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ORIGINAL ARTICLE

Resistance training using eccentric overload induces early adaptations in skeletal muscle size

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Abstract Fifteen healthy men performed a 5-week training program comprising four sets of seven unilateral, coupled concentric–eccentric knee extensions 2–3 times weekly. While eight men were assigned to training using a weight stack (WS) machine, seven men trained using a flywheel (FW) device, which inherently provides variable resistance and allows for eccentric overload. The design of these apparatuses ensured similar knee extensor muscle use and range of motion. Before and after training, maximal isometric force (MVC) was measured in tasks non-specific to the training modes. Volume of all individual quadriceps muscles was determined by magnetic resonance imaging. Performance across the 12 exercise sessions was measured using the inherent features of the devices. Whereas MVC increased ($P < 0.05$) at all angles measured in FW, such a change was less consistent in WS. There was a marked increase ($P < 0.05$) in task-specific performance (i.e., load lifted) in WS. Average work showed a non-significant 8.7% increase in FW. Quadriceps muscle volume increased ($P < 0.025$) in both groups after training. Although the more than twofold greater hypertrophy evident in FW (6.2%) was not statistically greater than that shown in WS (3.0%), all four individual quadriceps muscles of FW showed increased ($P < 0.025$) volume whereas in WS only m. rectus femoris was increased ($P < 0.025$). Collectively the results of this study suggest more robust muscular adaptations following flywheel than weight stack resistance exercise supporting the idea that eccentric overload offers a potent stimuli essential to optimize the benefits of resistance exercise.

Keywords Flywheel resistance training · Inertia · Muscle hypertrophy · Strength training · Weight stack

Introduction

Given that muscle stretch is a crucial stimulus promoting skeletal muscle growth (Goldspink 1999), there is also a general consensus that lengthening or eccentric (ECC) muscle actions should be emphasized in resistance training protocols aimed at governing increased muscle size (Hather et al. 1991; Hortobagyi et al. 1996) and strength (Komi and Buskirk 1972; Dudley et al. 1991; Hortobagyi et al. 1996). In support of this concept, in the rat it appears that muscles subjected to ECC exercise exhibit greater rate of myofibril protein synthesis (Wong and Booth 1990a, b) and hypertrophy (Wong and Booth 1990a, b) than muscles performing shortening or concentric (CON) actions. Likewise, the results of human studies show greater skeletal muscle protein synthesis following bouts of maximal ECC than CON exercise (Moore et al. 2005), and acute resistance exercise comprising ECC or CON actions only, elicited similar rate of protein synthesis despite the markedly less relative mechanical load employed in the ECC mode (Phillips et al. 1997; Gibala et al. 2000). Collectively the results of those studies and others (Hather et al. 1991; Higbie et al. 1996) would suggest that *both* the ECC action

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and high mechanical loading are essential stimuli in optimizing exercise-induced muscle hypertrophy. In fact, studies infer that resistance training protocols comprising ECC (Komi and Buskirk 1972; Hortobagyi et al. 1996) or coupled CON–ECC (Hather et al. 1991) high-force, not necessarily maximal actions, promote greater muscle hypertrophy than programs using CON actions only.

Inherently skeletal muscle, even during in vivo conditions, is capable of generating greater forces during ECC than CON actions (Katz 1939; Komi and Buskirk 1972; Tesch et al. 1990; Enoka 1996). Therefore, the idea, e.g., practiced by athletes for decades, that adding mechanical load during the ECC phase of a coupled CON–ECC action, i.e., ECC overload, would amplify the stimuli for growth, may be compelling. The results of the very few studies that have addressed the issue, suggest that resistance exercise paradigms, which implement ECC overload, induce more prominent strength increases than training with constant load during CON action only (Komi and Buskirk 1972; Colliander and Tesch 1990) or coupled CON–ECC actions (Hakkinen and Komi 1981; Hortobagyi et al. 2001; Brandenburg and Docherty 2002). However, studies aimed at revealing the effects on muscle size are inconclusive (Komi and Buskirk 1972; Colliander and Tesch 1990; Godard et al. 1998; Brandenburg and Docherty 2002). Therefore, while it is evident that the ECC action per se plays a decisive role in skeletal muscle adaptations to resistance exercise, it remains to be proven if employing ECC overload during training would further amplify the muscle hypertrophic response.

Spurred by the challenge to offer weight training to space travelers in a micro-gravity environment, an exercise device which uses the inertia of flywheel(s) to provide resistance was introduced (Berg and Tesch 1992; Berg and Tesch 1994), and subsequently employed in men and women, who were subjected to a 5-week training protocol. In both ambulatory (Tesch et al. 2004a) and, somewhat to our surprise, subjects who were unloaded and performed this particular regimen (Tesch et al. 2004b) muscle hypertrophied at a rate that exceeded what has been reported following traditional training programs of similar duration and intensity (Tesch et al. 2004a). This response may, at least in part, have resulted from the brief episodes of ECC overload, typically not offered with gravity-dependent weights, but elicited by this novel, loading approach.

To address this concept, and in an effort to compare the neuromuscular adaptations to flywheel and weight stack resistance training, two groups of men with comparable physical characteristics and training history were subjected to almost identical resistance exercise protocols (e.g., duration, frequency, sets and repetitions) isolating and targeting the knee extensor muscle group. However, while both exercise regimens comprised coupled CON–ECC actions, only the flywheel mode evoked brief episodes of ECC overload.

We hypothesized that 5 weeks of weight stack resistance exercise comprising knee extensions with the aid of a constant external load would result in increased muscle volume accompanied by marked increases in maximal isotonic force and power, and somewhat smaller increases in maximal voluntary isometric force. Because ECC actions performed in the weight stack mode does not call for near maximal forces, it was further hypothesized that quadriceps hypertrophy would be less evident compared with the response to a very similar resistance exercise program providing ECC overload. Indeed, the results of this particular study suggest that flywheel training promotes more robust neuromuscular adaptations than standard weight stack resistance training.

Methods

General design

Fifteen men performed 5 weeks of unilateral (left limb) knee extensor training 2–3 times × week^{-1} using either flywheel (FW) or weight stack (WS) resistance. Each session comprised four sets of seven repetitions. Seven men, who were part of a mixed-gender study reported elsewhere (Tesch et al. 2004a), accomplished training using a FW exercise device, allowing for brief episodes of ECC overload; eight men performed resistance training using a standard seated weight stack WS machine. While subjects assigned to FW, performed each repetition with maximal effort, training using WS employed a 4 × 7 RM protocol. Volume of individual quadriceps muscles and maximal isometric force were measured pre and post training. Also, task-specific performance was measured across the 12 training sessions. The procedures and possible risks and benefits of participation were explained, and informed written consent was obtained from each subject. The study protocols were approved by the Institutional Review Board of the University of Arkansas for Medical Sciences, Little Rock, AR and the Ethics Committee at the Karolinska Institutet, Stockholm, respectively.

Subjects

Seven men (mean, SD; 39.1 ± 9.1 years, 86.1 ± 7.6 kg, 178.3 ± 5.5 cm) were assigned to FW and performed resistance exercise using a flywheel (FW) device. Eight age- and strength- (MVC/quadriceps muscle cross sectional area) matched men (39.4 ± 8.1 years, 95.2 ± 16.4 kg, 186.7 ± 7.2 cm) with a similar past training history (none or limited experience of lower limb resistance training) trained using a weight stack (WS) machine. Subjects were apparently healthy, and reported no present or past knee pathology. All subjects complied with the prescribed training programs and the pre and post exercise tests.

Training protocol

Training equipment

FW carried out training using a seated knee extension flywheel device (YoYo® Technology Inc., Stockholm, Sweden; Fig. 1, Tesch et al. 2004a), equipped with a 4.2 kg flywheel with a moment inertia of 0.11 kg m^2. While seated and slightly reclined and using back support (hip angle 90°) and restraint, the trainee pushes against a crossbar mounted at the distal end of a pivoting moment arm, which rotation axis is aligned with the knee joint. From a starting position of about 90° knee angle, flywheel rotation is initiated through the pull of a strap anchored to the flywheel shaft and the distal part of the lever arm and looping around its curved cam. During knee extension the strap unwinds off the flywheel shaft and force and energy is imparted to the flywheel. Once the pushing concentric phase is completed at about 170° knee angle, the strap rewinds by virtue of the kinetic energy of the flywheel and thus, pulls the lever arm back. While attempting to resist the force produced by the pull of the rotating flywheel, which recoils the strap, the trainee then executes an eccentric muscle action. During training knee angle was measured using an electrogoniometer (Berg and Tesch 1994) fixed about the knee joint with a custom-built adjustable Velcro® strap system (Alfatex®, Deinze, Belgium). A miniature compression load cell (Model 276A, K-Toyo, Korea) measured force through the pull of the strap. Force and knee joint angle were measured at a sampling rate of 100 Hz, using a Windows™ based data acquisition system (MuscleLab™, Ergotest AS, Langesund, Norway).

The seated knee extension weight stack machine (World Class®, Stockholm, Sweden) used by WS, is equipped with a cam system which accommodates external torque through the range of motion. Similar to the flywheel device, it has a lever arm which rotational axis is aligned with the knee joint, and while seated with a 90° hip angle and grasping the handlebars, the trainee pushes against a perpendicular shin-padded, adjustable lever crossbar. A wire mounted onto the distal part of the lever arm and passing round the cam system and two pulley wheels is attached to the weight stack (Fig. 1). Weight plates of 5.0, 2.5 and 1.25 kg were used to set and adjust load. Load lifted and lowered, knee joint angle (see above) and vertical displacement of the weight, measured by means of a linear encoder, were recorded using the MuscleLab™ system (see above).

Loading principles of the flywheel device and the weight stack machine

Conventional gravity-dependent training devices rely on the weight of a load to provide resistance to the particular limb or muscle(s) subjected to exercise. Conversely, any flywheel apparatus generates resistance by opposing to the trainee's effort with the inertial force generated by a lightweight rotating flywheel such that the same inertia must be overcome during each repetition by means of accommodated loading. The more energy that is transferred from the lever arm to the flywheel during the CON action, the faster will the flywheel spin. When this kinetic energy is decelerated in a restricted part of the ECC action, force exceeding that generated during the corresponding CON phase, must be produced, i.e., ECC overload.

Devices designed for the one-joint knee extension mode, based on conventional weight stack architecture (a) or the flywheel concept (b), are schematically displayed in Fig. 1 (see also Fig. 4). On a weight stack machine, the work done by the trainee is converted into gravitational energy of the load that will vary through the range of motion. During a CON action, the weight is lifted and its gravitational energy increases; all this energy is removed during the ECC phase (given the initial and final position of the load is the same and no friction is imposed). The force F exerted by the trainee is expressed by:

$$F = kM(g + a) \tag{1}$$

with the notation of Fig. 1 and where k is a geometrical factor depending on the (variable) radius of the cam, g is the acceleration of gravity and a is the acceleration of the load. The cam is designed with a non-uniform radius (k decreases at increasing knee angles) to compensate for reduced efficiency at knee joints close to full extension. Though this cannot fully account for anthropometric differences among trainees, it is intended to reduce the "sticking point" effect, i.e., a joint angle which cannot be surpassed during the CON action due to such reduced efficiency. The minimum resistance required to perform a CON action is therefore:

$$F_{\min} = k_{\min}Mg \tag{2}$$

On a flywheel device, the CON action against the lever arm pulls the strap and imparts spin to the flywheel against its inertia. The device is adjusted such that, at the end of CON

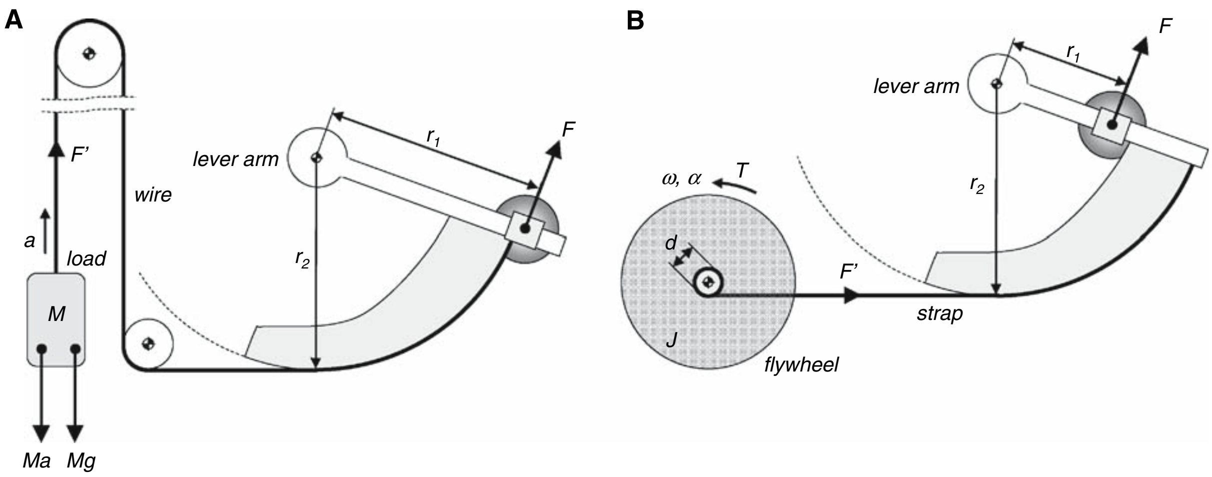

Fig. 1 Schematic representation of apparatuses designed for the one-joint knee extension exercise. **a** Weight stack machine equipped with variable radius cam to compensate for the lower efficiency of the knee joint close to full extension; here the radius (r_2) has been drawn constant for simplicity. **b** Flywheel device

action, the strap is completely unwounded, and the flywheel starts to recoil the strap by virtue of its rotary inertia, thus reversing the direction of the movement. In the ECC action the trainee resists to the recoil until the flywheel has come to a stop. Using a flywheel device, the energy generated in the CON action is converted into kinetic energy, which is accumulated in the flywheel and removed in the subsequent ECC action. The force F exerted by the trainee is expressed by:

$$F = zJ\alpha(t) \tag{3}$$

where z is a geometrical factor, J is the momentum of inertia of the flywheel and $\alpha(t)$ is the angular acceleration of the flywheel.

Resistance exercise protocol

Training was performed two (week 1, 3 and 5) or three (week 2 and 4) times weekly. Each session consisted of or aimed at four sets of seven maximal, CON–ECC knee extensions using the left limb. In FW, coupled actions were performed with a repetition cycle of about 3 s, with the CON and ECC action each lasting about 1.5 s. Similarly, in WS, the repetition cycle was about 3 s; yet the CON and ECC actions were about 1 and 2 s, respectively. Individual weights were chosen to result in failure to lift and control lowering the weight with seven repetitions. Load was increased in the subsequent set if the subject could perform more than 7 repetitions, or lowered if the subject failed to complete 7 repetitions with good form. CON–ECC and ECC–CON transition angle and CON and ECC angular velocity measured pre and post training in WS and FW are shown in Table 1. Sets were interspersed by 2 min rest periods. Every exercise session was preceded by a 5 min warm-up consisting of three sets of seven submaximal actions with progressively increased effort.

Test protocol

Maximal isometric force

Tests for maximal voluntary isometric knee extensor force (MVC) were executed in the seated position with hip joint at 90° using a load cell mounted on the apparatus also used for flywheel exercise (see above). MVC was determined with the lever arm fixed at 90° and 120° knee angle (180 = full knee extension), respectively. While grasping the handlebars at least two maximal isometric actions (2–3 s each), intervened by 1 min rest, were performed to assess MVC. If there was a difference in maximal force among the two best trials of more than 5%, the subject was given another attempt. The highest force value, averaged in a 1 s window showing a stable force level, was considered MVC. Both limbs were tested and in a revised randomized order across the subjects.

Power and work

Pre and post work/set and peak power were determined from separate tests comprising four (WS) or one (FW) set(s) of seven repetitions (left limb only), using weight stack and flywheel devices, respectively. Power and work of any coupled CON–ECC action were calculated from the displacement and the lifted and lowered weight (WS) or measured force (FW), respectively (Table 1). It should be noted that while power and work were measured directly in

Table 1 Eccentric–concentric (ECC–CON) and CON–ECC transition angle and CON and ECC average and peak angular velocity pre and post training in WS and FW

	WS		FW	
	Pre	Post	Pre	Post
ECC–CON transition	76 ± 3	80 ± 4	77 ± 5	76 ± 8
CON–ECC transition	161 ± 4	161 ± 5	169 ± 0.1	170 ± 1 †
CON average velocity	76 ± 15	77 ± 9	65 ± 5	66 ± 8 †
ECC average velocity	36 ± 7	45 ± 4*	67 ± 6	66 ± 9 †‡
CON peak velocity	130 ± 30	146 ± 15	162 ± 3	168 ± 6 †
ECC peak velocity	70 ± 16	102 ± 16 *	164 ± 5†	173 ± 15 †‡
Work/set	1,660 ± 386	2,323 ± 319 §	3,188 ± 414	3,466 ± 770
CON peak power	189 ± 59	318 ± 52 §	311 ± 70	339 ± 112
ECC peak power	94 ± 27	212 ± 43 §	308 ± 59	345 ± 123

Values are mean ± SD; knee joint transition angle (°), velocity (°/s), work/set (J), and power (W)

‡ Denotes difference in training response (pre to post) in WS compared with FW ($P < 0.05$). † Denotes difference between groups ($P < 0.05$). * Denotes significant increase from pre to post ($P < 0.025$). Because work and power were measured and calculated using different methods, there were no group comparisons performed. § Denotes significant increase from pre to post using Students *t* test ($P < 0.05$)

the flywheel mode, these performance indices were simply estimated in the weight stack mode based on the load being raised and lowered along with angular speed measurements. Thus, configuration and mass of the cam and lever arm were not taken into account. If anything, additional trials employing force sensor technique showed that within any subject examined the CON power or work generated in a set was very similar (<10%) across the two devices.

Magnetic resonance imaging

Volume of individual quadriceps muscles was assessed by magnetic resonance imaging (MRI). For FW, a 1.5 T MR (Signa, General Electric, Milwaukee, WI, USA) machine was used as described in detail elsewhere (Tesch et al. 2004a). WS was examined with use of a 1.5 T MR (Intera, Philips Medical Systems, Best, The Netherlands) unit employing the following sequence; Turbo spin echo, TE 110 ms, TR 5,723 ms, T2 weighted, NEX-NSA: 3 (3 excitations), FOV 485 × 315.25 mm, Matrix scan 448 × 291.2, Reconstruction 512 × 332.8, Pixel 0.95 × 0.95 mm. For all subjects, fifty images with slice thickness 10 mm and no spacing in between slices were obtained. To minimize the potential influence of any fluid shift on muscle size (Berg et al. 1993), subjects remained supine for 1 h prior to the start of scanning. Also a custom made adjustable foot restraint device was used to avoid compression of muscles during scanning and to keep the limbs in a fixed position. The graded foot-brace, and ink marks on the limbs aligned with the crosshairs of the imager, ensured accurate repositioning across sessions.

Analyses

Despite use of two MRI facilities and slightly different imaging sequences, analyses and procedures used were validated previously (Alkner and Tesch 2004; Tesch et al. 2004a, b). Hence, anatomical intervals and strategy to choose images for analyses were identical across the two study groups. After electronic data transfer of images to TIFF format, cross-sectional area measurements and calculations were performed using public domain software (Scion Image Beta 4.0.2 for Windows, Scion Corporation, Frederick, MD, USA). Using computerized planimetry (Intuos Graphic Tablet, Wacom Technology, Vancouver, WA, USA), areas of interest were identified from the displayed images and manually circumscribed and then automatically computed. The four quadriceps muscles (mm. rectus femoris, RF; vastus lateralis, VL; vastus medialis, VM; and vastus intermedius, VI) were encircled separately. The areas over the five circumscriptions, showing less than 2% difference between extreme values, were averaged. Anatomical landmarks were used to ensure the same segment of the thigh was measured pre and post training. From stacks of images beginning with the first not displaying m. gluteus maximus and ending with the last image in which RF appears, all (FW) or every third (WS) image was analyzed. This latter approach, reducing the number of images used for analyses, does not impact reliability of this method (Alkner and Tesch 2004). Muscle volume of the selected stack of images was subsequently calculated from the total sum of the cross-sectional areas determined in individual images × axial slice thickness.

Statistics

Within each study group, one-way or two-way repeated measures ANOVA were employed to make comparisons over the 12 training sessions for the left limb, and across limbs and time for pre and post measurements. Two-way repeated measures ANOVA were also used when comparing results for WS and FW. Since in neither study did the right limb show any changes, further comparisons across FW and WS comprised the left limb only. When an interaction over time and limb (within groups) or time and group (between groups) was found, planned comparisons were made employing a Bonferroni correction. When applicable, training induced changes within groups (work/set, CON and ECC peak power, and CON and ECC force in FW) were performed using a Students *t* test. Values reported are mean and standard deviation (SD). The significance level was set to $P < 0.05$.

Results

Repetition time, repetitions/set, transition joint angle and angular velocity

In FW, any CON–ECC repetition cycle was completed in about 3 s (Tesch et al. 2004a). Similarly, in WS repetition time averaged across the 12 training sessions (TR) was 3.0 ± 0.2 s; however repetition times were decreased somewhat over the trials (TR 1, 3.3 ± 0.4 s; TR 12, 2.8 ± 0.4 s). Whereas repetitions/set was fixed at 7 for FW, the number of repetitions/set over the 12 sessions averaged 7.2 ± 0.3 in WS. The ECC–CON transition angle was similar for WS and FW; however the CON–ECC joint transition angle (Table 1) was somewhat greater in FW ($P < 0.05$). In neither group did the joint transition angle change with training. WS showed higher ($P < 0.05$) CON average and peak velocity than FW. In neither group did training alter CON velocity. FW showed higher ($P < 0.05$) ECC average and peak velocity than WS. There was an interaction over time and group for ECC average and peak velocity. ECC average and peak velocity increased in WS ($P < 0.025$). It was unaltered in FW (Table 1).

Weight stack training

In WS there was an interaction across limbs and time for total quadriceps muscle volume (Fig. 2). Volume of the left quadriceps increased by 3.0% (Pre, 1,430 ± 364 cm^3; Post, 1472 ± 381 cm^3; $P < 0.025$). Quadriceps volume of the right limb was unchanged (Pre, 1,373 ± 309 cm^3; Post, 1,361 ± 300 cm^3; $P > 0.025$). There was an interaction across limbs and time for VL, VI and RF but not VM (Table 2). Only the left RF showed increased volume (Pre, 137 ± 43 cm^3; Post, 146 ± 47 cm^3; $P < 0.025$). Neither muscle of the right limb showed altered volume ($P > 0.025$).

Training load (Fig. 3) increased 48% over the 12 sessions (TR 1, 14.5 ± 3.1 kg; TR 12, 21.4 ± 3.2 kg; $P < 0.05$). Similarly, work/set and CON and ECC peak power increased by 40–126%; $P < 0.05$, Table 1). There was no interaction across limbs and time with regard to MVC at 90° (Pre left, 502 ± 87; Post left, 482 ± 63; Pre right, 488 ± 51; Post right, 489 ± 92). Neither did MVC at 120° show interaction across limbs and time (Pre left, 596 ± 114 N; Post left, 632 ± 112 N; Pre right, 593 ± 98 N; Post right, 578 ± 92 N).

Flywheel training

In FW there was an interaction across limbs and time for total quadriceps muscle volume (Fig. 2). The left limb showed a 6.2% increase (Pre, 1,300 ± 210 cm^3; Post, 1,380 ± 235 cm^3; $P < 0.025$). Quadriceps volume of the right limb showed no change (Pre, 1,276 ± 204 cm^3; Post, 1,263 ± 205 cm^3; $P > 0.025$). There was an interaction across limbs and time for individual quadriceps muscles such that all muscles of the left limb showed increased ($P < 0.025$) volume (Table 2). The right limb showed no change over time ($P > 0.025$).

ECC peak force (489 ± 86 N; 526 ± 106 N) exceeded ($P < 0.05$) CON peak force (447 ± 75 N; 481 ± 82 N) both pre and post training. CON and ECC peak force were unchanged ($P > 0.05$). Average force (ECC 401 ± 83 and 425 ± 120 N; CON 390 ± 73 and 407 ± 83 N) showed no significant increase ($P > 0.05$, Table 1). CON (Pre, 322 ± 67 N; Post, 338 ± 42 N) and ECC (Pre, 302 ± 60 N; Post, 320 ± 44 N) force averaged across the four training sets remained unchanged (+5.0 and +6.0%; $P > 0.05$) over

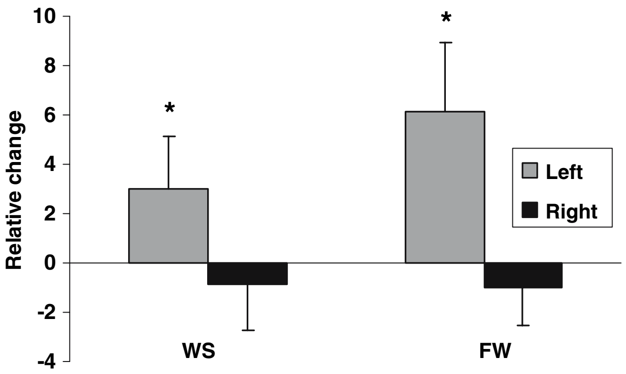

Fig. 2 Relative change in left (trained) and right (untrained) quadriceps muscle volume after 5 weeks of weight stack (WS) and flywheel (FW) training. * Denotes significant ($P < 0.025$) increase

Table 2 Muscle volume and relative change of individual quadriceps muscles (VL, m. vastus lateralis, VI, m. vastus intermedius, VM, m. vastus medialis, RF, m. rectus femoris) of the left limb pre and post training in WS and FW

Muscle	WS			FW		
	Pre	Post	Δ (%)	Pre	Post	Δ (%)
VL	479 ± 108	488 ± 112	+1.8	467 ± 97	494 ± 109	+5.8*§
VI	451 ± 133	462 ± 140	+2.4	400 ± 58	416 ± 61	+4.0*
VM	363 ± 97	377 ± 96	+3.8	308 ± 41	332 ± 46	+8.0*
RF	137 ± 43	146 ± 47	+6.7*	125 ± 34	137 ± 41	+9.9*
Quad	1,430 ± 364	1,472 ± 381	+3.0*	1,300 ± 210	1,380 ± 235	+6.2*

Values are mean ± SD muscle volume (ml), and percentage change from pre to post

* Denotes significant increase from pre to post ($P < 0.025$), § denotes trend to different response for VL in WS compared with FW ($P < 0.10$)

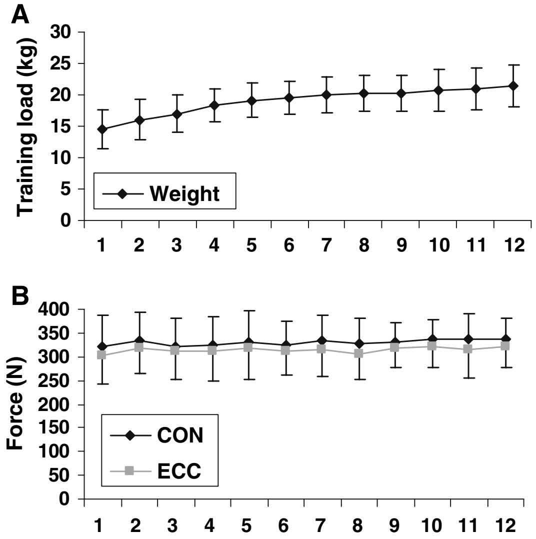

Fig. 3 Training load across the 12 training sessions in WS; weight (kg) lifted and lowered (**a**), and FW; average concentric or eccentric force (N) in a 30° window (**b**)

the 12 sessions (Fig. 3). Neither were the increases in work/set (+8.7%), or CON (+8.9%) and ECC (+12.0%) peak power significantly ($P > 0.05$) increased following training (Table 1). There was an interaction ($P < 0.05$) across limbs and time for MVC at 90°. The left limb showed an 11.6% increase (Pre, 537 ± 130 N; Post, 599 ± 156 N; $P < 0.025$). The right limb showed no change (Pre, 533 ± 141 N; Post, 560 ± 148 N; $P > 0.025$). There was no interaction across limbs and time with regard to MVC at 120° (Pre left, 545 ± 78 N; Post left, 617 ± 130 N; Pre right, 546 ± 88 N; Post right, 592 ± 115 N).

WS versus FW

There was no interaction ($P > 0.05$) over time and across groups for volume of quadriceps or any individual muscle (Table 2). Because force, work and power/set were measured and calculated using different methods for WS and FW, no direct group comparisons were performed. MVC at 90° showed interaction ($P < 0.05$) over time and group, such that FW, but not WS, had an increase. There was no interaction over time and group with regard to MVC at 120°. There was an increase over time ($P < 0.05$).

Discussion

Our interest in this study was spurred by the belief that, optimizing neuromuscular adaptations to resistance training programs requires the inclusion of muscle actions offering eccentric overload. Indeed, the current results suggest that flywheel training which allows for brief episodes of enhanced force in eccentric over concentric actions prompted more robust increases in maximal voluntary force and muscle size than weight stack training.

Thus, while all four individual quadriceps muscles showed increased size following flywheel training, only m. rectus femoris (RF) increased with weight stack training. Although there was no group difference, the 6.2% hypertrophy shown following flywheel training (Tesch et al. 2004a), was more than twofold greater than the 3.0% increase in quadriceps muscle volume evident in the weight stack group. Previous resistance training studies of men, comparable with the current subject sample regarding age and fitness level, and employing protocols of similar duration, intensity and frequency and emphasizing isolated maximal knee extensor use, have reported weekly increases in quadriceps muscle cross-sectional area or volume on the order of about 0.4–1.0% per week (Jones and Rutherford 1987; Narici et al. 1989; Ploutz et al. 1994). Given those findings, the increase observed in the subjects who completed the weight stack training protocol in the present study, equivalent to about 0.6% per week, was rather expected. However, few if any (Luthi et al. 1986), previous studies, have reported quadriceps muscle hypertrophy of that magnitude i.e., about 1.2% per week found with flywheel training. The fact that all individual quadriceps muscles increased with this novel approach and only RF showed increased volume with weight stack training infers that the flywheel training protocol promoted a more consistent degree of hypertrophy.

Although all individual quadriceps muscles are used in concert in the seated open-chain knee extension (Ploutz et al. 1994; Enocson et al. 2005), it appears this particular exercise inherently places an even greater demand on RF than on any of the three vastii muscles (Enocson et al. 2005). Thus, our finding of greater RF hypertrophy compared with the vastii complex during isolated knee extensor exercise is not new (Narici et al. 1996). However, because this pattern was evident regardless of loading mode being applied, it certainly provides evidence that the relative involvement among the four quadriceps muscles were, if not identical, very similar for the two exercise paradigms. In fact, despite the unique force-curve mechanics of each machine the loading history across the muscles using the two modalities could be replicated.

It is known that resistance exercise programs accompanied by muscle hypertrophy and task-specific performance may not necessarily increase maximal voluntary isometric strength (Brown et al. 1990; Sale et al. 1992; Higbie et al. 1996), yet a large number of studies have reported such an effect (Hakkinen and Komi 1983; Young et al. 1983; Jones and Rutherford 1987). The current finding of a somewhat greater increase in maximal voluntary isometric strength with enhanced eccentric compared with coupled concentric and eccentric resistance training is not at odds and consistent with other reports (Godard et al. 1998; Hortobagyi et al. 2001).

In contrast, chronic exercise increased average training load and work/set by nearly 50% and these effects were accompanied by an even greater increase in power. Given the minute hypertrophy, neuronal adaptations (Rutherford and Jones 1986; Sale 1988; Enoka 1997) during training must have been rather substantial. Thus, performance may increase out of proportion to muscle hypertrophy (Hakkinen et al. 1985; Sale 1988; Narici et al. 1989; Colliander and Tesch 1990; Dudley et al. 1991; Hather et al. 1991; Ploutz et al. 1994). This fact underscores the difficulty in choosing specific and valid tasks to assess and compare in vivo muscle function between different training protocols or modes. For example, and in frank contrast to the present results, other studies suggest that enhanced eccentric training protocols promote greater increases in task-specific performance than training using constant concentric and eccentric resistance (Hakkinen and Komi 1981; Brandenburg and Docherty 2002).

It should be acknowledged that the inertia the trainees had to overcome was kept constant over the 12 training sessions. This may in part explain the modest and non-significant 8–12% increase in force generated during training. At this time, it is not clear if progressively increasing inertia over the 5-week course could have added to this effect. There is also an inherent problem in standardizing a highly reproducible method to determine and compare force across subjects, or individual responses to e.g., long-term training or disuse, during exercise using flywheel technology. This is because neither range of motion nor the onset of the braking action and hence transition angles are controlled for (Berg and Tesch 1994). Hence, typically the strategy the trainee employs to conduct flywheel training is altered with progressive exposure and may also be impacted by any intervention in a non-systematic manner.

While reports show that strength increases with programs providing eccentric overload exceed those induced by constant concentric–eccentric load (Hakkinen and Komi 1981; Godard et al. 1998; Hortobagyi et al. 2001; Brandenburg and Docherty 2002) or concentric load only (Komi and Buskirk 1972; Colliander and Tesch 1990), related findings on muscle hypertrophy are equivocal (Godard et al. 1998; Brandenburg and Docherty 2002). Thus, the scarce reports have showed either failure to produce hypertrophy regardless of protocol (Brandenburg and Docherty 2002), or comparable hypertrophy, (Godard et al. 1998) with constant CON–ECC versus ECC overload training. Perhaps the non-uniform outcome of these reports indicates the complexity in designing valid training study protocols. The vast majority studies employed training which added load during the entire range of motion of the eccentric action. The fact that studies (Colliander and Tesch 1990; Petersen et al. 1990; Higbie et al. 1996) which used accommodated constant speed i.e., isokinetic resistance exercise allowing for markedly greater torque to be produced during the entire range of motion of the eccentric compared with concentric action have shown only modest (Higbie et al. 1996) or even failed to generate hypertrophy (Colliander and Tesch 1990), is further evidence that employing eccentric overload per se will not necessarily boost the stimulus for muscle growth.

The exercise kinematics provided by the two devices employed here are clearly different. When decelerating the energy stored in the flywheel in a very restricted part of the movement, the eccentric peak force is rather substantial (Fig. 4, right). Conversely, while resisting the weight stack being lowered in about 2 s, the eccentric peak force is less (Fig. 4, left) than the force required to lift the weight in the 1-s concentric action (Fig. 4, left). In this particular knee extension task the quadriceps muscle shows the greatest activation at completion of the concentric action or close to full extension of the knee joint (Fig. 4, left). However, regardless of knee angle there was no increase in maximal voluntary force resulting from this training, as would have

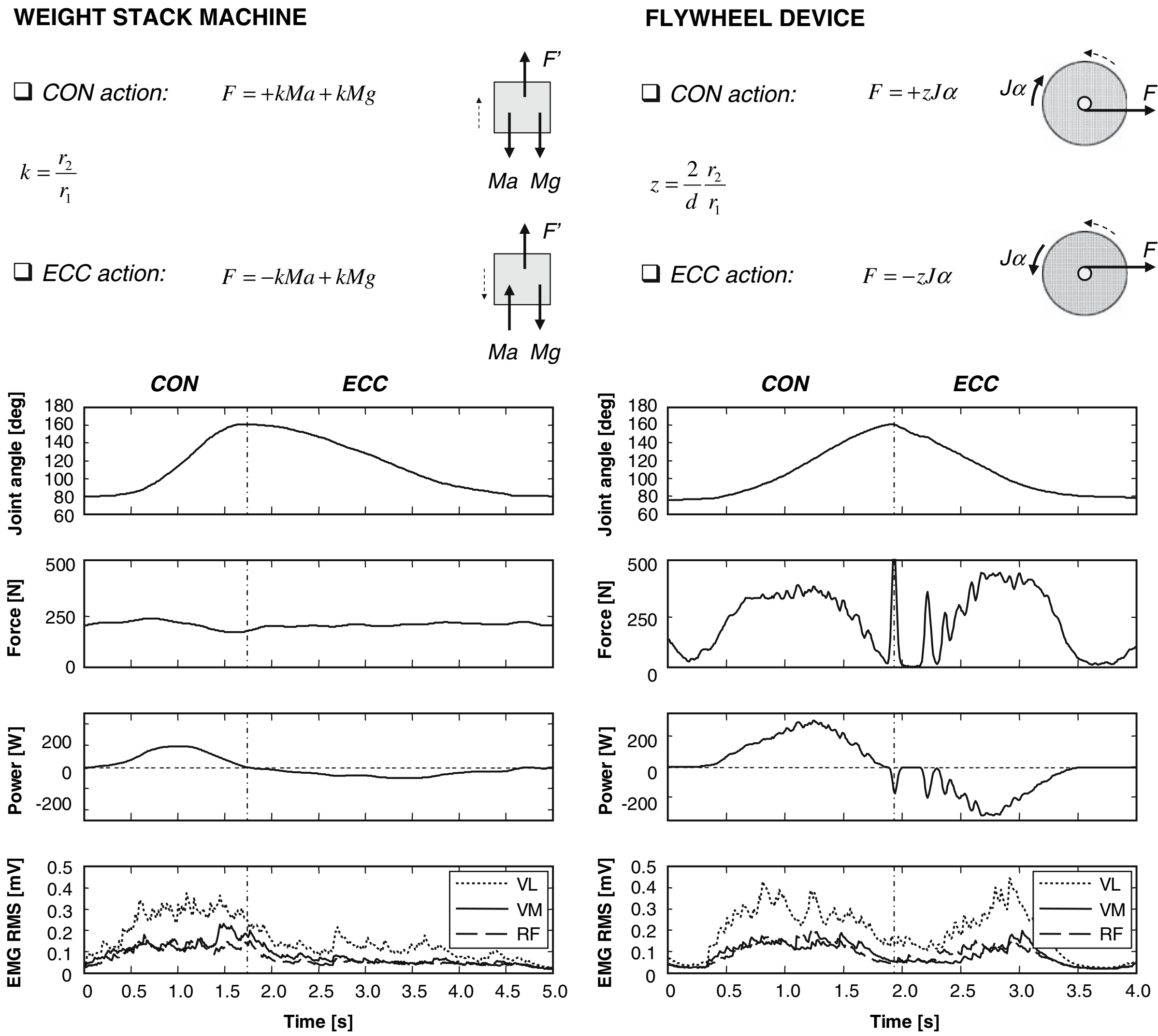

Fig. 4 Kinetics and surface electromyography (EMG) during exercise on weight stack (*left panels*) and flywheel (*right panels*) apparatuses in one subject. Simplified kinematics analysis; *F′* is the force applied to the load or flywheel, which is related to the force exerted by machine-dependent geometrical factors. Knee joint angle (°), force (N), power (W), and root mean square (RMS) EMG (mV) in one repetition cycle. EMG RMS was measured from mm. vastus lateralis (*VL*), medialis (*VM*) and rectus femoris (*RF*), respectively. *Vertical dashed–dotted line* denotes the CON–ECC deflection

been anticipated (Morrissey et al. 1995). The flywheel resistance training program however, did translate into increased non-specific, maximal voluntary force; an effect that may have been attributed to the high force produced, supported by the large EMG amplitude, particularly in the late eccentric phase performed at low angular velocity (Fig. 4, right). It should also be acknowledged that, contrary to weight stack exercise, flywheel exercise allows for performance of maximum or near maximum voluntary force actions from the very first repetition of a set. Again, given the complexity and specificity of neuronal adaptations to chronic resistance exercise (Enoka 1996), the significance of any group differences with regards to strength changes should not be overemphasized.

Inherently, EMG amplitude is markedly lower during eccentric than concentric actions (Moritani et al. 1987; Tesch et al. 1990; Enoka 1996; Komi et al. 2000; Grabiner and Owings 2002), given the same force or load is employed (Fig. 4, left). Interestingly, in comparison with weight stack exercise (Fig. 4), there was considerable activation during the eccentric action performed with flywheel exercise. Indeed EMG amplitude was comparable or sometimes even greater in the eccentric than the concentric action (Fig. 4, right). This finding supports the earlier demonstration of maximal or near maximal quadriceps activation during the eccentric action with use of the two-joint leg press flywheel exercise (Berg and Tesch 1994).

In explaining our finding of more pronounced hypertrophy with flywheel training, there is evidence that acute bouts of eccentric actions provoke more excessive myofibrillar disruption and muscle injury than those comprising concentric actions only (Newham et al. 1983; Friden and Lieber 1992; Gibala et al. 1995). Muscle damage, resulting from such types of loading, is believed to present an important stimulus triggering myofibrillar remodeling and hence muscle hypertrophy (Evans and Cannon 1991; Yu et al. 2003). Interestingly, an 8-week resistance training program comprising maximal, high-speed eccentric actions, and resulting in greater peak torque than an identical protocol emphasizing low-speed actions also induced the most significant hypertrophy (Farthing and Chilibeck 2003; Shepstone et al. 2005). Perhaps more importantly, those investigators reported that the magnitude of hypertrophy correlated with myofibrillar disruption including *Z*-line streaming, provoked by acute exercise with the two regimens. Whether those findings and the results of the current results are indicative that peak force during the eccentric deceleration rather than maintained enhanced eccentric force (Fig. 4, right) is a more important additional stimulus promoting muscle growth remains to be proven, but it is certainly an attractive hypothesis. Further, though both rat and human skeletal muscle show greater rate of protein synthesis (Wong and Booth 1990a, b) following lengthening than shortening actions (Phillips et al. 1997; Gibala et al. 2000; Moore et al. 2005), it remains to be proven if added eccentric load per se or other associated events or characteristics of contractile activity, e.g., high peak force and/or speed of action, are responsible for the more favorable adaptations that seem to result from resistance exercise regimens promoting eccentric overload.

We suggest our finding of superior results with flywheel training are due to the eccentric overload evident with flywheel but weight stack training. This is the most obvious feature difference between the two exercise modalities. Our suggestion that eccentric overload rather than greater work could explain our findings is based on the fact that (1) when we actually performed acute experiments allowing us to compare concentric work in the same subjects (not between the two training groups) on the two devices, there was no obvious systematic difference, (2) from past studies and training anecdotes concentric work per se does not appear to be a critical factor for inducing muscle hypertrophy and (3) while there was a marked increase (from 1,660 to 2,323 J) in work per set for the weight stack group; yet the flywheel group showed no significant increase. These results would infer there is no strong link between work produced and rate of hypertrophy.

In summary, 5 weeks of resistance exercise using flywheel induced similar or even more marked skeletal muscle adaptations than standard weight stack training. We suggest this effect was mainly due to the brief episodes of eccentric overload, elicited with flywheel resistance exercise. Combined it appears that in order to optimize the training responses to resistance exercise, inclusion of the eccentric action is not sufficient unless it also offers additional load over that provided by the coupled concentric action.

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