ORIGINAL ARTICLE

Flywheel resistance training calls for greater eccentric muscle activation than weight training

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Abstract Changes in muscle activation and performance were studied in healthy men in response to 5 weeks of resistance training with or without "eccentric overload". Subjects, assigned to either weight stack (grp WS; $n = 8$) or iso-inertial "eccentric overload" flywheel (grp FW; $n = 9$) knee extensor resistance training, completed 12 sessions of four sets of seven concentric–eccentric actions. Pre- and post-measurements comprised maximal voluntary contraction (MVC), rate of force development (RFD) and training mode-specific force. Root mean square electromyographic (EMG_{RMS}) activity of mm. vastus lateralis and medialis was assessed during MVC and used to normalize EMG_{RMS} for training mode-specific concentric (EMG_{CON}) and eccentric (EMG_{ECC}) actions at 90°, 120° and 150° knee joint angles. Grp FW showed greater ($p < 0.05$) overall normalized angle-specific EMG_{ECC} of vastii muscles compared with grp WS. Grp FW showed near maximal normalized EMG_{CON} both pre- and post-training. EMG_{CON} for Grp WS was near maximal only post-training. While RFD was unchanged following training ($p > 0.05$), MVC and training-specific strength increased ($p < 0.05$) in both groups.

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We believe the higher EMG_{ECC} activity noted with FW exercise compared to standard weight lifting could be attributed to its unique iso-inertial loading features. Hence, the resulting greater mechanical stress may explain the robust muscle hypertrophy reported earlier in response to flywheel resistance training.

Introduction

Skeletal muscle inherently possesses greater mechanical efficiency and ability to generate force in lengthening [eccentric (ECC)] than shortening [concentric (CON)] actions (Katz 1939; Komi and Buskirk 1972). Thus, the electromyographic (EMG) amplitude is less while lowering (ECC) than lifting (CON) a given weight (Moritani et al. 1987). In fact, the CON EMG amplitude may be more than twofold higher, inferring markedly less motor unit involvement in ECC than CON actions (Nardone et al. 1989). Such a response is paralleled by much less exercise-induced contrast shift of magnetic resonance images of muscle, following ECC actions (Adams et al. 1992). Thus, the metabolic demand is less when lowering (ECC) than lifting (CON) a given weight (Asmussen 1953; Dudley et al. 1991). EMG amplitude may also be lower in ECC than CON actions executed with maximal effort (Aagaard et al. 2000). Collectively, it appears that more load is placed upon each active muscle fiber in the ECC action. This may at least in part explain the greater hypertrophy reported following chronic resistance training comprising coupled ECC and CON actions or ECC actions compared with CON actions only (Hather et al. 1991; Higbie et al. 1996; Hortobagyi et al. 1996).

Given the greater mechanical efficiency of ECC actions during traditional weight training, no ECC action within a set will call for maximal activation. Additionally, and due to changes in biomechanical levers and muscle length, the ability to overcome the gravitational force of a weight is dictated by the "sticking point" occurring during the CON action. As a result, standard resistance exercise, employing a constant weight, calls for maximal activation only at the "sticking point" of the very last CON repetition resulting in failure to lift a particular weight. In contrast, the inertia of spinning flywheel(s) offers unrestrained resistance throughout the entire CON action and allows for brief episodes of ECC forces exceeding the CON forces, i.e., "ECC overload" (Norrbrand et al. 2008; Tesch et al. 2004). Thus, this exercise modality should evoke maximal muscle activation in the CON, and part of the ECC action, through each repetition of a set. Therefore, flywheel resistance exercise might elicit greater overall EMG amplitude than exercise using gravity-dependent weights. Because it is generally held that high mechanical loading, and in particular during ECC actions, is an essential stimulus to promote muscle hypertrophy (Hather et al. 1991; Higbie et al. 1996; Hortobagyi et al. 1996), features characteristic of flywheel exercise may also offer a more potent hypertrophic exercise stimulus than gravity-dependent weights. In fact, 3 and 5 weeks of flywheel knee extension training resulted in 4–5% (Seynnes et al. 2007) and 6–7% quadriceps hypertrophy (Norrbrand et al. 2008; Seynnes et al. 2007; Tesch et al. 2004). Traditional knee extension training programs, using weight stack, have failed to demonstrate comparable hypertrophy (Jones and Rutherford 1987; Narici et al. 1996; Ploutz et al. 1994).

Thus, muscle activation in the two loading modalities were compared before and after 5 weeks of seated open-chain knee extensor resistance exercise by controlling for, e.g., range of motion, time under tension per repetition and subject positioning.

The present experiments were set up with the assumption that the magnitude of muscle activation during resistance exercise correlates with the potential for skeletal muscle hypertrophy. Hence, this study aimed at comparing muscle activation, assessed by surface EMG, during flywheel and weight stack knee extension exercise. A second objective was to explore whether muscle activation would change following 5 weeks of flywheel or weight stack resistance training and, if so, compare neural training adaptations between exercise modes and in relation to potential changes in isometric and dynamic strength. Given the unique loading features of skeletal muscle prompted by flywheel inertia, we hypothesized that muscle activation during concentric and, more so, eccentric actions would be greater with resistance exercise using flywheel compared with standard weights. In view of readily induced neural adaptations with resistance training programs (Hakkinen et al. 1998; Moritani and deVries 1979), we further hypothesized that both exercise modes would induce marked increases in muscle strength.

Methods

General design

Seventeen healthy men performed 5 weeks of unilateral knee extensor training of the left limb. Subjects were assigned to 12 sessions of either flywheel (grp FW; $n = 9$) or standard weight stack (grp WS; $n = 8$) resistance exercise. Each session consisted of four sets of either seven maximal repetitions (grp FW) or seven RM (repetition maximum; grp WS) performed two to three times per week. Strength and root mean square EMG (EMG_{RMS}) of the left limb were determined during maximal voluntary contraction (MVC) and training mode-specific coupled CON–ECC actions pre- and post-training. In addition, the rate of force development (RFD) was assessed. Verbal encouragement and feedback regarding exercise form were given during all training sessions and tests. Written informed consent was obtained from all subjects. The study protocol was approved by the regional ethics committee at the Karolinska Institutet, Stockholm, Sweden. Selected data from the study of grp WS have been reported earlier (Norrbrand et al. 2008).

Subjects

Seventeen healthy men with no or limited experience of lower limb resistance training, and no present or past reported knee pathology, volunteered for this study (Table 1). Eight men were assigned to resistance exercise using a knee extension weight stack (grp WS) apparatus, while nine men trained using a knee extension flywheel (grp FW) device. All subjects complied with the familiarization procedures of at least two sessions, the prescribed training program, and pre- and post-training tests.

Table 1 Age, height and body mass of subjects in the flywheel (grp FW) and weight stack (grp WS) training groups

Subjects	Grp FW	Grp WS
Age (years)	38.8 ± 5.0	39.4 ± 8.1
Height (cm)	183.9 ± 8.7	186.7 ± 7.2
Body mass (kg)	85.4 ± 13.6	95.2 ± 16.2

Values are mean $\pm$ SD. No significant differences between groups were observed ($p > 0.05$)

Training equipment and resistance exercise protocol

The two devices used in the current study have been described in detail earlier (Norrbrand et al. 2008). Grp FW carried out unilateral training using a seated flywheel device (YoYo® Technology, Stockholm, Sweden (Tesch et al. 2004), equipped with a 4.2-kg flywheel with a moment inertia of 0.11 kg m². While seated slightly reclined with back support (hip angle 90°), using restraint and grasping the handlebars, the trainee pushes against a crossbar mounted at the distal end of a pivoting moment arm, with the rotational axis aligned with the knee joint. From a starting position of about 80° knee angle (180° = full knee extension), 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. While pushing (CON) against the crossbar, the strap unwinds off the flywheel shaft thereby imparting force and energy into the flywheel. Once the pushing CON phase has been completed at about 165° 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 executes an ECC action. After bringing the wheel to a stop at about 80° knee angle, a subsequent CON action is instantly initiated. 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, Seoul, 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, Langesund, Norway).

The seated knee extension weight stack machine (World Class®, Stockholm, Sweden), used by grp 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 with its rotational axis aligned with the knee joint. While seated (90° hip angle; 80° knee angle) and grasping the handlebars, the trainee pushed against a perpendicular shin-padded, adjustable lever crossbar and executed CON actions to about 165° knee angle. The weight was then lowered in a controlled manner and brought to a stop before being raised again. A wire mounted onto the distal part of the lever arm and passing around the cam and two pulley wheels was attached to the weight stack. 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 (Norrbrand et al. 2008).

Training was performed two (week 1, 3 and 5) or three (week 2 and 4) times weekly. Each session consisted of (grp FW) or aimed at (grp WS) four sets of seven CON–ECC knee extensions using the left limb. Grp FW performed coupled actions with a repetition cycle of about 3 s, with CON and ECC actions each lasting about 1.5 s. Similarly, in grp WS, the repetition cycle was about 3 s; the CON and ECC actions were about 1 and 2 s, respectively. During familiarization, grp FW were asked to perform FW exercise with increasing effort, while training requested maximal effort in each muscle action. Subjects were requested to push with maximal effort through the entire CON action, resisting gently in the initial third of the ECC action, and then aim at bringing the wheel to a full stop at about 80° knee angle. While being familiarized, individual weights for grp WS were chosen to result in failure to lift and lower the weight with seven repetitions, i.e., seven RM, in a controlled manner. Subjects were requested to lift the weight to a target ~165° knee angle in about 1 s, and then lower the weight in a controlled manner in approximately 2 s. Training load was increased by 1.25 kg in the subsequent set if the subject could perform more than seven repetitions, or lowered by 1.25 kg if the subject failed to complete seven repetitions with good form. Thus, whereas repetitions/set was fixed at seven for grp FW, the number of repetitions/set over the 12 sessions averaged 7.2 ± 0.3 in grp WS. Sets were interspersed by 2-min rest periods. Exercise sessions were preceded by a 5 min warm-up consisting of three sets of seven actions with progressively increased effort.

Test protocol

Maximal voluntary contraction (MVC)

This test, used to assess non-training-specific maximal strength and activation, was performed in the FW device. Maximal voluntary isometric knee extensor force (maximal voluntary contraction; MVC) along with EMG (maximal EMG amplitude; see below) was determined with hip angle at about 90° and the lever arm fixed at 120° knee angle. 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 across the two trials of more than 5%, the subject was requested to perform additional attempt(s). The highest force, averaged over a 1-s window showing a steady force level, was considered MVC.

Rate of force development

To assess RFD, tests were performed in the FW device, with hip angle at about 90° and the lever arm fixed at 120°

knee angle. While sustaining an isometric action at 20% of MVC, subjects were instructed to increase force as fast as possible to reach maximal force and maintain a steady force for about 2–3 s. At least two trials, intervened by 1 min rest, were performed to assess RFD. The force was analyzed at 0.1-s intervals within the first 0.5 s of each trial. The trial showing the highest force at 0.4 s was chosen for further analysis.

Dynamic coupled CON–ECC actions

To assess training mode-specific strength and EMG amplitude pre- and post-training, four sets of seven RM were performed in the WS (grp WS) and four sets of seven maximal actions in FW (grp FW) apparatuses. Sets were interspersed by 2-min rest periods. Both exercises were executed with a range of motion of 80–85°, starting the CON action at about 80° until about 165°. During pre- and post-tests, the range of motion of grp FW (pre: $81 \pm 5°$, post: $83 \pm 3°$)

and grp WS (pre: $86 \pm 6°$, post: $82 \pm 5°$) showed a trend to interaction over time and group ($p < 0.10$), but no significant differences were shown ($p > 0.05$). Mean, peak and angle-specific force are shown in Tables 2 and 3. Because force measurements performed in the two devices were not compatible there were no comparisons across groups with regard to force.

Surface EMG recordings

Pre- and post-test in grps WS and FW

Multichannel surface EMG signals were acquired from mm. vastus lateralis (VL) and vastus medialis (VM) using two 8-electrode, 5-mm interelectrode distance adhesive arrays (ELSCH008; SPES Medica, Salerno, Italy). These detection systems allow recording of multichannel surface EMG signals during movement, with negligible movement artifacts (Pozzo et al. 2004). Before array placement, the skin was shaved, rubbed with abrasive paste and cleansed with a paper towel.

The arrays were placed between the innervation zone and the proximal or distal tendon regions, along the fiber direction. Innervation zones and tendon regions were identified at about 90° and 160° knee joint angles in isometric test actions with the use of a 16-silver bar electrode array (1-mm length, 5-mm diameter, 5-mm interelectrode distance; SA16/5, Ottino Bioelettronica, Torino, Italy). Surface EMG signals were sampled at 2,048 samples/s per channel and amplified with a multichannel amplifier (−3 dB bandwidth: 10–500 Hz) (Farina et al. 2004; Pozzo et al. 2004). Signals were converted to digital data by a 12-bit acquisition board (National Instruments DAQCard-6024E; Austin, TX), displayed in real-time, and recorded

Table 2 Mean and peak force pre- and post-training for the flywheel (grp FW) and weight stack (grp WS) training groups

	Grp FW			Grp WS		
	Pre	Post	%	Pre	Post	%
Mean force (*N*)						
CON	227 ± 60	262 ± 57*	+15	142 ± 29	200 ± 29*	+41
ECC	207 ± 57	246 ± 51*	+19	143 ± 29	207 ± 31*	+45
Peak force (*N*)						
CON	344 ± 72	378 ± 64*	+10	185 ± 34	258 ± 32*	+39
ECC	368 ± 77	432 ± 78*	+17	165 ± 34	247 ± 35*	+50

No comparisons between groups were performed

Values are mean $\pm$ SD

* Increase over time with training ($p < 0.05$)

Table 3 Angle-specific force pre- and post-training for the flywheel (grp FW) and weight stack (grp WS) training groups

Angle-specific force (*N*)	Grp FW				Grp WS			
	Pre	Post		%	Pre	Post		%
CON								
90°	293 ± 60	316 ± 49	*	+8	174 ± 39	248 ± 28	‡ *	+43
120°	276 ± 86	329 ± 83	‡	+19	140 ± 34	233 ± 46	‡	+66
150°	129 ± 63	185 ± 77	‡	+43	101 ± 34	130 ± 36	‡	+29
ECC								
150°	67 ± 44	88 ± 58	*	+31	135 ± 29	190 ± 46	‡ *	+41
120°	220 ± 93	279 ± 110	†	+27	144 ± 31	221 ± 31	‡	+53
90°	319 ± 73	361 ± 71		+13	149 ± 33	215 ± 37	‡	+44

No comparisons between groups were performed

Values are mean $\pm$ SD

* Denotes overall force increase within the action ($p < 0.05$)

‡ Denotes increase over time with training ($p < 0.05$)

† Denotes trend to increase over time with training ($p < 0.10$)

on a computer equipped with EMG acquisition software (Pozzo et al. 2004). To ensure similar positioning of the EMG electrodes during the pre- and post-tests, the electrode location and anatomical landmarks were marked and transferred to a plastic sheet.

Processing of EMG data from the acute FW and WS test, and pre- and post-tests

The central bipolar signal of the VM and VL array were used to compute EMG_{RMS} values during MVC and dynamic actions. Maximal EMG_{RMS} was computed from the 1-s window that was chosen to determine MVC. In dynamic actions, EMG_{RMS} was assessed from the entire range of motion, and 150-ms windows at knee joint angles of 90°, 120° and 150° in the CON and ECC action, respectively. EMG_{RMS} at 90°, 120° and 150° knee angles were further averaged over repetitions and sets. Given the inherent methodological problems with surface EMG recordings (Duchateau et al. 2006), EMG_{RMS} was expressed relative to maximal EMG for each individual muscle, i.e., normalized angle-specific EMG_{CON} and EMG_{ECC}.

Statistics

All comparisons were made separately for the CON and ECC action and the VL and VM muscles. Group comparisons were made using three-way (over group, time and angle: normalized angle-specific EMG_{CON} and EMG_{ECC}, or over group, time and interval: RFD) and two-way (over group and time: MVC, MVC EMG_{RMS}, and range of motion) repeated measures ANOVA (Stat-Soft, Tulsa, OK, USA). Comparisons of angle-specific force within groups were made using two-way (over time and angle) repeated measures ANOVA. When a difference between training groups or an interaction was found, planned comparisons were executed, and Bonferroni correction employed. Hence, any *p* value obtained was multiplied by the number of planned comparisons and considered significant if lower than 0.05. A Student's *t* test was used for comparisons when applicable (mean and peak force over time within grp FW and grp WS). The significance level was set to 0.05. Values are expressed as mean ± standard deviation.

Results

MVC and maximal EMG_{RMS}

MVC increased by ($p < 0.05$) 8.1% (pre: 575 ± 90; post: 622 ± 91 N) in grp FW and 4.8% (pre: 594 ± 113; post: 623 ± 103 N) in grp WS in response to training. Maximal
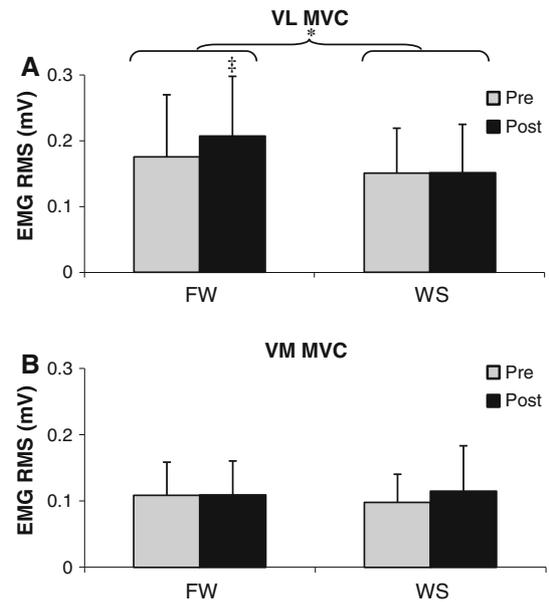

Fig. 1 Electromyographic amplitude (EMG_{RMS}) of mm. vastus lateralis (VL, **a**) and medialis (VM, **b**) during maximal voluntary contraction (MVC) performed by the flywheel (grp FW) and weight stack (grp WS) training groups pre- and post-training. *An interaction over group and time, where grp FW showed an increase (‡), but not grp WS
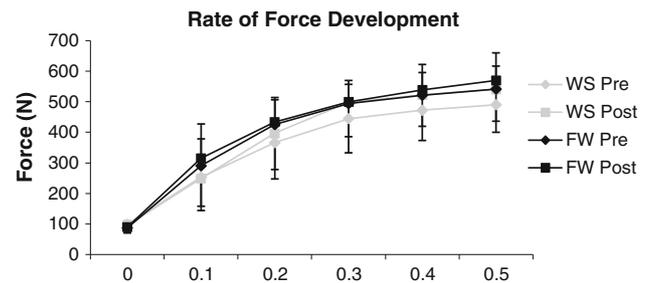

Fig. 2 Rate of force development (RFD) performed by the flywheel (grp FW) and weight stack (grp WS) training groups pre- and post-training

EMG_{RMS} of VL increased ($p < 0.05$) in grp FW, but not in grp WS (Fig. 1). VM showed no change.

Rate of force development

Force at 0.1–0.5 s, compared across groups and over time, showed a trend to increase ($p < 0.10$) from pre- to post-training (Fig. 2). There was no difference between groups.

Normalized angle-specific EMG

Grp FW showed greater ($p < 0.05$) normalized angle-specific EMG_{ECC} of both VL and VM compared with grp WS (Fig. 3). Specifically, grp FW showed greater ($p < 0.05$) normalized EMG_{ECC} of VL and VM at −90° pre- and post-training (Figs. 3, 4). In contrast, grp WS showed greater
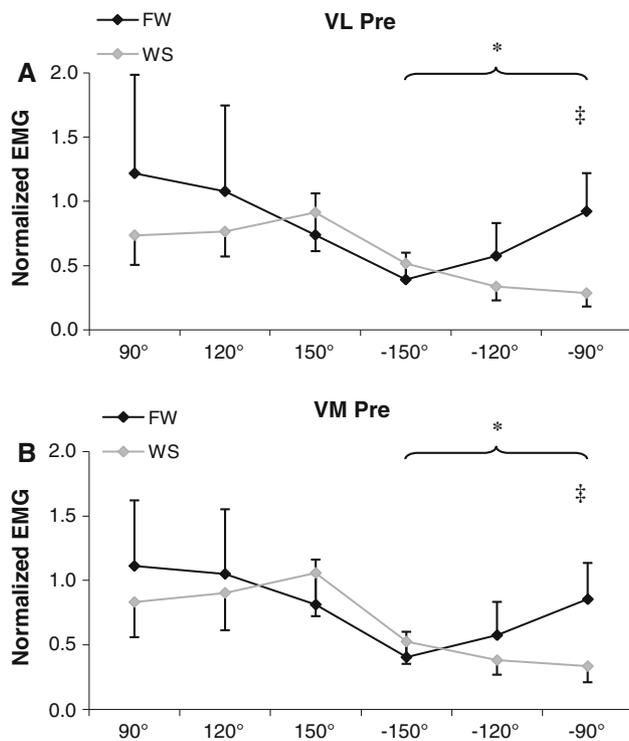
Fig. 3 Normalized angle-specific electromyographic (EMG) amplitude of mm. vastus lateralis (VL, **a**) and medialis (VM, **b**) during concentric (CON, 90° to 150°) and eccentric (ECC, −150° to −90°) actions of unilateral knee extension exercise, performed by the flywheel (grp FW) and weight stack (grp WS) training groups before the training period (pre-test). *Greater overall normalized angle-specific EMG with FW compared with WS exercise ($p < 0.05$). ‡Greater normalized angle-specific EMG with FW compared with WS exercise ($p < 0.05$)

normalized EMG$_{ECC}$ of VL and VM at −150° post-training ($p < 0.05$; Fig. 4). Normalized EMG$_{ECC}$ showed no changes from pre- to post-test in either group (Fig. 4). Overall, normalized angle-specific EMG$_{CON}$ showed no group difference. Grp WS showed a trend ($p < 0.10$) to increased normalized EMG$_{CON}$ of VL at 120° following training (Fig. 4). Collectively, following training, normalized EMG$_{CON}$ of grp WS was not different from that of grp FW. However, grp FW showed greater normalized EMG$_{ECC}$ than grp WS after training.

Discussion

The main finding of the present study was the markedly greater EMG, and in particular EMG$_{ECC}$ activity during flywheel (FW) compared with weight stack (WS) resistance exercise both before and after training. Hence, the greater muscle activation, and the resulting mechanical stress using
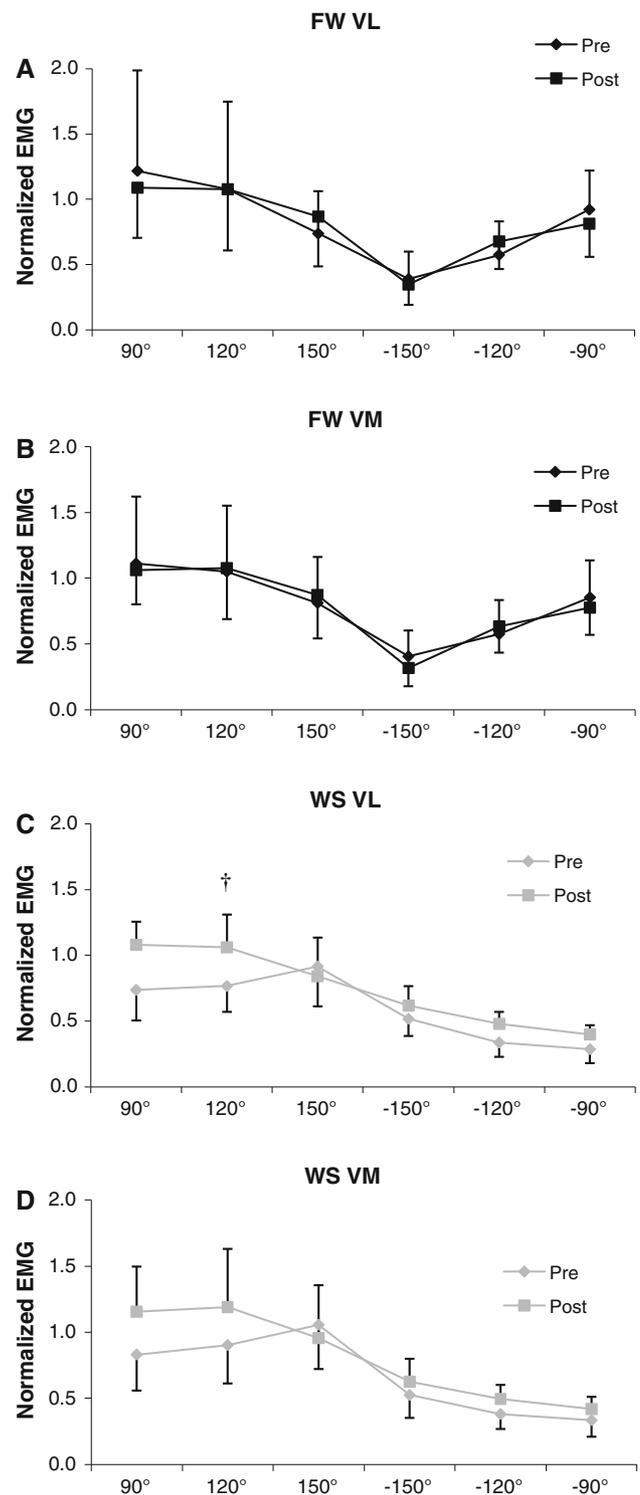

Fig. 4 Normalized angle-specific electromyographic (EMG) amplitude of mm. vastus lateralis (VL) and medialis (VM) during concentric (CON, 90° to 150°) and eccentric (ECC, −150° to −90°) actions of unilateral knee extension exercise, performed by the flywheel (grp FW, **a**, **b**) and weight stack (grp WS, **c**, **d**) training group pre- and post-training. Differences between groups are not indicated in the figure (see "Results" and Fig. 3). †Trend to increase over time with training ($p < 0.10$)

FW, may serve to explain the very robust muscle hypertrophy reported earlier in response to 5 weeks of flywheel resistance training (Norrbrand et al. 2008; Seynnes et al. 2007; Tesch et al. 2004).

To ensure comparable conditions for the two training groups, a 5-week unilateral open-chain knee extension exercise protocol standardized with regard to frequency and number of training sessions, number of sets and repetitions and rest was executed. In this context, the necessity and challenge of controlling conditions when comparing the outcome of different exercise paradigms should be acknowledged (Toigo and Boutellier 2006). Thus, body positioning, range of motion and time under tension per repetition was, if not identical, very similar for the two loading paradigms. It can only be speculated that training, at a different action speed (Matheson et al. 2001; Pincivero et al. 2008), requesting more repetitions per set (Pincivero et al. 2006), using other exercise modes (Andersen et al. 2006; Wilk et al. 1996) or employing other strategies (Sahaly et al. 2003), would have impacted the outcome of the current study.

Prior to training, the highest normalized EMG during WS occurred near completion of the CON knee extension. This coincided with the "sticking point", that inherently dictates the load that can be used in any exercise using weights. As a consequence, muscle activation during WS exercise is far from maximal through the major portion of the entire range of motion. Further, because the WS device uses constant resistance, only the last repetition of a set calls for maximal muscle activation at the point of failure to raise the weight. In contrast, the inertia of flywheel offers unrestrained resistance in each action, evoking maximal or near maximal activation from the onset and throughout a set, with force progressively decreasing with fatigue. The prescribed strategy used during FW training produced greater ECC than CON peak force ("ECC overload"). Thus, FW, but not WS resistance exercise, elicited maximal EMG throughout a large part of the CON action and maximal or near maximal EMG in the flexed position of the ECC action.

Interestingly, muscle activation was close to maximal already before training in grp FW. Grp WS showed a trend toward augmented EMG_{CON}, where the normalized EMG of VL and VM were maximal or near maximal in the low range of motion (90° and 120°) after training. Accordingly, force during WS training increased mainly in the acceleration phase (90°–120°) of CON actions. Thus, following training, EMG_{CON} was very similar across the two groups.

It is generally agreed that marked increases in MVC, as a result of resistance training, could occur through increased neural drive (Aagaard et al. 2002; Hakkinen and Komi 1983; Moritani and deVries 1979). The improved MVC (grp WS: 4.8%, grp FW: 8.1%) however appears to correlate with the associated hypertrophy (WS: 3.0%, FW: 6–7%) reported elsewhere (Norrbrand et al. 2008; Seynnes et al. 2007; Tesch et al. 2004), which contradicts the notion of increased neural drive. Further, the augmented maximal EMG_{RMS} of VL in response to FW resistance training may be indicative of increased neural drive. Yet, a concomitant boost in EMG_{RMS} of VM would have been expected (Aagaard et al. 2002; Moritani and deVries 1979). Instead, the EMG_{RMS} of only VL in grp FW may have been potentiated by reduced amplitude cancellations (Duchateau et al. 2006) due to increased MU synchronization (Milner-Brown et al. 1975), and/or enlarged surface area of the hypertrophied muscle fibers beneath the pick-up area of the surface electrode (Higbie et al. 1996). Finally, increased neural drive, resulting from training, may also be reflected in greater RFD (Aagaard et al. 2002), but neither group showed significant changes following training. In view of this, and regardless of exercise mode, any increase in neural drive must have been negligible and thus probably did not contribute to gain of MVC or training-specific strength.

Mechanisms responsible for the increased mode-specific strength, most evident following WS training, were therefore more likely attributed to more orchestrated coordination of agonist and stabilizing muscles (Duchateau et al. 2006; Rutherford and Jones 1986), excelled timing of individual motor unit activation (Cracraft and Petajan 1977) and/or attenuated antagonist co-activation (Hakkinen et al. 1998). The modest transfer of training-specific strength to MVC, most apparent in grp WS, conforms with the general notion of such neural adaptation occurring during the first weeks of training (Moritani and deVries 1979; Rutherford and Jones 1986).

The present study was prompted by previous reports of manifest hypertrophy following FW knee extension training (Norrbrand et al. 2008; Seynnes et al. 2007; Tesch et al. 2004). The quadriceps hypertrophy following FW training amounted to 4–5% (Seynnes et al. 2007) and 6–7% (Norrbrand et al. 2008; Seynnes et al. 2007; Tesch et al. 2004) after 3 and 5 weeks, respectively. This rate of quadriceps hypertrophy has rarely been reported (Luthi et al. 1986), while the hypertrophic response of 3% in grp WS after 5 weeks of training (Norrbrand et al. 2008) is in accordance with several earlier reports (Jones and Rutherford 1987; Narici et al. 1996; Ploutz et al. 1994). It is generally held that both high mechanical loading and inclusion of ECC actions are essential stimuli to promote muscle hypertrophy (Hather et al. 1991; Higbie et al. 1996; Hortobagyi et al. 1996). Since skeletal muscle signaling and remodeling for hypertrophy appears to be initiated by mechanical myofibrillar disruption (Friden et al. 1983; Newham et al. 1983), reports of potentiated Z-line streaming or myofibrillar disruptions (Friden et al. 1983; Newham et al. 1983) and protein synthesis (Moore et al. 2005; Wong and Booth

1990a, b) resulting from exercise favoring acute ECC actions, confirm this notion. Hence, the greater (1) ECC than CON peak force and (2) normalized EMG_{ECC} in grp FW, compared with grp WS, is commensurate with the hypothesis that FW resistance exercise offered a more powerful stimulus for hypertrophy than WS resistance exercise.

In an effort to control for range of motion, there was a brief pause between the ECC and CON actions during WS training. In contrast, actions in the FW mode were coupled and involved stretch–shortening cycling, most likely facilitating potentiated CON muscle activation and force (Komi and Bosco 1978). Given the inherent features of the exercise system, the subsequent CON action prompts more mechanical ECC work and hence muscle loading. Because grp WS did not perform coupled actions, it cannot be excluded that stretch–shortening actions executed in the FW mode in part were responsible for the greater muscle activation shown here and the more substantial hypertrophy reported elsewhere (Norrbrand et al. 2008) in response to FW exercise.

While the goal of this study was to compare neural adaptations in previously untrained subjects following resistance training using either flywheel inertia or standard weights, it became evident that muscle activation produced by FW exercise was near maximal in major portions of both CON and ECC actions prior to training. In contrast, WS exercise evoked far from complete activation. Following training, the EMG_{CON} was very similar between groups, while the normalized EMG_{ECC} remained much lower in grp WS. Thus, even after training, it appears that WS did not provide an optimal stimulus for hypertrophy. The current investigation may offer an explanation in support of previous notions of more substantial hypertrophy after flywheel than weight training. We suggest that the greater muscle activation, and particularly that during ECC muscle actions, is indicative of greater mechanical loading, resulting in more robust stimulus giving rise to signals promoting enhanced protein synthesis and eventually leading to greater muscle hypertrophy.

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