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Muscle Performance, Morphology and Metabolic Capacity During Strength Training and Detraining: A One Leg Model*

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Summary. To investigate biochemical, histochemical and contractile properties associated with strength training and detraining, six adult males were studied during and after 10 weeks of dynamic strength training for the quadriceps muscle group of one leg, as well as during and after a subsequent 12 weeks of detraining. Peak torque outputs at the velocities tested ($0-270° \cdot s^{-1}$) were increased ($p < 0.05$) by 39–60% and 12–37% after training for the trained and untrained legs, respectively. No significant changes in peak torques were observed in six control subjects tested at the same times. Significant decreases in strength performance of the trained leg (16–21%) and untrained leg (10–15%) were observed only after 12 weeks of detraining. Training resulted in an increase ($p < 0.05$) in the area of FTa (21%) and FTb (18%) fibres, while detraining was associated with a 12% decrease in FTb fibre cross-sectional area. However, fibre area changes were only noted in the trained leg. Neither training nor detaining had any significant effect on the specific activity of magnesium-activated myofibrillar ATPase or on the activities of enzymes of phosphagen, glycolytic or oxidative metabolism in serial muscle biopsy samples from both legs. In the absence of any changes in muscle enzyme activities and with only modest changes in FT fibre areas in the trained leg, the significant alterations in peak torque outputs with both legs suggest that neural adaptations play a prominent role in strength performance with training and detraining.

Key words: Strength training and detraining – Muscle performance – Muscle morphology – Muscle metabolic capacity

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Introduction

Strength training has been shown to result in significant improvements in muscle force output which have been associated with (MacDougall et al. 1980; Coyle et al. 1981) or not associated with (Thorstensson et al. 1976a; Costill et al. 1979) specific increases in muscle fibre cross-sectional areas. The consistent observations of improved muscle force production in strength training studies, irrespective of whether muscle hypertrophy has been noted, may reflect in large part neural adaptations as has been suggested previously (Moritani and DeVries 1979; Coyle et al. 1981). For example, Milner-Brown et al. (1975) demonstrated enhanced synchronization of motor unit firing in weightlifters, and also showed that a 6 week strength training program for the hand increased synchronization in normal subjects. In addition, strength training may provide a stimulus sufficient to increase the activities of certain enzymes of phosphagen (Thorstensson et al. 1976a) and glycolytic and oxidative (Costill et al. 1979) metabolism.

Short-term detraining following a strength training program has been shown to result in a significant retention of strength gained (Shaver 1975), whereas data reviewed by Müller (1970) reveal that strength is lost at a relatively constant rate when the training stimulus is withdrawn. However, the metabolic and morphological changes within the trained muscle have not been studied in the period following strength training. In the present experiment we have evaluated muscle performance, metabolic potential and morphology during and following strength training and detraining using a one leg model. It was anticipated that such an approach would facilitate a clearer understanding of the adaptations associated with strength training and detraining.

Methods

Subjects

Six males 73.1 ± 3.7 kg (mean ± SD), 177.3 ± 6.4 cm and 20.3 ± 0.9 year volunteered to participate in this study after being informed of the nature and the risks of the experiment and signing an approved consent form. All of these subjects completed the strength training and detraining phase of the study. They were occasionally active before the experiment, although they had never performed strength training. An additional group of six males 82.9 ± 6.6 kg, 180.1 ± 5.4 cm and 20.8 ± 0.7 year volunteered to participate as controls for the strength testing. These control subjects were occasionally to moderately active, but did not perform any strength training over the period in which they were tested.

General Protocol

Before any initial testing was performed, both the experimental and control subjects were allowed 2 days for instruction and practice in the strength testing procedures using the Cybex II Isokinetic Dynamometer (Lumex Corp.). Both legs of the experimental and control subjects were tested for maximum knee extension torque (week 0). At this time, muscle biopsy samples (ca. 40–60 mg) were obtained from the vastus lateralis muscle of both legs of the experimental subjects using the needle

technique (Bergström 1962). For the next 10 weeks, the experimental subjects performed strength training for the quadriceps muscle group of one leg, with three of the subjects training the left leg and three training the right leg. Muscle strength was assessed in both legs of the experimental subjects after 3, 6, and 10 weeks of training: identical measures were made on both legs of the control subjects at the same time intervals. In addition, muscle samples were obtained from both legs of the experimental subjects after 3, 6, and 10 weeks of training. Finally, strength assessments were made on, and muscle samples were taken from both legs of the experimental subjects after 4 (week 14) and 12 (week 22) weeks of detraining; a period in which the subjects resumed their normal pretraining activity levels.

Training Program

The training consisted of dynamic concentric exercises for the quadriceps muscle group using Universal exercise equipment (Kidde Inc.). Two exercises were performed, one leg knee extension and one leg press. The subjects were instructed to select a load such that they could only perform eight repetitions. When they could perform 10 repetitions the load was increased by 4.5 kg (leg press) or 2.2 kg (knee extension). The subjects trained 4 days/week, performing each exercise three times, and were instructed to use the heaviest loads possible. To test the effect of the two training exercises on the quadriceps muscle group of the inactive leg, integrated electromyographic (IEMG) activity was determined from surface electrodes placed longitudinally over the vastus lateralis muscle on both legs of control subjects at the conclusion of the experiment. The IEMG activity in the inactive leg was expressed as a percent of that in the active leg during the two exercises.

Strength Testing

Isometric and dynamic strength during knee extension was measured as peak torque output in Newton-metres (Nm) on a Cybex II Dynamometer (Thorstensson et al. 1976b). Isometric torque ($0° \cdot s^{-1}$) was measured at a knee angle of 90°, while dynamic torque was measured at velocities of 45, 90, 180, and $270° \cdot s^{-1}$. The unfiltered torque output was recorded on a pen recorder. From these traces the maximum torque from three trials was determined. Maximum torque values were corrected for the effects of gravity by measuring torque output during passive knee flexion from full extension to 90°. The angle at which the maximum torque occurred for each subject and at each velocity was matched to the corresponding angle from the gravitational torque measures. The resulting gravity torque was added to the maximum torque measured during knee extension, and the sum of these torques is reported as the peak torque. The significance of this correction has been documented recently (Winter et al. 1981).

Analysis of Muscle Samples

Two portions of muscle tissue from each biopsy sample were quickly frozen in liquid nitrogen and stored at −80° C for later enzyme analyses. The remaining portion of each muscle sample obtained before and after training and after detraining was mounted in an embedding medium, frozen in isopentane cooled in liquid nitrogen, and stored at −80° C for subsequent histochemical analysis. Histochemical procedures for typing fibres as slow twitch (ST) or fast twitch (FTa and FTb) were identical to those described previously (Houston et al. 1979). In addition, the mean cross-sectional areas of the fibre types were determined using a Numonics digitizer (Green et al. 1979). The activities of the enzymes succinate dehydrogenase (SDH), hexokinase (HK), 3-hydroxyacyl CoA dehydrogenase (HAD) and phosphofructokinase (PFK) were assayed using procedures described previously (Green et al. 1979). Lactate dehydrogenase (LDH) activity was assayed as described earlier (Houston et al. 1979), while creatine kinase (CK) activity was measured using a procedure described by Costill et al. 1979).

For the measurement of myofibrillar ATPase activity, myofibrils were isolated from muscle samples (minimum size 10 mg) using the procedure of Samaha (1967). The myofibrillar fraction was washed with 1% Triton X-100 (Solaro et al. 1971), centrifuged for 20 min at 1,000 *g*, and the supernatant was discarded. The sediment was then washed in 50 volumes of a solution containing 0.15 M KCl and 0.01 M histidine, pH 6.8, and the resulting suspension was centrifuged at 1,000 *g*. This was repeated three times. The sediment of washed myofibrils was suspended in 50 volumes of 0.05 M Tris-HCl, pH 7.8, containing 0.8 mM phospoenolpyruvate, 0.07 mM NADH, 0.016% BSA, and 50 mM KCl, and was kept at 0–4° C until analysis. Magnesium-activated myofibrillar ATPase activity was determined fluorometrically using the procedure of Takashi and Putnam (1979). The protein content of the myofibril fraction was determined by the procedure of Lowry et al. (1951). All enzyme activity analyses for each subject were made on the same day, and enzyme activities were expressed on the basis of wet muscle weight, with the exception of myofibrillar ATPase which was expressed per mg of myofibrillar protein.

Statistics

Significant differences ($p < 0.05$) between trained and control legs as well as differences over time were analyzed using analysis of variance for repeated measures. Duncan's multiple range test was employed to locate specific differences.

Results

Strength Test

Mean peak torque values at the various angular velocities tested for the trained and untrained leg of the experimental subjects are illustrated in Figs. 1 and 2, respectively over the training and detraining phases of the study. For the trained leg, knee extension strength as measured by peak torques was increased ($p < 0.05$) after 6 weeks compared to values obtained before training. An additional 4 weeks of training resulted in further increases ($p < 0.05$) in peak torque values at all angular velocities tested, such that by the end of training, knee extension peak torques were greater than those measured at the beginning of training by amounts ranging from 60% ($45° \cdot s^{-1}$) to 39% ($270° \cdot s^{-1}$). For the untrained leg peak torques were significantly increased after 10 weeks of training at all velocities tested by amounts ranging from 37% ($45° \cdot s^{-1}$) to 12% ($270° \cdot s^{-1}$). During training muscle strength of the trained limb significantly exceeded that of the untrained only after 10 weeks.

After 4 weeks of detraining (week 14) peak torque values for both the trained and untrained leg were not significantly different from those obtained after training (week 10). A further 8 weeks of detraining (week 22) resulted in a significant loss of muscle strength in the trained leg: decreases in peak torque over 12 weeks of detraining ranged from 21% ($90° \cdot s^{-1}$) to 16% ($270° \cdot s^{-1}$). For the untrained leg knee extension peak torque values after 12 weeks of detraining were significantly reduced compared to week 10 by 10 and 15% only for the 45 and $90° \cdot s^{-1}$ test velocities, respectively. However, for the trained leg, peak torque values after detraining were still significantly greater than those obtained before training for all test conditions except $270° \cdot s^{-1}$.

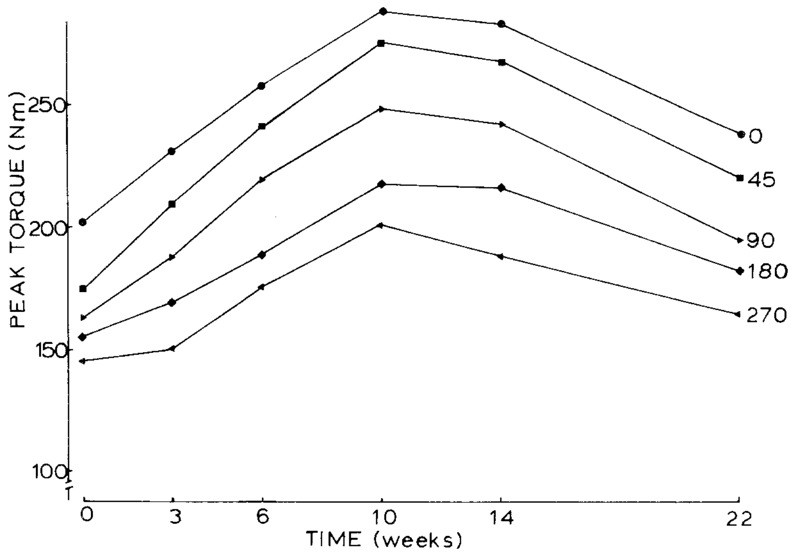

Fig. 1. Mean peak torque outputs of the trained leg using the Cybex II dynamometer at various angular velocities during strength training (weeks 0–10) and detraining (weeks 10–22)

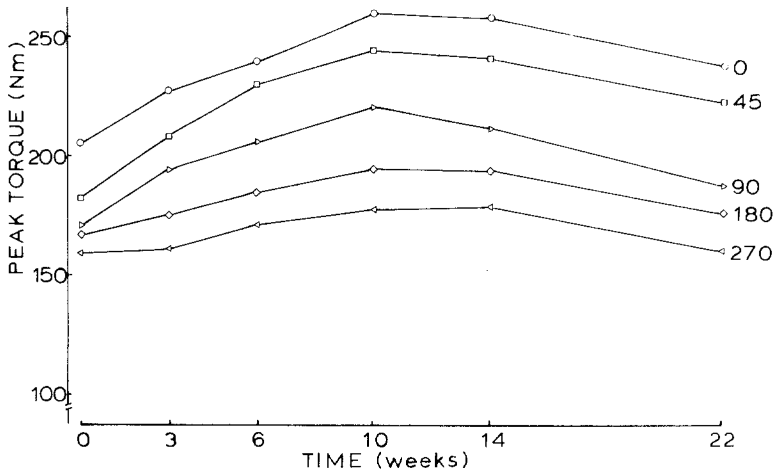

Fig. 2. Mean peak torque outputs of the untrained leg using the Cybex II dynamometer at various angular velocities during strength training (weeks 0–10) and detraining (weeks 10–22)

Peak torques measured on the left and right legs of the control subjects for the four testing periods over 10 weeks are shown in Table 1. Although there were small fluctuations in torque values at the four testing periods with initial values tending to be largest, there were no significant differences between the left and right leg or over time for the five velocities tested.

The IEMG activity in the vastus lateralis muscle of the active and inactive leg was measured in control subjects during one leg knee extensions and one leg

Table 1. Isometric and dynamic peak torque values of the left (L) and right (R) legs of control subjects measured at 0, 3, 6, and 10 weeks

Testing velocity ($^\circ \cdot s^{-1}$)	Peak torque values (N–m)			
	Time of measurement			
	Week 0		Week 3	
	L	R	L	R
0	280 ± 44	296 ± 30	260 ± 26	276 ± 13
45	262 ± 39	266 ± 22	240 ± 24	244 ± 14
90	230 ± 35	236 ± 20	214 ± 10	221 ± 13
180	209 ± 20	217 ± 27	194 ± 18	203 ± 25
270	192 ± 29	183 ± 23	174 ± 26	175 ± 24
	Week 6		Week 10	
	L	R	L	R
0	265 ± 29	262 ± 22	270 ± 36	278 ± 24
45	229 ± 17	239 ± 11	225 ± 17	241 ± 23
90	210 ± 13	211 ± 7	209 ± 21	218 ± 23
180	185 ± 16	195 ± 23	194 ± 23	193 ± 16
270	173 ± 20	174 ± 26	177 ± 25	173 ± 29

presses. For knee extension, the IEMG activity of the inactive leg averaged 6% (5–7, mean and range) of the active leg; the corresponding values for one leg press were 23% (18–31).

Fibre Type and Fibre Areas

There were no significant differences in muscle fibre composition of the vastus lateralis muscle in either leg over the duration of the experiment (Table 2). However, with training, the areas of both FTa and FTb fibres were increased ($p < 0.05$) by 21 and 18%, respectively in the trained leg only (Table 2). At the end of detraining, the mean cross-sectional area of type FTb fibres was 12% ($p < 0.05$) less than it was after training. Although there was a tendency toward smaller FTa fibres in the trained leg with detraining this was not significant.

Muscle Enzymes

The activities of the enzymes SDH, HAD and HK as well as CK, LDH and PFK in muscle samples obtained from the trained and untrained legs, before training and during and after training and detraining are illustrated in Figs. 3 and 4, respectively. The activities of each of these enzymes were similar in the trained

Table 2. Muscle fibre composition and fibre areas in the vastus lateralis muscle of the trained and untrained legs of the subjects, before training (week 0), after 10 weeks of strength training (week 10) and following 12 weeks of detraining (week 22)

Leg	Fibre type	Muscle fibre composition (%)		
		Week 0	Week 10	Week 22
Trained	ST	53 ± 6	49 ± 7	49 ± 6
	FTa	28 ± 9	35 ± 5	30 ± 7
	FTb	19 ± 8	16 ± 7	21 ± 8
Untrained	ST	46 ± 16	48 ± 14	50 ± 15
	FTa	32 ± 11	36 ± 13	29 ± 10
	FTb	22 ± 11	16 ± 10	20 ± 9
		Muscle fibre area ($\mu m^2 \times 10^{-3}$)		
		Week 0	Week 10	Week 22
Trained	ST	3.5 ± 1.2	3.6 ± 0.8	3.5 ± 1.1
	FTa	4.3 ± 1.3	5.2 ± 1.4[a]	4.8 ± 1.1[a]
	FTb	3.5 ± 0.8	4.2 ± 0.6[a]	3.7 ± 0.5[b]
Untrained	ST	3.3 ± 0.6	2.9 ± 0.4	3.0 ± 0.5
	FTa	4.6 ± 1.0	4.6 ± 0.8	4.5 ± 0.8
	FTb	3.9 ± 0.7	3.9 ± 1.1	3.8 ± 0.6

Values presented are means ± SD
[a] Significantly larger than week 0 ($p < 0.05$)
[b] Significantly smaller than week 10 ($p < 0.05$)

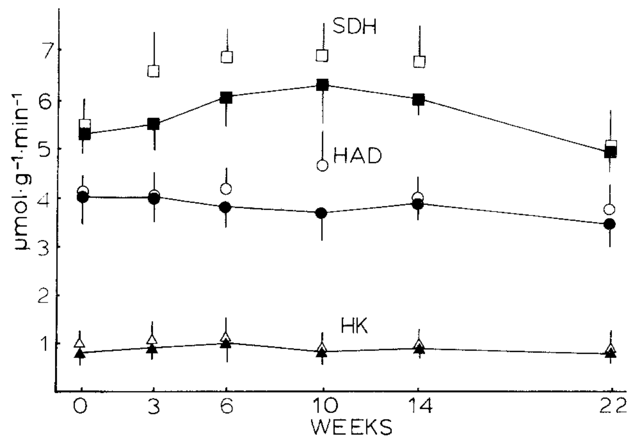

Fig. 3. Mean (± SD) activities of succinate dehydrogenase (SDH), 3-hydroxylacyl CoA dehydrogenase (HAD) and hexokinase (HK) in muscle biopsy samples obtained from the trained leg *(closed symbols)* and untrained leg *(open symbols)* during strength training (weeks 0–10) and detraining (weeks 10–22)

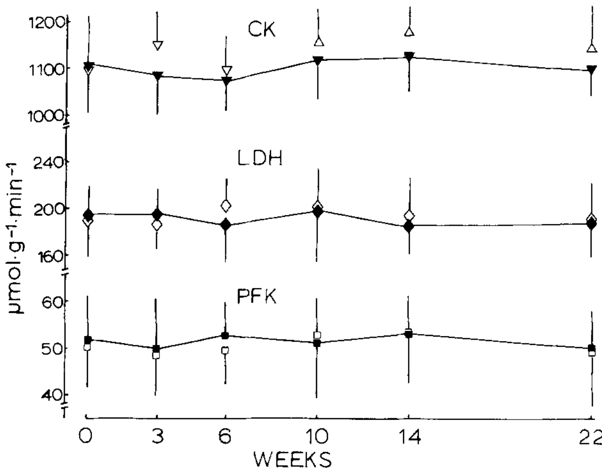

Fig. 4. Mean (± SD) activities of creatine kinase (CK), lactate dehydrogenase (LDH) and phosphofructokinase (PFK) in muscle biopsy samples obtained from the trained leg *(closed symbols)* and untrained leg *(open symbols)* during strength training (weeks 0–10) and detraining (weeks 10–22)

Table 3. Myofibrillar ATPase activity in the vastus lateralis muscle of the trained and untrained leg with strength training (weeks 0–10) and detraining (weeks 10–22)

Leg	Myofibrillar ATPase activity (μmol · mg protein^{-1} · min^{-1})					
	Week 0	Week 3	Week 6	Week 10	Week 14	Week 22
Trained	0.5 ± 0.1	0.5 ± 0.2	0.5 ± 0.2	0.5 ± 0.2	0.6 ± 0.2	0.5 ± 0.2
Untrained	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.2	0.6 ± 0.1	0.5 ± 0.2	0.6 ± 0.2

Values presented are means ± SD

and untrained legs at all muscle sampling times. Further, there were no significant changes in the activities of these enzymes in either leg during training and detraining. Myofibrillar ATPase activities (Table 3) were similar in the trained and untrained leg over the course of the experiment, and neither training nor detraining had any significant effect on these activities.

Discussion

The 10 week strength training program for the quadriceps muscle group was considered to be effective since significant improvements in knee extension peak torque were observed at all velocities tested with the trained leg, ranging from 39% at 270° · s^{-1} to 60% at 90° s^{-1}. These improvements in strength performance compare favourably to those observed in previous studies (Thorstensson et al. 1976a; Costill et al. 1979; Moritani and DeVries 1979;

MacDougall et al. 1980; Coyle et al. 1981). Moreover, the fact that there were no significant changes in strength performance in either leg of the control subjects when tested using identical procedures and at similar times suggests that the observed improvements in strength performance in the experimental subjects were due to the training program.

Significant increases in peak torque output were also observed with the untrained limb at all velocities tested following the training program. Indeed for the isometic ($0° \cdot s^{-1}$) and two slowest isokinetic velocities (45 and $90° \cdot s^{-1}$), the mean improvements in peak torque of the untrained leg were at least 55% of those noted with the trained leg. It has been proposed that co-contractions in the contralateral limb during contractions of the active limb may account for the improved strength performance that has been observed with untrained contralateral limbs (Shaver 1975; Komi et al. 1978). However, our observations that the IEMG activity of the contralateral leg averaged less than 10% and just over 20% of that of the active leg during one leg knee extensions and one leg press, respectively do not reflect sufficient muscular activity to account for improvements in torque output of up to 37% in the untrained limb.

It has been suggested previously (e.g., Moritani and DeVries 1979) that increases in muscle force production associated with strength training are due to neural factors without hypertrophy or neural factors in addition to hypertrophy. Although the precise locus of the neural adaptations is unclear (Komi et al. 1978), Milner-Brown et al. (1975) have described this as an improved synchronization of motor unit discharges in the trained muscle. The fact that significant hypertrophy of FTa and FTb fibres was observed only in the trained leg following training suggests that one component of the improved torque production by the trained limb was a larger muscle cross-sectional area. Moreover, the fact that the untrained leg could produce significantly greater torques after the training period without any evidence of hypertrophy provides a strong argument for neural adaptation in this limb. Accordingly, it is suggested that the improved strength performance of the trained limb was a consequence of both hypertrophy and neural adaptations, and that the latter effect was expressed bilaterally, accounting for the improved strength performance of the untrained limb.

Four weeks of detraining had no significant effect on peak torque outputs of either the trained or untrained leg. These data are in agreement with results presented by Shaver (1975), and demonstrate a notable capability for strength retention with short-term detraining. On the other hand, data reviewed by Müller (1970) would suggest that a 4 week absence of a strength training stimulus should result in an observable decrease in strength performance. However, we observed significant decrements in peak torque values at all velocities tested with the trained leg following an additional 8 weeks of detraining. For the untrained leg, 12 weeks of detraining resulted in significant decreases in peak torque only at 45 and $90° \cdot s^{-1}$; these being the velocities where torque improvements were largest after the training period. Since the detraining-induced decrement in strength performance of the trained leg was associated with a significant reduction in area of only the smallest fibre type group (i.e., FTb fibres) and since the decrease in strength performance of the untrained leg was not associated

with any changes in muscle fibre area, it may be reasonable to propose that the 12 week absence of a strength training stimulus resulted to some extent in the loss of a previously acquired neural adaptation.

A notable finding in the present study was the absence of any change in the activities of enzymes representative of phosphagen (CK), glycolytic (HK, PFK and LDH) or oxidative (HAD and SDH) metabolism in serial muscle biopsy samples, despite the fact that muscle strength performance was markedly altered with training and detraining. In addition, strength training and detraining had no significant effect on the specific activity of magnesium-activated ATPase in isolated myofibrils. These results provide strong evidence that strength training, at least in the manner employed in the present study, does not provide a suitable stimulus to modify the activity of the enzymes studied. Previous reports on the adaptive response of enzymes in skeletal muscle with strength training have been equivocal. For example, Thorstensson et al. (1976a) reported an increase only in the activity of myokinase after 8 weeks of strength training, while Costill et al. (1979) observed both significant increases and no changes in the activities of enzymes representative of glycolytic and oxidative metabolism in the legs of subjects who trained using repeated 30 s and 6 s isokinetic contractions, respectively.

In summary, the results of this study clearly demonstrate that 10 weeks of strength training using a one leg model results in large increases in muscle force production in both the trained and untrained legs, while 12 weeks of detraining leads to significant decreases in strength performance of both legs. Since there were no observable changes in muscle metabolic capacity with either training or detraining, plus the fact that changes in muscle fibre cross-sectional areas were confined to the trained leg only, it is evident that a major contribution to the increased force production with training and loss with detraining must involve systems outside of the affected muscles: these are likely in the neural processes controlling the firing of motor units.

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