Journal of Electromyography and Kinesiology xxx (2010) xxx–xxx

Contents lists available at ScienceDirect

Journal of Electromyography and Kinesiology

journal homepage: www.elsevier.com/locate/jelekin

Peripheral and central fatigue after muscle-damaging exercise is muscle length dependent and inversely related

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A R T I C L E I N F O

Article history:
Received 27 May 2009
Received in revised form 19 February 2010
Accepted 22 February 2010
Available online xxxx

Keywords:
Muscle length
Contraction
Central and peripheral fatigue
Damage

A B S T R A C T

Healthy untrained men performed 10 series of 12 knee eccentric extension repetitions (EE) at 160°/s. The maximal voluntary isometric contraction force of the quadriceps muscle, the maximal rate of electrically induced torque development (RTD) and relaxation (RTR), isokinetic concentric torque at 30°/s, the electrostimulation-induced torque at 20 and 100 Hz frequencies were established before and after EE at shorter and longer muscle lengths. Besides, voluntary activation (VA) index and central activation ratio (CAR) were tested. There was more peripheral fatigue than central after EE. We established more central fatigue as well as low frequency fatigue at a shorter muscle length compared to the longer muscle length. Relative RTD as well as relative RTR, improved after EE and did not depend on the muscle length. Finally, central fatigue is inversely significantly related with the eccentric torque reduction during eccentric exercise and with the changes in muscle torque induced by low frequency stimulation.

1. Introduction

Exercise-induced fatigue can be assessed by measuring a decrease in muscle force-generating capacity (Gandevia, 2001). It occurs due to limitations in skeletal muscles themselves or in the nervous system. It is now clear that peripheral fatigue occurs during many types of muscle exercises, but increasing evidence indicates that central fatigue is common as well (Gandevia, 2001; Prasartwuth et al., 2006; Sogaard et al., 2006; Stewart et al., 2008).

The well-documented symptoms of exercise-induced muscle damage include prolonged impairment of muscle function as measured in voluntary and electrically induced contractions (Byrne et al., 2004; Skurvydas et al., 2006; Warren et al., 1999). In addition, there is strong evidence for protein leakage from injured muscle fibres and delayed onset muscle soreness, stiffness and swelling (Chapman et al., 2008; Skurvydas et al., 2008). It is generally agreed that there are damages to the excitation–contraction coupling system (Proske and Morgan, 2001; Warren et al., 1999) in the muscle immediately after it has been subjected to a series of eccentric knee contractions (EE). Low frequency fatigue (LFF) is thought to reflect the impairment of the excitation–contraction coupling system (Skurvydas et al., 2006). LFF is characterized by proportionately greater reduction in tetanic force at low stimulation frequencies rather than at high ones (Jones, 1996; Rijkelijkhuizen et al., 2005; Skurvydas et al., 2008; Westerblad and Allen, 2002).

It has been established that muscle-damaging exercise decreases the muscle isometric, concentric and eccentric contraction forces (Byrne et al., 2004; Hubal et al., 2008; Michaut et al., 2003; Skurvydas et al., 2006; Warren et al., 1999), the rightward shift in the optimum joint angle for voluntary isometric (Chen et al., 2007; McHugh and Tetro, 2003; Philippou et al., 2004; Proske and Morgan, 2001) and the concentric strength (Yeung and Yeung, 2008) as well as greater voluntary activation impairment at a shorter elbow flexor length (Prasartwuth et al., 2006). The following issues, however, have not been cleared up, yet, namely (1) the length-dependent changes in quadriceps muscle voluntary and electrically induced force after eccentric exercise; (2) the length-dependent changes in muscle voluntary activation (VA) index and central activation ratio (CAR) after muscle-damaging exercise; (3) the relationship between changes in peripheral and central fatigues of quadriceps muscle. The primary aim of the present study is to clarify these issues. The indicator of peripheral fatigue was the decrease of electrically evoked muscle torque whereas central fatigue was assessed by using tetani stimulation superimposed on the voluntary contraction.

2. Methods

2.1. Subjects

Eleven healthy males (mean ± SD: age = 24.8 ± 3.7 years, body weight = 78.2 ± 4.7 kg, height = 179.9 ± 3.6 cm) took part in this study. The subjects were physically active but were not taking part

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doi:10.1016/j.jelekin.2010.02.009

in any formal physical exercise or sports program. They had not been involved in any specific fitness-training programs during recent years. Each subject read and signed a written informed consent form consistent with the principles outlined in the Declaration of Helsinki. The Ethics Committee of Kaunas Medical University approved this study.

2.2. Muscle-damaging eccentric exercise (EE)

The subjects performed EE in 10 series of 12 knee eccentric extension repetitions (the right leg) with the maximal intensity at angle velocity 160°/s (the range of knee angle was from 150° to 70°; full knee extension is equaled to 180°). The time period between series was 1 min. The subjects were asked to perform every repetition with maximal effort. The peak eccentric torque was taken for analysis.

2.3. Isometric torque and electrical stimulation

The isometric torque of knee extensor muscles of the right leg was measured by using an isokinetic dynamometer (System 3; Biodex Medical Systems, Shiley, New York). The resolution of the Biodex System 3 in torque measurements is ±1.36 Nm according to the manual provided with the dynamometer. The subjects sat upright in the dynamometer chair with the knee joint positioned at an angle of 130° or 90°. The equipment and procedure for electrical stimulation were essentially the same as previously described (Skurvydas et al., 2008; Streckis et al., 2007). Direct muscle stimulation was applied by using two carbonised rubber electrodes covered with a thin layer of electrode gel (ECG-EEG Gel; Medigel, Modi'in, Israel). One of the electrodes (6 × 11 cm) was placed transversely across the width of the proximal portion of the quadriceps femoris. Another electrode (6 × 20 cm) covered the distal portion of the muscle above the patella. A standard electrical stimulator (MG 440; Medicor, Budapest, Hungary) was used. The electrical stimulation was delivered in square-wave pulses, 0.5 ms in duration. The tolerance of volunteers to electrical stimulation was assessed on a separate occasion, and only these participants who showed good compliance with the procedure were recruited for the study. The intensity of the electrical stimulation was selected individually by applying single stimulus to the muscles tested. During this procedure, the voltage was increased until no increment in single twitch torque could be detected by an additional 10% increase in the current strength. The output from the force transducer was also displayed on a voltmeter in front of the subject.

The following data were measured: the torque at 20 Hz (P20) and 100 Hz (P100) of electrical stimulation using 1 s-length trains of stimuli at each frequency, with a knee angle of 90° and 130°; MVC at the knee angles of 90° and 130°, for longer and shorter muscle length, respectively, (top of the MVC was reached and maintained 5 s before relaxation, twice at each angle). During these attempts, the VA and CAR were measured (see VA and CAR measurements). In all cases, muscle torque registrations at different angles were taken randomly. The rest interval between the muscle electrostimulations was 10 s while that between MVC measurements was 2 min. The change in the ratio of P20/P100 after the exercise was used for the evaluation of LFF (Skurvydas et al., 2006, 2008). The fatigue index in percentage was calculated according to the formula: {(Torque value before EE − Value after EE)/Value before EE} × 100%. The maximal rate of torque development (RTD) was determined as the peak slope of torque per 10 ms (Δtorque/Δ10 ms). The relative RTD was determined as the RTD normalized relative to the maximal torque ((Δtorque/Δ10 ms)/peak torque, 1/s). The same methods were used to determine the rate of torque relaxation during muscle contractions evoked by stimulation at 100 Hz frequency (RTR).

2.4. Isokinetic concentric torque (IT) measurement

The subjects were asked to perform three continuous repetitions of knee extension with maximal intensity at an angle velocity of 30°/s. The angle range was from 70° to 150° (full knee extension is equaled to 180°). The knee was set passively at the starting position. The optimal knee angles which gave the greatest IT were established. IT (average of the three repetitions) at optimal knee angles was measured.

2.5. Voluntary activation (VA) index and central activation ratio (CAR) measurements

A volunteer was positioned in the dynamometer chair and the stimulating electrodes were placed on the right leg. Two 5-s MVCs (each at shorter and longer muscle lengths) were obtained with a 2-min rest between them. At ~3 s of MVC, a 250-ms test train of stimuli at 100 Hz (TT100Hz) was superimposed on the voluntary contraction. These TT100Hz contractions were used to assess the voluntary activation of knee extensors. We used tetani instead of single twitches since superimposed twitches are often difficult to detect and this may lead to erroneous conclusions about the voluntary activation. This is especially true in view of a progressive increase in voluntary force variation during continuous contractions (Streckis et al., 2007). The amplitude of the superimposed tetani was calculated from the baseline, estimated as the average torque over 1 s, just before the stimulation. The superimposed TT100Hz produced measurable torque increments in all subjects. For the VA, the TT100Hz torque of the relaxed muscles was used as the control torque, and the following formula was applied: VA (%) = {1 − (superimposed TT100Hz torque/control TT100Hz torque)} × 100%. In addition to VA, the CAR was calculated. The CAR is the ratio of the maximal voluntary torque to the peak torque generated with additional TT100Hz superimposed on an MVC (Bilodeau, 2006). We had applied the same method for CAR and VA measurements in an earlier study (Streckis et al., 2007).

2.6. Rectal and muscle temperature measurements

Rectal and muscle temperatures in six (only this number of subjects gave permission) subjects were measured before and after EE. Rectal temperature was measured with a thermocouple (Rectal Probe, Ellab, Hvidovre, Denmark) inserted to a depth of 12 cm past the anal sphincter. The intramuscular temperature was measured with a needle microprobe (MKA, Ellab, Hvidovre, Denmark) inserted into a 3-cm depth under the skin covering m. vastus lateralis of the right leg.

2.7. Plasma creatine kinase (CK) activity

Approximately 5 ml of blood was drawn from *vena cubiti media* of the arm at each time point of the measurement (before the exercise as well as 48 h after the exercise). Plasma samples were pipetted into microcentrifuge tubes and stored in a −20 °C freezer until the analysis. Plasma creatine kinase activity (IU/L) was determined by using the automatic biochemical analyzer "Monarch" (Instrumentation Laboratory SpA, USA–Italy).

2.8. Muscle soreness

Muscle soreness was reported subjectively by using a visual analogue scale of 0–10 where 0 represented "no pain" and 10 represented "intolerably intense pain". These muscle soreness

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evaluation methods had also been used in our previous research (Skurvydas et al., 2006).

2.9. Experimental protocol

Three to five days before the experiment, the subjects were introduced to electrical stimulation and to different tasks of voluntary performance. During the experimental day after measuring CK in the blood rectal and muscle temperatures, a subject was seated in the experimental chair, and after 5 min, muscle contractile properties were recorded at shorter and longer muscle lengths in the following sequence: P20, P100 and MVC. About 3 min later, three ITs at 30°/s were performed. About 3 min later, the EE was undertaken. Contractile properties were again measured at 2 min after EE. Besides, at 24 and 48 h after EE, muscle soreness and creatine kinase activity at 48 h after EE were determined.

2.10. Data and statistical analysis

Descriptive data are presented as means ± SD. Normality of data distribution was tested and confirmed by the Kolmogorov–Smirnov test. The level of significance calculated by paired *t*-test was set at 0.05. In order to evaluate the relationship between changes in different indicators of voluntary and electrically induced muscle performance after EE, Pearson correlation coefficient was established. Based on alpha level of 0.01 and the sample size ($n = 11$), standard deviations and average levels before and after the eccentric exercise, the statistical power was calculated for all the mechanical indicators. The statistical power in all cases was higher than 80%.

3. Results

The maximal eccentric torque decreased by 27.9 ± 9.9% ($P < 0.001$) at the end of the exercise. The rectal temperature increased from 37.1 ± 0.3 to 38.2 ± 0.2 °C ($P < 0.01$) while the muscle temperature rose from 36.9 ± 0.4 to 39.5 ± 0.3 °C ($P < 0.001$) after the exercise. Within 24–48 h after EE, the subjects felt acute muscle pain (5–6 points). The CK activity 48 h after EE increased up to 680.4 ± 594.2 IU/L ($P < 0.01$ compared to the before level, namely, 119.7 ± 48.7 IU/L).

3.1. The muscle length effect on changes in voluntary and electrically induced muscle performance after EE

MVC was significantly greater at a longer muscle length compared to the shorter muscle length before the exercise (Table 1). MVC as well IT decreased significantly ($P < 0.001$) after EE. There was no difference between MVC at longer and shorter muscle lengths. Before the eccentric exercise, the optimal angle for knee extension torque was 108.7 ± 4.7°. After the exercise, the optimal angle shifted to a significantly longer muscle length of 96.7 ± 12.6° (shift by 12.1 ± 10.1°). This shift to the longer optimal muscle length occurred in all subjects.

Electrically induced torque at 20 Hz stimulation (P20), P100 as well as relative RTD and RTR were significantly greater at the shorter muscle length compared to the longer muscle length before the exercise (Fig. 1, Table 2). Fig. 2 shows that all the criteria of electrically induced muscle performance changed significantly after EE: the torque decreased while relative RTD and RTR increased. There were no differences between shorter and longer muscle lengths in terms of change of relative RTD as well as relative RTR. The P20 at both shorter and longer muscle lengths decreased significantly more than P100. The LFF manifested itself after EE because P20/P100 decreased significantly after EE (Fig. 3). The LFF was significantly greater at 130° compared to 90°.

Table 1
Maximal voluntary contraction (MVC) torque at 130° and 90° knee angles and maximal isokinetic torque (IT) (mean ± SD).

	MVC-130 (N m)	MVC-90 (N m)	IT (N m)
Before exercise	246.4	280.3[†]	280.1
	33.1	47.5	43.4
After exercise	153.9[*]	164.7[*]	166.2[*]
	32.3	43.4	50.8
Changes (%)	38.2	41.7	41.4
	7.2	11.1	13.2

[*] $P < 0.05$ compared to the value before the exercise.
[†] $P < 0.05$ compared to MVC 130.

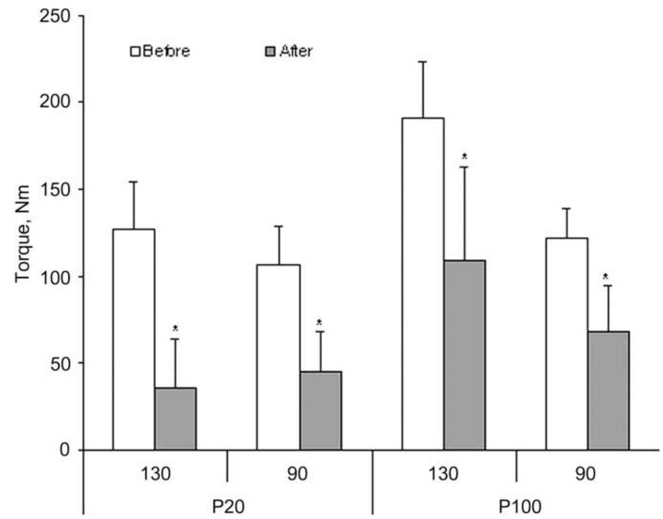

Fig. 1. The changes in quadriceps muscle torque evoked by electrostimulation at low (P20) and high (P100) frequencies at knee angle of 130° and 90° after the eccentric exercise (10 series of 12 repetitions) (mean ± SD). *$P < 0.05$ compared to the pre-exercise values.

3.2. VA and CAR

Prior to the eccentric exercise, VA and CAR were significantly lower at the shorter muscle length (Fig. 4). After the eccentric exercise, VA and CAR impaired significantly only at the shorter muscle length.

3.3. Relationship between central and peripheral fatigue

We established significant inverse relationship between the changes in maximal eccentric torque and the changes in VA and CAR (absolute difference in VA as well as CAR between before and after EE) at 130° ($r = -0.81$ and $r = -0.72$ respectively). It is of major interest that there was a significant inverse relationship between the changes in VA at 130° and the fatigue index of P20 at both shorter and longer muscle lengths ($r = -0.72$ and $r = -0.85$ respectively). Besides, there was a significant relationship between the changes in maximal eccentric torque and the changes in the optimal degree of IT ($r = 0.85$).

4. Discussion

The main findings of our study are (1) peripheral fatigue is higher than central fatigue of the quadriceps muscle after the eccentric exercise performed at high velocity (160°/s); (2) relative RTD as well as relative RTR induced by electrostimulation significantly improved after the muscle-damaging exercise and did not depend on the length of the muscle tested; (3) there is a central fatigue (in

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Table 2
The relative rate of torque development (RTD) and the relative rate of torque relaxation (RTR) at 130° and 90° of knee joint angles induced by 100 Hz electrostimulation (mean ± SD).

RTD-130 (1/s)	RTD-90 (1/s)	RTR-130 (1/s)	RTR-90 (1/s)
16.9*	12.2	20.1*	16.7
3.6	2.2	2.5	2.6

* $P < 0.05$ compared to 130° and 90° angles.

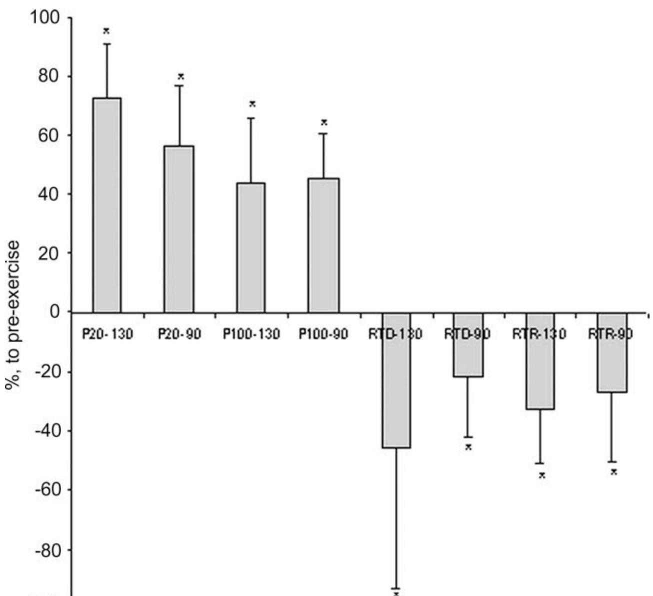

Fig. 2. The fatigue index after the eccentric exercise (10 series of 12 repetitions) (mean ± SD) P20 and P100 muscle torque evoked by electrostimulation at 20 and 100 Hz; RTD and RTR: relative rate of knee torque development and relaxation induced by 100 Hz electrostimulation; 130 and 90: indices at 130° and 90° of knee joint angles, respectively. *$P < 0.05$ compared to the pre-exercise values.

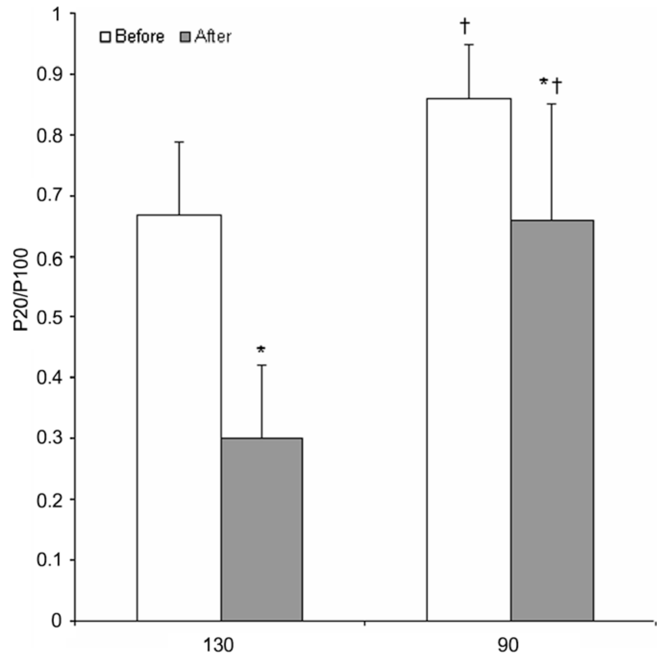

Fig. 3. The ratio P20/P100 before and after the eccentric exercise (10 series of 12 repetitions) (mean ± SD) P20 – muscle torque evoked by electrostimulation at 20 Hz; P100 – muscle torque evoked by electrostimulation at 100 Hz frequencies at knee angles 130° and 90°. *$P < 0.05$ compared to the pre-exercise values; †$P < 0.05$ between 130° and 90°.

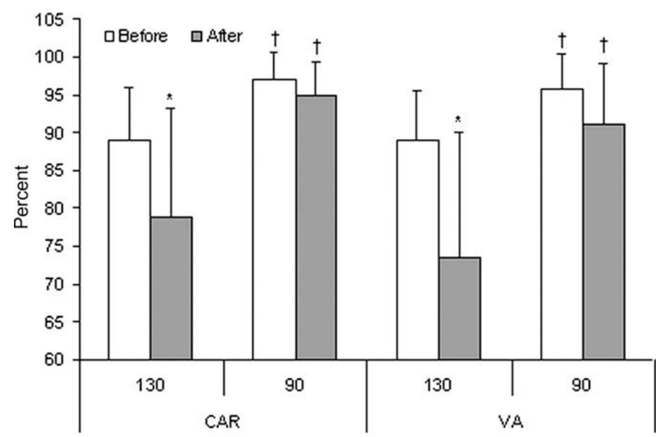

Fig. 4. The quadriceps muscle central activation ratio (CAR) and voluntary activation (VA) index before and after the eccentric exercise (10 series of 12 repetitions) at knee angles of 130° and 90° (mean ± SD). *$P < 0.05$ compared to the pre-exercise values; †$P < 0.05$ between CAR and VA.

both criteria, CAR and VA); however, it is manifested at the shorter muscle length only; (4) central fatigue is inversely significantly related with the eccentric torque reduction during the exercise as well as with changes in muscle torque induced by low frequency stimulation at both shorter and longer muscle lengths. The eccentric exercise induces significant muscle damage since indirect symptoms manifest themselves, namely, the rise of muscle soreness, the increased plasma creatine kinase activity, the decreased voluntary and electrically evoked performance. Besides, stimulation torque reduction was greater at low compared to high frequencies and the peak IT significantly shifted to the longer muscle length after EE.

4.1. Changes in voluntary and electrically induced muscle performance: effect of muscle length and stimulation frequencies

We have established a significant shift (12.1 ± 10.1°) of the optimal knee torque to the longer muscle length. The rightward shift in the muscle length vs. tension relationship is commonly attributed to an increased series compliance of the muscle due to disrupted sarcomeres (Gregory et al., 2007; Proske and Morgan, 2001), and this shift has been proposed as a reliable indicator of muscle damage (Chen et al., 2007; Philippou et al., 2004; Proske and Morgan, 2001) as well as of muscle fatigue (Butterfield and Herzog, 2006).

Yeung and Yeung (2008) also tested the optimal angle shift during isokinetic contraction (at 60°/s). They found that after a 10-min stepping eccentric exercise, there was a significant shift (about 4°) in the peak torque angle to the longer muscle lengths. A similar optimal angle shift (about 4°) in isometric contraction after 30 eccentric actions was found by Chen et al. (2007). However, in our case, the optimal angle shift to the longer muscle length was much greater (about 12°). This discrepancy might be explained by the fact that our eccentric exercise was much more intensive and therefore much greater muscle fatigue as well as muscle damage was induced. It is rather strange that there were no length-dependent changes in isometric MVC after EE. It might be related to the fact that we tested MVC only at two angles, i.e. 130° and 90°.

The results of our research have shown that P20 after EE decreases to a greater extent than the P100 (Figs. 1 and 2). This indicates that the muscles were subjected to LFF and especially at the shorter muscle length (Fig. 3). The decreased torque production of exercise-exposed muscle cells may, in principle, be due to (i) reduced Ca^{2+} release from the sarcoplasmic reticulum leading to decreased free myoplasmic [Ca^{2+}] ([Ca^{2+}]); (ii) decreased myofibrillar Ca^{2+} sensitivity, and (iii) reduced ability of contractile machinery to produce force (Allen et al., 2008). On a simplified model, factors (i) and (ii) would result in a larger force depression rather at low than at high stimulation frequencies due to the sigmoidal shape of the force-[Ca^{2+}]i relationship whereas factor (iii) would give a similar force decrease at all stimulation frequencies (Allen et al., 2008). We observed markedly larger force reductions during and after EE at 20 Hz than at 100 Hz stimulation (Fig. 2), which indicates important roles of factors (i) and (ii) in the EE-induced force depression. It should be noted, however, that sarcomere instability induced by eccentric contractions may shift the optimal length for the active force production to longer lengths, which may exaggerate the force depression at low stimulation frequencies (Parikh et al., 2004). Our finding that immediately after EE, LFF was greater at the shorter muscle length (Figs. 1–3) appears to be of interest. This can be accounted for by the fact that due to muscle damage, there is the optimal muscle torque shift in the direction of the longer muscle length, and it depends on sarcomere disruption (Proske and Morgan, 2001). However, we did not observe this shift in torque induced by electrostimulation at high frequencies (Figs. 1 and 2).

It is of great interest that relative RTD and RTR improved after EE while P20 and P100 significantly decreased (Fig. 2). Two main factors might influence these phenomena: (a) increased muscle temperature; and (b) reduced Ca^{2+} release from sarcoplasmic reticulum leading to decreased free myoplasmic Ca^{2+}. It has been clearly shown that muscle contraction and relaxation rates increase together with the increasing muscle temperature (De Ruiter et al., 1999; Sargeant, 1987; Todd et al., 2007). Therefore, the changes in relative RTD and RTR after EE might be increased by elevating the muscle temperature by about 2.6 ± 0.3 °C. It has been recently established that the quadriceps muscle contraction and relaxation rate increases during LFF (Skurvydas et al., 2002), and it might be explained by a reduced Ca^{2+} release from sarcoplasmic reticulum after the eccentric exercise (Nielsen et al., 2007).

4.2. Changes in CAR and VA

Two indices of muscle activation were used in this study and both produced similar results. The decrease in VA and CAR after EE shows that central fatigue occurs (Fig. 4) but only at the shorter muscle length. This is in accordance with the data of Prasartwuth et al. (2006) and Desbrosses et al. (2006). It is speculated that as twitch dynamics is faster and the force–frequency curve is shifted in such a way that a higher frequency is required to achieve the maximum force, voluntary activation would be reduced at the shorter muscle length (Gandevia and McKenzie, 1988). It has been concluded that the increasing muscle contraction and relaxation rate indicates that higher motor unit firing rates are required for the fusion of force (Todd et al., 2007). Therefore, increasing the relative RTD as well as relative RTR after EE might effect the muscle voluntary activation. We might speculate that changes in VA as well as CAR after EE might be effected by both muscle fatigue and elevated muscle temperature. Different mechanisms might operate to cause central fatigue in different types of exercise, and it is not clear whether the results of our study can be extended to other types of exercise. There are also uncertainties as to the applicability of the results of this study to other muscles.

4.3. Is there relationship between central and peripheral fatigue?

We can assume that peripheral fatigue is more expressed in our case than central fatigue because the changes in electrically and voluntarily induced torque were greater than the changes in CAR as well as VA. It is of great interest that the changes in VA after EE are inversely related with eccentric torque reduction during the exercise as well as with the changes in muscle torque induced by a low frequency stimulation at both shorter and longer muscle lengths. Thus we might speculate that the greater peripheral fatigue occurs, the more preserved the central fatigue is in order to avoid too high a stress on the neuromuscular system. It is similar to the data of Amann and Dempsey (2008), which showed that peripheral locomotor muscle fatigue development is a significant determinant of the magnitude of the central motor output during an exercise. Muscle fatigue may have an inhibitory influence on the central motor drive to keep the central output at a certain submaximal level presumably to avoid further accumulation of peripheral fatigue (Enoka and Duchateau, 2008). There is a possibility that magnitude of eccentric exercise-induced muscle damage is also associated with a reduction of the subject's ability to voluntarily activate the knee extensor muscles.

The relative contribution of central and peripheral fatigue after the muscle-damaging exercise is important for a practitioner. The present study provides information about the magnitude of the quadriceps muscle fatigue at different knee angles. The results refer to significant inverse relationship between the voluntary activation and the muscle torque reduction. This suggests that the development of peripheral fatigue might contribute to central fatigue.

5. Conclusion

Our exercise protocol induced both central and peripheral fatigue even though the central fatigue was observed at the shorter muscle length only. We observed a greater low frequency fatigue at the shorter muscle length compared to the longer length. Besides, the relative rate of torque development as well as the relative rate of torque relaxation induced by electrostimulation improved after the muscle-damaging exercise and did not depend on the length of the muscle tested. Finally, the changes in central fatigue are inversely significantly related with eccentric torque reduction during exercise and changes in muscle torque induced by low frequency stimulation at both shorter and longer muscle lengths.

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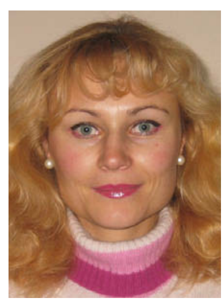

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