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ORIGINAL ARTICLE

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Specific effects of eccentric and concentric training on muscle strength and morphology in humans

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Abstract The purpose of this study was to compare pure eccentric and concentric isokinetic training with respect to their possible specificity in the adaptation of strength and morphology of the knee extensor muscles. Ten moderately trained male physical education students were divided into groups undertaking eccentric (ETG) and concentric (CTG) training. They performed 10 weeks of maximal isokinetic ($90° \cdot s^{-1}$) training of the left leg, 4 × 10 repetitions – three times a week, followed by a second 10-week period of similar training of the right-leg. Mean eccentric and concentric peak torques increased by 18% and 2% for ETG and by 10% and 14% for CTG, respectively. The highest increase in peak torque occurred in the eccentric $90° \cdot s^{-1}$ test for ETG (35%) whereas in CTG strength gains ranged 8%–15% at velocities equal or lower than the training velocity. Significant increases in strength were observed in the untrained contra-lateral leg only at the velocity and mode used in ipsilateral training. Cross-sectional area of the quadriceps muscle increased 3%–4% with training in both groups, reaching statistical significance only in ETG. No major changes in muscle fibre composition or areas were detected in biopsies from the vastus lateralis muscle for either leg or training group. In conclusion, effects of eccentric training on muscle strength appeared to be more mode and speed specific than corresponding concentric training. Only minor adaptations in gross muscle morphology indicated that other factors, such as changes in neural activation patterns, were causing the specific training-induced gains in muscle strength.

Key words Hypertrophy · Muscle · Specificity · Strength · Training

Introduction

An important consideration when designing strength training programmes is the specificity of a given training stimulus (see McCafferty and Horvath 1977). Numerous studies have investigated the concept of training specificity and observed adaptations specific to factors such as training task, muscle length and velocity of muscle shortening (e.g. Sale and MacDougall 1981; Thépaut-Mathieu et al. 1988; Behm and Sale 1993). An additional factor that can cause specific training effects is the muscle action type (mode) used, that is, if the training consists of isometric (constant length), concentric (shortening) or eccentric (lengthening) muscle actions, or combinations thereof.

Early studies have been primarily concerned with comparing the effects of isometric and dynamic (isotonic) training, the latter generally containing both concentric and eccentric muscle actions (McDonagh and Davies 1984). Dynamic training, usually consisting of lifting and lowering of weights, has been shown to be specific in the sense that it has resulted in large improvements in weight lifting performance but only marginal increases in isometric strength measured in a standardised test position (e.g. Thorstensson et al. 1976b). Pure concentric training has been reported to increase dynamic but not isometric strength (Kanehisha and Miyashita 1983), whereas pure isometric training has appeared to have the opposite effect (Lindh 1979). Some studies have compared pure concentric strength training with combined eccentric-concentric training, so-called hybrid training, and have found higher strength gains with the latter type of training (Colliander and Tesch 1990; Hather et al. 1991).

Studies investigating possible mode specificity in the training effects of pure eccentric and concentric muscle actions have been scarce and inconclusive (Kellis and

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Baltzopoulos 1995). Assuming that muscle tension per se is an important factor in increasing muscle strength during training, the fact that higher tension can be achieved in eccentric compared to other types of muscle actions (Westing et al. 1988; Westing and Seger 1989) would favour this type of training. However, it is important to note that eccentric actions also differ from concentric ones in other respects, such as electromechanical efficiency – that is it has been shown that a certain force, including that voluntarily possible, can be produced with a lower activation (electromyogram, EMG) level eccentrically than concentrically (Seger and Thorstensson 1994). Eccentric actions have also been found to be more metabolically efficient (Ryschon et al. 1997). Pertinent to the evaluation of the two training paradigms are also the differences in fatiguability and thus possible metabolic stimuli to gain in strength. Available data has indicated that the decline in strength with repeated maximal eccentric actions is considerably less than during corresponding concentric ones (Tesch et al. 1990; Westblad and Johansson 1993). Finally, it has been well established that eccentric muscle actions lead to an augmented risk for muscle damage and delayed muscle soreness (Stauber 1989).

Using weights as a training load, Johnson et al. (1976) have found no differences in strength gains between pure eccentric and concentric elbow flexor/extensor training, while Komi and Buskirk (1972) have recorded greater strength increases after an eccentric training regime. Employing the isokinetic technique, that is maximal voluntary muscle actions with constant movement velocity, a more pronounced mode specificity has been demonstrated for eccentric than for concentric muscle training (Duncan et al. 1989; Hortobágyi et al. 1996). It is interesting that a recent study by Hortobágyi et al. (1997) has indicated a similar mode specificity in the cross-education response, that is in the strength gain of the contra-lateral, untrained, leg using a single leg training paradigm.

There has been some experimental evidence of mode specific training adaptations in muscle morphology, mainly from animal studies, where muscle preparations have been subjected to electrical stimulation simulating strength training (Booth and Thomason 1991). Wong and Booth (1990a, b) have reported that such chronic stimulation of the rat gastrocnemius and tibialis anterior muscles resulted in muscle enlargement under eccentric but not concentric conditions. However, no clear picture has emerged from studies on humans. A supremacy of eccentric actions as stimulus for muscle hypertrophy has been reported by Higbie et al. (1994), whereas non-mode-specific muscle enlargements have been obtained in other studies (Jones and Rutherford 1987; Carey Smith and Rutherford 1995).

Also with respect to the effects on muscle fibre characteristics, the few available data present an inconsistent picture. No selective effects on cross-sectional area or relative number of type I (slow) or type II (fast) muscle fibres have been found in studies of Colliander and Tesch (1990) or Hather et al. (1991) who have compared pure concentric with combined concentric and eccentric isokinetic training. In contrast, Hortobágyi et al. (1996) have reported a specific increase in type II fibre area after pure eccentric training, which may be compatible with a unique activation strategy by the nervous system associated with eccentric muscle actions (Enoka 1996).

The purpose of this study was to compare pure eccentric and concentric isokinetic training with respect to possible specificity in the adaptation of strength parameters and muscle morphology, including total cross-sectional area as well as muscle fibre measurements. Using a single-leg cross-over training paradigm could also provide possibilities of comparing cross-education and detraining effects on these variables.

Methods

Subjects

Ten male, moderately trained, physical education students participated in the study. They were randomly assigned to groups undertaking two types of training, one eccentric (ETG) and the other concentric (CTG) exercise. The average age, body height and mass for ETG were 25 (SEM 2) years, 1.79 (SEM 0.01) m and 72.8 (SEM 2.5) kg, respectively. The corresponding values for CTG were 24 (SEM 2) years, 1.75 (SEM 0.03) m and 70.5 (SEM 2.9) kg. There were no significant differences in these body measurements between the two groups. None of the subjects had participated in systematic strength training before or had any history of knee problems. All the subjects gave their informed consent to participate prior to their inclusion in the study. The project was approved by the Ethics Committee of the Karolinska Institute, Stockholm.

Testing and training apparatus

The SPARK isokinetic dynamometer (Seger et al. 1988) was used to measure torque output during unilateral knee extensor actions. The same apparatus provided resistance in the training protocol. The experimental setup and the reliability and validity of the dynamometer have been described elsewhere (Seger et al. 1988; Westing et al. 1988). Briefly, the subjects were tested and trained in a seated position, restrained by straps at the upper thigh, pelvis and trunk. The lever arm of the dynamometer was attached distally on the lower leg via a pad. The subjects initiated a single movement of the lever arm by overcoming a preset low torque. During eccentric tests, the subjects maximally resisted the movement of the lever arm throughout the whole range of motion and, conversely, during concentric tests, the subjects pushed maximally in the direction of the lever arm movement. Despite the maximal efforts by the subjects to decelerate and accelerate the lever arm, the angular velocity was kept constant (isokinetic) by the machine.

Strength measurements

Maximal voluntary eccentric and concentric unilateral knee extensor actions were performed for each leg at the constant velocities of 30, 90 and 270° $\cdot$ s^{-1}. Acceleration and decelaration ramps were employed for the comfort of the subject and to avoid the effects of overshoot at high velocities (Gransberg and Knutsson 1983). An acceleration ramp of 5° was used for the 30 and 90° $\cdot$ s^{-1} tests and a 15° ramp for the 270° $\cdot$ s^{-1} test, respectively. A deceleration ramp of 5° was applied in all tests. The total range of motion was 85° (between 90 and 5°). In addition, an isometric measurement was made at a knee angle of 60° (0° = straight leg). The subjects were familiarized with the test procedures on a separate occasion before the first test. Actual tests were preceded by a warm-up session on the dynamometer consisting of 4–6 submaximal efforts at each velocity and action mode. The tests consisted of at least two trials for each eccentric, concentric and isometric action, administered in a random order. The test with the highest peak torque was chosen for further analysis. A rest of approximately 2 min separated each trial. Measurements taken from the torque curves were peak torque and the position (knee angle) for peak torque for each eccentric and concentric trial. The isometric trials consisted of 4 s of maximal effort. The highest stable torque was taken for analysis.

Magnetic resonance imaging

Measurements of the cross-sectional area of the quadriceps muscle were made using the magnetic resonance imaging (MRI) technique (1.0 T superconductive magnet). A T1 weighted fast focusing sequence was used to obtain 10-mm thick images. Echo time was 0.023 s and repetition time of axial scans was 0.5 s. Two axial scans were made of the thigh musculature of each leg with the subject resting in a supine position, one at half femur length (midpoint) and the other 12-cm distally from that point (distal point). Femur length was measured with a ruler between the lateral femoral epicondyle and the trochanter major and the midpoint was marked with waterproof ink to ensure the same measuring point on all test occasions. Care was taken to make sure that the legs were kept parallel by controlling the positions of the feet, knees and pelvis. The MRI images were analysed with an interactive software package, MIS 100 Image Analysis System (Radiofysik AB, Sweden) on a UNIX System. Quadriceps muscle areas were quantified on the transverse images by a pixel counting routine. All areas were measured on one occasion by the same person, working with unmarked images which were later decoded. Area ratios were calculated between trained and non-trained legs in order to avoid effects of possible inconsistencies in the exact location of the scans. One subject in CTG did not attend the MRI measurements.

Muscle biopsy and histochemical methods

Skeletal muscle samples were obtained at rest from the vastus lateralis muscle using a needle biopsy technique (Bergström 1962). Biopsies were immediately frozen in liquid nitrogen and stored at −70°C. Serial transverse sections (10 μm) were cut with a microtome at −20°C and stained for myofibrillar Adenosine triphosphatase activity after preincubation at different pH intensities (Padykula and Herman 1955) for fibre type classification into types I, IIa and IIb (Brooke and Kaiser 1970). The relative occurrence of fibre types and mean fibre areas were determined using an image analyser (COMFAS system, Bio-Rad, Denmark). The average number of fibres per section analysed was 143 (range 39–230). Biopsy data from one subject in each group are missing.

Training and testing protocol

All the subjects trained three times a week for a total of 20 weeks. During the first 10 weeks the left leg was trained and during the second 10-week-period the right leg was trained. The ETG always performed eccentric training and CTG concentric training. Each training session consisted of four sets of ten consecutive maximal isokinetic knee extensor actions. Sets were separated by a rest of about 2 min. The subjects were told to exert maximally over the whole range of motion (85°). The training velocity was $90° \cdot s^{-1}$, i.e. every single action lasted about 1 s with roughly 1 s of passive return until the next maximal effort. The other, non-training, leg hung freely. During the training period, data were collected once a week, including torque and work outputs for each single repetition. Training data are reported here as mean angle specific (60°) torques. The subjects were instructed not to do any additional specific strength training for the knee extensors during the period of the experiment.

Tests were carried out on three occasions: (i) before the first training period (pre), (ii) after the first training period (mid) and (iii) after the second training period (post). The tests were performed 2–6 days after the last training session of each period. On every test occasion strength and cross-sectional area were measured and biopsies taken from both legs.

In the Results section, data are reported for each leg separately (five trained and five non-trained legs per group). During the first 10-week period the left leg was the trained leg, the right leg being referred to as the control leg. In the second training period, during which the right leg was trained, the left leg was referred to as the detrained leg (Thorstensson 1977). In addition, all trained legs in each group were lumped together, i.e. left leg pre plus mid and right leg mid plus post, and the results presented as mean values for ten trained legs.

Statistics

Standard statistical methods were used to calculate means and standard error of the means (SEM). A Student's *t*-test for dependent samples was used to evaluate changes within training groups, and a Student's *t*-test for independent samples for inter-group comparisons. Significance was accepted at $P < 0.05$.

Results

Initial torques

A comparison between peak torques within velocity and muscle action type revealed no significant differences between training groups in the pre-test (Table 1).

Training progression

Both training groups performed an average of 25 training sessions per leg. Average torque (Fig. 1) and work output during training tended to increase over the training period for both training groups and for both legs. The subjects were told always to exert maximally, resulting in high training intensity and total training load, especially for ETG. Average overall torque values during training for CTG were 66% and 77% of those for ETG for the left and right leg, respectively. Corresponding values for average work output were 75% and 86%. It would appear that the ETG subjects performed at a lower intensity in the second training period when the right leg was trained (Fig. 1). It is noteworthy that of the five subjects in ETG, four exhibited knee pain during training. For three of them the pain involved the left leg and for one the right leg. Furthermore, the same three subjects reported knee pain during the mid-test of the left leg and one of them also during the post-test of the left leg.

Peak torques

Comparisons for five trained legs showed, for ETG, a significant increase in the eccentric $90° \cdot s^{-1}$ test for the left leg (43%, pre to mid), and in the eccentric $30° \cdot s^{-1}$

Table 1 Peak torques (N.m) in isometric (knee angle 60°), concentric (*C*) and eccentric (*E*) knee extensor actions at different velocities (30, 90 and 270° · s^{-1}), before (*pre*), in the middle of (*mid*) and after (*post*) the 20-week experimental period for the eccentric (*ETG*, $n = 5$) and concentric (*CTG*, $n = 5$) training groups. Training was performed at 90° · s^{-1}

Velocity	ETG Left leg						CTG Left leg					
	Pre		Mid		Post		Pre		Mid		Post	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Isometric	213	19	222	32[a]	251	24	209	5	250	10*[a]	227	8*
C 30	214	19	197	27[a]	243	20*	212	16	242	15*[a]	226	11
E 30	269	17	294	26[a]	331	44	256	13	301	18*[a]	273	13
C 90	186	10	198	13[a]	202	16	182	12	206	13*[a]	192	11*
E 90	240	12	344	36*[a]	352	37	262	14	309	18**[a]	270	11*
C 270	123	6	129	9[a]	132	11	118	6	133	11[a]	118	7
E 270	232	12	234	26[a]	288	15*	267	18	299	25[a]	259	13
	Right leg						Right leg					
Isometric	214	23	231	16	250	18[a]	189	19	220	14	237	8[a]
C 30	216	17	217	14	232	25[a]	197	15	204	15	238	10[a]
E 30	261	24	289	26	338	37*[a]	240	19	268	32	288	13[a]
C 90	191	11	193	9	214	16[a]	177	9	195	8*	199	8[a]
E 90	251	18	291	28*	369	36**[a]	236	19	275	31	295	6[a]
C 270	127	12	137	8	125	10[a]	115	3	130	10	122	4[a]
E 270	235	20	243	14	269	24[a]	255	15	257	36	267	11[a]

[a] Peak torque values after training. Significant changes with respect to the occasion of the previous measurement * $P < 0.05$, ** $P < 0.01$

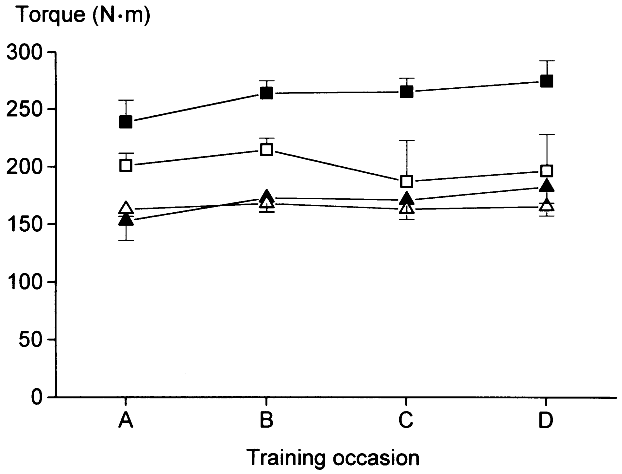

Fig. 1 Average angle specific (60°) torques (SEM) for four × ten repetitions on four training occasions (*A–D*) evenly distributed throughout the 10-week training periods for each leg and training group. *Solid squares* denote eccentric training group (ETG) left leg, *open squares* ETG right leg, *solid triangles* concentric training group (CTG) left leg and *open triangles* CTG right leg, respectively

and 90° · s^{-1} tests for the right leg (17% and 27%, respectively, mid to post; Table 1). For CTG, both concentric and eccentric torque values in the 30° · s^{-1} and 90° · s^{-1} tests as well as isometric torque were significantly increased after training for the left leg (13%–20%, pre minus mid). Similar tendencies were seen for the right leg (2%–17%, mid to post), although not reaching statistical significance (Table 1).

When ten trained legs per training group were compared before and after training (Table 2), significant increases in peak torque were present for ETG in the eccentric 30° · s^{-1} test as well as in the eccentric and concentric 90° · s^{-1} tests. The increase was clearly the largest in the eccentric 90° · s^{-1} test (35%). For CTG, significant increases were present in the isometric test and in the concentric and eccentric 30° · s^{-1} and 90° · s^{-1} tests (8%–15%; Table 2). In no case did the peak torques at the highest speed (270° · s^{-1}) change significantly with training.

Peak torques for the control (right) leg in ETG increased significantly after the left leg training period (pre to mid) in the eccentric 90° · s^{-1} test (16%). The corresponding comparison for CTG showed a significant increase in peak torque in the concentric 90° · s^{-1} test (10%). No other significant changes were present for the control leg (Table 1).

Peak torques for the detrained (left) leg (mid to post) in ETG increased significantly in the concentric 30° · s^{-1} and eccentric 270° · s^{-1} tests. For CTG, on the other hand, there were significant decreases in the concentric and eccentric 90° · s^{-1} and the isometric tests (Table 1).

Peak angles

No training induced changes were present for peak torque for either training group, leg or velocity. Averaged over both training groups and legs, knee angles for peak torque ranged from 76° to 62° for eccentric and from 74° to 66° for concentric trials, respectively, the highest values ocurring at the lowest velocities.

Cross-sectional areas (MRI)

In ETG, there was a significant increase (+5.7%) in quadriceps muscle cross-sectional area at the distal measuring point for the left trained leg in relation to the

Table 2 Peak torques (N.m) for ten trained legs (left + right) before and after 10 weeks of training for the two training groups. Training was performed at 90° · s^{-1}. Conditions and abbreviations are the same as in Table 1

Velocity	ETG				CTG			
	Before		After		Before		After	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Isometric	222	12	236	18	214	7	244	6**
C 30	215	11	215	18	208	10	240	8**
E 30	279	15	316	23*	262	16	295	11*
C 90	190	6	206	10*	188	7	203	7*
E 90	266	17	356	25***	269	16	302	9*
C 270	130	5	127	6	124	6	128	6
E 270	237	9	252	18	262	19	283	14

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

right, control, leg ($n = 5$). No other significant changes were seen for either measuring point or leg, including the control and detrained legs, in the two training groups.

For ten trained legs, ETG showed a significant increase in cross-sectional area after training (Fig. 2), again only for the distal measuring point (+3.5% vs the non-trained legs). A trend towards a corresponding increase was present for CTG ($n = 8$) at the midpoint, although not reaching statistical significance ($P = 0.061$).

Muscle fibre data

No significant changes in muscle fibre composition, absolute or relative areas were observed with training for either leg or training group, or for the control or detrained legs ($n = 4$). This was the case also when comparing eight trained legs (Table 3). Absolute areas tended to increase (although non-significantly) in all fibre types for ETG as well as for CTG. Small, but statistically significant decreases with training were present in ETG for the relative number and area of type IIa muscle fibres.

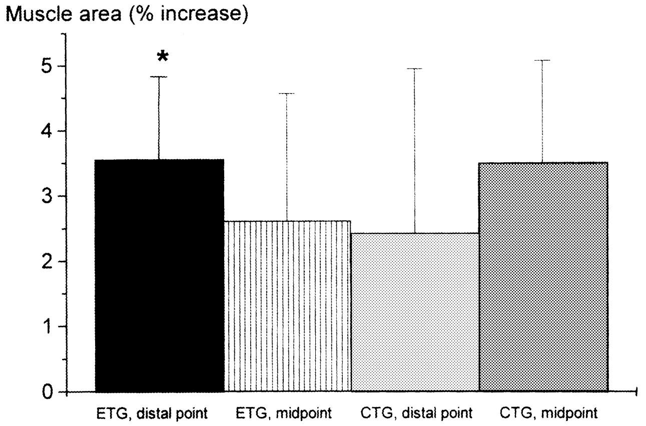

Fig. 2 Mean percentage increase (SEM) in cross-sectional area of the quadriceps muscle at two locations (distal and mid, see Methods) in trained versus non-trained legs, in the eccentric (*ETG*, $n = 10$) and concentric (*CTG*, $n = 8$) training groups, respectively. $P < 0.05$

Discussion

The major finding in this study was that training with pure eccentric and concentric muscle actions resulted in mode and velocity specific gains in strength in the trained leg, but also, and with an even more pronounced specificity, in the contralateral, non-trained leg.

Training stimulus

The training paradigm was chosen to enable the evaluation of specific effects related to muscle action type (mode), that is to training with pure eccentric and concentric muscle actions. Rather than using free weights, an isokinetic (constant velocity) technique was employed both for training and measuring muscle strength. This technique, as used here, implied that maximal voluntary efforts were to be produced and maintained over the major part of the range of motion in each repetition. Both the constant velocity and maximal actions represented deviations from common strength training paradigms. Using maximal efforts meant that the progression in the training, that is the successive increase of the submaximal load over the training period, keeping the relative load approximately constant (e.g. 60%–80% of maximum), could not be accomplished. It has been thought that such a progression may be a critical determinant of the increase in strength (Dudley et al. 1991). Otherwise, the training was performed with a perodicity, number of repetitions, sets and rest intervals, that is compatible with other common strength training routines.

It has been well established that maximal force output of a muscle varies with speed of shortening and lengthening. Similar relationships have also been documented for the torque (strength) output of muscle synergies and angular movement velocity at a certain joint, e.g. the knee joint, in humans (e.g. Westing et al. 1988). An isokinetic approach meant control of speed of motion in training and testing and also made possible conclusions about possible velocity specificity in the response to training.

Table 3 Muscle fibre composition, absolute and relative area per fibre type in biopsies taken from the vastus lateralis muscle before and after the 10 weeks of training for the eccentric (*ETG*, $n = 8$) and concentric (*CTG*, $n = 8$) training groups

	ETG				CTG			
	Before		After		Before		After	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Fibre composition (%)								
Type I	46	3.8	48	5.2	54	4.2	57	5.4
Type IIa	41	2.7	37	2.0*	33	3.2	31	4.3
Type IIb	13	2.9	15	4.0	13	1.7	12	2.4
Absolute area (μm^2)								
Type I	5585	386	6163	479	4595	325	5677	691
Type IIa	7336	445	7440	674	5792	571	6483	855
Type IIb	6648	696	6984	557	5355	628	5884	689
Relative area (%)								
Type I	40	3.7	44	5.3	49	3.6	55	5.2
Type IIa	47	2.4	40	2.2*	37	3.1	33	4.0
Type IIb	13	2.9	16	3.9	14	1.4	11	2.0

*$P < 0.05$

It is important to realize that the maximal strength output at a certain velocity is higher in eccentric than in concentric muscle actions (e.g. Westing et al. 1988; Westing and Seger 1989). Thus, the training stimuli for the two groups in the present study, and in most previous ones, do not only differ with respect to mode of muscle action (lengthening versus shortening), but also with respect to absolute load. Here, the absolute training load was clearly higher for the eccentric compared to the concentric training (Fig. 1). On the other hand, using the same absolute load would have resulted in a difference in relative load, which has been suggested to be an important determinant for the strength training effects (DeLorme 1945). This inherent variation in training load with muscle action type is a general dilemma found in studies aimed at comparing the effects of muscle action type per se.

The two muscle action types also differ with respect to electromechanical efficiency, that is, it has been shown that a certain force, including that voluntarily possible, can be produced with a lower activation (EMG) level eccentrically than concentrically (Westing et al. 1990). Eccentric actions have also been found to be more metabolically efficient (Ryschon et al. 1997). Pertinent to the evaluation of the two training paradigms are also the differences in fatiguability and thus possible metabolic stimuli to strength gain. Available data have indicated that the decline in strength with repeated maximal eccentric actions is considerably less than during corresponding concentric ones (Tesch et al. 1990; Westblad and Johansson 1993). This was also the case within the sets of repetitions applied here. Finally, it has been well established that eccentric muscle actions lead to an augmented risk for muscle damage (Stauber 1989). In fact, studies aiming at inducing muscle soreness have generally employed eccentric muscle actions (e.g. Fridén et al. 1983). In line with this, there were more frequent complaints about knee pain in ETG, particularly during the first 10 weeks of training of the left leg.

Effects on strength

Trained leg

The increases in peak torque with training in this study were of the same order of magnitude, or somewhat lower, than those that have been reported from training studies of similar intensity and duration (Duncan et al. 1989; Colliander and Tesch 1990; Hortobágyi et al. 1996). In ETG, four of the five subjects experienced knee pains most likely affecting both their training intensity and ability to perform maximally during testing (mid-test). This is further emphasised by the increases in peak torque observed for this group during the subsequent detraining period. In this perspective, the 35% increase in peak eccentric torque at the test velocity achieved by ETG is rather remarkable.

The present results indicated a mode-specific adaptation in peak torque for the eccentric training group, where the overall average torque increased over all three velocities by 18% for eccentric actions and by only 2% for concentric actions. For the concentric training there was a less clear specificity, with concentric and eccentric values being 14% and 10%, respectively. Other studies on eccentric and concentric isokinetic training of the knee extensors have produced similar results. Thus, a more pronounced mode-specific response with eccentric training has been reported by Duncan et al. (1989) and Hortobágyi et al. (1996) for young men and by Higbie et al. (1994) for young women training either eccentrically or concentrically at comparable speeds ($60–120° \cdot s^{-1}$) and durations (6–12 weeks).

Velocity specificity in the response to strength training has been extensively discussed but it has not been possible to draw any definite conclusions from available data, either for concentric or eccentric muscle actions (Bell and Wenger 1992; Behm and Sale 1993; Kellis and Baltzopoulus 1995). Some indications of velocity specificity were present in our data. Thus, there were no increases in strength at the highest testing velocity in either of the training groups. Furthermore, the effects of eccentric training were most marked at the training velocity (significant increases in both eccentric and concentric strength at $90° \cdot s^{-1}$), whereas strength gains with concentric training occurred at all velocities equal to and lower than the training velocity. The results on eccentric training are in contrast to the conclusion by Kellis and Baltzopoulos (1995) who have stated that "based on current knowledge, eccentric exercise does not appear to be velocity-specific". However, it appears that some of the discrepancies between various studies can be explained by the inconsistencies in definitions of speeds as "slow", "intermediate" or "fast". In this context it should be noted that even speeds classified as "fast", i.e. $180–300° \cdot s^{-1}$, still only correspond to about one-third of the maximal speed that has been achieved in knee extension with an unloaded lower leg (see Thorstensson et al. 1976a).

Non-trained leg (cross-education)

Perhaps the most conspicuous finding in the present study was the highly specific strength gains in the contralateral, untrained, leg during the initial 10 weeks of training. This increase in strength showed both mode and speed specificity. The spread of the training effects to the untrained limb, so-called cross-education, is a well-established phenomenon following training with isometric and concentric muscle actions (e.g. Moritani and deVries 1979; Kannus et al. 1992; see also Enoka 1988). In a recent study, Hortobágyi et al. (1997) have demonstrated cross-education also for eccentric strength training. These authors have also reported clearly greater mode-specific cross-education following training with lengthening rather than with shortening contractions (77% vs 30%). The present data showed a similar trend, although it was much less marked (15% vs 10%).

The mechanism underlying the cross-education phenomenon is still unknown. However, general agreement has been found in the literature (Enoka 1988) that the adaptations occur in the central nervous system. One piece of evidence for this is has been that there is essentially no activation of the corresponding muscles in the contra-lateral limb (Devine et al. 1981). In our experimental setup the contralateral leg hung freely, without straps, and seemed, from visual inspection, to be only marginally involved. If anything, there appeared to be contra-lateral knee flexion, which has been substantiated by EMG recordings from Hortobágyi et al. (1997). Other indirect evidence for central neural adaptation is the lack of changes occurring in the contralateral muscle itself. This was indicated by the present results as well as by previous studies (see below).

Naturally, the fact that there was cross-education from the trained left leg to the untrained right leg during the initial training period might have affected the magnitude of the training response in the right leg during the second training period. The relatively higher initial strength level for the right leg may explain the smaller training effects obtained during this training period. In addition, the lower training intensity, particularly for ETG (Fig. 1), may have contributed. Cross-education may also have caused a reduction of the detraining effects on the left leg during the second 10-week period. This should be borne in mind when evaluating the results, not least those obtained by pooling the training data for the left and right legs to obtain a larger basis for comparison.

Effects on muscle morphology

Muscle cross-sectional area

It has been well established that systematic strength training of a muscle eventually leads to an increase in its mass and cross-sectional area. Compared to what has been reported from previous strength training studies of similar intensity and duration, the currently observed increases in muscle cross-sectional areas of 3.5%–5.7% were relatively small. In comparison, Garfinkel and Cafarelli (1992) have found a 15% increase in cross-sectional area of the quadriceps muscle after 8 weeks of isometric training and Narici et al. (1989) have reported an 8.5% increase in knee extensor area after isokinetic concentric knee extensor training for 60 days.

Although by no means conclusive, our data could suggest a mode-specific training effect, in that a significant increase in muscle cross-sectional area was seen only after eccentric strength training. Such mode-specificity has been indicated in experiments on animal muscle preparations subjected to electrical stimulation simulating strength training. Wong and Booth (1990a, b) have reported that such chronic stimulation of the rat gastrocnemius and tibialis anterior muscles resulted in muscle enlargement under eccentric but not concentric conditions. It has been suggested that a supremacy of eccentric actions as a stimulus for muscle hypertrophy could be mediated by a mode-specific control of protein synthesis (Booth and Thomason 1991). However, studies on humans have not provided a coherent picture in this respect. Higbie et al. (1994) have trained female subjects for 10 weeks and found that eccentric training caused a significantly larger increase in knee extensor muscle area than concentric training (6.9% vs 5%). On the other hand, non-mode-specific muscle enlargements were obtained in studies of the quadriceps muscle (Jones and Rutherford 1987; Carey Smith and Rutherford 1995) as well as the upper arm (Hortobágyi and Katch 1990).

It is also noteworthy that there seems to be a location-specific response in hypertrophy of the quadriceps femoris muscle group. The increase in muscle cross-sectional area after eccentric training was located in the distal part of the thigh. This is in line with the common observation in our laboratory, that eccentric muscle actions cause initial discomfort mainly in the distal, medial part of the thigh, corresponding to the distal part of the vastus medialis muscle. In contrast, Narici et al. (1989) have applied concentric training of the knee extensors and found the largest increase in the quadriceps muscle area in the proximal portion of the muscle group. Our data for CTG showed a tendency towards an increase (mean 3.4%) in the mid-position of the thigh, that is a more proximal position than for ETG.

Muscle fibre characteristics

In line with the minor changes in total muscle cross-sectional area seen with training, the overall effects at the muscle fibre level were small. Absolute muscle areas did not show significant changes with any of the interventions. Although unchanged muscle fibre areas have been reported before (Colliander and Tesch 1990) the common observation has been that of hypertrophy of muscle fibres with heavy resistance training (MacDougall et al. 1980). It is interesting that Narici et al. (1996), in a concentric knee extensor training study, have found no changes in fibre cross-sectional area despite a considerable increase in proximal and distal quadriceps cross-sectional area (19%). This could have been due to the position of the sampling site since the site of the biopsy actually coincided with the portion of the vastus lateralis muscle which displayed the least hypertrophy (5%) after training.

Furthermore, this hypertrophy has in general been found to be more pronounced in the type II muscle fibres (Thorstensson et al. 1976b; MacDougall et al. 1980). This can be related to the size-principle that has been proposed for motor unit recruitment (Henneman 1957), in that larger motor units are brought in at higher tension levels and thus receive a higher relative loading than during activities of daily life. Generally, type II muscle fibres have not been subdivided into type IIa and IIb in studies on muscle hypertrophy or recruitment.

A change in recruitment order has been indicated for eccentric muscle actions in a study on single motor units at low force levels (Nardone et al. 1989). Provided that the preferential recruitment of large motor units (type II) occurs also at maximal or close to maximal eccentric muscle actions, it would imply that selective effects could be expected on the muscle fibre level. As mentioned, no such effects were seen in the present study nor in the studies of Colliander and Tesch (1990) or Hather et al. (1991) who have compared pure concentric training with hybrid training including both concentric and eccentric muscle actions. In contrast, Hortobágyi et al. (1996), employing a similar training paradigm as ours, have reported a 38% increase in type II fibre area after eccentric training, whereas concentric training had no effect on muscle fibre area at all. It is of interest that when training was performed at the same level of submaximal power (equivalent to 90% of maximal concentric torque, i.e. much lower in relation to eccentric maximum), concentric training has been reported to cause greater increases in type II muscle fibre area and maximal isometric strength than eccentric training (Mayhew et al. 1995). There was no indication of effects of cross-education at the muscle fibre level, which is in accordance with observations that have been made earlier (Housh et al. 1992; Hortobágyi et al. 1996).

It may be worth mentioning that the tendency towards a decrease in percentage of type IIa muscle fibres after eccentric training observed here is at variance with earlier studies. Hortobágyi et al. (1996) have found that the percentage of type IIa increased and type IIb decreased to a similar extent after both eccentric and concentric training. Similar results have been reported by Hather et al. (1991) in concentric and hybrid training. There is no obvious explanation for this discrepancy, or for the selective change in the number of type IIa muscle fibres. It should be realised that extrapolating results from muscle biopsy studies on humans, always raises a question as to the representativeness of the sample with respect to the whole muscle. This problem is accentuated when the number of fibres per sample is low, as in our study. Furthermore, two of our subjects did not fulfil their commitment regarding the biopsy tests and had to be excluded. Thus, a certain amount of caution is warranted in the interpretation of the muscle fibre results in the present, as well as in other studies. Also, training induced changes may well occur at the subcellular level in the muscle and in the connective tissue, which would not be revealed by a conventional histochemical analysis. Naturally, neural mechanisms are in addition likely candidates for explaining the specific gains in strength attained by training with different action types and speeds.

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