Muscle Adaptations to Plyometric vs. Resistance Training in Untrained Young Men

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ABSTRACT

Vissing, K, Brink, M, Lønbro, S, Sørensen, H, Overgaard, K, Danborg, K, Mortensen, J, Elstrøm, O, Rosenhøj, N, Ringgaard, S, Andersen, JL, and Aagaard, P. Muscle adaptations to plyometric vs. resistance training in untrained young men. J Strength Cond Res 22(6): 1799-1810, 2008-The purpose of this study was to compare changes in muscle strength, power, and morphology induced by conventional strength training vs. plyometric training of equal time and effort requirements. Young, untrained men performed 12 weeks of progressive conventional resistance training (CRT, n = 8) or plyometric training (PT, n = 7). Tests before and after training included one-repetition maximum (1 RM) incline leg press, 3 RM knee extension, and 1 RM knee flexion, countermovement jumping (CMJ), and ballistic incline leg press. Also, before and after training, magnetic resonance imaging scanning was performed for the thigh, and a muscle biopsy was sampled from the vastus lateralis muscle. Muscle strength increased by approximately 20-30% (1-3 RM tests) (p < 0.001), with CRT showing 50% greater improvement in hamstring strength than PT (p < 0.01). Plyometric training increased maximum CMJ height (10%) and maximal power (Pmax; 9%) during CMJ (p < 0.01) and Pmax in ballistic leg press (17%) (p < 0.001). This was far greater than for CRT (ρ < 0.01), which only increased Pmax during the ballistic leg press (4%) (p < 0.05). Quadriceps, hamstring, and adductor whole-muscle crosssectional area (CSA) increased equally (7-10%) with CRT and PT (p < 0.001). For fiber CSA analysis, some of the biopsies had to be omitted. Type I and IIa fiber CSA increased in CRT (n

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= 4) by 32 and 49%, respectively (p < 0.05), whereas no significant changes occurred for PT (n = 5). Myosin heavy-chain IIX content decreased from 11 to 6%, with no difference between CRT and PT. In conclusion, gross muscle size increased both by PT and CRT, whereas only CRT seemed to increase muscle fiber CSA. Gains in maximal muscle strength were essentially similar between groups, whereas muscle power increased almost exclusively with PT training.

KEY WORDS stretch shortening cycle, hypertrophy, strength training, long-term

Introduction

onventional resistance training (CRT) and plyometric training (PT) constitute two different strategies for improving maximal muscle strength and contractile power.

Conventional resistance training typically involves relatively slow and controlled movements against external loads of weight training apparatus or free weights and most often involves both concentric and eccentric contractions throughout the entire range of motion. Performing months of highresistance CRT has previously been shown to be effective for improving both muscle strength and power (2,6,9). These functional effects are caused by adaptive adjustments in neural circuitry function and muscle morphology, respectively (1). Thus, CRT has been shown to induce an increased neuronal input to agonist muscles (5,37) while sometimes also lowering antagonist muscle coactivation (16). The adaptive changes in muscle morphology induced by CRT have been shown to include increases in whole-muscle crosssectional area (CSA), increases in muscle fiber CSA of type I and especially type II fibers, upregulation of the relative amount of type IIa fibers and/or downregulation of type IIx fibers, and changes in muscle fiber pennation angle (2,9,18,23,26).

Plyometric training is employed by many athletes and coaches to increase muscle power in sports activities where muscle power is an important determinant of performance. Compared with CRT, PT more closely resembles the ballistic movement patterns (i.e., the body or implement is allowed to "take off") involved in athletic performance and is typically performed by use of high-impact jumping exercises (22). The principle of PT relies on exploitation of the stretchshortening cycle (SSC), in which a rapid eccentric muscle contraction facilitates an increased force and power output during the succeeding concentric contraction phase, provided that the movements are performed rapidly (24; pp. 184–199). Plyometric training has been reported to increase maximal vertical jump height effectively (30,33,35). This effect of PT is generally believed to be caused by neural adjustments in motor unit recruitment or neural firing frequency, enhanced reflex potentiation, and/or changes in muscle and connective tissue elastic properties (7,27). Reports on the effect of PT on muscle morphology are much scarcer. In strength trained individuals, smaller increases in both type I and type II fiber CSA were observed in response to PT (33), whereas somewhat greater increases in both type I and type II skinned muscle fibers have been reported after PT in subjects active in sports not involving high-impact jumping (30). Furthermore, a PT-induced downregulation of myosin heavy-chain (MHC) IIX has also been observed (30).

Thus, in contrast to the most common beliefs, the possibility exists that PT may induce changes in muscle morphology that resemble those of CRT. However, information on this aspect is very limited. Furthermore, direct comparisons on functional strength performance effects of CRT vs. PT also are scarce. Previous studies report similar increases in maximal vertical jump height with PT and CRT interventions, respectively (7,35). However, comparative information on PT vs. CRT is limited, especially for untrained individuals, because most studies on PT have recruited strength trained persons on account of an assumed risk of musculoskeletal injury with this type of training.

Comparisons of functional and morphological muscle responsiveness between PT and CRT are important for athletes in need of specific functional characteristics (e.g., strength or power) and/or muscle morphology effects (e.g., changes in hypertrophy and/or body weight).

The purpose of this study, therefore, was to compare possible changes in muscle strength, power, and morphology induced by PT vs. CRT of equal time and effort in individuals with no prior history of strength training or involvement in sports activities involving SSC movement patterns. More specifically, we wanted to 1) compare the adaptive changes both in single-fiber and whole-muscle morphology in PT vs. CRT, and 2) to compare the adaptive changes in maximal muscle strength and power induced by PT and CRT. It was hypothesized that PT would predominate over CRT in training-induced muscle power and that CRT would

predominate over PT in training-induced muscle hypertrophy and muscle strength.

Methods

Experimental Approach to the Problem

The study was designed to compare long-term training adaptations in muscle strength, power, and morphology to CRT vs. PT. To investigate this question, we recruited healthy young men who had not performed strength training of the lower extremities for an extended period and who were inexperienced with PT and sports involving a large degree of SSC patterns. Subjects were randomly divided in two groups and undertook 12 weeks of carefully controlled progressive CRT or PT. Muscle strength and power were evaluated by a number of functional tests, and muscle morphology changes were evaluated by whole-muscle scanning and muscle fiber analysis through protein chemistry procedures.

Subjects

Sixteen untrained healthy male subjects volunteered to participate in the study (age 25.1 ± 3.9 years [mean \pm SD], weight: 80.6 ± 16 kg, height: 181.3 ± 5.2 cm). None of the subjects had engaged in resistance training or sports activities involving SSC movement patterns for 6 months before their inclusion in the study. All participants were informed of the purpose and the risks of the study and gave their written consent to participate. The study was approved by the Danish Ethical Committee of Aarhus (j. no. 20050178) and conducted in accordance with the Declaration of Helsinki.

Experimental Design and Training Program

The subjects were randomly assigned as eight subjects to either a heavy CRT group or a PT group. The groups were not significantly different with respect to body mass (p = 0.354) or height (p = 0.592). Before and after a 12-week training period, all subjects underwent a magnetic resonance imaging scan of the thigh muscles, a muscle biopsy sampling from the middle part of the vastus lateralis muscle of one leg, and several strength and power tests dispersed on two succeeding days to allow recovery between tests. Subjects were given 2–3 days to recover between familiarization before pretesting, the pretesting procedures, and initiation of the training period. A similar length of recovery was given between the final training session and posttesting procedures.

The CRT training protocol was similar to a protocol reported by Andersen and Aagaard (9), with the aim of increasing maximal muscle strength and rate of force development and inducing hypertrophy in lower-extremity muscle groups. The PT training protocol was designed to include typically applied PT jumping exercises and progression in terms of the number of impacts and/or individually based height adjustments, as applied or recommended from the literature (30,33,34), to evaluate the potential changes in maximal muscle strength, rate of force development, and hypertrophy in similar muscle groups for this type of training intervention.

Session no.	1-5	6-15	16-20	21-25	26-30	31-35	35-36
Conventional s	strength trai	ning protoco	ol				
Incline leg pres	S						
Sets	3	4	4	4	5	5	4
Reps	12	10	10	10,10,10,8	8,8,8,6,6	8,8,6,6,6	8,6,6,4
Knee extension	า						
Sets	3	4	5	5	5	5	4
Reps	12	10	10,10,10,8,8	10,8,8,8,6	8,8,8,6,6	8,8,6,6,4	8,6,6,4
Hamstring curl							
Sets	3	4	4	4	5	5	4
Reps	12	10	10	10,10,10,8	8,8,8,6,6	8,8,6,6,6	8,6,6,4
2 minutes of re	ecovery bet	ween each	set				
Plyometric train	ning protoc	ol					
Hurdle jumps*							
Sets	6–8	8	10	10-12	12	12-15	15
Impacts	3	3	3	3	3-4	4	4
Countermoven	nent jumps						
Sets	3	3	3	4	4	4	4
Impacts	8	10	12	10	12	12-15	15
Drop jumps*							
Sets	2-3	3	3	4	4	4	4
Impacts	8	8-10	12	10	12	12-15	15

Fifteen seconds of recovery between impacts of countermovement jumps and drop jumps. Two minutes of recovery between each set. No recovery between hurdle jump impacts of each set.

The 12-week training regimens included a total of 36 training sessions. The CRT program consisted of three exercises using traditional strength training apparatus (leg press, knee extensions, and hamstring curl), and training followed a progression essentially similar to a previously applied protocol by Andersen and Aagaard (9) (see Table 1). In brief, the various exercises were essentially conducted in three to five sets of 4-12 repetitions (corresponding to 4- to 12-repetition maximum [RM] loads). All exercises were performed in a controlled manner at a self-selected pace using cyclic concentric and eccentric muscle contractions. Initial resistance was determined from each subject's 1 RM strength. The loading levels of each training session were monitored, and loads were continually adjusted to the intended relative levels throughout the training period (12 RM \rightarrow 4-6 RM). The PT program consisted of three commonly used plyometric jumping exercises (countermovement jumps [CMJ], hurdle jumps, and drop jumps). All three exercises were performed with emphasis on the eccentric-to-concentric transition, which was performed as quickly as possible during the ground-contact phase. Absolute PT loads were progressively increased by individually determined increases in the height of hurdles and the release height of the drop jump bench, respectively. Training progressed slowly in the early training phase,

whereas the number of impacts as well as jump height progressed in a steeper manner in the later training phase (see Table 1). All training sessions were closely supervised.

One major challenge was the attempt to design two very different training protocols that, despite the apparent dissimilarities, were comparable in terms of time and effort. To provide a rough estimate of this, the total training volumes were expressed as the total amount of work in joules (14; p. 7). Conventional resistance training volume was quantified as the weight resistance in newtons multiplied by the distance of weight displacement. In calculation of PT training volume, body weight constituted weight resistance. The amount of work per exercise repetition was then multiplied by the total number of repetitions for the training sessions. From such estimates, the average amount of work per training session turned out to be strikingly similar between groups, with CRT producing 33,747 J and PT producing 33,647 J of work, respectively. Furthermore, for the time under tension, estimates were obtained in two representative subjects by means of video recordings and timing of each specific exercise, in which the average time under tension was calculated by multiplying with repetitions/training sessions, as described above. Average total time under tension per CRT training session was approximately 200 seconds; in PT, it was approximately 20 seconds. Thus, estimated from the total

Repetitions (reps) corresponds to repetition-maximum loading.

^{*}Individually based height progression for hurdle jumps and drop jumps.

amount of work, the two training protocols were quite comparable, whereas time under tension was approximately 10 times greater in CRT than PT, indicating that power exertion (work/time) was 10 times greater in PT than CRT. Although other means for quantifying the PT stimulus exist, such as calculations of knee joint or ground-reaction forces (22), such analytic measures do not allow for a direct comparison with CRT.

Measurement Procedures

Muscle Strength and Power Assessment. Measurements of muscle strength and power were carried out on two consecutive days. On the first day, tests included maximal CMJs, 1 RM leg press, and ballistic leg press in said order. On the following day, tests included 3 RM knee extensions and 1 RM hamstring curl in said order. Before testing, the subjects warmed up on a cycle ergometer, and before each specific test the subjects performed two to three sets of two to five repetitions (depending on the specific exercise test) to enable habituation. Between warm-up and habituation sets, and again between the individual tests, 3–6 minutes were given (depending on the specific exercise test) to allow recovery.

The CMJs were performed on a force plate (AMTI OR6-7, AMTI, Watertown, Mass). Subjects were instructed to perform a maximal vertical CMJ with a preparatory downward motion from the upright standing position to a freely chosen flexion position with their hands on their waist/hip throughout the jump. Each participant was allowed five attempts; all attempts were recorded, and the highest jump was selected for subsequent analysis. The vertical groundreaction force signal was sampled at 240 Hz and was subsequently low-pass filtered at a 25-Hz cut-off frequency with a fourth-order Butterworth zero-lag low-pass filter (38; pp. 36-41). To avoid filter distortion at the sharp takeoff transient, the raw signal was clipped just before takeoff and then extended by multiplying the five last sampling points from the clipped signal by -1 and concatenating these five new negative values to the clipped signal (in effect rotating the last five-point part of the signal about the time axis). The filtered vertical force signal (F[t]) minus the subject's body weight (in newtons) was time integrated once to give vertical body center of mass (BCM) velocity (v[t]) and twice to give vertical BCM displacement during the time on the force plate. Vertical BCM displacement while airborne was calculated from the velocity at the instant of takeoff, assuming mechanical energy conservation during flight. The CMJ height was calculated by adding the vertical displacement of BCM while on the force plate and while airborne, respectively. Finally, F(t) and v(t) were multiplied to give power exerted by the leg extensor muscles on the BCM (P[t]). Maximal instantaneous power (Pmax) during the concentric part of the movement was determined from P(t) (13).

The procedures for RM testing were essentially similar to procedures reported in "Physiological tests for elite athletes," by the Australian Sports Commission (28; pp. 205–206).

According to these procedures, the validity and the test-retest reliability is high. Furthermore, it justifies our 3 RM procedures for other muscle groups to be a sound measure of maximal strength, because a high correlation exists between 1 RM and 3 RM measures. Each subject's 1 RM leg press strength was measured on a conventional incline leg press machine (Powerfit 45° inclined leg press, Powerfit, Italy). The load was increased in steps of approximately 7 kg (10-kg plates multiplied by the sine of the machine's 45° inclination) until the subject could no longer perform an accepted leg press-that is, start with straight knees, then flex the hips and knees to 90° knee angle and, finally, extend back to starting position. The machine's backrest inclination was adjusted individually so that the subject would reach a 90° knee angle just before the thighs would hit the chest. The 1 RM was defined as the combined mass of the plates and the machine's moveable foot plate (65 kg) lifted at the last accepted attempt.

Ballistic leg press was performed on the same machine we used for 1 RM leg press. Subjects were instructed to start the movement with stretched legs, then flex the knees to a freely chosen position, and then immediately push the foot plate upward with maximum effort. The machine was custom fitted so that the foot plate would not slide down again after being pushed away by the subject. Each subject performed ballistic leg presses with three to six different loads evenly distributed between no extra load and approximately 90% of 1 RM for the leg press movement. The different loads were lifted in randomized order between subjects, but in similar order preand posttraining for each individual subject, similar to previous studies (11,20); we chose a fixed absolute loading scheme instead of a scheme with fixed relative loadings because we simply wanted to detect possible changes in Pmax. By this procedure, we acknowledge that we are unable to discover possible shifts in force-velocity relations. However, for Pmax detection, absolute loads are equally adequate to relative loads; true maximal power might occur with a loading in between two of our absolute loadings, but this might as well occur when using fixed relative loadings. A force plate similar to the one used for CMJ was mounted on the foot plate. The force signal (F[t]) was sampled and filtered similarly to the procedures for CMJ. The ballistic leg press tests were filmed at 240 frames per second by four cameras placed at different angles to the left of the leg press machine (ProReflex MCU1000, Qualisys AB, Sweden). The digitized film recordings were low-pass filtered at a 10-Hz cut-off frequency with a fourth-order Butterworth zero-lag low-pass filter, and foot plate velocity (v[t]) was calculated using finite difference (38; pp. 47-48). Finally, F(t) and v(t) were multiplied to give power exerted by the leg extensor muscles on the foot plate (P[t]). The Pmax value during the concentric part of the movement was determined from P(t). Thus, except for the velocity determination, Pmax was determined similarly for CMJ and ballistic leg press. Subjects were allowed three attempts at each load; all attempts were

recorded, and the attempt with the highest Pmax was used in the statistical analysis.

Subjects' 3 RM dynamic knee extension and 1 RM hamstring curl were measured on a conventional combined knee extension/hamstring curl machine (Vasil Leg Curl/Extension-Combo, Vasil Gym, Ukraine). Three-repetition maximum tests were conducted for dynamic knee extension to avoid knee injury for this specific exercise. This is in accordance with procedures described to correlate strongly to 1 RM (28; pp. 201). Loading increments for hamstring curl and knee extension tests were 5 kg.

Whole-Muscle Cross-Sectional Area Analysis-Magnetic Resonance Image Scanning. All imaging was performed with a 1.5-T scanner (Philips Achieva, Best, the Netherlands). The subjects were placed in supine position with the feet first into the magnet. The images included both legs and were collected using a body coil. After an initial frontal scout scan, 50 transversal slices from the hip to the knees were acquired. A T1-weighted, fast spin echo sequence with the following parameters was used with scan matrix = 304×304 , field of view = 425×425 mm, number of slices = 50, slice thickness = 7 mm, slice gap = 3 mm, repetition time = 2 seconds, echo time = 5 milliseconds, echo train length = 18, number of signal averages = 2, and scan time = 3:12 minutes. Calculations of whole-muscle CSA were performed by manually segmenting the muscles at three axial positions using a custom-made analysis program. The analysis program was validated by comparing area analyses on phantom scans with analyses made with the standard Philips radiological analysis environment (ViewForum rel. 5.1, 2006). The analysis was performed blinded by randomizing data before the analysis. Whole-muscle CSA was obtained at proximal, middle, and distal levels corresponding to one-third, one-half, and two-thirds of femur length, respectively. The femur length was measured on the overview frontal scout scan as the distance from the most distal part of facies articularis on condylus lateralis to the most proximal part of caput femoris. Whole-muscle CSA of three muscle compartments was calculated for both legs: 1) m. quadriceps (mm. vastus lateralis, vastus medialis, vastus intermedius, and rectus femoris), 2) hamstrings (mm. semitendinosus, semimembranosus, and biceps femoris-caput longum and caput breve), and 3) the adductor compartment containing the three adductors (mm. adductor magnus, adductor longus, and gracilis). Finally, whole-muscle CSA-combined (proximal- + middledistal-level CSA) was calculated for each compartment.

Muscle Fiber Analysis—ATPase Histochemistry. Biopsies were obtained from the middle section of the vastus lateralis muscle by use of a conchotome. The muscle samples were immediately mounted with Tissue-Tek, frozen in isopentane cooled with liquid nitrogen, and stored at -80° C until further investigation. Serial sections (10 μ m) of the muscle biopsy samples were cut in a cryostat (-20° C), and cross-sections

from pre- and posttraining biopsies from the same subject were placed on the same slide and processed simultaneously for ATPase histochemistry. ATPase histochemistry analysis was performed after preincubation at pH of 4.37, 4.60, and 10.30 as described previously, to enable the determination of changes in the area of specific fiber types and fiber type distribution within the tissue sample (9). The serial sections were visualized and analyzed as described in detail by Andersen and Aagaard (9). Only fibers cut perpendicularly to their longitudinal axis were used in the determination of fiber size.

Muscle Homogenate Analysis—Sodium Dodecylsulfate Polyacrylamide Gel Electrophoresis. Analysis was performed on the muscle biopsies to investigate relative MHC isoform changes using sodium dodecylsulfate polyacrylamide gel electrophoresis (SDS-PAGE) as previously described (9). From each biopsy, 50–100 serial cross-sections (20 μm) were cut and placed in 100–200 μL of lysing buffer and heated for 3 minutes at 90°C. Between 5 and 20 μL of the myosin-containing samples were loaded on an SDS-PAGE gel containing 6% polyacryl polyacrylamide and 30% glycerol. Gels were run at 70 V for 42 hours at 4°C. Subsequently, the gels were Coomassie stained, and MHC isoform content was determined with a densitometric system (Cream 1D, KemEnTec Aps, Copenhagen, Denmark).

Statistical Analyses

Eight subjects were recruited for each training group to produce a statistical power of 0.800 for analytic measures such as strength and fiber CSA changes in response to CRT, for which we had realistic expectations from the literature. Results are presented as mean \pm *SEM* unless otherwise stated. All data were statistically analyzed using two-way ANOVA with repeated measures and Student-Newman-Keuls post hoc test when allowed. Level of significance was set at $\rho \leq 0.05$.

RESULTS

Compliance With the Training Program

Of the 16 subjects recruited, 1 had to be excluded because of exercise-unrelated illness. The remaining 15 subjects (RT, n = 8; PT, n = 7) all completed the prescribed exercise sessions without interruptions in the training protocol and without occurrence of muscle-tendon-bone injury.

Strength and Power Measurements

Maximal Muscle Strength. Relative changes in dynamic strength are shown in Figure 1. An overall training effect (p < 0.001) was observed for 1 RM inclined leg press, where CRT increased by $29 \pm 3\%$ (p < 0.001) and PT increased by $22 \pm 5\%$ (p < 0.01), with no differences between groups (Figure 1a). For 3 RM isolated knee extension, a training effect (p < 0.001) also was observed. Conventional resistance training increased by $27 \pm 2\%$ (p < 0.001) and PT increased by $26 \pm 5\%$ (p < 0.001), again with no differences between

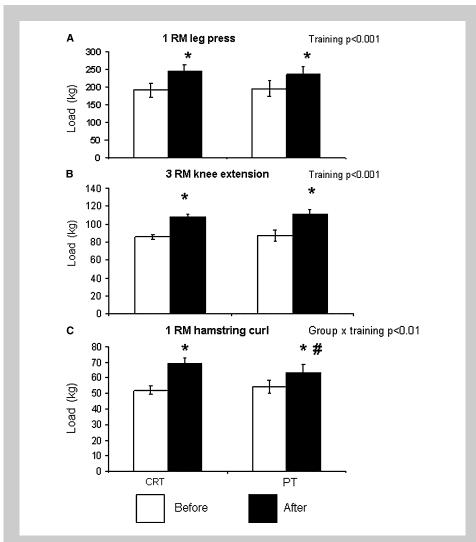


Figure 1. Maximal muscle strength. Loads (kg) \pm *SEM* before and after 12 weeks of either conventional resistance training (CRT) or plyometric training (PT) are shown for a) one-repetition maximum (RM) incline leg press, b) 3 RM knee extension, and c) 1 RM hamstring curls. The results from two-way analyses of variance are shown in the upper right corner of each diagram. *Significant difference before and after training (ρ < 0.001); #significant difference between groups (ρ < 0.01).

groups (Figure 1b). For the 1 RM hamstring curl, a group \times training interaction was observed (p<0.01) with an improvement in CRT by 33 \pm 3% (p<0.001), which was larger than the 18 \pm 4% improvement in PT (p<0.05) (Figure 1c).

Countermovement Jumping Height and Power. For maximum CMJ height, a group \times training interaction was observed (p < 0.05) (Figure 2a). The PT group improved their jumping height by approximately 10% (p < 0.01), whereas for CRT no increase in jumping height posttraining was observed. Also, for power measured as Pmax during CMJ, a group \times training interaction was observed (p < 0.05). The PT group improved Pmax by approximately 9% (p < 0.01), whereas for CRT no change was observed (results not shown).

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Ballistic Leg Press Power. For Pmax measured during ballistic 45° inclined leg press, a group \times training interaction was observed (p < 0.001). The PT group improved their power output by 17% (p < 0.001). This gain in peak power was greater than for CRT, which improved power output by 4% (p < 0.05) (Figure 2b).

Whole-Muscle Cross-Sectional Area

Whole-muscle CSA of the quadriceps muscle group, hamstring muscle group, and adductor muscle group were measured at three regional levels for both legs. The results of whole-muscle CSA combined for the three regional levels and also combined for the right and left legs are shown in Figure 3 for all three muscle groups. For all three muscle groups, an overall training effect was observed (p < 0.001), with no differences between groups. Quadriceps CSA of both legs combined increased by 8.4 ± 2.0% (p < 0.001) for CRT and by 7.5 \pm 1.9% for PT (p < 0.001) (Figure 3a). Hamstring CSA of both legs combined and averaged increased by $10.0 \pm 1.3\%$ for CRT (p < 0.001) and by $6.7 \pm 1.8\%$ for PT (p < 0.001) (Figure 3b). For the adductors, average

CSA of both legs combined increased by 7.8 \pm 2.7% for CRT (p < 0.001) and by 7.2 \pm 2.9% for PT (p < 0.001) (Figure 3c). No changes were seen between groups in terms of regionally measured whole-muscle CSA or between right- and left-leg whole-muscle CSA measures, respectively (results not shown).

Muscle Fiber Cross-Sectional Area and Distribution

Because of poor morphological integrity of some of the muscle biopsies, ATPase histochemical analysis could only be performed in four CRT subjects and five PT subjects. Whereas the results on fiber CSA changes rely on ATPase histochemical analysis on this limited sample size, fiber type distributional changes from MHC protein analysis include our entire sample size.

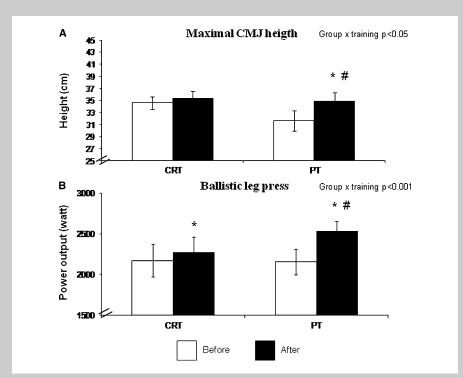


Figure 2. Peak power output. a) Maximal countermovement jump (CMJ) height (cm) \pm *SEM* and b) ballistic leg press peak power (W) \pm *SEM* are shown before and after 12 weeks of either conventional resistance training (CRT) or plyometric training (PT). The results from two-way analyses of variance are shown in the upper right corner. *Significant difference before and after training (ρ < 0.05); #significant difference between groups (ρ < 0.05).

For type I fiber CSA, an overall effect of training was observed (p < 0.05), with a 32 \pm 22% increase for the CRT group (p = 0.05) (Figure 4a). No significant changes were observed in the PT group. For type IIa fiber CSA, an overall effect of training was observed (p < 0.05), reflected by a 49 \pm 20% increase in the CRT group (p < 0.001), whereas no changes occurred in the PT group. For type IIa fiber CSA, a strong trend towards a group \times training interaction was observed (p = 0.061) (Figure 4b). No differences emerged in type IIx fiber CSA (Figure 4c).

When the relative distribution of MHC protein was evaluated by SDS PAGE electrophoresis, an overall effect of training was observed for MHC IIX (p < 0.05). The proportion of MHC IIX decreased from 10.4 ± 2.3 to $4.0 \pm 2.4\%$ in CRT (p < 0.05). In PT, MHC IIX exhibited a tendency to a decrease from 12.4 ± 5.0 to $7.1 \pm 2.9\%$ (p = 0.09) (Figure 5c). No changes were observed for MHC I and IIa in either group (Figures 5a and 5b).

DISCUSSION

The main findings of the present study were 1) that gains in whole-muscle CSA were induced to equal extent by both training regimens, with indications of greater gain in fiber CSA for CRT, and 2) that, except for hamstring strength, maximal strength gains were similar in CRT and PT, whereas

gain in power was much more markedly induced from PT than from CRT.

We applied PT to subjects with no prior strength training history or involvement in sports activities involving SSC patterns. Notably, no dropouts attributable to injury or injury symptoms were experienced in the PT group throughout the training period, whereas significant gains in maximal strength and power were achieved. Thus, PT training seems to constitute an applicable strength training alternative in subjects unfamiliar with this training regimen, at least when careful supervision and progression are provided.

Maximal muscle strength improved by 26–33% in response to CRT. The magnitude of improvement observed for the 1 RM leg press and 3 RM isolated knee extension was quite similar to the improvements observed in other CRT studies of comparable design

(i.e., comparable total duration of the training period, weekly session frequency, exercise types, and RM loadings) (8,15). Only a few studies have measured the impact of CRT on maximal hamstring strength. These studies report improvements within a 10–15% range for this specific exercise (21,32).

Plyometric training also induced improvement in all three tests of maximal strength. These PT improvements tended to be higher than the maximal strength changes observed in previous PT studies, which could be explained by shorter training periods and/or a higher initial training status of subjects in those previous studies (30,35). Yet, mean improvements in PT of isolated hamstring curl were 45% smaller than improvements in CRT. As all three test exercises were included in the CRT training protocol, larger CRT improvements compared with PT were expected, especially for hamstring curl, because the PT exercises probably loaded the hamstrings relatively less than the other muscle groups. However, in terms of a test exercise such as the isolated knee extension, the PT exercises collectively seemed to stimulate the quadriceps muscles similarly to CRT.

Countermovement jumping increased by 9–10% in response to PT, whereas no improvement was observed in response to CRT. These results are in accordance with previous reports of improvements in CMJ performance

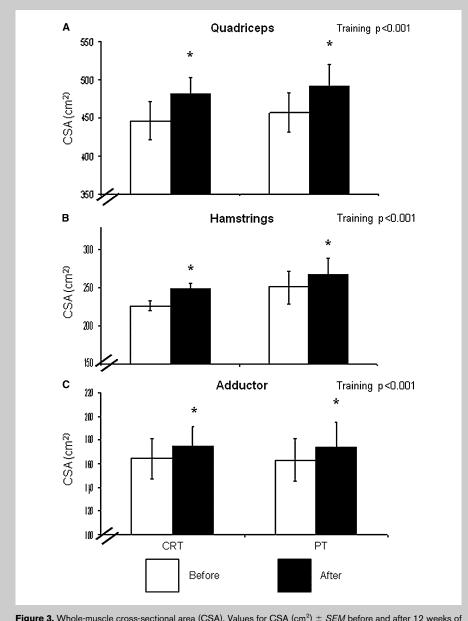


Figure 3. Whole-muscle cross-sectional area (CSA). Values for CSA (cm 2) \pm SEM before and after 12 weeks of either conventional resistance training (CRT) or plyometric training (PT) are shown for the proximal, central, and distal levels of both legs combined for a) quadriceps, b) hamstrings, and c) adductor muscle groups. The results from two-way analyses of variance are shown in the upper right corner for each muscle group. *Significant difference before and after training (ρ < 0.001).

within the 8–14% range in response to 8 weeks of PT training for untrained individuals (30,36), whereas PT studies including previously strength trained individuals or individuals familiar with activity including SSC exercise patterns report smaller improvements (29,33). The lack of improvement in CMJ performance with CRT observed in the present study is contradictive to some previous findings (9,10) but supported by others (17,25). Most likely, there is less transfer of training-induced learning from the CRT exercises than the PT exercises to the CMJ test (12). Other explanations comprise

subject variability within the limited number of subjects and/or the small relative alterations in CMJ performance.

It may be concluded that CRT and PT performance improvement, respectively, are greater in the tests that resemble most clearly the movement pattern of protocol-specific exercises. In the evaluation of power, we also conducted a ballistic leg press test, because this test may be regarded as a compromise between the movement pattern specificity of leg press exercise included in the CRT protocol and the ballistic element specifically inherent to the PT jumping exercises. Training-induced improvements in Pmax during ballistic leg press were observed to be substantially greater with PT than with CRT (17 vs. 4%). Thus, CRT and PT seem to constitute equally good strength training alternatives in male, untrained individuals for the development of maximal muscle strength of knee and for hip extensors other than the hamstring muscles. With reservation for our study design, maximal knee flexor strength seems to profit more from CRT than from PT. Plyometric training, on the other hand, seems to constitute a far better alternative for the development of peak power.

Training-induced changes in whole-muscle CSA were evaluated by magnetic resonance imaging. A strong relationship

between axial whole-muscle CSA obtained at 50% segment length and total muscle volume has previously been established for the quadriceps muscle (3,4), and increases of 5–15% in quadriceps CSA in response to prolonged heavy resistance training have previously been reported (4,16,18). Only one study that we are aware of has investigated whole-muscle CSA changes of conventional vs. plyometric exercise. In that study, 5–6% gains in whole-muscle CSA for calf muscles were equally induced by both training regimens (27). However, the design of the aforementioned study is very

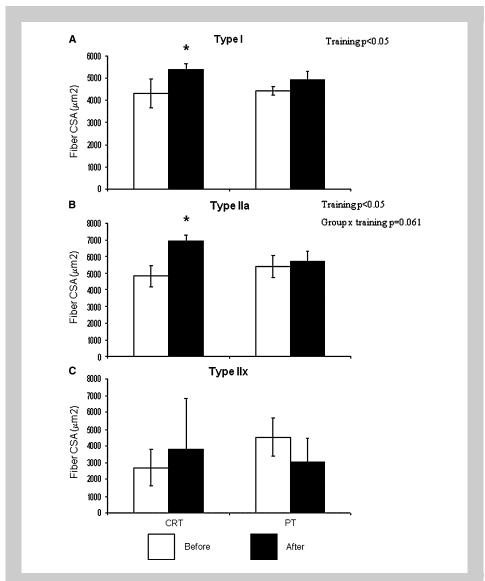


Figure 4. Single-fiber cross-sectional area (CSA). Values for CSA (μ m²) \pm *SEM* before and after 12 weeks of either conventional resistance training (CRT) or plyometric training (PT), as judged by ATPase histochemical analysis, are shown for a) type I, b) type IIa, and c) type IIx fibers. The results from two-way analyses of variance are shown in the upper right corner. *Significant difference before and after training (p < 0.05). Note that these results are based on only four CRT and five PT subjects (see Discussion).

different from ours, and, so far, no study has evaluated such comparative effects on the different thigh muscle groups and/or in response to training principles as they are commonly applied in real-life training situations. In the present study, quadriceps, hamstrings, and hip adductor muscle CSA increased to a similar extent with both CRT and PT. Thus, a similar change in hamstrings CSA was induced, and CRT still improved hamstring strength far more than PT. The most likely explanation for this is that only the CRT group had the hamstring curl exercise included in their training protocol, whereas both groups stimulated hamstring muscle hypertrophy through their respective exercises. The

observed change in hip adductor group CSA was somewhat unexpected. This finding could be interpreted as a high demand for hip stabilization during the leg press exercise of the CRT as well as during the jumping exercises of the PT training protocols.

The gain in muscle fiber CSA with resistance training, as evaluated by histochemical procedures, seems to vary considerably between studies depending on the types of subjects recruited and the training protocols applied. Increases of 15-30% in type I and type II fiber CSA have been reported after prolonged heavy resistance training (i.e., the CRT training protocol), typically with more pronounced hypertrophy of type II fibers (4,10,18,19). In the present study, 32 and 49% gains in type I and type IIa fiber CSA, respectively, were observed in response to CRT. In contrast, PT did not significantly increase type I or II fiber CSA. Few data exist on the change in fiber CSA in response to PT. Potteiger et al. (33) have reported 5-8% increases in type I and type II fiber area in response to 8 weeks of PT, but although the subjects included in this study were unfamiliar with plyometric exercise patterns, they had previously engaged in CRT. Gains as large as 20-30% in type I and type II skinned fiber

CSA have been reported with 8 weeks of PT in one study by Malisoux and coworkers (30). However, according to the training protocol of the study by Malisoux et al., 30–40% more jumping repetitions were performed with a 30–35% shorter average training session duration compared with our own training protocol (30). As limited recovery time between repetitions may in itself induce hypertrophy (15), the greater hypertrophic response of the study by Malisoux et al. (30) compared with the present study may partly be explained by this difference in recovery time.

Notably, after PT training, the increases in muscle CSA were not accompanied by increases in VL muscle fiber area.

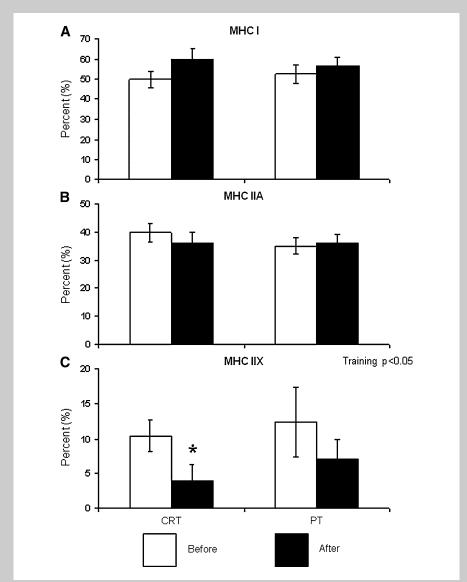


Figure 5. Myosin heavy-chain (MHC) isoform expression. Fiber type distribution of relative MHC expression in percent of total MHC expression (%) \pm *SEM*, as judged by sodium dodecylsulfate polyacrylamide gel electrophoresis gel electrophoresis before and after 12 weeks of either conventional resistance training (CRT) or plyometric training (PT), are shown for a) MHC I, b) MHC IIA, and c) MHC IIX isoforms. The results from two-way analyses of variance are shown in the upper right corner for each MHC isoform. *Significant difference before and after training (ρ < 0.05).

Obviously, this discrepancy could be caused by VL muscle biopsies not fully reflecting the overall change in anatomic quadriceps muscle size. Alternatively, fiber length (number of sarcomeres in-series) could have increased after PT training concurrently with an absence of single muscle fiber hypertrophy. Further, such potential adaptation would explain the marked gain in power observed in the PT group, as Pmax scales proportionally to maximal fiber shortening speed (Vo), which, in turn, scales linearly with the number of sarcomeres in-series (3). However, these theoretical considerations await experimental verification, and future studies

should be conducted to examine the potential influence of PT training on muscle fiber length.

Unfortunately, some of our biopsies were of less than optimal integrity, which left us with too small a sample size to allow strong conclusions based on ATPase histochemical procedures. Although the patterns of fiber CSA observed for the CRT group were within the expected range from the literature (9), our ability to judge fiber differences between CRT and PT groups by this method was inherently limited by sample size. However, previous studies on longitudinal PT by protocols similar to the present study have also failed to demonstrate substantial changes in muscle fiber CSA (33).

In light of our limited histochemical data, we evaluated fiber type distributional changes as the changes in MHC isoform composition by SDS-PAGE analysis. A strong correlation between MHC isoform expression and histochemical fiber typing profile has previously been reported (9), and prolonged CRT has previously been observed to induce MHC IIA upregulation and MHC IIX downregulation (9), whereas prolonged PT has been reported to induce either no changes or only a tendency toward MHC IIX downregulation (30,33). In the present study, we partly confirm this. Accordingly, we

observed downregulation in MHC IIX for CRT, and, for PT, a trend toward an MHC IIX downregulation was observed. Despite profound downregulation in MHC IIX, we did not observe the expected upregulation in MHC IIA content for CRT, for which we have no immediate explanation.

In conclusion, CRT and PT seemed to lead to similar gains in maximal strength, whereas PT induced far greater gains in muscle power. Notably, muscle hypertrophy can be induced by PT, with some indications of greater fiber hypertrophy induced with CRT. The information retrieved can be used in the design of strength training regimens for individuals with

different requirements of muscle strength and power, with or without a simultaneous requirement for hypertrophy.

PRACTICAL APPLICATIONS

Previous studies on PT have predominantly been conducted on athletes with substantial strength training history. The present data support the applicability of progressive PT for individuals with no prior history for this or any other type of strength training. From our results, PT in untrained individuals seems to improve not only muscle power but also muscle strength and hypertrophy. Thus, when carefully supervised, it constitutes an alternative training strategy to conventional strength training (which, to a lesser degree, improves muscle power) for the untrained. Depending on which qualities the practitioner wishes to improve, this knowledge can be useful to ensure effective training improvements.

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