

Human quadriceps cross-sectional area, torque and neural activation during 6 months strength training

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Quadriceps muscle and fibre cross-sectional areas (CSA), torque and neural activation were studied in seven healthy males during 6 months of weight training on alternate days with six series of eight unilateral leg extensions at 80% of one repetition maximum. After training, the quadriceps cross-sectional area increased by $18.8 \pm 7.2\%$ ($P < 0.001$) and $19.3 \pm 6.7\%$ ($P < 0.001$) in the distal and proximal regions respectively, and by $13.0 \pm 7.2\%$ ($P < 0.001$) in the central region of the muscle. Hypertrophy was significantly different between and within the four constituents of the quadriceps. Biopsies of the vastus lateralis at mid-thigh did not show any increase in mean fibre cross-sectional area. Maximum isometric voluntary torque increased by $29.6 \pm 7.9\%$ – $21.1 \pm 8.6\%$ ($P < 0.01$ – 0.05) between 100° and 160° of knee extension, but no change in the optimum angle (110° – 120°) for torque generation was found. A $12.0 \pm 10.8\%$ ($P < 0.02$) increase in torque per unit area together with a right shift in the IEMG-torque relation and no change in maximum IEMG were observed. Time to peak isometric torque decreased by 45.8% ($P < 0.03$) but no change in time to maximum IEMG was observed. In conclusion, strength training of the quadriceps results in a variable hypertrophy of its components without affecting its angle-torque relation. The increase in torque per unit area, in the absence of changes in IEMG, may indicate changes in muscle architecture. An increase in muscle-tendon stiffness may account for the decrease in time to peak torque.

Keywords EMG, exercise, hypertrophy, muscle, resistance training.

In most previous strength training studies human muscle hypertrophy has been described as an overall increase in the anatomical cross-sectional area (CSA) of an entire muscle group. Two recent studies (Narici *et al.* 1989, Housh *et al.* 1992) have also shown significant differences between the hypertrophy of the constituents of a muscle group as a result of strength training. An intriguing aspect of preferential muscle hypertrophy is its functional consequence on the angle-force relation. The angle-force curve of a muscle group is actually a composite curve consisting of the individual length-force relation of each of its con-

stituents (Gans & Bock 1965). Differences in the extent of hypertrophy of these constituents could therefore modify both the shape of the angle-force relation of a muscle group as well as the optimum angle at which maximum force is generated (Jones & Rutherford 1987). An even more fascinating aspect about hypertrophy is the finding that this process is uneven not only between the constituents of a muscle group but also along the belly of each individual muscle (Narici *et al.* 1989). The underlying causes for this phenomenon, whether architectural, biochemical or both are matter of discussion. In this context, it is

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noteworthy that hypertrophy of the rabbit tibialis anterior, induced by overload, features a greater increase in protein synthesis in the distal than in the central and proximal regions of this muscle (Goldspink *et al.* 1991).

Strength training has also been shown to lead to an increase in the force per unit CSA of the muscle. This effect has been attributed either to an increase in neural drive (Moritani & de Vries 1979, Häkkinen & Komi 1983, Narici *et al.* 1989) or to an actual increase in muscle specific tension due to a denser packing of muscle filaments, which might account for the observed increase in muscle radiological density (Jones & Rutherford 1987). A strategy to attain a denser packing of contractile tissue along the tendon, would be to increase the angle of pennation of muscle fibres (Gollinck *et al.* 1981). The recent findings of Kawakami *et al.* (1993), showing a greater fibre pennation angle in hypertrophied compared with normal human triceps, adds support to this hypothesis.

Although an increase in maximal neural activation with strength training has been reported by several authors (Moritani & de Vries 1979, Häkkinen & Komi 1983, Narici *et al.* 1989) this is not always the rule (Häkkinen *et al.* 1985, Garfinkel & Cafarelli 1992) and extremely well-motivated subjects often display full motor unit activation even before training (Jones & Rutherford 1987). Changes in motor unit activation during strength training seem therefore interesting to pursue.

Fibre hypertrophy is regarded as the main cause for the increase in muscle mass with training and is typically greater for fast- than for slow-twitch muscle fibres (Thorstensson 1976, MacDougall *et al.* 1979, Häkkinen *et al.* 1981, Häkkinen *et al.* 1985, Tesch *et al.* 1985). It has been suggested that there may be an optimum or ceiling size for hypertrophy of individual fibres above which any further increase in size may be obtained by fibre hyperplasia (MacDougall *et al.* 1982, Tesch & Larsson 1982). No direct evidence for humans exists to support this contention; it is intriguing, however, that swimmers and kayakers display hypertrophied deltoids despite surprisingly small fibre diameters (Nygaard & Nielsen 1978, Tesch & Karlsson 1985) and fibre numbers per motor unit (Larsson & Tesch 1986). It may be of interest, therefore, to compare both the degree and the time course of the hypertrophy of individual muscle fibres to those of the overall muscle mass.

Strength training has been shown to reduce the time to peak force and to increase the rate of force development (Häkkinen *et al.* 1981, 1985a, b). Therefore, in training protocols designed to improve muscle strength it is of interest, not only to analyse the effect on absolute muscle force, but also the effect on the

force-time characteristics of the contraction. As a matter of fact, rapid force production is an essential feature for fast performance tasks such as running or jumping in which each movement may last several hundred milliseconds.

With these considerations in mind we decided to conduct a 6-month strength training study on the human quadriceps with the following aims: (1) to gain further insight into the phenomenon of preferential hypertrophy within a muscle group as well as on regional differences along the belly of each constituent and (2) to investigate (a) the effect of preferential muscle hypertrophy on the quadriceps angle-torque relation, (b) possible relations between changes in torque and in neural activation (IEMG), (c) possible variations in the torque per cross-sectional area, (d) changes in muscle fibre CSA in relation to those of muscle CSA, and (e) the torque-time features of the quadriceps throughout training.

METHODS

Subjects

Seven healthy males (age 29.0 ± 3.6 years, height 1.82 ± 0.08 m, body mass 77.9 ± 10.4 kg, means \pm SD) volunteered, after giving informed consent, for this study. The risks and discomfort concerning the muscle needle biopsies were fully explained and the study was approved by the local Ethical Committee. At the time of the investigation the subjects were practising sports (soccer, jogging, swimming) at recreational level, no more than twice a week.

Training protocol

Subjects trained every other day for 6 months. Training consisted of six series of eight unilateral leg extensions carried out separately for each leg at an intensity of 80% of the individual one repetition maximum (1RM). This combination of loading and repetitions has been shown to be effective in increasing muscle size and strength (MacDougall 1986). Three minutes of rest were allowed between each set. The 80% 1RM was adjusted each week to match for the progressive increase in muscle strength. Training was carried out on a variable resistance leg extension machine (DAVID 200 Leg Extension, Vantaa, Finland) consisting of a seat, on a slight negative slope, with back support and hip fixation connected at the back to a vertical, low friction rail along which stacks of weights were lifted via a system of low friction pulleys and steel cables connected via a lever to an adjustable horizontal push bar in contact with

the leg at the level of the ankle. The movement only involved the extension of the knee joint and covered a tibio-femoral angle of 100° (from 80° to 180° , full knee extension). The exercise consisted of both a lifting phase and a lowering phase of the training weight. In the first series of eight repetitions the concentric phase lasted on average 1200 ms and the eccentric phase 1400 ms and the set of eight contractions lasted about 21 s with no rest interval in-between. In the last series, the set of eight contractions lasted, because of fatigue, about 27 s, the concentric being on average 1300 ms and the eccentric phase 2100 ms. By the end of the last series subjects could just about manage to complete full knee extension against the training load.

Measurements

All measurements concerned the knee extensor muscles and were carried out on the dominant leg only (right for all but one subject). Two separate practice sessions were introduced 2 weeks prior the baseline measurements.

Cross-sectional area

Measurement of quadriceps CSA was carried out before the start and every 2 months during training from nuclear magnetic resonance imaging (MRI) scans (1.5 Tesla, Gyroscan S15, Philips, the Netherlands) with a magnetic field resonance frequency for the protons of 63.86 MHz. Spin-echo, T1 weighted, multislice sequences with a slice thickness of 10 mm (axial scans) and 6 mm (coronal scans) were utilized. The length of the femur (Lf), taken as the distance from the upper border of the femur head to the lower border of the lateral femoral condyle, was measured on a coronal plane. Subsequently, seven axial scans interspaced by a distance of $1/10$ Lf were obtained from the level $2/10$ Lf (proximal to the greater trochanter) to $8/10$ Lf (proximal to the knee). To ensure the same location of the axial slices in successive sessions, the isocentre was positioned at $5/10$ Lf. Great care was taken to reproduce the same, individual femur length each time using the appropriate anatomical landmarks. The slice thickness, repetition time and echo time were 0.01 m, 0.496 s (fast feed echo) and 0.008 s, respectively, for the axial scans, and 0.007 m, 0.262 s, 0.015 s for the coronal scans. For each axial scan, CSA computation was carried out on the quadriceps as a whole and, individually, on the vastus lateralis (VL), vastus medialis (VM), vastus intermedius (VI) and on the rectus femoris (RF). Each contour was digitized with

a graphic tablet (Calcomp 2500, resolution 200 points per inch) and displayed on the monitor of a CAD workstation (Olivetti Personal Engineering 28) with a correspondence of one tablet point to one screen pixel. The area was then calculated by a pixel counting routine and by a scale conversion algorithm. The error in this technique, evaluated by digitizing shapes of known areas, was estimated to be 0.6% while the coefficient of variation (CV) for three CSA measurements, repeated on the same subject on 3 different days, was 0.3%. Digitization of muscle contours was carried out manually, a particularly time-consuming process. Therefore, out of the seven axial sections, only the five between $3/10$ and $7/10$ of Lf, were analysed.

Surface electromyographic activity (EMG)

Before the start and at 2 months intervals during training surface EMG of the vastus lateralis muscle of the dominant leg was recorded with a bipolar lead system during both maximal and submaximal isometric voluntary contractions. Two pre-gelled silver/silver chloride electrodes 10 mm in diameter, interelectrode distance 25 mm, were placed at half the distance between the point of attachment of the muscle tendon on the intertrochanteric line of the femur (about 30–40 mm below the greater trochanter) and its motor point (motorpoint-charts, TECA Corporation, Pleasantville, NY, USA). A reference electrode was placed at the wrist. In order to reduce the interelectrode resistance the skin was rubbed with ether and lightly abraded with fine emery paper before application of the electrodes. In all subjects skin resistance was kept below 1500Ω . To ensure the same recording site on successive sessions, an individual map of the thigh was made on acetate paper by marking the position of any moles and small angiomas, with respect to the two electrodes. The electrical activity of the vastus lateralis muscle recorded by the two surface electrodes was conveyed by screened leads to an instrumental amplifier (20 dB) and after further amplification (26 dB) was passed through an upper (10 Hz) and lower (1000 Hz) fourth-order cut-off filters of the electromyograph and stored on tape (RACAL S7, USA). The filtered signal, of frequency band 10–1000 Hz, was subsequently fed back to the electromyograph (Passerini, Italy) and full wave rectified and integrated (IEMG) with a Bessel filter of 10 time constant: this procedure did not introduce any phase shift. The IEMG signal was then sampled for 20 s at 555 Hz with an A/D card mounted on a personal computer (Olivetti PE 28, Italy). Integration of the EMG signal was done by a purposely designed

software over 1 s thus giving a signal in mVs. IEMG measurements repeated in the same subject in 3 separate days presented a coefficient of variation of 7%.

Strength measurements

Measurements of strength were carried out isometrically before the start and every 2 months during training. Subjects sat in an adjustable, straight-backed chair with the pelvis and trunk tightly secured by two velcro straps. A load cell (FGP Instruments, Model FN 3030, France) mounted on the chair frame was connected to a padded metal strap placed around the subject's ankle via a steel cable (3 mm in diameter) which was maintained at right angle to the leg by means of an adjustable pulley system as described by Narici *et al.* (1992). The moment arm (Rs) from centre of the the ankle strap to the head of the fibula was measured with a metal tape during the baseline data collection and reproduced to the nearest mm in successive sessions. The torque (units, Nm) developed by the knee extensors was calculated by multiplying the measured force (units, N) by the moment arm Rs (units, m). The following force and neural activation parameters were investigated.

Isometric maximal voluntary contraction (MVC) torque.

This was measured at 10° intervals from 90 to 160° of knee extension, chosen in a random order (full knee extension = 180°). This range of angles was chosen since it covered most of the ascending and descending force curve of the knee extensors (Narici *et al.* 1988) and overlapped with most of the movement range (80–180°) used in the training protocol. The torque at each joint angle was corrected for gravity as described by Narici *et al.* (1988). Knee angle was measured using an electronic goniometer (Penny and Giles, angle display unit ADU201, U.K.) fixed to the knee joint and aligned with the greater trochanter-knee space-lateral malleolus axis, according to the manufacturer recommendations. To ensure the same goniometer position each time, the sites of the greater trochanter, knee space and lateral malleolus were marked with indelible ink and the respective axis were drawn according to these markings. The knee angle could be visualized on the liquid crystal display of the transducer whose analogue output was stored on tape (RACAL S7, USA) together with the force and IEMG signals. Three MVCs were obtained at each joint angle and only the highest value was retained for analysis. A 3-min rest interval was allowed between each contraction. The subjects were strongly encouraged to produce the maximum possible effort and, having reached the top value, to make a brief all-out effort.

Each subject could monitor the generated torque on the screen of an oscilloscope placed in front and was constantly urged to improve his previous score.

In order to compare the joint angle-torque relation to the joint angle-training load relation, the load cell was connected to the horizontal push-bar used by the subject to lift the weight. The subject was asked to maintain the leg in contact with the bar, without pushing, while the operator lifted manually the bar attached to the load cell maintained normal to the leg. Knee angle was monitored with the goniometer throughout the trial. The outputs of the load cell and joint angles were stored on tape (RACAL S7, USA).

Time to peak torque (TPT), rate of torque development (RFD) and time to maximum EMG (TME).

These were assessed during a maximal isometric contraction carried out as rapidly as possible at a joint angle of 90°. TPT was measured as the time (ms) required to reach 95% of the maximum torque from the onset of the IEMG activity. The RFD was calculated as the maximum slope of torque-time curve. For the TME determination the raw EMG signal was integrated for nine 100 ms periods (0–100, 50–150, 100–200, 150–250, 200–300, 250–350, 300–400, 350–450 and 400–500 ms) from the start of the contraction as described by Häkkinen *et al.* (1985). For both parameters the best performance, i.e. that of shortest duration, was retained for data analysis.

IEMG/Torque relation.

This function was investigated by recording the IEMG activity during isometric contractions at 20, 40, 60, 80 and 100% of the MVC, at the optimum angle for maximum torque generation which, before training, was 110° in three subjects and 120° in four subjects. This range of quadriceps optimum angles are in agreement with those found by Lindahl *et al.* (1969). No other angles were tested since this operation would have required a considerably greater number of contractions likely to induce muscle fatigue. During the test the subject could monitor and grade his own torque to the target level imposed on the screen of an oscilloscope.

IEMG activity during the loading exercise.

To compare the pattern of activation between the four constituents of the quadriceps during the weight lifting exercise, the IEMG activities of the VL, VM and RF (VI not accessible with surface EMG) were recorded while lifting (concentric phase) and lowering (eccentric phase), the load of 80% of 1RM. Each activity was subsequently normalized for that recorded at 1 RM.

Torque/CSA. The torque per unit area (torque/CSA) of the quadriceps was calculated by dividing the

torque at the ankle by a mean value of quadriceps anatomical CSA calculated from 2/10 Lf to 7/10 Lf. This method gives an estimate of the actual specific tension of the knee extensors which is traditionally given by the fibre force component divided by the physiological CSA. This calculation, however, requires measurements of pennation angle, muscle volume, distance between the tendons as well as the mechanical advantage of the system (Narici *et al.* 1992). As none of these architectural parameters were evaluated in this study, it was decided to divide the torque at the ankle by the anatomical CSA of the quadriceps group and was hence expressed in Nm cm^{-2} .

Muscle biopsies. Biopsies of the vastus lateralis muscle of the dominant leg (right in all subjects but one) were taken at mid-thigh using the technique of Bergström (1962). The samples were processed for electron microscopy by fixation in a 6.25% solution of glutaraldehyde and transported in the fixing medium to the laboratory for processing. Morphometry was carried out on cross-sections of four randomly chosen tissue blocks from each biopsy. Fibre cross-sectional areas were estimated at a final $\times 1500$ magnification. Four pictures per block were taken in consecutive frames of slotted grids (type R 100 A, Veco, The Netherlands), yielding over 100 muscle fibres in each biopsy, as described in detail by Zumstein *et al.* (1983). For the morphometric analysis, contact prints of the 35-mm films were projected on a screen fitted with a quadratic grid of lines. Point counting was performed with a grid A100 (100 test points) (Weibel 1979). All stereological variables were estimated according to standard procedures (Weibel 1979).

All subjects agreed to undergo two biopsies, one at time zero and the second after 6 months of training. Four subjects volunteered for an additional biopsy 2 months after the beginning of training.

Statistics. Values are reported as means \pm SD. Two-way repeated analysis of variance (ANOVA) was used to test for differences in the absolute values of the angle-torque data, the cross-sectional areas and the IEMG/torque relation measured before and after 2, 4 and 6 months of training. One way ANOVA was used to test for differences in muscle fibre size measured before and after 2 and 6 months of training. One way ANOVA was also used to test for differences in the IEMG activity of VL, VM and RF in the concentric and eccentric weight lifting phases (see discussion). In the event of significant 'F' values from the ANOVA, post-hoc analysis was carried out with the Scheffé test of critical differences. Differences in TPT, consisting

of single measures repeated only before and after 6 months of training, were tested for significance with the Student's *t*-test. The level of statistical significance was set at $P < 0.05$.

RESULTS

Cross-sectional areas

Maximum CSA of the quadriceps (Q) was found both before and after training at 5/10 of femur length (Figure 1). Mean Q CSA increased significantly after 2 months ($P < 0.0001$) and steadily augmented thereafter. A non-uniform increase in Q CSA along the femur was observed after 6 months training. Indeed significant differences in Q CSA were found between 3/10 Lf and 6/10 Lf ($18.8 \pm 7.2\%$ vs. $13.0 \pm 7.2\%$, $P < 0.05$), between 4/10 Lf and 5/10 Lf ($17.9 \pm 4.2\%$ vs. $13.8 \pm 3.3\%$, $P < 0.05$), between 4/10 and 6/10 ($17.9 \pm 4.2\%$ vs. $13.0 \pm 7.2\%$, $P < 0.05$), and between 4/10 and 7/10 ($17.9 \pm 4.2\%$ vs. $19.3 \pm 6.7\%$, $P < 0.05$). This variable increase in Q CSA, reflected the combined hypertrophy of the four components of this muscle group. Moreover, significant differences in hypertrophy were found between VL, VM, VI and RF at 3/10 and 4/10 Lf (Figure 2). At 3/10 Lf, differences were significant ($P < 0.01$ – 0.05) between all muscles except for VL and VI. At 4/10 Lf the hypertrophic responses of VL vs. VM, VM vs. VI and VI vs. RF were significantly different ($P < 0.05$). In addition, hypertrophy was also not uniform within each muscle (Figure 2). Indeed, comparison of the increase in CSA at the five investigated levels along each muscle showed that certain sites (Figure 2) underwent hypertrophy to a significantly greater extent than others ($P < 0.05$).

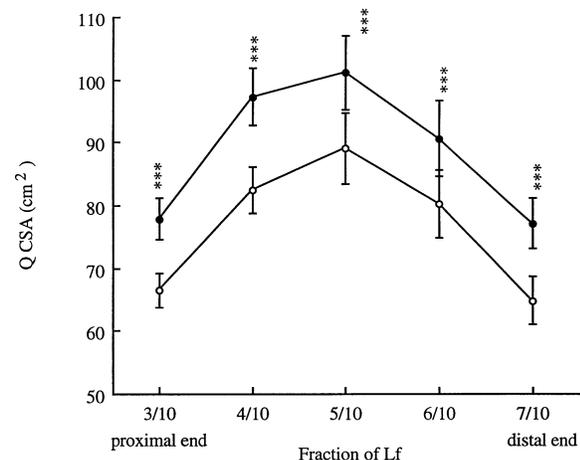


Figure 1 Quadriceps (Q) CSA from 3/10–7/10 of femur length (Lf) before (○) and after 6 months training (●) ($n = 7$, means \pm SD, *** = $P < 0.0001$).

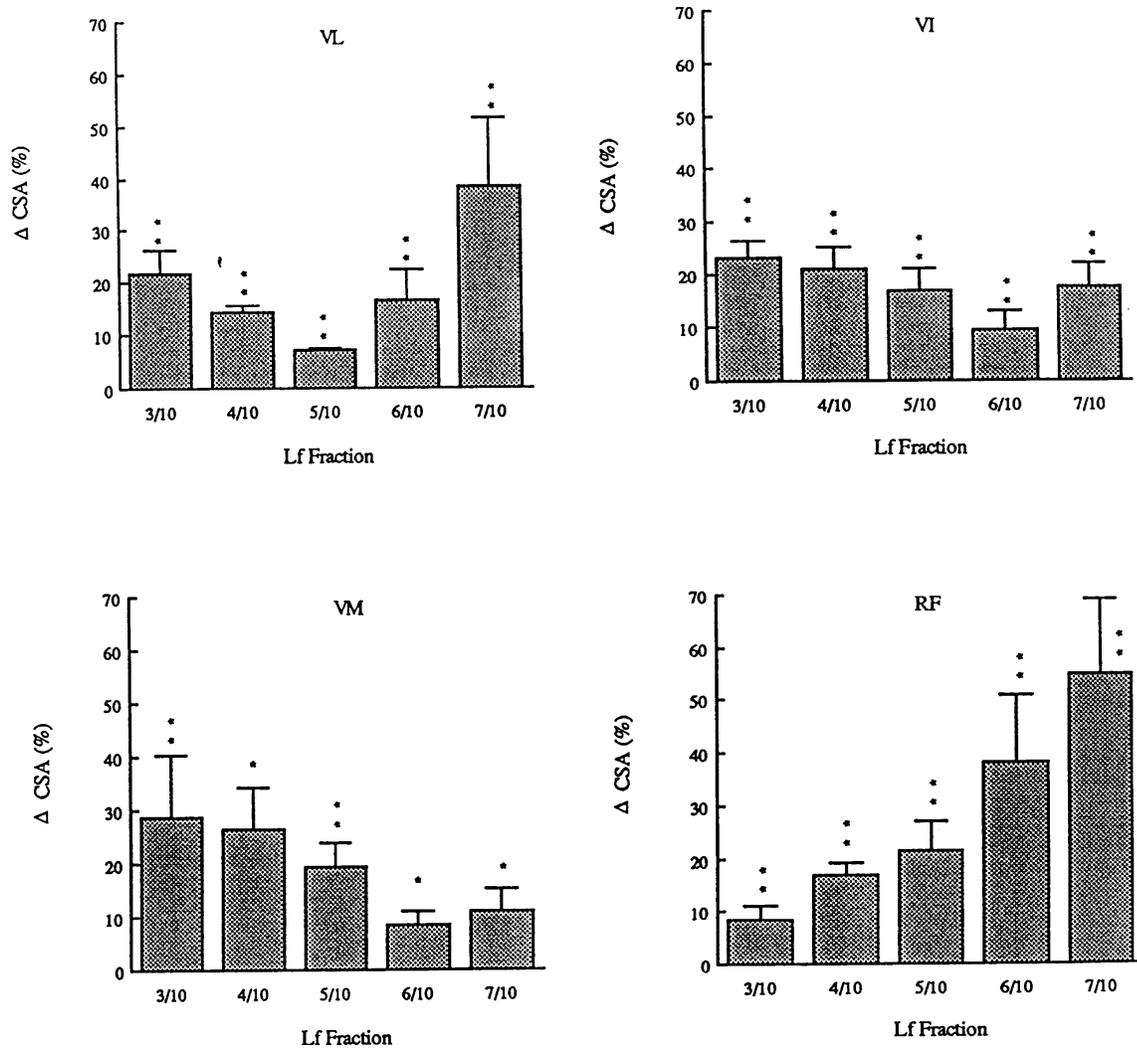


Figure 2 Percentage changes in cross-sectional area (Δ CSA) from 3/10–7/10 femur length for of the vastus lateralis (VL), vastus intermedius (VI), vastus medialis (VM) and rectus femoris (RF) muscles after 6 months strength training. ($n = 7$, means \pm SD, * = $P < 0.05$, ** = $P < 0.01$; asterisks denote statistical significance of differences between before and after training.)

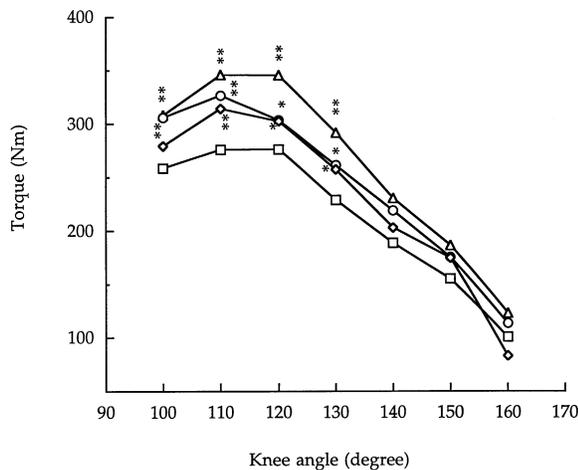


Figure 3 Quadriceps angle-torque relation before (\square) and at 2 (\diamond), 4 (\circ) and 6 months (\triangle) of training ($n = 7$, means \pm SD, * = $P < 0.05$, ** = $P < 0.01$).

Muscle fibre size

Mean fibre area of the VL at the investigated site (5/10 Lf) was $3436 \pm 645 \mu\text{m}^2$ before training and $3501 \pm 931 \mu\text{m}^2$ after 6 months training; no significant difference existed between the two measurements.

Angle-torque relationship

The isometric angle-torque (A-T) curves before training and after 2, 4 and 6 months of training are plotted in Figure 3. As can be seen from the A-T curve before training the optimum angle range for peak MVC was between 110° and 120° of knee extension. After 6 months of training, no shift in this optimum angle range was observed and the greatest increase in MVC was between 110° and 130° , ranging from $28.5 \pm 7.3\%$ to $29.6 \pm 7.9\%$ ($P < 0.01$ – 0.05).

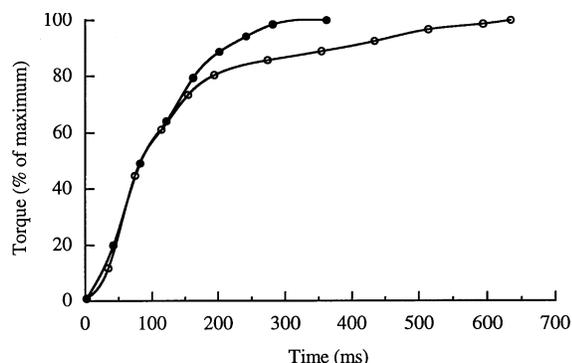


Figure 4 Time to 95% peak torque before (○) and after (●) 6 months quadriceps strength training ($n = 7$, means \pm SD).

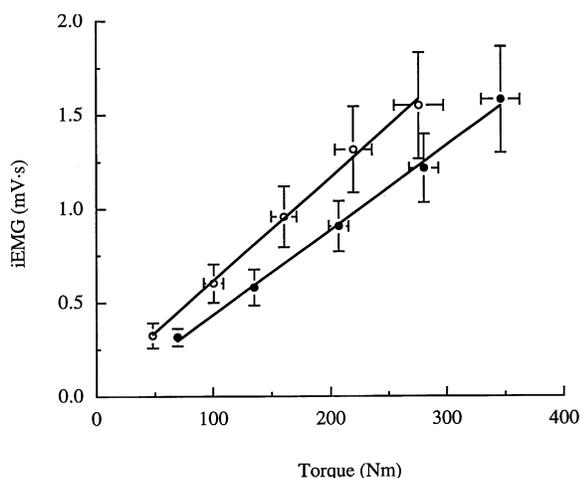


Figure 5 iEMG-torque relation before (○) and after (●) 6 months strength training ($n = 7$, means \pm SD). Experimental points are fitted with linear functions.

The increases in MVC within this angle range were significantly greater ($P < 0.01$) than those found at angles between 140° to 160° , at which changes in MVC were non-significant.

Comparison of the A-T curve, before training, and the joint angle-training load curve showed that both curves and the angle-training load curve reached a plateau at the same range of joint angles, namely between 100 and 110° .

Time to Peak Torque and time to maximum EMG development

The time to peak torque (TPT) was reduced from 528.6 ± 91.9 ms to 273.6 ± 19.4 ms ($P < 0.03$) after 6 months training (Figure 4). Up to 160 ms, no difference in RFD was found between the torque-time curves obtained before and after training. The reduction in TPT was not accompanied by any significant change in TME since maximum IEMG was attained, both before and after training, within 100 ms from the onset of the IEMG.

IEMG-Torque relation

The maximum absolute IEMG activity (IEMG max) during the isometric contraction at 100% MVC did not change significantly throughout the training period. Nevertheless, there was a right shift of the IEMG-Torque curve after 6 months, indicating an increase in torque output for the same level of neural activation (Figure 5).

IEMG activity during the loading exercise

Whereas no significant differences existed between the mean normalized IEMG activities (expressed in fractions of IEMG activity at 1 RM) of VL (0.52), VM (0.58) and RF (0.56) in the concentric phase, the activity of RF during the eccentric phase was greater, 0.41 ± 0.11 ($P < 0.001$), than those of VL and VM which were 0.31 ± 0.11 and 0.29 ± 0.12 , respectively.

Torque per cross-sectional area

A $12.0 \pm 10.8\%$ increase ($P < 0.02$) in specific tension from 3.3 ± 0.6 to 3.7 ± 0.5 Nm cm^{-2} was observed after training.

DISCUSSION

Selective muscle hypertrophy

The increase in muscle size proved to be a non-uniform process, not only between the individual components of the quadriceps group but also along the belly of each muscle, which is in agreement with our previous observations (Narici *et al.* 1989) and with those of Housh *et al.* (1992). The present results in fact show that if an average increase in CSA is calculated for each muscle, then hypertrophy can be ranked as follows: RF (27.9%) > VL (19.5%) > VM (18.7%) > VI (17.4%). Intuitively, the different hypertrophic response of muscles belonging to the same group could either be attributed to differences in activation, or to differences in contractile proteins synthesis along the muscle belly. The results show that while no differences in the normalized IEMG activities of VL, VM and RF were present in the concentric phase, there was a significant tendency for a greater activity of the RF during the eccentric phase. These results seem of particular interest since they not only suggest that the RF exerted, in these conditions, a greater braking action than VM and VL but also that the greater hypertrophy of RF may originate not as much from loading in the concentric phase but rather from loading in the eccentric phase. Whether this greater activity of RF is of either cortical or reflex origin cannot be defined at the present time.

In the present study each of the four components of the quadriceps displayed a greater increase in CSA in the proximal and distal than in the middle region of each muscle. This regional hypertrophy, most marked in the RF, seems in line with the observations on protein synthesis of over-loaded rabbit muscle. Goldspink *et al.* (1991) have indeed shown that the incorporation of [³H]phenylalanine into myosin of electrically stimulated, stretched tibialis anterior (TA) was accompanied by a marked increase in new myosin synthesis occurring mainly in the distal segments of this muscle. This observation is of particular interest since it shows that the assembly of new myosin to form new sarcomeres occurs preferentially in the distal end of the TA. It is also noteworthy that during a tetanus in stretched muscles, the proximal and distal sarcomeres generate more tension than those at the centre of the muscle fibres (Gordon *et al.* 1966a). Although in our case a rather modest stretch would be expected to have occurred in the eccentric phase of the movement (lowering of the weight) compared with the above experimental conditions, it cannot be excluded that this greater hypertrophy in the proximal and distal portions of the muscle were due to higher tensions generated in these regions.

Angle-torque relationship

The greatest increase in muscle strength observed in the present study, $28.5 \pm 7.6\%$, was between 110° and 130° of knee extension and was comparable to that reported by Häkkinen *et al.* (1985) for the same muscle group after five and a half months' weight training. The above angle range almost corresponded to the optimum angle for peak torque generation (110–120°) which was not modified by training. The fact that the shape of the quadriceps A-T curve was unchanged by training suggests that, despite regional muscle hypertrophy, either no changes in the length-tension relation of any of its components did occur or that these were not sufficiently large to modify the overall A-T relation. In any case, the specific increase in torque at angles between 100 and 130° was independent of the neural drive since maximum IEMG activity did not change significantly after training. The absence of changes in the optimum angle for torque generation may also be explained by the fact that the shape of the joint angle-load curve quite closely followed the A-T curve of the quadriceps, the maximum loading of the quadriceps coinciding with the optimum joint angle for quadriceps torque generation. It should be pointed out, however, that any training machine with a radically different loading principle from this ideal situation could lead to different results.

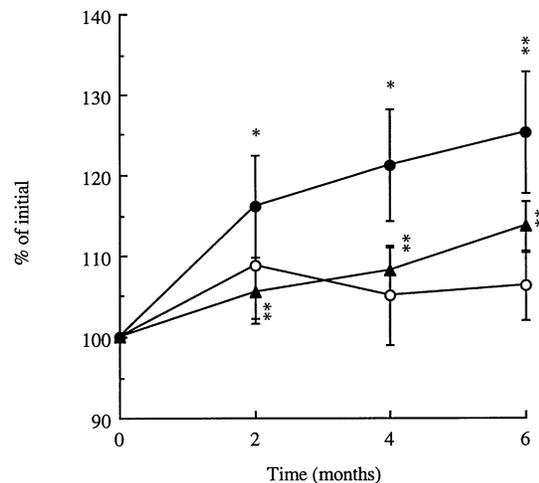


Figure 6 Isometric MVC (●), IEMGmax (○) at 120° and quadriceps CSA at 5/10 Lf (◆) during 6 months strength training, normalized for the initial values. ($n = 7$, means \pm SD, * = $P < 0.05$, ** = $P < 0.01$.)

As for previous studies (Sale & MacDougall 1981, Jones & Rutherford 1987) the increase in dynamic force (1 RM) was far greater (about 150%) than the increase in isometric MVC (28.5%). This effect, showing the specificity of the movement pattern in strength training, probably involves task-specific learning effects and improved coordination (Rutherford & Jones 1986).

Neural activation

The absence of any change in maximum IEMG activity after training implies that the investigated subjects were able to reach full motor unit activation even before training. Similar conclusions were reached by Jones & Rutherford (1987) after 12 weeks of strength training. In our study however, training produced a right shift in the IEMG/torque relation (Figure 5). This indicates that for the same level of motor unit activation a greater torque was generated as a result of muscle hypertrophy which is in agreement with the findings of Moritani & de Vries (1979) on the elbow flexors and of Garfinkel & Cafarelli (1992) on the knee extensors.

Changes in MVC, CSA and IEMG

From the comparison between the relative changes in MVC (at the optimum angle), CSA (at 5/10 Lf) and IEMG max (Figure 6) it was observed that no delay existed between the onset of hypertrophy and changes in muscle strength. Confirming our previous findings (Narici *et al.* 1989), muscle hypertrophy evolved essentially in a linear fashion with time clearly

indicating that the plateau of this process is reached well beyond 6 months of training. It is noteworthy that after the second month of training, quadriceps torque and CSA increased in parallel, indicating a constant contribution of hypertrophy towards the increase in strength (Figure 6). The concerted action of other factors such as improved coordination, reduced antagonist co-activation and an increase in force/CSA, possibly to greater density of contractile tissue, may account for the discrepancy between the increase of torque compared with that of CSA (Figure 6). Neural factors have previously been shown to substantially contribute to the increase in muscle strength during training (Komi *et al.* 1982, Moritani & De Vries 1979, Häkkinen *et al.* 1985), particularly before hypertrophy takes place (Sale 1990). Although the present data indicate that the IEMG max at 2 and 6 months was not statistically different from that before training, possibly due to the rather large methodological error of this measure, a sizeable increase in IEMG max at 2 months was observed. This may also explain the fact that during the first 2 months torque increased at a much higher rate than CSA. This observation seems consistent with the results of Häkkinen & Komi (1983) of an increase in IEMG in the early phases and a decrease in the later phases of a 4 months strength training study. An initially greater and then lower motor unit synchronization has been proposed to explain this finding (Häkkinen & Komi 1983).

Torque per unit cross-sectional area

The muscle hypertrophy observed in the present study, only partly accounted for the increase in MVC obtained after training. In fact, a mean increase in MVC of $28.5 \pm 7.6\%$ (pooled mean from 110 to 130°) was accompanied by a change in quadriceps mean CSA of $16.1 \pm 3.4\%$. This 12.4% discrepancy seems to be explained by the $12.0 \pm 10.8\%$ rise in torque/CSA. This finding is consistent with that of Jones & Rutherford (1987) who reported a 27% rise in force per unit area after 84 days strength training of the same muscle group. An increase in specific tension could theoretically ensue from changes in muscle architecture. Hypertrophy might in fact lead to an increase in the angle of pennation of muscle fibres (Gollnick *et al.* 1981) and recent evidence by Kawakami *et al.* (1993), showing greater pennation angles in hypertrophied than in normal human triceps brachii, supports this hypothesis. Although this should decrease the useful vector of the force running along the tendon, it will allow packing of a greater number of contractile elements along the tendon (Gans & Bock 1965) thus generating more force per unit area.

An additional factor that may contribute to the increase in torque/CSA is represented by a decrease in the activity of the antagonist muscles, the hamstring group in this case. Co-contraction of the antagonist group is often observed in strong and/or rapid contractions (Smith 1981) and may impair, through reciprocal inhibition, full activation of the agonists (Tyler & Hutton 1986) as well as by decreasing the net torque in the intended direction (Baratta *et al.* 1988). The latter authors have indeed shown that during maximal knee extension the antagonist knee flexors will generate a torque equal to 10% of total extensor torque. Few studies have investigated the effect of training on antagonists co-contraction; however, athletes with hypertrophic quadriceps display less co-contraction of the knee flexors during low velocity isokinetic knee extensions than control subjects (Baratta *et al.* 1988). Also, strength and power athletes vs. endurance athletes have less knee flexors co-contraction during low velocity knee extensions (Ostering *et al.* 1990). Therefore, it cannot be ruled out that some of the increase in quadriceps torque observed in this study was due to a reduction in antagonists activity brought by strength training.

Muscle fibres size

In the present study, muscle biopsy data did not show any change in fibre CSA. This seems surprising since several previous studies have shown fibre hypertrophy as a result of functional overload (Thorstensson 1976, Häkkinen *et al.* 1981, MacDougall *et al.* 1982, Tesch *et al.* 1985, Hather *et al.* 1991). Most of all, the highly significant increase in CSA of the VL observed in this study clearly indicates that fibre hypertrophy must have occurred but was simply not detected. This finding is plausibly explained by the fact that the site of biopsy at mid-muscle belly used in the present study actually coincided with the portion of the VL (5/10 Lf) which displayed the least hypertrophy (c.a. 5%) after training. Changes of fibre size of less than 10% have been regarded as the limit of what can be detected with morphometric techniques from biopsies (Zumstein *et al.* 1983). Furthermore, Viitasalo *et al.* (1980) showed that biopsy measurements have a low reproducibility and are characterized by a coefficient of variation of about 17%. Should the present findings be confirmed, care should be taken when drawing conclusions concerning the whole muscle mass from changes occurring at a single biopsy site.

Time to peak torque

A 45.8% reduction in time to peak isometric torque (TPT) was observed after training. This agrees with

the observations of a shorter time for force generation in power athletes (Komi 1979) and after strength training (Hakkinen *et al.* 1981). The TPT depends both on the stiffness of the series elastic component (SEC) and on the force-velocity (F-V) characteristics of the contractile component (CC) which shortens at the expense of the SEC (Jewell & Wilkie 1958). A change in maximum contraction velocity (V_{\max}) or alteration in the FT/ST fibre ratio may potentially lead to changes in the F-V features of the CC. Scanty data exist on the effects of strength training on V_{\max} , but it is noteworthy that Duchateau & Hainaut (1984) reported an increase in V_{\max} after dynamic training. Weak dependence has instead been found between muscle fibre composition and the force-time characteristics of the quadriceps (Viitasalo & Komi 1978). An increase in spontaneous motor neurone firing frequency could also be a cause for the decrease in TPT after training. Synchronous artificial stimulation of the muscle at 100 Hz has indeed been shown to lead to a faster rate of tension rise than at 50 Hz (Grimby *et al.* 1981). Comparison of the rate of rise of IEMG before and after training did not show any changes; however, since surface EMG depends both on recruitment and firing frequency no conclusions on firing frequency may be made.

An increase in SEC stiffness could also be a likely factor responsible for the decrease in TPT. Since the experiments of Wilkie in 1950, it has been known that adding a compliance to the muscle decreases the rate of rise of tension. As suggested by Wilson *et al.* (1994), an increase in SEC stiffness should result in a higher force and rate of force development. This is because a stiffer SEC would require less shortening of the CC and force would be developed closer to optimum muscle length. Also, less shortening of the CC will be reflected by a decrease in contraction velocity and thus the muscle would work in an advantageous part of the F-V curve to develop high forces. A stiffer SEC would also transmit force to the bone more rapidly and thus a higher rate of force development would be expected. Since the SEC does not obey Hooke's law, its stiffness will increase with tension, being particularly high when the contraction is at a maximum. An increase in SEC stiffness could therefore explain the observation made, that up to about 160 ms the RFD after training was the same as before training, namely of 1.73 Nm ms^{-1} and differences in RFD only became apparent at torque levels above 70% MVC. This observation is consistent with the findings of Hakkinen *et al.* (1985) after 24 weeks of leg extensors strength training showing a decrease in time to reach maximal force levels with little change at low force levels. Consistent with this hypothesis seem the findings of Pousson *et al.* (1990) who described an increase in

SEC stiffness following a period of eccentric strength training. In this respect, an increase in collagen content and in tensile strength in response to functional overload has been reported both in animal (Booth & Gould 1975) and human (MacDougall *et al.* 1984) skeletal muscles.

CONCLUSIONS

Long-term (6 months) strength training results in an uneven distribution of hypertrophy amongst and within the components of the human quadriceps. This effect does not seem to modify the shape of the angle-torque relation of the quadriceps; the same optimum angle for maximum torque generation was observed after training. The increase in muscle torque does not seem to be necessarily accompanied by an increase in neural activation which was unmodified after training. An increase in pennation angle is called upon to explain the greater increase in torque compared with quadriceps CSA. A significant decrease in time to peak torque was observed after training; this observation could indicate an increase in musculotendinous stiffness.

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