Central Versus Peripheral Adaptations Following Eccentric Resistance Training

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Introduction

The physiological modifications induced by strength training have been widely investigated and it has been suggested that the resultant torque gains can be attributed to peripheral and/or central factors [7,12,15,17,18,31]. A common approach used to distinguish neural versus muscle-morphological adaptations is the analysis of the relationship between electromyographic (EMG) activity and voluntary torque output. Indeed, as suggested by Moritani and de Vries [26], changes in the slope of this relationship could result from peripheral adaptations (e.g. hypertrophy), whereas increases of the maximal EMG activity with no modification of the slope could be more particularly associated to an increased central neural drive to the agonist muscles. More recently, it has been demonstrated that training-induced increases of the torque can also be attributed to a reduction in the level of coactivation of the antagonist muscles [6]. As a practical recommendation, the EMG activity from the antagonist muscles must necessarily be recorded, especially when focusing on the adaptations induced by training. On the other hand, modifications in agonist EMG activity could be related to local processes such as changes of the membrane ionic mechanisms [13]. Only EMG-recording during voluntary contractions is therefore unable to discriminate the origin of the adaptations (central versus peripheral).

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Abstract

Aim of the present investigation was to study the effects of an eccentric training on the neuromuscular properties of the plantar-flexor muscles. The experiment was carried out on 14 males divided into two groups (eccentric and control). Eccentric training consisted of six sets of six eccentric contractions at 120% of one maximal concentric repetition and it was performed four times a week during four weeks. Before and after the 4-wk period, the plantar-flexor torque and the associated electromyographic activity were recorded during voluntary contractions (isometric, concentric and eccentric) and electrically induced contractions (twitch and tetanus), in order to distinguish central from peripheral adaptations. For the eccentric group, voluntary torque significantly increased after training independent of the action mode (relative gains 14 – 30%, p < 0.05). This was associated with an increase in agonist EMG activity during isometric action and a decrease in antagonist coactivation in concentric (~27%) and eccentric actions (~22%) (p < 0.05). Voluntary activation level significantly increased from 80 ± 5% to 91 ± 2% (p < 0.05). Some of the twitch contractile properties (peak torque and maximal rate of twitch tension relaxation) were significantly modified (p < 0.05), but no changes were observed for the tetanus characteristics. These results allowed to conclude that the torque gains observed after the present training were more likely associated to central adaptations, affecting both agonist and antagonist muscles.

Key words
Plantar-flexor muscles · M wave · coactivation · tetanus · activation

Introduction

The physiological modifications induced by strength training have been widely investigated and it has been suggested that the resultant torque gains can be attributed to peripheral and/or central factors [7,12,15,17,18,31]. A common approach used to distinguish neural versus muscle-morphological adaptations is the analysis of the relationship between electromyographic (EMG) activity and voluntary torque output. Indeed, as suggested by Moritani and de Vries [26], changes in the slope of this relationship could result from peripheral adaptations (e.g. hypertrophy), whereas increases of the maximal EMG activity with no modification of the slope could be more particularly associated to an increased central neural drive to the agonist muscles. More recently, it has been demonstrated that training-induced increases of the torque can also be attributed to a reduction in the level of coactivation of the antagonist muscles [6]. As a practical recommendation, the EMG activity from the antagonist muscles must necessarily be recorded, especially when focusing on the adaptations induced by training. On the other hand, modifications in agonist EMG activity could be related to local processes such as changes of the membrane ionic mechanisms [13]. Only EMG-recording during voluntary contractions is therefore unable to discriminate the origin of the adaptations (central versus peripheral).
A simple way to study the local adaptations induced by training consists of recording the mechanical (twitch) and EMG (M wave) responses obtained after electrical stimulation of the motor nerve [14]. This method induces muscle contraction with no influence from central factors, therefore providing information concerning the peripheral origin of adaptations by the analysis of muscle excitation–contraction coupling and contractile kinetics [11]. Peripheral adaptations are also often analysed by expressing the amplitude of the twitch or tetanus evoked at rest with respect to the maximal voluntary contraction (MVC) [15]. Two other methods are commonly used to investigate the adaptations affecting the peripheral part of the neuromuscular system: the train-of-stimuli (i.e. tetanus), which recruits all the motor units at their maximal level, and the post-contraction potentiation (PCP), i.e. the enhancement of the twitch evoked after a maximal voluntary contraction, which allows to study the intramuscular mechanisms such as the Ca²⁺ movements [13,29,36]. Electrically evoked single twitches could also be useful for the analysis of central adaptations. Indeed, one or more twitches superimposed to a MVC allow to quantify the voluntary level of muscle activation [1]. This technique, called twitch interpolation, has so far been used by a limited number of studies to examine the plasticity of the activation level to training [20]. In addition, the EMG activity recorded during voluntary contractions can be normalized with respect to the surface of the action potential electrically evoked (M wave). This ratio allows not only to account for differences in electrodes placement and electrical impedance, but also to exclude all modifications induced at peripheral level from the EMG values.

To the best of our knowledge, no research has previously associated the ensemble of these techniques to study the adaptations induced by eccentric training. Moreover, the nature of the adaptations (central versus peripheral) associated to short-term eccentric training has not yet been clearly elucidated. Aim of the present investigation was therefore to examine the effects of an eccentric training performed over a 4-wk period on the neuromuscular properties of the plantar-flexors. In order to differentiate the relative contribution of the central and peripheral adaptations to potential torque gains, plantar-flexor torque and EMG activity from agonist and antagonist muscles were recorded during voluntary contractions and after electrical stimulation of the motor nerve.

**Methods and Materials**

**Subjects and training program**

The experiment was carried out on 14 male students divided into two groups: the eccentric training group (EG), composed of eight subjects (mean age ± SD 23.1 ± 5.2 years; height 175.6 ± 3.8 cm; mass 73.4 ± 10.0 kg) and the control group (CG; n = 6; age 26.0 ± 5.1 years; height 176.7 ± 4.8 cm; mass 69.5 ± 4.6 kg). All subjects were normally active, and they volunteered and signed informed consent prior to involvement in the investigation. Approval for the project was obtained from the local Committee on Human Research.

Training for EG was carried out four times a week during four weeks. Each subject realized six sets of six eccentric contractions at 120% of one maximal concentric repetition. This latter was determined at the beginning of the first and third session of each week. Subjects performed the training contractions sitting in a calf machine (Multi-Form, La Roque d’Anthéron, France), with a 90° angle at the knee and trunk joints. They performed 3-s eccentric actions, starting from the position of complete plantar flexion. A metronome imposed the duration of exercise, and motion amplitude ranged from 50° to 60°, which corresponded to an angular velocity comprised between 15° × s⁻¹ and 20° × s⁻¹. At the end of each eccentric action the load was returned to the initial position by the experimenter. A 3-min rest was allowed between each set.

**Isometric and isokinetic voluntary strength testing**

Two testing sessions were organized, each separated by at least 48 hours. During each session, plantar-flexor torque and EMG data were recorded concurrently. In the first testing session, strength measurements were carried out using an isokinetic dynamometer (Biodex Shirley Corporation, NY, USA), which records instantaneous muscular torque at different angular positions and at various constant angular velocities [33]. Subjects were seated with the trunk inclined 30° with respect to the vertical and with a 90° angle at the knee and ankle joints. To minimise hip and thigh motion during the contractions, straps were applied across the chest, pelvis, mid-thigh and lower leg. The dominant foot (i.e. the take-off-foot) was also firmly secured to the dynamometer’s footplate by means of straps. In this position, three maximal voluntary plantar-flexions were performed under isometric, concentric and eccentric conditions. Under isometric conditions the ankle was fixed at 0°, which corresponds to an angle of 90° between the ankle and the leg. The angular velocity adopted for concentric and eccentric contractions was 60° × s⁻¹ and the range of motion was 50°, i.e. 20° in dorsi-flexion and 30° in plantar-flexion. Three maximal isometric dorsi-flexions were also realized at 0°. Between each contraction, 1-min rest was allowed to eliminate the effects of fatigue.

**Electrical stimulation**

During the second testing session, subjects were stimulated at rest to evoke an EMG response (M wave, see EMG activity below) associated to a plantar-flexor mechanical response. This latter was recorded by a pedal equipped with strain gauges and specifically developed for the study by the local engineer school. The dominant foot was fixed to the pedal by two straps. Subjects were examined under sitting conditions with the trunk inclined 60° with respect to the vertical and the hip, knee and ankle joints flexed at 90°. The posterior tibial nerve was stimulated using a cathode ball electrode (0.5 cm diameter) pressed in the poplitea fossa. The anode was a large rectangular electrode (5 cm × 10 cm – Medicompex SA, Eaublens, Switzerland), placed on the anterior surface of the knee. The percutaneous electrical stimulus was a rectangular pulse (1 ms duration) delivered by a Digitimer stimulator (Model DS7, Herthfordshire, England). Each subject was initially familiarised with several submaximal (range 1 – 20 mA) electrical stimuli over a period of 10 min. The current intensity was then progressively increased until plantar-flexor twitch torque and M wave amplitude reached a maximal value. When this optimal intensity was determined, four single stimuli were delivered, each separated by a 5-s interval. The individual intensity was then maintained for the entire session of electrical stimulation.

The level of maximal voluntary activation was estimated using the twitch interpolation technique [1], and concomitantly, the post-contraction potentiation (PCP) was assessed as follows. Subjects performed two maximal isometric plantar-flexions lasting 3 s. One second before each contraction, in the middle of the isometric plateau and one second after the end of the contraction, two stimuli were delivered at an interval of 10 ms (paired stimuli). Finally, a 250-ms tetanus was electrically evoked at rest (25 stimuli, i.e. 100 Hz). Fig. 4b shows torque traces obtained after tetanic stimulation for one subject. For the activation level estimation, PCP and tetanus, two trials were performed, with 1-min rest between each.

EMG activity
The EMG activity from the soleus (SOL), gastrocnemius medialis (GM), gastrocnemius lateralis (GL) and tibialis anterior (TA) muscles, was recorded by means of two silver-chloride surface electrodes of 10-mm diameter, with an inter-electrode (centre-to-centre) distance of 2 cm. For the SOL, the recording electrodes were placed along the mid-dorsal line of the leg, about 5-cm distal from where the two heads of the gastrocnemius join the Achilles tendon. For the GM, GL and TA, electrodes were fixed lengthwise over the middle of the muscle belly [10]. The reference electrode was attached in a central position on the same leg. The placement of the electrodes was marked on the skin with indelible ink, so that it could be exactly repeated between experiments. In order to reduce the differences in the EMG signal due to changes at the skin level, the RMS values were normalised to the surface of the M wave of the session. This normalisation procedure allows to account for individual differences in electrical impedance and electrode placement from session to session. Moreover, the results obtained on the control group before and after the 4-wk period, clearly confirm the reliability of the present EMG data. Low impedance (<5 kΩ) at the skin-electrode interface was obtained by abrading the skin with emery paper and cleaning with alcohol. EMG signals were amplified with a bandwidth frequency ranging from 1.5 Hz to 2 kHz.

Data analysis
Whatever the testing session, the single traces and the average of electrical and mechanical signals were digitised on-line (sampling frequency 2 kHz), and stored with commercially available software (Tida, Heka Elektronik, Lambrecht/Pfalz, Germany) for data analysis. Constant angular torque at 0° (i.e. 90° of flexion at the ankle) was included in the torque/angular velocity (T/AV) relationship. During isometric actions, torque and EMG were analysed over a 1-s period after the torque had reached a plateau. During isokinetic actions, the torque was considered as the highest value of three trials, and the root mean square (RMS) EMG activity was calculated over 10° around the constant angular torque (i.e. between −5° and +5°). For the SOL, GM and GL muscles, the RMS values were normalised with respect to the surface of the respective M wave recorded at the optimal intensity (EMG_Ratio). For the TA muscle, the RMS values were normalised with respect to the RMS obtained at 0° when this muscle contracted as agonist (EMG_TA).

Concerning the electrically evoked twitches, the average of four EMG signals and mechanical responses (Fig. 4a) was considered and peak-to-peak amplitude (A), duration (D), and surface (SAP) of the SOL, GM, and GL M wave were calculated. The SAP was obtained after numerical integration of the entire compound action potential. The following twitch contractile properties were computed: 1) peak twitch (Pt_max), the highest value of twitch tension production; 2) maximal rate of twitch tension development (RDp0), the highest value of the first derivative of the force signal; 3) maximal rate of twitch tension relaxation (RRP0), the lowest value of the first derivative of the force signal; 4) contraction time (CT), the time to twitch maximal force, calculated from the origin of the mechanical signal and 5) half-relaxation time (1/2 RT), the time to obtain half of the decline in twitch maximal force.

In order to estimate the individual level of voluntary activation, the ratio of the amplitude of the superimposed twitch over the size of the twitch evoked at rest was calculated, as suggested by Allen et al. [1]:

Voluntary activation (%) =

\[
1 - \frac{\text{superimposed twitch}}{\text{twitch evoked at rest}} \times 100
\]

Paired stimulations were however used for the superimposed twitch and for the twitch evoked at rest. The twitch interpolation technique assumes that a voluntary activation of 100% indicates full activation, whereas a value less than 100% indicates that the activation is not complete. Post-contraction potentiation (PCP) was calculated as the ratio between the twitch evoked after the MVC and the twitch evoked before the same contraction (paired stimuli). The following properties were measured from the tonic torque traces: the peak torque (Pp0), and the maximum rate of torque development and relaxation, respectively called RDp0 and RRP0.

Statistical analysis
Ordinary statistical methods including means and their standard errors (SE) were calculated for each parameter. The differences between CG and EG, and between pre- and post-test values were analysed by means of a two-ways Anova followed by LSD post-hoc analysis. The level of significance was fixed at p ≤ 0.05 for all the procedures.

Results
Torque/angular velocity relationship and associated EMG activity
Before training and irrespective of the action mode, the torque developed by the EG and CG groups were not significantly different. Fig. 1 shows the plantar-flexor T/AV relationship for EG and CG group. After training, the constant angular torque significantly increased (p < 0.05) in all action modes, and these values were significantly different from the CG. The maximal isometric torque increased from 89.7 ± 9.5 N·m to 115.7 ± 13.5 N·m, the concentric torque from 85.2 ± 11.1 N·m to 98.6 ± 9.0 N·m, and the eccentric torque from 98.8 ± 8.9 N·m to 114.5 ± 11.5 N·m. The relative gains averaged 30 ± 8% for isometric, 14 ± 5% for concentric and 16 ± 5% for eccentric torque, but no significant difference was observed between the three action modes. No significant changes in isometric, concentric and eccentric torque were noted in the CG before and after the 4-wk period.
Fig. 1  Plantar-flexor T/AV relationship for EG and CG, before (○) and after (■) training. Values are means ± SE. Significantly different from values before training: *p < 0.05.

Fig. 2  Normalised EMG activity (EMG\textsubscript{RATIO}), for soleus (SOL), gastrocnemius medialis (GM) and gastrocnemius lateralis (GL), during eccentric (−60° × s\textsuperscript{-1}), isometric (0°) and concentric (60° × s\textsuperscript{-1}) contractions, in EG and CG before and after training. Values are means ± SE; EG n = 8, CG n = 6. Significantly different from values before training: *p < 0.05.

Fig. 3  Normalised EMG activity (EMG\textsubscript{TA}) for antagonist muscle, during eccentric (−60° × s\textsuperscript{-1}), isometric (0°) and concentric (60° × s\textsuperscript{-1}) contractions, in EG and CG, before (○) and after (■) training. Values are means ± SE. Significantly different from values before training: *p ≤ 0.05.

Fig. 4  Example of twitch torque associated with maximal M wave response (a), and tetanic torque obtained at a frequency of 100 Hz, with stimulation intensity corresponding to maximal twitch response (b), before (thin lines) and after training (thick lines) for one representative subject (average of four acquisitions).

Fig. 2 shows the normalised EMG activity recorded from SOL, GM and GL before and after the 4-wk period, for EG and CG. At baseline, no significant difference in EMG\textsubscript{RATIO} for the three plantarflexors was noted between CG and EG. After training, the EMG\textsubscript{RATIO} of the agonist muscles showed a tendency to increase...
whatever the action mode. A significant (p < 0.05) increase was observed under isometric conditions for the three plantar-flexors (Fig. 2), while no modifications of the EMG ratio were observed during concentric or eccentric contractions, except for the GM. Before training, the antagonist coactivation appeared essentially constant irrespectively of the action mode (Fig. 3). The level of coactivation during eccentric and concentric contractions was affected by training. Indeed, the EMG activity significantly decreased in eccentric (–22%, p < 0.05) and concentric (–27%, p < 0.05) action modes, while no modification was observed in isometric contractions. For the CG, there were no significant differences between the two testing sessions in normalised EMG for the agonist (Fig. 2) and antagonist muscles (Fig. 3).

**Twitch contractile properties, M waves, activation level, PCP and tetanus**

Before training, no significant differences were observed in plantar-flexor twitch contractile properties, between CG and EG (Table 1). Fig. 4 shows typical changes induced by eccentric training on the twitch torque and on the 100 Hz-tetanic torque, for one representative subject. The maximal amplitude of the plantar-flexor twitch (Ptmax) significantly increased in EG after training (p < 0.05). We also noted a significant increase in RRpt (p < 0.05) but no changes for RDpt, CT and 1/2 RT (Table 1). No significant modifications were observed on the M wave characteristics for the SOL, GM and GL (Table 3) after training. Twitch contractile properties (Table 1) and M wave characteristics were not significantly different in CG between the two testing sessions (Table 3).

Before training, activation level, PCP and tetanus properties were not different between CG and EG. The activation level estimated during maximal voluntary isometric contraction significantly increased in EG (p < 0.05), and the average relative gain was 17 ± 7% (Table 2). Post-contraction potentiation was significantly higher (p < 0.05) after the training period (Table 2), and increased from 1.03 ± 0.01 to 1.20 ± 0.03 (relative gain 18 ± 4%)

The overall characteristics (P0, RD0, RR0) of the torque evoked by 100-Hz tetanic stimulation were not affected by training (Table 2). The RD0 (from 0.86 ± 0.07 N·m·s⁻¹ to 0.85 ± 0.07 N·m·s⁻¹) and RR0 (from 0.75 ± 0.11 N·m·s⁻¹ to 0.79 ± 0.11 N·m·s⁻¹) were not significantly different between CG and EG. Before training, activation level, PCP and tetanus properties were not different between CG and EG. The activation level estimated during maximal voluntary isometric contraction significantly increased in EG (p < 0.05), and the average relative gain was 17 ± 7% (Table 2). Post-contraction potentiation was significantly higher (p < 0.05) after the training period (Table 2), and increased from 1.03 ± 0.01 to 1.20 ± 0.03 (relative gain 18 ± 4%).

Table 1

| Plantar-flexor twitch contractile properties for the eccentric group (EG) and control group (CG) before and after training |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                  | Ptmax (N·m)     | CT (ms)         | 1/2 RT (ms)     | RDpt (N·m·s⁻¹)  | RRpt (N·m·s⁻¹)  |
| EG Before        | 14.57 ± 1.60    | 131.93 ± 3.98   | 93.94 ± 2.44    | 0.21 ± 0.02     | 0.12 ± 0.02     |
| After            | 17.38 ± 1.65*   | 131.39 ± 3.33   | 91.06 ± 1.74    | 0.25 ± 0.03     | 0.15 ± 0.02*    |
| CG Before        | 17.48 ± 1.48    | 136.02 ± 3.76   | 94.43 ± 4.43    | 0.24 ± 0.02     | 0.14 ± 0.02     |
| After            | 16.28 ± 2.25    | 135.11 ± 3.91   | 98.64 ± 3.43    | 0.24 ± 0.04     | 0.13 ± 0.02     |

Twitch peak torque (Ptmax), contraction time (CT); half-relaxation time (1/2 RT); maximal rate of twitch tension development (RDpt); maximal rate of twitch tension relaxation (RRpt). Significantly different from values before training: *p < 0.05.

Table 2

<table>
<thead>
<tr>
<th>P0 (N·m)</th>
<th>RD0 (N·m·m·s⁻¹)</th>
<th>RR0 (N·m·m·s⁻¹)</th>
<th>MVC/P0</th>
<th>Activation (%)</th>
<th>PCP</th>
</tr>
</thead>
<tbody>
<tr>
<td>EG Before</td>
<td>88.89 ± 11.55</td>
<td>0.86 ± 0.07</td>
<td>0.75 ± 0.11</td>
<td>1.04 ± 0.06</td>
<td>80 ± 5</td>
</tr>
<tr>
<td>After</td>
<td>85.99 ± 8.38</td>
<td>0.85 ± 0.09</td>
<td>0.79 ± 0.07</td>
<td>1.34 ± 0.08*</td>
<td>91 ± 2*</td>
</tr>
<tr>
<td>CG Before</td>
<td>96.54 ± 8.86</td>
<td>0.79 ± 0.08</td>
<td>0.70 ± 0.09</td>
<td>1.08 ± 0.15</td>
<td>72 ± 7</td>
</tr>
<tr>
<td>After</td>
<td>105.82 ± 17.12</td>
<td>0.94 ± 0.10</td>
<td>0.73 ± 0.15</td>
<td>0.97 ± 0.06</td>
<td>79 ± 4</td>
</tr>
</tbody>
</table>

Maximal tetanic torque (P0); maximal rate of torque development (RD0); maximal rate of torque relaxation (RR0); MVC/P0; activation level (%); post-contraction potentiation (PCP). Significantly different from values before training: *p < 0.05.

Table 3

| M wave characteristics obtained for the eccentric group (EG) and control group (CG) on the soleus (SOL), gastrocnemius medialis (GM) and gastrocnemius lateralis (GL), before and after training |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                  | Amplitude (mV) | Duration (ms)   | Before          | Before          | Before          |
|                  | Before          | After           | Before          | After           | Before          |
|                  | Before          | After           | Before          | After           | Before          |
|                  |                 |                 |                 |                 |                 |
| EG SOL           | 9.90 ± 0.94     | 9.90 ± 1.30     | 2.67 ± 0.25     | 2.69 ± 0.22     | 0.12 ± 0.04     |
| GM               | 6.32 ± 1.43     | 3.93 ± 0.58     | 1.75 ± 0.13     | 2.22 ± 0.22     | 0.05 ± 0.02     |
| GL               | 5.28 ± 0.67     | 5.11 ± 0.62     | 3.11 ± 0.39     | 3.90 ± 0.53     | 0.04 ± 0.01     |
| CG SOL           | 10.93 ± 1.13    | 10.34 ± 1.22    | 2.60 ± 0.22     | 2.79 ± 0.32     | 0.13 ± 0.03     |
| GM               | 7.80 ± 1.60     | 7.42 ± 1.65     | 2.76 ± 0.20     | 2.15 ± 0.28     | 0.08 ± 0.04     |
| GL               | 4.72 ± 0.54     | 6.47 ± 1.07     | 3.47 ± 0.30     | 3.75 ± 0.51     | 0.03 ± 0.003    |

Peak-to-peak amplitude (A); Peak-to-peak duration (D); Surface Action Potential (SAP); Values are means ± SE; EG n = 8, CG n = 6. Significantly different from values before training: *p < 0.05.
Training & Testing EMGRATIO and under eccentric conditions EMGRATIO significantly increased (p < 0.05) (Table 2). In CG, no changes were observed for activation level, PCP and tetanus properties between the two testing sessions (Table 2).

Discussion

The aim of the present study was to investigate the origin of the adaptations (central versus peripheral) induced by eccentric resistance training on the plantar-flexor muscles. In agreement with previous studies focusing on eccentric training [7,22,23], the present training protocol significantly increased maximal eccentric (16%), isometric (30%) and concentric (14%) torque. Although no action mode effects were observed, the greater torque gains were recorded under isometric conditions. This unexpected result could be explained, at least in part, by the slow velocity adopted during the training contractions (from 15 to 20° × s⁻¹). Torque production capacity is influenced by several factors. For instance, it has been demonstrated that torque increases resulting from strength training could be related to central adaptations, e.g. modifications of the neural drive to agonist and/or antagonist muscles [6,16,17,22,23], and/or peripheral adaptations, e.g. modifications affecting the muscular structure and/or intramuscular processes [22,31].

In the present study, central adaptations were analysed with two different methods: the estimation of the maximal voluntary activation level and the ratio between the EMG RMS value recorded during voluntary contractions and the M wave surface (EMG_ratio). The first method is associated to the compound response of the ensemble of the plantar-flexors, while the second permits to discriminate the relative contribution of each muscle participating to the plantar-flexion. After 4 wk of eccentric training a significant decrease in the amplitude of the superimposed twitch was recorded and therefore, the estimated level of maximal voluntary activation significantly increased from 80 ± 5% to 91 ± 2% [2]. This result was confirmed by the higher EMG_ratio observed under isometric conditions for the three plantar-flexors, which in turn indicated an increased neural drive [34]. Moreover, considering that no variations occurred in the surface of the maximal M wave, increases in EMG_ratio were essentially linked to an increased central neural drive to the agonist muscles. One could therefore conjecture that a greater number of active motor units and/or a higher firing frequency were responsible for the results observed here [4]. The first argument seems likely, according to the increases observed for the activation level. Even though firing frequency has not been assessed with the present methodology, it is nevertheless interesting to suggest that Van Cutsem et al. [35] have reported an increased discharge rate of the motor units after 12 weeks of ballistic dorsiflexions.

While isometric EMG_ratio significantly increased for the three agonist muscles, no changes were observed in concentric EMG_ratio and under eccentric conditions EMG_ratio significantly increased exclusively for the GM. Based on these results, it is obvious that factors other than the agonist neural drive are likely to account for the eccentric and concentric torque gains. Antagonist EMG activity (i.e. coactivation level) significantly decreased during eccentric and concentric contractions but not during isometric ones. It is well known that torque output is influenced by the behaviour of the antagonist muscles [25,32]. For example, Carolan and Cafarelli [6] showed that a reduced antagonist EMG activity after 8 wk of isometric training resulted in an increased torque production. In the same way, Hakkinen et al. [19] showed a reduction in coactivation after 6 months of strength training in elderly subjects. Our results corroborate these findings and confirm that the antagonist coactivation is sensitive to training. The unchanged coactivation level observed for the control group could also reinforce this last assumption. Another factor that could explain torque increases observed under dynamic contractions is the contribution of synergistic plantar-flexor muscles to the compound torque output. Indeed, synergistic muscles other than soleus and gastrocnemius (e.g. plantaris, peroneus longus, tibialis posterior, flexor hallucis longus, and flexor digitorum) are likely to contribute to the total plantar-flexor torque [9,28]. Due to specific characteristics (e.g. architecture, insertions, and/or) their relative contribution could be more important during dynamic contractions than during static contractions. However, since EMG activity from these muscles was not recorded with the present methodology, this latter assumption remains to be validated.

The present eccentric training also affected the twitch contractile properties. In fact, Pₜ max and RRₚ could be related to several adaptations such as hypertrophy, modifications in passive stiffness of series-elastic component or intramuscular modifications connected to contractile protein activation. Several studies have shown that eccentric resistance training, longer that the present, induced muscle hypertrophy [21,24]. In our study, we observed no changes in M wave characteristics, so that the hypothesis of peripheral adaptations at the membrane level could be excluded. The increases in Pₜ max and RRₚ could be related to several adaptations such as hypertrophy, modifications in passive stiffness of series-elastic component or intramuscular modifications connected to contractile protein activation. Several studies have shown that eccentric resistance training, longer that the present, induced muscle hypertrophy [21,24]. In our study, we observed no changes in M wave characteristics, so that the hypothesis of peripheral adaptations at the membrane level could be excluded. The increases in Pₜ max and RRₚ could be related to several adaptations such as hypertrophy, modifications in passive stiffness of series-elastic component or intramuscular modifications connected to contractile protein activation. Several studies have shown that eccentric resistance training, longer that the present, induced muscle hypertrophy [21,24]. In our study, we observed no changes in M wave characteristics, so that the hypothesis of peripheral adaptations at the membrane level could be excluded. The increases in Pₜ max and RRₚ could be related to several adaptations such as hypertrophy, modifications in passive stiffness of series-elastic component or intramuscular modifications connected to contractile protein activation. Several studies have shown that eccentric resistance training, longer that the present, induced muscle hypertrophy [21,24].
tractile kinetics. Post-contraction potentiation significantly increased by 18% after the training period, which could be a sign of an intensification of the contractile-protein activation 29 and/or a prolongation of the excitation-contraction coupling [13]. Because twitch contraction time was not significantly modified, the improved excitation-contraction coupling cannot be related to a prolongation, but rather to an intensification of the contractile protein activation. The intracellular Ca\(^{2+}\) movements play a role in the control of the twitch time course [5]. As a speculation, the increase in twitch torque amplitude observed here could be explained by changes in Ca\(^{2+}\) release by the sarcoplasmic reticulum [13] and/or variations in the Ca\(^{2+}\) sensitivity of contractile proteins 29,36. In addition, changes in muscular contraction kinetics could also be explained by an enhancement in myosin ATPase activity [3]. However, no significant modification occurred in P\(_0\) and in the other tetanic parameters (RD\(_{P0}\), RR\(_{P0}\)) after training. The fact that potential intensification in contractile protein activation has not affected the tetanic parameters is not a surprising result. Indeed, during maximal activation, the Ca\(^{2+}\) concentration is higher than the one required to fully activate the contractile proteins [5]. Since maximal voluntary torque significantly increased and maximal tetanic torque was not modified by training, the MVC/tetanus ratio significantly increased. As a consequence, peripherals adaptations, witnessed by the modifications of twitch contractile properties cannot alone account for the present voluntary torque gains.

In conclusion, the present study demonstrated that a 4-wk eccentric resistance training significantly increased the maximal voluntary torque of the plantar-flexor muscles under isometric, eccentric and concentric conditions. The torque gains were associated to neural adaptations more particularly, affecting EMG activity of both agonist and antagonist muscles. Isometric torque gains were explained by an increased neural drive to agonists, while torque gains observed under eccentric and concentric conditions. The torque gains were also explained by an increased neural drive to agonists, while torque gains observed under eccentric and concentric conditions. The torque gains were also explained by an increased neural drive to agonists, while torque gains observed under eccentric and concentric conditions. The torque gains were also explained by an increased neural drive to agonists, while torque gains observed under eccentric and concentric conditions.

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