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ORIGINAL ARTICLE

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Training-induced changes in muscle architecture and specific tension

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Abstract Five men underwent unilateral resistance training of elbow extensor (triceps brachii) muscles for 16 weeks. Before and after training, muscle layer thickness and fascicle angles of the long head of the triceps muscle were measured in vivo using B-mode ultrasound, and fascicle lengths were estimated. Series anatomical cross-sectional areas (ACSA) of the triceps brachii muscle were measured by magnetic resonance imaging, from which muscle volume (V_m) was determined and physiological cross-sectional area (PCSA) was calculated. Elbow extension strength (isometric; concentric and eccentric at 30, 90 and $180° \cdot s^{-1}$) was measured using an isokinetic dynamometer to determine specific tension. Muscle volumes, ACSA, PCSA, muscle layer thickness and fascicle angles increased after training and their relative changes were similar, while muscle and fascicle length did not change. Muscle strength increased at all velocities; however, specific tension decreased after training. Increase in fascicle angles, which would be the result of increased V_m and PCSA, would seem to imply the occurrence of changes in muscle architecture. This might have given a negative effect on the force-generating properties of the muscles.

Key words Muscle hypertrophy · Pennation angle · Physiological cross-sectional area

Introduction

The architecture of skeletal muscles, that is the geometric design by which muscle-fibres are arranged in the muscle-tendon complex, has been shown to affect tension development characteristics of muscles as well as the intrinsic properties of muscle fibres themselves (Lieber 1992). Muscle architecture has been studied with respect to fibre cross-sectional area (CSA), muscle and fibre length, and their arrangements (Alexander and Vernon 1975; An et al. 1981; Wickiewicz et al. 1983).

In a pennate muscle, fibres terminate at the tendon at a certain angle to the line of pull of the muscle. This configuration allows for more contractile materials to be attached to the limited areas, but the direction of force exerted by muscle fibres is at variance with that of the tendon transmitting force to bones (Alexander and Vernon 1975). Thus the pennation angle, which determines the component of force of fibres to the line of pull, is considered to be an important architectural parameter. Pennation angles have been derived from reports on human cadavers (Amis et al. 1979), but recently, they have been measured in vivo by ultrasound (Rutherford and Jones 1992; Kawakami et al. 1993).

Among a number of studies on resistance training and the resultant changes in muscles, some indirect evidence has been presented suggesting changes in muscle architecture (Gollnick et al. 1981; Maughan et al. 1984; Jones and Rutherford 1987; Davies et al. 1988; Narici et al. 1989). Maughan et al. (1984) have observed an inverse relationship between strength per unit of anatomical CSA (ACSA) of muscles and ACSA, and attributed it to the increase in pennation angles in larger muscles. More recently, Kawakami et al. (1993) have shown in subjects with hypertrophied muscles that pennation angles are greater than in those with normal muscles.

Physiological CSA (PCSA), that is the total cross-sectional area of all the muscle fibres at right angles to their long axes, has recently been determined in vivo from muscle volume measurement by magnetic resonance imaging (MRI) (e.g. Fukunaga et al. 1992). By dividing muscle force by PCSA, specific tension of human skeletal muscles has been determined to evaluate the force-producing capacity of the muscle (Kawakami et

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al. 1994). However, information on the training-induced changes in PCSA and specific tension has been rather limited (e.g. Narici et al. 1989).

In the present study, we investigated changes in PCSA, pennation angles and specific tension of human muscles resulting from resistance training. The possibility was tested that changes in muscle architecture occur after training and that the altered architecture affects the force-producing capacity of the muscle.

Methods

Subjects

Five healthy men [age 29 (SD 4) years, height 169 (SD 8) cm, mass 63.4 (SD 11.2) kg] volunteered for the study. Informed consent was obtained from each subject before the study began. They had no orthopaedic abnormality in their upper extremities and all were physically active and fully motivated and well-accustomed to the development of maximal voluntary force. All of them were right-handed. The study had been approved by the Department of Life Sciences, The University of Tokyo.

Training

Unilateral resistance training of elbow extensor muscles was administered 3 days a week for 16 weeks. The training exercise was "French Press": each subject stood and moved their forearms upward then downward, concentrically and eccentrically, with a load-adjustable dumb-bell in his left hand. The left upper arm was kept upright to avoid movements of the shoulder. Prior to training, the maximal mass each subject could raise (1 repetition maximum, 1RM) was measured. During training, the mass of the dumb-bell was set at 80% of 1RM and five sets of exercises were done with eight repetitions each. Measurement of 1RM was made every 2 weeks to adjust the training load. The right arm was not trained and served as a control.

Muscle layer thickness measurement

Muscle layer thickness of the triceps brachii muscle was measured with a B-mode ultrasound apparatus (SSD-500, Aloka, Japan). Precision and linearity of the image reconstruction have been confirmed elsewhere (Kawakami et al. 1993). A single cross-sectional plane was imaged at 40% of the distance from the lateral epicondyle to the acromion process of the scapula, starting at the lateral epicondyle. The muscles measured included parts of the long, lateral, and medial heads of the triceps brachii. Measurements were carried out while the subjects stood with their arms relaxed and hands at their sides. The elbow was in an extended position. A transducer with a 5-MHz scanning head was placed perpendicular to the tissue interface and to the underlying humerus. The scanning head was coated with water-soluble transmission gel, which provided acoustic contact without depressing the dermal surface. The subcutaneous adipose tissue-muscle interface and the muscle-bone interface were identified from the ultrasonic image, and the distance from the adipose tissue-muscle interface and the muscle-bone interface was adopted as muscle layer thickness (Weiss and Clark 1987; Kawakami et al. 1993).

Measurement of fascicle angles

On the same site where muscle layer thickness was measured, the centre of the ultrasonic transducer was placed parallel to the long head of the triceps. The angles between the echo of the deep aponeurosis of the triceps muscle and echoes from interspaces among the fascicles of the long head of triceps muscle were measured as fascicle angles (Kawakami et al. 1993). Measurements of muscle layer thickness and fascicle angles were done both for the right and left arms of each subject.

From the muscle layer thickness and the fascicle angle, the length of fascicles (l_f) across the deep and superficial aponeuroses was estimated from the following equation:

$$l_f = \text{muscle layer thickness} \cdot \sin^{-1} \theta$$

where θ is the fascicle angle of the long head determined by ultrasound.

Measurement of triceps CSA

Before and after training, series cross-sectional images of the upper extremities were obtained by MRI scans with a body coil (Signa 1.5T, GE Electronics, USA). Spin-echo, multislice sequences with a slice thickness of 10 mm were used with a repetition time of 900 ms and an echo time of 17 ms. Each subject lay supine in the body coil with his arms extended and relaxed. Transverse scans were carried out with an interspaced gap of 0 mm, from the elbow joint to the head of humerus. Figure 1 shows an example of series cross-sectional images of the upper extremity for one subject.

From each cross-sectional image of the upper extremity, outlines of the triceps brachii muscle were traced according to Bo et al. (1980), and digitized by using a personal computer (PC-9801, NEC, Japan) and ACSA was calculated. Digitizing and area calculation were repeated three times for a single image and an averaged value was adopted as representative of ACSA. Coefficients of variation of the three measurements were less than 5%. Muscle length was defined as the distance between the most proximal and the most distal images in which the muscle was visible. Subcutaneous adipose tissue and tendinous tissue, which were imaged in different tones from the muscle tissue, were excluded when digitizing. By summing the ACSA of the muscle along its length and then multiplying the sum by the interval of 10 mm, muscle volume (V_m) was determined. From l_f and V_m, PCSA of the triceps brachii muscle was obtained (An et al. 1981), i.e. $PCSA = V_m \cdot l_f^{-1}$.

Measurement of strength

Maximal voluntary isometric, concentric, and eccentric strength of elbow extensors were measured before and after training using an isokinetic dynamometer (Kawakami et al. 1994), To standardize the measurement and localize the action to appropriate muscles, the subject was seated on an adjustable chair with support for the back, elbow, shoulders, and hips. The measurement of elbow extension torque was carried out with the subject seated, with the arm supported on the horizontal plane on a padded table. The axis of rotation of the elbow joint was visually aligned to the axis of the lever arm of the dynamometer. The subject's wrist was fixed at the end of the lever arm in a position halfway between supination and pronation. The torque was corrected for gravitational moments of the forearm and the lever arm. Isometric torques were measured twice to three times at the elbow joint angle in the range of 45–70° (full extension corresponds to O°) and the maximal value was adopted. Concentric and eccentric peak torque was also measured at velocities 30, 90, and 180°$\cdot$s^{-1}, in the range of joint angles between 25° and 90°. The torque was recorded on a strip recorder (RECTI-HORIZ, NEC San-ei, Japan). The order of the measurements was randomized and a rest of approximately 1 min was allowed between trials to exclude an effect of fatigue.

Determination of specific tension

Torque output was divided by the moment arm of the triceps brachii musles which was derived from the previous study (Kawa-

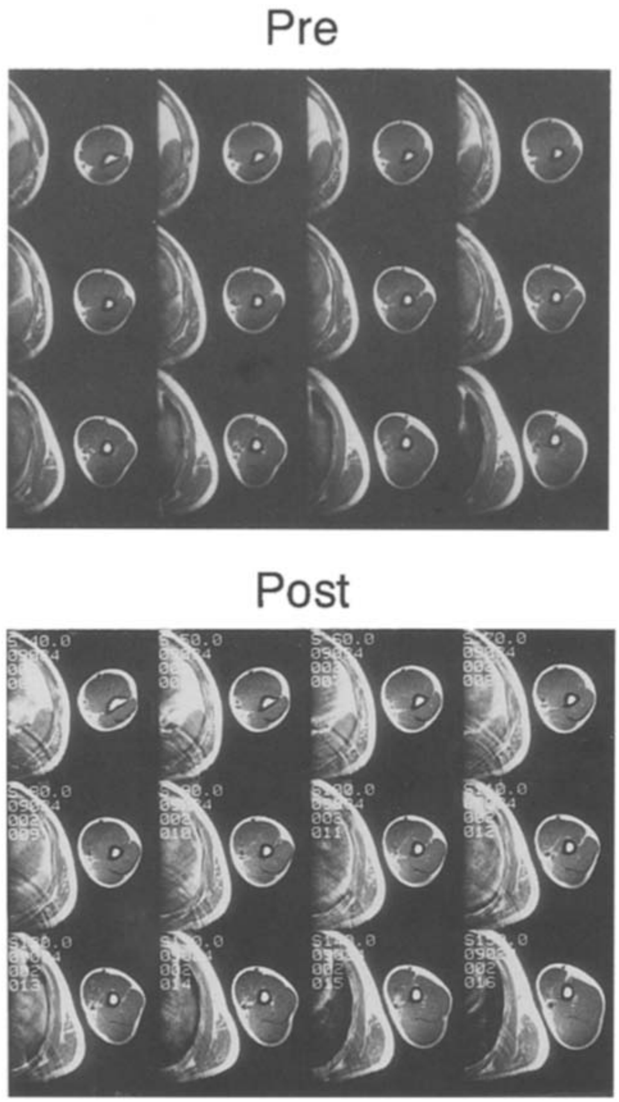

Fig. 1 Series cross-sectional magnetic resonance images of the upper extremity before (*Pre*) and after (*Post*) training for one subject. The scanning was carried out from the elbow joint to the head of humerus, with a slice thickness of 10 mm. In this figure, images including the middle portion of the triceps brachii muscle are shown, from the *top left* to the *bottom right*

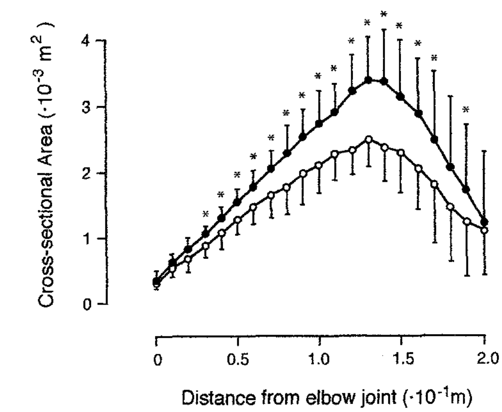

Fig. 2 Series anatomical cross-sectional areas (mean and SD of five subjects) of triceps brachii muscle along the length of the upper (*left*) arm before and after training (pre ○, post ●). Significance from pretraining values, * $P<0.05$

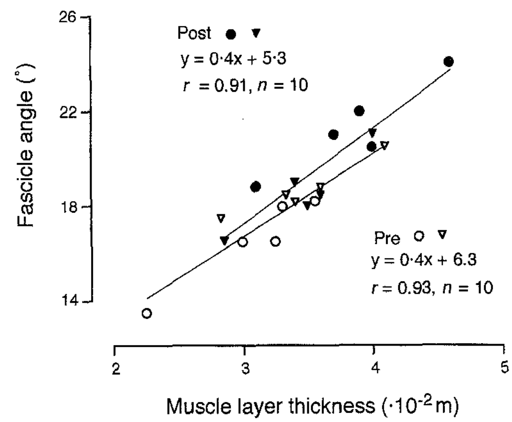

Fig. 3 The relationship between muscle layer thickness and fascicle angles. Both parameters were measured by ultrasound and plotted for trained (pre ○, post ●) and untrained (pre ▽, post ▼) arms. A regression line was drawn for the data of pre- and post-training

kami et al. 1994), correcting for difference in forearm length, and the force acting on the triceps tendon was estimated. The tendon force was then divided by the PCSA of the total triceps muscle to give specific tension.

Statistical analyses

Statistical analysis of the data was accomplished with two-way analyses of variance (ANOVA): arm (left, right) × time (pre, post); for relative changes, arm × variables (V_m, $ACSA_{max}$, PCSA, muscle layer thickness, fascicle angles, and l_f); arm × velocities (for torque and specific tension). The homogeneity of variance was confirmed by a Bartlett test. When the data were not normally distributed, a paired Student's *t*-test and a Friedman test were performed for the significance of the difference. The relationship between muscle layer thickness and fascicle angles was tested by a simple linear regression analysis. In each statistical analysis the level of significance was set at $P<0.05$.

Results

Figure 2 shows series ACSA of the triceps muscle (including three heads) before and after training with mean values for five subjects. Maximal ACSA ($ACSA_{max}$) was observed at about distal 40% of the muscle length. In the trained arm, ACSA increased significantly except for the proximal and distal ends. In the control arm, no significant changes in ACSA were observed throughout the entire length of the muscle.

Muscle layer thickness was significantly correlated to fascicle angles (pre-training: $r=0.93$, post-training: $r=0.91$; $P<0.05$, Fig. 3). The slopes and intercepts of the two regression lines did not differ significantly. In the trained arm, both muscle layer thickness and fascicle angles increased after training ($P<0.05$) whereas in the control arm, no statistical difference was noted. The mean l_f, estimated from the muscle layer thickness and fascicle angles, ranged from 9.6 to 11.7 cm and was

Table 1 Architectural parameters of the triceps brachii muscle before and after training. Relative change was calculated as: [(post-training value) − (pretraining value)]·(pretaining value)$^{-1}$·100. V_m Muscle volume, $ACSA_{max}$ maximal anatomical cross-sectional area, *PCSA* physiological cross-sectional area, l_f length of fascicle

	Subject	Left (trained) arm Pre	Post	Relative change (%)	Right (control) arm Pre	Post	Relative change (%)
V_m ($\cdot 10^{-4}$ m^3)	A	4.28	5.73	33.8	4.02	4.26	5.8
	B	3.73	5.35	43.7	4.09	4.15	1.6
	C	3.20	4.31	34.5	3.95	4.40	11.5
	D	2.13	2.85	33.6	2.77	2.72	−1.6
	E	3.57	4.03	12.7	4.39	4.37	−0.5
	Mean	3.38	4.45	31.7	3.84	3.98	3.4
	SD	0.80	1.14	11.4	0.62	0.71	5.3
$ACSA_{max}$ ($\cdot 10^{-3}$ m^2)	A	3.23	4.16	28.6	3.04	3.12	2.4
	B	2.86	4.03	41.0	2.97	3.05	2.6
	C	2.34	3.38	44.3	3.17	3.41	7.4
	D	1.80	2.38	32.5	2.42	2.28	−5.5
	E	2.82	3.16	11.9	3.31	3.61	9.2
	Mean	2.61	3.42	31.7	2.98	3.09	3.2
	SD	0.55	0.72	12.7	0.34	0.51	5.7
PCSA ($\cdot 10^{-3}$ m^2)	A	4.01	5.06	26.4	3.83	4.08	6.3
	B	3.26	5.14	57.9	3.75	3.67	−2.4
	C	3.03	3.77	24.4	3.54	3.88	9.8
	D	2.21	2.96	33.9	2.94	2.72	−7.7
	E	3.14	3.90	24.1	3.75	3.92	4.4
	Mean	3.13	4.17	33.3	3.56	3.65	2.1
	SD	0.64	0.93	14.3	0.36	0.54	7.0
Muscle layer thickness ($\cdot 10^{-2}$ m)	A	3.3	4.6	39.4	3.3	3.4	2.1
	B	3.3	3.9	20.0	3.4	3.5	2.9
	C	3.0	4.0	33.3	3.6	3.6	0.0
	D	2.3	3.1	37.8	2.8	2.9	0.7
	E	3.6	3.7	4.2	4.1	4.0	−2.4
	Mean	3.1	3.7	27.0	3.5	3.4	0.7
	SD	0.5	0.5	14.8	0.4	0.4	2.1
Fascicle angle (°)	A	18.0	24.0	33.3	18.5	19.0	2.7
	B	16.5	22.0	33.3	18.2	18.0	−1.1
	C	16.5	20.5	24.2	18.8	18.5	−1.6
	D	13.5	18.8	39.3	17.5	16.5	−5.7
	E	18.2	21.0	15.4	20.5	21.0	2.4
	Mean	16.5	21.3	29.1	18.7	18.6	−0.7
	SD	1.9	1.9	9.4	1.1	1.6	3.4
l_f ($\cdot 10^{-2}$ m)	A	10.7	11.3	5.9	10.5	10.4	−0.5
	B	11.4	10.4	−9.0	10.9	11.3	4.1
	C	10.6	11.4	8.1	11.2	11.3	1.6
	D	9.6	9.6	−0.2	9.4	10.0	6.6
	E	11.4	10.3	−9.2	11.7	11.2	−4.7
	Mean	10.7	10.6	−0.9	10.7	10.9	1.4
	SD	0.7	0.8	8.1	0.9	0.6	4.3

comparable to that of human cadavers (10.2±1.9 cm; An et al. 1981). Both in the trained and control arms, no significant changes were observed in l_f.

Table 1 shows mean values of $ACSA_{max}$, V_m, PCSA, muscle layer thickness, fascicle angles and l_f before and after training as well as their relative changes. In the trained arm, all parameters except l_f increased significantly after training. The ANOVA of relative increases in these parameters for each subject showed that the effect of arms (left, right) was significant ($P<0.05$); however, there were no statistically significant differences in the relative changes in the trained arm.

Isometric and isokinetic peak torque of elbow extension increased significantly ($P<0.05$) in the trained arm at all velocities (Fig. 4). Relative increases in torque after training were 16% (isometric), 20%–32% (concentric), and 15%–16% (eccentric). In the control arm, no significant changes were observed. The angles of the elbow joint at which peak torque appeared did not change significantly either in the trained [pre: 58 (SD 11)°, post: 62 (SD 10)°] and control [pre: 55 (SD 6)°, post: 60 (SD 8)°] arms. There were no significant relationship between the relative changes of peak torque and those of $ACSA_{max}$, V_m, and PCSA.

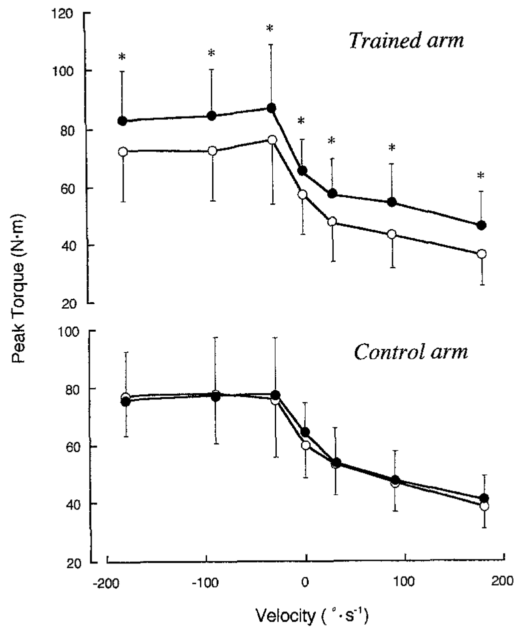

Fig. 4 The relationships between angular velocities of elbow joint and peak torque in the trained (*top*) and control (*bottom*) arms (pre ○, post ●). Significance from pretraining values, $* P<0.05$

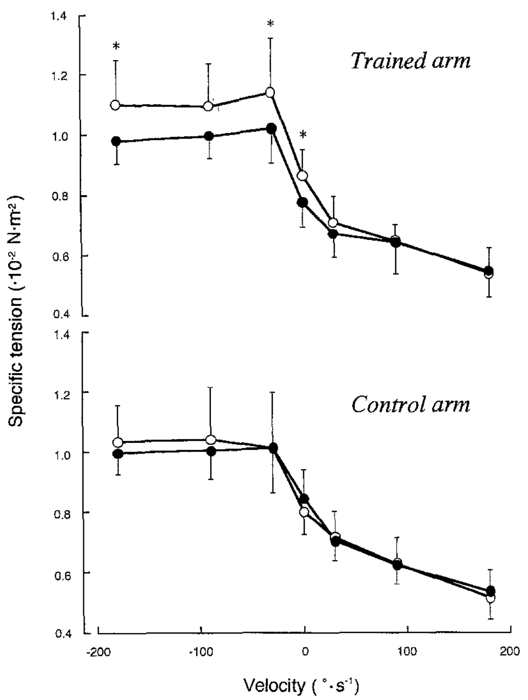

Fig. 5 The relationships between angular velocities of elbow joint and specific tension in the trained (*top*) and control (*bottom*) arms (pre ○, post ●). Significance from pretraining values, $* P<0.05$

As illustrated in Fig. 5, no significant change occurred in specific tension in the control arm while in the trained arm, specific tension decreased after training, especially in isometric and eccentric action. The ANOVA of the relative changes in specific tension data for each subject showed that the effect of arms (left, right) was significant. The velocity did not affect the relative changes both in the left and right arms. Similar results were observed when the tendon force was divided by $ACSA_{max}$.

Discussion

The ACSA increased after training in the middle portion of the muscle while remaining unchanged near the proximal and distal ends. These results imply that muscle hypertrophy does not occur equally throughout the entire length of the muscle. But because relative increases in muscle layer thickness, $ACSA_{max}$, V_m, and PCSA did not differ significantly, it is suggested that the change in CSA from a single slice reflects that of all the muscle-fibres. Thus, ACSA measurement for only one slice which has frequently been done in previous studies (e.g. Jones and Rutherford 1987) seems to be a correct approach for the evaluation of muscle size. One study however exists (Roman et al. 1993) showing dissimilar changes in V_m and ACSA after resistance training. They have concluded that evaluation of muscle size based on a single ACSA overestimates the degree of hypertrophy. In their study, biceps brachii and brachialis muscles were combined to give $ACSA_{max}$. Because the positions where $ACSA_{max}$ has been observed differ between these two muscles (Kawakami et al. 1994), divergence of their results from those of the present study might have been due to their methodology in ACSA calculation. Another possibility is that they have used elbow flexors muscles (biceps and brachialis) which are parallel-fibred muscles, in which the manner of enlargement might be different from that of pennate muscles such as the triceps muscle. Effect of differences in muscle architecture on muscle enlargement patterns deserves further investigation.

The result that there was a positive correlation between muscle layer thickness and fascicle angles is in accordance with a previous study by Kawakami et al. (1993), in which, like the present study, fascicle angles were measured in vivo using ultrasound and a comparison was made between normal subjects and highly-trained bodybuilders. The present study also showed that the training resulted in similar increases in muscle layer thickness and fascicle angles. These results imply that muscle hypertrophy accompanies an increase in pennation angles, that is changes in muscle architecture, the possibility of which has only been supposed so far (Gollnick et al. 1981; Maughan et al. 1984; Jones and Rutherford 1987; Davies et al. 1988; Jones et al. 1989; Narici et al. 1989) and actually observed in rats during growth (Heslinga and Huijing 1990). The slight variability in the plots in Fig. 3 might have been due to the difference in muscle length of the subjects, because fascicle angles are considered to depend on the muscle length.

Maxwell et al. (1974) have predicted that for a muscle of constant muscle length, fibre length, and fibre numbers, hypertrophy (increase in the diameter of muscle fibres) would accompany increases in pennation angles and muscle layer thickness. Maughan et al. (1984) have observed an inverse relationship between ACSA and strength per unit ACSA. They have argued that the observed relationship might have been due to changes in the internal architecture of the muscles: an increase in pennation angles. The present results support their supposition. It has been suggested that an increase in fascicle (pennation) angles would result in more contractile material attached to a larger area of the tendon (Alexander and Vernon 1975). Thus the greater pennation angles would be the result of increased V_m and PCSA. Changes in muscle architecture might have resulted in the relative changes in V_m and PCSA similar to that of $ACSA_{max}$ although ACSA did not increase near the proximal and distal ends of the muscle.

Rutherford and Jones (1992), using similar techniques to this study have not found any increase in fascicle angles after resistance training of 3 months. We suppose that the training intensity they adopted (6RM, six repetitions × four sets, three times a week) was not enough to cause changes in muscle architectures and/or that the degree of training-induced changes are muscle-specific. The latter possibility might be indirectly supported by the results of Henriksson-Larsen et al. (1992) that have shown no correlation between muscle-fibre angulation and fibre CSA for the vastus lateralis muscle.

In the literature muscle fibre splitting (hyperplasia) has been documented as one of the mechanisms of the increase in V_m (Mikesky et al. 1991; Antonio and Gonyea 1993). But, as Maxwell et al. (1974) and Gollnick et al. (1981) have suggested, the apparent increase in fibre number might be a result of the way muscles with pennated architectures are cross-sectioned. We consider that hyperplasia, if any, would be of minor importance on the overall enlargement of skeletal muscles. Increase in water content or connective tissue may contribute to the increase in V_m; however, previous reports (Mikesky et al. 1991; Roman et al. 1993) have not supported that possibility. Increased fibre length could also contribute to the increase in V_m. In fact, in a model of chronic stretch of animal muscles, elongation of fibre length has been observed (Williams and Goldspink 1973). But, after resistance training in human skeletal muscles the occurrence has not been confirmed (Gollnick et al. 1981; Mikesky et al. 1991). Likewise, in the present study, the estimated l_f did not change after training. Thus the increase in V_m would be predominantly due to muscle fibre hypertrophy.

Estimated l_f were similar to fibre lengths which have been reported on human cadavers (An et al. 1981). Although muscles in the embalmed cadavers change their morphological characteristics after fixation procedures (Friedrich and Brand 1990), shrinkage of fibre length does not occur (Cutts 1988). Thus, the present calculation might well be used to evaluate muscle-fibre lengths. Validation of the present method by comparison with the direct measurement of l_f on cadaver muscles would be necessary and currently experiments are under way. In the present study, only the long head was measured for l_f. It has been shown in a cadaver study (An et al. 1981) that fibre lengths differ slightly among three heads of the triceps muscle. Information on the other two heads would be required for more precise PCSA calculation.

Peak torque increased at all velocities. On the other hand, specific tension, determined as the force at the tendon divided by PCSA, changed significantly in the trained arm: specific tension decreased after training. Similar results were obtained for the force divided by $ACSA_{max}$. These results suggest that force-generating capacity of the muscle changes after training. The degree of force development might be determined primarily by PCSA, as suggested by Powell et al. (1984). Increase in fascicle angles allows an increase in PCSA by packing more contractile material attached to the tendon, but on the other hand it is disadvantageous for force transmission from the muscle fibres to the tendon due to the decreased component of force by fibres to the line of pull of the muscle. Decreased specific tension might reflect a reduced efficiency in force transmission. Sale et al. (1992) have observed muscle hypertrophy without an increase in strength. Their results, as they have speculated, might also be due to changes in muscle architecture which decreased the net force acting along the line of the tendon. It should be noted, however, that when representing the muscle by a parallelogram, angles such as those made by the aponeuroses and the line of action of the muscle also need to be incorporated when considering muscle function in detail (see Zuurbier and Huijing 1992). Furthermore, it has been found that the fascicles are not arranged completely in parallel within a muscle (Scott et al. 1993). Thus, to study the accurate effect of muscle geometry on muscle function the arrangement of fascicles needs to be determined over the whole muscle, and this awaits further studies.

Alexander and Vernon (1975) have presented a model to estimate the force at the tendon from V_m, muscle layer thickness, fascicle angles and specific tension. If the measured changes in these parameters were used for the isometric muscle action, the computed change in force would be 13%, which is close to the present results in the change of isometric force of 16%. The changes in V_m, muscle layer thickness, and fascicle angles cause by themselves a 37% increase in force in the model, but the decreased specific tension lessened the relative increase by 21%.

We have demonstrated increases in size and strength as well as changes in architecture of a muscle as a result of resistance training. It is likely that the altered muscle architecture reduced specific tension of the muscle. In highly hypertrophied muscles as observed in bodybuilders, the specific tension, that is the force-producing capacity of muscles, might be smaller than that of less hypertrophied muscles.

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References

Alexander RM, Vernon A (1975) The dimensions of knee and ankle muscles and the forces they exert. J Hum Mov Stud 1:115–123

Amis AA, Dowson D, Wright V (1979) Muscle strengths and musculo-skeletal geometry of the upper limb. Eng Med 8:41–48

An KN, Fui FC, Morrey BF, Linshceid RL, Chao EY (1981) Muscles across the elbow joint: a biomechanical analysis. J Biomech 14:659–669

Antonio H, Gonyea WJ (1993) Progressive stretch overload of skeletal muscle results in hypertrophy before hyperplasia. J Appl Physiol 75:1263–1271

Bo WJ, Meschan I, Krueger WA (1988) Basic atlas of cross-sectional anatomy. Saunders, Philadelphia, pp 283–299

Cutts A (1988) Shrinkage of muscle fibres during the fixation of cadaveric tissue. J Anat 160:75–78

Davies J, Parker DF, Rutherford OM, Jones DA (1988) Changes in strength and cross sectional area of the elbow flexors as a result of isometric strength training. Eur J Appl Physiol 57:667–670

Friedrich JA, Brand RA (1990) Muscle fiber architecture in the human lower limb. J Biomech 23:91–95

Fukunaga T, Roy RR, Schellock FG, Hodgson JA, Day MK, Lee PL, Kwong-Fu H, Edgerton VR (1992) Physiological cross-sectional area of human leg muscles based on magnetic resonance imaging. J Orthop Res 10:926–934

Gollnick PD, Timson BF, Moore RL, Riedy M (1981) Muscular enlargement and number of fibers in skeletal muscles of rats. J Appl Physiol: Respir Environ Exerc Physiol 50:936–943

Henriksson-Larsen K, Wretling M-L, Lorentzon RL, Oberg L (1992) Do muscle size and fibre angulation correlate in pennated human muscles? Eur J Appl Physiol 64:68–72

Heslinga JW, Huijing PA (1990) Effects of growth on architecture and functional characteristics of adult rat gastrocnemius muscle. J Morphol 206:119–132

Jones DA, Rutherford OM (1987) Human muscle strength training: the effects of three different regimes and the nature of the resultant changes. J Physiol 391:1–11

Jones DA, Rutherford OM, Parker DF (1989) Physiological changes in skeletal muscle as a result of strength training. Q J Exp Physiol 74:233–256

Kawakami Y, Abe T, Fukunaga T (1993) Muscle-fiber pennation angles are greater in hypertrophied than in normal muscles. J Appl Physiol 74:2740–2744

Kawakami Y, Nakazawa K, Fujimoto T, Nozaki D, Miyashita M, Fukunaga T (1994) Specific tension of elbow flexor and extensor muscles based on magnetic resonance imaging. Eur J Appl Physiol 68:139–147

Lieber RL (1992) Skeletal muscle structure and function. Williams and Wilkins, Baltimore, pp 33–46

Maughan RJ, Watson JS, Weir J (1984) Muscle strength and cross-sectional area in man: a comparison of strength-trained and untrained subjects. Br J Sports Med 18:149–157

Maxwell LC, Faulkner JA, Hyatt (1974) Estimation of fibers in guinea pig skeletal muscles. J Appl Physiol 37:259–264

Mikesky AE, Giddings CJ, Matthews W, Gonyea WJ (1991) Changes in muscle fiber size and composition in response to heavy-resistance exercise. Med Sci Sports Exerc 23:1042–1049

Narici MV, Roi GS, Landoni L, Minetti AE, Cerretelli P (1989) Changes in force, cross-sectional area and neural activation during strength training and detraining of the human quadriceps. Eur J Appl Physiol 59:310–319

Powell PL, Roy RR, Kanim PM, Bello A, Edgerton VR (1984) Predictability of skeletal muscle tension from architectural determinations in guinea pig hindlimbs. J Appl Physiol 57:1715–1721

Roman WJ, Fleckenstein J, Stray-Gundersen J, Alway SE, Peshock R, Gonyea WJ (1993) Adaptations in the elbow flexors of elderly males after heavy-resistance training. J Appl Physiol 74:750–754

Rutherford OM, Jones DA (1992) Measurement of fibre pennation using ultrasound in the human quadriceps in vivo. Eur J Appl Physiol 65:433–437

Sale DG, Martin JE, Moroz DE (1992) Hypertrophy without increased isometric strength after weight training. Eur J Appl Physiol 64:51–55

Scott SH, Engstrom CM, Loeb GE (1993) Morphometry of human thigh muscles. Determination of fascicle architecture by magnetic resonance imaging. J Anat 182:249–257

Weiss LW, Clark FC (1987) Ultrasonic measurement of upper-arm skeletal muscle thickness. J Sports Med 27:128–133

Wickiewicz TL, Roy RR, Powell PL, Edgerton VR (1983) Muscle architecture of the human lower limb. Clin Orthop Rel Res 179:275–283

Williams P, Goldspink G (1973) The effect of immobilization on the longitudinal growth of striated muscle fibers. J Anat 116:45–55

Zuurbier CJ, Huijing PA (1992) Influence of muscle geometry on shortening speed of fibre, aponeurosis and muscle. J Biomech 25:1017–1026