contractions, a period corresponding to a 15° angular displacement (i.e., 250 ms) before the stimulus was considered to calculate RMS. For the EMG power spectrum, fast Fourier transformations were used to obtain MF. The window length was set at 1,024 data points during the isometric condition and 512 data points during the concentric condition (from 70 to 55° knee flexion).

Electrical stimulations were delivered using a high-voltage stimulator (Digitimer DS7, Hertfordshire, UK) to determine 1) the mechanical properties of the knee extensors and 2) the voluntary activation level by using the twitch interpolation technique. The cathode (ball probe, 10-mm diameter) was pressed onto the femoral triangle over the femoral nerve and moved to the position giving the greatest visible contraction of the whole quadriceps muscle group. The anode (self- adhesive electrode, 10 × 5 cm) was positioned midway between the superior aspect of the greater trochanter and the inferior border of the iliac crest. To determine each subject’s maximal stimulation intensity, a series of single square-wave stimuli (1-ms duration, 400-V maximal voltage) were delivered by progressively increasing the current until there was no further increase in the evoked isometric twitch response (55° knee flexion). The plateau in twitch torque, so obtained, was taken as the maximal stimulation intensity. Then supramaximal stimulations (maximal intensity + 10%) were applied strictly with paired stimuli (10-ms interstimuli intervals) under isometric and concentric conditions. During concentric actions, either at rest or during voluntary contractions, electrical impulses were delivered using a trigger connected to the joint angular position channel. Because of varying intersubject contraction times and electromechanical delays, the trigger was carefully and individually adjusted so as to obtain the peak mechanical response as close as possible to a 55° knee flexion angle, i.e., joint angle used for isometric (see Ref. 4).

To calculate the activation level, paired impulses were also superimposed during voluntary isometric and concentric contractions (A) and delivered immediately after each voluntary contraction on resting muscles using the same muscular condition as the superimposed doublet twitch (i.e., at rest under isometric conditions or during passive leg extensions for concentric) (B). The activation level was quantified with the formula, activation level (%) = 100 − (A/B) × 100. During isometric contractions, superimposed paired stimuli were elicited ~1 s after the maximal voluntary torque plateau had been reached. The superimposed torque was calculated as done previously (4) by subtracting the torque that would have occurred in absence of stimulation. The latter was estimated by linear extrapolation of the slope of the voluntary torque measured before the stimulation beyond the stimulus artifact. Stimulations delivered on resting muscles immediately after each voluntary contraction were also used to calculate the doublet twitch contractile properties, i.e., the maximal doublet twitch amplitude (Pt), contraction time, half-relaxation time, and maximal rate of tension development (RD) and relaxation. For all torque measurements, appropriate corrections were made for the gravitational effect of the lower leg by recording and subtracting the resistive torque of the leg on relaxed subjects under isometric or concentric conditions. Torque, angular position, and EMG signals were digitized online (sampling frequency 2,000 Hz) using a digital computer and stored on hard disk for further analysis.

Experimental design. The experimental procedure consisted of two sessions, separated by at least 3 wk, conducted on the right leg extensor muscles. It was designed to induce neuromuscular fatigue following concentric and isometric contractions that resulted in a quite similar torque decrease. Because torque decreases could be more easily controlled during isometric contractions, the first session was always performed under concentric conditions. Torque decreases, so obtained, were reproduced during the second session in isometric conditions.

Each session began with the determination of the stimulus intensity. Then subjects carried out a standardized warm-up composed of 10–12 concentric or isometric contractions (depending on the test session) with increasing intensity until the maximal voluntary contraction (MVC). During the concentric session (CON), the warm-up was followed by two series of three 60°/s concentric MVC interspersed with 2 min of rest between series. For the isometric session (ISO), three 5-s isometric MVC were performed with 1 min of rest between MVC. Each MVC was superimposed with one paired stimuli and immediately followed by two paired stimuli delivered at rest (0.5 Hz). Then subjects performed the fatiguing procedure. During CON, three series of 30 maximal concentric leg extensions (S1, S2, and S3) were performed. The three last contractions of each series were superimposed with paired stimuli, and series were immediately followed with two doublet twitches delivered at rest. During ISO, subjects performed three continuous isometric contractions (also noted S1, S2, and S3). Each contraction was maintained until the S1, S2, and S3 torque reductions, previously registered during CON, were attained. When isometric torque reductions were similar to those obtained during each series of the CON, three superimposed paired stimuli were delivered with 2-s intervals. Contractions were then stopped and followed by two resting paired stimuli (0.5 Hz). For both sessions, a 1-min rest period was allowed between each series or MVC, respectively, during CON and ISO. The maximal voluntary torque activation level, EMG activity, and contractile properties of the doublet twitches (when evoked at rest) were thus studied before fatigue and at the end of each series.

Statistical analysis. Maximal voluntary torque, corresponding activation levels, RMS and MF values, and the doublet twitch contractile properties were expressed as means ± SD. Percentage changes of these variables with fatigue (end of S1, S2, and S3) were determined as a function of the pret fatigue value. The statistical differences between contraction mode and/or series (pret fatigue, S1, S2, and S3) were tested using a two-way ANOVA with repeated measures. F
ratios were considered significant at a $P$ level of $<0.05$. A Newman-Keuls post hoc test was conducted if significant main effect or interactions were present.

RESULTS

Fatiguing procedure. Before fatigue, the voluntary torque was significantly ($P < 0.05$) higher during isometric than concentric MVC (Table 1). During the fatiguing protocol, torque reductions increased significantly ($P < 0.05$) with series. Compared with the prefatigue maximal voluntary torque, torque reductions were $35.9 \pm 12.1, 51.5 \pm 8.6$, and $59.0 \pm 8.1$% during the CON procedure for S1, S2, and S3, and $37.8 \pm 11.5, 46.4 \pm 9.2$, and $57.9 \pm 8.6$% during ISO for S1, S2, and S3, respectively. As planned by the experimental procedure, torque decreases, following the three fatiguing series, were similar for both CON and ISO protocols. These torque decreases were obtained with similar contraction durations for each of the three series and total contraction durations (135 ± 0 and 144.4 ± 32.8 s for CON and ISO, respectively).

Activation level. Under fresh conditions (before the fatiguing procedure), the twitch interpolation technique demonstrated similar activation levels during maximal voluntary isometric and concentric contractions (Table 1). With fatigue, the voluntary activation level was significantly reduced compared with the fresh conditions (Fig. 1). For ISO, activation level changes were significantly greater ($P < 0.001$) during S2 and S3 compared with S1, and no difference was observed between S2 and S3. During CON, activation level changes were not different between S1 and S2. CON activation level reduction measured during S3 was significantly greater ($P < 0.05$) compared with S1 and S2. When the two fatiguing procedures were compared, ISO actions yielded a significantly greater reduction in activation levels than CON during S1, S2, and S3 (Fig. 1). Compared with prefatigue, activation levels decreased by $11.2 \pm 3.3, 15.2 \pm 7.0$, and $27.0 \pm 6.0$% during CON for S1, S2, and S3, and $27.5 \pm 6.6, 33.6 \pm 6.4$, and $36.3 \pm 11.3$% during ISO for S1, S2, and S3, respectively.

EMG. In fresh conditions, no difference was observed between isometric and concentric MVC, either for RMS amplitudes or for MF values of vastus lateralis muscle (Table 1). During the CON fatiguing procedure and whatever the series, RMS amplitudes did not change significantly compared with prefatigue values (Fig. 2A). For ISO, RMS was significantly reduced ($P < 0.01$) compared with the fresh condition. No difference was obtained between series. When comparing both fatiguing procedures, RMS changes were significantly greater ($P < 0.01$) during ISO ($-24.9 \pm 14.9, -24.7 \pm 24.8$, and $-23.3 \pm 24.1$, respectively, for S1, S2, and S3) than during CON ($5.9 \pm 14.7, -5.8 \pm 13.3$, and $-3.9 \pm 7.9$, respectively, for S1, S2 and S3).

<table>
<thead>
<tr>
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<th>ISO</th>
<th>CON</th>
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<tbody>
<tr>
<td>Maximal voluntary torque, N·m</td>
<td>$244.5 \pm 31.5$</td>
<td>$216.8 \pm 26.5^{*}$</td>
</tr>
<tr>
<td>Activation level, %</td>
<td>$89.4 \pm 3.1$</td>
<td>$88.3 \pm 3.0$</td>
</tr>
<tr>
<td>VL RMS</td>
<td>$0.83 \pm 0.18$</td>
<td>$0.88 \pm 0.23$</td>
</tr>
<tr>
<td>VL MF, Hz</td>
<td>$74.2 \pm 9.2$</td>
<td>$70.3 \pm 8.4$</td>
</tr>
<tr>
<td>Pt, N·m</td>
<td>$107.2 \pm 15.4$</td>
<td>$98.1 \pm 10.7$</td>
</tr>
<tr>
<td>CT, ms</td>
<td>$56.4 \pm 6.9$</td>
<td>$51.6 \pm 4.6$</td>
</tr>
<tr>
<td>HRT, ms</td>
<td>$107.9 \pm 13.2$</td>
<td>$96.2 \pm 13.1$</td>
</tr>
<tr>
<td>RD, N·m/ms</td>
<td>$2.94 \pm 0.67$</td>
<td>$2.78 \pm 0.38$</td>
</tr>
<tr>
<td>RR, N·m/ms</td>
<td>$-1.41 \pm 0.23$</td>
<td>$-1.44 \pm 0.18$</td>
</tr>
</tbody>
</table>

Values are means ± SD. ISO, isometric; CON, concentric; VL, vastus lateralis; RMS, root mean square; MF, median frequency; Pt, maximal doublet twitch amplitude; CT, doublet twitch contraction time; HRT, doublet twitch half-relaxation time; RD and RR, maximal rate of doublet twitch tension development and relaxation, respectively. *Significant difference between ISO and CON ($P < 0.05$).
During both fatiguing procedures, the MF was significantly reduced (on average $-20.0 \pm 10.0\%$; $P < 0.001$) compared with the fresh condition (Fig. 2B). No difference was obtained either between the three series of each fatiguing procedure or between the ISO and CON fatiguing procedures. When collapsed among action modes, MF decreased from $72.3 \pm 9.1$ to $55.3 \pm 7.6$ Hz, respectively, before and at the end of the fatiguing procedure (S3).

Doublet twitch mechanical properties at rest. Before fatigue, doublet twitch contractile properties, when explored on resting muscles, did not demonstrate any significant difference between isometric and concentric conditions (Table 1). During the fatiguing procedure, Pt was significantly reduced ($P < 0.01$) compared with prefatigue values during both ISO and CON (Table 2). During ISO, Pt reduction was significantly greater ($P < 0.05$) during S2 and S3 compared with S1. No difference was observed between all three series during the CON session. Comparing the two fatiguing procedures revealed a significantly greater Pt reduction ($P < 0.05$) during CON than ISO for both S1 and S2. No difference was observed between ISO and CON for S3. The doublet twitch contraction time did not exhibit any modification with fatigue. Therefore, no difference was obtained between the two fatiguing sessions. S1 and S2 half-relaxation time were significantly increased ($P < 0.05$) compared with prefatigue values, but no significant difference was obtained between the two fatiguing procedures. The doublet twitch rate of tension development and rate of relaxation decreased significantly with fatigue. No difference was observed between series and between ISO and CON.

Table 2. Percent changes of the doublet twitch contractile properties during the two fatiguing sessions

<table>
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<tr>
<th></th>
<th>ISO</th>
<th>CON</th>
<th>$P$ Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pt</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S1</td>
<td>$-18.3 \pm 10.6$</td>
<td>$-32.8 \pm 7.6$</td>
<td>0.0004</td>
</tr>
<tr>
<td>S2</td>
<td>$-26.0 \pm 10.8$</td>
<td>$-35.9 \pm 8.4$</td>
<td>0.022</td>
</tr>
<tr>
<td>S3</td>
<td>$-33.5 \pm 6.4$</td>
<td>$-38.5 \pm 9.5$</td>
<td>0.27</td>
</tr>
<tr>
<td>CT</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S1</td>
<td>10.9 $\pm 13.4$</td>
<td>6.4 $\pm 7.2$</td>
<td>0.26</td>
</tr>
<tr>
<td>S2</td>
<td>6.0 $\pm 11.7$</td>
<td>5.3 $\pm 5.8$</td>
<td>0.85</td>
</tr>
<tr>
<td>S3</td>
<td>6.1 $\pm 11.1$</td>
<td>4.3 $\pm 9.2$</td>
<td>0.96</td>
</tr>
<tr>
<td>HRT</td>
<td></td>
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<tr>
<td>S1</td>
<td>39.1 $\pm 26.0$</td>
<td>33.1 $\pm 20.8$</td>
<td>0.54</td>
</tr>
<tr>
<td>S2</td>
<td>25.5 $\pm 16.0$</td>
<td>29.7 $\pm 25.8$</td>
<td>0.65</td>
</tr>
<tr>
<td>S3</td>
<td>14.7 $\pm 15.0$</td>
<td>9.2 $\pm 19.9$</td>
<td>0.56</td>
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<tr>
<td>RD</td>
<td></td>
<td></td>
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<tr>
<td>S1</td>
<td>$-28.3 \pm 17.9$</td>
<td>$-35.9 \pm 11.1$</td>
<td>0.23</td>
</tr>
<tr>
<td>S2</td>
<td>$-27.7 \pm 22.8$</td>
<td>$-38.8 \pm 9.7$</td>
<td>0.15</td>
</tr>
<tr>
<td>S3</td>
<td>$-31.2 \pm 20.3$</td>
<td>$-39.8 \pm 13.1$</td>
<td>0.26</td>
</tr>
<tr>
<td>RR</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S1</td>
<td>$-41.4 \pm 16.5$</td>
<td>$-48.4 \pm 8.1$</td>
<td>0.51</td>
</tr>
<tr>
<td>S2</td>
<td>$-36.3 \pm 13.4$</td>
<td>$-49.3 \pm 8.7$</td>
<td>0.26</td>
</tr>
<tr>
<td>S3</td>
<td>$-32.0 \pm 19.1$</td>
<td>$-42.7 \pm 6.6$</td>
<td>0.33</td>
</tr>
</tbody>
</table>

Values are means $\pm$ SD. Pt, CT, HRT, and maximal RD and RR changes (%) are after the 3 series (S1, S2, and S3) of the ISO and CON fatigue protocol. Paired stimuli were evoked under the same contraction mode as during the fatiguing exercise. Differences between ISO and CON conditions are presented by the $P$ values of the repeated-measures ANOVA. Significant differences with the fresh conditions are also shown: *$P < 0.05$; †$P < 0.01$. During ISO, the doublet twitch amplitude reduction was significantly greater during S2 and S3 compared with S1: ‡ $P < 0.05$.

**DISCUSSION**

The present study revealed different central and peripheral fatigue profiles when performing CON and ISO exercises. During CON exercise, fatigue was preferentially peripheral in origin and then central. The opposite fatigue profile was obtained when performing the ISO procedure since fatigue was firstly central, then peripheral.

In fresh conditions (i.e., on unfatigued muscles), the concentric maximal voluntary torque was lower than isometric, but no difference was obtained for activation levels and EMG values. This finding was surprising since our laboratory previously recorded lower activation levels during slow concentric MVC ($60^\circ$/s) compared with isometric and faster ($120^\circ$/s$^{-1}$) concentric MVC (3). Such apparent disagreement could be, to some extent, attributed to various neural strategies to produce maximal voluntary torque. Moreover, one must keep in mind that the twitch interpolation technique was associated here with paired stimuli, whereas single impulses were previously used.

In the present experiment, the equivalent torque decreases imposed during both procedures were obtained with quite similar contraction durations. However, these ISO and CON muscular actions were associated with distinct fatigue developments as exhibited by the different neural activation failures. Central fatigue changes were investigated by using the twitch interpolation technique and EMG activity. Compared with fresh conditions, at the end of S3, the activation level reduction was $>25\%$ for CON and ISO. This reduction may appear relatively high compared with some studies that obtained no (19, 21) or slight activation declines ($-12\%$; Ref. 27) but was in accordance with others (17, 28). Differences may be partly attributed to the fact that activation level was determined at the end of fatiguing exercises while measurements were performed after the fatiguing procedure in the previously cited experiments (19, 21, 27). Moreover, fatigue was induced using varying exercises, such as high-intensity uphill running (21) or submaximal contractions (19). For all three series, lower activation level and RMS reductions are shown following the CON condition compared with ISO. Moreover, the central fatigue time course appeared to be slower during CON compared with ISO. Activation level reductions progressed more during all three series for the CON procedure and plateaued from the end of S2 for ISO (no difference was obtained between S2 and S3). This finding corroborates the experiment reported by Kay et al. (18), who recorded huge EMG activity reductions after isometric exercises ($-60\%$) and only slight modifications after concentric actions ($-7\%$). The fatigue time course dependency on muscular contractile condition is therefore verified (24, 26, 30, 32).

The different central fatigue development, observed between ISO and CON, is revealed throughout the protocol and may originate from either or both spinal and supraspinal factors. These differences could be partly the consequences of increased metabolite concentrations (8). Indeed, the increased intracellular H$^+$ and Pi concentrations resulting from the ATP hydrolysis, for example, are known to alter force production capacity (5, 13). Metabolite accumulation, via small-diameter afferents (14, 33), is likely involved in a $\alpha$-motoneuron inhibition and a reduction of supraspinal descending drive (for reviews, see Refs. 13, 36). The two muscular action modes.
used in the present study might evoke small-diameter afferent inhibition to variable extents. Indeed, compared with the continuous ISO contraction, the intermittent nature of the CON procedure (muscular actions followed by a passive movement) may favor blood flow (20) and, therefore, the evacuation of metabolic by-products. Accordingly, metabolite concentration might be higher during the ISO fatiguing procedure compared with CON and would increase the inhibitory effect of small-diameter afferents. As suggested by Walton et al. (40), differences observed between ISO and CON central fatigue may not solely be explained by the indirect effects of by-products. Recurrent inhibition (25), presynaptic inhibition of Ia afferents (29), stretch-reflex disfacilitation (2), and responsiveness of Golgi tendinous organs (15) may be involved. However, their influence on α-motoneuron pool inhibition is ambiguous and not clear (6). Supraspinal phenomena, such as suboptimal cortical output (11, 34), might also account for the different ISO and CON fatigue development. Nevertheless, failures in motor cortex excitability may not explain the different central fatigue obtained during CON and ISO, since an increase in cortical excitability has already been observed during isometric and concentric fatiguing contractions (26, 35).

EMG has also been used to evaluate MF modifications with fatigue to help identify various neural strategies. For instance, Linnamo et al. (24) registered greater MF reductions for eccentric than concentric fatiguing procedure, which could be attributed to selective damage of fast-twitch fibers. In the present study, the MF significantly decreased after all three series without any difference between the ISO and CON conditions. These decrements could, to some extent, be attributed to motor unit synchronization (7) and fiber conduction velocity impairments; this latter could be related to $H^+$ accumulation (22). Therefore, higher MF reductions would have been expected during ISO. However, it seems that proton and lactate accumulation is not primarily responsible for spectral changes of the EMG (39). Actually, these authors registered an almost immediate MF recovery, whereas pH recovered slower. Thus ISO and CON MF changes with fatigue might be unrelated to metabolic by-products. The lack of difference in MF with fatigue between ISO and CON could additionally be attributed to methodological considerations, such as interelectrode distance and fast Fourier transformation determination. For example, concentric power spectrum could be influenced by the quadriceps shortening and, therefore, by the changing joint angles. Indeed, MF has been suggested to depend on the joint angle used for power spectrum calculation (24). Moreover, possible configuration changes of the muscle fibers within the recording volume of the electrodes as a result of angular displacement could also affect MF results.

The present experimental procedure revealed the development of distinct central but also peripheral fatigue. Although no difference was registered between ISO and CON for the doublet twitch kinetics, the peripheral fatigue time course appeared to be markedly faster during CON compared with ISO as revealed by the doublet twitch amplitude. Indeed, the contractile speed decrease, previously registered (21, 27), was similar with ISO and CON fatigue, and the doublet twitch amplitude reductions plateaued from S1 during CON, whereas during ISO this reduction was progressive so as to attain similar values as CON only after the last series of the fatiguing procedure (S3). As previously registered after eccentric contractions (27), this difference could be attributed to alterations of the excitation–contraction coupling partly originating from decreased Ca$^{2+}$ release by the sarcoplasmic reticulum or contractile protein sensitivity to Ca$^{2+}$, as well as to a reduced number of strong binding cross bridges. Metabolite accumulation might also be involved and could explain the slower doublet twitch amplitude reduction obtained during ISO (16). Indeed, in their recent experiment, Karelis et al. (16) showed that lactate infusion had a protective effect on muscle force production with fatigue (e.g., maximal and submaximal force decrease, M-wave characteristic alteration). Lactate seems to alleviate peripheral fatigue. According to this study (16), the likely lower by-product evacuation during ISO might, therefore, partly account for the slower peripheral fatigue compared with CON. Similarly, M-wave changes might be expected. Studies related with fatigue generally agreed (e.g., Ref. 17) with the fact that M waves remained unchanged during intermittent isometric or isokinetic contractions (19), whereas M waves usually progressively decreased during sustained isometric contractions (10). Therefore, the progressive peripheral fatigue increase registered during ISO may additionally be related to failures of sarcolemmal excitation and neuromuscular transmission. However, these assumptions could not be verified because paired stimuli, used before and after fatigue for the present study, made M-wave measurements unfeasible.

In conclusion, in both ISO and CON conditions, central and peripheral fatigue played a significant role in the loss of muscle strength. Fatigue was, however, dependent on the muscular contractile condition, with inverse fatigue time courses being observed during ISO and CON. ISO conditions first produced central fatigue that was much more pronounced than during CON. Peripheral fatigue grew secondarily so as to attain similar decays as with the CON procedure at the end of the fatiguing exercise. The fatigue development was the inverse during CON.

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