Prolonged Mental Exertion Does Not Alter Neuromuscular Function of the Knee Extensors

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Abstract

PAGEAUX, B., S. M. MARCORA, and R. LEPERS. Prolonged Mental Exertion Does Not Alter Neuromuscular Function of the Knee Extensors. Med. Sci. Sports Exerc., Vol. 45, No. 12, pp. 2254–2264, 2013. Purpose: The aim of this study was to test the hypotheses that prolonged mental exertion (i) reduces maximal muscle activation and (ii) increases the extent of central fatigue induced by subsequent endurance exercise. Methods: The neuromuscular function of the knee extensor muscles was assessed in 10 male subjects in two different conditions: (i) before and after prolonged mental exertion leading to mental fatigue and (ii) before and after an easy cognitive task (control). Both cognitive tasks lasted 90 min and were followed by submaximal isometric knee extensor exercise until exhaustion (endurance task), and a third assessment of neuromuscular function. Results: Time to exhaustion was 13% ± 4% shorter in the mental fatigue condition (230 ± 22 s) compared with the control condition (266 ± 26 s) (P < 0.01). Prolonged mental exertion did not have any significant effect on maximal voluntary contraction torque, voluntary activation level, and peripheral parameters of neuromuscular function. A similar significant decrease in maximal voluntary contraction torque (mental fatigue condition: −26.7% ± 5.7%; control condition: −27.6% ± 3.3%, P < 0.001), voluntary activation level (mental fatigue: −10.6% ± 4.3%; control condition: −11.2% ± 5.2%, P < 0.05), and peripheral parameters of neuromuscular function occurred in both conditions after the endurance task. However, mentally fatigued subjects rated perceived exertion significantly higher during the endurance task compared with the control condition (P < 0.05). Conclusions: These findings provide the first experimental evidence that prolonged mental exertion (i) does not reduce maximal muscle activation and (ii) does not increase the extent of central fatigue induced by subsequent endurance exercise. The negative effect of mental fatigue on endurance performance seems to be mediated by the higher perception of effort rather than impaired neuromuscular function. Key Words: PERCEPTION OF EFFORT, MUSCLE ACTIVATION, MENTAL FATIGUE, PERIPHERAL FATIGUE, CENTRAL FATIGUE, ENDURANCE PERFORMANCE

Prolonged mental exertion is well known to induce mental fatigue, a psychobiological state characterized by subjective feelings of “tiredness” and “lack of energy” (3). The negative effects of mental fatigue on cognitive performance are well established and include impairments in attention, action monitoring, and cognitive control (e.g., 3, 37). On the contrary, the effects of mental fatigue on physical performance have been scarcely investigated. In 1906, Mosso (25) reported that two of his colleagues did poorly in a muscle fatigue test performed after delivering long physiology lectures and viva examinations. More recently, Bray et al. (5,6) showed that performing a demanding cognitive task before or between isometric contractions significantly reduces the endurance and strength of isolated upper limb muscles. However, in these studies, mental exertion was not prolonged enough to induce subjective feelings of mental fatigue. Furthermore, neuromuscular function was assessed with EMG, a method that does not provide a valid measure of maximal voluntary activation of muscle (15). Therefore, the link between the prolonged mental exertion and the central component of muscle fatigue is still unclear. Marcera et al. (21) conducted the first experimental study on the effect of prolonged mental exertion on endurance performance during dynamic whole-body exercise. These investigators induced mental fatigue in a group of healthy and fit subjects using a prolonged demanding cognitive task performed for 90 min and found a significant reduction in time to exhaustion during subsequent high-intensity cycling exercise. However, the physiological mechanisms underlying the negative effect of prolonged mental exertion on endurance performance are currently unknown. Marcera et al. (21) did not find any effect of mental fatigue on the cardiovascular, respiratory, and metabolic responses to

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high-intensity cycling exercise. Motivation related to the time to exhaustion test was also unaffected by mental fatigue. In this study, the only factor that could explain a premature exhaustion was the higher perception of effort experienced by mentally fatigued subjects during high-intensity cycling exercise. According to the psychobiological model of endurance performance, exhaustion is not caused by muscle fatigue (20), that is, by the failure of the fatigued neuromuscular system to produce the force/power required by the endurance task despite a maximal voluntary effort. On the contrary, it is proposed that exhaustion results from a conscious decision to disengage from the endurance task. In highly motivated subjects, this effort-based decision is taken when the perception of effort is maximal and continuation of the endurance task seems impossible.

Although this explanation is plausible, Marcera et al. (21) did not measure neuromuscular function. Therefore, a reduction in maximal muscle activation or an increase in the extent of central fatigue induced by endurance exercise may also explain the negative effect of mental fatigue on endurance performance. Central fatigue is an exercise-induced reduction in the capacity of the central nervous system (CNS) to fully recruit the active muscles (muscle activation) during a maximal voluntary contraction (MVC) and occurs at both spinal and/or supraspinal level (15). Central fatigue is thought to negatively affect endurance performance (1), and several authors have proposed a strong link between mental and central fatigue (e.g., 5, 11, 26). Because supraspinal fatigue seems to occur in brain areas upstream of the primary motor cortex (34), it is plausible that prolonged mental exertion can alter maximal muscle activation and, thus, impair endurance performance.

The main aim of the present study was to test experimentally this hypothetical link between mental fatigue, maximal muscle activation, and central fatigue. Specifically, we hypothesized that prolonged mental exertion leading to mental fatigue (i) would reduce maximal muscle activation and (ii) would increase the extent of central fatigue induced by subsequent endurance exercise. We tested these two main hypotheses by measuring maximal muscle activation of the knee extensor muscles before and after prolonged mental exertion and immediately after subsequent submaximal isometric contraction of the knee extensor muscles until exhaustion (endurance task). In addition, we hypothesized that prolonged mental exertion would reduce endurance performance via a higher perception of effort during the endurance task.

METHODS

Subjects and Ethical Approval

Ten physically active male adults (mean ± SD; age = 22 ± 2 yr, height = 177 ± 6 cm, weight = 70 ± 8 kg) volunteered to participate in this study. None of the subjects had any known mental or somatic disorder. Each subject gave written informed consent before the study. Experimental protocol and procedures were approved by the local ethics committee of the Faculty of Sport Sciences, University of Burgundy in Dijon. All subjects were given written instructions describing all procedures related to the study but were naive of its aims and hypotheses. Participants believed that the study was on the effects of two different cognitive activities (a computerized task and watching a movie) on the neuromuscular responses to an endurance task. To ensure high motivation during the cognitive and endurance tasks, a reward (ticket to a professional sport event) was given to the best performances in both the cognitive and endurance tasks. At the end of the last session, subjects were debriefed and asked not to discuss the real aims of the study with other participants. The study conformed to the standards set by the World Medical Association Declaration of Helsinki “Ethical Principles for Medical Research Involving Human Subjects” (2008).

Experimental Protocol

Subjects visited the laboratory on three different occasions. During the first visit, subjects were familiarized with the laboratory and the experimental procedures. During the second and third visit, subjects performed either a mental fatigue task or a control task (for more details, see Cognitive Tasks section) in a randomized and counterbalanced order. After the cognitive task, subjects performed submaximal isometric knee extensor exercise until exhaustion (for more details, see Endurance Task section). The neuromuscular function of the knee extensor muscles was tested before and after the cognitive task and after the subsequent endurance task. Mood was assessed before and after the cognitive task, whereas motivation was measured before the subsequent endurance task (Fig. 1). For more details, see Neuromuscular Function Tests and Psychological Questionnaires sections.

Each participant completed all three visits for a period of 3 wk, with a minimum of 72 h of recovery period between

FIGURE 1—Graphical overview of the protocol for one session. Order and timing was the same for each subject and each session. Q, psychological questionnaires; CT, cognitive task; MVC, maximal voluntary contraction.
visits. All participants were given instructions to sleep for at least 7 h, refrain from the consumption of alcohol, and not to practice vigorous physical activity the day before each visit. Participants were also instructed not to consume caffeine and nicotine at least 3 h before testing and were asked to declare if they had taken any medication or had any acute illness, injury, or infection.

### Cognitive Tasks

**Mental fatigue task.** Mental fatigue was induced by asking the subject to perform the AX-Continuous Performance Test (AX-CPT) (8) for 90 min on a personal computer. In this cognitive task, sequences of letters were visually presented one at a time in a continuous fashion on a computer screen with black background. All letters were presented centrally, for a duration of 300 ms in 24-point uppercase Helvetica font. Each letter was followed by a 1200-ms interval, for a total of a 4500-ms delay between the presentation of cue and probe stimuli. Participants sat in front of the computer screen and were instructed to press the keyboard space bar on target trials and the control button otherwise. Any missed or incorrect response activated a beep sound from two speakers as a prompt to increase speed and accuracy. To further increase engagement in the mental fatigue task, a ticket for a professional sporting event was given as a prize for the best performance. Feedback on performance was presented on the computer screen every 30 min as a percentage of the maximum possible score. Performance was scored automatically by the computer on the basis of correct responses and response time. Target trials were defined as a cue-probe sequence in which the letter A (in red) appeared as a cue and the letter X (in red) as the probe. To increase task difficulty, two white distractor letters (except A, K, X, or Y) were presented between the cue and the probe (in white). All other cue-probe sequences served as invalid cues and nontarget probes. Letter sequences were presented in pseudorandom order, such that target (AX) trials occurred with 70% and nontarget trials occurred with 30% frequency.

**Control task.** The nonfatiguing cognitive task consisted of watching *Earth*, a documentary following the migration paths of four animal families (Alastair Fothergill and Mark Linfield, 2007), for 90 min on the same computer. During both cognitive tasks, HR was recorded continuously using an HR monitor (Polar RS400; Polar Electro Oy, Kempele, Finland).

**Endurance task.** To evaluate endurance performance, subjects performed one prolonged submaximal isometric contraction of the knee extensor muscles until exhaustion. Equipment and subject position was similar to that used for mechanical recordings during the neuromuscular function tests. A target value of 20% MVC torque was chosen. The MVC before the cognitive task was used to calculate the target torque. Visual feedback of the torque exerted during the endurance task was clearly displayed on a computer screen located 1 m in front of the subject. Torque feedback was represented as a horizontal line, and subjects were required to reach an upper target line fixed at the target level. The endurance task terminated when torque fell below the required target value for more than 3 s despite strong verbal encouragement (exhaustion) given by a research assistant blind to the nature of the cognitive task previously performed by the subject. Endurance performance was measured as time to exhaustion. Subjects were not aware of time during the endurance task, and they were made aware of their times to exhaustion after the study was completed. The perception of effort defined as “the conscious sensation of how hard, heavy, and strenuous exercise is” (18) was measured using the 15-point RPE scale (4). Standardized explanations of the scale were given to each subject before the warm-up. Briefly, subjects were asked to rate how hard they were driving their leg during the endurance task. Leg RPE was assessed every 20 s. HR and electromyographic (EMG) signal (see Electromyographic recordings section) for the knee extensor muscles were continuously recorded during the endurance task. HR was calculated for consecutive sampling intervals of 20 s.

### Neuromuscular Function Tests

**Electrical stimulation.** Both single and double (100 Hz frequency) stimulation were used for assessment of neuromuscular function. Transcutaneous electrically evoked contractions of the knee extensor muscles were induced by using a high-voltage (maximal voltage, 400 V) constant-current stimulator (model DS7 modified; Digitimer, Hertfordshire, UK). The femoral nerve was stimulated using a monopolar cathode ball electrode (0.5-cm diameter) pressed into the femoral triangle by the same experimenter during all tests. The site of stimulation producing the largest resting twitch amplitude and compound muscle action potential (M-wave) was located and was marked on the skin so that it could be repeated reliably before and after the cognitive task and after the endurance task. The anode was a 50-cm² (10 × 5 cm) rectangular electrode (Compex SA, Ecublens, Switzerland) located in the gluteal fold opposite the cathode. The optimal intensity of stimulation (i.e., that which recruited all knee extensors motor unit) was considered to be reached when an increase in the stimulus intensity did not induce a further increase in the amplitude of the twitch torque and of the peak-to-peak amplitude of the knee extensors compound muscle action potentials (M-waves). The stimulus duration was 1 ms, and the interval of the stimuli in the doublet was 10 ms. Once the optimal intensity was found, 130% of this intensity was used and kept constant throughout the session for each subject. The supramaximal intensities ranged from 60 to 140 mA. Methodology and supramaximal intensities are according to previous studies (e.g., 29,30).

**Mechanical recordings.** Mechanical parameters were recorded using a Biodex isokinetic dynamometer (Biodex Medical Systems Inc., Shirley, NY). The axis of the dynamometer was aligned with the knee axis, and the lever arm
was attached to the shank with a strap. The extraneous movement of the upper body was limited by two crossover shoulder harnesses and a belt across the abdomen. Neuromuscular function tests were performed with the right leg at a knee joint angle of 90° of flexion (0° = knee fully extended) and a hip angle of 90°. The following parameters were analyzed from the twitch response (average of three single stimulation interspaced by 3 s): peak twitch (Tw), time to peak twitch (contraction time, Ct), and half-relaxation time. The peak torque of the doublet (potentiated doublet, 5 s after the MVC) was also analyzed. MVC torque was considered as the peak torque attained during the MVC. Voluntary activation level (VAL) during the MVC was estimated according to the following formula:

$$\text{VAL} = 100 \left(1 - \frac{\text{superimposed doublet amplitude}}{\text{potential doublet amplitude}}\right)$$

(MVC at stimulation/MVC) corresponding to the Strojnik and Komi correction (4) was used if the stimulation appears not at the MVC torque value. All VAL calculations were performed for an MVC at stimulation between 95% and 100% MVC to ensure reliability of measurement. Mechanical signals were digitized online at a sampling frequency of 1 kHz using a computer and stored for analysis with commercially available software (Acqknowledge 4.1 for MP Systems; Biopac Systems Inc., Goleta, CA). The timing of stimulation could be found in Figure 1.

**Electromyographic recordings.** The EMG of the vastus lateralis (VL) and rectus femoris (RF) muscles was recorded with pairs of silver chloride circular (recording diameter of 10 mm) surface electrodes (ref 1066, Swaromed; Nessler Medizintechnik, Innsbruck, Austria) with an interelectrode (center-to-center) distance of 20 mm. Recording sites were then carefully adjusted by eliciting the greatest M-wave amplitude for each muscle at a given intensity via femoral nerve stimulation at the beginning of each testing session. The low resistance between the two electrodes (<5 kΩ) was obtained by shaving the skin, and dirt were removed from the skin using alcohol swabs. The reference electrode was attached to the patella of the left knee. Myoelectrical signals were amplified with a bandwidth frequency ranging from 1 Hz to 5 kHz (common mode rejection ratio = 110 dB, impedance input = 1000 MΩ, gain = 1000 for RF and 500 for VL), digitized online at a sampling frequency of 2 kHz using a computer, and stored for analysis with commercially available software (Acqknowledge 4.1 for MP Systems; Biopac Systems Inc.). The root mean square (RMS), a measure of EMG amplitude, was automatically calculated with the software.

Peak-to-peak amplitude and duration of the M-waves were analyzed for VL and RF muscles, with the average of the three trials used for analysis. The EMG amplitude of VL and RF muscles during the knee extensors MVC was quantified as the RMS for a 0.5-s interval at peak torque (250-ms interval either side of the peak torque). The maximal RMS values for VL and RF muscles were then normalized by the M-wave peak-to-peak amplitude for the respective muscles to obtain the RMS/M-wave ratio. This normalization procedure accounted for peripheral influences including neuromuscular propagation failure and changes in impedance from the EMG recordings. RMS EMG was calculated for consecutive sampling intervals of 20 s during the endurance task for both VL and RF. The RMS EMG during endurance task was normalized to the RMS EMG determined during the MVC precognitive task.

**Psychological Questionnaires**

**Mood.** The Brunel Mood Scale developed by Terry et al. (36) was used to quantify current mood (“How do you feel right now?”) before and after the cognitive tasks. This questionnaire contains 24 items (e.g., “angry, uncertain, miserable, tired, nervous, and energetic”) divided into six respective subscales: anger, confusion, depression, fatigue, tension, and vigor. The items are answered on a 5-point scale (0 = not at all, 1 = a little, 2 = moderately, 3 = quite a bit, and 4 = extremely), and each subscales, with four relevant items, can achieve a raw score in the range of 0 to 16. Only the scores for the fatigue and vigor subscales were considered in this study as subjective markers of mental fatigue.

**Motivation.** Motivation related to the endurance task was measured using the success motivation and intrinsic motivation scales developed and validated by Matthews et al. (23). Each scale consists of 7 items (e.g., “I want to succeed on the task” and “I am concerned about not doing as well as I can”) scored on a 5-point scale (0 = not at all, 1 = a little bit, 2 = somewhat, 3 = very much, and 4 = extremely). Therefore, total scores for these motivation scales ranged between 0 and 28.

**Statistics.** All data are presented as means ± SEM. Assumptions of statistical tests such as normal distribution and sphericity of data were checked as appropriate. The Greenhouse–Geisser correction to the degrees of freedom was applied when violations to sphericity were present. Paired t-tests were used to assess the effect of condition (mental fatigue vs control) on time to exhaustion, motivation scores, HR at exhaustion, leg RPE at exhaustion, and RMS at exhaustion. One-way repeated-measures ANOVA was used to test the effect of time (15-min blocks) on the number of incorrect answers, reaction time, and HR during the AX-CPT task. Fully repeated-measure 2 × 2 ANOVAs were used to test the effect of condition and time on mood before and after the cognitive tasks. Fully repeated-measure 2 × 3 ANOVAs were used to test the effect of condition and time on MVC torque, VAL, M-wave parameters for each muscle, RMS/M-wave ratio, twitch properties, and peak doublet torque before and after the cognitive tasks and after the endurance task. Fully repeated-measure 2 × 7 ANOVAs were used to test the effect of condition and time on HR, leg RPE, and RMS at isotime (time elapsed from the beginning of the
endurance task to the last measurement before exhaustion of the shortest performance). Significant main effects of time and significant interactions were followed up with Bonferroni tests as appropriate. Significance was set at 0.05 (two-tailed) for all analyses, which were conducted using the Statistical Package for the Social Sciences, version 19 for Mac OS X (SPSS Inc., Chicago, IL).

RESULTS

Manipulation Checks

HR decreased over time in both conditions \((P < 0.001)\), but it was significantly higher in the mental fatigue condition \((73 \pm 1 \text{ beat per minute})\) compared with the control condition \((69 \pm 1 \text{ beat per minute})\) \((P = 0.004)\) (Fig. 2B). The number of incorrect responses (Fig. 2C) and reaction time (Fig. 2D) did not change significantly over time during the AX-CPT task.

The mood questionnaire revealed a significant decrease in vigor after both the AX-CPT task \((9.0 \pm 0.9 \text{ to } 6.5 \pm 0.9)\) and the control task \((9.7 \pm 0.6 \text{ to } 7.1 \pm 0.7)\) \((P = 0.003)\) with no significant difference between conditions. However, there was a significant interaction for the subjective fatigue \((P = 0.033)\). Follow-up tests demonstrated that fatigue increased significantly only after the AX-CPT task \((P = 0.007)\) with no significant change after the control task (Fig. 2A).

There were no significant differences between conditions in intrinsic motivation (mental fatigue condition 16.5 \(\pm 1.3\), control condition 16.5 \(\pm 1.1\), \(P = 1.000\)) and success motivation (mental fatigue condition 18.8 \(\pm 1.6\), control condition 15.8 \(\pm 1.8\), \(P = 0.111\)).

Effects of Mental Fatigue on Time to Exhaustion, HR, EMG Amplitude, and Perception of Effort during the Endurance Task

Time to exhaustion (Fig. 3A) was 13\% \(\pm 4\%\) shorter in the mental fatigue condition compared with the control condition \((P = 0.008)\). Individual times to exhaustion were shorter in the mental fatigue condition compared with the control condition in 8 of 10 subjects (Fig. 3B). HR (Fig. 3D) increased significantly during the endurance task \((P < 0.001)\), with no significant differences between conditions at both isotime and exhaustion. EMG amplitude (RMS/RMS pre-cognitive task MVC) of the VL muscle (Fig 3C) increased significantly during the endurance task \((P = 0.003)\) with no significant difference between conditions at isotime. At exhaustion, however, VL EMG amplitude tended to be higher in the control condition \((52.8\% \pm 6.8\%)\) compared with the mental fatigue condition \((41.5\% \pm 5.9\%)\) \((P = 0.095)\). Leg
RPE (Fig. 3E) increased significantly during the endurance task ($P < 0.001$), and it was significantly higher in the mental fatigue condition compared with the control condition ($P = 0.045$), without interaction effect ($P = 0.353$). Leg RPE at exhaustion was not significantly different between conditions.

Effects of Mental Fatigue and the Endurance Task on Neuromuscular Function

**MVC.** There was no significant main effect of condition or interaction on knee extensors MVC (Fig. 4A). Follow-up tests of the significant main effect of time ($P < 0.001$) revealed that the cognitive tasks did not affect MVC torque.

The endurance task caused a significant reduction in MVC torque in both the mental fatigue and control condition (mental fatigue condition $-26.7\% \pm 5.7\%$, control condition $-27.6\% \pm 3.3\%$) ($P < 0.001$). The MVC torque of the knee flexors was not significantly affected by the cognitive tasks and the endurance task (precognitive task: mental fatigue condition $94 \pm 5$ N·m, control condition $91 \pm 6$ N·m; postcognitive task: mental fatigue condition $86 \pm 5$ N·m, control condition $93 \pm 6$ N·m; postendurance task: mental fatigue condition $89 \pm 6$ N·m, control condition $93 \pm 7$ N·m).

**Peripheral fatigue.** There were no significant main effects of condition or interactions on all twitch parameters. Follow-up tests of the significant main effects of time (all $P < 0.010$) revealed that the cognitive tasks did not affect Tw (Fig. 4C), Ct, and doublets (Fig. 4B). Half
relaxation time of the twitch peak force was significantly higher after the cognitive tasks ($P = 0.047$). The endurance task significantly affected $Tw$ ($P = 0.021$) (Fig. 4C), $Ct$ ($P = 0.021$), half relaxation time of the twitch peak force ($P = 0.034$), and doublet ($P = 0.035$) (Fig. 4B). M-wave amplitude and duration for VL and RF (Table 1) muscles were not significantly affected by the cognitive tasks and the endurance task (amplitude: $P = 0.352$ and $P = 0.444$; duration: $P = 0.488$ and $P = 0.792$). M-wave amplitude and duration for VL and RF muscles did not change between condition (amplitude: $P = 0.177$ and $P = 0.740$, duration: $P = 0.088$ and $P = 0.177$) and did not show any interaction effect (amplitude: $P = 0.804$ and $P = 0.972$, duration: $P = 0.804$ and $P = 0.360$).

**Central fatigue.** There was no significant main effect of condition or interaction on VAL (Fig. 4D). Follow-up tests of the significant main effect of time ($P = 0.027$) revealed that the cognitive tasks did not significantly affect VAL.

**TABLE 1.** Peak-to-peak amplitude and duration of the maximal M-wave associated with the single twitch.

<table>
<thead>
<tr>
<th></th>
<th>Mental Fatigue</th>
<th>Control</th>
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<tbody>
<tr>
<td></td>
<td>Pre-CT</td>
<td>Post-CT</td>
</tr>
<tr>
<td>Amplitude VL (mV)</td>
<td>12.19 ± 2.52</td>
<td>11.81 ± 2.37</td>
</tr>
<tr>
<td>Duration VL (ms)</td>
<td>8.85 ± 0.48</td>
<td>9.08 ± 0.47</td>
</tr>
<tr>
<td>Amplitude RF (mV)</td>
<td>7.70 ± 1.35</td>
<td>7.46 ± 1.22</td>
</tr>
<tr>
<td>Duration RF (ms)</td>
<td>8.03 ± 0.57</td>
<td>8.68 ± 0.86</td>
</tr>
</tbody>
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CT, cognitive task; ET, endurance task; VL, vastus lateralis; RF, rectus femoris.

**FIGURE 4**—Effects of cognitive tasks and endurance task on central and peripheral parameters of neuromuscular function. A. Maximal voluntary contraction (MVC) torque of the knee extensors (KE). B. Peak torque of the doublet. C. Peak twitch ($Tw$). D. Voluntary activation level (VAL). E. Root mean square (RMS)/$M_{\text{max}}$ (M-wave) ratio of the vastus lateralis (VL) muscle. Values are expressed as a percentage of baseline values (precognitive task values). CT, cognitive task; ET, endurance task. *Significant main effect of time ($P < 0.05$). **Significant main effect of time ($P < 0.01$). ***Significant main effect of time ($P < 0.001$). Data are presented as means ± SEM.
However, the endurance task significantly reduced VAL ($P = 0.024$). Similarly, there was no significant main effect of condition or interaction on RMS/M-wave ratio of the RF and VL (Fig. 4E) muscles. Follow-up tests of the significant main effects of time (all $P < 0.009$) revealed that the cognitive tasks did not affect RMS/M of the RF and VL muscles. However, RMS/M decreased significantly after the endurance task for both the RF ($P < 0.001$) and VL ($P = 0.010$) muscles.

**DISCUSSION**

The main aim of the present study was to test the hypotheses that prolonged mental exertion leading to mental fatigue (i) would reduce maximal muscle activation and (ii) would increase the extent of central fatigue induced by subsequent endurance exercise. Contrary to our hypotheses, this study demonstrates that prolonged mental exertion does not lead to any impairment in neuromuscular function. In accordance with previous findings (21), the negative effect of prolonged mental exertion on endurance performance seems to be mediated by the higher perception of effort experienced by mentally fatigued subjects during the endurance task.

**Prolonged mental exertion and mental fatigue.** The higher HR observed during the AX-CPT task compared with watching a movie confirms the demanding nature of this cognitive task. In fact, an increase in HR and other cardiovascular changes are associated with exertion of effort during cognitive tasks (32). Given its demanding nature, it is not surprising that 90 min of the AX-CPT task induced a significant increase in subjective feelings of fatigue. This effect is in accordance with previous studies (21,38) and demonstrates we were successful in experimentally inducing a state of mental fatigue in our subjects. However, we did not observe any significant decrease in cognitive performance during the AX-CPT task. It is possible that the reward we gave for best performance in the AX-CPT task made our subjects able to overcome the negative effects of mental fatigue on cognitive performance (2).

**Prolonged mental exertion does not reduce maximal muscle activation.** Our first hypothesis was that prolonged mental exertion would reduce maximal muscle activation. It is well known that endurance exercise can reduce maximal muscle activation (15); but until now, it was not known whether prolonged mental exertion could also reduce the capacity of the CNS to maximally recruit the active muscles. We tested this hypothesis by examining neuromuscular function before and after the two cognitive tasks. Because small changes in maximal muscle activation may be hard to detect using the twitch interpolation technique (33), careful consideration of numerous experimental details was taken (e.g., use of pair stimuli or high resolution measurement of torque). Contrary to our hypothesis, the present study failed to show a decrease in knee extensors muscles MVC torque following the fatiguing cognitive task (90-min AX-CPT). Furthermore, VAL and RMS/M-wave ratio during MVC were not affected by mental fatigue. These novel results suggest that, unlike endurance exercise, prolonged mental exertion does not reduce maximal muscle activation. However, in the present study, the 90-min AX-CPT induced a relatively moderate level of mental fatigue. Therefore, we cannot exclude that cognitive tasks leading to higher levels of mental fatigue may reduce maximal muscle activation.

Interestingly, some literature suggests that mental fatigue can have systemic effects such as alterations of amino acids concentration in the blood (24,27). These and other unknown systemic effects of mental fatigue could theoretically cause some peripheral fatigue. Our experimental study, however, failed to find any significant effect of prolonged mental exertion on Twitches and M-waves properties.

Our findings are in contrast with those of Bray et al. (5), who found a negative effect of a demanding cognitive task on MVC of the hand flexor muscles. These authors suggested an interaction between the demanding cognitive task and an alteration of the ability of the CNS to maximally recruit the active muscles. However, no valid measure of maximal muscle activation was included in their study. The discrepancy between our results and those of Bray et al. (5) may also be explained by the difference in muscle group tested to measure neuromuscular function (hand flexor muscles vs knee extensor muscles). Furthermore, the increase in MVC observed by Bray et al. (5) in the control condition suggests that their subject did not exert a maximal voluntary effort during all tests of neuromuscular function. Lack of maximal voluntary effort is well known to negatively affect measures of neuromuscular function (12). Further research is required to get better insights on the possible effect of prolonged mental exertion on maximal muscle activation in different muscle groups.

**Prolonged mental exertion does not increase the extent of central fatigue induced by subsequent endurance exercise.** Although prolonged mental exertion did not reduce maximal muscle activation, it may be possible that exercising in a mental fatigue state would increase the extent of central fatigue measured at exhaustion. To investigate the hypothetical interaction between mental and central fatigue, we chose a submaximal isometric knee extensor exercise protocol known to induce a reduction in VAL, that is, to induce central fatigue (e.g., 30). Moreover because timing for neuromuscular assessment is crucial (13), submaximal isometric exercise immediately followed by an MVC of the same muscle group provides us with the fastest way to accurately quantify the extent of central fatigue at exhaustion. As expected, the endurance task induced significant central and peripheral fatigue in both the mental fatigue and control conditions. However, the similar reduction in VAL at exhaustion in both conditions is against our hypothesis that prolonged mental exertion would increase the extent of central fatigue induced by subsequent endurance exercise. Because time to exhaustion was significantly different
between the mental fatigue and control conditions, further investigations on the effect of prolonged mental exertion on the time course of central fatigue during endurance exercise are required. However, it should be pointed that any small difference in voluntary activation between mental fatigue and control conditions may be hard to detect. Further research is also needed to investigate whether higher levels of mental fatigue or different endurance tasks (e.g., dynamic whole-body exercise) are associated with an increase in the extent of central fatigue induced by subsequent endurance exercise.

**Prolonged mental exertion versus endurance exercise.** Our findings demonstrate for the first time that prolonged mental exertion and endurance exercise have different effects on neuromuscular function. The fact that prolonged mental exertion, unlike endurance exercise, does not alter peripheral muscle function is not surprising because the fatiguing cognitive task (90-min AX-CPT) does not involve the knee extensor muscles. However, we expected that prolonged mental exertion would reduce maximal muscle activation of the knee extensors. As in previous studies (30), our submaximal isometric knee extensor exercise protocol induced a significant reduction in maximal muscle activation, a phenomenon called central fatigue (15). However, the 90-min AX-CPT did not reduce maximal muscle activation of the knee extensors despite leading to a significant level of mental fatigue. The different effects of prolonged mental exertion and endurance exercise on maximal muscle activation suggest that different mechanisms are involved. One possibility is that prolonged mental exertion and endurance exercise are associated with different neurochemical changes in the brain. However, both prolonged mental exertion (14,17) and endurance exercise (9,22) have been associated with an increase in brain adenosine and a reduction in brain glycogen. Therefore, at present, the most likely explanation for the different effects of prolonged mental exertion and endurance exercise on maximal muscle activation suggest that different mechanisms are involved. One possibility is that supraspinal fatigue during maximal and submaximal isometric contractions is localized in brain areas upstream of the primary motor cortex (34), there are few neuroimaging studies investigating the brain areas associated with supraspinal fatigue. Some studies have shown progressive increase in activity in several brain areas such as the sensorimotor cortex, supplementary motor areas, frontal cortex, and the insular cortex during submaximal fatiguing exercise (16,31,39,40). However, it is not clear whether the concept of central fatigue is meaningful during submaximal muscle contractions (35). In fact, these changes in cerebral activity during submaximal fatiguing exercise are likely to reflect brain adaptations to compensate for spinal and/or peripheral muscle fatigue rather than mechanisms of supraspinal fatigue. To the best of our knowledge, only van Duinen et al. (39) have investigated the brain areas associated with supraspinal fatigue by measuring their activity during MVCs performed before and after fatiguing exercise. These authors showed a significant decrease in activity of the supplementary motor areas and, to a lesser extent, in parts of the paracentral gyrus, right putamen, and in a small cluster of the left parietal operculum. The fact that central fatigue was not associated with changes in ACC activity suggests that the brain areas affected by prolonged mental exertion and endurance exercise are different.

Furthermore, we have to consider that the neurochemical changes induced by prolonged mental exertion are likely to be confined to the brain, and some of the neurochemical changes leading to central fatigue may also occur at spinal level (15). Therefore, the different effects of prolonged mental exertion and endurance exercise on maximal muscle activation could be explained by (i) the different brain areas affected by prolonged mental exertion and endurance exercise and (ii) the spinal alterations likely to occur during endurance exercise but not during prolonged mental exertion.

**Mental fatigue, perceived exertion, and the psychological model of endurance performance.** Finally, the present results provide experimental evidence that the higher perception of effort induced by prolonged mental exertion is not associated with lower muscle activation before exercise. In fact, the higher perception of effort experienced by mentally fatigued subjects occurs despite no reduction of maximal muscle activation before the endurance task, and similar extent of central fatigue at exhaustion in the mental fatigue and control conditions. However, the increase in the perception of effort occurring over time during the endurance task in both conditions may be caused, at least in part, by the central and peripheral fatigue induced by endurance exercise. In fact, in the presence of significant muscle fatigue, an increase in central motor command is required to maintain the same submaximal force. Because the sensory signal for the perception of effort is the corollary discharge of the central motor command, the increase in central motor command required to overcome muscle fatigue is reflected in a significant increase in the perception of effort (10,19). A previous study (21) suggests that the higher perception of effort experienced by mentally fatigued subjects during the endurance
task may be due to altered central processing of sensory signals. However, further research is required to understand the neurophysiological mechanisms underlying the negative effect of mental fatigue on the perception of effort during endurance exercise.

Similar to previous findings on the effect of mental fatigue on endurance performance during dynamic whole-body exercise (21), we found that mental fatigue significantly reduces time to exhaustion during submaximal isometric knee extensor exercise. These results suggest that mental fatigue has a negative effect on endurance performance regardless of the type of contraction and muscle mass active during endurance exercise.

A plausible explanation for the negative effect of mental fatigue on endurance performance is provided by the psychobiological model of endurance performance (20) based on Motivational Intensity Theory (7). This model postulates that exhaustion is a form of task disengagement that occurs when subjects perceive the task as being impossible to complete despite their maximal effort, or when the effort required by the task exceeds the upper limit of what people are willing to do (potential motivation). Accordingly, a reduction in time to exhaustion can occur either because of an increase in the perception of effort or a reduction in potential motivation. In accordance to a previous study (21), we did not measure any negative effect of mental fatigue on intrinsic and success motivation related to the endurance task. Therefore, the only mechanism that can explain the negative effect of prolonged mental exertion on time to exhaustion is the higher perception of effort experienced by mentally fatigued subjects during the endurance task. As leg RPE increased similarly over time in both conditions, mentally fatigued subjects reached their maximal level of perceived exertion and disengaged from the endurance task earlier than that in the control condition.

CONCLUSIONS AND PERSPECTIVES

The present study provides the first experimental evidence that prolonged mental exertion does not alter neuromuscular function measured as maximal muscle activation and central fatigue induced by subsequent endurance exercise. These findings suggest that prolonged mental exertion and endurance exercise affect different areas of the CNS. Future studies on brain and endurance performance should investigate the specific mechanisms of mental fatigue and central fatigue without making the wrong assumption that these two phenomena are two different aspects of the same central alterations. Because the perception of effort is the most likely mediator of the negative effect of mental fatigue on endurance performance, further studies are required to investigate the neurophysiological alterations associated with the higher perception of effort experienced by mentally fatigued subjects during endurance exercise. On a more practical perspective, the present study suggests that the negative impact of mental fatigue on physical performance is limited to endurance and may not have a negative impact on performance of short maximal voluntary efforts such as sprint or jump.

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