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ORIGINAL ARTICLE

Gerson E.R. Campos · Thomas J. Luecke
Heather K. Wendeln · Kumika Toma
Fredrick C. Hagerman · Thomas F. Murray
Kerry E. Ragg · Nicholas A. Ratamess
William J. Kraemer · Robert S. Staron

Muscular adaptations in response to three different resistance-training regimens: specificity of repetition maximum training zones

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Abstract Thirty-two untrained men [mean (SD) age 22.5 (5.8) years, height 178.3 (7.2) cm, body mass 77.8 (11.9) kg] participated in an 8-week progressive resistance-training program to investigate the "strength–endurance continuum". Subjects were divided into four groups: a low repetition group (Low Rep, $n=9$) performing 3–5 repetitions maximum (RM) for four sets of each exercise with 3 min rest between sets and exercises, an intermediate repetition group (Int Rep, $n=11$) performing 9–11 RM for three sets with 2 min rest, a high repetition group (High Rep, $n=7$) performing 20–28 RM for two sets with 1 min rest, and a non-exercising control group (Con, $n=5$). Three exercises (leg press, squat, and knee extension) were performed 2 days/week for the first 4 weeks and 3 days/week for the final 4 weeks. Maximal strength [one repetition maximum, 1RM), local muscular endurance (maximal number of repetitions performed with 60% of 1RM), and various cardiorespiratory parameters (e.g., maximum oxygen consumption, pulmonary ventilation, maximal aerobic power, time to exhaustion) were assessed at the beginning and end of the study. In addition, pre- and post-training muscle biopsy samples were analyzed for fiber-type composition, cross-sectional area, myosin heavy chain (MHC) content, and capillarization. Maximal strength improved significantly more for the Low Rep group compared to the other training groups, and the maximal number of repetitions at 60% 1RM improved the most for the High Rep group. In addition, maximal aerobic power and time to exhaustion significantly increased at the end of the study for only the High Rep group. All three major fiber types (types I, IIA, and IIB) hypertrophied for the Low Rep and Int Rep groups, whereas no significant increases were demonstrated for either the High Rep or Con groups. However, the percentage of type IIB fibers decreased, with a concomitant increase in IIAB fibers for all three resistance-trained groups. These fiber-type conversions were supported by a significant decrease in MHCIIb accompanied by a significant increase in MHCIIa. No significant changes in fiber-type composition were found in the control samples. Although all three training regimens resulted in similar fiber-type transformations (IIB to IIA), the low to intermediate repetition resistance-training programs induced a greater hypertrophic effect compared to the high repetition regimen. The High Rep group, however, appeared better adapted for submaximal, prolonged contractions, with significant increases after training in aerobic power and time to exhaustion. Thus, low and intermediate RM training appears to induce similar muscular adaptations, at least after short-term training in previously untrained subjects. Overall, however, these data demonstrate that both physical performance and the associated physiological adaptations are linked to the intensity and number of repetitions performed, and thus lend support to the "strength–endurance continuum".

Keywords Human skeletal muscle · Fiber types · Histochemistry · Capillarization · Myosin heavy chains

G.E.R. Campos · T.J. Luecke · H.K. Wendeln · K. Toma
F.C. Hagerman · R.S. Staron (✉)
Department of Biomedical Sciences,
College of Osteopathic Medicine,
Ohio University, Irvine Hall, rm 430,
Athens, OH 45701, USA
E-mail: staron@ohio.edu
Tel.: +1-740-5932409
Fax: +1-740-5972778

T.F. Murray
Com-Admin and Diagnostic Services,
College of Health and Human Services,
Ohio University, Athens, OH 45701, USA

K.E. Ragg
Student Health Service, Ohio University,
Athens, OH 45701, USA

N.A. Ratamess · W.J. Kraemer
Human Performance Laboratory,
Department of Kinesiology,
The University of Connecticut, Storrs, CT 06269, USA

Introduction

Human skeletal muscle is a heterogeneous tissue composed of functionally diverse fiber types (Staron 1997). This mixture of different fiber types enables the muscle to fulfill a variety of functional demands. An additional unique feature of skeletal muscle is the ability to alter its phenotypic profile in response to specific stimuli (Pette and Staron 2001). For resistance training, these alterations usually contribute to significant increases in muscle strength and size (McDonagh and Davies 1984; Tesch 1988; Abernethy et al. 1994). Research in this area has often focused on various combinations of sets and repetitions to optimize these specific adaptations (Tan 1999). For example, an early study by Berger (1962) suggested that three sets of 4–8 repetitions produced optimal gains in strength compared to various other set/repetition combinations. These data suggest that specific muscle-fiber adaptations are associated with differential strength gains.

It is clear that manipulation of the various acute resistance-training variables (e.g., number of sets, length of rest periods between sets and exercises, intensity, or load) can stress the muscles in very different ways. As such, there appears to be a specific relationship between the training stimulus and the adaptive response. Taking resistance training to various extremes, DeLorme's classic work (1945) suggested that a resistance-training program using low repetition/high resistance favored adaptations for strength/power, whereas training with high repetition/low resistance increased muscular endurance.

Anderson and Kearney (1982) tested DeLorme's hypothesis by investigating the effects of three very different resistance programs on strength adaptations. Forty-five college-aged men were randomly assigned to one of three groups: high resistance/low repetition (three sets of 6–8 repetitions maximum, RM), medium resistance/medium repetition (two sets of 30–40 RM), and low resistance/high repetition (one set of 100–150 RM). After 9 weeks of training for 3 days/week, the high resistance/low repetition group showed the greatest improvement in maximal strength (one-repetition maximum, 1RM) and the poorest in relative endurance (maximum number of repetitions using 40% 1RM) compared to the other two groups. Similar results were obtained in a more recent study using women (Stone and Coulter 1994). This study, although modeled after Anderson and Kearney (1982), used a less extreme "endurance" protocol for the low-resistance/high repetition group. Forty-five college-aged women were assigned to one of three groups: high resistance/low repetitions (three sets of 6–8 RM), medium resistance/medium repetitions (two sets of 15–20 RM), and low resistance/high repetitions (one set of 30–40 RM). After 9 weeks of training for 3 days/week, the high resistance/low repetition training resulted in greater strength gains, whereas low resistance/high repetition produced greater muscular endurance gains. From these studies, a "repetition training continuum" (Anderson and Kearney 1982) or "repetition maximum continuum" (Fleck and Kraemer 1988) has been hypothesized such that the number of repetitions allowed by the resistance will result in very specific training adaptations.

Although various resistance-training studies have been published demonstrating specific muscular strength and endurance adaptations (e.g., Anderson and Kearney 1982; Stone and Coulter 1994), there is scant information concerning specific intramuscular adaptations in response to different set and repetition combinations. The purpose of the present investigation was to compare the effects of three different resistance-training programs on adaptations within the vastus lateralis muscle. To this end, routines at three different points along the theorized strength–endurance continuum were chosen to investigate and compare specific muscular adaptations. The design of the present study more closely resembles that of Stone and Coulter (1994), and utilizes a more practical resistance-training regimen on the endurance end of the continuum compared to that of Anderson and Kearney (1982).

Methods

Subjects

Thirty-two healthy men [mean (SD) age 22.5 (5.8) years, height 178.3 (7.2) cm, body mass 77.8 (11.9) kg] volunteered to participate in the present study. All subjects were informed of the procedures, risks, and benefits, and signed an informed consent document approved by the Ohio University Institutional Review Board before participation. Although physically active, all subjects were considered untrained and had not participated in a regular exercise program for at least 6 months prior to the start of the study. Twenty-seven healthy men were randomly divided into three training groups: a low repetition group [Low Rep, $n=9$; mean (SD) age 21.1 (1.5) years, height 179.8 (6.5) cm], an intermediate repetition group [Int Rep, $n=11$; mean (SD) age 20.7 (2.9) years, 179.6 (7.4) cm], and a high repetition group [High Rep, $n=7$; mean (SD) age 20.4 (3.5) years, height 174.3 (8.6) cm]. Six additional individuals served as non-exercising controls (Con). One Con subject began endurance training during the course of the study and was dropped from the study, leaving a final Con group comprising five individuals [mean (SD) age 31.6 (9.8) years, height 178.1 (5.5) cm].

Anthropometric assessments

Anthropometric measurements (total body mass, estimated fat-free mass, and estimated percentage body fat) were determined before and after the 8-week training period (Table 1). Skinfold measurements were obtained from three sites (anterior thigh, axillary fold, and abdomen) prior to extraction of the muscle biopsy samples and were used in the equation proposed by Jackson and Pollock (1978) for body composition analyses (e.g., estimation of percentage body fat).

Maximal oxygen consumption

A previous study from this laboratory (Hagerman et al. 2000) demonstrated significant improvements in maximum oxygen consumption ($\dot{V}O_{2max}$) and time to exhaustion following 16 weeks of resistance training in elderly men. Therefore, aerobic capacities

Table 1. Total body mass and estimated percentage body fat. Values given are mean (SD). (*LOW REP* Low repetition group, *INT REP* intermediate repetition group, *HIGH REP* high repetition group, *Pre* pre-training, *Post* post-training)

Training condition	Body mass (kg)	% Body fat
CONTROL		
Pre	80.8 (23.3)	14.6 (6.6)
Post	81.4 (24.3)	14.0 (6.5)
LOW REP		
Pre	80.1 (8.4)	13.9 (3.7)
Post	82.4 (8.3)	14.3 (4.0)
INT REP		
Pre	79.5 (7.8)	14.7 (4.8)
Post	81.2 (8.3)	16.0 (5.3)
HIGH REP		
Pre	70.2 (9.5)	11.2 (3.9)
Post	71.5 (9.2)	11.4 (3.7)

were determined for all subjects at the beginning and end of the study. Testing was administered on a Monark cycle ergometer using a graded protocol that increased the intensity at regular intervals. The subjects began pedaling at a frequency of 60 rpm at 60 W. Every minute the workload was progressively increased by 30 W. Termination of the test occurred when the subject could no longer maintain the required power or stopped voluntarily due to exhaustion. A test was considered valid if one of the following criteria was observed: (1) predicted maximal heart rate was attained, (2) oxygen consumption ($\dot{V}O_2$) leveled off or declined, or (3) a respiratory exchange ratio (R) of greater than 1.1 was reached (see Howley et al. 1995). $\dot{V}O_2$ was measured every 20 s. Heart rate and rate of perceived exertion were measured at each exercise intensity. $\dot{V}O_{2max}$, pulmonary ventilation ($\dot{V}_E$), expired carbon dioxide, and R were measured using semiautomated-computerized open-circuit spirometry (Vacumed, Ventura, Calif., USA) that included a Parkinson-Cowan dry gas meter, and carbon dioxide infrared and oxygen paramagnetic gas analyzers. Heart rate was monitored every minute using Polar CIC transmitters and receivers. Time to exhaustion was recorded as a multiple of 20 s from the initiation of the test. Immediately following the cycle test, the subjects were seated for a 5-min recovery period before a blood sample was obtained for analysis of whole-blood lactate.

Maximal strength and muscular endurance tests

All subjects (including the controls) participated in a 1-week orientation program for familiarization with the equipment and exercises (Dudley et al. 1991). Proper lifting technique was demonstrated and practiced for each of the three lower-limb exercises (leg press, squat, and knee extension). Both maximal dynamic strength (1RM) and local muscular endurance (maximum number of repetitions performed with 60% of 1RM) were assessed for each of the exercises at the beginning and end of the study. Because of the exhaustive nature of the endurance test, the maximal strength test was always performed first. After warming up, the load was set at 90% of the predicted 1RM, and was increased after each successful lift until failure (Staron et al. 1990). Periods of rest (approximately 4–5 min) were allotted between each attempt to ensure recovery. A test was considered valid if the subject used proper form and completed the entire lift in a controlled manner without assistance. Once the 1RM was determined, 60% of this value was calculated for the local muscular endurance test. After a sufficient recovery period (≅4–5 min), the subjects performed as many repetitions as possible with 60% of 1RM until failure.

Strength-training protocols

The training subjects participated in an 8-week high-intensity training program for the lower extremities. Workouts were performed 2 days/week for the first 4 weeks and 3 days/week for the final 4 weeks. The training subjects used one of three different regimens. The training programs were adapted from several previous studies (Anderson and Kearney 1982; Jackson et al. 1990; Stone and Coulter 1994), and were designed to be approximately equal in volume (resistance×repetitions×sets) with the rest periods between sets and exercises adjusted according to the strength–endurance continuum (Fleck and Kraemer 1997). Therefore, those individuals working on the endurance end of the continuum performed fewer sets and had shorter rest periods compared with the other training groups. The exercises were performed in the fixed order of leg press, squat, and knee extension. After warming up, the Low Rep group performed 3–5 repetitions maximum (3–5 RM) for four sets with 3 min rest between sets and exercises, the Int Rep group performed 9–11 RM for three sets with 2 min rest, and the High Rep group performed 20–28 RM for two sets with 1 min rest. During the study, the resistance was progressively increased to maintain these ranges of repetitions per set. For each set, the training subjects performed repetitions until failure. If the subject performed repetitions beyond the prescribed training zone, the weight was sufficiently increased to bring the number of repetitions back within the RM training zone. All subjects were supervised and verbally encouraged during each set. Maximal heart rates were measured during training in weeks 2 and 7 to compare the cardiorespiratory stress of each group's workout. Training heart rates were calculated as a percentage of the maximal heart rate obtained during the and cycle ergometer $\dot{V}O_{2max}$ pre- and post-training tests. Values from week 2 were calculated as a percentage of the maximal heart rate obtained from the pre-training maximal test and those from week 7 as a percentage of the post-training maximal test. Workouts began and ended with 10–15 min of calisthenics, stretching, and low-intensity cycling.

Muscle biopsy sampling

Muscle biopsy samples (80–160 mg) were extracted from the superficial region (depth of 3–4 cm) of the vastus lateralis muscle (approximately mid-shaft) using the percutaneous needle biopsy technique (Bergström 1962). The muscle samples were removed from the needle, oriented in tragacanth gum, immediately frozen in isopentane cooled by liquid nitrogen to –159°C, and stored at –74°C until further analyses could be performed. Biopsy samples were obtained at the beginning and end of the study. Because of possible variations in fiber-type distribution from superficial to deep and proximal to distal (Blomstrand and Ekblom 1982), attempts were made to extract pre-training and post-training tissue samples from within a small area of the muscle using the pre-biopsy scar and depth markings on the needle. As such, successive incisions were made approximately 0.5 cm apart. The pre-training and post-training biopsy sites were far enough apart so that the insertion of the first biopsy needle and extraction of tissue did not affect the area of the second biopsy. To ensure adequate sample sizes, large biopsy specimens were obtained using a double-chop method (Staron et al. 1990, 1991, 1994) combined with suction (Evans et al. 1982).

Fiber-type and cross-sectional area determinations

The frozen biopsy specimens were thawed to –24°C and sectioned serially (12 µm thick) for histochemical analysis. To determine the muscle fiber-type composition, myofibrillar adenosine triphosphatase (mATPase) histochemistry was performed using preincubation pH values of 4.3, 4.6, and 10.4 (Guth and Samaha 1969; Brooke and Kaiser 1970). Six fiber types (I, IC, IIC, IIA, IIAB, and IIB) were distinguished based on their staining intensities (Fig. 1a–c). Fiber types IIAB and IIB have more recently been referred to as IIAX and IIX, respectively (Smerdu et al. 1994; Ennion et al. 1995). Cross sections of pre-training and post-training biopsy specimens from an individual were placed on the same glass coverslip so that they could be assayed simultaneously for mATPase activity. A composite photomontage of each mATPase preparation after

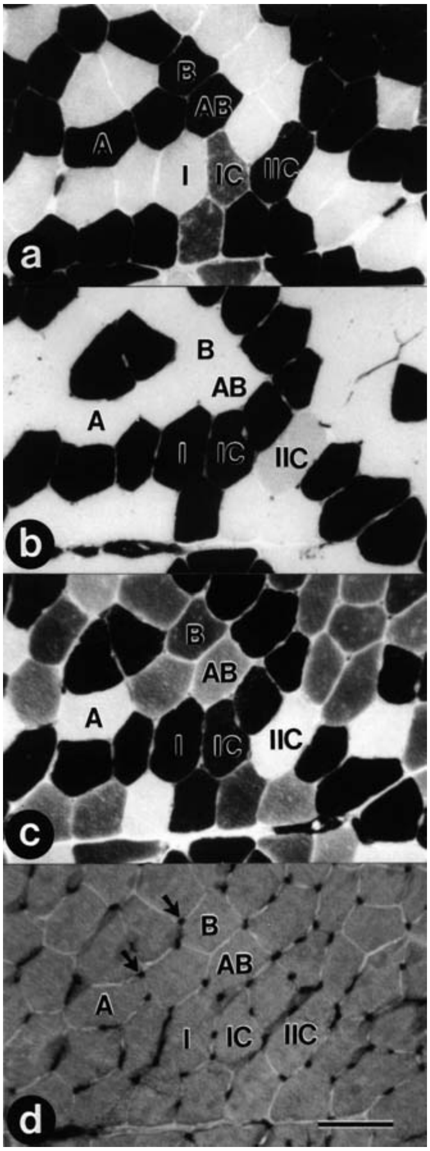

Fig. 1. Serial cross sections of muscle samples taken from a control subject demonstrating fiber-type delineation using myofibrillar adenosine triphosphatase histochemistry after preincubation at pH 10.4 (**a**), 4.3 (**b**), and 4.6 (**c**), and capillary supply using *Ulex europaeus* agglutinin lectin histochemistry (**d**). *Arrows* in **d** indicate capillaries. (*I* Type I muscle fiber, *IC* type IC muscle fiber, *IIC* type IIC muscle fiber, *A* type IIA muscle fiber, *AB* type IIAB muscle fiber, *B* type IIB muscle fiber). Bar = 100 μm

preincubation at pH 4.6 was made using Polaroid micrographs (×56 magnification). These were used in combination with the other mATPase preparations to determine fiber-type percentages and total fiber number in each biopsy sample. Cross-sectional area was determined on at least 50 fibers per major fiber type (I, IIA, and IIB) per biopsy sample using the NIH imaging software program (version 1.55).

Myosin heavy chain (MHC) analysis

MHC analyses were performed on the biopsy samples using sodium dodecylsulfate (SDS)-polyacrylamide electrophoretic techniques (Fig. 2). The protocol for analyzing the specimens was based on procedures of Perrie and Bumford (1986) with modifications used for single-fiber analysis (Staron 1991; Staron and Hikida 1992). Briefly, four to six serial cross sections (20 μm thick) from each biopsy sample were placed into 0.5 ml of a lysing buffer containing 10% (wt/vol) glycerol, 5% (vol/vol) 2-mercaptoethanol, and 2.3% (wt/vol) SDS in 62.5 mM tris (hydroxymethyl) aminomethane HCl buffer (pH 6.8) and heated for 10 min at 60°C. Small amounts of the extracts (3–5 μl) were loaded on 4–8% gradient SDS-polyacrylamide gels with 4% stacking gels (Bär and Pette 1988), run overnight (19–21 h) at 120 V, and stained with Coomassie Blue. MHC isoforms were identified according to their apparent molecular masses compared with those of marker proteins and migration patterns from single-fiber analyses. Relative MHC isoform content was subsequently determined using a laser densitometer.

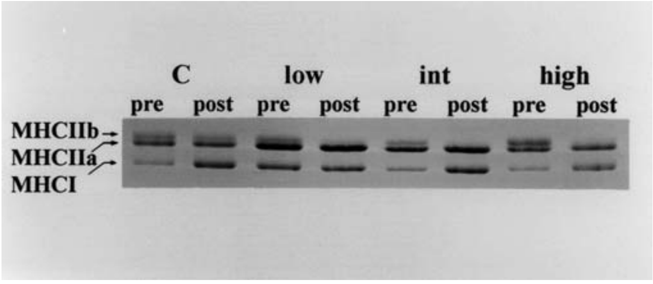

Fig. 2. Myosin heavy chain (MHC) analysis of muscle biopsy samples obtained from a representative subject in each of the four groups (*C* control, *low* low repetition, *int* intermediate repetition, *high* high repetition) at the beginning (*pre*) and end (*post*) of the study. Note the decrease in the band corresponding to MHCIIb from pre to post for the training subjects. (*MHCIIb* Myosin heavy chain IIb, *MHCIIa* myosin heavy chain IIa, *MHCI* myosin heavy chain I)

Capillary assessment

Capillaries were identified on cross sections serial to those used for fiber-type determination by *Ulex europaeus* agglutinin I (UEA-I) lectin histochemistry, according to the procedure of Holthöfer et al. (1982) (Fig. 1d). UEA-I is a sensitive and reliable marker for endothelium. Capillary data were collected from at least 50 fibers per major fiber type (I, IIA, IIB) per biopsy sample. Fibers that lay on the border of a muscle fascicle were not included in the analysis. Also, capillaries on the edge of a sampling area were added together and divided by two to correct for fiber sharing, according to Plyley and Groom (1975). Several measures of muscle capillarity were used in the present investigation. The number of capillaries per unit area (capillary density, CD = capillaries/mm^2) was measured to give an indication of the number of capillaries present in a standard area. The number of capillaries per fiber (CF) was measured as a global representation of capillary supply, whereas the number of capillaries per fiber-type area (CFTA) was determined to assess relative differences in capillary supply to individual fiber types. Finally, the number of capillaries per fiber type (CFT) was reported to demonstrate an absolute measure of capillary supply to each fiber type.

Statistical analysis

Descriptive statistics were used to derive means and standard deviations (SD) for all variables, and data are presented in the form mean (SD). Statistical analyses for each dependent variable were accomplished using a separate two-way analysis of variance (ANOVA) with repeated measures (3×2 design: 3 groups by 2 time points). When a significant F value was achieved, post-hoc comparisons were accomplished via a Fisher's least significant differences (LSD) test. Using the nQuery Advisor software (Statistical Solutions, Saugus, Mass., USA), the statistical power for the n size used ranged from 0.76 to 0.87. Differences were considered significant at $P = 0.05$.

Results

Anthropometric data

No significant differences were detected either between or within any of the groups for the anthropometric measurements (Table 1).

Cardiorespiratory measurements

$\dot{V}O_{2\max}$, $\dot{V}_E$, time to exhaustion, and aerobic power were monitored at the beginning and end of the study (Table 2). All subjects completed valid $\dot{V}O_{2\max}$ tests (see Methods). The average maximal heart rates were 188.2 (16.1) and 189 (9.6) beats/min for the pre- and post-training tests, respectively. Lactate measurements did not differ between the groups, and averaged 12.4 (1.7) and 11.6 (2.5) mmol/l for the pre- and post-training tests, respectively. $\dot{V}O_{2\max}$ and $\dot{V}_E$ were unchanged at the end of the study for all training groups. The High Rep group was the only training group to show a significant increase in both time to exhaustion [from 7.6 (1.8) to 9.1 (1.3) min] and maximal aerobic power [from 265 (47) to 308 (41) W] in the cycle endurance test. As expected, the Con group demonstrated no significant changes for the various cardiorespiratory parameters with the exception of a significant decrease in $\dot{V}_E$ at the end of the study (Table 2).

Workout volume and cardiorespiratory stress

The average volume of total work accomplished (resistance×repetitions×sets) was calculated for each training group every week. No significant differences in volume were found between the training groups. Volumes had a tendency to rise slightly for all three training groups for each exercise throughout the duration of the training period. However, no significant differences in volume occurred over time. Likewise, no differences between the groups were found when comparing heart rates obtained during training in weeks 2 and 7. The average training heart rates for week 2 were 87%, 86%, and 93%, and for week 7 were 88%, 87%, and 91% for the Low Rep, Int Rep, and High Rep groups, respectively.

Maximal dynamic strength and muscular endurance

All three training groups showed significant increases in maximal dynamic strength (1RM) for all three exercises compared to their pre-training values (Fig. 3). Although not shown, this was also true for maximal dynamic strength relative to total and lean body mass. No significant changes in 1RM were demonstrated pre- to post-training for the Con group (Fig. 3). In a comparison between groups, the relative and absolute increases in maximal dynamic strength for the leg press and squat exercises were significantly greater for Low Rep compared to the other groups (Fig. 3). For the leg extension, the post-training 1RM value for the Low Rep group was significantly greater than for both the High Rep and Con groups (Fig. 3).

Compared to the results obtained for maximal dynamic strength, the reverse was true for the assessment of local muscular endurance. High Rep performed significantly more repetitions using 60% 1RM after training for all three exercises, and these post-training values were greater than all other corresponding group values (Fig. 4). Although all three training groups significantly increased the number of repetitions using 60% of the 1RM in the squat exercise after training, neither the Int Rep nor Low Rep groups demonstrated a significant improvement at 60% 1RM after training for the leg press or leg extension (Fig. 4). Indeed, the Low Rep group performed significantly fewer repetitions for the leg press after training (Fig. 4). No significant changes in local muscular endurance were found for the Con group (Fig. 4).

Fiber-type distribution and MHC content

For all three training groups, the percentage of type IIB fibers decreased, with a concomitant increase in the percentage of fibers classified as type IIAB (Table 3). No

Table 2. Cardiorespiratory data obtained from pre- and post-training endurance tests. Values given are mean (SD). ($\dot{V}O_2$ Oxygen consumption, $\dot{V}O_{2\max}$ maximum oxygen consumption, $\dot{V}_E$ minute ventilation, *Max power* maximal aerobic power, *t* time to exhaustion)

Training condition	$\dot{V}O_{2\max}$ (ml/kg/min)	$\dot{V}O_2$ (l/min)	$\dot{V}_E$ (l/min)	Max power (W)	*t* (min)
CONTROL					
Pre	48.7 (9.6)	3.81 (0.77)	152.0 (28.5)	276 (58)	8.5 (1.8)
Post	44.8 (7.6)	3.32 (0.70)	123.6 (38.6)*	276 (39)	8.4 (1.6)
LOW REP					
Pre	50.3 (5.6)	4.00 (0.45)	140.1 (22.9)	297 (41)	8.9 (1.3)
Post	48.5 (6.6)	3.97 (0.46)	132.1 (25.6)	307 (36)	9.2 (1.2)
INT REP					
Pre	48.1 (3.7)	3.88 (0.41)	149.8 (17.2)	290 (34)	9.0 (1.0)
Post	45.7 (4.4)	3.76 (0.45)	137.8 (25.2)	293 (33)	9.0 (1.2)
HIGH REP					
Pre	51.0 (10.4)	3.52 (0.55)	140.3 (33.5)	266 (47)	7.6 (1.8)
Post	52.5 (5.7)	3.74 (0.50)	153.7 (21.7)	309 (41)*	9.1 (1.3)*

*Significantly different from corresponding pre-training value

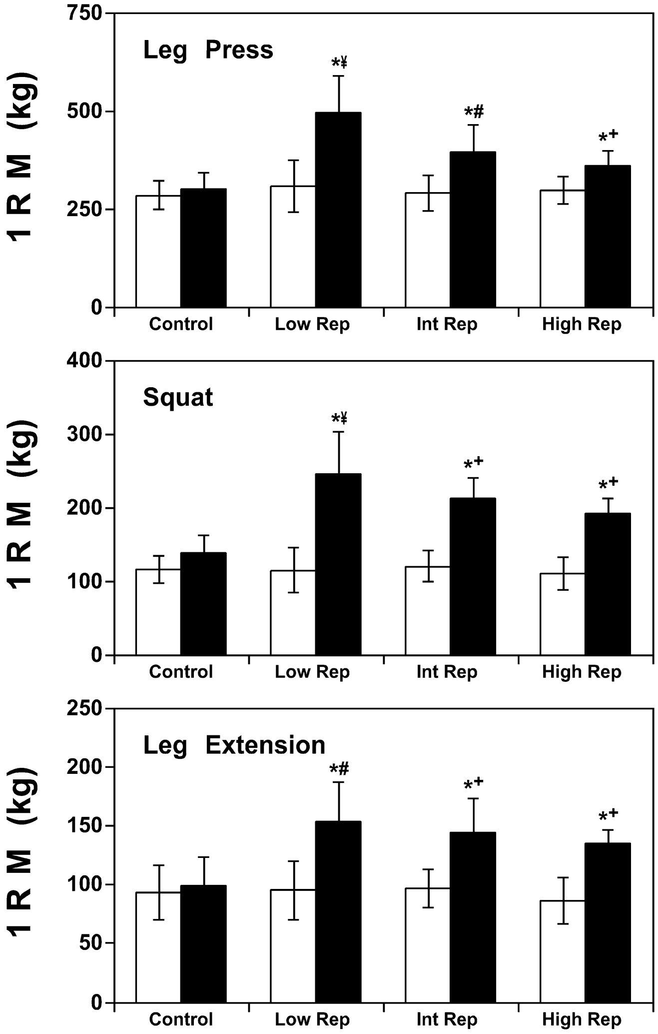

Fig. 3. Bar graphs comparing maximal strength (1-repetition maximum, *1RM*) values [mean (SD)] for the three lower-limb exercises pre- (■) and post-training (■). (*C* Control group, *Low Rep* low repetition group, *Int Rep* intermediate repetition group, *High Rep* high repetition group). *Significantly greater than corresponding pre-training value; ¥significantly greater than all corresponding post-training values; #significantly greater than corresponding High, Rep and Control post-training values; +significantly greater than corresponding Control post-training values

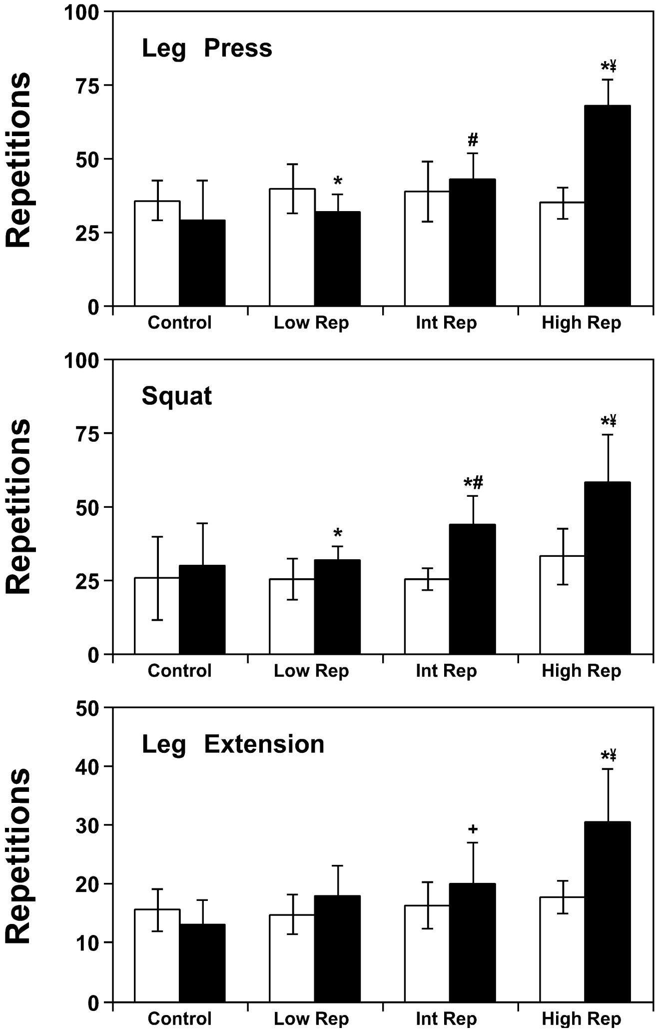

Fig. 4. Bar graphs comparing the maximal number of repetitions using 60% 1RM [mean (SD)] for the three lower-limb exercises pre- (■) and post-training (■). *Significantly different from corresponding pre-training value; ¥significantly greater than all corresponding post-training values; significantly greater than Low, Rep and Control corresponding post-training values; +significantly greater than corresponding Control post-training values

changes in fiber-type distribution were found for the Con group. These data were supported by the changes in the relative percentages of MHC isoforms. The biopsy specimens from all three training groups showed a significant decrease in MHCIIb and a concomitant increase in MHCIIa (Fig. 2, Table 4). No change was found in MHC content for the Con group.

Cross-sectional area

A hypertrophic effect was observed after resistance training for only the Int Rep and Low Rep groups (Table 5). For these two training groups, the cross-sectional areas of all three major fiber types (I, IIA, and IIB) were significantly larger after training. The 8-week progressive resistance training program caused the cross-sectional areas of the major fiber types to increase by approximately 12.5% for type I, 19.5% for type IIA, and 26% for type IIB, for both the Int and Low Rep groups. No significant area changes were found for the High Rep and Con groups (Table 5). However, there was a tendency for the type IIB cross-sectional area to increase after training for the High Rep group ($P = 0.13$).

Capillarization

Comparing pre- to post-training values for all groups, no significant differences were found in either CD or CF (Table 6). Likewise, no significant changes occurred in

Table 3. Muscle fiber type percentages determined using myofibrillar adenosine triphosphatase histochemical methods. Values given are mean (SD). (*n* Mean number of fibers per biopsy sample)

Training condition	Muscle fiber type						
	I	IC	IIC	IIA	IIAB	IIB	*n*
CONTROL							
Pre	35.6 (11.3)	1.0 (1.7)	0.7 (1.2)	28.2 (10.3)	4.6 (2.6)	29.9 (5.6)	1040 (451)
Post	39.9 (9.6)	1.4 (1.9)	0.6 (0.5)	31.2 (10.3)	3.2 (0.9)	23.7 (2.8)	1100 (452)
LOW REP							
Pre	38.3 (10.9)	0.3 (0.6)	0.6 (0.9)	33.3 (7.3)	5.4 (2.1)	22.1 (9.0)	1022 (255)
Post	42.8 (11.3)	1.6 (1.6)	3.9 (3.3)	31.0 (11.7)	12.1 (7.0)*	8.6 (6.1)*	912 (542)
INT REP							
Pre	38.6 (9.3)	0.5 (0.6)	0.5 (0.8)	33.1 (7.7)	6.1 (4.1)	21.2 (9.0)	953 (463)
Post	40.7 (9.9)	1.8 (2.1)	1.6 (1.3)	34.1 (11.8)	11.3 (2.8)*	10.5 (9.8)*	885 (471)
HIGH REP							
Pre	34.9 (13.3)	0.7 (1.1)	2.4 (4.8)	28.5 (10.5)	5.8 (5.1)	27.7 (15.8)	1110 (561)
Post	40.4 (6.0)	1.8 (3.6)	3.0 (2.8)	32.2 (9.5)	12.0 (6.1)*	10.6 (5.8)*	1342 (549)

*Significantly different from corresponding pre-training value

Table 4. Relative myosin heavy chain isoform percentages from homogenate muscle samples determined using sodium dodecylsulfate-polyacrylamide gel electrophoresis. Values given are mean (SD). (*MHCI* Myosin heavy chain I, *MHCIIa* myosin heavy chain IIa, *MHCIIb* myosin heavy chain IIb)

Training condition	MHCI	MHCIIa	MHCIIb
CONTROL			
Pre	34.4 (14.0)	41.4 (11.1)	23.2 (4.9)
Post	36.9 (12.0)	40.7 (8.7)	22.4 (5.0)
LOW REP			
Pre	32.8 (8.2)	44.6 (6.7)	22.6 (5.6)
Post	35.3 (11.3)	55.4 (9.3)*	9.3 (2.9)*
INT REP			
Pre	28.6 (7.9)	47.1 (6.9)	24.3 (8.4)
Post	31.6 (8.0)	57.6 (6.6)*	10.8 (3.7)*
HIGH REP			
Pre	30.1 (10.2)	42.4 (4.7)	27.5 (11.6)
Post	33.2 (6.3)	53.9 (5.3)*	12.9 (3.5)*

*Significantly different from pre-training values

Table 5. Cross-sectional area (μm^2) of the three major muscle fiber types. Data are presented as mean (SD)

Training condition	Muscle fiber type		
	I	IIA	IIB
CONTROL			
Pre	5208 (1494)	6070 (1944)	4648 (1043)
Post	5155 (1239)	5982 (1547)	4813 (672)
LOW REP			
Pre	4869 (1178)	5615 (1042)	4926 (942)
Post	5475 (1425)*	6903 (1442)*	6171 (1436)*
INT REP			
Pre	4155 (893)	5238 (787)	4556 (877)
Post	4701 (809)*	6090 (1421)*	5798 (1899)*
HIGH REP			
Pre	3894 (1085)	5217 (1009)	4564 (1179)
Post	4297 (1203)	5633 (596)	5181 (714)

*Significantly different from corresponding pre-training values

CFTA for any group (data not shown). With the exception of a significant increase after training for CFT for type IIA for the Int Rep group, no significant changes occurred in CFT for any of the three types (I, IIA, or IIB; Table 6).

Discussion

Strength adaptations

Although a few resistance-training studies have challenged DeLorme's (1945) theory of a strength–endurance continuum (DeLateur et al. 1968; Clark and Stull 1970; Stull and Clark 1970), most research in this area supports the idea of task specificity related to specific set/repetition combinations (e.g., Stull and Clark 1970; Anderson and Kearney 1982). The results from the present investigation support the findings of these earlier studies on strength adaptations. Although maximal dynamic strength significantly improved for all three training groups, the Low Rep group improved the most. For example, maximal dynamic strength improvements in the leg press exercise amounted to 61% for Low Rep compared to 36% for Int Rep, 32% for High Rep, and 6% for Con (Fig. 3). On the other hand, local muscular endurance in the leg press improved the most for High Rep compared to the other groups: 94% improvement for High Rep, 10% for Int Rep, –20% for Low Rep, and –19% for Con (Fig. 4).

Cardiorespiratory adaptations

Although traditional resistance training involves heavy resistance combined with low numbers of repetitions, low resistance/high repetition regimens must still be regarded as a form of resistance training. Even working on the "extreme" endurance end of the strength–endurance continuum (performing as many as 150 repetitions) usually means performing submaximal repeated contractions for less than 5 minutes/set (e.g., Stull and Clark 1970; Anderson and Kearney 1982). However, improvements in short-term endurance following a resistance-training program have been reported. After 10 weeks of a heavy-resistance-training program, Hickson et al. (1980) found a significant increase in time

Table 6. Muscle capillary supply as determined using *Ulex europaeus* agglutinin I lectin histochemistry. Values given are mean (SD). (*n caps/I* Number of capillaries per type I fiber, *n caps/IIA* number of capillaries per type IIA fiber, *n caps/IIAB* number of capillaries per type IIAB fiber, *n caps/IIB* number of capillaries per type IIB fiber, *n caps/fiber* number of capillaries per fiber, *n caps/mm*^{2} number of capillaries per millimeter squared)

Training condition	*n* caps/I	*n* caps/IIA	*n* caps/IIAB	*n* caps/IIB	*n* caps/fiber	*n* caps/mm^2
CONTROL ($n=5$)						
Pre	4.1 (0.3)	3.9 (0.6)	3.6 (0.5)	3.2 (0.5)	1.7 (0.6)	268 (89)
Post	4.7 (0.6)	4.3 (0.3)	4.4 (1.0)	3.6 (0.9)	1.6 (0.3)	273 (29)
LOW REP ($n=7$)						
Pre	4.5 (0.7)	4.7 (0.7)	3.9 (0.9)	3.7 (0.6)	1.6 (0.4)	273 (32)
Post	4.7 (0.8)	4.8 (0.7)	4.2 (1.1)	4.5 (1.0)	1.7 (0.4)	251 (39)
INT REP ($n=6$)						
Pre	3.7 (0.4)	3.7 (0.4)	3.5 (0.5)	3.2 (0.4)	1.2 (0.2)	244 (50)
Post	4.4 (0.5)	4.7 (0.5)*	4.5 (0.8)	4.1 (0.4)	1.5 (0.2)	254 (39)
HIGH REP ($n=5$)						
Pre	3.7 (0.3)	3.8 (0.7)	3.7 (0.3)	3.6 (0.7)	1.3 (0.1)	263 (44)
Post	4.1 (0.4)	4.7 (0.7)	4.7 (0.6)	3.9 (0.2)	1.5 (0.3)	282 (34)

*Significantly different from corresponding pre-training value

to exhaustion for both cycling and running with no significant changes in $\dot{V}O_{2\max}$. Likewise, Marcinik et al. (1991) reported that 12 weeks of circuit strength training improved cycle endurance performance independent of changes in $\dot{V}O_{2\max}$. Similar findings have also been reported when resistance training is added to an aerobic endurance-training program in young individuals (Hickson et al. 1988; Paavolainen et al. 1999), as well as in elderly men (Grimby et al. 1992) and women (Ferketich et al. 1998). Results from the present study support these findings. The High Rep group significantly improved their cycling performance (both maximal aerobic power and time to exhaustion) without changes in $\dot{V}O_{2\max}$ (Table 2). Although this may seem to contradict the basic principles of training specificity, enhanced long-term work capacity also requires muscular strength and anaerobic power (Tanaka and Swensen 1998). In addition, resistance training has been shown to improve running economy (Johnston et al. 1995; Paavolainen et al. 1999) and may, thus, also improve cycling economy. Such improvements in endurance performance following a resistance-training program may be related to increases in lactate threshold and lower-limb strength (Marcinik et al. 1991), and therefore, may not necessarily be related to increases in aerobic capacity.

Muscle fiber type and cross-sectional area

Although strength and performance adaptations to varied resistance training programs are fairly well documented, scant information exists regarding specific neuromuscular adaptations. Our hope was to gain some insight into what may be happening within the muscle (i.e., changes in fiber size, fiber type, and capillarity) that could potentially contribute to these documented differences in maximal strength, local muscular endurance, and performance.

Very few studies have attempted to document muscular changes following different modes of resistance training. Some studies have used indirect methods to measure changes in cross-sectional area (magnetic resonance imaging and ultrasound scanning) and have reported similar area and strength adaptations in young men (Chestnut and Docherty 1999), young women (Hisaeda et al. 1996), and early postmenopausal women (Bemben et al. 2000) subjected to different sets/repetition maximum training protocols. To our knowledge, only two studies have investigated the effects of different types of resistance training programs on skeletal muscle utilizing muscle biopsy sampling (Jackson et al. 1990; Taaffe et al. 1996), and neither of these specifically addressed the "strength–endurance continuum".

Advantages of the present study compared with previous work in this area include a non-exercising control group, the full range of histochemical fiber types, relative MHC content to validate the histochemical data, cross-sectional area determined from at least 50 fibers per major type, free weights for training and testing, and the inclusion of various cardiorespiratory parameters. In addition, in the present study we chose three different, yet practical, resistance-training protocols to specifically focus on muscular adaptations at different points along the strength–endurance continuum.

Similar to previous resistance-training studies (see Staron and Johnson 1993), the present study found exercise-induced fiber-type conversions within the fast fiber population in the direction of type IIB to IIA. This fiber type transformation occurred to the same extent in all three training groups, amounting to approximately a two-fold increase in the percentage of fibers classified as type IIAB with a concomitant decrease in fibers classified as "pure" type IIB. This finding of similar fiber-type conversions between the three training groups is perhaps not surprising considering previously published data on both aerobic and anaerobic conditioning in humans (Staron and Johnson 1993). It appears that any exercise stimulus (e.g., resistance or endurance) that is sufficient in duration and/or intensity has the potential to ultimately cause conversions within the fast fiber population from type IIB to type IIA (Staron and Johnson 1993; Kraemer et al. 1995). Although this transformation took place in the present study following all three training protocols, significant differences between the groups were noted regarding the extent of exercise-induced hypertrophy.

The logical and often sought after outcome of a resistance-training program is increased size and force output of the exercised muscles. Hypertrophy appears to be the result of an increased rate of protein synthesis (Chesley et al. 1992; Phillips et al. 1997), which contributes to an absolute increase in the amount of contractile elements (MacDougall et al. 1979, 1982; Lüthi et al. 1986). Numerous studies have demonstrated a hypertrophic response for all three major fiber types (I, IIA, and IIB) following short-term resistance training in previously untrained young and elderly individuals (e.g., Staron et al. 1990, 1991; Hikida et al. 2000). However, this exercise-induced hypertrophy appears to affect the fast fibers to a greater extent than the slow, type I fibers (see Tesch 1987). In the present study, the hypertrophic response was minimized (essentially negated) in those individuals in the High Rep group. On the contrary, the cross-sectional area of all three major fiber types significantly increased for those subjects training at the strength end of the continuum (Table 5). Interestingly, the hypertrophic response was similar between both the Low Rep and Int Rep groups. It has often been accepted that improved strength/power results from high intensity/low volume training, whereas low intensity/high volume training maximizes muscle hypertrophy (Hisaeda et al. 1996). Based on data from the present investigation, this may not be entirely true. Indeed, data from the present investigation suggest low and intermediate RM training induces similar muscular adaptations, at least after short-term training in previously untrained subjects.

Capillarity

Results from resistance-training studies investigating capillary changes are equivocal, with reports of increases, decreases and no changes (e.g., Schantz 1982; Tesch et al. 1984, 1990; Hather et al. 1991; Wang et al. 1993; McCall et al. 1996; Hagerman et al. 2000). In the present study, there was a tendency for the number of capillaries per fiber to increase with training, indicating the formation of new capillaries within the muscle (Table 6). Such findings have been reported previously following resistance training in humans (Hather et al. 1991; McCall et al. 1996; Hepple et al. 1997; Green et al. 1998), and suggest that capillary changes are proportional to changes in fiber size. In other words, capillary growth may have been masked by the increase in area occupied by the muscle fibers. As such, capillary density did not change in the present study, even though a significant amount of hypertrophy occurred following training for the Low Rep and Int Rep groups.

Although there were no significant differences in either CD or CF after training in the present study, there was a trend suggesting potential differences between groups. CD went down 8% for Low Rep and went up 4% for Int Rep and 7% for High Rep. Likewise, there was a tendency for CF to increase a greater amount post-training for Int Rep and High Rep (23% and 18%, respectively) compared to Low Rep and Con (4%). Taken together, these data suggest that continued training may have resulted in significant differences between the groups, lending support to the idea that capillary adaptations occur on a continuum that is based on the duration and intensity of training. As such, high repetition/light resistance training appears to cause capillary adaptations more similar to aerobic endurance training compared to low repetition/heavy resistance training.

In conclusion, all three training regimens caused similar alterations within the fast fiber-type population (IIB to IIA fiber conversions) and in MHC content. Differences were, however, apparent between the three training groups in the hypertrophic response, and for various cardiorespiratory parameters. These specific post-training adaptations obviously contributed to the differences found between the groups for maximal dynamic strength and local muscular endurance. Those individuals training with heavier loads improved the most in maximal strength, whereas those who trained with the lighter loads improved the most using 60% of 1RM. Interestingly, both groups working on the strength end of the strength–endurance continuum (Low Rep and Int Rep) had a similar hypertrophic response. It has often been accepted that gains in strength/power result from high intensity/low volume training, whereas low intensity/high volume training maximizes muscle hypertrophy (Hisaeda et al. 1996). Based on data from the present investigation, low and intermediate RM training appears to induce similar muscular adaptations, at least after short-term training in previously untrained subjects. Overall, however, data from the current investigation demonstrate that both physical performance and the associated physiological adaptations are linked to the intensity and number of repetitions performed.

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