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ORIGINAL ARTICLE

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The effect of varying the time of concentric and eccentric muscle actions during resistance training on skeletal muscle adaptations in women

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Abstract This study investigated the effect of manipulating the time to complete both the concentric (CON) and eccentric (ECC) muscle actions during resistance training on strength, skeletal muscle properties and cortisol in women. Twenty-eight women (mean ± SE age = 24.3 ± 1.1 year) with strength training experience completed three training sessions per week for 9 weeks. Two sets of four lower body exercises (leg press, parallel squat, knee extension and knee flexion) were completed using 6–8 RM intensity. The long CON (LC) group performed the CON action for 6 s and the ECC action for 2 s, while the long ECC (LE) group completed the CON and ECC phases for 2 and 6 s, respectively. Both groups experienced significant increases in leg press CON only, ECC only and combined ECC and CON maximal strength (1 RM). Immunohistochemical analyses demonstrated that both types I and IIA vastus lateralis fibre areas significantly increased following LC training while only type I fibre area increased following LE training. There was a decrease in MHCIId(x) with a concomitant increase in MHCIIa ($P < 0.05$) in both groups. Twenty-four hour urinary cortisol significantly increased after LC training only. It was concluded that LC resistance training was more effective than LE for increasing both types I and IIA fibre area and cortisol when time under tension and intensity of muscle actions were matched between the two modes of resistance training in young healthy women.

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Introduction

Dynamic constant external resistance (DCER) training, in which the concentric (CON) and eccentric (ECC) load is the same for both muscle actions, is the most commonly used mode of resistance training. However, it has been shown that CON and ECC muscle actions differ with regard to their maximal force generating capabilities, metabolic energy cost, neural activation and the extent to which they induce muscle damage (Dudley et al. 1991a; Nakazawa et al. 1993; Ryschon et al. 1997; Aagaard et al. 2000; Gibala et al. 2000). It has also been suggested that both these actions are necessary for optimal development of muscular strength and hypertrophy (Dudley et al. 1991b; Hather et al. 1991). Despite this knowledge, the underlying mechanisms and the influence of these opposing muscle actions on strength development and fibre hypertrophy are still not completely understood, especially with respect to the relative time devoted to each action (Gillies and Docherty 1999).

The effect of manipulating the relative time under tension (TUT) of the CON and ECC actions during DCER training on muscle strength and fibre hypertrophy has received little attention. The few investigations that have manipulated the TUT for CON muscle actions have used 2 s or less (Young and Bilby 1993; Morrissey et al. 1998) or a longer CON TUT of 8 vs. 2 s (Gillies and Docherty 1999). These investigations reported equivocal effects with different CON TUT during training on combined maximal strength. However, the use of a longer time to complete the CON muscle action during training resulted in significantly greater muscle hypertrophy compared to a shorter CON protocol (Gillies and Docherty 1999). The results of this latter investigation suggest that muscle hypertrophy may be maximized with slower movements that emphasize the CON phase, although

this remains to be substantiated. Consistent with this latter research, Mikesky et al. (1989) reported that muscle hypertrophy was highly correlated with the length of time to complete the CON movement using a rodent weight lifting model. Collectively, these studies indicate that TUT during the CON muscle action is important to maximize hypertrophy. Nevertheless, the influence of ECC TUT during DCER exercises on strength development and muscle fibre hypertrophy has not been elucidated. Furthermore, comparing the effects of TUT longer than 2 s for either the ECC or CON muscle actions, also has not been adequately investigated.

Therefore, the purpose of this study was to investigate the effects of resistance training, with different times for the CON and ECC muscle actions but with the total TUT equated, on maximal strength development, muscle fibre cross-sectional areas (CSA), patterns of myosin heavy chain (MHC) expression and urinary cortisol concentrations. It was hypothesized that prolonging the relative TUT of the CON and ECC actions while equating the time spent performing the different actions would improve strength, increase muscle fibre area and raise cortisol levels. Additionally, it was hypothesized that there may be a differential training-induced adaptation in muscle fibre type morphology and MHC isoforms as a result of manipulating the TUT for CON and ECC muscle actions. Alterations in MHC isoforms were hypothesized to mirror the changes in fibre type area and MHCIId(x) isoform would be decreased in both training groups.

Methods

Subjects description and experimental design

Twenty-nine women with current resistance training experience, defined as adhering to a program of multiple sets of various upper and lower body exercises performed with 8–12 repetitions to failure, 2–3 times per week for a minimum of 8 weeks prior to recruitment to the study, volunteered to participate in this study. All subjects were initially ranked in order by leg press one repetition maximal (1 RM) strength and each consecutive pair of subjects were randomly assigned to one of the two experimental training protocols to ensure that both groups had similar strength levels prior to training. Initial randomization resulted in one additional subject assigned to the group that emphasized the long CON (LC) muscle action during training ($n = 15$). One subject assigned to the group that emphasized the ECC muscle action during training long ECC (LE) was unable to complete all training and testing requirements for reasons not related to the study and this data was removed (final $n = 13$). The remaining 28 subjects had a mean ($\pm$ SE) age of 24.3 (1.1) year, height of 164.6 (1.4) cm, body mass of 66.7 (1.7) kg, BMI of 24.7 (0.7) kg m^{-2}) and body fat of 17.6 (0.9)% calculated from the sum of six skin-fold sites (subscapular, tricep, iliac crest, abdominal, front and rear thigh) performed in triplicate by the same tester before and after training. The body fat prediction formula used was: [(sum of six skin-folds $\times$ 0.217)$-$4.47] as it was based on Canadian college-aged women (Yuhasz 1966). A University Research Ethics Board approved this study and written informed consent was obtained from each subject.

All subjects continued with their usual resistance-training regimen albeit at a frequency reduced to 1–2 times per week for 4–6 weeks before commencing training so that the start of study could be coordinated with the menstrual cycle. Each subject was stratified according to menstrual status of pharmacological contraceptive use or no use. Subjects not using contraceptives commenced training between days 4 and 6 of their menstrual cycle (i.e. early follicular phase) while those using contraceptives began training during days 22–24 of their cycle. This enabled the onset of training to occur at a time when circulating estrogen levels were low.

Strength testing

Three different maximal voluntary strength (1 RM) tests were conducted prior to, mid-way and after training: 1 RM CON, 1 RM ECC and a combined ECC/CON 1 RM for incline (0.785 rad) bilateral leg press exercise. The CON only test started with a knee joint angle of 1.57 rad (90°) for leg press and the load was fully supported at the start position by fixed supports. Following a verbal command from the subject, the load was released and momentarily supported ($\sim$1 s) by the subject prior to the CON lift phase. The ECC only 1 RM was assessed in a similar fashion by release of the load being supported by assistants and after the subject's verbal indication. After a momentary support of the load, it was lowered through the ECC phase. Both the CON only and ECC only 1 RM strength tests were performed throughout the same standardized range of motion (ROM). Additionally, the subjects were instructed to perform the CON strength test phase "as hard and fast as possible" while the ECC strength test required a controlled timing of 3 s duration (using a handheld stopwatch) through the full ROM. The combined ECC/CON test involved lowering the load over a 3 s duration and then raising it to full extension throughout the same ROM. Failure during the CON and combined ECC/CON 1 RM attempts was determined by inability of the subject to achieve full extension while failure during the ECC 1 RM test was determined when the subject was unable to control the descent in the required time throughout the full ROM. Verbal encouragement was consistently given during all 1 RM attempts and subjects were instructed to "push up as hard and fast as possible" during the CON actions of the CON and combined action tests and to "maintain control and lower the load with an even velocity" throughout the ROM during the ECC strength tests. Five minutes of rest was given between subsequent 1 RM attempts. Test order for the

CON, ECC and combined strength tests were randomized for the pre-training session and this order was maintained for subsequent tests. Test-retest reliability for combined, CON and ECC 1 RM was assessed using five subjects tested 3–5 days apart and produced intraclass coefficients (ICC) of 0.986, 0.994 and 0.965, respectively (Maguire and Hazlet 1969).

Muscle biopsy procedure

Muscle samples were obtained before and after training using the needle biopsy technique as previously described for our lab (Bell et al. 2000). Tissue samples were taken from a site approximately one-third of the length from the proximal lateral edge of the patella to the anterior superior iliac spine of the lateral aspect of the left vastus lateralis muscle. Once obtained, the samples were immediately oriented and mounted on cork in embedding medium (OCT, Tissue Tek, Miles Laboratories, Naperville, IL, USA), frozen in melting isopentane (−159°C) pre-cooled in liquid nitrogen and stored in an ultra low freezer at −80°C until analysis. Note that muscle biopsies of two subjects (one from each training group) were of insufficient size for the analyses. Due to this, all analyses regarding muscle fibre CSA, fibre type proportions and MHC isoform content is based on a sample 26 subjects.

Immunohistochemistry

Serial 8-μm thick transverse sections were cut at −20°C in a cryostat (Tissue Tek, Miles Laboratories, Elkhart, IN, USA), mounted on poly-L-lysine coated slides (Cedarlane Laboratories, Hornby, ON, Canada) for analysis of fibre type identification. The samples from both before and after training were mounted and assayed on the same slide to avoid inter-assay variation. Fibre types were classified using the following monoclonal antibodies (mAb) directed against adult MHC isoforms: MHCIβ (clone BA-D5), MHCIIa (clone SC-71) and MHCIIb (BF-F3). As well, mAb directed against $MHC_{embryonic}$ (clone BF-45) was used to detect regenerating muscle fibres. Positive staining using the corresponding mAb identified pure fibre types. Mixed type I/IIA fibres were identified as staining positive for both MHCI and MHCIIa. As no mAb for human MHCIId(x) was available, type IID(X) fibres were identified by the absence staining using this panel of antibodies. The immunohistochemical procedures were identical to those previously detailed for our lab by Putman et al. (2003, 2004).

Morphometric fibre analysis

Serial sections immunohistochemically stained for various MHC isoforms were visualized with a computer inter-faced light microscope (Leitz Diaplan, Ernst Leitz Wetzlar GmbH, Wetzlar, Germany) fitted with a Pro Series High Performance CCD camera (Media Cybernetics, Silver Springs, MD, USA) for analysis as previously described for our laboratory (Putman et al. 2004). Fibre CSA measurements were made using a semi-automated image-analysis software program (Image-Pro Plus 4.0, Media Cybernetics) with the same magnification for all analyses. The camera was calibrated with a known measurement scale. All fibres within a given section were used to determine fibre type proportions (for all subjects combined; mean (SE), minimum–maximum: 695 (71), 101–1,705 fibres/sample) while CSA measurements were made on 1–2 images of the section (~60–100 fibres per image) or on all fibres of one type if there were less than 50 fibres of a type. For all subjects combined, CSA was measured on [mean (SE), minimum–maximum number of fibres] 65 (4), 12–123 type I fibres and 58 (5), 20–151 type IIA fibres. Mixed type I/IIA fibres and IID(X) fibres were too few in number to confidently analyse CSA.

Myosin heavy chain isoform content

Myosin heavy chain isoform analyses were completed according Putman et al. (2003, 2004). An amount of 10 μl of standardized muscle extract (1.5 μg/10 μl sample vol) was loaded in each lane and run for 24 h at 10°C at 275 V using a Hoefer SE 600 electrophoresis system (Amersham Biosciences, Montreal, Que., Canada). All samples were measured in duplicate and the coefficient of variation (CV) of duplicate measurements of total protein content was 6.5%. The CV for the relative MHC isoform content on duplicate gels was 3.9, 3.3 and 10.4% for MHCI, IIa and IId(x), respectively.

Radio-immunoassay for cortisol

Twenty-four hour urinary cortisol was measured before and after training as a physiological indicator of training stress. Urine collection commenced 6 h post-training session and continued until 30 h after the training session. During week 1, the collection period followed the second training session, and during week 9, the collection period followed the third training session of the week. The total volume of urine was measured and an aliquot was stored at −80°C until analysed. Urinary cortisol was measured using a commercially available kit (DiaSorin, Stillwater, MN, USA). All samples were run in duplicate with a mean intra-assay CV of 8.2% for duplicate samples.

Resistance training programs

Both groups were matched for the total time spent under muscular tension (TUT) defined as the time to complete the CON muscle action plus the time to complete the ECC action, along with a 1 s pause between actions. The CON group performed the CON action in 6 s and the ECC action in 2 s, while the ECC group performed the CON action in 2 s and the ECC action in 6 s. This was based on average velocities of approximately 0.2 and 0.8 rad s^{-1}. These velocities were chosen in order to attempt to match the total time of both muscle actions

and minimize or equalize the effects of muscle activation related to the velocity of the muscle actions as determined in our laboratory (Gillies et al. 2000). Acceleration at the start of each repetition was not strictly controlled other than each action was preceded with a 1 s pause to minimize the effects of the stretch-shortening cycle and each subject was consistently reminded to maintain an even velocity throughout the ROM and avoid any rapid acceleration at the initiation of each movement during supervision of training.

Each training session consisted of the primary four lower body exercises performed in the following order: bilateral incline leg press, parallel squat, bilateral leg extension and leg flexion. To provide some balance to the training program and because the subjects were previously accustomed to doing both upper and lower body resistance training, bench press and a choice one of three other upper body exercises (bilateral bicep curl, lat pull down or seated row) were performed each session. Thus, a total of six exercises were completed per session. Subjects performed two sets of each exercise with a resistance that elicited technical failure within 6–8 repetitions (6–8 RM) with 2.5 min of rest between sets. The load was progressively increased approximately 2.5–5% when subjects were able to complete eight or more repetitions during the second set of an exercise. Each training and testing session was preceded by a 5 min warm-up on a cycle ergometer and 5 min of general static and dynamic stretching. Each subject used a metronome to control the timing of each muscle action during training. Training load and repetitions for all exercises were recorded in a logbook and all training sessions were supervised.

The resistance training sessions were performed three times a week for 9-weeks except for the fifth week which consisted of one training session, a "rest" day and a 1 RM testing session. The relative training load of leg press was determined as the mean training load during the second training session of week 1 and the third session of weeks 5 and 9, and expressed relative to the 1 RM combined strength of each respective 1 RM test. The weekly mean number of repetitions per set was determined as the mean number of repetitions completed during all sets of an exercise during each week. Training load for each week was determined as the mean load utilized during all sets of each exercise. Training volume for each week was calculated by the sum of load x repetitions for each set.

Dietary monitoring

Dietary intake was monitored over a 3 days period, every 2 weeks throughout the duration of the investigation (total of five recording periods). Subjects were provided with a checklist of the amount of protein in various foods in an attempt to maintain a daily protein intake of 1.5 g kg^{-1} body mass day^{-1} throughout the study. It was deemed important to monitor protein intake as protein requirements are increased with resistance training (Lemon 1991; Andersen et al. 2005). Food intake, quantity and time ingested were recorded in booklets, with caloric and macronutrient intake determined using The Food Processor software (ESHA Research, Salem, OR, USA).

Statistical analyses

An independent sample Student's t-test was used to determine whether there was a difference between training groups for all baseline measurements. Separate two-way analysis of variance (ANOVA) with repeated measures was used to determine whether there were differences between groups over time (repeated measure) for the dependent variables of strength, training variables (% of 1 RM, average repetitions per set, average load per set and training volume), cortisol response and protein intake. Separate three-way ANOVA's were performed to analyse the effects of group and time with the variables of muscle fibre type area, proportions of muscle fibre type and MHC isoform proportions. A between factor of oral contraceptive use or non-use was initially included in all analyses but this factor did not demonstrate any significant main effects and thus the groups were collapsed across menstrual status. A Newman–Keuls multiple comparison procedure was used to locate differences when significant main effects or interactions were found. Results are reported as means ± SE. All statistical analyses were carried out using the statistical software program Statistica 5.1 (StatSoft, Tulsa, OK, USA) and actual P-values are reported.

Results

Baseline comparisons

Before training, there was no difference between groups for age, height or other physical measurements (see Table 1). Mean (SE) menstrual cycle length with no oral contraceptive use during the cycle preceding commencement of training and over the training duration was 27.9 (0.6) and 28.3 (0.4) days for LC and LE, respectively, and did not differ between groups. Training compliance for the supervised 24 training sessions did not significantly differ between groups and was 99.4 (0.4) and 98.4 (0.6)% of total training sessions for LC and LE, respectively. Body composition was altered similarly in both groups following training (Table 1).

Strength

Figure 1 shows the combined ECC/CON, CON and ECC leg press 1 RM values before, midway and after training. For all strength assessments, a significant main effect for time indicated that both groups experienced a similar increase (all $P < 0.001$) in maximal leg press strength with training. The relative increases in leg press 1 RM strength for combined ECC/CON, CON and ECC were 25.2 (2.6), 21.3 (2.9) and 43.6 (4.0)%, respectively.

Table 1 Anthropometric measurements and body composition for the long concentric (LC) and long eccentric (LE) training groups, before and after training in young women

Variable	LC ($n = 15$)		LE ($n = 13$)	
	Before	After	Before	After
Body mass (kg)	65.4 (2.1)	65.2 (1.8)	68.1 (2.9)	68.9 (2.9)
Sum of six skin-folds (mm)[a]	90.9 (5.0)	86.7 (3.3)*	105.9 (6.4)	100.4 (5.0)*
Thigh skin-folds (mm)[b]	38.4 (3.2)	34.1 (1.9)*	41.5 (2.4)	38.1 (1.7)*
Mid-thigh girth (cm)	49.4 (0.7)	49.8 (0.7)*	50.7 (0.9)	51.3 (0.8)*
Body fat (%)[a]	16.2 (1.3)	15.1 (0.8)*	19.2 (1.5)	18.0 (1.2)*
BMI (kg m^{-2})	23.9 (0.8)	23.8 (0.7)	25.6 (1.2)	25.8 (1.1)

All values are mean (SE)
* indicates significant ($P < 0.05$) difference from previous measurement. Note that there were no significant differences between groups
[a] Sum of six skin-folds = subscapular, tricep, iliac crest, abdominal, front and rear thigh (Yuhasz 1966)
[b] Thigh skin-folds are the sum of front and rear skin-fold thickness

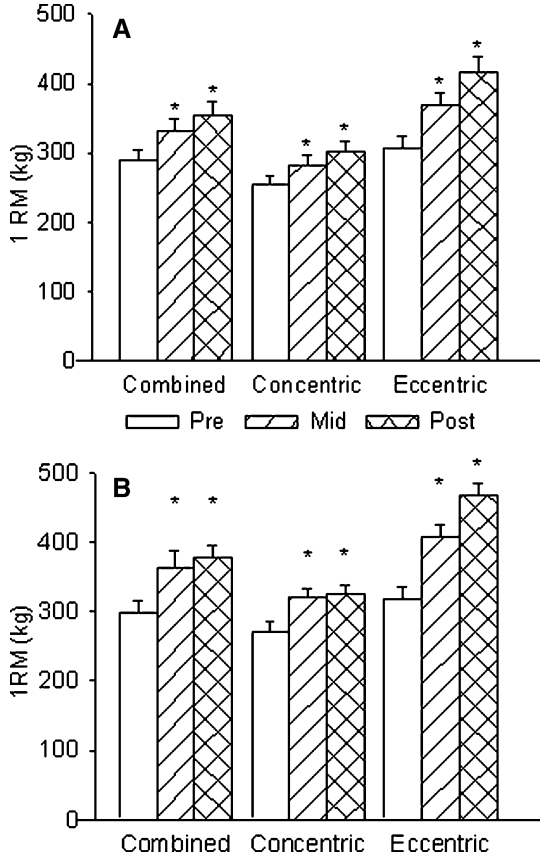

Fig. 1 Leg press maximum strength (1 RM) of the three strength tests at pre-, mid- and post-training for the long concentric training group (**a**) and the long eccentric training group (**b**). Values are in kg [mean (SE)]. *indicates significant ($P < 0.001$) difference from previous measurement. Differences between groups were not significant

The increase in ECC strength was greater ($P < 0.001$) than the increase of combined or CON strength for both groups.

Fibre type cross-sectional areas and proportions

Representative MHC immunohistochemical stains of serial cross-sections identifying different fibre types of the vastus lateralis muscle are shown in Fig. 2. The CSA for hybrid type I/IIA fibres and type IID(X) fibres are not reported due to the low number of these fibres types (mean of two mixed fibres and less than one type IID(X) fibre per sample). Muscle biopsy samples of only seven subjects contained mixed fibres both pre- and post-training and only one subject displayed type IID(X) fibres pre- and post-training. Embryonic or type IIB fibres were not observed in any of the samples.

There was a significant three-way interaction between groups, training and fibre type area of types I and IIA fibres (Fig. 3). While both groups experienced an increase in the CSA of type I fibres post-training (both $P < 0.004$), only the LC group demonstrated an increase ($P < 0.001$) in CSA of type IIA fibres following training. In the LC group, type I fibres were larger ($P < 0.004$) than type IIA fibres before training, but there was no difference ($P = 0.48$) in CSA between these fibre types after training due to the proportionally greater increase in CSA of type IIA fibres. In the LE group, the CSA of both fibre types were initially similar ($P = 0.43$) but following training, the type I fibres were larger ($P < 0.001$) than IIA fibres. Prolonged ECC training induced an 11.1 ($\pm$ 4.4)% increase in the CSA of type I fibres ($P < 0.004$) but did not induce a change in the CSA of IIA fibres ($P = 0.86$). Both groups demonstrated similar increases in the percentage change in CSA of type I fibres. However, the percentage change in size of type IIA fibres was different ($P < 0.001$) between groups (see Fig. 3). In the LC condition, the relative changes in muscle fibre CSA of types I and IIA fibres were 16.4 ($\pm$ 7.2) and 25.8 ($\pm$ 8.4)%, respectively.

Fibre type distribution is shown in Fig. 4. Both training groups possessed greater proportions of type I than IIA fibres before and after training (all $P < 0.001$), which comprised the majority of fibres. The proportion of IIA fibres was greater ($P < 0.05$) in the LC group compared with LE after training. LE training was associated with an increase ($P < 0.05$) in the proportion of fibres expressing MHCI and a proportional decrease ($P < 0.04$) in IIA fibre content while training did not alter fibre type proportions in LC (all $P > 0.81$).

Myosin heavy chain isoform content

Representative MHC gels are shown in Fig. 5. The proportion of MHCIId(x) was less than that of MHCIIa and MHCI (both $P < 0.001$), which did not change after training (Fig. 6). Both groups responded with a similar shift in the pattern of MHC isoform expression, namely a decrease ($P < 0.03$) in the proportion MHCIId(x) accompanied by an increase ($P < 0.03$) in the proportion of MHCIIa. There were no detectable changes ($P = 0.48$) in the proportion of MHCI after C or E training.

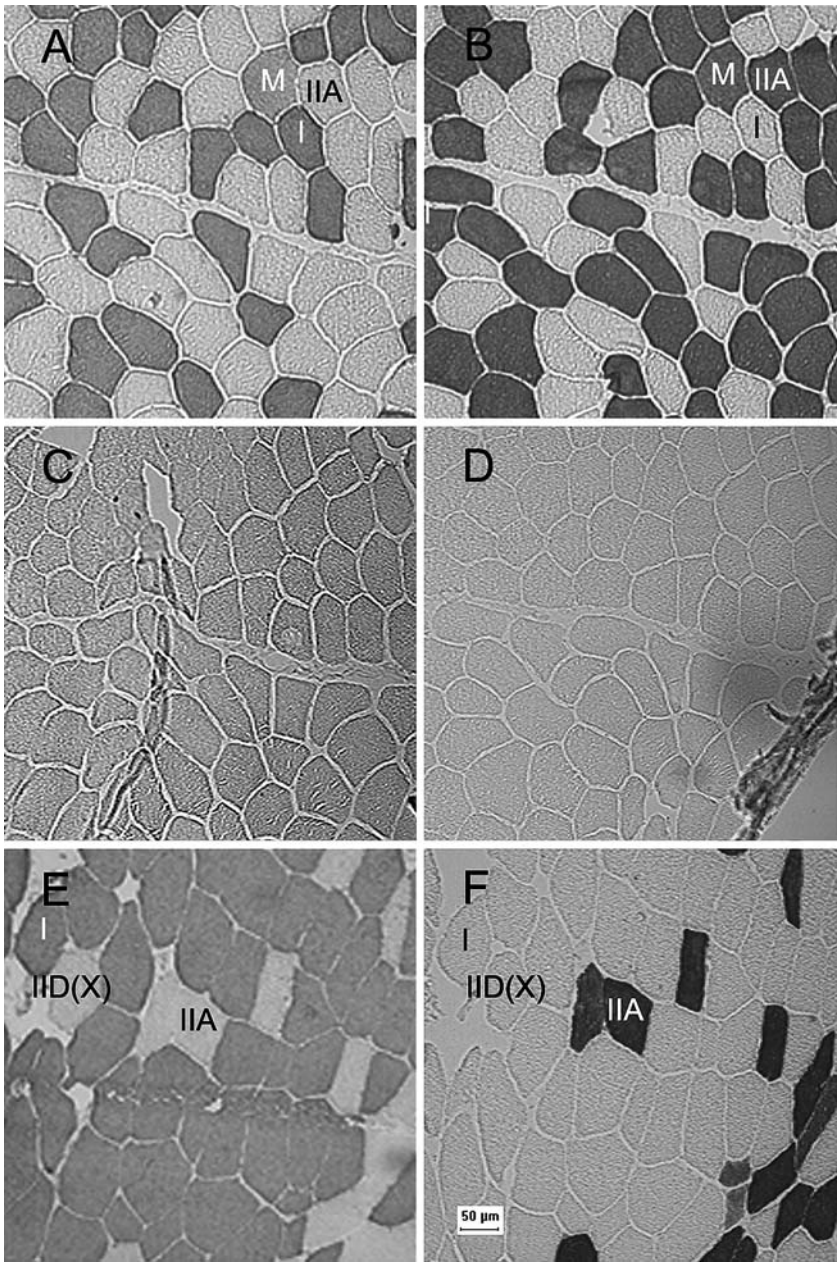

Fig. 2 Representative MHC immunohistochemical stains of serial cross-sections of the vastus lateralis muscle. Sections were stained for MHCI with monoclonal antibody (mAB) clone BA-D5 (**a**, **e**); MHCIIa with mAB clone SC-71 (**b**, **f**); $MHC_{embryonic}$ with mAB clone BF-45 (**c**). Non-specific mouse IgG was used as a negative control (**d**). One typical fibre of each type is labelled [*I*, *IIA*, *Mixed I and IIA-M*, *IID(X)*]

Cortisol

Values for 24-h urinary cortisol levels during the first and last week of training are shown in Fig. 7. A significant interaction of group and time showed that LC training produced an increase ($P < 0.05$) in urinary 'cortisol at week 9 while there was no change with LE training ($P = 0.98$).

Dietary intake

Macronutrient and caloric intake did not differ ($P > 0.58$) between groups during the five dietary recording periods and there was no alteration ($P > 0.42$) in macronutrient and caloric intake throughout the training program. For all recording periods, the percentages of total caloric intake derived from protein, carbohydrate and fat were16 (0.8), 60 (1.1) and 23 (1.1) %, respectively. Average daily caloric intake was 2,280 (56) kcals. Similarly, protein intake did not differ ($P = 0.77$) between groups during any of the dietary recording periods and did not change ($P = 0.07$) throughout the recording periods. Protein intake averaged 1.40 (0.03) g kg^{-1} body mass day^{-1}.

Training variables

The relative training load of leg press increased ($P < 0.001$) between weeks 1, 5 and 9 and was the same ($P = 0.96$) for both groups. The leg press relative

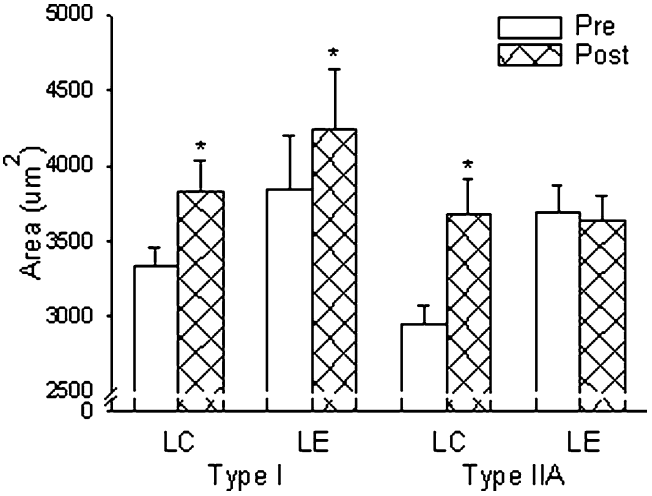

Fig. 3 Muscle fibre CSA (μm^2) pre- and post-training. Values are mean (SE). Long concentric training group (*LC*), long eccentric training group (*LE*). * indicates significant ($P < 0.01$) difference from previous measurement. Differences between groups were not significant

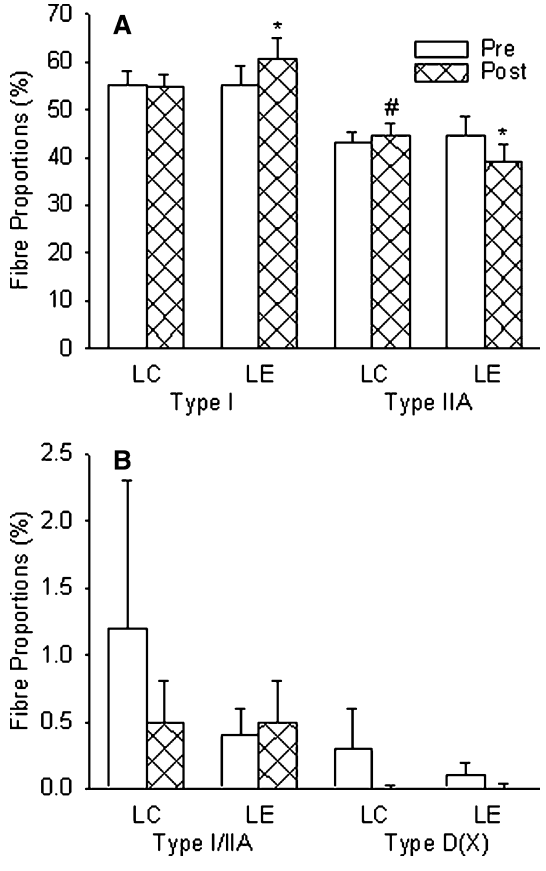

Fig. 4 Muscle fibre type proportions (%) pre- and post-training for the long concentric training group (**a**) and the long eccentric training group (**b**). Values are mean (SE). Mixed fibres are types I/IIA. * indicates significant ($P \leq 0.05$) difference from previous measurement. # indicates significant ($P \leq 0.05$) difference between groups

training load for both groups combined was 56 ($\pm$ 1.4), 61 ($\pm$ 1.9) and 67 ($\pm$ 2.2)% for weeks 1, 5 and 9, respectively. The mean number of repetitions per set for leg press did not differ ($P = 0.77$) between groups or throughout ($P = 0.27$) the 9 weeks of training [7 (0.1) repetitions per set]. Both groups responded similarly ($P = 0.34$) to the training regimens with a gradual increase in load per set such that the load used during the last 4 weeks of training was heavier (all $P < 0.03$) than that used during the first 5 weeks of training. Likewise, total training volume increased with training [volume of weeks 6–9 were all greater (all $P < 0.04$) than weeks 1–5]. The training response to squat exercise and leg extension was similar to that of leg press (data not

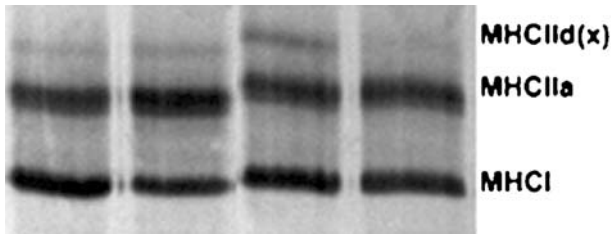

Fig. 5 Representative gels showing MHC isoforms separated by SDS-PAGE. Bands are shown from two subjects before (pre) and after (post) 9 weeks of resistance training. *Left two lanes* are from a concentric group subject and *right two lanes* are from an eccentric group subject

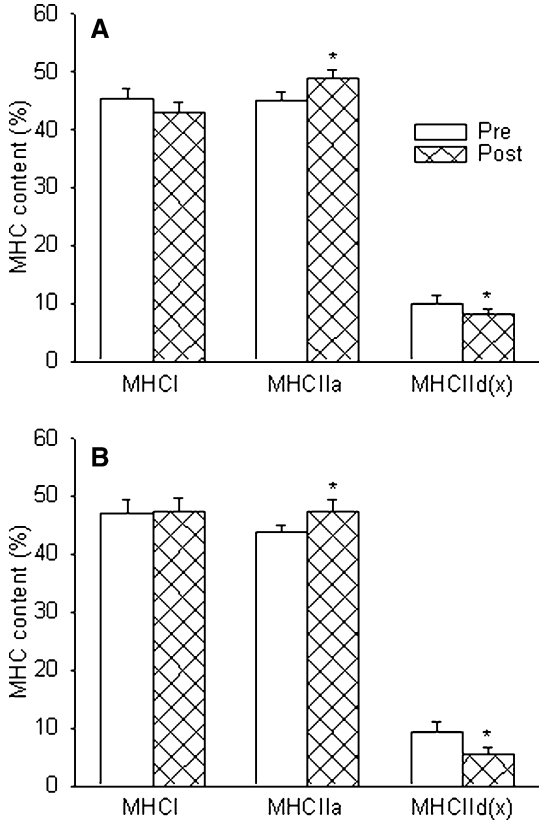

Fig. 6 Myosin heavy chain composition (% of total *MHC*) pre- and post-training for the long concentric training group (**a**) and the long eccentric training group (**b**). Values are mean percentage (SE). * indicates significant ($P = 0.02$) difference from previous measurement

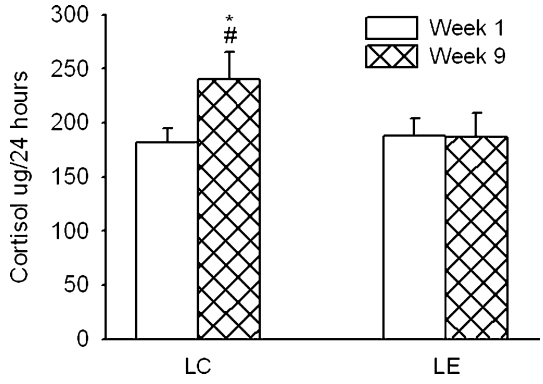

Fig. 7 Twenty-four hour urinary cortisol (μg per 24 h) during weeks 1 and 9 of training. Values are mean (SE). Long concentric training group (*LC*), long eccentric training group (*LE*). * indicates significant ($P \leq 0.05$) difference from previous measurement. # indicates significant ($P \leq 0.05$) difference between groups

shown). Likewise, total training volume for all three exercises stressing the quadriceps muscle group increased ($P < 0.001$) over training (Fig. 8).

Discussion

The purpose of this study was to investigate the effect of varying the time spent using CON and ECC muscle actions during resistance training on strength, skeletal muscle adaptations and urinary cortisol. In an attempt to ensure that any observed differences were due to the manipulation of the TUT, the training prescription used in this study equated the total time for the CON and ECC muscle actions, used the same relative intensity for training and progressively overloaded the training stimulus in the same fashion for both groups. Furthermore, diet was monitored and similar between groups and any potential effects of menstrual cycle on the observed findings was also controlled for and eliminated as a confounding factor. Thus, we are confident that the observed changes and differences observed in the present study were due to the manipulation of the time to complete the CON and ECC muscle actions and not due to differences in training prescription variables. Our findings support our hypothesis that both training programs would improve strength and result in skeletal muscle hypertrophy. The most novel findings of the present study was that slow CON training produced significant increases in both types I and IIA muscle fibre CSA and urinary cortisol while slow ECC training only significantly increased type I fibre area with no observed changes in cortisol.

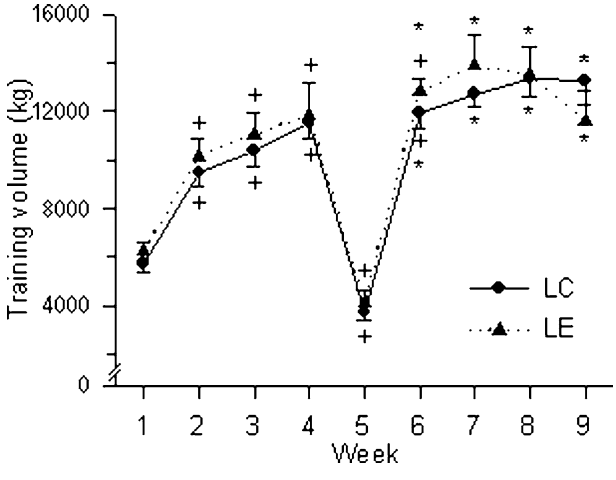

Fig. 8 Total training volume (weekly sum of load × repetitions for each set of leg press, squat and leg extension) throughout the nine training weeks. Values are mean (SE). Long concentric training group (*LC*), long eccentric training group (*LE*). Note that there were no significant differences between groups at all weeks. + indicates significant ($P \leq 0.05$) difference from previous week. * indicates significant ($P \leq 0.05$) difference from weeks 1 to 5. There was one training session only during week 5

Our finding of a similar increase in strength in both groups regardless of which muscle action was emphasized was supported by other research that have examined strength responses following resistance training utilizing a load based on a percentage of submaximal CON strength with either CON or ECC actions only, or both actions combined (Dudley et al. 1991b; Ben-Sira et al. 1995). The increases in maximal strength for the three test modes varied from 21 to 44% in the present study and are comparable to reports of increases ranging from 12 to 67% with other investigations using similar muscle actions during training (Dudley et al. 1991b; Ben-Sira et al. 1995) or with manipulation of muscle action completion time (Young and Bilby 1993; Morrissey et al. 1998; Gillies and Docherty 1999). Contrary to this, Raue et al. (2005) found a significant increase in CON 1 RM strength after 4 weeks of CON resistance training but no changes with ECC training. Unfortunately, this latter research did not perform an ECC strength test. The use of "slow" muscle actions certainly did not limit strength gains in the present study, as similar increases in combined or CON strength have been shown with other more "typical" resistance training protocols using combined muscle actions (Staron et al. 1994; Bell et al. 2000; Williamson et al. 2001). Another interesting finding of the present study was that the greatest relative change in leg press strength occurred within the ECC action (i.e. a 44% increase). This greater change in ECC strength may be partially explained by a reduction of an inhibitory neural drive/protective mechanism and/or an increase in maximal motor unit recruitment that occurs as a result of training that emphasizes ECC muscle actions (Aagaard et al. 2000; Linnamo et al. 2002). It may also be due to a greater potential to increase ECC strength, as most individuals do not emphasize heavy, prolonged ECC actions during recreational resistance training to the extent prescribed in the present study or during activities of daily living.

The current study also found some evidence of preferential muscle fibre type hypertrophy as a result of the

manipulation of CON and ECC muscle action time. The use of a slow CON muscle action time during training resulted in significant hypertrophy of both types I and IIA fibres, which was similar to the findings of other investigations that have not manipulated TUT but have employed combined actions based on the same submaximal CON load (Hather et al. 1991; Staron et al. 1991; Bell et al. 2000; Putman et al. 2004). While hypertrophy of type II fibres (or subpopulations of type II fibres) following resistance training has not always been shown to be accompanied by type I fibre hypertrophy (Kadi et al. 2000; Sharman et al. 2001), we found that training with an emphasis on the ECC action resulted in significant hypertrophy of type I fibres only. It is possible that this latter finding was partially because the cross sectional area of type IIA fibres was not significantly different than type I fibres prior to training in the slow ECC training group. Although this was the result of the random assignment of the subjects to the experimental groups, it must be considered a limitation of the present study.

However, there are several possible explanations for the finding of differential hypertrophy with the training regimens in the present study. It has been shown that muscle activation is lower during ECC than CON actions when the same submaximal load is used (Nakazawa et al. 1993; Gillies et al. 2000) suggesting that fewer motor units are required during the ECC action. Since the relative training intensity was the same between groups and based on CON strength in the present study, the ECC training protocol may have activated fewer motor units than the group that emphasized CON muscle actions despite the same time of muscle activation. Second, research has shown that there is a greater metabolic demand during CON compared to ECC actions (Dudley et al. 1991a; Ryschon et al. 1997). Thus, it was reasonable to assume that the metabolic demand of prolonged CON muscle action training in the present study was likely greater than that of the prolonged ECC training protocol. The significantly higher 24-h urinary cortisol levels observed after prolonged CON training group provided indirect evidence of a greater physiological stress during prolonged CON training. This significantly elevated urinary cortisol levels produced by the prolonged CON only protocol study may also suggest a greater extent of muscle protein turnover and possible greater muscle damage. This latter response has been proposed to elicit a physiological signal initiating some type of mechanistic cascades for stimulating muscle fibre hypertrophy (Staron et al. 1992; Fiatarone Singh et al. 1999) that may (Macpherson et al. 1996) or may not be fibre type specific (Staron et al. 1992; Fiatarone Singh et al. 1999; Gibala et al. 2000). As such, muscle damage is likely not the explanation for the observed differences in fibre hypertrophy in the present study especially since muscle damage can be reduced over the time course of resistance training mediated in part by regeneration and subsequent resistance to further damage (Staron et al. 1992; Fiatarone Singh et al. 1999; Gibala et al. 2000). This is further supported by the lack of fibres expressing the embryonic form of MHC, an indicator of muscle regeneration, in the present study. Further research is necessary to elucidate the underlying factors that would help explain fibre type specific hypertrophy to training with different muscle actions and time spent under tension.

Despite a differential response in fibre hypertrophy, our results suggest that resistance training primarily influences the fast MHC isoforms, and that the endpoint of fibre type transformations following resistance training favours an increased MHCIIa content. This finding is supported by research in our laboratory (Putman et al. 2004) as well as by other investigators (Adams et al. 1993; Sharman et al. 2001; Williamson et al. 2001). Conversely, Raue et al. (2005) did not observe many changes in MHC content of single fibres after 4 weeks of either CON only or ECC only resistance training. The alteration in MHC content observed in the present study may be related to a reduction in hybrid fibres co-expressing multiple MHC isoforms, resulting in an increase in the proportion of fibres expressing MHCIIa only (Williamson et al. 2001; Putman et al. 2004). However, it must also be considered that the observed shift in MHC isoforms may not represent a true shift in proportions but may be a reflection of relative fibre type hypertrophy.

The apparent mismatch between the changes in fibre type proportion and MHC content with the ECC training protocol of the present study is not in agreement with the few investigations that have examined both fibre phenotype and MHC expression (Hather et al. 1991; Adams et al. 1993; Kadi and Thornell 1999; Kadi et al. 2000). These latter studies found that changes in fibre type proportions mirrored changes in MHC content. This discrepancy in our results is difficult to explain but it is possible that a slight increase in MHCIIa expression in fibres classified as type I may not have been a sufficient enough change to influence the classification of fibres from type I to mixed but this minor alteration was able to be detected by MHC quantification. However, the findings of Williamson et al. (2001) would not support this suggestion. It is also possible that the mismatch of fibre phenotype and MHC expression found with our ECC training protocol would have dissipated with a longer training program since MHC transformation in muscle fibres has been shown to precede hypertrophy (Staron et al. 1991). Conversely, there was a slight (although not significant) increase of MHCI with the prolonged ECC training in the present study that may provide some evidence that a transformation towards MHCI might be in process and match the alteration in fibre phenotype with longer-term resistance training. Finally, it must also be considered that the increased proportion of MHCIIa after prolonged CON training may be a reflection of the greater relative increase in the size of type IIA fibres, and not just a shift in the proportion of the fast MHC's. Further research is also needed to confirm these possibilities.

In conclusion, our investigation has shown a similar increase in CON, ECC and combined CON–ECC strength with prolonged CON or ECC muscle actions at the same relative intensity during resistance training in young women. Both groups also exhibited a significant decrease in MHCIId(x) and a concomitant significant increase in MHCIIa after training. The novel finding of this study was that a differential fibre type hypertrophy occurred with the manipulation of the time to complete the CON or ECC muscle actions. An emphasis of time spent performing the CON action during resistance training appeared to significantly increase CSAs of both types I and IIA muscle fibres while an emphasis on the ECC action limited hypertrophy to type I fibres only. Urinary cortisol levels were only significantly elevated after the CON training protocol. In summary, these observed differences in fibre type hypertrophy and cortisol response were not accompanied by a differential response in strength, MHC protein expression or differences in training variables and may be related to different factors due to an emphasis on the specific type of muscle action used during resistance training in young women.

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