Muscle Morphological and Strength Adaptations to Endurance Vs. Resistance Training

Jean Farup,[1] Tue Kjølhede,[1] Henrik Sørensen,[1] Ulrik Dalgas,[1] Andreas B. Møller,[1] Poul F. Vestergaard,[1] Steffen Ringgaard,[2] Jens Bojsen-Møller,[3] and Kristian Vissing[1]

[1]*Department of Sport Science, Aarhus University, Aarhus, Denmark;* [2]*MR-Research Center, Institute of Clinical Medicine, Aarhus University Hospital, Aarhus, Denmark; and* [3]*Norwegian Research Center for Training and Performance, Norwegian School of Sport Sciences, Oslo, Norway*

Abstract

Farup, J, Kjølhede, T, Sørensen, H, Dalgas, U, Møller, AB, Vestergaard, PF, Ringgaard, S, Bojsen-Møller, J, and Vissing, K. Muscle morphological and strength adaptations to endurance vs. resistance training. *J Strength Cond Res* 26(2): 398–407, 2012–Fascicle angle (FA) is suggested to increase as a result of fiber hypertrophy and furthermore to serve as the explanatory link in the discrepancy in the relative adaptations in the anatomical cross-sectional area (CSA) and fiber CSA after resistance training (RT). In contrast to RT, the effects of endurance training on FA are unclear. The purpose of this study was therefore to investigate and compare the longitudinal effects of either progressive endurance training (END, $n = 7$) or RT ($n = 7$) in young untrained men on FA, anatomical CSA, and fiber CSA. Muscle morphological measures included the assessment of vastus lateralis FA obtained by ultrasonography and anatomical CSA by magnetic resonance imaging of the thigh and fiber CSA deduced from histochemical analyses of biopsy samples from m. vastus lateralis. Functional performance measures included $\dot{V}O_2$max and maximal voluntary contraction (MVC). The RT produced increases in FA by 23 ± 8% ($p < 0.01$), anatomical CSA of the knee extensor muscles by 9 ± 3% ($p = 0.001$), and fiber CSA by 19 ± 7% ($p < 0.05$). RT increased knee extensor MVC by 20 ± 5% ($p < 0.001$). END increased $\dot{V}O_2$max by 10 ± 2% but did not evoke changes in FA, anatomical CSA, or in fiber CSA. In conclusion, the morphological changes induced by 10 weeks of RT support that FA does indeed serve as the explanatory link in the observed discrepancy between the changes in anatomical and fiber CSA. Contrarily, 10 weeks of endurance training did not induce changes in FA, but the lack of morphological changes from END indirectly support the fact that fiber hypertrophy and FA are interrelated.

Key Words fascicle angle, pennation angle, fiber cross-sectional area, anatomical cross-sectional area, cycling, hypertrophy

Introduction

Several morphological parameters have been shown to be related to skeletal muscle performance (15). Such parameters include, for example, muscle anatomical and fiber cross-sectional area (CSA) and fascicle angle (FA) (1,15,32). In recent years, FA has been devoted increased interest (8). The FA is defined as the angle between the longitudinal directions of the muscle fascicles and the aponeurosis, respectively (Figure 1). The FA influences muscle force–generating capacity and is adaptable to chronic loading (1,3,8,33,37). Because the force transmission to the aponeurosis is proportional to cos(FA) (33), an increase in FA per se would penalize the transmitted force. However, the increase in FA allows for more contractile tissue contained within a given anatomical CSA (33) or volume (27). Alexander and Vernon (3) suggested that the fiber CSA increases in proportion to sin(FA). Combining the penalizing effect of increased FA with the benefits from the increased fiber CSA suggests that an increase in FA up to 45° (cos(FA) × sin(FA) = (1⁄2) × sin(2 FA) would increase the total contractile force on the aponeurosis (4).

Several studies on resistance training (RT) have verified the adaptability of FA, anatomical CSA and fiber CSA of different skeletal muscles (1,10,21,37). A discrepancy has been observed among the relative changes in fiber CSA, anatomical CSA, and maximal voluntary contraction (MVC) after RT (29,37). It has been suggested that the discrepancy between the relative increases in fiber and anatomical CSA could be explained by the concomitant increase in FA (1,29); however, only 1 study has measured FA and anatomical and fiber CSA simultaneously (1). Accordingly, Aagaard et al. (1) found a relative change of 35% in FA, 16% in fiber CSA, and

Address correspondence to Kristian Vissing, vissing@sport.au.dk.

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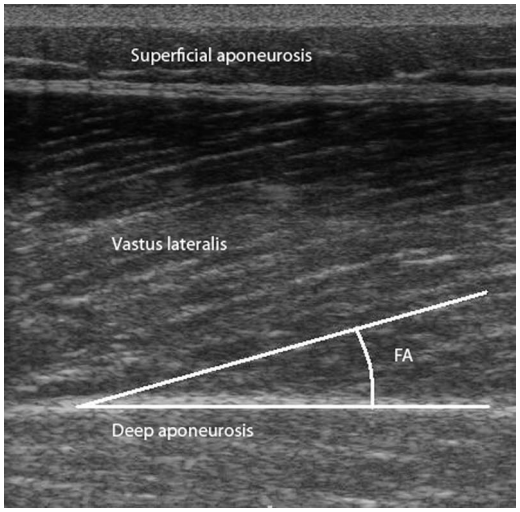

Figure 1. Representative sagital ultrasound image from m. vastus lateralis. Fascicle angle (FA) is determined as the angle between the fascicles and the deep aponeurosis.

10% in anatomical CSA of m. vastus lateralis after 14 weeks of RT in young untrained men. This, however, is to date the only in vivo study to confirm such a possible relationship between FA, fiber CSA, and anatomical CSA. The explanation for the adaptations in FA is suggested to be related to the changes in fiber CSA (10).

Knowledge on adaptations in FA after endurance training is currently lacking, that is, no longitudinal studies have investigated chronic adaptations of endurance training on FA (8). Because both force-generating capacity and contraction velocity (and thus mean power) are affected by FA, this could be of importance for endurance performance, and hence, potential changes in FA after endurance training are interesting to reveal. One cross-sectional study has compared baseline levels in experienced distance runners (~7 years training) with experienced sprinters and controls and has found greater FA in m. vastus lateralis in long-distance runners (3). Neither anatomical nor fiber CSA was measured; however, the assessment of muscle thickness (expressed as the distance between the deep and superficial aponeurosis) did not identify any differences between controls and distance runners. The measurement of muscle thickness is rather difficult to compare with measurements of fiber CSA, and from this study, it cannot be concluded if the distance runners actually have a higher fiber CSA than do the controls. Furthermore, the cross-sectional design of this study does not reveal whether the observed differences in FA were caused by different training regimens, long-term exposure to running, or genetic factors.

The purpose of this study was therefore to compare muscle strength and morphological adaptations of 10 weeks of endurance cycling with 10 weeks of lower body RT, with primary focus on potentially chronic adaptations in FA and fiber CSA.

We hypothesized that 10 weeks of endurance training would not change fiber CSA and thus would cause no adaptation in FA. Furthermore, we hypothesized that 10 weeks of RT would induce increases in fiber CSA with related increases in FA, constituting the explanatory link between relative changes in anatomical and fiber CSA.

Methods

Experimental Approach to the Problem

The study was designed to compare the adaptations in muscle morphology and muscle mechanics after 10 weeks of either endurance (END) or RT. Eighteen healthy young men were included. The subjects performed a maximal oxygen uptake test on a cycle ergometer to ensure that the $\dot{V}O_2$max values corresponded to values within the range of untrained healthy young men (<50 ml·min^{-1}·kg^{-1}). Inclusion was based on a combination of this result and a questionnaire to ensure against too high an activity level. The subjects were randomly distributed into 1 of 2 training groups, consisting of either 10 weeks of endurance training on cycle ergometers or progressive RT for the lower extremity muscle groups. $\dot{V}O_2$max and maximal muscle strength were assessed with an incremental maximal oxygen uptake test, an isokinetic dynamometer, and repetition maximum, respectively. Muscle morphology was measured using ultrasonography (US), whole-muscle magnetic resonance imaging (MRI) scanning, and muscle fiber analysis through histochemical procedures. Throughout the training period, the subjects were instructed to refrain from nutritional and ergogenic supplements but otherwise to sustain unaltered habits of activity and diet as done before the inclusion in the study.

Subjects

Eighteen untrained, young, healthy, male subjects volunteered to participate in the training study (body mass 78.3 ± 3.4 kg, height 1.81 ± 0.02 m, age 23.4 ± 0.8 years; [mean ± SEM]). The subjects were excluded if they had engaged in structured resistance or endurance training within the last 6 months before inclusion. Other exclusion criteria comprised any history of musculoskeletal injuries and current prescription medicine intake. All the participants were informed of the purpose and the risks of the study and gave written, informed consent to participate. The study was approved by the ethics committee of Region Midtjylland (j. no. M-20080177) and conducted in accordance with the Declaration of Helsinki.

Procedures

Training Program. Both END and RT performed 3 weekly training sessions for 10 weeks. Three sessions per week has previously been suggested as optimal for untrained subjects (26).

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Table 1. Training protocol for resistance training.*

Session	1–4	5–10	11–15	16–20	21–25	26–29
Leg press						
Sets	4	4	5	5	5	5
Reps‡	10,10,10,10	10,10,10,8	8,8,8,6,6	8,8,6,6,6	8,6,6,4,4	6,6,4,4,4
Knee extension						
Sets	5	5	5	5	5	5
Reps‡	10,10,10,8,8	10,8,8,8,6	8,8,8,6,6	8,8,6,6,4	8,6,6,4,4	6,6,4,4,4
Hamstring curl						
Sets	4	4	5	5	5	5
Reps‡	10,10,10,10	10,10,10,8	8,8,8,6,6	8,8,6,6,6	8,6,6,4,4	6,6,4,4,4

*Two to 3 minutes of recovery was allowed between each set.
‡Reps = repetitions; RM = repetition maximum.
Reps (repetitions) correspond to RM (repetition maximum) loading.

RT completed a training program consisting of 3 different lower body exercises (leg press, hamstring curl, and knee extension), each performed as 3–5 sets of 4–10 repetitions with repetitions corresponding to RM loading (Table 1). The recovery time between sets was set to 2 minutes during the first 15 training sessions, increasing to 3 minutes for the remaining 15 training sessions. During the last 15 sessions, the subjects were instructed to perform the concentric part of the exercises as fast as possible to induce changes in maximal power and rate of force development (RFD). Thus, the principles of the training program were aimed at producing changes in muscle strength, power, RFD, and changes in muscle morphology (i.e., hypertrophy) as previously done by others (7). All the training sessions were initiated with a light warm-up on a rowing ergometer (Concept 2 Model D, Concept 2, Morrisville, VT) followed by 2 submaximal warm-up sets in the incline leg press.

END completed a training program performed on stationary bicycles (Kettler Ergoracer GT, Kettler, Enseparsit, Germany). Based on the $\dot{V}O_2$max test, target watt and heart rate for each training session were calculated, to aid maintenance of intended training intensity. To further aid this, the subjects wore a heart rate monitor throughout each training session. Each session began with a 5-minute warm-up on the bike followed by 1 of 3 different weekly exercise sessions. At the end of all the sessions, the subjects performed 5–10 minutes of light cycling. The first weekly session consisted of continuous cycling of 30–45 minutes at 60–75% of watt-max. The second weekly session consisted of 2 intervals of 20 minutes at 70–80% of watt-max interspaced by 5 minutes of light cycling. The third weekly session consisted of eight 4 minutes intervals at 80–90% of watt-max interspaced by 1 minute of light cycling (Table 2). Two of the short interval sessions were replaced with midway maximal oxygen uptake tests to allow adjustments of relative intensity according to gradual training improvements.

All the training sessions were supervised to ensure proper progression and intensity for both groups. All the training sessions were separated by at least 1 day.

Whole-Muscle Cross-Sectional Area Analysis—Magnetic Resonance Imaging. All imaging was performed with a 1.5-T scanner (Philips Achieva, Best, the Netherlands). The subjects were placed in the supine position with the feet entering the scanner first. The MRI scans were performed on the left leg by using a cardiac coil. After an initial frontal scout scan, 20 transversal slices were acquired, of which only one was used for this study. The first slice was 215 mm proximally to the fossa intercondylaris, and the following images were acquired distally from this point. A T1-weighted, fast spin echo sequence with the following parameters was used: scan matrix = 288 × 282, field of view = 230 × 230 mm^2, number of slices = 20, slice thickness = 7.5 mm, slice gap = 1 mm, repetition time = 2 seconds, echo time = 5.3 milliseconds, echo train length = 18, number of signal averages = 3, and scan time = 3:12 minutes. Whole-muscle CSA was obtained from the most proximal slice at a position corresponding to one-half of the femur length. Whole-muscle CSA of 3 muscle compartments was calculated using custommade software. The first compartment was the knee extensors (mm. vastus lateralis, vastus medialis, vastus intermedius, and rectus femoris), the second was the knee flexors (mm. semitendinosus, semimembranosus, and biceps femoris–caput longum and caput breve), and the third was the hip adductors (mm. adductor magnus, adductor longus, and gracilis). Furthermore, the total thigh muscle CSA was calculated as the sum of the 3 compartments. Two investigators performed blinded area measurements on all images and intraclass correlation coefficients (ICCs) were calculated. The final CSA for the 3 compartments used for later analysis was taken as the mean of the results from the 2 investigators (ICC = 0.95).

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Table 2. Repetitions × duration of work at intensity of watt-max.*

Week	Session 1	Session 2	Session 3
1	30–40 min at 60%	2 × 20 min at 70%	
2	30–40 min at 60%	2 × 20 min at 60–70%	8 × 4 min at 70–80%
3	45 min at 60–65%	2 × 20 min at 60–70%	Maximal oxygen uptake test
4	45 min at 65–70%	2 × 20 min at 70–75%	8 × 4 min at 80–85%
5	45 min at 70%	2 × 20 min at 70–75%	8 × 4 min at 80–85%
6	45 min at 75%	2 × 20 min at 80–85%	Maximal oxygen uptake test
7	45 min at 70%	2 × 20 min at 70–75%	8 × 4 min at 80–85%
8	45 min at 70%	2 × 20 min at 75-80%	8 × 4 min at 85–90%
9	45 min at 70–75%	2 × 20 min at 75–80%	8 × 4 min at 85–90%
10	45 min at 75%	2 × 20 min at 80%	8 × 4 min at 90%

*Pause between 2 × 20-minute interval was 5 minutes and 1 minute between 8 × 4-minute intervals.

Muscle Fiber Analysis—ATPase histochemistry. Biopsies were obtained from the middle section of the m. vastus lateralis muscle by applying the Bergström needle technique. The same person performed all invasive procedures and attempted to reach the same sample depth. The muscle samples were dissected free of visible fat and connective tissue, and a part of the biopsy was immediately mounted with Tissue-Tek, frozen in isopentane cooled with liquid nitrogen, and stored at −80°C until further analysis. Serial sections (10 μm) of the muscle biopsy samples were cut in a cryostat (−20°C), and cross-sections from pretraining and posttraining biopsies from the same subject were placed on the same slide and processed simultaneously for ATPase histochemistry analysis. ATPase histochemistry analysis was performed after preincubation at pH of 4.37, 4.60, and 10.30 as described previously (12), to enable the determination of fiber type–specific CSA and fiber type distribution. The serial sections were visualized and analyzed as described in detail by Andersen and Aagaard (5). The serial sections were visualized and analyzed using a Leica DM2000 microscope (Leica, Stockholm, Sweden) and a Leica Hi-resolution Color DFC camera (Leica) combined with image-analysis software (Leica Qwin ver. 3, Leica) as described by Dalgas et al. (14). The investigator was blinded to pre- and post samples and to subject information.

The muscle fibers were categorized as 1 of 5 fiber types (I, I/IIa, IIa, IIax, and IIx) and then grouped into the 3 main fiber types (I, IIa, IIx) according to the following formula: type I = I + ½I/IIa; type IIa = ½I/IIa + IIa + ½IIax; type IIx = ½IIax + IIx. For the area measurements, a general mean fiber size for all fiber types was combined, and a type I and type II (type IIa + type IIx)–specific area measure was calculated (14).

Only fibers cut perpendicularly to their longitudinal axis were used in the determination of fiber size in accordance with the study of Andersen and Aagaard (5). The mean number of fibers used for the area analysis was 132 ± 8.

Ultrasonography Measurements. Sagittal US images of m. vastus lateralis were recorded with a Siemens real-time scanner with a 7.5-MHz linear array transducer. The images were obtained in a seated position with 90° hip flexion and 70° knee flexion in the isokinetic dynamometer to ensure correct and reproducible joint angles (representative image is depicted in Figure 1). The US probe was placed at 50% of femur length over the midbelly of the m. vastus lateralis. The images were saved and later analyzed for FA by using Scion Image (Scion Image, Scion Corporation, MD). The m. vastus lateralis FA was measured as the angle between muscle fascicles and the deep aponeurosis at the insertion, which according to previous studies is suggested to be the most valid and reliable method (1,19,20,33). To avoid the influence from other tests, the US test was performed on a separate day. All the images were analyzed twice by 2 investigators to ensure reliability. The mean values were used for further analysis.

Maximal Oxygen Uptake Test. The $\dot{V}O_2$max test was performed pre- and post training. To determine $\dot{V}O_2$peak during bicycling, all the subjects performed an incremental exercise test on a Monark Ergomedic 834E bicycle ergometer (Monark ergometic 894 E, Monark, Varberg, Sweden). The test was conducted at 70 rpm with 35-W increments every minute. The rate of oxygen uptake and carbon dioxide release was determined every 10 seconds by means of an online respiratory gas exchange analyzer (AMIS 2001, Innovision, Odense, Denmark). The protocol was a standardized, stepwise progressive test to exhaustion. $\dot{V}O_2$max was defined as the highest mean of 3 consecutive measurements of 10-second intervals, including the $\dot{V}O_2$peak. Watt-max was estimated according to the principles of Andersen (6). The heart rate was monitored continuously with a heart rate monitor (Polar, Oulu, Finland).

Strength Measurements. Isometric strength was determined as follows: Subsequent to a standardized warm-up consisting of 5 minutes of light aerobic exercise (100 W) on a stationary

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bicycle (Monark, Varberg, Sweden), the subjects were seated in an isokinetic dynamometer (Humac Norm, CSMI, Stoughton) with 90° hip flexion and restraining straps crossing the torso and the right leg. The transverse axis of the subject's knee was aligned with the axis of the dynamometer. The right leg was placed behind a stabilization bar while the left leg was attached to the dynamometer arm. The subjects were instructed to grab the chair handles. The dynamometer was adjusted individually so that the contact point between the subjects' leg and the dynamometer arm was 3 cm proximal to the malleolus medialis. The MVC was measured by 3 maximal isometric knee extensor contractions at 70° knee flexion (0° equals full extension) and 3 maximal isometric knee flexor contractions at 20° knee flexion. All the contractions were interspaced with 1-minute recovery time. All the trials were sampled at 100 Hz. The peak torque from the best of the 3 trials was used for further analysis.

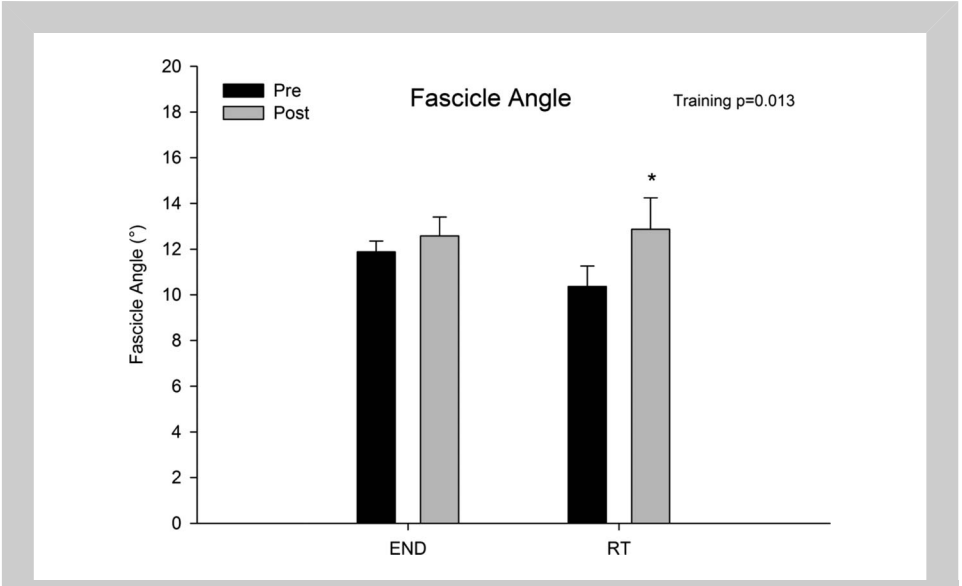

Figure 2. Fascicle angle (FA). Values for m. vastus lateralis FA (°) ± *SEM* pre- and post-10 weeks of either endurance training (END) or resistance training (RT). The results from 2-way analysis of variance are shown in the upper right corner. *Significant difference pretraining vs. posttraining for RT ($p < 0.01$).

Dynamic strength repetition maximum (RM) was determined as follows: The subjects performed a light aerobic warm-up on a rowing ergometer. After the warm-up, the subjects completed the RM testing: 3RM and 1RM incline leg press, 3RM hamstring curl, and 3 RM knee extension (all ergometers from Nordic Gym, Bollnäs, Sweden). Before each RM test, the subjects performed 2–3 sets of 2–5 repetitions to enable habituation. Between all the trials, approximately 3 minutes of recovery was allowed. In the incline leg press, the subjects were instructed to lower the weight until 90° knee flexion. In hamstring curl and knee extension, the subjects performed a full range of motion. The RM trials continued until the subject could no longer complete the predetermined range of motion.

Statistical Analyses

The dependent variables included morphological (FA, anatomical and fiber CSA) and functional (MVC, $\dot{V}O_2$max, and 1 and 3RM) results. The independent variables included treatment (END vs. RT) and time (pre vs. post). After passing a test for normality and equal variance of distribution, data were expressed as mean ± SEM. A 2-way repeated measures analysis of variance was used to analyze time and group interactions. When a significant overall time or group effect was observed, the Tukey post hoc analysis was used to analyze for individual pairwise differences. Significance was set at an alpha level ≤0.05. All statistical analyses were performed using SigmaPlot (SigmaPlot v 11.0, Systat Software Inc., Chicago, IL).

Results

Two exercise-unrelated dropouts occurred in each training group. Thus, all presented data are from the remaining 14 subjects ($n = 7$ in each training group).

Baseline Values

No differences between RT and END were observed before commencing training in any of the variables.

Changes in m. Vastus Lateralis Fascicle Angle

The results for FA are shown in Figure 2. For RT, m. vastus lateralis FA increased from ~10.4 ± 0.9° before training to ~12.9 ± 1.4° after training ($p < 0.01$) corresponding to a relative increase of ~23 ± 8%. No changes in FA were observed for END.

Changes in Fiber Cross-Sectional Area

Results for fiber CSA are shown in Figure 3. In the RT group, the overall fiber size increased from ~5,207 ± 266 μm^2 before training to ~6,125 ± 342 μm^2 after training ($p < 0.05$), corresponding to a relative increase of ~19 ± 7%. The average Type II area increased in RT pretraining to posttraining from ~5,516 ± 433 to ~6,657 ± 526 μm^2 ($p = 0.011$), corresponding to a relative increase of ~22 ± 7%. No changes in the mean or specific fiber CSA were observed for END.

Changes in Anatomical Cross-Sectional Area

The results for anatomical CSA are shown in Figure 4. Total thigh anatomical CSA for RT increased from ~137 ± 5 cm^2

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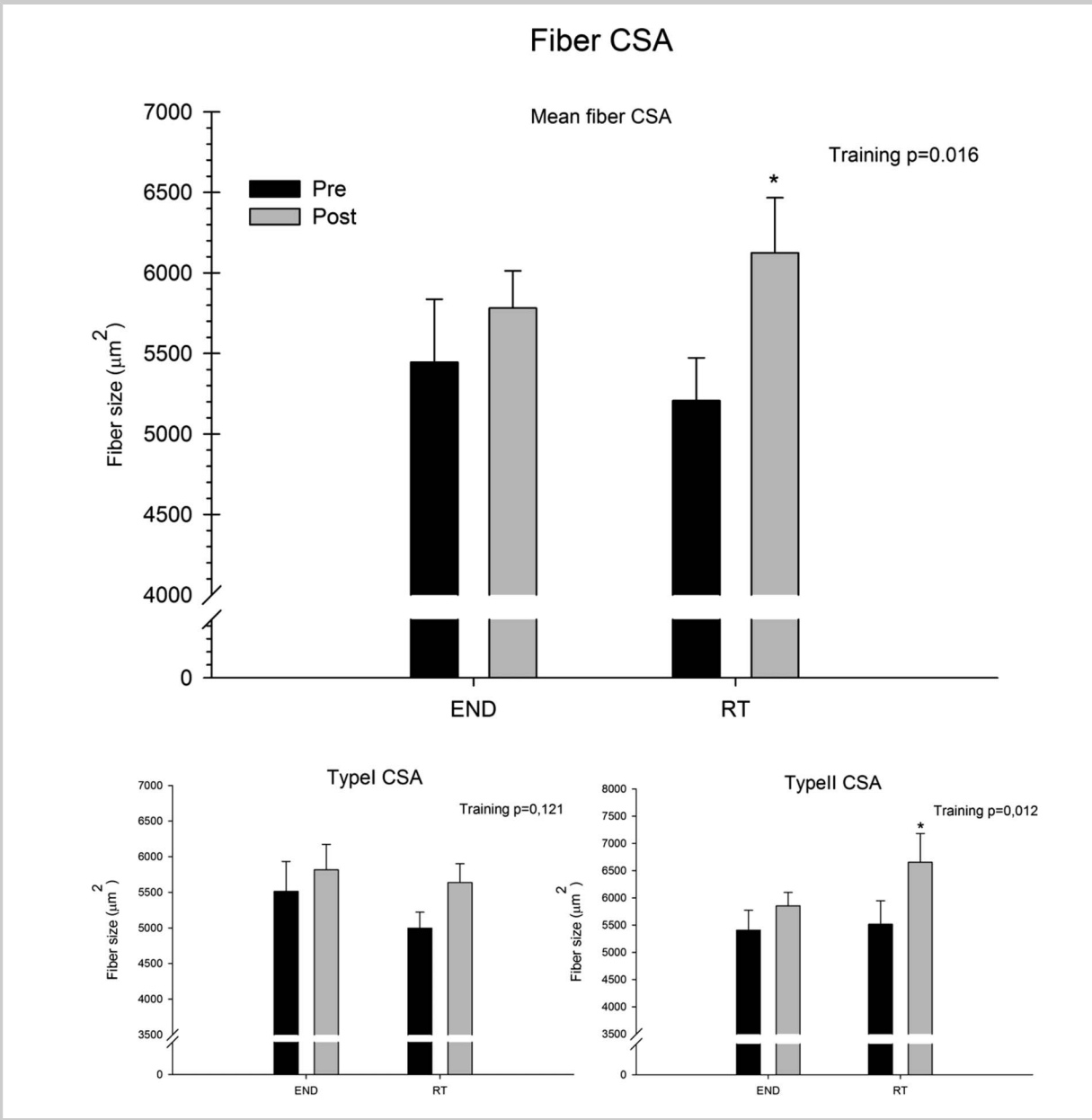

Figure 3. Fiber cross-sectional area (CSA). Values for m. vastus lateralis mean fiber, type I and type II CSA (μm^2) ± *SEM* pre- and post-10 weeks of either endurance training (END) or resistance training (RT). The results from 2-way analysis of variance are shown in the upper right corner. *Significant difference pretraining vs. posttraining for RT ($p < 0.05$).

before training to ~153 ± 5 cm^2 after training ($p < 0.001$), corresponding to a relative increase of ~11 ± 3%. The RT increased anatomical CSA for the knee extensor compartment from ~77 ± 3 cm^2 before training to 84 ± 2 cm^2 after training ($p = 0.001$), corresponding to a relative increase of ~9 ± 3%. The anatomical CSA for the knee flexor compartment for RT increased from ~33 ± 2 cm^2 before training to ~38 ± 2 cm^2 after training ($p < 0.001$), corresponding to a relative increase of ~14 ± 2%. No changes were observed for the adductor compartment for RT. In END, no changes were observed in any of the muscle compartments and thus neither in total thigh anatomical CSA.

Body Mass

The RT increased their body mass pre to post from 76.5 ± 4 to 78.8 ± 4 kg ($p < 0.05$), whereas no changes were observed for END ($p = 0.633$).

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Changes in Maximal Oxygen Uptake

The END increased from ~45 ± 2 ml·min^{-1}·kg^{-1} before training to ~50 ± 2 ml·min^{-1}·kg^{-1} after training ($p < 0.001$), corresponding to a relative increase of ~10 ± 2%. No changes were observed for RT. The values for RT pre and post were 46.9 ± 3 and 46.9 ± 3 ml·min^{-1}·kg^{-1} ($p = 0.958$), respectively.

Changes in Maximal Muscle Strength

Isometric Strength. The RT increased knee flexor MVC from ~151 ± 14 N·m before training to ~176 ± 7 N·m after training ($p < 0.001$) and knee extensor MVC from ~238 ± 17 N·m before training to ~280 ± 21 N·m after training ($p < 0.001$), corresponding to relative increases of ~28 ± 6% and ~20 ± 5%, respectively. No changes were observed for END. The knee flexor strength for RT was significantly greater than END posttraining ($p < 0.05$).

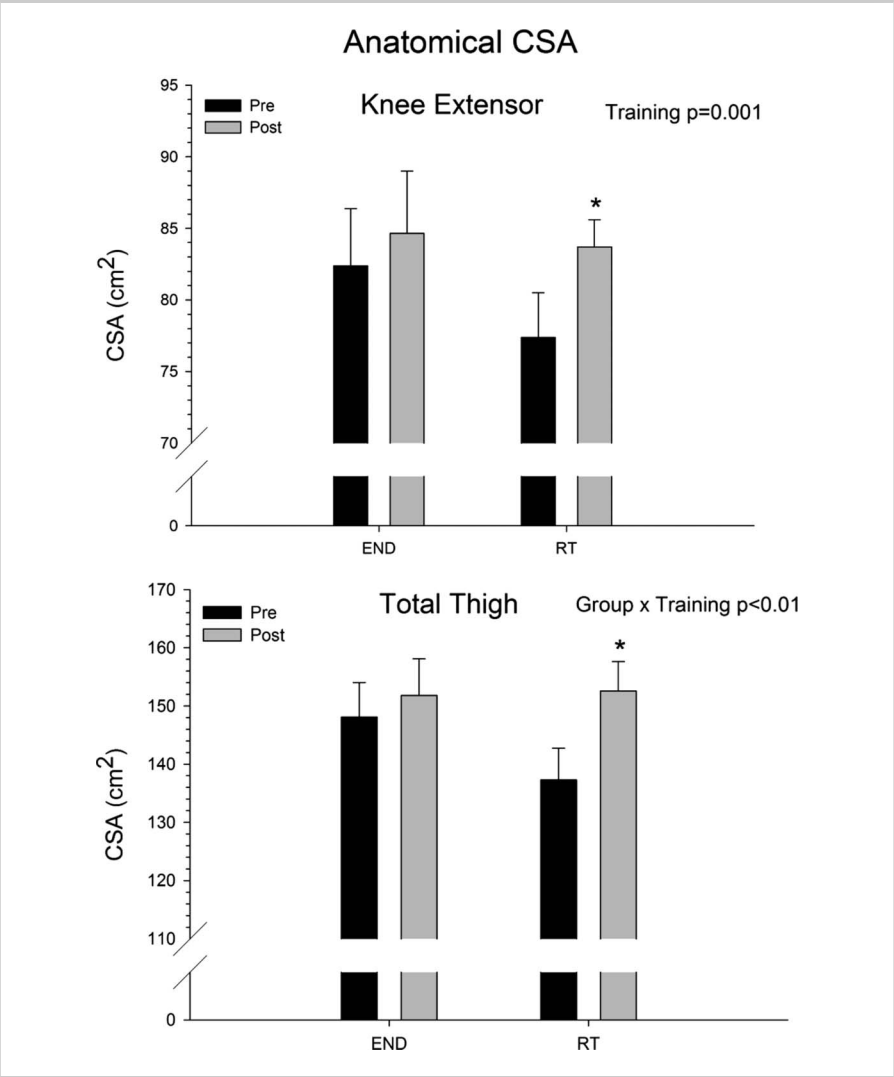

Figure 4. Anatomical cross-sectional area (CSA). Values for knee extensor and total thigh anatomical CSA (cm^2) ± *SEM* pre- and post-10 weeks of either endurance training (END) or resistance training (RT). The results from 2-way analysis of variance are shown in the upper right corner. *Significant difference pretraining vs. posttraining for RT ($p < 0.01$).

Dynamic Strength Repetition Maximum. The results for RM are shown in Figure 5. The RT increased 3RM and 1RM in the leg press pretraining to posttraining from ~160 ± 10 to ~284 ± 12 kg ($p < 0.001$) and ~179 ± 11 to ~305 ± 13 kg ($p < 0.001$) corresponding to ~81 ± 12% and ~74 ± 11% increases in 3RM and 1RM, respectively. The END increased 3RM and 1RM in the leg press pretraining to posttraining from ~161 ± 12 to ~219 ± 19 kg ($p < 0.001$) and ~180 ± 14 to ~239 ± 19 kg ($p < 0.001$), corresponding to ~36 ± 8% and ~34 ± 7% for the 3RM and 1RM, respectively. In both 3RM and 1RM, the RT was significantly stronger than END posttraining ($p < 0.01$). The RT increased 3RM in the knee extension pretraining to posttraining from ~96 ± 5 to ~133 ± 4 kg ($p < 0.001$), corresponding to an ~40 ± 4% increase. The RT was significantly stronger than the END posttraining ($p < 0.01$). The RT increased 3RM in the hamstring curl pretraining to posttraining from ~48 ± 4 to ~65 ± 3 kg ($p < 0.001$), corresponding to ~39 ± 6%. The RT was significantly stronger than the END posttraining ($p = 0.008$).

Discussion

The main finding of this study is that 10 weeks of resistance, but not endurance training, is able to produce changes in FA, fiber CSA, and anatomical CSA. Accordingly, 10 weeks of RT increased FA by 23%, mean fiber CSA by 19%, and anatomical CSA by 9%. These training-specific morphological adaptations are supported by the results from strength measurements in which RT increased strength at all conditions, whereas only minor changes were observed for END. Our

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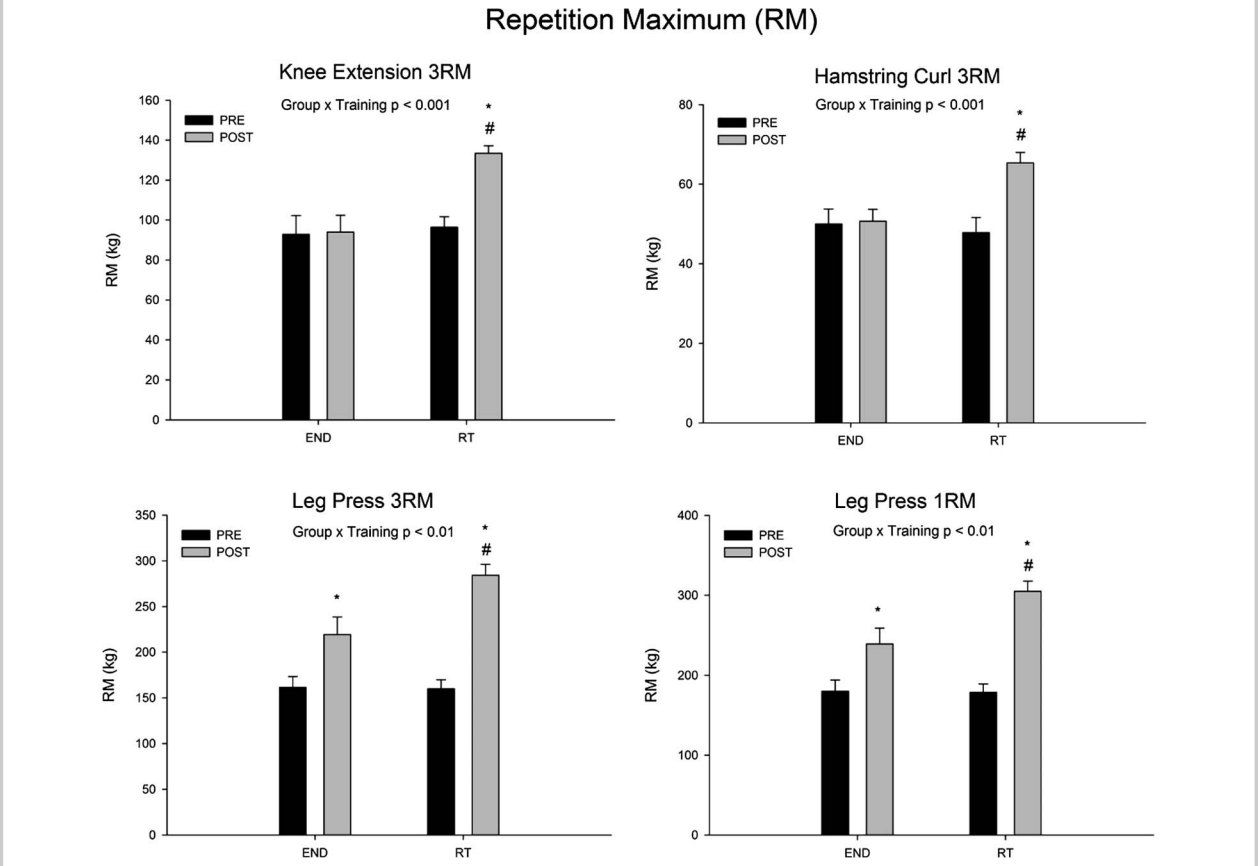

Figure 5. Repetition maximum (RM). Values for 1 and 3RM (kg) ± *SEM* pre- and post-10 weeks of either endurance training (END) or resistance training (RT) in knee extension, hamstring curl, and leg press. The results from 2-way analysis of variance are shown in the upper right corner. *Significant difference pretraining vs. posttraining within group ($p < 0.001$). #Significant group differences posttraining ($p < 0.01$).

results confirm those of only a previous study on RT that the explanation for the discrepancy between increases in fiber and anatomical CSA is FA (1). The results for END serve to indirectly confirm that the changes in muscle fiber hypertrophy and FA are closely related.

Although knowledge concerning the changes in FA in response to RT is substantial, the changes in FA in response to endurance training is virtually nonexistent. In the 1 cross-sectional study we are aware of, Abe et al. (3) found increased FA baseline levels in experienced distance runners compared with that in controls. In this study, we did not observe an increased FA after 10 weeks of endurance training. However, in our study, endurance training was performed as cycling, whereas the endurance athletes in the study by Abe et al. (3) were distance runners. One major difference between cycling and running is the eccentric part of the stretch-shortening cycle during running, which could potentially induce specific morphological adaptations compared with the concentric exercise modality practiced through cycle training (17,31). Furthermore, our subjects were untrained before the 10 weeks of training, whereas the distance runners had approximately 7 years of running experience. One study reported acute increases in FA after a single-bout incremental (increments of 25 W every 2 minutes) cycloergometer protocol to exhaustion and suggested edema and perfusion as a possible mechanism (11). Our results suggest that no chronic change in FA takes place after 10 weeks of endurance cycling. We believe that the influence of edema or perfusion were avoided in our study by several days interspacing the US measurements from test or exercise procedures.

In general, the morphological results from this study are in agreement with those in the literature. Concerning m. vastus lateralis, we observed increases in FA after 10 weeks of RT. Both the absolute values pre (10 ± 1°) and post (13 ± 1°) and the relative increase (23 ± 8%) of FA correspond well with those of the literature (1,9,37). The absolute values for fiber CSA at pretraining (~5,500 μm^2) are higher than those of one study (1) (~3,754 μm^2) but are in accordance with those of other studies (25,36). However, the relative increase of approximately 19% for the mean fiber CSA in the RT group is within

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the range of that of most similar previous training studies (1,25,36). The absolute values before and after training for the anatomical CSA and the relative improvement for RT are also in accordance with those of previous studies (1,29,38).

As for END, no changes in mean fiber CSA or fiber type–specific CSA were observed. This is somewhat in contrast to the findings of Kraemer et al. (25) who observed a significant decrease in type I fiber area after 12 weeks of endurance running and Gollnick et al. (16) found an increase in type I fiber area after 5 months of endurance cycling. The variability in the results on fiber CSA after endurance training might be attributed to differences in the initial training status of the subjects in the studies, the type of exercise performed (running vs. cycling), number of fibers analyzed, etc. Considering the results from Kraemer et al. (25) and Gollnick et al. (16), we find that there is no general consensus that endurance training is able to elicit changes in fiber CSA.

With respect to the changes in strength measures, the observed increases in isometric MVC for RT were as expected and similar to those reported in earlier studies of a similar duration (1,2,29). Unlike RT, END did not improve isometric MVC for knee extension and flexion. When comparing increases in knee extensor MVC with increases in m. vastus lateralis mean fiber CSA, Aagaard et al. (1) found a 1:1 relation between the parameters. Similarly, our results from RT exhibit a relative increase in the mean fiber CSA of 19% and a relative increase in knee extensor MVC of 20%. As for dynamic strength, the improvements in the knee extension and hamstring curl for RT are very similar to results from earlier studies (13,24,38). Both RT and END increased leg press strength, with RT values being significantly higher than those of END. Considering the fact that the subjects were untrained, the strength increase in endurance-trained individuals could be caused by a minor degree of initial learning effect from the pretesting combined with an increase in knee and hip extensor strength from the high-intensity endurance intervals. The latter explanation seems more likely, because END produced no strength changes in isolated knee extension or in hamstring curl (18).

From a mechanical point of view, an increase in hypertrophy of the muscle increases the passive stiffness (27). This point of view is supported by the cross-sectional study of Ryan et al. (34) who reported significant correlations between the anatomical CSA and passive stiffness of the plantar flexors. Furthermore, Klinge et al. (22) observed an approximately 15% increase in stiffness of the hamstrings after 13 weeks of isometric RT. If no change occurs in the aponeurosis or tendon stiffness, the increased passive stiffness of the muscle fibers could theoretically stretch the aponeurosis, the tendon or both, and increase the FA. Thus, it can be speculated that increased muscle stiffness caused by hypertrophy provides an explanation as a mechanism for the changes in FA. On the other hand, the increases in tendon stiffness after RT (23,32) can therefore be argued to counteract the increased muscle stiffness from hypertrophy and render it insufficient to increase FA. Structural proteins such as titin and desmin are strongly connected to passive stiffness (28,35). An increase in desmin protein concentration after RT (but not after endurance cycling) has previously been observed by Parcell et al. (30) and could serve as an explanation to further increase the passive stiffness of the muscle tissue. We speculate that this could possibly overcome the increased stiffness of the tendinous tissue and ultimately increase the FA. To explore such a question, further studies are needed to investigate possible relations between FA and structural proteins such as desmin, titin, or functionally related proteins.

In conclusion 10 weeks of endurance training was unable to produce changes in fiber CSA, anatomical CSA, and FA. This is in direct contrast to the changes in and interdependence of muscle morphological parameters observed in response to 10 weeks of RT.

Practical Applications

The present data demonstrate the specific adaptations to 10 weeks of endurance vs. that to RT. When conducting cycling-based endurance training, the primary functional adaptation is an increase in maximal oxygen uptake, whereas only minor increases in muscle strength can be expected. These minor strength increases can probably only be expected in movements similar to the ones exercised and is not reflected in any permanent muscle morphological changes, that is, changes in FA or fiber CSA. On the contrary, when conducting high-intensity RT, the adaptations in morphology and therefore also in maximal strength (both isometric and repetition maximum) occur and are highly interrelated. Depending on which qualities the practitioner wishes to improve, this knowledge can be useful to ensure effective training improvements.

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