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ABSTRACT

Weight training typically offers constant external load during coupled shortening (concentric) and lengthening (eccentric) muscle actions in sets of consecutive repetitions until failure. However, skeletal muscle inherently has the capability to produce greater force in the eccentric compared with the concentric action, which allows for greater loading during the eccentric action, i.e. “eccentric overload”. Thus, traditional weight training uses a loading strategy, which appears to result in incomplete motor unit recruitment and muscle use during most concentric actions and all eccentric actions of a set. In contrast, the flywheel device, using the inertia of flywheel(s) to generate resistance, allows for maximal voluntary force to be produced throughout each concentric action with brief episodes of eccentric overload. This type of loading may potentially increase motor unit recruitment and muscle use during acute resistance exercise, and as a result may induce greater training adaptations when bouts are repeated.

The aim of the present thesis was to explore the fatigue response of the quadriceps muscle during flywheel exercise, and to compare quadriceps muscle use and adaptations to training in response to acute or chronic resistance exercise using traditional free weights/weight stack machine or a flywheel apparatus.

Multichannel surface electromyographic (EMG) signals were recorded from the quadriceps muscle of nine men, to assess fatigue during consecutive concentric-eccentric actions performed using the flywheel device. There was marked fatigue during both the concentric and eccentric actions. Results further showed a discrepancy between normalized rate of decrease of instantaneous mean power spectral frequency (iMNF) and conduction velocity (CV), which may imply that iMNF will not accurately reflect changes in CV during dynamic actions. Furthermore, to assess and compare quadriceps muscle use in the two loading features, five resistance trained men performed free weight and flywheel resistance exercise on separate days. Flywheel exercise induced greater over all muscle use, showing greater over all EMG activity and increase in transverse relaxation time (T₂) of magnetic resonance images, compared with free weight exercise. The greater muscle use shown with flywheel exercise appeared to result from the greater forces produced during the flywheel compared with free weight exercise. Furthermore, when fifteen healthy men were assigned to five weeks of unilateral knee extension training using either a flywheel device or a weight stack machine, flywheel training induced more robust muscular adaptations, i.e. increased volume of all four individual quadriceps muscles and increased maximal isometric strength, compared with weight stack training.

In summary, flywheel resistance exercise resulted in more robust muscular adaptations compared with traditional resistance exercise using weights. Furthermore, the flywheel device induced greater forces and muscle use during acute exercise. The marked fatigue response during the coupled concentric-eccentric flywheel exercise is supported of near maximal effort and hence muscle use, which is further suggested to, at least in part, explain the more robust muscular adaptations following chronic flywheel resistance exercise compared with traditional weight training.

LIST OF PUBLICATIONS

- I. Pozzo M, Alkner B, **Norrbrand L**, Farina D, Tesch PA, Muscle-fiber conduction velocity during concentric and eccentric actions on a flywheel exercise device. *Muscle Nerve* 34: 169-177, 2006.
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LIST OF ABBREVIATIONS

ARV	Average rectified value
ATP	Adenosine triphosphate
BS	Barbell squat
CON	Concentric, shortening muscle action
CSA	Cross-sectional area
CV	Conduction velocity
ECC	Eccentric, lengthening muscle action
EMG	Electromyography
FS	Flywheel squat
FW	Flywheel / Flywheel training
iMNF	Instantaneous mean power spectral frequency
MRI	Magnetic resonance imaging
MU	Motor unit
MVC	Maximal voluntary contraction/maximal isometric strength
ROM	Range of motion
RF	M. rectus femoris
RMS	Root mean square
T2	Transverse relaxation time
VI	M. vastus intermedius
VL	M. vastus lateralis
VM	M. vastus medialis
WS	Weight stack training
1 RM	One repetition maximum; the maximum amount of weight that can be lifted during one repetition

DICTIONARY

Isoinertial action	A dynamic action against constant inertia
Isokinetic action	A dynamic action at constant velocity
Isometric action	An action where neither joint angle nor muscle length changes
Isotonic action	A dynamic action against a constant external load

1 INTRODUCTION

1.1 BACKGROUND OF RESISTANCE EXERCISE

Chronic resistance exercise induces increases in skeletal muscle strength and mass (27, 103). Typically, such exercise is performed with use of coupled concentric (CON) and eccentric (ECC) actions to enhance athletic performance (2) or to prevent injury (12) during sports. Further, it has been proven to reduce the consequences of several of the welfare diseases/disorders, such as coronary heart disease, Type 2 diabetes, and osteoporosis (71), and may thus benefit health in recreationally active.

It is generally agreed that the neural adaptations prevail during the first weeks of resistance training programs (52, 80, 94), with muscle hypertrophy evident after a few weeks of training (53, 73, 84, 101), gradually contributing to improved strength and performance (94). Cellular signaling for hypertrophy and increased protein synthesis may however occur after a single bout of resistance exercise (21, 79, 86).

1.2 CONCENTRIC AND ECCENTRIC ACTIONS

Inherently skeletal muscle possesses the capability to produce greater force in the ECC compared with the CON action (40, 56, 65). The utilization of elastic energy stored in the cross-bridges formed by actin and myosin filaments is thought to provide a major part of the force produced in the active muscle fibers during stretch (40, 63). Thus mechanical efficiency is greater (19, 29, 68), and the metabolic cost lower (13, 19, 29) during ECC compared with CON actions. Since the type of action potentially involves diverse stimuli dictating hypertrophy, neural drive and metabolism (see below), it has been suggested that resistance exercise should incorporate both CON and ECC actions (30).

1.3 ACUTE RESPONSE OF RESISTANCE EXERCISE

1.3.1 Motor unit recruitment and muscle involvement

According to the size principle (54), smaller/slower motor units (MUs) with lower twitch force and recruitment threshold are recruited before larger/faster MUs in response to increased force demand. Hence, force is modulated by recruitment of additional MUs and increased discharge rate of recruited MUs (34, 94). Despite indications of recruitment with respect to size, exceptions to this concept have been reported, suggesting an altered recruitment strategy during ECC actions (33, 47, 76, 111).

Heavy resistance exercise enhances the energy demand with increased breakdown of ATP and creatine phosphate (48). The accumulation of related metabolic by-products initiates osmotically driven fluid shift within the muscle and is believed to explain the acute increase in contrast shift, signal intensity and transverse relaxation time (T2) in muscles involved in exercise (39, 77, 85), when assessed by means of functional magnetic resonance imaging (MRI). Exercise-induced changes in T2 appear to correlate with the intensity of the CON actions (4, 98), and thus the metabolic changes, which may be attributed to greater MU involvement (13, 29) during CON compared with ECC actions. The greater electromyographic (EMG) amplitude typically reported

during CON compared with the ECC actions, also suggests greater MU involvement during shortening than lengthening actions (19, 33, 69, 81).

1.3.2 Neuromuscular fatigue

Neuromuscular fatigue appears to be of either central or peripheral origin, but depending on e.g. type of action and relative force level, the mechanisms inducing fatigue varies. Proposed mechanisms include decreased neural drive (42, 92), motoneuron inhibition (42), as well as impaired transmission of the action potential along the membrane, limited calcium ion concentration, or impaired cross-bridge cycling (18, 96, 113).

In order to maintain force output during a sustained isometric action at 50 % of maximal voluntary force, MU recruitment and discharge rate increases (115), which is reflected by a gradually increasing EMG amplitude (51). The following accumulation of metabolites and extra cellular potassium (78, 96), have been proposed to decrease membrane excitability, and thereby impair the transmission of the action potential. When assessing multichannel EMG signals, this will be recognized as decreased conduction velocity (CV). Furthermore, the decreased CV has been suggested to be the main cause to decreased EMG frequency spectrum during a sustained submaximal isometric action (11, 37, 102). Since the changes of CV and EMG frequency spectrum appear to correlate (10, 11), frequency spectrum parameters have been used to infer changes in CV.

While the EMG fatigue response during isometric actions has been extensively reported (11, 18, 24, 28, 37, 88, 102, 115), the neuromuscular fatigue during different types of dynamic actions has not been thoroughly examined (36, 70, 75, 105). Marked decline in force and mean power frequency (MNF), and increased EMG amplitude/force relationship, have been reported during consecutive CON actions (70, 105). Further, these indices of fatigue showed greater changes during CON than ECC actions (105). The greater mechanical efficiency of the ECC actions (19, 29, 68) and altered recruitment strategy used during ECC actions (33, 47, 76, 82, 105, 111), may be responsible for the unaltered force output, power spectrum frequency and EMG amplitude/force relationship, reported during consecutive ECC actions (105). When performing coupled CON-ECC actions, the fatigue response, mainly induced by the CON actions, may potentially affect also the fatigue response of the ECC actions. However, the fatigue response during maximal coupled CON-ECC actions, and specifically with regard to the relationship between spectral parameters and CV, remains to be studied.

1.3.3 Cellular signaling for muscle hypertrophy

The net increase in contractile protein following resistance exercise is modulated through increased protein synthesis and reduced protein degradation (45). Cellular signaling for hypertrophy has been reported after a single bout of resistance exercise (21, 79, 86), and protein synthesis increases multi-fold within hours after acute resistance exercise (79, 86).

The ECC actions provoke Z-line streaming (23, 38, 41, 99), and greater rate of myofibril disruption compared with CON actions (41, 43). This ultrastructural damage following ECC actions appears to be part of the remodeling of the muscle fibril (118). In fact, human and rat muscles subjected to ECC exercise exhibited both greater rate of myofibril protein synthesis and cellular signaling for protein synthesis than muscles performing CON actions (31, 79, 116, 117). Hence, collectively these results suggest that the ECC action is important for inducing the hypertrophy process.

1.4 TRAINING RESPONSE OF RESISTANCE EXERCISE

1.4.1 Strength and neural adaptations

Following strength training programs the increase in maximal strength is typically greater than the rate of hypertrophy (27, 73, 84). This response has been attributed to the neural adaptations, e.g. by enhanced ability to coordinate muscle agonists (34, 93), reduced inhibition (1), and/or increased recruitment ability (34, 73, 84, 93, 109), especially of the high threshold fast/large MUs (94). According to the concept of specificity (34, 91), it is generally held that increases in strength are most evident in the training mode. Therefore, dynamic strength typically increases more compared with isometric strength after dynamic resistance exercise (83, 90, 95). As a result, the neuromuscular efficiency improves, i.e. a given force is produced with less muscle involvement (52, 83, 87, 93, 108).

The mentioned greater capability of force production during the ECC action allows for greater loading during the ECC compared with CON action (33, 67, 105), i.e. ECC overload, in a given exercise mode. Although this training concept has been employed by athletes for decades, only a few studies have aimed at assessing the efficacy of chronic training using ECC overload. Results show that training-specific (20, 25, 50, 67) and isometric strength (67) increases more after ECC overload compared with constant load during CON actions only (25, 67), or coupled CON-ECC actions (20, 50, 58), which suggests that the neural adaptation may be augmented with chronic ECC overload training.

1.4.2 Hypertrophy

Hypertrophy after weight training (50, 74) is reflected in increased volume, cross-sectional area (CSA) of the whole muscle or muscle fibers, and in particular the Type II fibers (53, 74, 104, 108). The number of sarcomeres is believed to increase both in parallel and in series (114, 119), which appears to improve both force production and ability to withstand stress (119). The following increased fiber pennation angle (66) may contribute to improved neuromuscular efficiency (83).

Mechanical loading and ECC actions appears to be crucial for optimizing hypertrophy (46, 53, 55). Although some contradictory data have been reported (61, 64), several studies have shown that ECC training induces greater rate of hypertrophy than CON training in humans (59, 67), and rats (116, 117). Therefore, the rate of hypertrophy may potentially be optimized by employing ECC overload training. However, the responses to ECC overload compared with constant load resistance training are inconclusive with

regard to muscle hypertrophy (20, 25, 44, 67). Thus, it is not clear whether ECC overload optimizes the hypertrophy response following resistance training, or not.

1.5 LOADING DURING RESISTANCE EXERCISE

1.5.1 Loading during weight training

Traditional weight training, using coupled CON and ECC actions, employ constant external load, i.e. isotonic loading. Thus, with increasing exertion throughout each set, maximal loading is only offered in the very last repetition, resulting in failure to raise the load. Given this and the greater force capability during the ECC action, infer that the majority of CON actions and all ECC actions are executed with a load that is far from maximal. Despite shortcomings, knee extension weight stack training (Study III) and barbell squat exercise (Study II) has been proven effective to increase muscle strength and size (14, 49, 83, 87).

1.5.2 Loading during flywheel training

The flywheel device (FW) allows for maximal CON force throughout the range of motion (ROM), brief episodes of ECC overload, and maximal exertion from the first repetition. The fatigue response will result in decreased force production throughout the set. The concept of using the inertia of spinning flywheels to generate resistance and used by A. W. Hill in the early 20's (57), was introduced to provide a resistance exercise device for space travelers working in a non-gravity environment (16, 17). The isoinertial loading has been proven effective to induce hypertrophy during unloading (107) and ambulation (97, 106), and to prevent muscle atrophy during long-term bed rest (7, 8).

2 AIMS

The overall aim of the present thesis was to evaluate the fatigue response during isoinertial loading, and to compare muscle involvement and training adaptations following resistance exercise using traditional isotonic or isoinertial loading.

More specifically the aims of this thesis were:

- By using a novel EMG technique, describe the fatigue response during coupled CON-ECC actions performed during isoinertial loading, and more specifically to evaluate changes of EMG spectral frequency parameters and conduction velocity.
- To compare muscle involvement between the isoinertial and isotonic loading during acute resistance exercise.
- To compare the training effect on muscle volume and function following 5 weeks of resistance exercise, executed with identical programs, but employing either isoinertial or isotonic loading.

3 METHODS

3.1 DESIGN OF STUDY I, II AND III

3.1.1 General design

Subjects received information about the study protocol before a written consent was given. The study protocols were approved by the Ethics Committee at the Karolinska Institutet Study, Stockholm (Study I-III) and by the Institutional Review Board of the University of Arkansas for Medical Sciences, Little Rock, AR (Study III).

3.1.1.1 Study I

Nine healthy men performed maximal voluntary isometric actions (MVC), a sustained isometric action at 50 % of MVC, isometric force ramps (0-100 % of MVC), and 30 dynamic coupled CON-ECC actions, while seated in the FW knee extension device. To assess the fatigue response, multichannel surface EMG signals were recorded from mm. vastus lateralis (VL) and vastus medialis (VM). The average rectified value (ARV), instantaneous mean power spectral frequency (iMNF), and CV were estimated from the sampled 8 channel EMG signals. The same experimental protocol was repeated on two non-consecutive days.

3.1.1.2 Study II

Five resistance trained subjects performed three MVCs followed by 5 sets of 10 maximal repetitions (RM) of squat exercises using either a traditional barbell (BS) with weights or a flywheel device (FS) on separate days. Quadriceps muscle use was assessed by means of functional MRI scans, acquiring a dual echo sequence prior to and within 2-3 minutes after finishing the exercise. The obtained images were analyzed by measuring average SI and calculating T2. Force, linear displacement and EMG from the three superficial quadriceps muscles were recorded during exercises.

3.1.1.3 Study III

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 quadriceps muscle group. The 5 week training protocol were comprised of unilateral CON-ECC knee extensions using either a flywheel device or a weight stack machine. Training load/force production was measured during every training session. Prior to and at completion of the training period, quadriceps muscle volume was assessed by means of MRI, and MVC, as well as training specific strength and performance were tested in both limbs separately.

3.1.2 Subjects

3.1.2.1 Study I

Nine men (age: 30±4 yrs; height: 182±4 cm; weight: 84±10 kg) with no previous history of lower limb pathology and no known neuromuscular or cardiovascular disease, volunteered for this study.

3.1.2.2 Study II

Five healthy resistance trained male subjects (age: 33 ± 2 yrs, height: 178 ± 9 cm, weight: 88 ± 15 kg) participated in this study. Mean 10 RM for the subjects in the barbell half squat was 146 ± 18 kg.

3.1.2.3 Study III

Seven men (age: 39 ± 9 yrs, height: 178 ± 6 cm, weight: $86\pm$ kg,) were assigned to perform resistance exercise using a FW device (FW), while eight age- and strength-matched men (age: 39 ± 8 yrs, height: 187 ± 7 cm, weight: 95 ± 16 kg) 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. The FW group was a subgroup from an earlier reported study (106).

3.1.3 Exercise protocol

3.1.3.1 Study I

The tasks performed involved unilateral knee extension of the dominant leg. At least two MVCs at 120° knee angle were performed. While grasping the handlebars at least 2 maximal isometric actions (2-3 s each), intervened by 1 min rest. 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 one second window showing a stable force level, was considered MVC. Then the subjects performed two isometric ramp actions (attaining 100 % of MVC in less than 10 s), one 60 s isometric action at 50 % of MVC, and finally 30 dynamic coupled CON-ECC actions, while seated in the FW knee extension device. Verbal encouragement was given during all actions. Visual force feedback was provided on a computer screen during the ramp and sustained isometric actions. The two ramp actions were separated by 2-min rest, while 10-min rest followed the second ramp action and the sustained isometric action. During the CON/ECC actions, the subject was requested to exert the maximal force over the entire range of motion for each repetition.

3.1.3.2 Study II

Familiarization with the equipment and 10 RM was determined prior to tests. Subjects performed squat exercises with both equipments on separate days one week apart, starting with either the flywheel or the free weight exercises in a randomized order. Following a warm-up consisting of two sets of squats of moderate intensity, subjects performed three MVCs at 90° knee angle in YoYo Multi Gym (YoYo[®] Technology Inc., Stockholm, Sweden). The MVC trial with the greatest overall EMG (averaged over 4 s) was considered as maximal EMG. This was followed by 5 sets of 10 RM of either FS or BS with 3 min rest in between sets. Verbal encouragement to ensure maximal effort and proper technique was given.

3.1.3.3 Study III

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. In order to control for ROM, the ECC-CON turning point in WS was limited to the same angle as was used during FW training.

Verbal encouragement was given during all actions. Sets were interspersed by 2 min rest periods. Any exercise session was preceded by a 5 min warm-up with progressively increased effort. All subjects complied with the prescribed training programs.

Prior to and after completion of the training period tests of unilateral knee extension of both limbs were executed. Tests for knee extensor MVC were executed in the seated position with hip joint at 90°, and with the lever arm fixed at 90 and 120° knee angle, respectively (see description above). Training specific strength and performance were tested while performing CON-ECC knee extensions at 7 RM in either the FW device (FW) or the weight stack device (WS). Both limbs were tested and in a revised randomized order across the subjects.

3.2 RESISTANCE EXERCISE DEVICES

3.2.1 Flywheel training devices

In Study I and III all tests and FW training were performed in a seated knee extension flywheel device (YoYo® Technology Inc., Stockholm, Sweden; (106), equipped with a 4.2 kg flywheel with a moment inertia of 0.11 kg·m². While seated and slightly reclined and using back support (hip angle 90°) and restraint, the trainee pushes against a cross-bar 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. The strap unwinds off the shaft and energy is imparted to the flywheel in the CON action. 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, and the trainee then executes an ECC action while trying to resist.

In Study II flywheel squat was performed in a YoYo Multi Gym (YoYo® Technology, Stockholm, Sweden) equipped with 2 · 2.7 kg flywheels with a moment inertia of 0.07 kg·m² each. The configuration employed is designed for use in space and allows for multiple exercises involving upper- and lower-body as well as back muscles. Using a harness connected through a strap to the flywheel axle, the seat slides back and fourth on a rail in the coupled CON-ECC action. With feet on the foot plate and flexed knees, the trainee initiates flywheel rotation through the pull of the strap. The strap unwinds and the trainee slides backwards. Once the concentric phase has been completed, the eccentric muscle action is performed by trying to resist the pull of the flywheels, which recoils the strap onto the axle. This equipment has been described in detail elsewhere (6).

3.2.2 Weight training devices

In Study II back barbell half squats (BS) were performed in coupled ECC-CON actions using a 20 kg Olympic barbell (Eleiko, Halmstad) with additional weights. With the bar centered across the upper back, the subject descend in a continuous motion by flexing the knees, ankles and hip until the posterior surface of the thighs are parallel to the floor, and then ascend to the upright position.

In Study III group WS used a seated knee extension weight stack machine (World Class®, Stockholm, Sweden) during training, 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. Weight plates of 5.0, 2.5 and 1.25 kg were used to set and adjust load.

3.3 MAGNETIC RESONANCE IMAGING

To minimize the potential influence of any fluid shift on muscle size (15), subjects remained supine for 1 h prior to the start of any of the resting MRIs. A custom made adjustable foot restraint device was used during all scans to avoid compression of muscles during scanning and to keep the limbs in a fixed position. The graded foot-brace and detailed description of placement ensured accurate repositioning across sessions.

3.3.1.1 Study II

A 1.5 T MRI (Intera, Philips Medical Systems, Best, The Netherlands) was used to acquire spin-echo scans (double echo sequence, proton density with TR/TE: 1500/30 msec, T2 weighted with TR/TE: 1500/60 msec, FOV: 455 · 341 mm, Voxel: 1.78 · 1.78 · 10 mm, Matrix: 256 · 128, Thickness: 10 mm, Gap: 10 mm, NEX/NSA: 1, Acquisition time: 2 min 25 s) prior to and within 2-3 minutes after finishing the exercise. Starting where m. gluteus maximus was not seen and then distally, quadriceps (rectus femoris; RF, vastus intermedius; VI, VL, and VM) were analyzed. Five of the 17 slices obtained, were analyzed by measuring average signal intensity (SI) in the regions of interest using custom made software (DimView, Nordic Ice Medical, Bergen, Norway). Average SI in each slice was obtained and T2 was calculated, and further mean T2 over the 5 slices ($T2 = (\Delta TE) / \ln (SI_{TE\ 30} / SI_{TE\ 60})$). Care was taken not to include non-muscular tissues such as fat and blood vessels.

3.3.1.2 Study III

Volume of individual quadriceps muscles was assessed by MRI. For FW, a 1.5 T MRI (Signa, General Electric, Milwaukee, WI, USA) machine was used. WS was examined with use of a 1.5 T MRI (Intera, Philips Medical Systems, Best, The Netherlands) unit. For all subjects, fifty images with slice thickness 10 mm and no spacing in between slices were obtained. Despite use of two MRI facilities and slightly different imaging sequences, analyses and procedures used has been validated previously (7, 106, 107). 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 (RF, VL, VM, and 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, has no impact reliability of this measurement (7). Muscle volume of the selected stack was subsequently calculated from the areas determined in individual images.

3.4 ELECTROMYOGRAPHY

3.4.1.1 Study I

The used detection systems (Laboratory for Engineering of the Neuromuscular System (LISiN), Politecnico di Torino, Italy), allow for recordings of multichannel surface EMG signals during movement, assessing ARV and iMNF, and detecting propagating potentials for the estimation of CV (36, 88). Using two 8-electrode, 5-mm interelectrode distance adhesive arrays (ELSCH008; SPES Medica, Salerno, Italy), multichannel surface EMG signals were acquired from the VL and VM muscles (Fig. 1). After detection of the innervation zone and the tendon regions, the arrays were placed along the fiber direction between the innervation zone and the proximal or distal tendon regions. Before array placement, the skin was shaved, rubbed with abrasive paste, and cleaned with a paper towel. Electromyographic electrode location was marked with an ink pen after the first experimental session, ensuring similar electrode positioning. Surface EMG signals were amplified with a multichannel amplifier (-3 dB bandwidth: 10-500 Hz, LISiN), sampled at 2048 samples/s per channel, converted to digital data, displayed in real-time, and recorded on a computer equipped with an EMG acquisition software developed at LISiN.

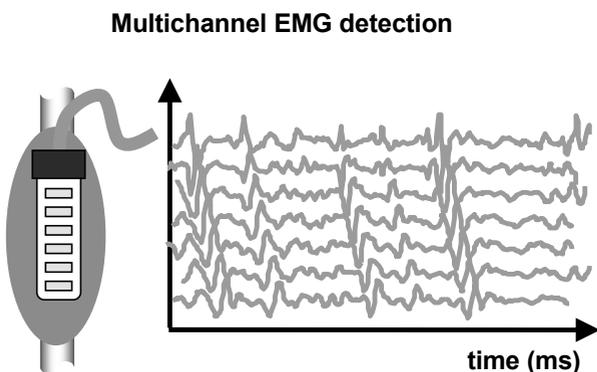


Figure 1. Schematic picture of multichannel EMG detection using arrays.

Double-differential derivations were obtained from the single-differential EMG signals and used to estimate muscle fiber CV with a developed algorithm (36). In this way, CV could be estimated from very short signal epochs (88), providing estimates that are local in time. For VM and VL, values of iMNF were computed from the central bipolar signal of each array. In order to reduce estimation variance, each value of iMNF was calculated from 30 consecutive values corresponding to 14.6 ms. Using the same bipolar signal, values of ARV were calculated from 250 ms time interval (8192 consecutive values). Conduction velocity, iMNF, and ARV were estimated at time instants corresponding to the force levels 10 %-100 % MVC (10 % increments) in the isometric ramp action and at time instants separated by 1 s in the 50 % of MVC constant force contraction. During the dynamic task, the same variables were estimated for each repetition of CON and ECC actions, at time instants corresponding to a joint angle of 120°. Knee joint angular velocity and force were computed at the same time instants. The first value of CV, iMNF, and ARV obtained during the 50 % of MVC action and the dynamic exercise were considered as initial value (and 100 %). For the estimates of CV, iMNF, and ARV, a trend line, i.e. slope, was calculated. To allow for comparisons, the slopes were normalized to the initial values and expressed in percentage.

3.4.1.2 Study II

Disposable bipolar Ag-Ag/Cl surface electrodes (Multi Bio Sensors Inc., El Paso, TX, USA) with 25 mm inter-electrode distance were placed aligned longitudinally to the fibre direction over VM, VL and RF of the dominant limb. Single differential surface EMG signals were amplified using bipolar EMG probes (MuscleLab™, Ergotest AS, Langesund, Norway; -3 dB bandwidth = 6-1500 Hz; input impedance = 2 GΩ; CMRR = 100 dB; gain = 600). Root mean square (RMS) of the raw signal was sampled using a Windows™ based data acquisition system (MuscleLab™, Ergotest AS, Langesund, Norway). The MVC trial with the greatest overall EMG (EMG RMS averaged over 4 s) was considered as maximal EMG. For the following dynamic actions, EMG RMS was measured over the CON and ECC actions, averaged over repetitions and sets, and expressed relative to maximal EMG for each specific muscle.

3.5 FORCE, WORK, POWER, RANGE OF MOTION AND VELOCITY

3.5.1.1 Study I

The FW was equipped with a force sensor (Model 276A, K Toyo, Seoul, Korea) to measure the force developed by the subject. A potentiometer mounted on the lever arm measured the knee joint angle. The force signal was also fed onto a computer-based oscilloscope (ADC42; Pico Technology, St. Neots, UK), used as a visual force feedback for the subject during isometric actions. Force and joint angle were acquired at a sampling rate of 2048 Hz, simultaneously with the surface EMG signals.

3.5.1.2 Study II

For force measurements during BS, the weight of the bar and added load together with recordings from a linear encoder (Ergotest AS, Langesund, Norway) were used, while a force strain gauge (Model 333A, K Toyo, Seoul, Korea) placed in between the harness and the pulley was used during FS. The linear displacement (FS: attached to the harness; BS: attached to the bar), velocity and duration of the CON and ECC actions were measured during both exercises. All parameters were recorded by MuscleLab™ (see above).

3.5.1.3 Study III

In WS, mean and peak work and power were calculated from training load lifted and angular velocity. Thus, configuration and mass of the cam and lever arm were not taken into account, when calculating training load, work or power. To evaluate mean and peak angular velocity, and ROM in WS, knee angle was measured using an electrogoniometer (16) fixed about the knee joint with a custom-built adjustable Velcro® strap system (Alfatex®, Deinze, Belgium). In FW, a force sensor (see Study I) and knee angle, measured by a mounted potentiometer in the FW device, were used to calculate mean and peak angular velocity, work and power. The FW device was used for testing MVC in both groups. Force, vertical displacement and knee joint angle were measured using MuscleLab™ (see above).

3.6 STATISTICS

3.6.1.1 Study I

Data were analyzed with repeated measures ANOVA. When appropriate, the Student-Newman-Keuls (SNK) post-hoc test was used for multiple pair-wise comparisons. Statistical significance was set to $p < 0.05$. Data are presented as mean ± standard error (SE) of the mean.

3.6.1.2 *Study II*

A repeated measures, three-factorial ANOVA (Statsoft, Tulsa, OK, USA) was employed to compare T2 over exercise mode, time and muscle (VM, VL, VI, RF), and to compare EMG activity over exercise mode, action, and muscle (VM, VL, RF). A repeated measures, two-factorial ANOVA was used to compare force, displacement, velocity and duration over exercise mode and action, and also for comparisons of relative T2 increase over exercise mode and muscle. Planned comparisons were performed from pre to post within exercises for all muscles. Planned comparisons for normalized EMG RMS, force, displacement, velocity and duration were performed between exercises within the CON or ECC action, and between CON and ECC actions within exercises. The significance level was set to $p < 0.05$, and when planned comparisons were executed the significance level was set to $p < 0.025$. Values are expressed as mean \pm standard deviation (SD).

3.6.1.3 *Study III*

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. The significance level was set to $p < 0.05$. Values presented as mean \pm standard deviation (SD).

4 RESULTS

4.1 STUDY I

4.1.1.1.1 Isometric ramp actions

While iMNF was not affected by the force level ($p > 0.05$), CV increased ($p < 0.05$) as the force was increased during the ramp action. At 10 % and 20 % of MVC ($p < 0.05$), CV was lower than at any other force level. The ARV increased with force ($p < 0.05$), and values differed from each other at any force level at or above 30 % of MVC ($p < 0.05$).

4.1.1.1.2 Sustained isometric actions

The initial value of CV was lower ($p < 0.05$) in VL (5.13 ± 0.23 m/s) than in VM (5.51 ± 0.16 m/s). The negative slope of CV over time was not different ($p > 0.05$) between days or muscles (-0.0052 ± 0.0018 m/s²). The initial value of iMNF (76.7 ± 1.1 Hz), iMNF slope (-0.065 ± 0.024 Hz/s), initial value of ARV (38.8 ± 6.0 μ V), and ARV slope (0.29 ± 0.05 μ V/s) were not different across days or muscles. Furthermore, there was no difference between the negative normalized slopes of iMNF and CV ($p > 0.05$).

4.1.1.1.3 Dynamic actions

During the 30 coupled CON-ECC actions, all parameters were analyzed at the time instants corresponding to 120° knee joint angle. In this knee joint angle, average CON force (135.7 ± 11.1 N) was greater ($p < 0.05$) than averaged ECC force (128.5 ± 10.9 N), and the negative slope was greater ($p < 0.05$) for CON (-0.99 ± 0.08 N/s) than ECC actions (-0.91 ± 0.09 N/s). The normalized slope of iMNF and CV was different during both CON and ECC actions ($p < 0.05$). The relative decrease of CV was greater compared with iMNF ($p < 0.05$). Initial values of CV was higher ($p < 0.05$) in CON (5.42 ± 0.16 m/s) compared with ECC (5.28 ± 0.20 m/s) actions. The slope of CV was greater ($p < 0.05$) for VL (-0.0096 ± 0.0023 m/s²) than VM (-0.0073 ± 0.0022 m/s²). Initial values of iMNF was not different ($p > 0.05$) across muscles, days, or type of action. The negative slope of iMNF showed larger decrease over time ($p < 0.05$) in VL (-0.077 ± 0.022 Hz/s) than VM (-0.056 ± 0.013 Hz/s). Initial values of ARV was greater ($p < 0.05$) in VM (42.2 ± 8.1) compared with VL (38.0 ± 6.5 μ V). The ARV was greater ($p < 0.05$) during CON (59.5 ± 12.0 μ V) than ECC (27.7 ± 3.7 μ V) actions, but the negative slope of ARV (-0.070 ± 0.03 μ V) was not different between actions.

During any of the tests did the EMG parameters vary from day to day, inferring good reproducibility.

4.2 STUDY II

4.2.1.1.1 Peak and mean force

There was a difference between exercises in peak force ($p < 0.05$), with greater CON ($p < 0.025$) and ECC ($p < 0.025$) peak force during FS compared with BS. There was an interaction across exercise mode and action for mean force ($p < 0.05$), with a trend to greater CON mean force for FS compared with BS ($p = 0.080$). There were no differences between FS and BS with respect to ECC mean force ($p > 0.025$). As expected, there were no differences between CON and ECC actions with regard to either peak or mean force ($p > 0.025$) during the isotonic BS. There was no difference in CON and ECC peak force during FS ($p > 0.025$). However, mean force was greater in the CON compared with the ECC action ($p < 0.025$).

4.2.1.1.2 Functional Magnetic Resonance Imaging

T2 increased in all individual quadriceps muscles after both exercises ($p < 0.025$). Mean T2 across the four quadriceps muscles also showed an increase after both exercises ($p < 0.025$). There was an interaction over time and mode for quadriceps ($p < 0.05$), where T2 increased more with FS (Pre: 28.2 ± 0.4 , Post: 34.3 ± 2.1) than with BS (Pre: 28.6 ± 0.3 , Post: 31.9 ± 2.0 , Fig. 2). Among individual muscles, T2 of RF increased more ($p < 0.025$) with FS than with BS, and a trend ($p = 0.083$) to greater increase with FS was found for VM. Further, the relative T2 increase in RF tended to be greater compared with vastii in FS ($p = 0.037$). Such difference was not shown with BS ($p > 0.05$).

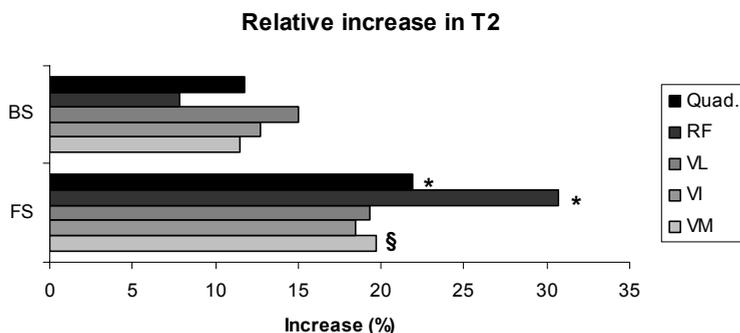


Figure 2. Relative T2 change in individual quadriceps muscles (mm. rectus femoris (RF), vastus lateralis (VL), intermedius (VI) and medialis (VM)) with flywheel (FS) or barbell squat (BS). * denotes greater T2 increase in FS compared with BS ($p < 0.05$). § denotes trend to greater T2 increase ($p < 0.10$).

4.2.1.1.3 Electromyography

There was an interaction over action and muscle ($p < 0.05$), and a trend for interaction over exercise mode, action and muscle ($p = 0.061$). The overall normalized EMG RMS of quadriceps (VM, VL and RF) was greater with FS compared with BS ($p < 0.05$), and greater during the CON compared with the ECC action ($p < 0.05$). When planned comparisons were made for quadriceps, a trend to greater CON ($p = 0.035$) and ECC ($p = 0.087$) normalized EMG RMS was seen during FS compared with BS. Further, greater normalized EMG RMS was seen in the CON compared with the ECC action with BS ($p < 0.025$), while a trend to greater normalized EMG RMS in the CON action was seen with FS ($p = 0.041$). Further, there was a trend to greater normalized EMG

RMS with FS compared with BS in RF (CON; $p=0.066$, ECC; $p=0.037$) and VM (CON; $p=0.056$, Fig. 3). No difference between normalized EMG RMS of RF compared with the vastii muscles where present in either exercise ($p>0.05$).

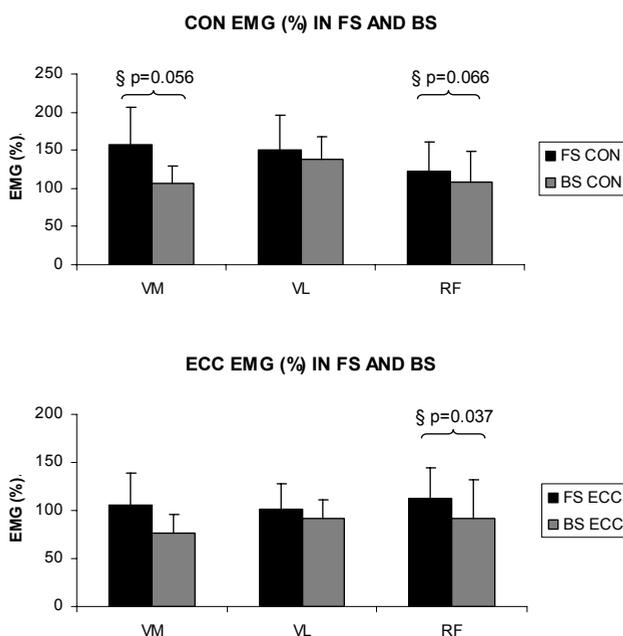


Figure 3. Normalized electromyographic activity (EMG) in individual quadriceps muscles (mm. vastus medialis (VM), vastus lateralis (VL), and rectus femoris (RF)) in the concentric (CON; upper) and eccentric (ECC; lower) actions during flywheel squat (FS) and barbell squat (BS), respectively. § denotes trend to greater normalized EMG activity in FS compared with BS.

4.3 STUDY III

4.3.1.1.1 Muscle volume

There was no interaction ($p>0.05$) over time and across groups for volume of quadriceps or any individual muscle (Fig. 4). There was a trend to interaction over time and group for VL volume ($p=0.054$).

In FW, there was an interaction across limbs and time for total quadriceps muscle volume, where the left quadriceps showed a 6.2 % increase (Pre: 1300 ± 210 cm³, Post: 1380 ± 235 cm³; $p<0.025$), while the right quadriceps showed no change (Pre: 1276 ± 204 cm³, Post: 1263 ± 205 cm³; $p>0.025$). 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. The right limb showed no change over time ($p>0.025$). In WS, there was an interaction across limbs and time for total quadriceps muscle volume, where the left quadriceps increased by 3.0 % (Pre: 1430 ± 364 cm³, Post: 1472 ± 381 cm³; $p<0.025$), while the right quadriceps was unchanged (Pre: 1373 ± 309 cm³, Post: 1361 ± 300 cm³; $p>0.025$). There was an interaction across limbs and time for VL, VI and RF but not VM. Only the left RF showed increased volume (Pre: 137 ± 43 cm³, Post: 146 ± 47 cm³; $p<0.025$). Neither muscle of the right limb showed altered volume ($p>0.025$).

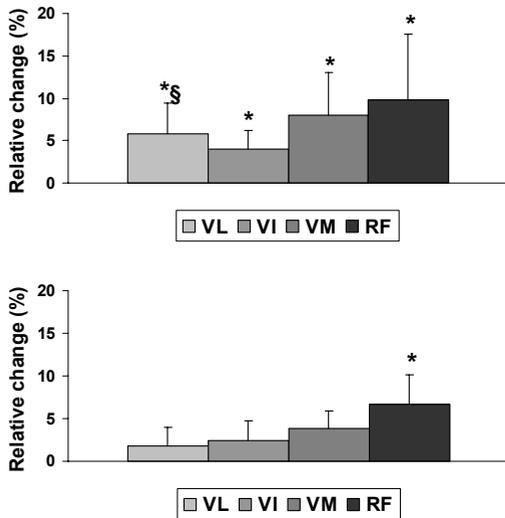


Figure 4. Relative change of muscle volume in individual quadriceps muscles (VL, m. vastus lateralis, VI, m. vastus intermedius, VM, m. vastus medialis, RF, m. rectus femoris) of the left limb following training in FW (upper graph) and WS (lower graph). * denotes significant increase from pre to post ($p < 0.025$), § denotes trend to different response for VL in WS compared with FW ($p < 0.10$).

4.3.1.1.2 Dynamic strength

Because WS and FW training load were measured and calculated using different methods, no direct group comparisons were performed.

The 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 in FW. CON and ECC peak force was unchanged ($p > 0.05$). From pre to post training, ECC mean force (Pre: 401 ± 83 N, Post: 425 ± 120 N) and CON mean force (Pre: 390 ± 73 , Post: 407 ± 83 N) showed no significant increase ($p > 0.05$). Similarly, CON (Pre: 322 ± 67 N, Post: 338 ± 42 N) and ECC (Pre: 302 ± 60 N, Post: 320 ± 44 N) mean force averaged across the four training sets was unchanged ($+5.0\%$ and $+6.0\%$; $p > 0.05$) over the 12 sessions (Fig. 5). Neither were the work/set ($+8.7\%$), or CON ($+8.9\%$) and ECC ($+12.0\%$) peak power significantly ($p > 0.05$) increased following training. In WS, the training load (Fig. 5) increased 48% over the 12 sessions (Training 1: 14.5 ± 3.1 kg, Training 12: 21.4 ± 3.2 kg; $p < 0.05$). Similarly, work/set and CON and ECC peak power increased by 40 - 126% ($p < 0.05$).

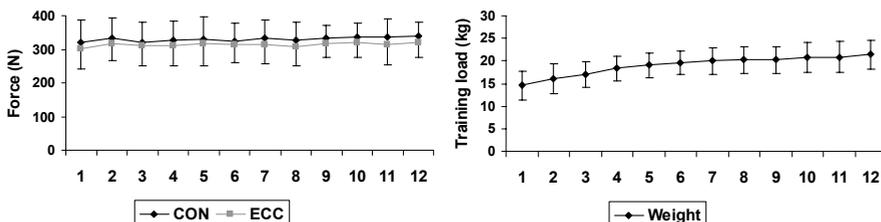


Figure 5. Training load used during the 12 resistance exercise sessions in FW; average concentric (CON) and eccentric (ECC) force (N) in a 30° window (left), and WS; weight (kg) lifted and lowered (right).

4.3.1.1.3 Maximal isometric strength

There was an interaction ($p < 0.05$) over time and group with regard to MVC at 90° , such that FW, but not WS, had an increase (Fig. 6). There was no interaction over time and group with regard to MVC at 120° .

In FW, 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; $p < 0.025$), while the right limb showed no change (Pre: 533 ± 141 N, Post: 560 ± 148 N; $p > 0.025$). Furthermore, 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), but there was a trend to an increase over time ($p < 0.10$). In WS, there was no interaction across limbs and time with regard to MVC at 90° (Pre left: 502 ± 87 N, Post left: 482 ± 63 N, Pre right: 488 ± 51 N, Post right: 489 ± 92 N). 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).

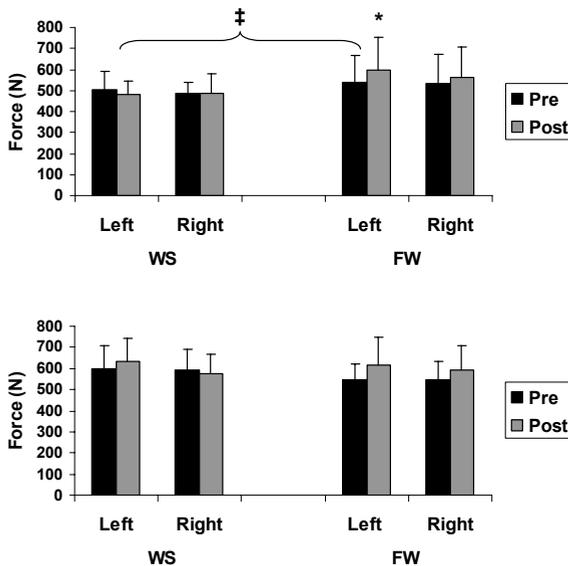


Figure 6. Maximal isometric force (MVC) at 90° (upper graph) and 120° (lower graph) knee angle of left (trained) and right (untrained) limb pre and post training in WS and FW. * denotes increase from pre to post ($p < 0.025$); ‡ denotes different response for left limb across groups ($p < 0.05$).

5 DISCUSSION

The overall aim of this thesis was to assess acute fatigue response during isoinertial loading, and to compare effects of resistance exercise performed with either isotonic or isoinertial loading with regard to acute muscle use and training response. The acute fatigue response during dynamic actions showed that force declined during both actions, but to a somewhat greater extent during the CON than ECC actions. Furthermore, there was a decrease of both CV and iMNF, yet the normalized rate of change over time of CV and iMNF differed. The isoinertial FW resistance exercise showed greater muscle use, as assessed by means of surface EMG activity and exercise-induced changes in T2, compared with the isotonic free weight exercise. This difference in muscle use could most likely be attributed to the greater force elicited with FW compared with free weight exercise. In healthy men assigned to a 5 wk training paradigm comprising unilateral knee extensions using either a flywheel device or a weight stack machine, flywheel training resulted in more robust muscular adaptations, i.e. increased volume of all four individual quadriceps muscles and increased maximal isometric strength, compared with weight stack training.

5.1 LOADING

Isotonic loading, offering constant external load throughout a set of repetitions, will not call for maximal activation during most CON or ECC actions. Thus, although there is progressive exertion, only the very last successful repetition of a set could be regarded as maximal. Further, given that the ability to produce force is greater in the ECC compared with the CON action, and the weakest position within the CON ROM is joint-angle specific, would imply that all ECC actions and most of the CON actions are executed with a load that does not require complete MU involvement. In the squat exercise, this “sticking-point”, occurs early in the CON action, as reflected in high EMG amplitude shown here (Study II) and elsewhere (35, 100). In the knee extension, this position is evident close to full extension of the knee (35). Weight stack devices, used in the current study (Study III) and by others (9, 83), have been designed such that a cam with a variable radius aim at compensating for this “sticking-point”, which is due to the inherent muscle length-tension relationship and more importantly, variations in the lever during movement about the joint.

In contrast, isoinertial loading allows for accommodated and maximal muscle use throughout the entire ROM of the CON action. In the subsequent ECC action, the imparted energy and the resulting action is gently resisted in the early part of ROM and prior to applying maximal force to bring the flywheel(s) to a full stop. Thus, the spinning flywheel(s) is decelerated during a part of the ECC action, and consequently inducing brief episodes of ECC overload. Furthermore, loading is maximal from the very first repetition, and given maximal effort, the force declines during each set as a result of fatigue. The FW loading thus provide unrestrained resistance, and any increase in force production will induce more energy in the spinning flywheel(s), and result in greater spinning velocity and angular velocity of the movement. In the knee extension configuration (Study III) this strategy was evident with greater ECC than CON peak force. However, in Study II there was no difference between CON and ECC peak force. It may be easier to achieve the desired ECC overload in the controlled single-joint knee extension exercise compared with the multi-joint squat exercise. In fact, the peak CON force during FS (Study II) occurred close to fully extended position, and peak ECC

force during FS was, as always with FW loading, produced close to the fully flexed position, which is more unfavorable for force production in the multi-joint squat exercise. Collectively these factors may explain the similar peak CON and ECC peak forces during FS.

The unrestrained force produced throughout the CON actions imparted kinetic energy to the spinning flywheel(s), which was decelerated during only a part of the subsequent ECC action. In this way, high peak and mean forces were produced during FW resistance exercise, resulting in marked fatigue (Study I), most likely due to greater muscle use in FS compared with BS (Study II), and further resulting in robust muscular adaptations in FW compared with WS (Study III), as discussed below.

5.2 HYPERTROPHY

Greater protein synthesis, cellular signaling for protein synthesis, disruption, Z-line streaming and ultrastructural changes have been reported following ECC compared with CON actions (23, 31, 41, 43, 79). These ultrastructural changes after ECC exercise have been suggested to stimulate skeletal muscle remodeling and hence being an important part of the hypertrophy process (118). Since mechanical loading and the ECC action appears to be crucial for hypertrophy (46, 53, 55), the approach of optimizing the hypertrophy stimuli by applying ECC overload seems logical. The hypertrophic rate of about 1.2 % per week shown in FW has rarely been reported (73), while the hypertrophy in WS (Study III) of about 0.6 % per week is in concordance with earlier studies (64, 84, 87), suggesting that ECC overload is indeed necessary to optimize the hypertrophy response.

Few studies that have assessed the possible enhancement of training response with ECC overload compared with constant CON-ECC resistance, show similar (44) or greater (20, 50) increases in strength after weight training, but no (20) or similar (44) rate of hypertrophy. The discrepancy between the results of these past studies and the current findings are not readily explained, but it may be the pre-training status of subjects chosen (20), or speed of action (44) and the resulting peak forces (38, 60) during training, that could have impacted the outcome.

The open-kinetic knee extension exercise involve all quadriceps muscles, with heavy emphasis on the RF (5, 32, 112). This fits with the prominent hypertrophy in RF over that of vastii muscles in earlier studies (83), and following 5 weeks of WS or FW training (Study III). While hypertrophy of individual muscles was present in RF only after WS, volume of all quadriceps muscles increased after FW. The robust 6.2 % hypertrophy shown after FW knee extension training was recently confirmed by the ~7 % increase shown after 5 weeks training using a identical FW knee extension device (97). These authors reported a significant ~4 % increase in cross-sectional area after 20 days (97). Collectively these results suggest that the high peak forces developed, especially during deceleration of the flywheel(s) in the ECC action, is responsible for the more significant hypertrophy after isoinertial compared with isotonic training (64, 84, 87).

5.3 MUSCLE INVOLVEMENT AND MOTOR UNIT RECRUITMENT

The fact that the knee extension appears to use RF more than any other knee extensor muscle, and that RF shows the greatest hypertrophy after training, would infer that training adaptation correlates with muscle use. Thus, to evaluate if isoinertial resistance exercise induced greater muscle use than isotonic resistance exercise, the squat exercise was compared between loading principles (Study II). The greater over all muscle use during FS compared with BS seemed to be result of the greater peak forces achieved during FS compared with BS. The higher over all normalized EMG amplitude during FS, also suggests greater MU involvement (34, 94) during FS compared with BS. The greater normalized EMG amplitude during CON actions, and given that T2 mainly increases with intensity of the CON action (4, 98), may further suggest more significant MU involvement (13, 29) and metabolic change (77, 85, 89, 110, 112), mainly resulting from the maximal CON actions during FS compared with BS.

It is generally held that the low threshold MUs are recruited before the larger/faster high threshold MU, containing Type II fibers, when increasing force (54). However, the typically reported lower EMG amplitude during ECC compared with CON actions (Study I and II) and earlier studies (69, 81, 105), suggest a different recruitment pattern (33, 47, 62, 76, 82, 105, 111), or control strategy of the CNS (33, 47) during ECC compared with CON actions. In fact, selective recruitment of high threshold MU during ECC actions has been proposed (33, 72, 76, 82). Since, ECC actions induce greater hypertrophy compared with the CON actions (116, 117), and the acute ultrastructural damage (41) and hypertrophy following training including ECC actions (53) are most prominent in Type II fibers, the suggestion of selective recruitment of high threshold MU (Type II fibers) in the ECC action is attractive (33, 72, 76, 82). The current study (Study II) did not reveal the mechanism, but the brief episodes of high ECC peak force during FW training may have increased high threshold MUs/Type II fiber recruitment, potentially affecting the rate of hypertrophy.

5.4 NEUROMUSCULAR FATIGUE

Since MU recruitment is thought to be important also above 50 % of maximal force in quadriceps (18, 26, 115), the increased ARV (Study I) during both the ramp action and the sustained submaximal isometric action suggests that, probably both MU recruitment and discharge rate increased (34, 94) in order to increase or maintain force, respectively. Furthermore, in accordance with several earlier reports, the fatigue response of VL and VM during sustained submaximal isometric action was reflected by a decreased iMNF/power spectrum (11, 24, 37, 102, 115), and decreased CV (11, 37, 88), respectively. There was no difference between the normalized rate of change between iMNF and CV, which concurs with earlier reports (10, 11), and may further indicate that decreased iMNF was probably due to the decline in CV (11, 37).

During the 30 coupled CON-ECC actions, the CON actions showed a somewhat greater decline in force and greater increase in ARV/force relationship compared with the ECC actions, confirming an earlier report on fatigue response during maximal isokinetic CON and ECC actions (105). The greater ARV during the CON compared with the ECC actions, indicated greater MU involvement and thus metabolic cost of the CON actions (also EMG RMS in Paper III, Fig 4). Thus, preferentially the CON actions resulted an accumulation of metabolites (3, 13, 19, 29, 68), e.g. inorganic

phosphate, which appears to reduce the ability to produce force (113). Consequently, the comprised CON force production imparted less kinetic energy into the flywheel, and thus less ECC force was produced to bring the flywheel to a full stop during deceleration. Therefore, we can not elucidate if the ability to produce ECC force was impaired or unaffected (105). It should be noted, that while the force and ARV may have been maximal throughout the CON action, the greatest EMG amplitude and peak force during the ECC action took place closer to the ECC-CON transition angle (also shown in Fig. 4 in Paper III), which suggests that the loading was maximal at 120° knee angle during the CON, but not the ECC, action. Given this and the higher CV during the CON than ECC actions, results suggest that the fast/large MUs may have been recruited to a greater extent at 120° knee angle during the CON than ECC actions, contrasting the proposed selective recruitment of fast/large MUs during the ECC actions.

Yet, the fast/large MUs were potentially recruited from the very first repetition during the maximal CON and ECC actions, and gradually de-recruited due to fatigue, which could partly explain the similar decrease of CV during the CON and ECC actions. De-recruitment may also explain the decreased ARV throughout the exercise bout. Moreover, the discrepancy between normalized rate of decrease of iMNF and CV, would suggest that not only changed membrane properties affected the estimations of CV and iMNF. Since MU de-recruitment is thought to affect the CV while EMG spectral parameters has been reported unchanged (22), this is most likely the mechanism explaining the decreased ARV, and the divergence between negative slope of CV and iMNF. A difference in the negative slope of CV and spectral EMG parameters has been reported during brief isometric actions interrupting the dynamic exercise (75). The current findings suggest this fatigue response prevails during coupled CON-ECC actions as well, and imply that iMNF can not indirectly estimate changes in CV during dynamic actions.

The fatigue response during maximal coupled CON-ECC actions was probably provoked mainly by the CON actions. Results further showed a discrepancy between normalized rate of decrease of iMNF and CV. This might imply that iMNF will not accurately reflect changes in CV during dynamic or variable force tasks.

5.5 NEURAL ADAPTATIONS AND INCREASED STRENGTH

The fatigue response demonstrated during dynamic actions (Study I), and the greater muscle use during FS than BS (Study II), indicate a high demand on the neural drive induced by the maximal CON actions and brief episodes of high ECC force. Furthermore, since it is generally held that the neural changes are greater compared with the hypertrophy during early adaptations to resistance exercise, and that training specific strength typically increases much more than non-specific strength (55, 64, 95), one would expect that training specific strength increases more than the muscle size (FW: 6.2 %, WS: 3.0 %, Study III). This was true for WS, but not for FW (Study III). There training load increased by almost 50 % in WS, indicating substantial neural adaptations, yet MVC showed no significant increase. In contrast, the FW training resulted in increased MVC, but only non-significant increases in specific dynamic strength (8-12 %).

Although similar strength increase has been reported (44), a majority of the studies evaluating ECC overload training, suggests greater strength increases compared with constant load during CON action only (25, 67), or coupled CON-ECC actions (20, 50). Further, greater training-specific (20, 50, 67) or isometric strength (67) increase were reported in the ECC overload group compared with the constant load group. The ECC overload training was therefore expected to increase strength more compared with constant load training.

The unchanged dynamic strength in the FW group may rather be explained by the fact that the isoinertial resistance was kept constant throughout the training period. Further, since the FW force production is unrestrained, the onset of breaking is not controlled for, and thus it might be difficult to measure training specific strength in a standardized way during FW training. In addition, the substantial neural adaptations in WS, would also have been expected to induce a concomitant increase the MVC (49, 64). Hence, the results of the two groups illustrate the difficulties to choose a valid test for strength measurements. We chose to test the training specific strength, but since short term ECC overload training has been reported to induce greater increase in ECC strength and similar increase in CON strength compared with constant load training (58), results may have been different if specific strength had been measured during CON and ECC actions separately.

Though, there is a correlation between MVC and muscle CSA, and the increased MVC to a large extent could be attributed to the increased CSA, clearly increased recruitment may increase MVC as well (34, 73, 84, 93, 109). The peak loading and EMG amplitude during FW training was greatest in the low knee angle of the CON and ECC action, while peak loading during WS training occurred closer to full extension, which probably contributed to the increased MVC in FW, but not in WS. In accordance with the results of the current study, Seyenne et al. (97) recently reported a substantial increase in MVC (+38 %) after 5 weeks of FW knee extension training, suggesting that maximal or near maximal CON-ECC training promotes important muscular adaptations.

5.6 SUMMARY

The fatigue response during the maximal coupled CON-ECC actions performed in the FW device was probably mainly induced by the CON actions. Since there was a discrepancy between normalized rate of decrease of iMNF and CV, this might imply that iMNF will not accurately reflect changes in CV during dynamic or variable force tasks. Moreover, isoinertial resistance exercise resulted in more prominent hypertrophy of individual quadriceps muscles and greater improvement of non-specific strength compared with isotonic loading, which may, at least in part, be explained by the greater muscle use produced with isoinertial than isotonic resistance exercise.

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