Evidence of neuromuscular fatigue after prolonged cycling exercise

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ABSTRACT

LEPERS, R., C. HAUSSWIRTH, N. MAFFIULETTI, J. BRISSWALTER, and J. VAN HOECKE. Evidence of neuromuscular fatigue after prolonged cycling exercise. Med. Sci. Sports Exerc., Vol. 32, No. 11, pp. 1880–1886, 2000. Purpose: The purpose of this study was to analyze the effects of prolonged cycling exercise on metabolic, neuromuscular, and biomechanical parameters. Methods: Eight well-trained male cyclists or triathletes performed a 2-h cycling exercise at a power output corresponding to 65% of their maximal aerobic power. Maximal concentric (CON; 60, 120, 240° s−1), isometric (ISO; 0° s−1), and eccentric (ECC; −120, −60° s−1) contractions, electromyographic (EMG) activity of vastus lateralis (VL) and vastus medialis (VM) muscles were recorded before and after the exercise. Neural (M-wave) and contractile (isometric muscular twitch) parameters of quadriceps muscle were also analyzed using electrical stimulation techniques. Results: Oxygen uptake (VO2), minute ventilation (VE), and heart rate (HR) significantly increased (P < 0.01) during the 2-h by, respectively, 9.6%, 17.7%, and 12.7%, whereas pedaling rate significantly decreased (P < 0.01) by 21% (from 87 to 69 rpm). Reductions in muscular peak torque were quite similar during CON, ISO, and ECC contractions, ranging from 11 to 15%. M-wave duration significantly increased (P < 0.05) postexercise in both VL and VM, whereas maximal amplitude and total area decreased (VM: P < 0.05, VL: NS). Significant decreases in maximal twitch tension (P < 0.01), total area of mechanical response (P < 0.01), and maximal rate of twitch tension development (P < 0.05) were found postexercise. Conclusions: A reduction in leg muscular capacity after prolonged cycling exercise resulted from both reduced neural input to the muscles and a failure of peripheral contractile mechanisms. Several hypothesis are proposed to explain a decrease in pedaling rate during the 2-h cycling with a constancy of power output and an increase in energy cost. Key Words: TRIATHLETES, MUSCULAR TORQUE, M-WAVE, MUSCULAR TWITCH, OXYGEN UPTAKE, PEDALING RATE

The effects of prolonged exercise such as running or cross-country skiing upon neuromuscular performance has previously been investigated (11,23,24,29). Nicol et al. (24) showed that repeated stretch-shortening cycles during the running of a marathon affected force production by reducing neural input to the muscles and deteriorating the efficiency of the contractile mechanism. Reductions in muscle strength and maximal myoelectrical activity of knee extensor muscles were also observed after prolonged skiing (29), where both glycogen depletion and muscle fiber volume changes are probably involved. Little is known, however, about alterations to the neuromuscular system after prolonged cycling, where leg muscles act only concentrically. Nevertheless, Sahlin and Seger (25) found a reduction in force-generation capacity of the quadriceps muscle under isometric, concentric, and eccentric conditions after an 85-min cycling exercise, but the absence of myoelectrical data limited the possible explanations for such a reduction. However, several mechanisms, either central or peripheral could play a role in the decrease of force production, but their relative involvement after a prolonged cycling exercise needs to be clarified. To our knowledge, changes in neural and contractile properties of the quadriceps muscle, such as the muscle compound action potential (M-wave) and isometric twitch force after a prolonged cycling exercise has not previously been investigated. From this perspective, it would thus seem interesting to further examine changes in neuromuscular performance after prolonged cycling.

Within this framework, the reduction in neuromuscular capacity associated with long-duration exercise could induce changes in movement patterns themselves. More specifically, it has been shown that both stride length and frequency change at the end of a prolonged run (17). To optimize energy costs during locomotion, the choice of a particular cadence in running or cycling is often evoked by coaches or athletes. However, even if the adoption of patterns of locomotion associated with the lowest energy cost during running has been well documented (18), a similar relationship has not been shown for cycling. Typically, cyclists are unaware of why they have chosen a particular pedaling rate and, indeed, feel that this rate should be
maintained despite variations in power output. In addition, the effect of an exercise duration longer than 6 min on the cycling economy—cadence relationship has not been well studied. Only Coast et al. (8) have reported no differences in optimal pedaling rate, for five cyclists for a 20-min ride at 85% of their VO_{2}\text{max}. Thus, there would appear to be a scarcity of data concerning the effects of prolonged ergocycle exercise (lasting more than 1 h) on both neuromuscular performances and pedaling rate.

Therefore, the aim of the present study was to 1) analyze the effects of prolonged cycling exercise upon contractile and neural properties of the quadriceps muscle, and 2) examine the choice of the freely-chosen cycling cadence with the apparition of a state of fatigue due to exercise duration.

MATERIALS AND METHODS

Subjects

Eight well-trained males (either cyclists or triathletes), volunteered to participate in this study. They were informed before the tests in detail as to the nature of the experiment and possible risks. Written consent was given by each subject, and a local Ethics Committee for the protection of individuals gave prior approval to the project before its initiation.

The average age of the subjects was 26 ± 4 yr (with a range of 22–32). Their body weight was 75 ± 7 kg, and their average height was 182 ± 5 cm. All subjects had regularly trained in cycling for at least 4 yr previous the study, and their average weekly training distance during the 2 months before testing was 180 ± 80 km.

Data Collection and Analysis

Strength measurement. Instantaneous torques of the quadriceps muscle at various preset constant angular velocities were recorded using a Biodex isokinetic dynamometer (Biodex Shirley Corp., New York, NY). Subjects were placed in a sitting position, securely strapped into the test chair. Extraneous movement of the upper body was limited by two cross-over shoulder harnesses and an abdomen belt. The trunk/thigh angle was 90°. The axis of the dynamometer was lined up with the right knee flexion-extension axis, and the lever arm was attached to the shank by a strap. During eccentric testing, each subject maximally resisted the downward movement of the lever arm through the full range of motion. Conversely, during concentric testing, each subject extended his knee as forcefully as possible through the full range of motion.

Muscular twitch and surface action potential. To test the effects of the 2-h cycling exercise on muscular twitch (MR) and surface action potential (AP) or M-wave, the quadriceps muscle was electrically stimulated using the femoral nerve in the seat position previously mentioned. Measurement of isometric tension developed by the MR was achieved by the isokinetic dynamometer. Electrical stimulations were given using a high-voltage stimulator (model DS7, Digitimer Stimulator, Hertfordshire, England). The femoral nerve was stimulated using a monopolar cathodal electrode pressed in the femoral triangle. The anode was a rectangular electrode (Medicompex SA, Ecublens, Switzerland), 50 cm² (10 cm × 5 cm), located in the gluteal fold opposite the cathode. The amperage (20–100 mA) of a 400-V rectangular pulse (2 ms in duration) was progressively increased in order to obtain a plateau in the twitch torque. Once this was achieved, a train-of-five stimulus was given over a 25-s period. We measured from mechanical twitch: maximal twitch tension (Pt), maximal rate of tension development (Rt) and relaxation (St), twitch time to peak (Ct), and time to half relaxation (Hrt), as well as total twitch area (A_{RM}). EMG signals were analyzed to determine for both vastus lateralis (VL) and vastus medialis (VM) muscles: duration (D), peak-to-peak amplitude (V), as well total area (A_{AP}) of the surface AP.

EMG and mechanical recording. Recording of muscle electrical activity (EMG) and surface potential action on the VL and VM muscles was achieved by means of two pairs of silver-chloride surface electrodes fixed to the right leg. Low impedance at the skin-electrode surface was obtained (Z < 1 kΩ) by light abrasion of the skin. Electrodes were coated with electrode gel and fixed lengthwise over the motor points (approximately 20 cm above the knee) with an interelectrode distance of 16 mm, and with the reference electrode being fixed on the right wrist. Myoelectric signals were amplified with a bandwidth frequency ranging from 1.5 to 500 Hz (common mode rejection ratio (CMRR) = 90dB; Z input = 100 MΩ; gain = 1000). Torque and EMG signals were digitized on-line (sampling frequency 1000 Hz) by using a digital computer (IPC 486). All data were stored on hard disk for further analysis.

Maximal peak angular torque (PT) during concentric, eccentric, and isometric contractions were determined from the highest values of the two trials. During isokinetic actions, EMG signals were quantified using the root mean square (RMS), which was calculated over a range of 30° extension (±15) around the peak angular torque. For both muscles (VL, VM), normalized RMS amplitude data were expressed as a percentage of the RMS value obtained during the maximal isometric contraction before the 2-h cycling exercise. During isometric actions, the RMS was calculated over a 1-s period after the torque had reached a plateau.

Triangular protocol: maximal oxygen uptake (VO_{2}\text{max}) evaluation. After a 48-h restriction upon strenuous physical activity, each of the eight subjects performed a continuous, incremental cycling test on an electromagnetically braked ergocycle. The test began with a warm-up at 150 W for 10 min, after which the power output was increased by 25 W every 2 min until volitional exhaustion. During this incremental exercise, oxygen uptake (VO_{2}), minute ventilation (VE), and respiratory exchange ratio (RER) were continuously measured every 15 s using a telemetric system collecting gas exchanges (Cosmed K_{4}R, Rome, Italy), previously validated by Hausswirth et al. (16). The criteria used for the determination of VO_{2}\text{max} were: a plateau in VO_{2} despite an increase in power output, a RER
above 1.1 and a heart rate (HR) over 90% of the predicted maximal HR (4). VO$_{2\text{max}}$ was the average of the last three highest VO$_2$ values recorded. It amounted on average to 66.5 ± 8.4 mL·min$^{-1}$·kg$^{-1}$. The maximal aerobic power output (mean arterial pressure (MAP)) was the highest power completed for 2 min (385 ± 25 W). The data collected indicate that the subjects chosen for this study are comparable with competitive cyclists (21) or triathletes (15).

**Bicycle ergometer.** All experiments were conducted on an electromagnetically braked cycle ergometer (Type Excalibur, Lode, Groningen, The Netherlands) where seat and handlebars are fully adjustable both vertically and horizontally to replicate conditions known to subjects from their own bicycles. The ergometer was also equipped with racing pedals and toe clips allowing subjects to wear cycling shoes. Pedaling rate was recorded instantaneously from the ergocycle by using a computer. The ergometer allowed subjects to keep power output constant independent of the pedal rate they naturally adopted (ranging from 40 to 180 rpm). No feedback was given to the subjects concerning their self-selected cadence during the entire experiment. Inside air temperatures ranged from 21 to 23°C. Two fans were placed in front of the ergocycle to reduce sweating during cycling. Subjects drank on average 1000 mL of water during the experiment.

**Protocol and Experimental Procedures**

**Rectangular protocol of experiment.** The subjects were all familiar with the test protocol and the ergocycle. A load designed to elicit 65% of MAP was used for this test. Unpublished observations showed that this level corresponds to the highest power output that could be maintained for 2 h. The power output was constant during the 2-h testing sessions. The test consisted of sustaining 65% of MAP for 2 h (excluding the 10-min warm-up period at 33% of MAP) at a free pedaling rate. The interval between calculations of respiratory parameters was set at 15 s using the Cosmed K4b$_2$. Data were collected between the 5th and 20th minute of cycling (5–20, start: T1), between the 55th and 70th min (55–70, middle: T2), and between the 105th and 120th min (105–120, end: T3); this was done in order to give the cyclists a maximal amount of respiratory comfort and to enable them drink during the test. Pedaling rate was continuously recorded and heart rate was monitored using a cardiofrequency meter (type BHL 6000, Bauman-Haldi SA, Fleurier, Switzerland) connected to the telemetric device of the Cosmed K4b$_2$.

**Blood sampling.** Capillary blood samples were collected from subjects’ earlobes in 25-μL heparinized capillary tubes before and after each period (i.e., T1, T2, T3). Blood lactate concentration was then assayed using an enzymatic method (7).

**Neuromuscular performances.** During the primary session which took place at least 3 d before the experiment, 30 min after the VO$_{2\text{max}}$ test, subjects familiarized themselves with the strength measurement apparatus and the transcutaneous stimulation. A standardized warm-up period was carried out by each subject before the test session. It consisted of 10-min cycling at 33% of MAP, followed by several submaximal concentric contractions of the quadriceps muscle in the testing position. After the warm-up period, the femoral nerve of the right quadriceps muscle was electrically stimulated. The subjects were then asked to perform two maximal isokinetic knee extensions at five angular velocities (−120, -60°·s$^{-1}$ under eccentric conditions and 60, 120, 240°·s$^{-1}$ under concentric conditions) presented randomly (starting position corresponded to thigh/shank angle of 90°; range of motion was 90°, full extension being 0°). The highest peak torque values of the two trials were considered. After this, a set of two maximal isometric voluntary contractions at a knee angle of 60° extension was executed. A 1-min rest period was permitted between each set of muscular actions to minimize the effects of recuperation especially post test. The same experimental procedure was carried out before and immediately after the 2-h cycling exercise.

**Statistical Analysis**

The global statistical analysis allowing the correct identification of the evolution of all parameters studied in relation to the various period of time identified (T1: 5–20 min; T2: 55–70 min; T3: 105–120 min) was performed by means of a repeated measures ANOVA. The comparison of variables between the experimental conditions was conducted using a Student’s t-test for paired samples. The statistical significance of differences between values of PT and RMS for a given angular velocity, and between the parameters of muscular action potential and muscular twitch before and after the 2-h cycling, was also determined using a Student t-test for paired samples. All values are expressed as mean ± standard deviation (SD). In all statistical tests the level of significance was set at $P < 0.05$.

**RESULTS**

**Physiological Parameters**

ANOVA revealed a significant effect of exercise duration ($P < 0.01$) upon ventilatory parameters. VO$_2$, VE, and HR increased respectively by 9.6%, 17.7%, and 12.7%, whereas RER decreased from 0.94 ± 0.02 to 0.88 ± 0.02 (see Table 1A). Blood lactate concentration significantly increased ($P < 0.01$) during the bike exercise compared with rest values (see Table 1B).

**Pedaling Rate**

The free chosen cadence decreased from 87 ± 9 to 69 ± 7 rpm (−21%, $P < 0.01$), whereas the output power remained constant (see Table 1A). On average, subjects initially lost 9 rpm during the 1st h (from T1 to T2), and similarly 9 rpm during the 2nd h (from T2 to T3).
**MUSCULAR STRENGTH**

In preexercise condition, values obtained for knee muscular torque agreed with the torque/angular velocity relationship (see Table 2). Indeed, PT values obtained under eccentric conditions were greater than under isometric and concentric conditions and concentric torque decreased with increases in angular velocity. After the 2-h cycling, PT values were significantly lower ($P < 0.05$) at each angular velocity. This decrease in muscular torque was quite similar regardless of the kind of contractions and angular velocity: from 11 to 15% under CON, from 12 to 14% under ECC, and 13% under ISO conditions.

**MUSCULAR ACTIVITY**

Figure 1 demonstrates that, after the 2-h cycling exercise, the RMS activity was lower at each angular velocity but the reduction was only significant ($P < 0.05$) from $-60^\circ \text{s}^{-1}$ to $120^\circ \text{s}^{-1}$ for VM muscle and at $120^\circ \text{s}^{-1}$ and $240^\circ \text{s}^{-1}$ for VL muscle. The absence of significant differences at the other angular velocities was due to the large SEM values. These data confirmed a reduction of neural input to quadriceps muscles regardless of kind of muscular solicitation.

**CONTRACTILE AND ELECTRICAL PARAMETERS**

Characteristics of muscular action potential of VL and VM muscles changed after the 2-h cycling exercise (see Table 3). A significant ($P < 0.05$) increase of AP duration ($0.01$) reduced body weight ($2.1\%$), which corresponds to an effective increase from 66.9 to 73.3% $\dot{V}O_2$max ($9.6\%$), despite a constant power output and a significantly ($P < 0.01$) reduced body weight ($-2.1\%$). The body weight loss primarily due to sweating accentuated the rise in $\dot{V}O_2$ when expressed in terms of mL per kg per minute to 11.9%. An increase in energy cost with exercise duration had already been observed for prolonged exercises such as running (11) or triathlon (15), but relatively little data exist concerning prolonged cycling exercise. The gradual rise in aerobic metabolism observed during the 2-h cycling exercise was undoubtedly due to several factors. During exercise RER was found to decline, which suggested that the metabolic mixture gradually switched from carbohydrate to fat substrates. The utilization of fat as substrate is known to increase the $\dot{V}O_2$ requirement of exercise. Thermoregulation is also known to participate in increased energy cost during prolonged cycling exercise (13).

**DISCUSSION**

Our results have shown that a 2-h cycling exercise induced changes in physiological, biomechanical (pedaling rate), and neuromuscular (neural and contractile properties of quadriceps muscle) parameters.

**EFFECTS ON ENERGY COST**

During the 2-h cycling exercise, the mean rise in relative $\dot{V}O_2$ was 4.3 mL kg$^{-1}$ min$^{-1}$, which corresponds to an effective increase from 66.9 to 73.3% $\dot{V}O_2$max ($9.6\%$), despite a constant power output and a significantly ($P < 0.01$) reduced body weight ($-2.1\%$). The body weight loss primarily due to sweating accentuated the rise in $\dot{V}O_2$ when expressed in terms of mL per kg per minute to 11.9%. An increase in energy cost with exercise duration had already been observed for prolonged exercises such as running (11) or triathlon (15), but relatively little data exist concerning prolonged cycling exercise. The gradual rise in aerobic metabolism observed during the 2-h cycling exercise was undoubtedly due to several factors. During exercise RER was found to decline, which suggested that the metabolic mixture gradually switched from carbohydrate to fat substrates. The utilization of fat as substrate is known to increase the $\dot{V}O_2$ requirement of exercise. Thermoregulation is also known to participate in increased energy cost during prolonged cycling exercise (13).

**EFFECTS ON NEUROMUSCULAR PERFORMANCES**

**Isokinetic strength.** Results also showed that the decrease in maximal muscular torque ranged from 11 to 15% depending upon the type of contraction. As in Sahlin and Seger’s (25) study, no difference was observed between ECC, ISO, or CON. Because the eccentric component during cycling is negligible, this indicates that in cycling the impairment of muscle function was not specific to the type of contraction performed. The decline under ISO (13%), CON (11–15%), and ECC (12–14%) conditions was less pronounced than those reported by Sahlin and Seger (25), who found, respectively, losses of 34%, 26%, and 20% after a cycling exercise at about 75% of $\dot{V}O_2$max. Nevertheless in the present study, the subjects were not experts in cycling and reached exhaustion after 1 h 25 min. On the contrary, in our experiment the subjects were well trained cyclists or triathletes and had managed 2 h at approximately 70% of $\dot{V}O_2$max without exhaustion. Abernethy (1) had also examined the reduction in muscular torque after a 2 h 30 min exercise.
cycling exercise, but the relatively low intensity used (35% of \( \dot{V}_{O_2\max} \)) may explain the small torque losses (~4%) that were recorded.

In comparison with other prolonged activities, in this study muscular torque losses after 2-h cycling exercise were smaller than those reported after prolonged running exercise (18–35% decrement) (23,24,26) but closer to those observed after prolonged cross-country skiing (7–28%) (29). The importance of strength loss appears to be dependent on the kind of muscular solicitations during the prolonged exercise with greater reductions being recorded after running, an activity that is known to induce severe muscular damage (14).

The decrease in leg maximal muscular torque was associated with a reduction in the maximal electromyographic activity in VL and VM muscles. Similar observations have been made by Nicol et al. (24) after a marathon and by Viitassalo et al. (29) after 85 km of cross-country skiing. The reduced neural input to the muscles after a prolonged cycling exercise, as with other long duration activities, could be partly responsible for the reduction in force production.

**Neural and contractile parameters.** Our results provided evidence that some peripheral mechanisms could also be involved in force reduction. Indeed, the 2-h cycling exercise induced changes in neural and contractile properties of the quadriceps muscle such as alterations of the M-wave and isometric muscular twitch. Post exercise, the peak-to-peak amplitude of the surface action potential (AP), as well as the total area of the surface AP were reduced, whereas the duration of the AP increased. The alteration of the M-wave in the quadriceps muscle has apparently never been investigated after prolonged exercise. Arnaud et al. (3) showed reduced M-wave amplitude with lengthening of the duration in VL muscle but in untrained subjects executing a 5-min high-level cycling exercise. The effects of a prolonged exercise (marathon running) on M-wave has been examined by Avela et al. (5) but only on triceps surae muscle for which no change was observed in the maximal M-wave peak-to-peak amplitude. Impairment of neuromuscular propagation has been showed by numerous studies in different muscles after sustained or intermittent fatiguing contractions at maximal or submaximal forces (12,20). Nevertheless, the alteration of M-wave in human muscle with fatigue is still controversial. For example, Bigland-Ritchie et al. (6) found no change in the M-wave after sustained voluntary contractions; other authors (19,30) found a potentiation of the action potential after fatigue. This discrepancy may be partially due to differences in the tasks performed to induce fatigue and in the type of contractions (isometric, concentric, eccentric).

The cellular mechanism responsible for the alteration of the M-wave could be impaired neuromuscular transmission or decreased excitability of the muscle fiber plasmalemma. Increase of AP duration in VM and VL muscles observed after 2-h cycling exercise can be interpreted as a slowing of conduction velocity along membranes of muscle fibers whereas, decrease of AP amplitude and total area suggests the presence of presynaptic and/or endplate fatigue. Nevertheless, the cellular mechanisms that might account for the

<table>
<thead>
<tr>
<th>Angular velocity (°s(^{-1}))</th>
<th>ECC</th>
<th>ISO</th>
<th>CON</th>
<th>ECC</th>
<th>ISO</th>
<th>CON</th>
</tr>
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<tbody>
<tr>
<td>Before 120°</td>
<td>338 ± 56</td>
<td>329 ± 67</td>
<td>303 ± 70</td>
<td>235 ± 37</td>
<td>194 ± 28</td>
<td>134 ± 19</td>
</tr>
<tr>
<td>After 120°</td>
<td>290 * ± 41</td>
<td>290 * ± 67</td>
<td>262 * ± 48</td>
<td>206 * ± 29</td>
<td>164 * ± 21</td>
<td>119 * ± 18</td>
</tr>
<tr>
<td>Loss (%)</td>
<td>14</td>
<td>12</td>
<td>13</td>
<td>12</td>
<td>15</td>
<td>11</td>
</tr>
</tbody>
</table>

* \( P < 0.05; \) ** \( P < 0.01; \) significant differences compared with “Before” values.
Values are means ± 1 SD.
TABLE 3. Characteristics of muscular action potential before and after the 2-h cycling exercise for both VM and VL muscles.

<table>
<thead>
<tr>
<th></th>
<th>Vastus Lateralis</th>
<th>Vastus Medialis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>D (ms)</td>
<td>V (V)</td>
</tr>
<tr>
<td>Before</td>
<td>8.6 ± 1.3</td>
<td>12.66 ± 4.91</td>
</tr>
<tr>
<td>After</td>
<td>10.7* ± 2.7</td>
<td>10.87 ± 4.09</td>
</tr>
</tbody>
</table>

D, duration; V, amplitude; AAP, total area of action potential.
Values are means ± 1 SD.
* P < 0.05; ** P < 0.01 = significant differences compared with “Before” values.

Changes observed in the M-wave such as reduced Na\(^+\)-K\(^+\) pump activity, impaired inactivation of Na\(^+\) channels, or physical damage to the muscle membrane were not directly measured in the present study.

Significant decreases in maximal isometric twitch tension, total area of mechanical response, and maximal rate of twitch tension development have been observed after the 2-h cycling exercise. Contractile kinetics of the quadriceps muscle have been investigated by Sahlin and Seger (25) after a 1 h 25 min cycling exercise using electrical stimulation, but these authors did not find significant changes in the kinetics of the evoked isometric contraction (rise time of contraction force and half relaxation time). Davies and White (10) showed alterations of human muscle contractile properties after prolonged running exercise but in the triceps surae. Numerous studies have shown a mechanical failure of human muscle after fatigue (12,20), but the specific mechanisms involved are still unclear. Possible changes in the excitation-contraction coupling could have several explanations such as changes in metabolites (H\(^+\), inorganic phosphate Pi) or a reduction in the release Ca\(^{2+}\) from the sarcoplasmic reticulum (22). These mechanisms might be represented by the changes observed in the M-wave duration and amplitude from the present study.

**Effects on Self-Selected Cadence**

Results showed that the self-selected cadence progressively decreased (-18 rpm) throughout the 2 h-cycling exercise while power output remained constant. This muscular strategy which consisted of applying greater forces to the pedals with reducing the pedaling rate as the exercise duration increase had, to our knowledge, never been observed and appeared to contradict results concerning a decrease of maximal muscular strength postexercise.

A change in muscle type fiber recruitment during the 2-h cycling exercise could be advanced. The fiber type recruitment in cyclists seems to depend upon pedaling rate. Indeed, Ahlquist et al. (2) have shown that cycling (30 min, 85% of \(\text{VO}_{2\text{max}}\)) with the same metabolic cost at 50 rather 100 rpm resulted in greater glycogen depletion of type II fibers. These authors suggested that force development, as opposed to velocity of contraction, determines the degree of type II fiber recruitment. According to this hypothesis, a decrease in pedaling rate observed during the 2-h cycling exercise in the present study could have indicated that type II fibers were increasingly recruited. Even through for prolonged cycling at an intensity of greater than 50% of \(\text{VO}_{2\text{max}}\), higher final glycogen loss was observed in the type I fibers of the vastus lateralis, type I and II fibers seem to be recruited right from the beginning (28). Moreover, specific recruitment of type II fiber as the duration of exercise increased is limited by the fact that endurance trained cyclist are known to have a low percentage of type II fibers in quadriceps muscle (9). Therefore, the hypothesis of a progressive increase in type II fiber recruitment during the 2-h cycling exercise, while the pool of type I fibers became more and more depleted in glycogen, appears not be relevant.

Another hypothesis to explain the shift to lower cadence could be proposed from data concerning the relationship between cadence and energy cost. In experienced cyclists, for relatively short-duration exercise (less than 15 min), free-chosen cadence appears higher than the cadence that minimizes their oxygen uptake. Takaishi et al. (27) has suggested that the reason that cyclists prefer a higher pedaling is closely related to the neuromuscular factors because the adopted cadence corresponded to a minimum of the integrated EMG slope for vastus lateralis muscle which could be associated to a lower “neuromuscular cost.” The reduction of cadence with an increase in duration of exercise with muscle fatigue progressively occurring could be interpreted as an adaptation of the movement pattern in order to minimize the energy cost rather than the “neuromuscular cost”. Nevertheless, this hypothesis cannot be verified here with the absence of EMG recording during the cycling exercise.

**TABLE 4. Contractile parameters measured on muscular twitch of the quadriceps muscle before and after the 2-h cycling exercise.**

<table>
<thead>
<tr>
<th></th>
<th>A(_{\text{MM}}) (Nm·s)</th>
<th>Ct (ms)</th>
<th>Pt (N·m)</th>
<th>HRT (ms)</th>
<th>Rt (Nm·ms(^{-1}))</th>
<th>St (ms)</th>
</tr>
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<tbody>
<tr>
<td>Before</td>
<td>3.15 ± 0.99</td>
<td>93.8 ± 14.6</td>
<td>25.6 ± 6.6</td>
<td>69.6 ± 12.5</td>
<td>0.61 ± 0.15</td>
<td>0.30 ± 0.10</td>
</tr>
<tr>
<td>After</td>
<td>2.30* ± 0.80</td>
<td>85.2 ± 5.45</td>
<td>19.4* ± 6.9</td>
<td>74.0 ± 6.8</td>
<td>0.50* ± 0.19</td>
<td>0.25 ± 0.14</td>
</tr>
</tbody>
</table>

A\(_{\text{MM}}\), total area of mechanical response; Ct, contraction time; Pt, maximal twitch tension; HRT, half relaxation time; Rt, maximal rate of twitch tension development; St, maximal rate of twitch tension relaxation.
Values are means ± 1 SD.
* P < 0.05; ** P < 0.01 = significant differences compared to “Before” values.
In conclusion, the deteriorating force generating capacity of the quadriceps muscle after a prolonged cycling exercise resulted from both reduced neural input to the muscles and peripheral mechanisms such as a failure in muscle membrane excitation and in excitation-contraction coupling. The increase of energy cost during the 2-h cycling exercise was associated with a progressive reduction in the self-selective cadence. Further investigations are necessary to target the mechanisms involved in the decrease in pedaling rate with the duration of exercise.

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