A mechanism for increased contractile strength of human pennate muscle in response to strength training: changes in muscle architecture

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1. In human pennate muscle, changes in anatomical cross-sectional area (CSA) or volume caused by training or inactivity may not necessarily reflect the change in physiological CSA, and thereby in maximal contractile force, since a simultaneous change in muscle fibre pennation angle could also occur.

2. Eleven male subjects undertook 14 weeks of heavy-resistance strength training of the lower limb muscles. Before and after training anatomical CSA and volume of the human quadriceps femoris muscle were assessed by use of magnetic resonance imaging (MRI), muscle fibre pennation angle (θ_p) was measured in the vastus lateralis (VL) by use of ultrasonography, and muscle fibre CSA (CSA_{fibre}) was obtained by needle biopsy sampling in VL.

3. Anatomical muscle CSA and volume increased with training from 77.5 ± 3.0 to 85.0 ± 2.7 cm^2 and 1676 ± 63 to 1841 ± 57 cm^3, respectively ($\pm$ S.E.M.). Furthermore, VL pennation angle increased from 8.0 ± 0.4 to 10.7 ± 0.6 deg and CSA_{fibre} increased from 3754 ± 271 to 4238 ± 202 μm^2. Isometric quadriceps strength increased from 282.6 ± 11.7 to 327.0 ± 12.4 N m.

4. A positive relationship was observed between θ_p and quadriceps volume prior to training ($r = 0.622$). Multifactor regression analysis revealed a stronger relationship when θ_p and CSA_{fibre} were combined ($R = 0.728$). Post-training increases in CSA_{fibre} were related to the increase in quadriceps volume ($r = 0.749$).

5. Myosin heavy chain (MHC) isoform distribution (type I and II) remained unaltered with training.

6. VL muscle fibre pennation angle was observed to increase in response to resistance training. This allowed single muscle fibre CSA and maximal contractile strength to increase more (+16 %) than anatomical muscle CSA and volume (+10 %).

7. Collectively, the present data suggest that the morphology, architecture and contractile capacity of human pennate muscle are interrelated, *in vivo*. This interaction seems to include the specific adaptation responses evoked by intensive resistance training.

Many, if not most, human muscles are characterized by a pennate arrangement of the muscle fibres relative to the points of origin and insertion at the aponeurosis or tendon (Steno, 1667). In terms of muscle CSA the phenomenon of muscle fibre pennation allows *physiological muscle CSA*, which is defined as the magnitude of muscle fibre area perpendicular to the longitudinal axis of individual muscle fibres multiplied by the cosine of the angle of pennation (Wickiewicz *et al.* 1983; Powell *et al.* 1984), to greatly exceed the *anatomical muscle CSA* measured in a plane axial to the longitudinal axis of the muscle. Since the physiological CSA represents the maximal number of acto-myosin crossbridges that can be activated in parallel during contraction, the maximal force-generating capacity of a given muscle is proportional to its total physiological CSA. Based on parallelogram models of

bipennate muscle, total physiological muscle CSA increases in proportion to $\sin(\theta_p)$, where θ_p is the muscle fibre pennation angle (Alexander & Vernon, 1975; Rutherford & Jones, 1992; Narici *et al.* 1992). On the other hand, the effective contractile force exerted onto the aponeurosis or tendon will obviously decrease when angular pennation is increased, thereby causing muscle force to decrease proportionally to $\cos(\theta_p)$. From the overall result of these two opposing effects (i.e. $\sin(\theta_p) \times \cos(\theta_p) \propto \frac{1}{2}\sin(2\theta_p)$), maximal muscle force is expected to increase with increases in muscle fibre pennation angle to an upper limit of 45 deg (Alexander & Vernon, 1975; Rutherford & Jones, 1992). Consequently, pennate muscles are able to exert significantly greater contractile force compared to non-pennate muscles. It should be recognized that the above estimates are based on simplistic planar geometric models, which do not fully describe the 3-dimensional and non-linear architecture of pennate muscle *in vivo* (Van Leeuwen & Spoor, 1992, 1993). However, the models may still be considered useful as an approximation.

Previously, muscle fibre pennation angle has been obtained from dissection of cadaveric specimens. However, more adequate measuring methods based on ultrasound sonography have been recently introduced, which makes it possible to perform *in vivo* recordings of fibre pennation at specific muscle lenghts (joint angles) and at specific levels of muscle tension (Herbert & Gandevia, 1995; Narici *et al.* 1996*a*; Maganaris *et al.* 1998) (i.e. Fig. 1).

The physiological CSA and thereby the maximal force-generating capacity of human pennate muscles is not easily estimated *in vivo*, since it is impossible to measure the total area constituted by all the muscle fibres situated in parallel within the muscle directly. In contrast, anatomical muscle CSA and volume can be assessed with reasonable accuracy by the use of nuclear MRI (Narici *et al.* 1989, 1992, 1996*b*). However, it should be recognized that changes in anatomical CSA or total muscle volume caused by training or inactivity may not be representive of the change in physiological CSA, and thereby in force-generating capacity, since muscle fibre pennation angle θ_p could also change in response to specific regimes of training or physical inactivity. Recent studies using ultrasound imaging have indicated that the architecture (i.e. θ_p) and the morphology (i.e. anatomical CSA) of human skeletal muscle *in vivo* are more closely associated than previously recognized (Rutherford & Jones, 1992; Kawakami *et al.* 1993; Ichinose *et al.* 1998). Furthermore, the findings of these studies suggest that the changes in muscle architecture and morphology evoked by resistance training may be closely coupled (Kawakami *et al.* 1993, 1995). Positive relationships have been observed *in vivo* between anatomical muscle CSA and muscle fibre pennation angle for the human triceps brachii (Kawakami *et al.* 1993; Ichinose *et al.* 1998) and quadriceps femoris (Rutherford & Jones, 1992). In addition, greater CSA and steeper fibre pennation angles were observed in bodybuilders compared to age-matched sedentary subjects (Kawakami *et al.* 1993) which suggests that the muscle hypertrophy induced by resistance training may be associated with an increase in muscle fibre pennation angles. However, only few and conflicting data exist regarding the influence of resistance training on muscle fibre pennation angle. Using ultrasound sonography Kawakami *et al.* (1995) reported a significant increase in fibre pennation angle from 16.5 deg to 21.3 deg in the triceps brachii muscle following 16 weeks of resistance training. In contrast, no increase in fibre pennation angle was observed for the quadriceps muscle (vastus lateralis) following 12 weeks of resistance training (Rutherford & Jones, 1992).

Measures of muscle morphology may be obtained both at the *microscopic scale* by the determination of single muscle fibre CSA from muscle biopsy samples (Fig. 1) and at the *macroscopic scale* by an estimation of total anatomical muscle CSA or volume using MRI (Fig. 3), computer tomography (CT) or ultrasound imaging techniques. It has previously been demonstrated that muscle morphology evaluated at the microscopic level (i.e. myosin isoform composition) is related to *in vivo* mechanical muscle function at the macroscopic level (Harridge *et al.* 1995; Aagaard & Andersen, 1998). On the other hand, no association may necessarily exist between microscopic and macroscopic measures of muscle morphology, since single muscle fibre cross-sectional area seems to be unrelated to the magnitude of total anatomical muscle CSA (Henriksson-Larsén *et al.* 1992).

Collectively the above findings suggest that some degree of association exists between the morphology and architecture of human pennate muscle *in vivo*. However, at the same time a significant degree of complexity and heterogeneity appears to be present as well. In order to describe more closely the potential interaction between muscle morphology, muscle architecture and contractile capacity, the present study examined the relationship between anatomical cross-sectional area and volume, physiological cross-sectional area of individual muscle fibres and fibre pennation angle in the human quadriceps muscle before and after a prolonged period of resistance training. It was hypothesized that an extensive regime of heavy-resistance strength training would cause muscle fibre pennation angle to increase. As a result, the magnitude of training-induced increase in physiological muscle fibre CSA and thus in maximal contractile strength was expected to exceed the increase in anatomical muscle CSA and volume. The present study is the first in which measurements of muscle fibre pennation angle (ultrasound imaging), macroscopic muscle dimensions (MRI) and single muscle fibre morphology (biopsy sampling) were combined in order to examine the specific adaptation responses in muscle morphology, architecture and contractile function evoked by intense strength training. Preliminary findings have been reported previously (Aagaard *et al.* 2000*a*).

METHODS

Subjects

Eleven male subjects volunteered to participate in the study (body mass, 72.8 ± 4.0 kg; height, 180.7 ± 7.3 cm; age, 27.0 ± 5.3 years; means ± S.D.). None of the subjects had previously participated in systematic resistance training. The conditions of the study were approved by the local Ethics Committee. All the experimental procedures were performed in accordance with the Declaration of Helsinki and all subjects gave their written informed consent to participate in the study.

Muscle fibre pennation angle

Sagittal ultrasound images were recorded in the quadriceps femoris muscle using of a Toshiba Sonolayer SSA-270A real-time scanner with a 7.5 MHz linear array transducer. Images were recorded at 50% femur length (90 deg flexion at the hip and knee joint), according to procedures previously described (Rutherford & Jones, 1992; Fukunaga *et al.* 1997). VL fibre pennation angle (θ_p) was measured as the angle between VL muscle fibre fascicles and the deep aponeurosis of insertion, i.e. the fascia separating VL and the vastus intermedius muscle (Rutherford & Jones, 1992; Henriksson-Larsén *et al.* 1992; Fukunaga *et al.* 1997) (Fig. 1). At every test occasion three ultrasound images were obtained in each subject for which θ_p was determined as the average fibre pennation angle.

Muscle biopsy sampling

Needle biopsies (100–150 mg) were obtained from the middle portion of m. vastus lateralis (Bergström, 1962). The muscle samples were divided into two parts; one part was frozen in liquid nitrogen for later analysis of MHC composition (Andersen *et al.* 1994) and the remaining part was trimmed, mounted and frozen in isopentane, and cooled with liquid nitrogen at −80 °C for later histochemical analysis.

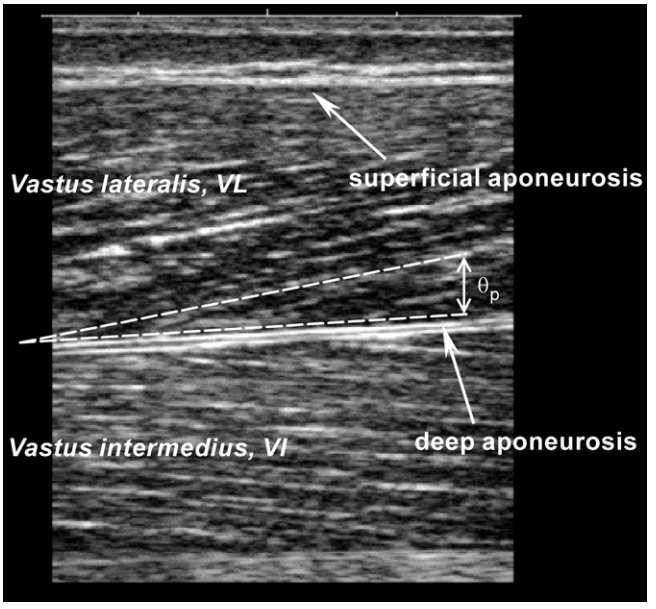

Figure 1

Sagital ultrasound image obtained in the quadriceps femoris muscle at 50% femur length. VL muscle fibre pennation angle (θ_p) was determined as the angle between vastus lateralis muscle fibre fascicles and the deep aponeurosis separating vastus lateralis and vastus intermedius.

MHC composition

Muscle samples of 20–40 mg were homogenized as described in detail elsewhere (Andersen *et al.* 1994). Subsequently, the homogenates were loaded on SDS-PAGE gels containing 37.5% glycerol and 6% polyacrylamide and were run overnight at 70 V, followed by a 3–4 h session at 200 V. Following Coomassie Blue staining densitometric quantification of the MHC isoforms was performed.

Myofibrillar ATPase histochemistry

Serial transverse sections (10 μm) were cut in a cryotome at −20 °C. Subsequently the sections were stained for myofibrillar ATPase at pH 9.4 after both alkaline (pH 10.3) and acid (pH 4.3 and 4.6) preincubations (Brooke & Kaiser, 1970). Based on the ATPase staining pattern muscle fibres were characterized as type I, IIA and IIX (Fig. 2).

Physiological muscle fibre area

CSA_{fibre} was analysed from the ATPase-stained sections (pH 4.6) using a COMFAS image scanner (SBsysCOMFAS, Scan Beam, Hadsund, Denmark). On average 282 ± 25 fibres (± S.E.M.) were examined in each subject. CSA_{fibre} was determined separately for the type I and II fibres. In addition, the average type I+II muscle fibre area was calculated as:

$$(\%\,\text{type I} \times CSA_{typeI}) + (\%\,\text{type II} \times CSA_{typeII}).$$

Anatomical muscle CSA and volume

Muscle CSA and volume were determined from spin-echo, T1-weighted axial MR images recorded with a 0.3-T magnet (Fonar Equipment, Melville, NY, USA). The femur length, defined as the distance from the most proximal prominence of the greater trochanter to the most distal border of the lateral femur condyle, was carefully determined in coronary scout scans. Subsequently, seven axial slices (slice thickness 10 mm, repetition time 480 ms, echotime 30 ms) interspaced by a distance of 1/10 femur length were obtained at 20, 30, 40, 50, 60, 70 and 80% femur length (Higbie *et al.* 1996) (Fig. 3). The perimeter of the quadriceps muscle was digitized in each axial image, allowing anatomical muscle CSA to be calculated (Scion Image, Frederick, MD, USA; NIH Image, National Institutes of

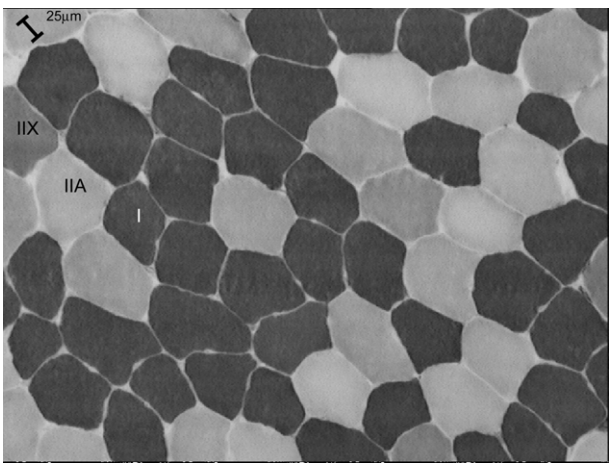

Figure 2

Muscle biopsy cross section stained for myofibrillar ATPase after preincubation at pH 4.6. Type I, IIA and IIX muscle fibers are marked for illustration. Type I and II muscle fibre area, average fibre area, fiber type composition and myosin heavy chain (MHC) isoform composition was determined before and after the period of resistance training.

Health, USA). Volumes were calculated by the summation of successive CSA values, each multiplied by the respective interslice distance. The different quadriceps components (i.e. VL, VM, VI and RF) may be identified along their entire length, to calculate the volume of the individual compartments (Narici *et al.* 1989, 1992). However, such a differentiation is not always possible, since substantial fusion may be found between adjacent vastii (Willan *et al.* 1990). Based on cadaveric dissection, 57 of 75 quadriceps muscles showed fusion between the lateral and deep vastii (VL and VI, respectively) at more than 50% of the entire length of the muscle (Willan *et al.* 1990). In the present study, the proximal axial MR scans typically showed a lack of distinct fascial boundaries between the lateral and deep vastii (postero-laterally) and between the medial and deep vastii (antero-medially) (Fig. 3). Consequently, pre- and post-training muscle CSA was identified along the perimeter of the common muscle fascia.

Maximal quadriceps strength

Maximal isometric quadriceps muscle strength was measured as maximal isometric knee extension moment exerted at 70 deg knee joint flexion (KinCom, Kinetic Communicator, Chattecx Corp., Chattanooga, TN, USA). Subjects were seated 10 deg reclined in a rigid chair and firmly strapped at the hip and distal thigh. The rotational axis of the dynamometer was aligned to the lateral femoral epicondyle of the subject and the lower leg was attached to the dynamometer lever arm 2 cm above the lateral malleolus. Three successive trials were performed, each lasting 2 s and separated by a minimum of 45 s of rest. All recorded moment-signals were corrected for the effect of gravity (Aagaard *et al.* 1995). The maximal knee extension moment was identified in each trial and the highest value was accepted as maximal quadriceps strength.

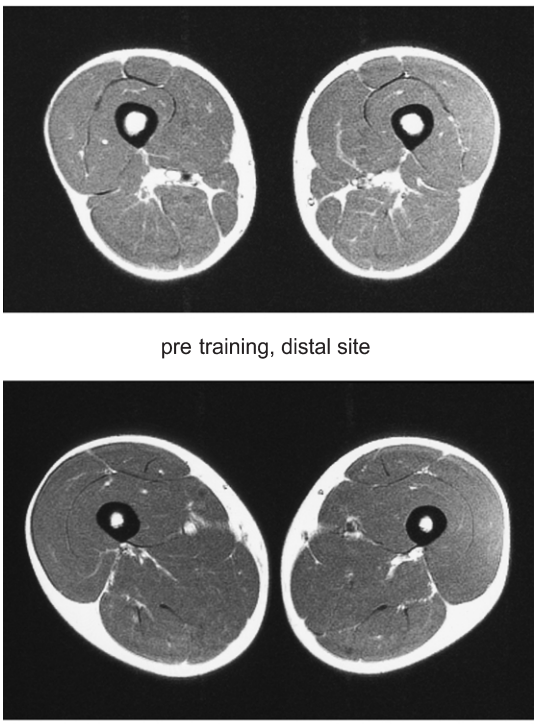

Figure 3

Axial MRI images of the thigh obtained at 50% femur length (proximal slice, bottom panel) and 30% femur length (distal slice, top panel). Axial images were obtained at 20, 30, 40, 50, 60, 70 and 80% femur length, before and after the period of training. Quadriceps femoris muscle volume was calculated by stacking of successive axial images.

Resistance training

Details of the training regime have been reported previously (Andersen & Aagaard, 2000). In brief, progressive heavy-resistance strength training was performed for 14 weeks in a total of 38 sessions. All training was surveyed and supervised by the authors of the study. Training loads ranged between 3 and 10 repetion maximum (RM), except for the first 10 days (4 sessions) where lower loadings were used (10–12 RM). Very heavy loadings (4–6 RM) and an increased number of sets (ensuring unchanged total work load) were used in the final 4 weeks of the study. Obligatory leg training exercises were hack squats, incline leg press, isolated knee extension, hamstring curls and calf raises. Four (weeks 1–10) or five (weeks 11–14) sets were performed for each exercise.

Statistics

Pre- to post-training changes in muscle fibre area (type I, type II and average I+II) and muscle fibre composition (proportion of type I and II MHC isoforms) were evaluated by using the Friedman two-way analysis of variance by ranks for multiple related samples (Conover, 1980). Changes in VL fibre pennation angle and maximal muscle strength were evaluated by using the Wilcoxon signed rank test for paired samples (Conover, 1980). Linear regression analysis was performed using the Pearson product-moment relation. Multifactor regression analysis was performed on selected variables. Spearman's rho (r_s) was determined to test the presence of any rank-order association between variables. A 0.05 level of statistical significance (two-tailed) was used.

RESULTS

Changes in VL muscle fibre pennation angle

VL fibre pennation angle increased pre- to post-training, from 8.0 ± 0.4 to 10.7 ± 0.6 deg ($P < 0.01$; Fig. 4), corresponding to a relative change of 35.5 ± 8.3%.

Changes in muscle fibre CSA

Average muscle CSA_{fibre} increased pre- to post-training, from 3754 ± 271 to 4238 ± 202 μm^2 ($P < 0.001$; Fig. 5*A*), corresponding to a relative change of 15.5 ± 5.1%. For the type I fibres the change in CSA_{fibre} was not statistically significant; 3582 ± 293 before training and 3910 ± 216 μm^2 after training ($P = 0.07$; Fig. 5*B*). In contrast, type II CSA_{fibre} increased with training from 3952 ± 290 to 4572 ± 243 μm^2 ($P < 0.001$; Fig. 5*C*), which corresponded to a relative change of 18.4 ± 5.6%. Prior to training CSA_{fibre} did not differ between fibre types ($P > 0.05$). Following the period of training, however, greater CSA_{fibre} was observed for the type II fibres as compared to the type I fibres ($P < 0.001$).

Changes in anatomical muscle CSA and volume

Anatomical quadriceps CSA obtained at mid-femur increased from 77.5 ± 3.0 to 85.0 ± 2.7 cm^2 following the period of resistance training ($\pm$ S.E.M., $P < 0.001$; Fig. 6). Averaged between subjects this corresponded to a relative change of 10.2 ± 2.2%. Likewise, quadriceps volume

increased from 1676 ± 63 to 1841 ± 57 cm^3 ($P < 0.001$) (Fig. 7), corresponding to an average relative change of 10.3 ± 2.2 %.

Changes in MHC composition

Muscle fibre type composition remained unaltered with training as revealed by no change in myosin heavy chain (MHC) isoform distribution: percentage MHC I was 45.2 ± 3.1 and 48.4 ± 3.1 ($P > 0.05$) and percentage MHC II was 54.8 ± 3.0 and 51.6 ± 3.2 ($P > 0.05$) pre- and post-training. Individual subject range in MHC isoform composition was 26.5–58.3 % MHC I, 41.7–73.5 % MHC II (pre-training) and 31.9–65.3 % MHC I, 34.7–68.1 % MHC II (post-training).

Changes in maximal muscle strength

Maximal quadriceps strength increased 16 % from 282.6 ± 11.7 to 327.0 ± 12.4 N m following training ($P < 0.01$; Fig. 8), corresponding to a relative change of 16.2 ± 3.0 %.

Correlation analysis

To eliminate the influence of inter-individual differences in body size, correlation analysis was performed on CSA and volume data, which were normalized to femur length raised to the second and third power, respectively. Identical scaling procedures have been employed in previous studies (Kawakami *et al.* 1993; Kanehisa *et al.* 1994; Ichinose *et al.* 1998).

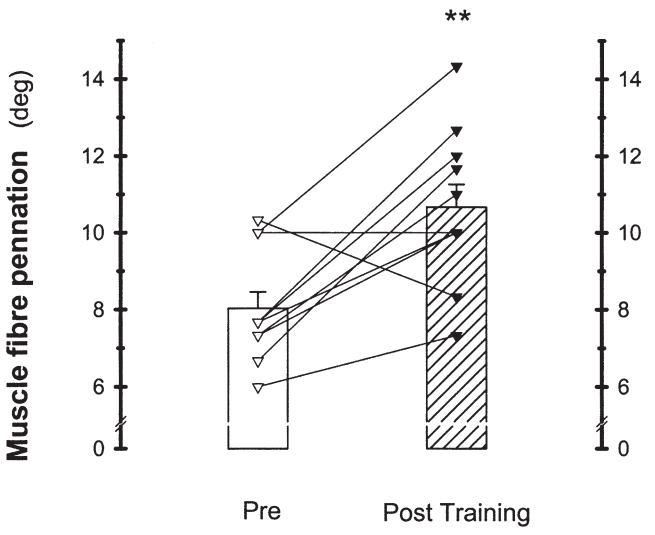

Figure 4

Muscle fibre pennation angle obtained in vastus lateralis at 50 % femur length by use of ultrasound sonography imaging, before and after the period of training. Open symbols and column show pre-training individual values and group mean value, respectively, and S.E.M. is indicated by error bars. Closed symbols and hatched column show post-training values. Pre- to post-training differences, ** $P < 0.001$.

Muscle CSA and volume were unrelated to muscle fibre CSA (CSA_{fibre}) ($P > 0.05$). In contrast, a positive relationship was observed between θ_p and quadriceps volume prior to training ($r = 0.622$, $P < 0.05$). When θ_p was combined with CSA_{fibre} in a multiple regression model the relationship to quadriceps volume was improved ($R = 0.728$, $P < 0.05$).

Pre-to post-training increases in CSA_{fibre} were positively related to increases in quadriceps volume ($r = 0.749$, $r_s = 0.755$; $P < 0.01$) and CSA ($r = 0.580$, $r_s = 0.564$; $P = 0.05$).

DISCUSSION

The present study was the first to employ simultaneous measurements of muscle fibre pennation angle (ultrasound imaging), macroscopic muscle dimensions (MRI) and single muscle fibre dimensions (biopsy sampling) to address the change in muscle morphology, architecture and contractile function induced by intense resistance training. Based on these measurements significant alterations were demonstrated in response to 14 weeks of heavy-resistance strength training, as shown by increases in anatomical CSA and volume, increase in physiological CSA of single muscle fibres, increased VL muscle fibre pennation angle and increase in maximal contractile muscle strength. The main and novel findings were (i) that quadriceps muscle (VL) fibre pennation angle increased with training and (ii) that this allowed physiological muscle CSA and thereby maximal force-generating capacity to increase significantly more (+16 %) than anatomical muscle CSA and volume (+10 %).

Maximal muscle strength

An average relative increase of 16 % in maximal isometric quadriceps strength was observed following the period of resistance training (Fig. 8). Comparable changes (20–23 %) were seen for the increase in maximal dynamic muscle strength as evaluated using isokinetic dynamometry (Aagaard *et al.* 2000*b*). Previous studies have demonstrated similar changes in maximal quadriceps muscle strength following intensive heavy-resistance strength training (Häkkinen & Komi, 1983; Narici *et al.* 1989, 1996*b*; Colliander & Tesch, 1990; Aagaard *et al.* 1996).

VL muscle fibre pennation angle

Resistance training resulted in a marked increase in VL fibre pennation angle (Fig. 4). Prior to training, VL fibre pennation angle corresponded closely to the 7.9 deg reported earlier for the VL muscle using similar recording conditions (i.e. 90 deg knee joint angle and images taken at 50 % femur length; Rutherford & Jones 1992). Steeper pennation angles have been reported in conditions of shortened muscle length, i.e. during full knee extension (18 deg, Fukunaga *et al.* 1997; 17.1 deg, Narici *et al.* 1992; 11–23 deg, Henriksson-Larsén *et al.* 1992). In addition, contraction of the muscle will affect the degree of muscle fibre angulation, especially when the quadriceps muscle is

shortened, as manifested by a marked difference in θ_p between the relaxed and the contracted state at full knee joint extension (18 deg *vs.* 21 deg, respectively; Fukunaga *et al.* 1997). At longer muscle length, i.e. in 90 deg knee joint flexion, this difference in angular pennation is greatly reduced ($\Delta\theta_p = 0.8$–1.0 deg; Fukunaga *et al.* 1997). Thus, fibre pennation measurements at flexed knee joint positions, as performed in the present study, are likely to be close to those that would be obtained during active muscle contraction. Interestingly, Fukunaga *et al.* (1997) reported surprisingly steep fibre pennation angles of 14 deg for the vastus lateralis muscle at 90 deg knee flexion. It is possible that this discrepancy could be explained by relatively smaller limb dimensions in their subjects, which in turn may be associated with greater angles of muscle fibre pennation. This possibility was partly supported by the findings of the present study, since an inverse relationship was observed between femur length and VL muscle fibre pennation angle ($r = -0.493$; $P < 0.05$).

The greater anatomical muscle CSA and steeper muscle fibre pennation angles of the triceps brachii in body-builders compared to untrained subjects (Kawakami *et al.* 1993) suggest that the muscle hypertrophy induced by resistance training may be associated with an increase in fibre pennation angles. This was confirmed in a longitudinal study by Kawakami *et al.* (1995) who reported a significant increase in muscle fibre pennation angle from 16.5 to 21.3 deg in the triceps brachii muscle in response to 16 weeks of resistance training. In contrast, no increase in fibre pennation angle was observed for the quadriceps muscle (VL) in response to 12 weeks of resistance training despite the fact that

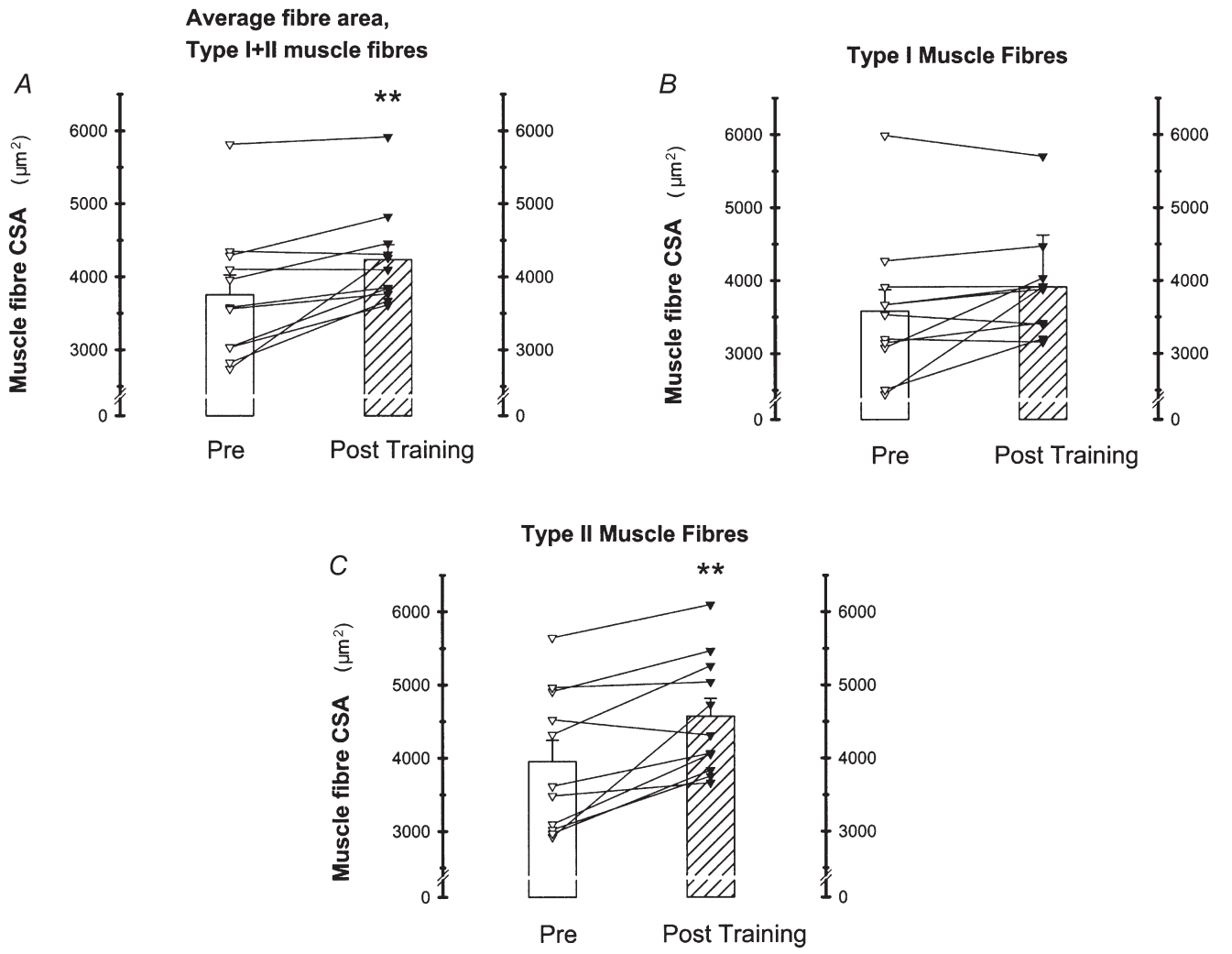

Figure 5.

Single muscle fibre cross-sectional area, (CSA), before and after the period of training. *A*, average muscle fibre CSA, *B*, type I fibre CSA, *C*, type II fibre CSA. CSA_{fibre} was measured in biopsy samples obtained from the vastus lateralis muscle. Open symbols/column show pre-training individual values and group mean value, respectively, and S.E.M. is indicated by error bars. Filled symbols and the hatched column show post-training values. Pre- to post-training differences: ** $P < 0.001$. A trend towards an increase in type I fibre CSA was observed post training ($P = 0.074$).

anatomical CSA and maximal isometric strength increased 5% and 13%, respectively (Rutherford & Jones, 1992). This lack of increase in pennation angle may have been due to a relatively modest total training load performed by their subjects, corresponding to about one-third of the total load performed in the present study. Alternatively, based on the geometric parallelogram models (Alexander & Vernon, 1975), Rutherford & Jones (1992) estimated that the 13% increase in maximal quadriceps strength along with a 5% increase in anatomical CSA observed in their study could be explained by a 0.6 deg increase in fibre pennation angle, which may not have been detectable (Rutherford & Jones, 1992).

Muscle fibre CSA

Average muscle fibre cross-sectional area increased 16% following training (Fig. 5*A*). When separated into fibre types, type II fibre area increased 18% (Fig. 5*C*), whereas the change in type I fibre area did not reach statistical significance ($P = 0.07$; Fig. 5*B*), indicating a more readily evoked hypertrophy response for the type II fibres. These relative changes are in agreement with those previously observed with heavy-resistance strength training regimes (Hather *et al.* 1991; Staron *et al.* 1994; Volek *et al.* 1999). Comparable evidence of a preferential or more pronounced type II fibre hypertrophy in response to heavy resistance training has been reported previously (e.g. Hather *et al.* 1991; Roman *et al.* 1993; Volek *et al.* 1999; Kadi *et al.* 1999; Andersen & Aagaard, 2000; Hortobagyi *et al.* 2000). Apparently, type II muscle fibres seem to possess a greater adaptive responsiveness to the intense muscle-loading regimes associated with heavy-resistance training. In contrast to the above findings, few studies have been unable to demonstrate muscle fibre hypertrophy in response to strength training (Colliander & Tesch, 1990; Narici *et al.* 1996). Probably this was due, at least in part, to the biological and statistical variability of the specific muscle biopsy procedures employed.

Anatomical muscle CSA and volume

The present study demonstrated an increase in anatomical quadriceps CSA with training (Fig. 6). In previous reports quadriceps CSA obtained at 50% femur length have ranged from 68 to 88 cm^2 (Narici *et al.* 1989, 1996*b*; Rutherford & Jones, 1992; Kanehisa *et al.* 1994). In terms of changes evoked by resistance training, moderate increases (5–12%) in anatomical CSA have been observed following 10–15 weeks of resistance training (Narici *et al.* 1989; Rutherford & Jones, 1992; Higbie *et al.* 1996; Häkkinen *et al.* 1998), whereas somewhat greater changes (13%) were reported following more prolonged periods of training (26 weeks; Narici *et al.* 1996*b*). In comparison, 14 weeks of resistance training resulted in a 10% increase in anatomical CSA in the present study.

Prior to training quadriceps muscle volume was 1676 cm^3 ± 63 cm^3, S.E.M. (Fig. 7). After the period of resistance training muscle volume increased to 1841 ± 57 cm^3 (S.E.M.). Compared to these data, slightly greater volumes have been reported for habitually active male subjects in previous studies also based on multiple axial MRI imaging (i.e. 1823 ± 150 cm^3, S.E.M.; Narici *et al.* 1992). The apparent discrepancy between these results (~10%)

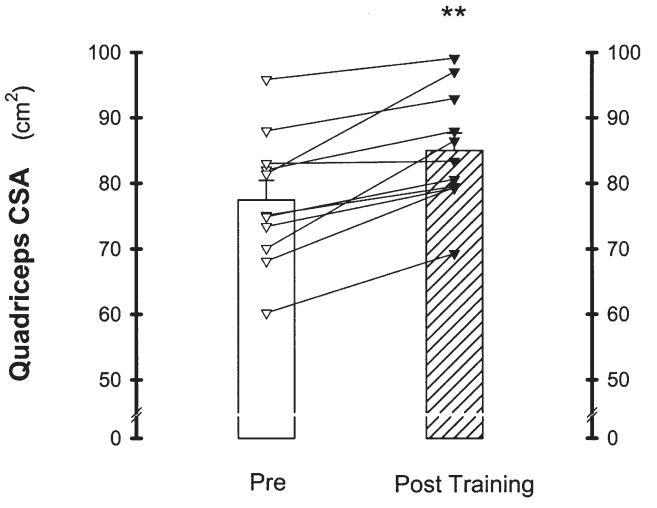

Figure 6

Anatomical quadriceps muscle CSA measured at 50% femur length by use of MRI, before and after the period of training. Open symbols show individual values, open column shows group mean value prior to training, and S.E.M. is indicated by error bars. Filled symbols and hatched column show individual values and group mean value, respectively, following training ($n = 11$). Pre- to post-training differences: ** $P < 0.001$.

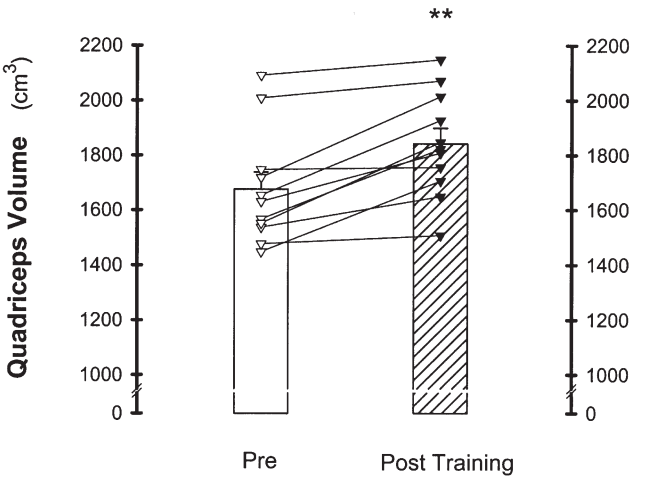

Figure 7

Quadriceps muscle volume measured by MRI. Open symbols and column show pre-training individual values and group mean value, respectively, and S.E.M. is indicated by error bars. Filled symbols and hatched column show post training values. Pre- to post-training differences: ** $P < 0.001$.

likely resides from inter-study differences in subject age, size and training status, which obviously will have a strong influence on muscle CSA and volume. It is interesting to note that the above discrepancy also was apparent at the muscle fibre level, as pre-training muscle fibre areas were ~10 % lower than those frequently observed for physically active young males (Hather *et al.* 1991; Staron *et al.* 1994).

Relationships between measures of muscle morphology and architecture

It has previously been demonstrated that muscle morphology evaluated at the microscopic level (i.e. MHC isoform composition) can be related to *in vivo* mechanical muscle function at the macroscopic level (Harridge *et al.* 1995; Aagaard & Andersen, 1998). On the other hand, others have been unable to find any association between microscopic and macroscopic measures of muscle morphology. Thus, no relationship was observed between single muscle fibre cross-sectional area (CSA_{fibre}) and total anatomical muscle CSA in a study by Henriksson-Larsén *et al.* (1992). Similar to these findings, the present study did not find any correlation between CSA_{fibre} and anatomical quadriceps CSA or volume. In contrast, relationships between macroscopic measures of muscle morphology and architecture were found to exist; prior to training a correlation between VL fibre pennation angle (θ_p) and muscle volume was observed ($r = 0.622$). This association became stronger when θ_p and CSA_{fibre} were combined using multifactor regression analysis ($R = 0.728$).

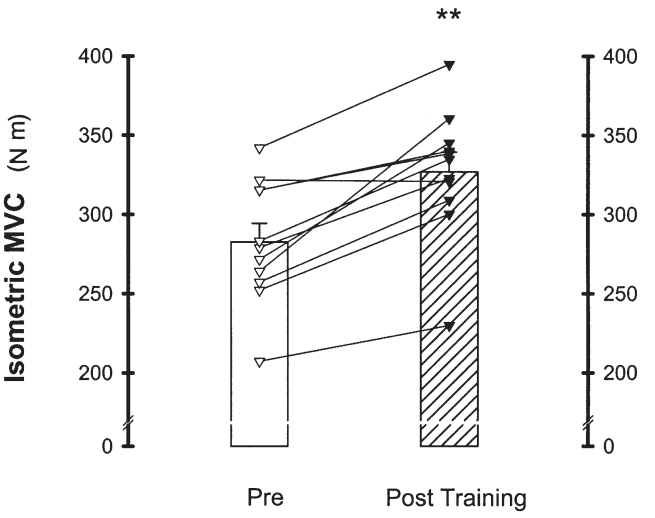

Figure 8

Maximal isometric quadriceps strength (MVC), before and after training. Open symbols and column show pre-training individual values and group mean value, respectively, and S.E.M. is indicated by error bars. Filled symbols and hatched column show post-training values. Pre- to post-training differences: $^{**}P < 0.001$.

Similar relationships between muscle fibre pennation angle and macroscopic measures of muscle size have been reported previously, in terms of positive correlations between VL fibre pennation angle and anatomical CSA in the quadriceps muscle ($r = 0.63$, Rutherford & Jones, 1992) and correlations between fibre pennation angle and muscle thickness in the triceps brachii ($r = 0.83$–0.88, Kawakami *et al.* 1993; $r = 0.91$–0.93, Kawakami *et al.* 1995; $r = 0.72$, Ichinose *et al.* 1998).

Despite the lack of any association between CSA_{fibre} and anatomical quadriceps CSA (or volume) in the present study, the *change* in CSA_{fibre} with training was related to the *change* in quadriceps volume and CSA. Taken together these data suggest that the different morphological adaptation responses evoked by heavy resistance-training are to some extent interlinked. At the same time, however, correlations were not very strong ($r = 0.58$–0.76, $r^2 = 0.33$–0.58) which may indicate that no simple relationship exists.

Disproportionate changes in fibre CSA and anatomical muscle CSA

In the present study a mismatch was observed between the increase in muscle fibre CSA (+16 %) and anatomical CSA or volume (+10 %). Since steeper muscle fibre pennation angle allows for a greater physiological fibre area for a given volume of muscle, the post-training increase in VL muscle fibre pennation angle alone may explain the present observation of disproportionate changes in physiological *versus* anatomical muscle CSA. In fact, previous studies that have examined the human quadriceps femoris muscle by combined muscle biopsy sampling and macroscopic muscle imaging techniques (MRI, CT) also have demonstrated the increase in muscle fibre CSA to be greater than that of anatomical muscle CSA with resistance training (Frontera *et al.* 1988; Hakkinen *et al.* 1998; Esmarck *et al.* 2001). Unfortunately, fibre pennation angle was not obtained in any of these studies. Alternatively, the above findings could be explained by a change in the ratio of contractile to non-contractile muscle tissue. Against this notion, however, speaks the fact that the relative proportion of non-contractile tissue appears to remain unchanged in response to resistance training (Mikesky *et al.* 1991; Wang *et al.* 1993; Roman *et al.* 1993).

Implications for specific muscle tension

It is highly difficult to provide a precise measure of the total physiological muscle fibre area (CSA_{phys}) of pennate muscle, *in vivo*. However, an estimate of CSA_{phys} can be obtained by combining data from the present and previous studies, thereby allowing maximal contractile force (F) per unit physiological muscle area (specific tension: F_{fibres}/CSA_{phys}) to be estimated. Several models have been proposed for the estimation of total CSA_{phys} (Alexander & Vernon, 1975; Powell *et al.* 1984; Narici *et*

al. 1992; Kawakami *et al.* 1993, 1994). As suggested by Edgerton *et al.* (Wickiewicz *et al.* 1983, Powell *et al.* 1984, Fukunaga *et al.* 1996), CSA_{phys} can be found from muscle volume, fibre length and fibre pennation angle. In the present calculations a muscle fibre length of 7 cm (Wickiewicz *et al.* 1983, 1984) was used in combination with the muscle volumes and pennation angles obtained experimentally. Total muscle fibre force (F_{fibres}) was calculated from $F_{quad}/\cos(\theta_p)$, where quadriceps force (F_{quad}) was estimated from the measurement of maximal knee extension moment, assuming a 4.0 cm moment arm for the patella tendon (Wickiewicz *et al.* 1984; Marshall *et al.* 1990) and a ratio of patella tendon force to quadriceps tendon force of 0.70 at 70 deg knee flexion (Nisell *et al.* 1989). As a result, values of 42.6 and 45.3 N cm^{-3} were derived for maximal specific muscle tension before and after the period of strength training, respectively. It is important to notice, however, that the above estimations are highly sensitive to even small changes in muscle fibre length. For example, a 5% change in muscle fibre length (~0.4 cm) would result in a specific muscle tension of 42.5 N cm^{-3} post-training. Values of 16–47 N cm^{-3} have previously been reported for the maximal specific muscle tension of mammalian muscle (Saltin & Gollnick, 1981). For human skeletal muscle, values of 11–32 and 24–47 N cm^{-3} were observed for the plantar flexors and extensors, respectively (Fukunaga *et al.* 1996). Interestingly, substantially higher values of 65–75 N cm^{-3} have been reported for the elbow flexors and extensors (Kawakami *et al.* 1994, 1993). Compared to the present data, a substantially lower value of 25 N cm^{-3} previously was found for the quadriceps femoris muscle (Narici *et al.* 1992). However, in their study muscle fibre length and pennation angle were obtained at full knee joint extension, i.e. at highly reduced fibre lengths and steep fibre pennation angles (thereby overestimating CSA_{phys}), whereas maximal quadriceps contraction force was recorded in a rather flexed knee joint position (65 deg; position of maximal force generation) characterized by long fibre lengths and reduced pennation angle.

Although the maximal contractile force per physiological CSA appears to be fairly similar among different muscles in various animal species (Close, 1972), the above data seem to suggest that a considerable variation may exist for human skeletal muscle. However, muscle fibre forces may not summate according to the simplified geometric arrangement assumed by most models, as considerable contractile force can be transmitted laterally via the interfibrillar matrix (Street, 1983; Trotter, 1993). Thus, it is possible that the force-generating capacity of the sarcomeres is relatively uniform among various human skeletal muscles, whereas transmission of sarcomere force to the aponeurosis-tendon may differ considerably due to differences in muscle architecture, thereby giving rise to marked differences in force per CSA (Fukunaga *et al.* 1996).

Conclusions

Significant increases were observed for anatomical CSA and volume of the quadriceps muscle as well as for individual muscle fibre area in response to 14 weeks of heavy-resistance training. Training-induced alterations in quadriceps muscle architecture were demonstrated, as manifested by an increase in VL muscle fibre pennation angle. This increase in fibre pennation angle allowed physiological CSA, and thereby maximal force-generating capacity, to increase significantly more than anatomical CSA and volume, as supported by a 16% change in CSA_{fibre} and maximal muscle strength together with a only 10% change in muscle CSA and volume. Consequently, measurements of anatomical muscle CSA or volume using macroscopic imaging techniques (e.g. MRI and CT) cannot replace the information obtained by assessing physiological muscle fibre area via biopsy sampling, or vice versa. From the present data it was also clear that the adaptive plasticity of muscle fibre pennation angle should be taken into account when examining the training-induced change in maximal muscle strength, *in vivo*. Prior to training a positive relationship was found to exist between quadriceps muscle volume and VL muscle fibre pennation angle. Furthermore, training-induced changes in quadriceps muscle size were associated with changes in single muscle fibre size. Collectively, the present data suggest that the morphology, architecture and contractile capacity of human pennate muscle are interrelated. This interaction seems to include the specific adaptation responses evoked by intensive resistance training.

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