NEUROMUSCULAR ADAPTATIONS TO SINGLE-SESSION COMBINED STRENGTH AND ENDURANCE TRAINING IN UNTRAINED MEN: AN EXAMINATION OF THE "ORDER EFFECT"

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ABSTRACT

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Understanding the adaptations to single-session combined strength (S) and endurance (E) training has received increased attention in scientific literature through the expanding use of combined training programs for practical purposes. However, the intra-session exercise order when performing both E and S in the same training session may limit potential strength development, as the neuromuscular adaptations to either training mode alone are very different. Research on the effect of the intra-session exercise order of combined training on various training-induced adaptations, i.e. the order effect, is currently limited, especially with regard to the neuromuscular adaptations. Therefore, the purpose of this study was to investigate the order effect to single-session combined strength and endurance training on the long-term neuromuscular adaptations.

Thirty-two young adult male subjects (29 ± 4 years) completed a 24-week progressive single-session combined strength and endurance-training program. The subjects were split into two groups performing opposite intra-session exercise orders, endurance before strength (E+S; n = 14) or strength before endurance (S+E; n= 18) by pairwise matching of basal maximum strength results. All subjects were tested on three separate occasions (*0*, *12* and *24 weeks*). A group of subjects (n = 8) participated in a two-week control period performed before week 0 (*-2* to *0 weeks*) to ensure reproducibility and stability of important dependent variables. Maximal voluntary activation (VA), surface electromyography (sEMG), one-repetition maximum concentric strength (1-RM), maximal voluntary isometric force (MVC) and rapid force production (AV_{500}) of the leg extensors and flexors were evaluated.

No changes occurred in strength during the two-week control period, while after the 24-week training period significant increases in 1-RM load of 13% ($p<0.001$) and 17% ($p<0.001$), knee extension MVC of 7% ($p<0.05$) and 14% ($p<0.01$) and leg press MVC of 15% ($p<0.01$) and 13% ($p<0.01$) were observed for E+S and S+E, respectively. There were no significant between group differences in strength gains. After 24 weeks a significant increase took place in VA of quadriceps femoris of 4% ($p<0.01$) in S+E only whereas no significant changes occurred in E+S. There were differences between groups in changes in maximum sEMG activity of the vastus lateralis after 24 weeks as large increases took place in S+E whereas non-significant changes occurred in E+S.

The present data provide some evidence of an order effect on training induced adaptations to combined strength and endurance training. Maximum voluntary activation of trained leg muscles appeared to be interfered after training E+S when compared to S+E. Additionally, strength development appeared to be affected by training order as larger strength gains were continually observed for S+E when compared to E+S, however, strength gains were not statistically significant. These findings highlight the importance of combined training order as the level or neural activation governs muscular strength.

Keywords: order effect, combined training, interference effect, neural activation, strength, super-imposed twitch technique

LIST OF ABBREVIATIONS

1-RM – One repetition maximum

AV_{500} – Average isometric leg press force during first 500 ms of contraction

α-MN – Alpha motoneuron

BF – Biceps femoris

E – Endurance training

E+S – Combined training, endurance before strength

M_{max} – Maximum compound muscle-action potential

MU – Motor unit

MVC – Maximal voluntary contraction

N – Newtons

QF – Quadriceps femoris

RFD – rate of force development

S – Strength training

sEMG – Surface electromyography

SIT – Super-imposed twitch method

S+E – Combined training, strength before endurance

VA – Voluntary activation

VL – Vastus lateralis

VO_2max – Maximal oxygen consumption

CONTENTS

1 INTRODUCTION

Training for either strength or endurance results in better abilities to perform both everyday tasks and sport performance. However, endurance and strength training result in distinct acute responses and chronic adaptations. These select adaptations have been shown to be specific to the type of training, i.e. *specificity of training*, which is a general principle of all training programs. (DeLorme 1945; Coyle et al. 1981; Rutherford & Jones 1986.) Therefore, the performance of either endurance or strength training results in specific responses to both the cardio-respiratory (Holloszy & Coyle 1984; Howald et al. 1985; Ahtiainen et al. 2003) and neuromuscular systems (Moritani & deVries 1979; Pérot et al. 1991).

The combining of endurance and strength training into single programs, either single or separate-day sessions, is gaining popularity in both scientific literature (Hickson 1980; McCarthy et al. 1995; Häkkinen et al. 2003) and practical usage (Haskell et al. 2007; Garber et al. 2011). However, combined training may be problematic for performance gains (e.g. Hickson 1980). Leveritt et al. (1999a) proposed that in order to successfully employ a combined training program, the acute responses and chronic adaptations to the two different types of training must be organized so as to not negatively affect one another, but rather increase performance. Thus, the dissimilarities of adaptations between the two training modalities have lead researchers into investigating how to successfully combine strength and endurance training into a single program (Wilson et al 2012). This is especially true with respect to the influence of the intra-session exercise sequence of single-sessions of combined strength and endurance training (i.e. *order effect*).

Neural adaptation alone to either strength or endurance training is highly complex and particular, resulting in distinct changes at the supraspinal and spinal levels (Gandevia 1999). To date, there is very little research examining, what has been termed, the *order effect* of combined strength and endurance training (e.g. Sale et al. 1990b), especially with respect to neural adaptation (e.g. Cadore et al. 2012). Therefore, the purpose of this thesis is to examine the neural adaptations to moderate volume single-session combined strength and endurance training, with regard to the order effect.

2 VOLUNTARY FORCE PRODUCTION

Voluntary force production is the result of a complex but coordinated interaction between the nervous and musculoskeletal systems. This interaction involves the process of initiation, transmission and translation of neural signals to activate muscles causing mechanical contractile responses resulting in force production. (Zajac 1989.) Furthermore, because of the relationship voluntary force production is largely dependent on the level of neural input, or neural activation, of muscle.

2.1 Development of force production

Voluntary force production is the product of interconnected anatomical systems organized in a hierarchical, descending fashion beginning within the brain and ending with a muscle action (figure 1). Descending motor commands are initiated, defined, planned and delivered from a specialized region of the brain known as the cerebral cortex (e.g. supraspinal or central command). During the defining and planning stages of commands, the motor cortex receives input from the basal ganglia, cerebellum and thalamus regarding the integration and coordination of muscle activation of the intended action. The motor cortex delivers motor commands either directly to the spinal cord (e.g. spinal or lower command), or to the brain stem, where motor commands can be further modulated. (Ghez & Krakauer 2000, 664-667.) Commands are then transmitted along the spinal cord activating the corresponding bundle of alpha-motoneurons (α-MN), i.e the *motoneuron pool*, of the target muscle. (Loeb & Ghez 2000, 677; Squire et al. 2008, 673.) Once activated, a single α-MN propagates electrical impulses (action potentials) along its axon to the variable number of muscle fibers it innervates. This functional entity of a single α-MN and the muscle fibers it innervates is known as a *motor unit* (MU; Sale 1987). Action potentials are translated at the neuromuscular junction between the α-MN and muscle fiber to a physiological response at the muscle membrane where a mechanical response is triggered through the excitation-contraction coupling mechanism (Sandow 1952).

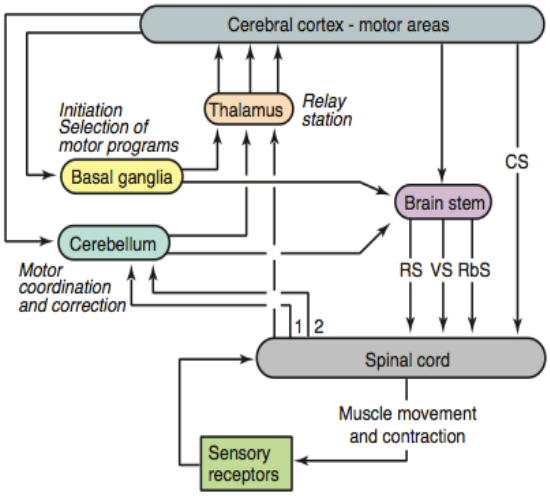

FIGURE 1. Human motor control scheme (Squire et al. 2008, 673).

2.2 Structural properties of the neuromuscular system

The level of neural activation of a muscle is positively related to its potential force output capability (Bigland & Lippold 1954). The properties of central and peripheral structures of the neuromuscular system potentially dictate the level of neural activation of muscle (Adkins et al. 2006; Duchateau et al. 2006; Vila-Chã et al. 2010).

2.2.1 Central control properties

The motor control scheme illustrates how the brain, and more specifically the motor cortex is responsible for initiating, planning, and commanding muscle actions (i.e. force production) while receiving input from other regions of the brain regarding specifics of the planned movement (Georgopoulos et al. 1992; Squire et al. 2008, 673). The cerebral cortex is split into interconnected left and right hemispheres each controlling the contralateral side of the body (e.g. left hemisphere controls right-side limbs). The motor cortex is organized in a somatotopic fashion meaning body parts are represented on the cortex by a specific region (figure 2). (Squire et al. 2008, 670.) There is evidence that supraspinal mechanisms undergo functional and structural changes to the learning and acquisition of fine and complex motor skills (Karni et al. 1995; Pascual-Leone et al. 1995), as well as to strength- and endurance training (Muellbacher et al. 2001; Adkins et al. 2006). However, the plasticity of the supraspinal mechanisms may depend on the

difficulty and intensity of the imposed motor task (Pearce & Kidgell 2009; Smyth et al. 2010). Therefore, changes to supraspinal mechanisms may result in enhanced supraspinal input to muscle that increases force production of intended tasks through more efficient strategies of MU activation (Griffin & Cafarelli 2005) and / or increased endurance for prolonged motor output (Muellbacher et al. 2001).

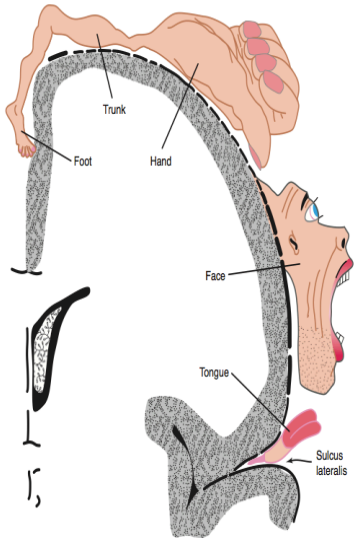

FIGURE 2. Somatatopic organization of body parts on the motor cortex (Squire et al. 2008, 671).

2.2.2 Peripheral control properties

Sale (1987) defined a MU as a single α-MN and the muscle fibers it innervates. Force production is ultimately regulated by the recruitment and firing rates of various MUs. The *common drive concept* states that the same net supraspinal command activates the entire MU pool of a muscle, but, individual MUs respond individually based on their properties (De Luca & Erim 1994). The properties of the α-MN and the muscle fibers it innervates determine how the MUs respond to the imposed motor command.

MUs can be classified into two categories Type I (slow) and Type II (fast). Classification of MU is based on the make-up and properties of the corresponding α-MN its muscle fibers (figure 3). Type I, or slow, MUs consist of small, highly excitable α-MNs with low firing frequencies; slow action potential conduction velocities; muscle fibers that are weak in twitch strength and highly resistant to fatigue making these units ex-

tremely beneficial for endurance exercise (e.g. long-distance running or cycling). Type II, or fast, MUs can be split into two subtypes, Type IIa or Type IIb. Type IIb, or fast-fatigable, MUs consist of large, less-excitable α-MNs with high firing frequencies; fast conduction velocities; muscle fibers that exhibit very strong twitch strength but have little-to-no fatigue resistance. However, Type IIa, or fast fatigue-resistant, MUs are considered intermediate, sharing traits from both Type I and IIb units. Type IIa MUs consist of large α-MNs that are also less excitable and have high firing frequencies; fast conduction velocities; the corresponding muscle fibers, however, exhibit strong twitch forces but have a high capability of fatigue resistance. Type II MUs are very functional for anaerobic activities such as weightlifting and sprinting. (Henneman et al. 1957; Burke et al. 1973; Garnett et al. 1979.)

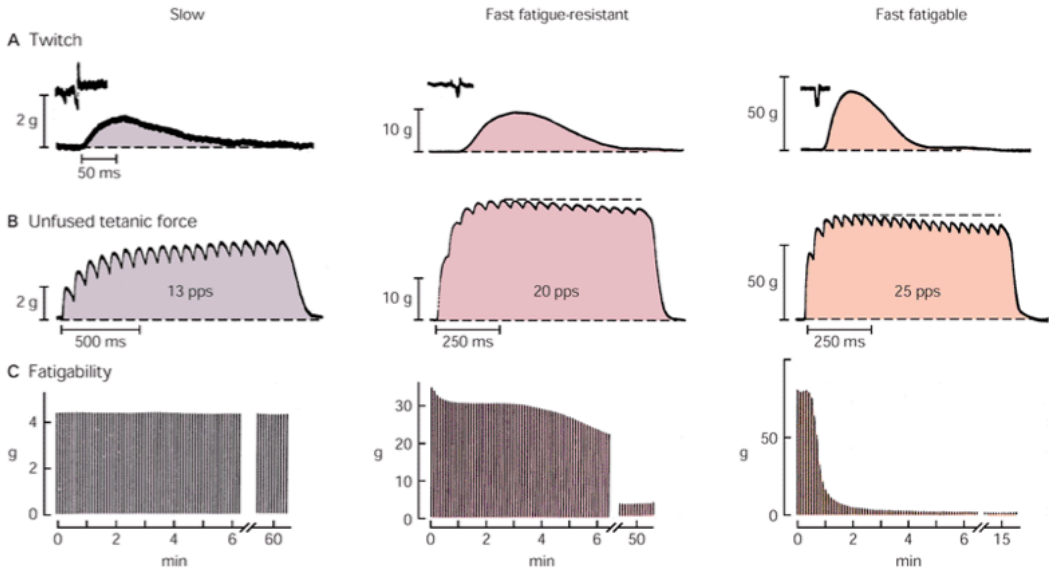

FIGURE 3. Characteristics of Type I (slow), IIa (fast-fatigue resistant) and IIb (fast-fatigable) MUs. **(A)** muscle twitch force and contraction time responses of the three MUs. **(B)** Unfused tetanic contractions of the three MUs. **(C)** Fatigability of each type of MU during sustained contractions. (Burke et al. 1973.)

As force production increases the number of recruited MUs increases as well. Recruitment of MUs has been observed to occur in an orderly fashion based on the MUs corresponding α-MN size (figure 4). This orderly recruitment of smallest to largest MUs is known as *Henneman's Size Principle*. The first recruited MUs consist of small α-MN and are more excitable than the larger MUs. Type I MUs have low force-recruitment thresholds while Types IIa and IIb have high force recruitment thresholds. (Henneman

et al. 1957.) However, there is evidence of a reversal in the orderly recruitment of MUs during explosive contractions, so that Types IIa and IIb are recruited before Type I MUs (Grimby & Hannerz 1968). Although, the observation of reversed MU recruitment has been scrutinized and additional investigations have indicated that the orderly recruitment, first proposed by Henneman et al. (1957), remains intact during explosive contractions (Desmedt & Godaux 1977; Desmedt & Godaux 1979).

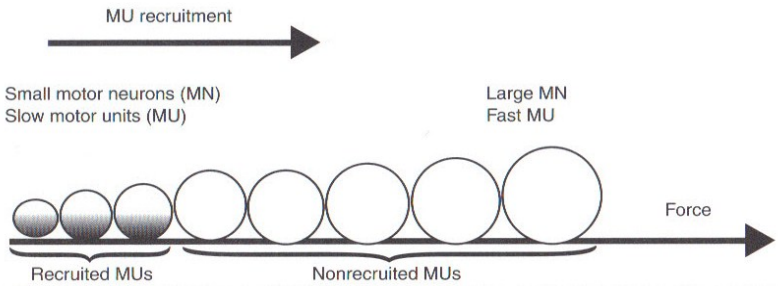

FIGURE 4. Schematic of Henneman's Size Principle during increasing force production (Zatsiorsky & Kraemer 2006, 62).

The firing rates of MUs increase as force output increases (figure 5). The three types of MUs each have different minimum and maximum firing rates. There is a positive relationship between the MU recruitment thresholds and maximal firing rates. Although, Type IIa and IIb MUs are recruited last during maximal muscle actions they display the highest firing rates. (Monster & Chan 1977; Sale 1987.)

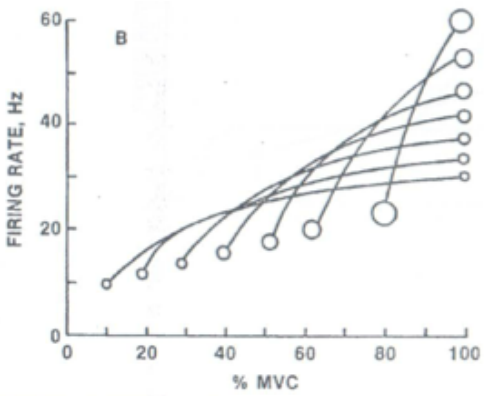

FIGURE 5. Relationship of MU recruitment threshold and firing rates up to MVC (Sale 1987).

MUs are highly adaptable structures. Numerous suggestions have indicated that any type of physical activity modifies the make-up MUs. Similar to the supraspinal changes, the difficulty and intensity of exercise determine the changes that MUs undergo. (e.g. Edström & Grimby 1986; Gardiner 1991; Duchateau et al. 2006.)

3 STRENGTH AND ENDURANCE TRAINING

The human neuromuscular system is highly adaptable and can be modified distinctly to imposed stimuli (Adkins et al. 2006). Thus, manipulation of specific training stimulus variables, such as the intensity and time of exposure, evoke multiple neural adaptations that contribute to enhance motor performance of desired tasks (Vila-Chã et al. 2010). Strength training has been described as the use of resistance exercises in an effort to enhance force production characteristics by employing maximal to near-maximal intensities of motor output for short durations. In contrast, endurance training can be defined as rhythmic extension and flexion exercise utilizing sub-maximal intensities of motor output aiming to increase capacity for prolonged performance. (Adkins et al. 2006; Knuttgen 2007.) Consequently, because these two types of training represent the extremes of physical activity, the training-induced neural and strength adaptations are be very different (Sale et al. 1990a; Vila-Chã et al. 2010).

3.1 Force production characteristics after strength or endurance training

The training differences between strength and endurance exercise have been shown to result in unique adaptations in force production characteristics. Investigations of muscle twitch properties have observed differences between endurance and strength-trained individuals. Researchers viewed that years of strength training (5-11 years) resulted in significantly greater electrically evoked maximal force and rate of force development (RFD) than endurance-trained athletes. (Pääsuke et al. 1999.) The observed dissimilarities of the twitch properties reveal the prospect of distinct voluntary maximal strength adaptations that occur to in response to strength or endurance training. Differences in maximal voluntary isometric contraction (MVC) force and RFD have been observed between short-term strength and endurance training (Vila-Chã et al. 2010; Vila-Chã et al. 2012). Additionally, long-term strength or endurance training studies have shown an extension of the differences in force production characteristics seen after short-term training (Viitasalo & Komi 1978; Häkkinen & Keskinen 1989).

Generally, strength training results in far greater MVC than endurance training (figure 6A; Viitasalo & Komi 1978; Kyröläinen & Komi 1994). Several comparative studies confirm these ideas in the training-dependent increase in strength (e.g. Maughan et al. 1983; Izquierdo et al. 2004). Maximal RFD is also affected differently between strength and endurance training. Mainly, the variables of strength training permit far more improvement in RFD capabilities than endurance training (figure 6B). (Häkkinen & Keskinen 1989.)

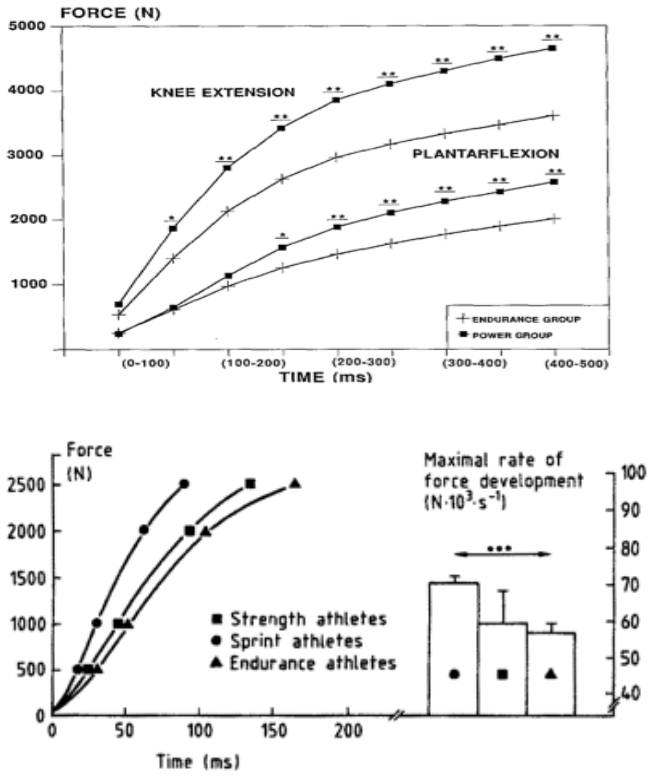

FIGURE 6. *Top*, MVC force curves of knee extensor and plantar flexion musles of endurance (+) and power (■) trained athletes (Kyröläinen & Komi 1994). *Bottom*, Maximal RFD to a force level of 2500N of strength (■), endurance (▲), and sprint athletes (●). (Häkkinen & Keskinen 1989.) *p<0.05, **p<0.01, ***p<0.001.

The different force production characteristics suggest distinct training-induced neuromuscular adaptations to strength or endurance training. It is suggested that the neural adaptations that occur to strength or endurance training play a large role in the development of force, both maximally and rapidly, especially during the beginning stages of a training program (Moritani & deVries 1979; Häkkinen & Komi 1983; Vila-Chã et al 2010).

3.2 Neural adaptations to strength training

Muscular strength is the result of an integrated communication between the nervous and musculoskeletal systems (Zajac 1989). Research has extensively clarified that maximal strength characteristics are closely related to morphological (hypertrophy; Ikai & Fukunaga 1970), architectural (pennation angle; Aagaard et al. 2001) and mechanical characteristics of muscle (tendon stiffness; Reeves et al. 2003). However, during the very initial stages of a strength-training program (< 2 months) there have been various observations of disproportionately large increases in strength prior to any physical changes in musculature (Moritani & deVries 1979; Narici et al. 1989). Therefore, considering the relationship of the nervous and musculoskeletal systems in strength development, several noteworthy investigations have interpreted these early, rapid strength gains, with no concomitant changes in muscle size or contractile characteristics, as an indication of neural adaptations in response to strength training (figure 7; Moritani & deVries 1979; Häkkinen & Komi 1983; Narici et al. 1989).

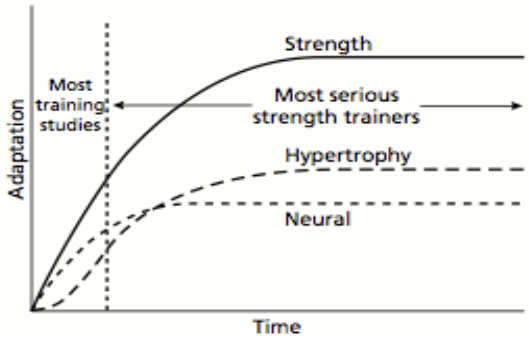

FIGURE 7. A schematic of the time-course of adaptations and strength gains to resistance training (Sale 2003).

3.2.1 Agonist activation

Several investigations examining maximal strength properties have observed that untrained individuals sub-maximally activate agonist muscles during maximal voluntary muscle actions through the observance of fluctuations in MVC in response to electrical stimulation and surface electromyography (sEMG) (Dudley et al. 1990; Strojnik 1995; Harridge et al. 1999; Knight & Kamen 2001). Strojnik (1995), as well as Knight and

Kamen (2001), observed significant activation deficits of the quadriceps femoris muscle group in untrained individuals while applying *super-imposed electrical twitches* (SIT; Merton 1954) onto maximal voluntary knee extensions (figure 8). The observances of small rises in force, with the application of SIT, suggest that muscle activation is typically sub-maximal in untrained individuals, despite there being maximal effort. Theoretically, sub-maximal activation portrays a deficiency in the central nervous system's ability to recruit MUs and / or evoke optimal firing rates of individual MUs (Kent-Braun & LeBlanc 1996; Gandevia 2001). Conversely, in an earlier study using identical methods, no activation deficit was observed in the adductor pollicis during thumb adduction movements (Merton 1954). However, the level of voluntary activation has been may be muscle specific, as different voluntary activation levels have been reported for the plantar flexors, dorsiflexors and elbow flexors (Behm et al. 2002). Nonetheless, muscle activation deficits in untrained individuals may be reduced via strength training, alluding to the potential of strength training-induced increases in neural input to trained muscle leading to strength gains (Jones & Rutherford 1987; Strojnik 1995).

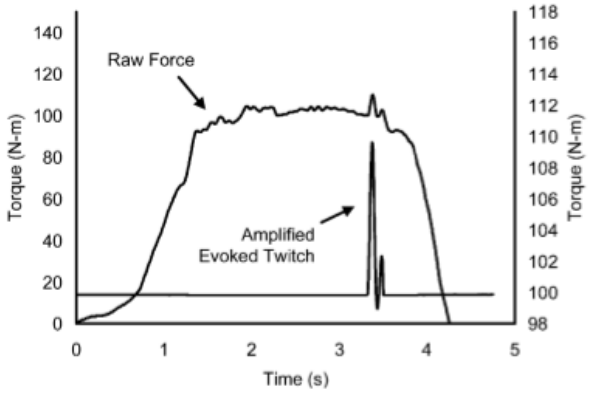

FIGURE 8. A measurement example of the SIT method, with the super-imposed twitch and resting twitch vertically aligned. The twitch in voluntary force from the SIT represents voluntary activation deficit through an inability of the central nervous system to fully recruit all available MUs or the sub-maximal firing rate of individual units. (Knight & Kamen 2001.)

Numerous studies have reported strength training-induced increases in sEMG activity of agonist muscle during the first weeks of training before physical changes in muscle, suggesting increases in agonist neural activation (Moritani & deVries 1979; Häkkinen & Komi 1983; Häkkinen et al. 1985c; Häkkinen & Komi 1986; Narici et al. 1989; Häkkinen et al. 1998a; Häkkinen et al. 1998b; Häkkinen et al. 2000; Häkkinen et al. 2001).

Increases in sEMG activity have been documented as early as 3-4 weeks after the start of strength training, occurring alongside increases in maximal strength in both previously untrained, healthy middle-aged and elderly individuals (figure 9; Häkkinen & Komi 1983; Häkkinen et al. 1998a; Häkkinen et al. 2003; Reeves et al. 2004; Tillin et al. 2011). However, similar results have not always been documented, as some researchers have observed increases in maximal strength whilst no alterations in sEMG activity occurred after training (Thorstensson et al. 1976; Carolan & Cafarelli 1992; Narici et al. 1996). Methodological and technical errors may partly explain the inconsistent reports of sEMG results, as changes in electrode placement or changes in tissue properties (e.g. adipose tissue or muscle fiber pennation angle) between testing sessions can influence sEMG recordings, posing difficulties in interpreting longitudinal adaptations in sEMG activity (De Luca 1997).

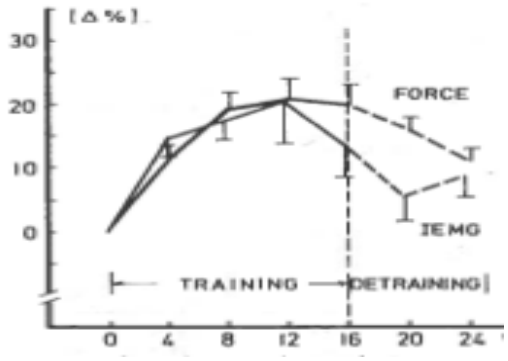

FIGURE 9. Relative changes in average bilateral isometric leg extension force and integrated EMG (IEMG) averaged from the rectus femoris, vastus lateralis and vastus medialis during 16-weeks of strength training and 8-weeks of detraining (Häkkinen & Komi 1983).

Futhermore, a means of reducing these confounding factors has been to normalize sEMG to a maximal compound muscle-action potential, i.e. *M-wave* (Gandevia 2001). An M-wave response is produced through supramaximal stimulation of a peripheral nerve resulting in the electrical equivalent of recruiting all MUs of the MN pool of a given muscle and, presumably, does not change in response to training (Palmieri et al. 2004; Calder et al. 2005). Recently, several strength-training studies have utilized this normalization procedure and have reported increases in the normalized sEMG activity concomitantly with strength gains after short training periods of 4-12 weeks (Van Cutsem et al. 1998; Cannon et al. 2007; Tillin et al. 2011). Alternatively, however, Pucci and colleagues (2006) observed simultaneous increases in both sEMG and M-wave after

three-weeks of isometric strength training resulting in the authors suggesting peripheral rather than central adaptations (i.e. muscle properties) inducing the concurrent strength increases. Nevertheless, if sEMG measurements are methodologically strict, the training-induced increases in non-normalized and normalized sEMG activity may represent increases in descending neural activation to trained agonist muscle (Tillin et al. 2011).

In addition to sEMG, the SIT method (Merton 1954) has been moderately used to assess changes in voluntary activation levels (i.e. descending neural drive) in agonist muscle after strength training. Initially, studies have indicated no changes in voluntary activation after short periods of strength training when measured by SIT (Jones & Rutherford 1987; Brown et al. 1990). However, the techniques used to assess voluntary activation in these early studies may have been too insensitive to detect changes. Since these early studies, however, there have been significant advancements in both the technology and methods of analyzing voluntary activation (Herbert & Gandevia 1999; Suter & Herzog 2001; Shield & Zhou 2004; Folland & Williams 2007b). Therefore, several studies from the past decade have noted small but significant 2 - 5% increases in voluntary activation concurrently with increases in maximal strength of the knee extensors and plantar flexors following short-term heavy-resistance training in previously untrained young and elderly individuals (figure 10; Knight & Kamen 2001; Scaglioni et al. 2002: Reeves et al. 2004). Additionally, other studies have reported non-significant increases of similar magnitudes for the knee extensors (Harridge et al. 1999; Tillin et al. 2011).

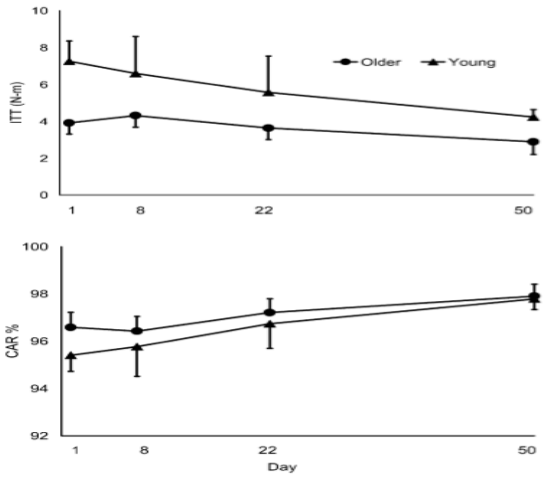

FIGURE 10. Changes in super-imposed twitch torque (ITT; *top)* and central activation ratio (CAR), i.e. voluntary activation (*bottom*) of older (●) and younger (▲) individuals during a control (1-8 days) and 50-days of strength training (day 50). (Knight & Kamen 2001.)

Through the careful application of sEMG and SIT, there is mounting support that an early adaptation to strength training is an increased descending neural drive enhancing the activation of trained muscle (Häkkinen & Komi 1983; Knight & Kamen 2001). Furthermore, these findings give credence to the suggestions made earlier in the seminal study by Moritani and deVries (1979), that in the absence of physical changes to musculoskeletal properties neural changes must account for the rapid increases in strength at the onset of strength training for untrained individuals. These neural adaptations may be central and / or peripheral in origin. Therefore, many researchers have proposed that increases in neural drive to agonist muscle, examined by SIT, signify alterations in mechanisms along the central neuraxis, i.e. spinal and supraspinal mechanisms (Adkins et al. 2006; Carroll et al. 2009). Moreover, changes to central nervous system mechanisms may optimize the activation strategies of the agonist, synergist and antagonist muscles enhancing muscle coordination during various muscle actions (Rutherford & Jones 1986; Folland & Williams 2007a). Enhanced muscle activation strategies and coordination during muscle actions may be caused by a facilitation of MU recruitment and / or their firing rates (Gabriel et al. 2006; Knight & Kamen 2008; Carroll et al. 2011).

3.2.2 Changes in agonist motor unit behavior

Motor unit recruitment. As was first indicated by Henneman et al. (1957), while force output and effort increases, so does the number of recruited MUs. There are suggestions, however, that with the occurrence of incomplete activation in untrained individuals during maximal muscle actions, full MU recruitment may be rarely achieved (Reeves et al. 2004). Therefore, since initial gains in strength are minimally influenced by changes in morphological properties of muscle (Moritani & deVries 1979; Narici et al. 1989), an increase in the number of recruited MUs has been suggested as a cause of the initial increases in strength (Akima et al. 1999; Patten et al. 2001; Sale 2003).

Akima and colleagues (1999) observed a greater portion of the vastus lateralis muscle was active during isokinetic and isometric knee extensions after two-weeks of isokinetic strength training. The researchers proposed that the increased area of vastus lateralis activation represented increase in the number of recruited MU. However, this hypothe-

sis implies that previously inactive MUs, most likely Type II units held in a "reserve" state, become activated following strength training during maximal muscle actions through improved descending neural drive. Presently, there is a lack of evidence establishing the existence of a collection of "reserve" units in large muscles like the quadriceps femoris during maximal muscle actions in untrained individuals, as current technology and methods are incapable of identifying any populations of inactive MUs during maximal muscle actions (Folland & Williams 2007a). Additionally, it seems unlikely that increased MU recruitment is a training-induced adaptation given that complete MU recruitment has been observed in various lower-limb muscles up to 90-95% of MVC in individuals with no prior strength training experience (Van Cutsem et al.1997; Oya et al. 2009). Considering these findings, it can be speculated that the occurrence of rapid strength increases during the early phases of training may not be primarily caused by increased recruitment but rather alterations in MU discharge properties (e.g. Strojnik 1995; Knight & Kamen 2008).

Motor unit firing rate. Several researchers have suggested that the mechanism responsible for the rapid gains in strength characteristics at the onset of exercise may be increases in individual MU firing rates (Sale 1987; Strojnik 1995). However, the relationship between changes in force production and MU firing rate adaptations after strength training is rather ambiguous as the studies available examining these changes during maximal and sub-maximal muscle actions are equivocal (Rich & Cafarelli 2000; Patten et al. 2001; Kamen & Knight 2004; Pucci et al. 2006; Knight & Kamen 2008; Christie & Kamen 2010; Vila-Chã et al. 2010).

Increases in maximal MU firing rates after strength training have been observed in the vastus lateralis, tibialis anterior and abductor digiti minimi of the fifth finger (Van Cutsem et al. 1998; Patten et al. 2001; Kamen & Knight 2004; Christie & Kamen 2010). Using intramuscular EMG techniques several studies have observed increases in maximal strength occur concurrently with increases in maximal MU firing rates after a single strength testing session for both old and young individuals (Patten et al. 2001; Kamen & Knight 2004; Christie & Kamen 2010). Moreover, there appears to be a strong relationship between the early, rapid increases in strength and changes in individual MU firing (figure 11; Kamen & Knight 2004). The strength training-induced increases in maximal firing rates of trained muscles were also highly correlated with increases in voluntary

neural drive of those muscles, as measured by SIT (Knight & Kamen 2008). However, after the initial gains following the first strength testing session, the influence of MU firing rates on strength seems to diminish. It is suggested then that the adaptation(s) to neural mechanism(s) initially enhancing MU firing rates are moderated as other adaptations begin to occur, continuing strength development. (Gabriel et al. 2006.) Conversely, Pucci et al. (2006) did not observe similar changes in maximal MU firing rates in the vastus lateralis although knee extension strength increased after three weeks of isometric strength training. However, because testing was done only before and after the three weeks of training, any alterations in MU firing rates may have been diluted as changes may occur only during the first days of training and then are replaced as other adaptations begin to occur (e.g. changes in antagonist co-activation).

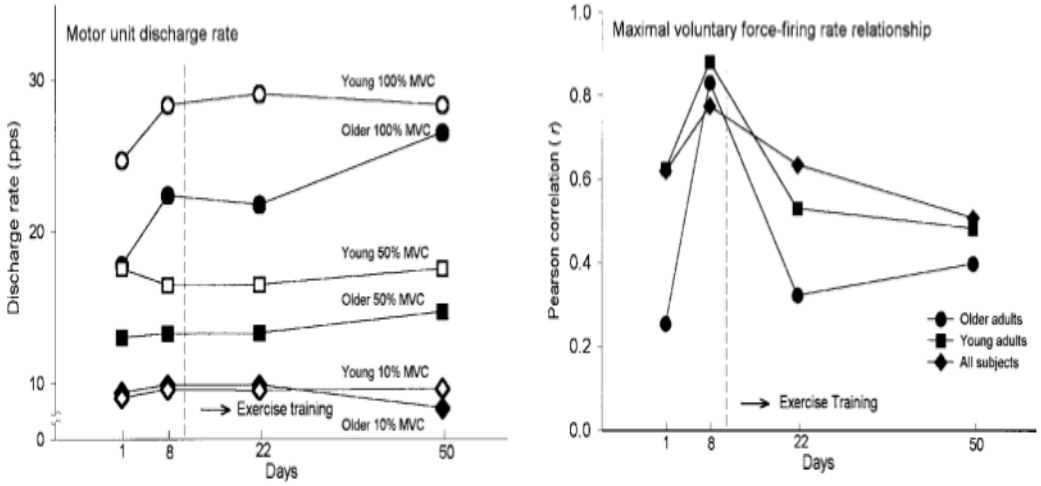

FIGURE 11. *Left*, Motor unit discharge rates in pulses per second (pps;) during 10%, 50% and 100% MVC of the vastus lateralis muscle between young (*white*) and older adults (*black*) during a control period (1-8 days) and over 6-weeks (50 days) of strength training. *Right*, The Peasrson correlation coefficient (r) between maximal force and motor unit discharge rates in young (■) and older (●) adults during the same period. (Kamen & Knight 2004.)

Motor unit doublet firing. The beginning patterns of MU recruitment may be just as important as the number of recruited MUs, as either a single extra or missed MU action potential may have significant effects at the onset of force production (Gabriel et al. 2006). Van Cutsem et al. (1998) observed the occurrence of single MU discharges with short interpulse intervals at the beginning of rapid muscle actions, which have been termed doublets. Doublet firings, which the researchers defined as double discharges of a single MU less than 5 ms apart, practical significance was proposed as a mechanism

to greatly enhance both RFD at the onset of muscle actions. Using intramuscular EMG to detect patterns of MU firing rates, Van Cutsem et al. (1998) observed an increased rate of doublet firings during ballistic contractions concomitantly with enhanced RFD and MVC after 12-weeks of dynamic explosive type strength-training in the tibialis anterior muscle (figure 12). Increases in the occurrence doublets may be one mechanism facilitating the initial rapid gains in maximal strength.

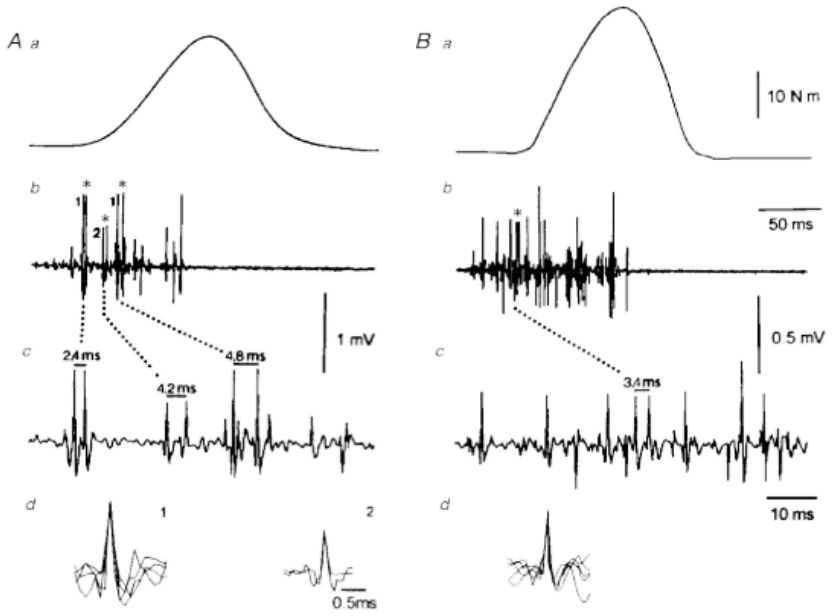

FIGURE 12. Examples of doublet discharges from two **(A)** and one **(B)** MU(s) during ballistic muscle actions after 12-weeks of dynamic explosive strength training. **(a)** force; intramuscular EMG plotted at slow **(b)** and fast **(c)** speeds. * = indication of doublet. (Van Cutsem et al. 1998.)

Motor unit synchronization. Synchronization, the simultaneous discharge of several MUs, may be another strength training-induced adaptation in MU behavior augmenting strength characteristics. In an early study by Milner-Brown et al. (1975), the effect of strength-training on MU synchronization of the first dorsal interosseous muscle was investigated. This study found that synchronization increased following six-weeks of isometric strength training in untrained individuals. Additionally, in a comparative study of strength-trained athletes and untrained persons, greater MU synchronization was observed within the group of strength-trained individuals, adding to the assumption that strength training-induces MU synchronization (Semmler & Nordstrom 1998).

However, more recently there is evidence indicating MU synchronization does not enhance force production (e.g. Kidgell et al. 2006).

3.2.3 Antagonist co-activation

There are at least two opposing muscles actively controlling movement: the muscle initiating the action (agonist) and the muscle resisting (antagonist). The co-activation of antagonist muscle during muscle actions is important for both the integrity and stability of the joint(s) around which the action occurs (Baratta et al. 1988). However, in terms of muscular strength, the co-activation of antagonist muscle is contradictory, as the strength of a muscle action is the net force between the agonist and antagonist muscle. Furthermore, antagonist co-activation also inhibits the ability of the central nervous system to fully activate the agonist muscle via reciprocal inhibition, further attenuating the strength of muscle actions (Basmajian & De Luca 1985, 223-228). Therefore, decreasing the co-activation level of antagonist muscle may contribute to increased strength characteristics (e.g. Carolan & Cafarelli 1992). However, the willingness of the central nervous system to compromise joint stability for muscular strength is unknown (Gabriel et al. 2006).

Strength training-induced reductions in antagonist co-activation during maximal muscle actions coinciding with strength gains have been documented on several occasions in both young and old individuals (Carolan & Cafarelli 1992; Häkkinen et al. 1998b; Häkkinen et al. 2000; Tillin et al. 2011). Tillin et al. (2011) found that increases in knee extensor strength after four-weeks of unilateral strength training were related to a downward shift in the agonist – antagonist activation relationship (figure 13). Though, individually both agonist and antagonist activation increased during knee extension after the training intervention. It was suggested that the increase in antagonist activation was likely a protective mechanism maintaining joint stability and integrity to compensate for increased agonist activation and knee extensor strength.

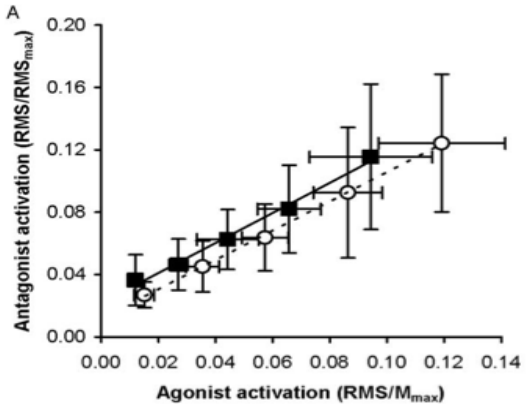

FIGURE 13. The relationship between agonist and antagonist activation during isometric knee extensions at 20%, 40%, 60%, 80% and 100% of MVC before (■, solid line) and after (○, dotted line) four-weeks of isometric strength training (Tillin et al. 2011).

Strength training-induced reductions of antagonist co-activation seem to occur irrespective of gender and age (Häkkinen et al. 1998b). Conversely, reductions in antagonist co-activation have not always been found, as 14-weeks of strength training the knee extensors elicited no changes in biceps femoris co-activation (Reeves et al. 2004). Nevertheless, there seems to be an augmentation of strength as co-activation of antagonist muscle decreases. Furthermore, the mechanisms controlling reductions may be spinal and / or supraspinal moderating undesirable activation and movement of antagonist muscle (e.g. Hortobagyi & DeVita 2006).

3.2.4 Spinal adaptations to strength training

Changes in spinal α-MN excitability have been suggested to alter supraspinal drive activating MUs (Gardiner 1991; Duchateau et al. 2006). It is reported that α-MN excitability is mediated by changes of intrinsic properties of α-MN and / or afferent feedback induced by spinal reflexes. Various nerve stimulation techniques have been used to examine the effect of training on α-MN and spinal reflex properties. The Hoffman reflex (*H-reflex*), which is an artificially evoked spinal reflex through a sub-maximal stimulation of a peripheral nerve, has been utilized to examine spinal α-MN excitability as well as pre-synaptic Ia afferent inhibition (Palmieri et al. 2004). Additionally, an electrophysiological variant of the H-reflex known as the *V-wave* has been used to assess the efficiency of efferent neural drive caused changes in spinal α-MN excitability. V-wave responses are evoked using supramaximal stimulation of peripheral nerve during maxi-

mal muscle actions. (Aagaard et al. 2002; Vila-Chã et al. 2012.) In a number of cross-sectional studies, when compared to untrained individuals strength athletes were reported to exhibit greater responses in both H-reflex and V-wave in suggesting enhanced spinal α-MN excitability in strength trained athletes (Milner-Brown et al. 1975; Maffiuletti et al. 2001). These findings of greater H-reflex and V-wave responses in strength athletes suggest that strength training may cause functional changes to the excitability of spinal α-MNs.

Initial increases in strength during strength training may be caused by changes in spinal α-MN excitability. H-reflex responses have tended to remain unchanged after a period of strength training when taken in a resting condition (Aagaard et al. 2002; Maffiuletti et al. 2003; Gondin et al. 2006; Beck et al. 2007; Del Balso & Cafarelli 2007). However, it is suggested that H-reflex responses should be measured during the trained muscle actions, as opposed to at rest, considering the specificity of training adaptations (Aagaard & Mayer 2007). In this case, H-reflex amplitudes were observed to increase after a period of strength training when taken at multiple levels of MVC (Aagaard et al. 2002; Holterman et al. 2007; Vila-Chã et al. 2012). These observations suggest possible changes in α–MN excitability and / or pre-synaptic inhibition of Ia afferents. Additionally, increases in evoked V-wave responses following a short strength-training period have also been observed (Aagaard et al. 2002; Gondin et al. 2006; Del Balso & Cafarelli 2007; Fimland et al. 2009; Vila-Chã et al. 2012) indicating that an increase in α–MN activation may take place. The observed changes in both H-reflex and V-wave responses are consistent with early suggestions that training may cause increased α–MN excitability and activation (Sale et al. 1983). These changes in α–MN activation may cause the leftward shift observed in the torque-recruitment threshold relationships by Van Cutsem et al. (1998) (figure 14). The decreases in α–MN force-recruitment thresholds may indicate the increased activation of MUs and the changes in behavior during a muscle action cause the sharp rises in both MVC and RFD during the beginning stages of strength training. (Van Cutsem et al. 1998; Holtermann et al. 2007). These observations might help explain the findings of increased firing rates and doublets in response to strength training.

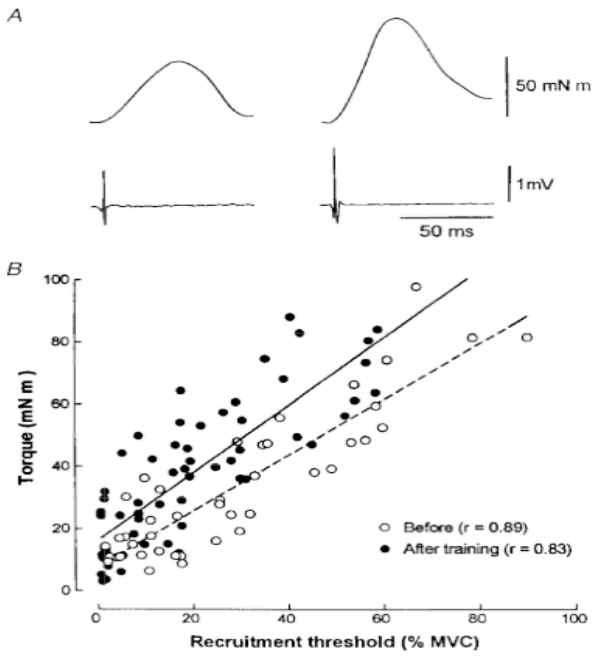

FIGURE 14. **(A)** Twitch torque before (○) and after (●) 12-weeks of dynamic explosive strength training. **(B)** Torque-recruitment threshold relationship before and after 12-weeks of dynamic explosive strength training. (Van Cutsem et al. 1998.)

The changes in the reflex measurements suggest that changes in spinal mechanisms may assist with the early increases in strength during training. However, if both V-wave and H-reflex increases are detected concomitantly, this may represent increased influence of descending drive from supraspinal mechanisms (figure 15). (Aagaard et al. 2002.)

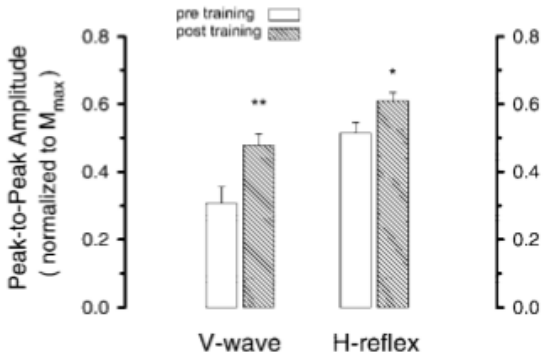

FIGURE 15. Mean peak-to-peak V-wave and H-reflex amplitudes normalized to M_{max} of the soleus muscle during isometric plantar flexion MVC pre- (white) and post- (shaded) 14-weeks of strength training (*p<0.05; **p<0.01). (Aagaard et al. 2002.)

3.2.5 Supraspinal adaptations to strength training

There appears to be training-induced increases in descending supraspinal drive positively influencing strength. Changes in supraspinal influence has been suggested through observations of increased strength after training with imagined contractions (Yue & Cole 1992) and increases in the evoked spinal reflex measurements, H-reflex and V-wave (Aagaard et al. 2002). These observations imply that possible changes in supraspinal drive may lead to the alterations in MU behavior and increased maximal and explosive strength. Research has suggested that the plasticity of supraspinal mechanisms is modified to various forms of motor learning (Muellbacher et al. 2001), from which changes in cortical activity and economy of neural output may occur in response to resistance training (Farthing et al. 2007; Carroll et al. 2009; Falvo et al. 2010)

An increase in net descending cortical drive may optimize the pattern of MU activation, causing improved force production through changes in the activation properties of the agonist and synergist muscles (del Olmo et al. 2006; Beck et al. 2007; Del Balso & Cafarelli 2007; Griffin & Cafarelli 2007; Carroll et al. 2009). Using electroencephalographic (EEG) techniques, the increased force production after short-term of heavy- and explosive strength training was observed to be the result of changing spatially distributed motor activity at the motor cortex to a more specific and localized region that centers around the motor areas of the trained muscles (Falvo et al. 2010), outlined by the somatatopic organization of the motor cortex (Squire et al. 2008, 671). This change may result in the observations of increased in cortical excitability (figure 16) and decreased intracortical inhibitory influences acting on the motor areas of the trained muscle measured by transcranial magnetic stimulation (TMS; Griffin & Cafarelli 2007; Weier et al. 2012) Thus these changes may reduce the cortical activity controlling the antagonist or other unintended muscle(s) for the movement and thus reducing the activation level of those muscles (Giacobbe et al. 2011; Dal Maso et al. 2012).

Enhanced cortical excitability may also be reflected by the phenomenon of increased strength of untrained limbs after unilateral training, i.e. cross-education. The increased neural activation and force output of untrained limbs, may be caused by a “spill over” effect of unilateral activation resulting in bilateral cortical activation through the connections of the left and right cerebral hemispheres. (Farthing et al. 2007; Carroll et al.

2009; Lee et al. 2009.) The increases in cortical excitability of the trained motor areas may thus increase net descending volitional drive to the target MN pool and ultimately enhance force production characteristics (Beck et al. 2007; Del Balso & Cafarelli 2007; Griffin & Cafarelli 2007).

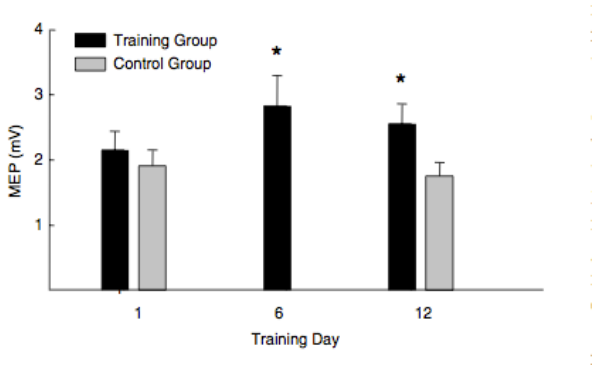

FIGURE 16. Peak-to-peak TMS motor evoked potential (MEP) amplitudes during 12 days of strength training from the tibialis anterior muscle in training (*black*) and control groups (*gray*) (*p<0.05). (Griffin & Cafarelli 2007.)

3.3 Neural adaptations to endurance training

Endurance training is typically distinguished by improvements in fatigue resistance, maximal oxygen consumption (VO_2max), minimal changes in strength (Hickson 1980). The increases in VO_2max are generally attributed to changes in the cardio-respiratory, cardiovascular and metabolic systems (e.g. mitochondrial density), as well as, muscle composition (e.g. increased Type I muscle fibers) that enable greater energy efficiency (Hollszy & Coyle 1984; Howald et al. 1985). However, the basis of motor control outlines a close relationship between the nervous- and musculoskeletal systems (Zajac 1989). Therefore, neural adaptations to endurance training may allow for a more skilled control of movements (e.g. running and cycling) optimizing motor system characteristics for greater endurance exercise performance while strength improvement is attenuated (Bonacci et al. 2009).

3.3.1 Motor unit behavior after endurance training

There is surprisingly very little research focusing on the changes of MU recruitment and firing rates in response to endurance exercise. However, of the few investigations, MU

behavior has been observed to change after periods of endurance training (Lucía et al. 2000; Chapman et al 2008; Vila-Chã et al. 2010). Investigations of short and long-term endurance training have observed increases in sEMG activity (Lucía et al. 2000). However, the increases in sEMG were observed only during sub-maximal muscle actions, while no changes were observed during maximal muscle actions (figure 17A; Vila-Chã et al. 2010). Additionally, during the sub-maximal muscle actions, there is evidence that MU firing rates decrease following endurance training (figure 17B; Vila-Chã et al. 2010). It is speculated that the observations of decreased MU firing rates and increased sEMG activity likely meant the number of activated MUs increased during the sub-maximal muscle actions. Contrary to strength training though, researchers have speculated that the increased recruitment was likely increases in low-threshold Type I MUs through changes that may specifically be mediated through spinal properties (Kyröläinen & Komi 1994).

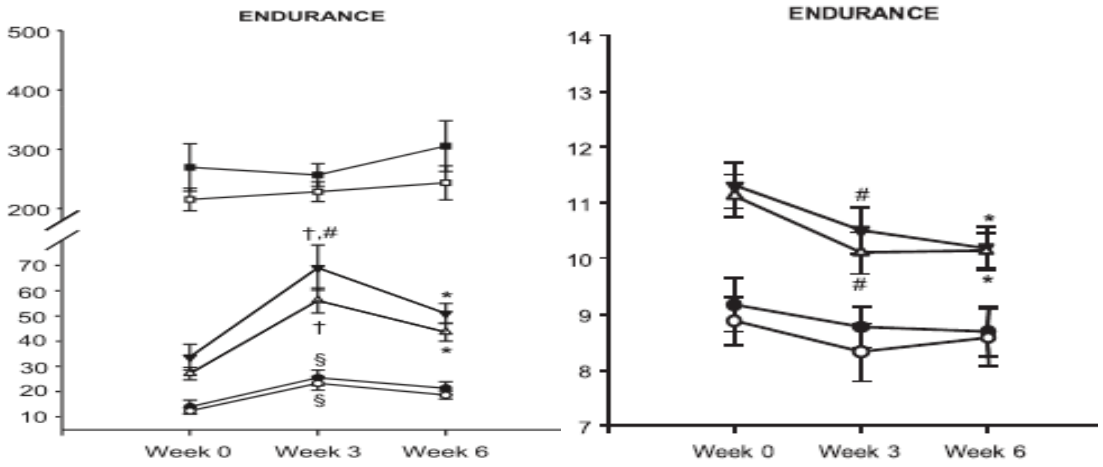

FIGURE 17. *Left*, mean average rectified value EMG (μV) and *right*, motor unit firing frequencies (pps) of the vastus medialis obliquus (VMO; *black*) and vastus lateralis (VL; *white*) during knee extension at 10% (circles), MVC (triangles) and 100%MVC after 6-weeks of endurance training (§p<0.01; †p<0.0001 from *week 0* to *week 3*. #p<0.01 from week 3 to week 6. *p<0.05; **p<0.001 from week 0 to week 6). (Vila-Chã et al. 2010.)

3.3.2 Spinal adaptations to endurance training

Short-term endurance training was observed to increase H-reflex amplitudes (figure 18; Pérot et al. 1991; Vila-Chã et al. 2012). However, in contrast to strength training, V-wave responses went unchanged after a period of endurance training (Vila- Chã et al.

2012). The training-induced adaptations in spinal reflex measurements are in agreement with multiple cross-sectional studies that observed larger H-reflex amplitudes from endurance athletes when compared to experienced strength athletes and untrained individuals (e.g. Nielsen et al. 1993; Maffiuletti et al. 2001). Considering the properties and responses of the H-reflex and V-wave spinal reflex measurements, neural adaptations to endurance training seem to alter spinal properties rather than supraspinal. The observed increases in H-reflex amplitudes are considered to be the result of increased motoneuron excitability and / or decreased inhibition of pre-synaptic Ia afferents (Vila- Chã et al. 2012).

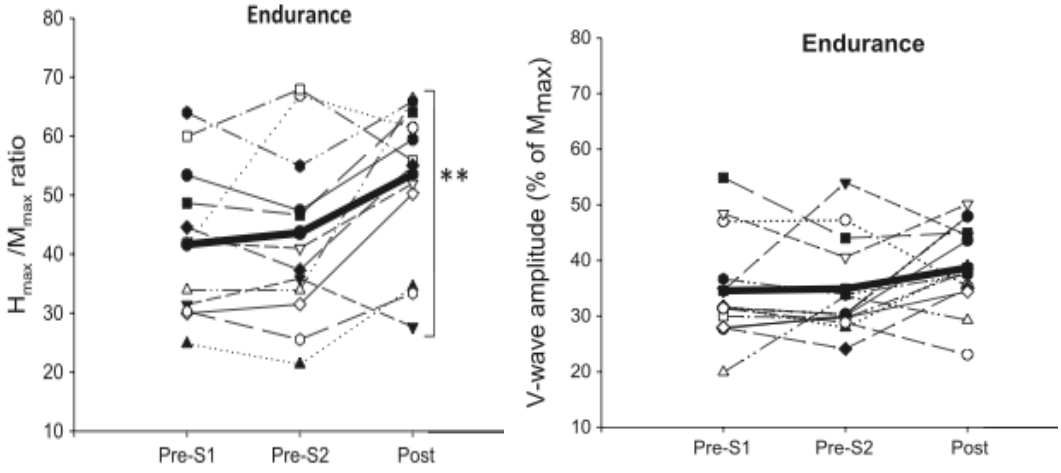

FIGURE 18. H_{max} / M_{max} ratio (*left*) and V-wave amplitude normalized to M_{max} (*right*) of individual subjects during control period (Pre-S1), before (Pre-S2) and after (Post) 6-weeks of cycling endurance training (**p<0.01). (Vila-Chã et al. 2012.)

The increased excitability of motoneurons could reflect an increase in representation of low-threshold Type I MUs (small α-MN and Type I muscle fibers), as increased Type I MU proportions have been seen in endurance athletes (Goubel & Marini 1987). This change would allow for the suggested increases in MU recruitment and the observed decreases in firing rates at sub-maximal force levels, as Type I MUs are more easily excitable because of its corresponding α-MN properties. Based on the Type I MU properties, energy utilization would be more efficient and, this, prolonging the onset of fatigue**.** Additionally, the decreased pre-synaptic inhibition of Ia afferents to α-MNs could result in changes observed in MU behavior, as this property has been perceived to

modulate MU recruitment thresholds and firing rates during sub-maximal contractions (Grande & Cafarelli 2003).

3.3.3 Supraspinal adaptations to endurance training

Spinal reflex measurement studies suggest that neural adaptations to endurance training may only occur within spinal rather than supraspinal mechanisms (Pérot et al. 1991; Maffiuletti et al. 2001; Vila-Chã et al. 2012). This is especially true for maximal force production efforts as strength levels and supraspinal mechanisms seem to undergo no changes after endurance training (Vila-Chã et al. 2010; Vila-Chã et al. 2012). Alternatively, endurance training may only affect the blood flow to supraspinal mechanisms (i.e. cerebrovasculature) rather than modify the cortical activity. Investigations have shown that even short-term endurance training increased the blood flow to the motor cortex and also causes angiogensis, or the formation of new blood vessels, within the cortex. Endurance exercise may then generate a more supportive and nutrient rich environment for the motor cortex in response to the demand of prolonged motor output rather than change any cortical activity after a period of endurance training. (Kleim et al. 2002; Swain et al. 2003.)

4 COMBINED STRENGTH AND ENDURANCE TRAINING

Strength, power, and endurance are important characteristics for successful elite athletic performance as well as for general health (Nader 2006). Moreover, with regard to the general population, these traits are essential in the prevention of disease, injury and dependency in young and elderly age groups (Haskell et al. 2007; Garber et al. 2011). Therefore, per recommendations by the American College of Sports Medicine (ACSM), coaches and trainers have been encouraged to integrate both strength and endurance components into training programs (Garber et al. 2011). This coupling of strength training (to increase strength and power) and endurance training (to enhance cardiorespiratory and cardiovascular performance) into a single program is known as combined or concurrent training (Wilson et al. 2012).

A problem arises, however, with the combined training paradigm as strength training involves short duration activities employing near maximal-to-maximal force production whereas endurance training typically involves repetitive sub-maximal force production for prolonged periods (Knuttgen 2007). The differences between strength and endurance training result in adaptations with considerably few similarities and may ultimately conflict one another in many cases (figure 19; Wilson et al. 2012). This is especially true regarding both neural adaptations and strength characteristics (e.g. Vila-Chã et al. 2010; Vila-Chã et al. 2012). Consequently, these inherent dissimilarities may be problematic in the effort to improve strength, power and endurance components of fitness simultaneously compared to either training mode alone (Wilson et al. 2012).

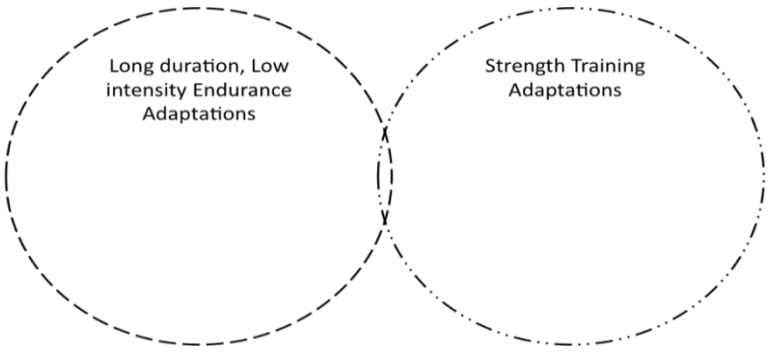

FIGURE 19. Relation of long-term adaptations between endurance (l*eft*) and strength training (*right*) modified from Wilson et al. 2012.

4.1 Interference effect

One of the most consistent findings of combined strength and endurance training studies is the attenuation of strength characteristics following combined training when compared to strength training alone (Hickson 1980; Hunter et al. 1987; Hennessy & Watson 1994; Kraemer et al. 1995). In one of the first combined training studies, Robert Hickson (1980) reported that a combined strength and endurance-training program impaired the development of strength. In this study, after a 10-week training program consisting of high-volume and high-intensity combined strength and endurance training, it was apparent that lower-body maximal strength gains were profoundly reduced compared to gains achieved through strength training alone (figure 20). This attenuation of strength gains as a result of combined strength and endurance training defines what is known as *the interference effect*. Since the seminal study by Hickson (1980) there has been extensive evidence acknowledging the role of high volume combined strength and endurance training in causing the interference effect phenomenon on strength development compared to what typically occurs with strength training alone (e.g. Hunter et al. 1987; Hennessy & Watson 1994; Kraemer et al. 1995).

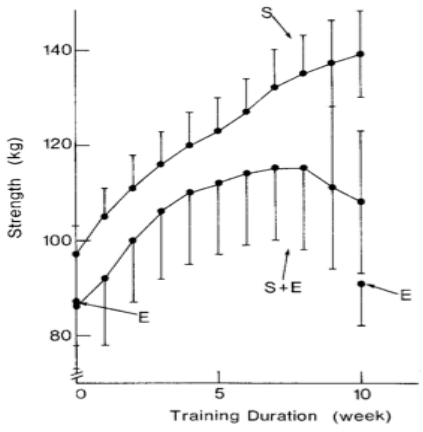

FIGURE 20. Parallel squat 1-RM load changes in strength-only (S), endurance-only (E) and combined strength and endurance (S+E) training groups during a 10-week training period (Hickson 1980).

Despite the tendency of inhibited strength development, endurance performance appears to be unimpeded by combined training as endurance indices, such as VO_2max, have been regularly reported to improve in magnitudes similar to endurance training alone

(Hickson 1980; Hunter et al. 1987; Kraemer et al. 1995; Häkkinen et al. 2003; Mikkola et al. 2011). The consistent findings that combined training does not compromise endurance performance but rather strength development, has led some researchers to suggest that endurance exercise as the factor limiting strength gains (Leveritt et al. 1999a; Cadore et al. 2010; Wilson et al. 2012).

Acute endurance training variables of combined training, such as training mode and intensity, may determine the extent of strength interference (Leveritt & Abernethy 1999b; De Souza et al. 2007; Gergley 2009). It has been suggested that endurance exercises biomechanically similar to strength exercises performed in combined programs may minimize the interference of strength development. For example, cycling may be more beneficial in minimizing the antagonistic effects of concurrent training on strength compared to running. This may particularly be due to differences in muscle actions of the quadriceps between the two exercises, as cycling closely resembles the concentric actions in various strength exercises, such as leg press and knee extension, whereas running involves high amounts of eccentric actions which causes greater muscle damage limiting the frequency of successive training sessions and, by consequence, potential strength improvements. (Gergley 2009; Wilson et al. 2012.) Moreover, the intensity of the endurance exercise performed during combined training may be the greatest contributing factor to the hindrance of strength gains (De Souza et al. 2007).

Based on training descriptions of studies reporting strength interference, a common trait between the studies appears to be that endurance exercise was performed at rather high-intensities (Hickson 1980; Hennesy & Watson 1994; Kraemer et al. 1995). Hence, endurance exercise that is strenuous both metabolically and neurally, such as intensities near VO_2max, may exacerbate strength interference (Docherty & Sporer 2000). Specifically, high-intensity interval type endurance training has been shown to cause acute decrements in strength performance, which may lead to a reduction in the quality of subsequent strength training sessions (Leveritt & Abernethy 1999b; De Souza et al. 2007). Thus, during prolonged combined training programs, if strength-training sessions are repeatedly performed sub-optimally, chronic strength development may be compromised (Craig et al. 1991). Therefore, low-intensity continuous endurance training (i.e. below aerobic threshold) may minimize the degree of interference on strength development (Docherty & Sporer 2000; De Souza et al. 2007).

The extent of strength interference may not only depend on acute endurance training variables, but also the current training status of individuals beginning combined training must be considered (Leveritt et al. 1999a). Strength interference following high-intensity combined strength and endurance training has been reported for both previously untrained (e.g. Hennessy & Watson 1994) and athletically trained individuals (Kraemer et al. 1995). However, the level of strength interference seems be attenuated for persons with endurance training backgrounds (Hunter et al. 1987). Additionally, increases in maximal strength, power and endurance performance simultaneously have been reported in endurance trained following periods of combined training (Aagaard & Andersen 2010). These findings suggest that the training history of an individual may influence the level of tolerance and adaptability to high intensity combined training (Hunter et al. 1987).

In non-endurance trained individuals, however, interference of strength gains after high volume and intensity combined training may be cause by overreaching or overtraining syndromes (Leveritt et al. 1999a). It is proposed that the overreaching and overtraining effects stimulate competing adaptations over a long-term program resulting in diminished performance, such as alterations in anabolic and catabolic hormone concentrations, shifts in the make-up of muscle proteins, and / or a reorganization of motor unit recruitment and behavior (Chromiak & Mulvaney 1990; Wilson et al. 2012).

Reducing the volume and / or intensity of combined strength and endurance-training, through careful programming / periodization, may be imperative in preventing overreaching or overtraining and, therefore, negating the strength interference for non-endurance trained individuals (Häkkinen et al. 2003). Several studies have shown that reduced volumes of combined training, by reduced frequency and / or intensity of training sessions, for untrained persons, are associated with maximal strength gains typically observed with strength training alone (McCarthy et al. 1995; Häkkinen et al. 2003; Glowacki et al. 2004; Shaw et al. 2009). Moreover, it seems that lower training volumes during single training sessions, by performing strength or endurance training on separate days as opposed to both in a single session, may be more beneficial for strength development (Sale et al. 1990b). However, it seems that interference of strength development persists despite reductions in training volume as several investigations have reported attenuated explosive strength properties (figure 21; Dudley & Djamil 1985;

Häkkinen et al. 2003; Mikkola et al. 2012). The unaffected maximal strength and attenuated RFD responses to reduced volumes of combined training suggests that the cause of interference may most likely be neural adaptations, typically associated with pure strength training, are possibly impaired with the inclusion of endurance training rather than the suggestion of alterations in hormone concentrations or expression of muscle proteins (Kraemer et al. 1995; Leveritt et al. 1999a; Häkkinen et al. 2003.)

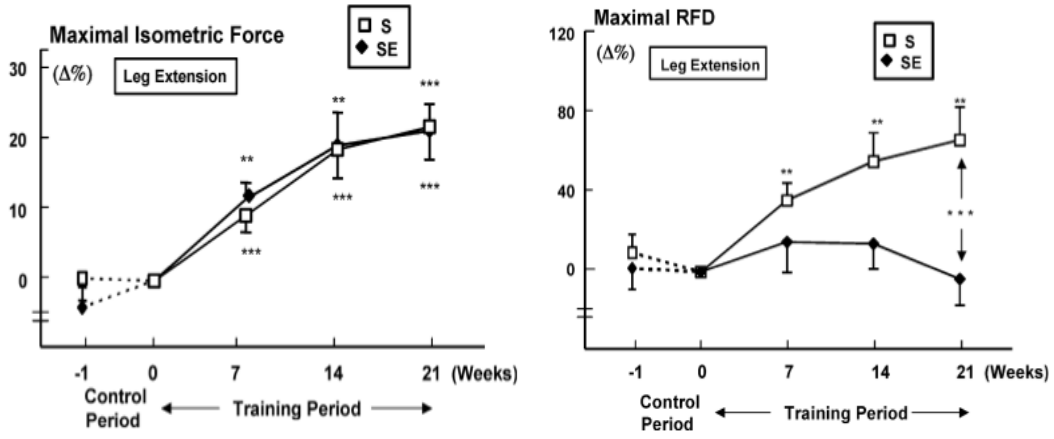

FIGURE 21. Mean changes in maximal voluntary bilateral isometric leg extension force (*left*) and RFD (*right*) between strength-only (S, □) and separate-day combined strength and endurance (SE, ♦) training groups during a 1-week control period and 21-weeks of training (**p<0.01; ***p<0.001). (Häkkinen et al. 2003.)

4.2 Neural adaptations to combined training

There is widespread acceptance that strength training causes neural adaptations altering MU behavior that enhance maximal strength characteristics, often observed by concurrent increases in sEMG activity and strength characteristics (e.g. Häkkinen & Komi 1983; Van Cutsem et al. 1998). Conversely, endurance training has been observed to result in neural adaptations that change MU behavior to benefit prolonged sub-maximal force output while there seems to no changes in maximal strength (e.g. Vila-Chã et al. 2010; Vila-Chã et al. 2012). Therefore, attenuated strength development, due to the incompatibility of combined strength and endurance training, has been suggested to be a result of altered neural activation strategies that do not enhance maximal strength development (Chromiak & Mulvaney 1990).

The absence of interference on maximal strength after low to moderate volume combined training has been viewed in relation to increases in sEMG activity for untrained individuals. Additionally, antagonist co-activation has been observed to decrease with combined training. Despite maximal sEMG increases, rapid neural activation has been reported to go unchanged after the same training regimens (figure 22), which reflects the observations of attenuated rapid force characteristics following combined strength and endurance training. (Häkkinen et al. 2003; Mikkola et al. 2012.)

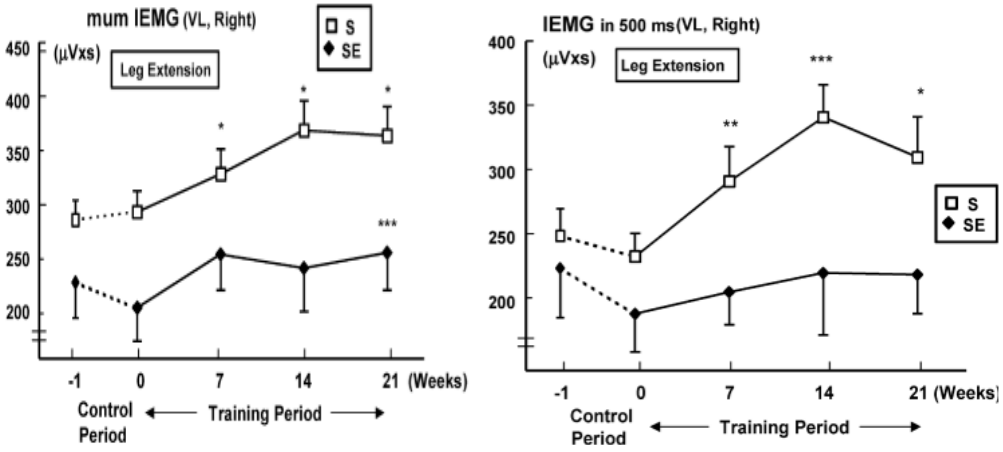

FIGURE 22. Changes in maximum integrated electromygraphic activity (iEMG; *left*) and rapid neural activation during the first 500 ms (*right*) of maximal voluntary bilateral isometric leg extension in the vastus lateralis of the right leg in the strength-only (S, □) and combined strength and endurance training (SE, ♦) groups during a 1-week control and 21-week training period (*p<0.05; **p<0.01; ***p<0.001). (Häkkinen et al. 2003.)

The design of a combined training program may influence the expression of neural adaptations. Considering concurrent training program design, increases in maximal sEMG activity were not similarly observed by either McCarthy et al. (2002) or Cadore et al. (2010) in untrained young adults and elderly individuals, respectively, when strength and endurance training were performed during the same session. The increases in maximal sEMG activity by Häkkinen et al. (2003) were observed with a 4-days / week, separate-day strength and endurance training program design (2-days endurance + 2-days strength). However, attenuated changes in maximal sEMG activity were viewed when both strength and endurance exercises were performed during single-sessions 3-days / week (e.g. McCarthy et al. 2002; Cadore et al. 2010). The combined single-session training studies utilized training programs where intra-session exercise order

was either endurance followed by strength (Cadore et al. 2010) or a mixed order throughout the training period (McCarthy et al. 2002). Cadore et al. (2010) speculated that performing endurance exercise first, during a single-session, may limit the ability of the neuromuscular system to produce maximal and rapid force during the following strength training period, thus, altering the full expression of neural adaptations typically observed from strength training alone. However, it should be pointed out that comparing these studies is difficult as study and training designs are unique for each.

4.3 The order effect

The major problem of combined training seems to be the limited expression of force generating properties and neural adaptations typically observed by strength training alone, whereas endurance performance tends to improve regardless (e.g. Hickson 1980; Kraemer et al. 1994). The interference of strength appears to be the consequence of added endurance training inducing limitations on the neuromuscular system's force generating characteristics (Häkkinen et al. 2003) especially if performed before strength training (Nelson et al. 1990). Furthermore, the critical factor for optimal strength development is the degree in which muscular strength is produced during training (Atha 1981). Therefore, it may be important to understand the effect of intra-session exercise sequence of single-session combined training programs (i.e. strength-endurance or endurance-strength) on strength development (i.e. *order effect*; Sale et al. 1990a; Cadore et al. 2012). However, research examining the influence of the intra-session exercise order on strength characteristics and, more particularly, neural adaptations over a long-term combined strength and endurance-training program is currently limited.

4.3.1 Influence of the order effect on strength development

It has been suggested that the mode (e.g. cycling, running) and intensity of the endurance exercise utilized during a combined training program are the causal links determining the extent of interference of strength characteristics (De Souza et al. 2007; Gergley 2009). However, the timing of endurance exercise relative to strength training may be more important for the design of combined training programs (Collins & Snow 1993). Performing lower-body endurance exercise has regularly been shown to result in acute

decreases in lower-body strength (Abernathy 1993; Lepers et al. 2001). The acute strength decreases after endurance exercise may reduce the quality of subsequent strength training sessions in the single-session combined training paradigm (Leveritt & Abernethy 1999b). Therefore, repeated bouts of training endurance immediately prior to strength training may compromise long-term adaptations strength development (Craig et al. 1991). Thus, it may be suggested that single-session combined training programs with an intra-session exercise order of strength prior to endurance might result in strength gains similar to those of strength training alone (Nelson et al. 1990), and possibly greater than gains achieved from an intra-session combined training order of endurance before strength (Cadore et al. 2010).

The limited number of studies investigating the order effect on strength adaptations has been relatively inconsistent (Sale et al. 1990a; Collins & Snow 1993; Gravelle & Blessing 2000; Cadore et al. 2012). After 12-weeks of single-session combined training unequal strength gains have been observed between inverse intra-session exercise orders in sedentary elderly individuals (Cadore et al. 2012). Cadore et al. 2012 reported that 12-weeks of periodized strength training combined with moderate-intensity endurance exercise, individuals performing a strength-endurance exercise order exhibited significantly greater increases in 1-RM knee extension strength than individuals training an endurance-strength order (35% to 22%, respectively). However, it is proposed that the age and the previous health status of the individuals may influence training results. Sedentary elderly persons may be more susceptible to training improvements and endurance exercise induced acute fatigue, thus, affecting subsequent strength training performance and chronic adaptations. (Cadore et al. 2010.) Alternatively, young to middle-aged males and females have displayed equal improvements in leg press 1-RM, irrespective of the different intra-session exercise orders of combined low to moderate-intensity endurance and strength training after short and prolonged periods (figure 23; Sale et al. 1990a; Collins & Snow 1993; Gravelle & Blessing 2000).

FIGURE 23. The percent change in the 1-RM of bilateral concentric leg press over 7-weeks of concurrent strength and endurance training with groups practicing different intra-session training orders; strength-endurance (ST / ET, ○) and endurance-strength (ET / ST, ●) groups (Collins & Snow 1993).

It has also been observed that endurance performance increases similarly regardless of intra-session loading order, gender and age. Therefore, for young to middle-aged healthy untrained men and women there seems to be no influence of the intra-session exercise sequence on either maximal strength or endurance gains after low to moderate single-session concurrent training (Collins & Snow 1993; Gravelle & Blessing 2000). Conversely, the intra-session exercise sequence of concurrent training may influence strength development in elderly individuals (Cadore et al. 2012). The lack of studies investigating the order effect of concurrent strength and endurance training programs employing periodized maximal and / or explosive strength training, as well as, the response of rapid force production over a prolonged period of time leaves some differences unanswered.

4.3.2 Influence of order effect on neural adaptations

Häkkinen et al. (2003) observed increases in maximal sEMG alongside attenuated rapid neural activation in response to separate-day combined strength and endurance training. However, there is an inability of the neuromuscular system to produce maximal force immediately after endurance exercise (Abernathy 1993; Sidhu et al. 2009) These observations may indicate the potential for differences in neural adaptations to alternate orders of intra-session exercise sequences of combined strength and endurance training.

An attenuation of maximal sEMG activity in elderly subjects has been observed after a 12-week concurrent training program of moderate-intensity endurance exercise performed prior to periodized strength training (endurance-strength) in relation to sEMG changes to a strength-training only group (Cadore et al. 2010). Conversely, when the intra-session exercise order was switched (strength-endurance) for similar subjects, there were indications using indirect methods (e.g. muscle quality = maximal strength / muscle thickness) that neural adaptations and strength occur to a greater magnitude than the an endurance-strength training order (figure 24; Cadore et al. 2012). Researchers have speculated that the attenuated changes in maximal sEMG activity observed in the endurance-strength group may be the result of performing strength training in a fatigued state through the inhibition of full MU recruitment, as well as, maximal firing rates resulting in sub-optimal expression of strength training-induced neural adaptations (Cadore et al. 2010).

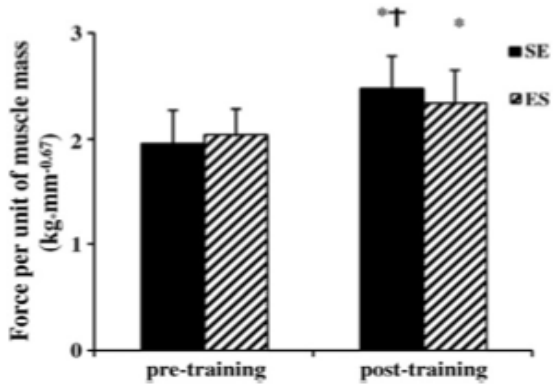

FIGURE 24. The quadriceps femoris force per unit of muscle mass or muscle quality changes before and after 12-weeks of concurrent training with intra-session training orders of strength prior to endurance (SE) and endurance prior to strength (ES). (Cadore et al. 2012.)

Therefore, performing concurrent training with an intra-session exercise order of strength-endurance may save the neuromuscular system from acute fatigue and result in positive neural adaptations benefiting strength in the elderly (Cadore et al 2012). Currently, however, there is a lack of research using more sensitive measures to detect differences in neural adaptations to single-session concurrent strength and endurance training, in relation to responses to strength training alone. Moreover, knowledge of the effects of different intra-session exercise order of concurrent training on neural adaptations in untrained young to middle-aged individuals is limited.

5 PURPOSE OF THE STUDY

The purpose of the present study was to investigate the neuromuscular adaptations over 24-weeks of concurrent endurance (E) and strength (S) training performed during single training-sessions (e.g. 1E + 1S = a single training session) in young to middle-aged healthy, untrained men. This study gave special attention to examining the "order effect" of concurrent training (E+S vs. S+E).

5.1 Research questions

1) Are gains in maximal dynamic and isometric strength reduced when endurance exercise precedes strength training after 24-weeks of single-session combined training?

2) What is the effect of the intra-session exercise order of concurrent training on adaptations to maximum voluntary activation (i.e. descending neural drive)?

3) Do changes in maximal surface electromyographic activity express the specific training-induced adaptations of the exercise performed first during single-session combined training after 24-weeks, as well as, do these changes mimic those observed in maximal voluntary activation?

4) What is the effect of different intra-session exercise orders of prolonged concurrent training on the neuromuscular adaptations of explosive strength?

5.2 Research hypotheses

The hypotheses to the proposed research question are as follows:

1) Performing an intra-session exercise order of endurance-strength will inhibit strength capabilities during subsequent strength training exercises, resulting in chronic sub-optimal performance and, thus, attenuated maximal strength

development compared to gains accumulated by training strength-endurance after 24-weeks (e.g. Craig et al. 1991; Leveritt & Abernethy 1999b; Cadore et al. 2012).

2) Maximal descending neural drive, measured by super-imposed electrical stimulation and presented as quadriceps femoris voluntary activation, during maximal isometric strength does not change after performing an endurance-strength intra-session exercise while, alternatively, training strength-endurance voluntary activation increases over 24-weeks (e.g. Craig et al. 1991; Sidhu et al. 2009).

3) Maximal sEMG activity will mirror the changes in voluntary activation. The group training strength-endurance will increase maximal sEMG activity during maximal strength exercises while maximal sEMG activity in the endurance-strength groups does not change (e.g. Lepers et al. 2001; Cadore et al. 2010; Cadore et al. 2012).

4) Regardless of training order, explosive neural activation as well as explosive strength characteristics will be inhibited following the 24 week training period (e.g. Häkkinen et al. 2003; Mikkola et al. 2012).

6 METHODS AND MATERIALS

6.1 Study design

The total duration of the study was 26 weeks. To investigate the effects of the intra-session exercise sequence of concurrent training on both neural and strength characteristics adaptations, two training groups performed single-session concurrent strength and endurance training interventions with opposite exercise orders for a total of 24 weeks with a one-week preparatory training phase before the experimental training period (-1 to 0 weeks). All subjects were tested on three separate occasions during the 24-week training intervention, once before (0 weeks), in the middle (12 weeks) and at the end (24 weeks) of the training intervention using identical protocols for each testing session. However, some subjects were randomly selected and tested twice before the start of the training intervention (-2 and 0 weeks), which served as a control period, to ensure reliability and stability of certain performance measures. The overview of the study design is outlined in figure 25. During the control period no experimental training was carried out but subjects maintained their normal daily physical activities (e.g. walking and biking). All testing was completed on the same equipment with identical subject / equipment settings, at the same time of day and conducted by the same investigator. Only the methods used for the present study are described, as the study was part of a larger Ph.D. project for Moritz Schumann, M.Sc.

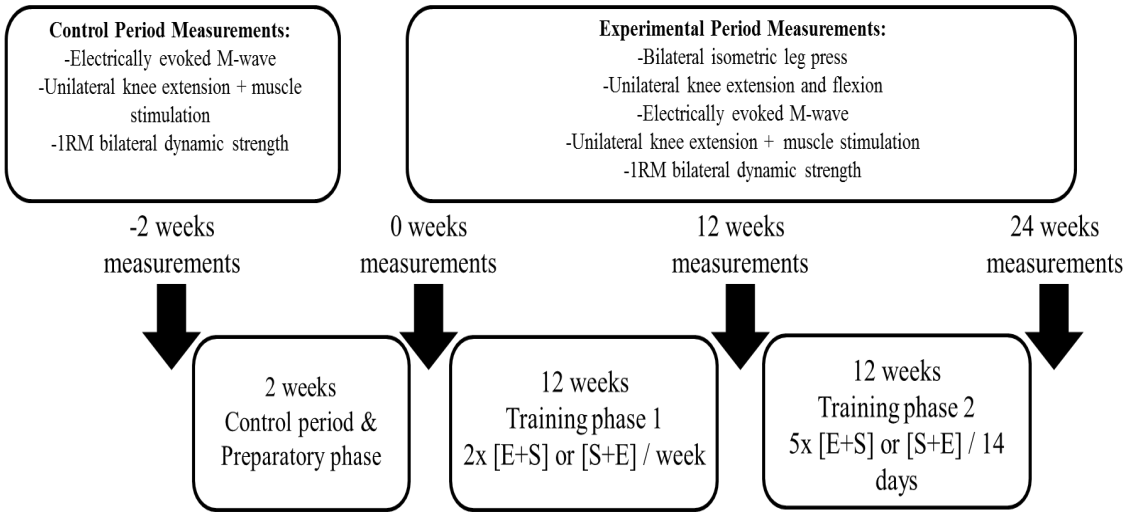

FIGURE 25. Schematic of the overall study design.

6.2 Subjects

Forty-two untrained, healthy men aged 18-40 years old were recruited for the study from the region around the city of Jyväskylä. Recruitment consisted of several public postings and notifications. To be eligible for participation, subjects needed to be recreationally active with no prior participation in a systematic / progressive strength or endurance training program for at least 12 months prior to the start of the study. Additional inclusion criteria required candidates to have a BMI less than 30kg/m^2, abstained from smoking for a minimum of 12 months prior to the study and free from pathology.

Candidate subjects completed phone interviews pertaining to their general health as well as underwent ECG and blood pressure testing conducted by project staff. All health questionnaires, ECG and blood pressure results were analyzed and approved by a cardiologist before subjects were allowed participation in the study. All approved subjects were carefully informed on the overall study design during a meeting with project coordinators and staff, which highlighted the possible benefits, risks and discomforts of participation. All subjects who understood and agreed to the information they had been given subsequently signed informed consent forms prior to the start of the study.

The subjects were assigned to one of the two training groups, either endurance exercise prior to strength training (E+S) or strength training prior to endurance exercise (S+E), by pairwise matching of anthropometric characteristics and results from measurements conducted at 0-weeks. However, due to subjects having to drop out for various reasons (e.g. injuries or personal reasons), 32 subjects completed the entire 24-week training intervention. In the end 14 subjects remained in the E+S groups (n = 14) and 18 in the S+E group (n = 18). The control period was completed by eight subjects (n = 8), randomly selected before experimental testing or training. The anthropometric data for the final 32 subjects, divided into their respective training groups, is presented in Table 1. Height was measured by a tape measure fastened to a wall (0.1 cm accuracy) with subjects standing up-right with feet hip width apart, heels against a wall and head in a neutral position. Weight was measured while subjects were in a 12-hour fasted stated with all heavy clothing and shoes removed (0.1 kg accuracy).

TABLE 1. Subject anthropometrics divided into training groups (E+S or S+E).

Group	n	Age (years)	Height (cm)	Weight (kg)	BMI (kg/m^2)
E+S	14	28.7 ± 5.5	178 ± 6	77.9 ± 9.3	24.6 ± 2.7
S+E	18	29.8 ± 4.4	179 ± 5	75.2 ± 8.5	23.5 ± 2.1

6.3 Strength and power measurements

A familiarization session took place one week before any testing sessions were completed. During the familiarization session subjects were carefully measured and set for all strength devices according to individual physical characteristics and were encouraged to complete several practice contractions in each device to familiarize themselves with the movements. Specific knee joint angles were manually measured for each of the strength measurement devices using a hand held goniometer, using the greater trochanter and lateral malleolus as the reference points. All settings, for each subject, were stored both manually on paper and digitally on a Windows-operated desktop computer to ensure settings were the same for each testing session (-2, 0, 12, and 24 weeks). All of the measurements described below were completed during each testing session, starting at 0 weeks, in the same order. However, the control period (-2 to 0 weeks) only tested certain performance variables (figure 25). During the testing sessions, subjects were reminded of proper technique for each strength measurement and were allowed to perform several warm-up contractions prior to maximal tests trials. Subjects were given strong verbal encouragement during all measurements to promote maximal effort.

6.3.1 Isometric strength

Isometric tests were performed for bilateral leg press, unilateral knee extension, and unilateral knee flexion. All strength measurements were completed with hip and knee joint angles of 110° and 107°, respectively. At least three maximal trials were completed with 1-minute rest in between trials for all measurements. If the third trial was greater than 5 % different from a previous trial then an additional trial was performed. A maximum of five trials was allowed. The best performance, in terms of maximal force, measured in Newtons (N), was used for further analysis. All maximum isometric force signals were passed in real-time to an analog-to-digital (AD) converter (Micro

1401, Cambridge Electronic Design, UK) and transferred to a Windows-operated desk-top computer and recorded by Signal 2.16 software (Cambridge Electronic Design, UK). Force signals were sampled at 2000 Hz and low-pass filtered (20 Hz).

Maximum bilateral isometric leg press force (MVC_{LP}) of the leg extensors (hip, knee, and ankle) was measured in a seated position using an electromechanical isometric leg press dynamometer device (figure 26; designed and manufactured by the University of Jyväskylä, Finland). Upon verbal command subjects were instructed to exert their maximal force as fast as possible maintaining for 3-4 seconds with correct form. Along with maximal force, the average force (N) produced during first 500 ms of the same contraction (AV_{500}) was measured to examine changes in rapid force production which was calculated from the force curve. A customized script was used to analyze the force curves for MVC_{LP} and AV_{500} (Signal version 2.16 software, Cambridge Electronic Design, UK).

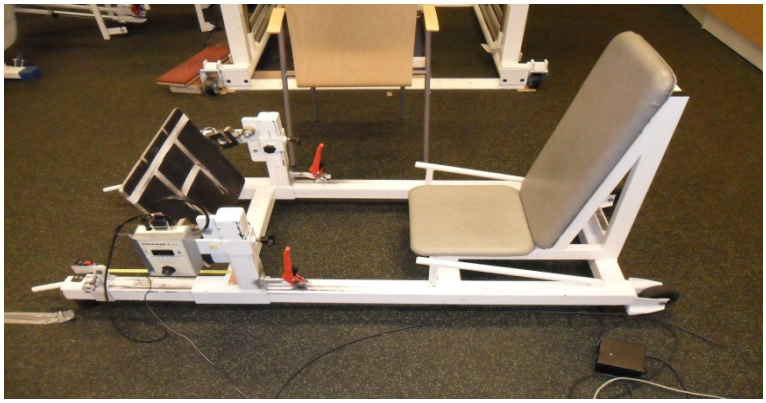

FIGURE 26. The bilateral isometric leg press device used in the study (designed and manufactured by the Department of Biology of Physical Activity, University of Jyväskylä, Finland).

A David 200 knee extension / flexion device (David Health Solutions Ltd., Helsinki, Finland) modified for isometric strength testing (Department of Biology of Physicial Activity, University of Jyväskylä, Finland) was used to measure maximum unilateral isometric knee extension (MVC_{KE}) and flexion (MVC_{KF}) force production from the right knee extensor and flexor muscles, respectively (figure 27). To avoid unrelated movements subjects were secured at the hip with a seatbelt and a pad across the top of the knee. For isometric knee extension, the ankle pad was located on anterior side for the leg in the curvature of the ankle above the dorsal side of the foot, and to avoid

swinging the ankle was strapped to the pad with a non-elastic band. During isometric knee extension, subjects were instructed to attempt to fully straighten their knee (straight knee joint angle = 180°). For isometric knee flexion the ankle pad was located on the posterior side of the leg, above the calcaneus, in the curvature of Achilles tendon. During the knee flexion measurement, subjects were instructed to try and touch their heel to the back of their leg. Upon verbal command subjects were instructed to exert their maximal force as fast as possible maintaining for 3-4 seconds with correct form for both contractions. The trials yielding the best performance in terms of maximal force production (N) were used for further analysis. Maximal force trials were analyzed by a customized script (Signal 2.16 software, Cambridge Electronic Design, UK).

FIGURE 27. David 200 knee extension and flexion device used in the study (David Health Solutions Ltd, Helsinki, Finland) modified for isometric strength testing (Department of Biology of Physical Activity, University of Jyväskylä, Finland).

Maximal isometric unilateral knee extension force (MVC_{VA}) for the right knee extensor muscles was also measured with muscle stimulation assessing voluntary activation using a low-compliant electromechanical isometric knee extension device (designed and manufactured by the Department of Biology of Physical Activity, University of Jyväskylä, Finland). Subjects were seated with a hip and right knee joint angle of 110° and 107°, respectively. The subjects left leg was lifted off the ground so that it was straight and supported by a chair (figure 28). Subjects were secured by a seatbelt at the hip, by a strapped pad over the right knee and with a Velcro strap, 2 cm above the lateral malleolus of the right leg, which secured the ankle and was connected to a strain gauge. Subjects performed three maximal knee extension trials and were instructed to increase

force gradually, reaching maximum voluntary force in ~3 s and maintaining for ~4 s. Force signals were sampled at 2000 Hz and low-pass filtered (20 Hz) and recorded on a Windows-operated desktop computer. Maximal force was manually analyzed on Signal version 4.04 (Cambridge Electronic Design, UK) as the greatest force value voluntarily achieved prior to the super-imposed muscle stimulation (see *Muscle stimulation* section for details).

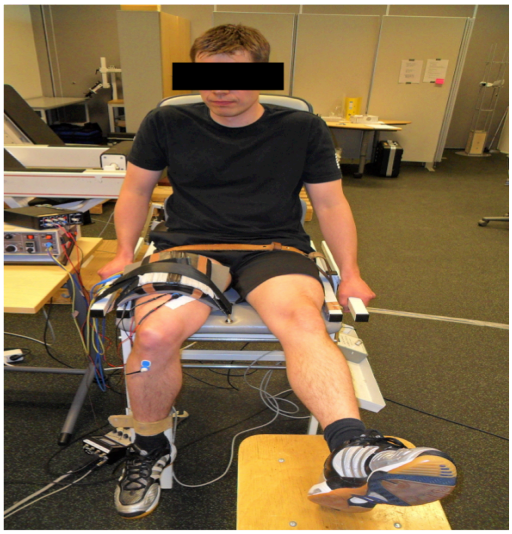

FIGURE 28. The electromechanical isometric knee extension device (designed and manufactured by the Department of Biology of Physical Activity, University of Jyväskylä) used to measure maximal isometric knee extension force during the assessment of voluntary activation through super-imposed muscle stimulation.

6.3.2 Dynamic strength

One repetition-maximum (1-RM) bilateral concentric strength of the leg extensors (hip, knee, and ankle) was measured using a David 210 leg press (figure 29; David Health Solutions Ltd., Helsinki, Finland). The subjects were in a seated position with starting knee angles of ~60º (± 2°). Subjects performed three warm-up sets with progressively increasing loads (1 x 5 x 70-75% estimated 1-RM, 1 x 3 x 80-85% estimated 1-RM, 1 x 2 x 90-95% estimated 1-RM) in preparation for the maximal trials. On verbal command, subjects performed a dynamic concentric leg extension trying to reach full leg extension (straight knee joint angle = 180° and hip angle = 110°) against a resistance determined by a load (kg) keeping constant contact with the seat and back rest of the leg press. After each successful repetition, the load was increased in increments until the subject was

no longer able to reach full leg extension with an accuracy of 1.25 kg. A 1-minute rest period was given in between each warm-up and maximal trial. The last acceptable trial with the highest load was determined as the 1-RM. A maximum of five trials was allowed. In addition to the bilateral isometric leg press, concentric leg press strength was measured because the strength training during the intervention was dynamic.

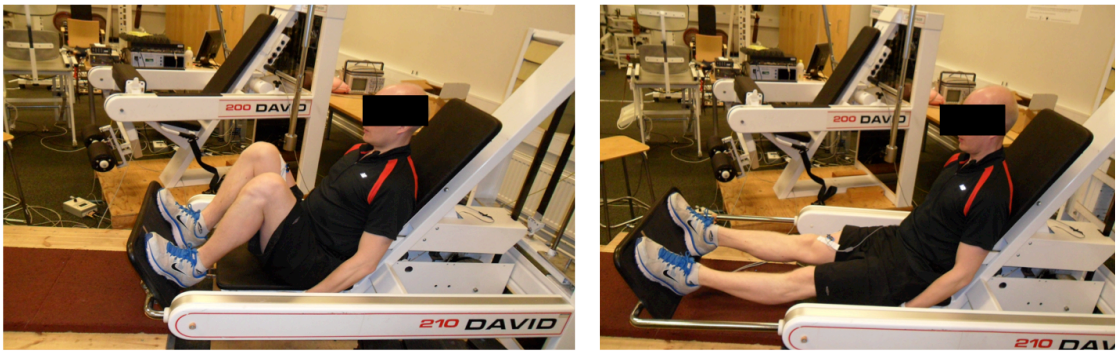

FIGURE 29. *Left*, Bilateral concentric leg press starting position (knee joint angle of ~60 ± 2°) on a David 210 leg press device (David Health Solutions Ltd, Helsinki, Finland). *Right*, The final position with full leg extension (straight knee joint angle = 180°).

6.4 Electrical stimulation

6.4.1 Nerve stimulation.

Maximal peak-to-peak M-wave amplitude (M_{max}) of the right leg vastus lateralis muscle (VL) was assessed using femoral nerve stimulation (figure 30). Maximal M-wave is the electrical equivalent of recruiting all MUs of the MN pool of a given muscle and presumably does not change in response to training (Palmieri et al. 2005; Calder et al. 2005). Subjects were instructed to stand fully upright with feet hip width apart and their bodyweight dispersed equally between both legs. A hand-held stimulating cathode (1 cm diameter) was placed firmly into the femoral triangle at the point that gave the strongest response to sub-maximal stimulation pulses of 30 - 50 mA. The anode (5.08 x 10.16 cm V-trode, Mettler Electronic Corp, USA) was placed over the greater trochanter of the right leg. Stimulation intensity was increased in 10 mA stages (1-ms single-pulse, 400 V) by a constant-current stimulator (Model DS7AH, Digitimer Ltd, UK) until there was a clear plateau in the M-wave peak-to-peak amplitude. Thereafter, an additional 25% of stimulation intensity was applied to ensure maximal effect. At this

point three supra-maximal stimulations were taken with 10 s between each pulse. The mean of the three supra-maximal stimulations was used to represent M_{max}. During all measurement sessions (-2, 0, 12, and 24 weeks) M_{max} was measured. All sEMG variables (see *EMG measurements* for details) for the VL muscle were normalized to the corresponding testing session's M_{max} response to account for inter-session sEMG measurement sources of error (e.g. De Luca 1997; Gandevia 2001).

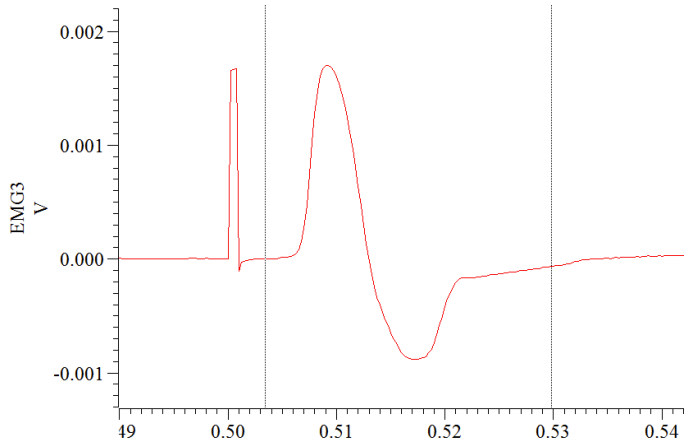

FIGURE 30. An example of the recorded maximal M-wave response of VL muscle from femoral nerve stimulation, between the two vertical cursors.

6.4.2 Muscle stimulation.

Voluntary activation (VA) of the quadriceps femoris muscles (QF), was evaluated using muscle stimulation performed by placing four self-adhesive electrodes (6.98 cm V-trodes, Mettler Electronics Corp, USA) on the proximal and mid regions of the quadriceps muscle belly of the right leg (figure 31). Single 1-ms rectangular pulses, increasing in 5 mA increments were delivered during rest, by the same constant-current stimulator as nerve stimulation (400V, Model DS7AH, Digitimer Ltd, UK) until a plateau in twitch force was observed. An additional 25 % of stimulation intensity was added to the current identified to produce maximum twitch force to ensure maximal effect for the knee extension trials. During the unilateral maximum isometric knee extension trials the supra-maximal single-pulse electrical stimulation was delivered three separate times: 3 s before voluntary knee extension while at rest, during the plateau of maximal voluntary force during knee extension and then again 5 s after the end of the contraction (e.g. Merton 1954). The level of QF VA was manually analyzed from the additional force

produced by the electrical twitch superimposed during the maximum knee extension (P_{ts}) and the maximum force produced by the subsequent resting twitch (P_t) using the formula by Harridge et al. (1999): VA % = (1 – (P_{ts} / P_t)) × 100. This technique is otherwise known as the super-imposed twitch method (SIT).

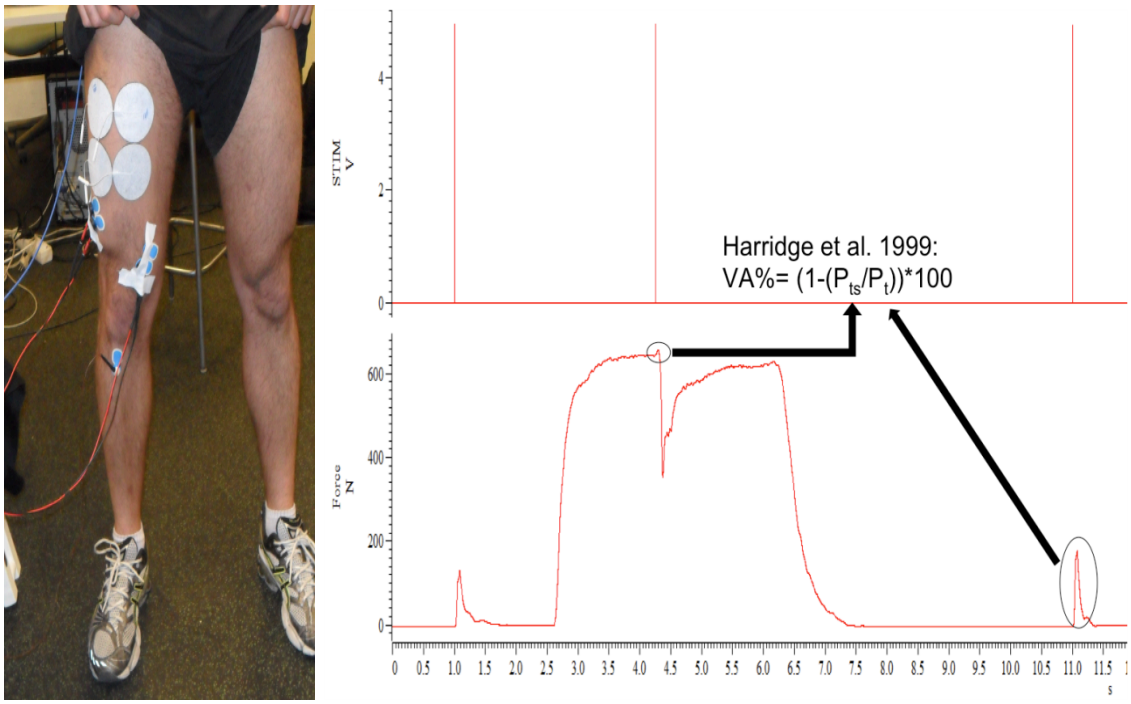

FIGURE 31. *Left*, The positioning of stimulating electrodes and sEMG electrodes for the muscle stimulation. *Right*, Signals from super-imposed twitch method using muscle stimulation: stimulation recordings (*top*) and force recording with the twitches used for VA% assessment highlighted (*bottom*).

6.5 Electromyography

Surface Electromyography (sEMG) was used to measure muscle activity of the VL and biceps femoris (BF) muscles of the right leg during the multiple strength measurements. During the familiarization session the VL and BF motor points of the right leg were measured according to Surface Electromyography for the Non-Invasive Assessment of Muscles (SENIAM) guidelines, and marked with indelible ink tattoos to ensure electrode position was similar throughout the 26-week period (Häkkinen & Komi 1983). The VL sEMG position was on the motor point, two-thirds of the distance on the line between the anterior spina iliaca superior to the lateral side of the patella. The BF sEMG position was on the motor point, one-half of the distance on the line between the

ischial tuberosity and the lateral epicondyle of the tibia. (Hermens et al. 1999.) Shaving, skin abrasion and application of alcohol, to clean the skin, preceded electrode placement. A Bipolar configuration of Al / AgCl electrodes (20mm inter-electrode distance, inter-electrode resistance < 5 kΩ, Blue Sensor N ECG Electrodes, Ambu A/S, Denmark) were adjusted over the motor points so that the tattoo was directly between the detecting surfaces of the electrodes and were placed parallel to the assumed pennation angle of the underlying muscle fibers of the corresponding muscle.

The sEMG activity of the agonist VL muscle was recorded during bilateral isometric leg press tests and unilateral knee extension (performed without the super-imposed electrical stimulation). Additionally, during the same unilateral knee extension measurement, the BF muscle was recorded for the assessment of antagonist co-activation. The raw sEMG signals from these measurements were amplified by 1000 and sampled at 3000 Hz. The signals were passed from a portable transmitter, worn around the subjects' waist to a receiver box (Telemyo 2400R, Noraxon, Scottsdale, AZ, USA) from which the signal was relayed to a desktop computer via an AD converter (Micro 1401, Cambridge Electronic Design, UK). Analysis of the isometric sEMG was performed using a customized script (Signal 2.16, Cambridge Electronic Design, UK) and converted to integrated sEMG (iEMG). Maximum iEMG, in mV•s, was determined from the 500-1500 ms time period of contractions representing the peak force phase for isometric bilateral leg press (VL) and unilateral knee extension (VL and BF). The iEMG from the isometric bilateral leg press was also analyzed for the first 500 ms of the contraction (0-500 ms), to assess rapid neural activation. To assess changes in antagonist co-activation during knee extension, similar analysis was completed to measure the maximal iEMG while the BF acted as an agonist during unilateral isometric knee flexion. Antagonist co-activation during the isometric knee extension action was calculated as a percentage through the Häkkinen et al. (1998a; 1998b) equation: co-activation % = (iEMG of the BF during isometric knee extension / iEMG of the BF during isometric knee flexion) * 100.

During the assessment of M_{max} and VA, sEMG was measured from the VL muscle and multiplied by 1000 by a preamplifier (NeuroLog Systems NL844, Digitimer Ltd, UK) and sampled at a frequency of 2000 Hz. Signals were passed to an AD converter (Micro 1401, Cambridge Electronic Design, UK) and recorded by Signal 4.04 software (Cam-

bridge Electronic Design, UK) on a Windows-operated desktop computer. The raw sEMG signals from the unilateral isometric knee extension with super-imposed electrical twitch, were band-pass filtered (20–350 Hz) and, due to technical reasons, converted to root mean square (rmsEMG; mV) during a 500 ms epoch (i.e. time frame) immediately before the super-imposed twitch (figure 32) manually on Signal 4.04 software (Cambridge Electronic Design, UK). The raw sEMG signals from nerve stimulation, assessing M_{max}, were only analyzed for peak-to-peak amplitude in mV (i.e. largest positive peak to largest negative peak).

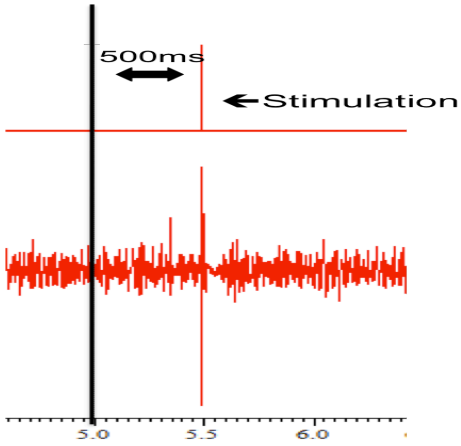

FIGURE 32. Example of 500 ms epoch sEMG from MVC_{VA}.

6.6 Training

Training consisted of 24 weeks of single-session combined strength and endurance training, divided into two 12-week phases (phase I and II). Prior to the start of the experimental training period there was a one-week preparatory training phase in which all subjects completed one session of combined training. The experimental training period consisted of progressive and periodized strength and endurance training. During training phase one subjects completed training 2 - combined training sessions / week of either [1E + 1S] or [1S + 1E], depending on their assigned groups. During training phase two, training frequency was increased to 5 - combined sessions / 14 - days, continuing in the same training groups. All training sessions were supervised by project staff.

The strength-training program targeted mainly muscle hypertrophy and maximal strength components of fitness. Strength exercises were performed for all major muscle

groups with special focus on the knee extensors and flexors. Three leg exercises (leg press, leg extension and leg curl) and seven exercises for the other main muscle groups (dumbbell flys, lateral pulldowns, military press, bicep curls, triceps pushdowns as well as trunk flexor and extensor exercises). Strength exercises utilized both resistance exercise machines and free weights.

Endurance training was continuous cycling exercise completed using magnetic resistance cycle ergometers. Training intensity for endurance exercise was controlled by heart rate zones that had been determined by bicycle ergometer endurance tests on a separate occasion (*endurance performance data not shown in this study*).

Preparatory training (-1 – 0 weeks): Strength training consisted of exercises using intensities between 30 - 50% 1-RM targeting strength-endurance as well as including 1 to 2 sets with load intensities of 80-95% 1-RM. Additionally, the endurance exercise was performed below the aerobic threshold for 45 min per session.

Combined training phase I (0 - 12 weeks): Strength training began with light resistances using 40 - 60% 1-RM loads during the first 2 weeks and systematically increased to 60 - 80% 1-RM loads during weeks 4 - 7 and continuing to 80 - 95% for weeks 7 - 12. Explosive power exercises were included during weeks 10 - 12 ranging in intensity from 30 to 40% 1-RM. Endurance training was continuous cycling set at intensities for subjects to train between the aerobic and anaerobic thresholds for 30 – 50 minutes per session.

Combined training phase II (13 - 24 weeks): The training program from the combined training phase I was repeated, however, the training frequency (5 x [1E + 1S] or [1S + 1E] / 14 days) and intensities were increased. Endurance training was continuous and interval-type cycling set at intensities for subjects to train between the aerobic and anaerobic thresholds and above for 30 – 50 minutes per session.

6.7 Statistical analysis

All data was analyzed and graphed on Microsoft Excel 2008 (Microsoft Corporation, Redmond, Washington, USA), as well as, calculating the means and standard deviation (SD). All data is presented as mean ± SD. Normal distribution of the data was calculated using the Shapiro-Wilk test for normality. To assess stability of important dependent variables, results from the two-control period measurement sessions (-2 and 0 weeks) were compared using Student's paired t-tests as well as calculating the coefficient of variation (CV) to check reproducibility. The training-related differences, between 0, 12 and 24 weeks, were checked using repeated measures multivariate analysis of variance (RM-MANOVA) for within-group and between-group differences. All within-group data changes were analyzed using the absolute values, while between-group differences were calculated using relative values to 0-weeks and 12-weeks. Pearson product-moment correlations coefficients were assessed for VA and MVC_{VA}. IBM SPSS Statistics version 20 (IBM Corporation, Armonk, New York, USA) was used for all statistical analysis. Significance was accepted when *$p<0.05$, **$p<0.01$ and ***$p<0.001$.

7 RESULTS

7.1 Control measurements and reproducibility

There were no significant increases in any variables measured during the control period (-2 to 0 weeks) ($p>0.05$) except for normalized maximum VL rmsEMG (rmsEMG/ M_{max}) during isometric knee extension (MVC_{VA}) in which muscle activity increased (paired t-test, $p<0.05$). VA and 1-RM significantly decreased during the control period ($p<0.05$). Results and CV of the measured variables are presented in Table 2.

TABLE 2. Results and CV of measurements from the control period (-2 to 0 weeks). *$p<0.05$.

	n	-2 weeks	0 weeks	CV (%)
1-RM (kg)	8	151.3 ± 31.4	142.8 ± 32.6*	4.8
MVC_{VA} (N)	8	608 ± 88	595 ± 97	6.9
M_{max} (mV)	5	1.39 ± 0.17	1.37 ± 0.51	20.3
VL rmsEMG (mV)	7	0.29 ± 0.09	0.31 ± 0.07	28.1
Normalized VL rmsEMG ratio (rmsEMG/ M_{max})	4	0.22 ± 0.06	0.28 ± 0.06*	12.2
VA (%)	8	91.3 ± 5.8	87.3 ± 10.5*	5.8

7.2 Maximal strength and power

7.2.1 Maximal unilateral isometric knee extension force with muscle stimulation

The E+S group significantly increased maximum isometric knee extension force (MVC_{VA}) during weeks 0 to 12 by 8% ($p<0.05$) and by 7% ($p<0.05$) from 618 ± 66N during weeks 0 to 24 (figure 33, table 3). The S+E group significantly increased MVC_{VA} by 9% during weeks 0 to 12 ($p<0.05$) and during weeks 0 to 24 by 14% ($p<0.01$) from 560 ± 91N. There were no significant differences between the E+S and S+E at any time point ($p>0.05$).

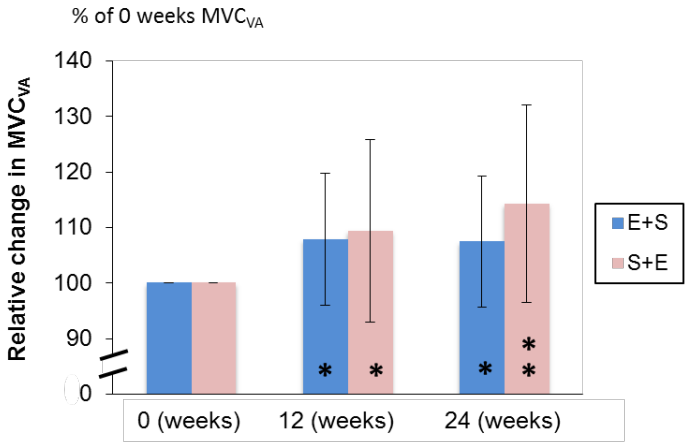

FIGURE 33. Mean (± SD) relative changes in MVC_{VA} for E+S and S+E during the 24-week training period. Data presented as a percentage of the initial value at 0 weeks. * = significant from 0 weeks. *p<0.05; **p<0.01.

7.2.2 Bilateral concentric leg press 1-RM

The E+S group significantly increased bilateral concentric 1-RM leg extension (1-RM) load by 8% during 0 to 12 weeks (p<0.001) and by 13% during 0 to 24 weeks from 160.0 ± 28.5 kg (figure 34, table 3). During weeks 0 to 12 the S+E group significantly increased 1-RM load by 12% (p<0.001) and by 17% during weeks 0 to 24 (p<0.001) from 143.0 ± 23.2 kg. Both groups also significantly increased 1-RM load (p<0.01) during weeks 12 to 24. No significant between group differences were found at any time point (p>0.05).

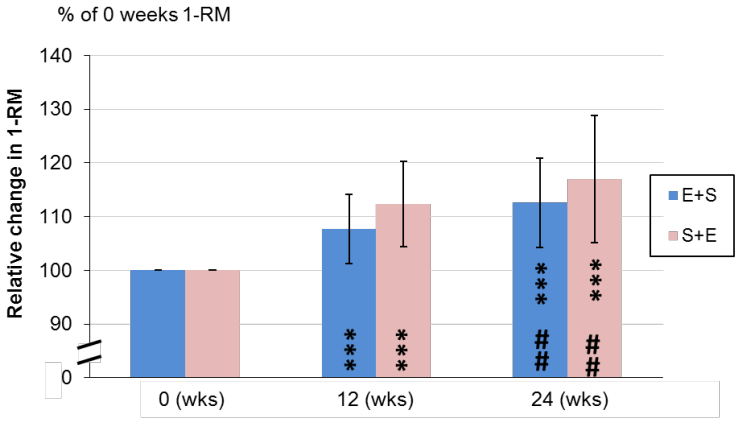

FIGURE 34. Mean (± SD) relative changes in 1-RM for E+S and S+E during the 24-week training period. Data presented as a percentage of the initial value at 0 weeks. * = significant from 0 weeks; # = significant from 12 weeks. ***p<0.001; ##p<0.01.

TABLE 3. Mean absolute values (± SD) from all strength tests during training weeks 0 to 24 for E+S and S+E. Data is presented as mean ± SD. * = significant from 0 weeks; # = significant from 12 weeks; † = significant between groups. *p<0.05; **p<0.01; ***p<0.001; #p<0.05; ##p<0.01; †p<0.05.

	E+S				S+E			
	n	**0-week**	**12-week**	**24-week**	**n**	**0-week**	**12-week**	**24-week**
1-RM (kg)	14	160.0 ± 28.5	171.3 ± 26.9***	178.8 ± 27.0 ***##	18	143.0 ± 23.2	159.6 ± 21.4***	165.6 ± 20.4***##
MVC_{VA} (N)	14	618 ± 66	681± 120*	690 ± 150*	18	560 ± 91	602 ± 58*	632 ± 32**
MVC_{LP} (N)	14	2689 ± 671	3051 ± 783**	3080 ± 824***	18	2345 ± 537	2545 ± 533**	2611 ± 564**
AV_{500} (N)	14	1794 ± 480†	2060 ± 472***	2022 ± 521*	18	1521 ± 378	1744 ± 274***	1813 ± 327**
MVC_{KE} (N)	14	861 ± 152	892 ± 113	924 ± 125#	18	789 ± 163	827 ± 96	868 ± 155*#
MVC_{KF} (N)	14	383 ± 96†	412 ± 59	421 ± 71	17	327 ± 71	353 ± 70*	368 ± 67**

1-RM = One-repetition maximum bilateral concentric leg press

MVC_{VA} = Maximal unilateral isometric knee extension force performed before SIT

MVC_{LP} = Maximum bilateral isometric leg press force

AV_{500} = Average force produced during the first 500 ms of MVC_{LP}

MVC_{KE} = Maximum unilateral isometric knee extension force without SIT

MVC_{KF} = Maximum unilateral isometric knee flexion force

7.2.3 Maximal and rapid bilateral isometric leg press force

The E+S group significantly increased maximal isometric leg press force (MVC_{LP}) by 14% and 15% ($p<0.01$) from 2689 ± 671N during weeks 0 to 12 and 0 to 24, respectively (figure 35, table 3). The S+E group significantly increased MVC_{LP} by 10% and 13% ($p<0.01$) during weeks 0 to 12 weeks and 0 to 24 weeks, respectively, from 2345 ± 537N. There were no significant between group differences detected at any time point ($p>0.05$).

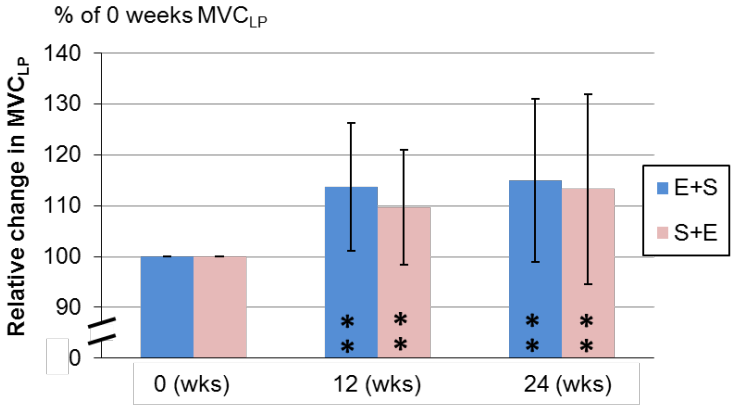

FIGURE 35. Mean (± SD) relative changes in MVC_{LP} for E+S and S+E during the 24-week training period. Data presented as a percentage of the initial value at 0 weeks. * = significant from 0 weeks. **$p<0.01$.

There was a significant difference at 0-week for the average force produced during the first 500ms of isometric leg press (AV_{500}) between the E+S [1794 ± 480 N] and S+E [1521 ± 378 N] groups ($p<0.05$). During weeks 0 to 12 and 0 to 24 E+S significant increased AV_{500} by 17% ($p<0.01$) and 16% ($p<0.05$), respectively, from 1794 ± 480N (figure 36, table 3). The S+E group increased AV_{500} by 19% ($p<0.001$) and by 24% ($p<0.01$) from 1521 ± 378N during weeks 0 to 12 and 0 to 24 weeks, respectively. There were no significant differences detected between E+S or S+E during the experimental training period ($p>0.05$).

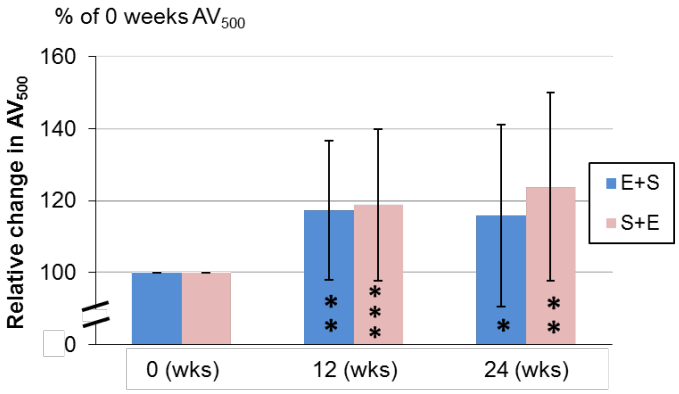

FIGURE 36. Mean (± SD) relative changes in AV_{500} for E+S and S+E during the 24-week training period. Data presented as a percentage of the initial value at 0 weeks. * = significant from 0 weeks. *p<0.05; **p<0.01; ***p<0.001.

7.2.4 Maximal unilateral isometric knee extension and flexion force

The E+S training group significantly increased maximal isometric knee extension force (MVC_{KE}) by 4% (p<0.05) from 892 ± 113N during weeks 12 to 24 (figure 37, table 3). Over the entire 24-week training period an increase of 9% from 861 ± 152N in the E+S group approached significance (p=0.066). S+E significantly increased MVC_{KE} by 12% (p<0.05) from 789 ± 163N during weeks 0 to 24. There were no significant differences at any time point between the E+S or S+E groups (p>0.05).

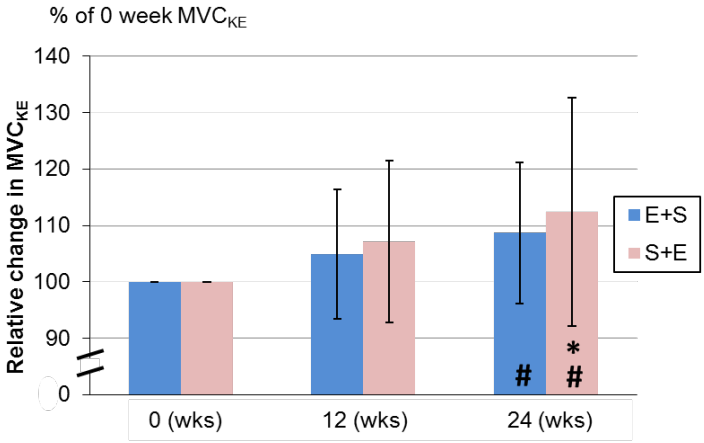

FIGURE 37. Mean (± SD) relative changes in MVC_{KE} for E+S and S+E during the 24-week training period. Data presented as a percentage of the initial value at 0 weeks. * = significant from 0 weeks; # = significant from 12 weeks. *p<0.05; #p<0.05.

At week 0 maximal isometric knee flexion strength in E+S was significantly greater than in the S+E group ($p<0.05$). Unilateral isometric knee flexion force (MVC_{KF}) significantly increased in S+E by 9% ($p<0.05$) and by 15% ($p<0.01$) from 327 ± 71N during weeks 0 to 12 weeks and 0 to 24, respectively (figure 38, table 3). There were no significant increases for E+S in MVC_{KF}. There were no significant differences between E+S and S+E over the course of the entire training period ($p>0.05$).

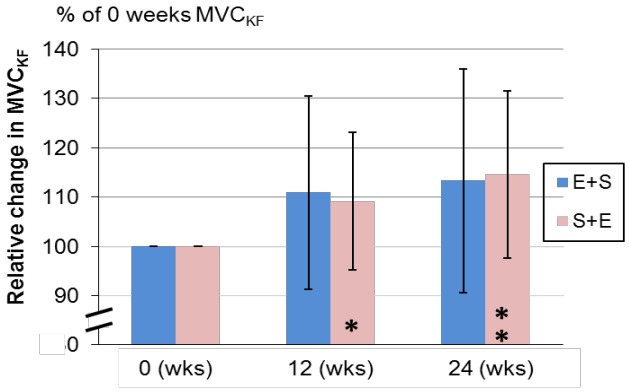

FIGURE 38. Mean (± SD) relative changes in MVC_{KF} for E+S and S+E during the 24-week training period. Data presented as a percentage of the initial value at 0 weeks. * = significant from 0 weeks. *p<0.05;**p<0.01.

7.3 Neural measurements

7.3.1 Maximal M-wave

There were no significant changes in M_{max} of the VL muscle during weeks 0 to 24 weeks in either E+S [1.10 ± 0.55mV to 1.26 ± 0.55mV] or S+E [1.23 ± 0.55mV to 1.37 ± 0.55mV] ($p>0.05$) (figure 39).

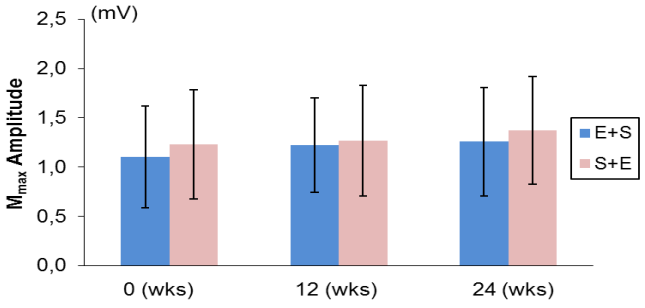

FIGURE 39. Mean absolute (± SD) M_{max} amplitudes of the right VL muscle during the 24-week training period for E+S and S+E.

7.3.2 Maximal VL rmsEMG

Over the entire 24-week training period the E+S group experienced a non-significant 2% increase in rmsEMG amplitude of the VL during MVC_{VA} [0.30 ± 0.08mV to 0.30 ± 0.09mV] (figure 42). E+S displayed a significant increase during weeks 0 to 12 by 16% [0.30 ±0.08mV to 0.34 ± 0.10mV] ($p<0.01$), but during weeks 12 to 24 a significant decrease of 11% in maximal rmsEMG amplitude was observed [0.34 ± 0.10mV to 0.30 ± 0.09mV] ($p<0.05$). A significant increase of 26% [0.27 ± 0.08mV to 0.33 ± 0.08mV] ($p<0.01$) in maximal rmsEMG amplitude of VL was observed in the S+E group during weeks 0 to 24. This change over the whole 24-week period was coupled with a significant increase of 11% [0.31 ± 0.09mvV to 0.33 ± 0.09mV] ($p<0.05$) in maximal rmsEMG amplitude from weeks 12-24 in the S+E group. During the last 12-week training period (12-24 weeks) a significant difference between groups was detected in the change of maximal rmsEMG amplitude as S+E had increased maximal rmsEMG of the VL by 32% and E+S by 2% ($p<0.001$).

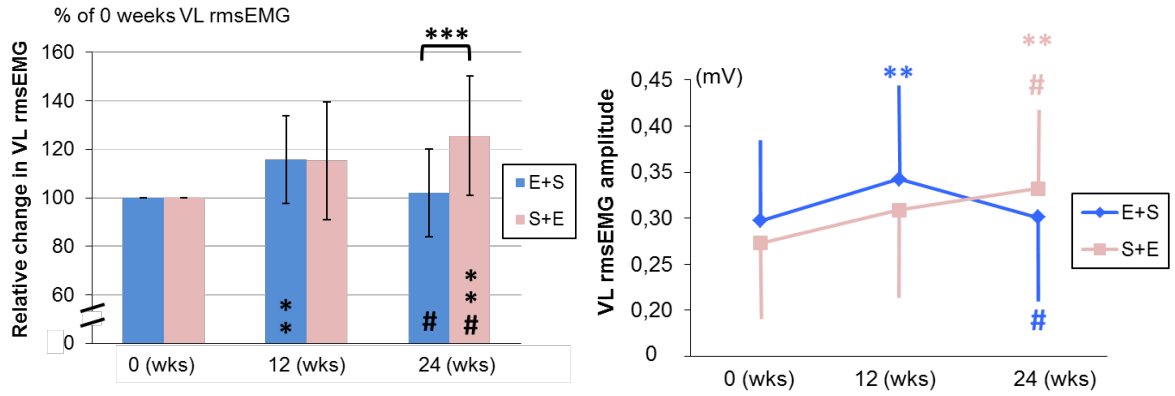

FIGURE 42. Mean (± SD) relative changes (*left*) in maximal rmsEMG amplitude and mean (± SD) absolute values (*right*) of the right VL muscle during a 500 ms epoch of unilateral isometric knee extension during the 24-week training period for E+S and S+E. Relative changes are presented in relation to 0 weeks values. * = significant from 0 weeks # = significant from 12 weeks. ⌐ = between group differences. ***$p<0.001$ and #$p<0.05$.

When maximal rmsEMG amplitude of the VL was normalized to M_{max} (rmsEMG / M_{max}) there were non-significant changes of -11% [0.29 ± 0.12 to 0.25 ± 0.11] in E+S and 10% [0.28 ± 0.11 to 0.30 ± 0.15] in S+E ($p>0.05$) after 24 weeks of training (figure 43). A large difference in changes to normalized rmsEMG of VL approached significance ($p=0.058$) between the E+S and S+E groups during weeks 12 to 24.

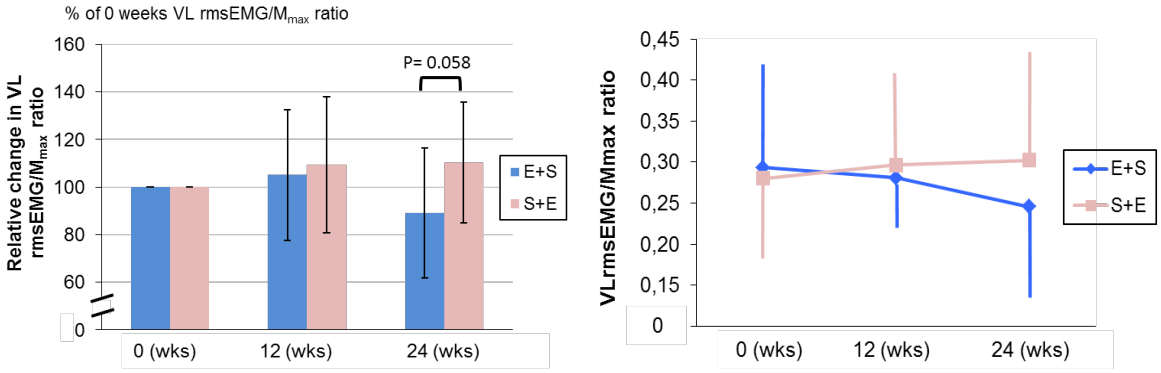

FIGURE 43. Mean (± SD) relative changes (*left*) in maximal rmsEMG amplitude normalized to M_{max} and the mean (± SD) rmsEMG / M_{max} ratios (*right*) of the right VL muscle during a 500 ms epoch of unilateral isometric knee extension during the 24-week training period for E+S and S+E. Relative changes are presented in relation to 0 weeks values.

7.3.4 Bilateral isometric leg press iEMG

Bilateral isometric leg press VL iEMG 500-1500 ms. The E+S training group displayed a significant increase of 23% [0.28 ± 0.12 mV•s to 0.33 ± 0.09mV•s] in maximal VL iEMG during the peak force phase during weeks 0 to 12 (figure 44). Over the entire 24-week training period a non-significant increase of 23% [0.28 ± 0.12 mV•s to 0.32 ± 0.10mV•s] ($p>0.05$) in E+S was observed. Significant increases took place in the maximal iEMG amplitude of the VL muscle during the peak force phase in the S+E group as a significant increase of 38% [0.30 ± 0.15 mV•s to 0.39 ± 0.15mV•s] ($p<0.001$) during weeks 0-24. This increase in maximal iEMG amplitude over the whole 24-week training period in S+E was coupled with a significant increase of 16% [0.35 ± 0.09 mV•s to 0.39 ± 0.15mV•s] ($p<0.05$) during weeks 12 to 24 weeks. There were no significant differences detected between E+S or S+E at any time point.

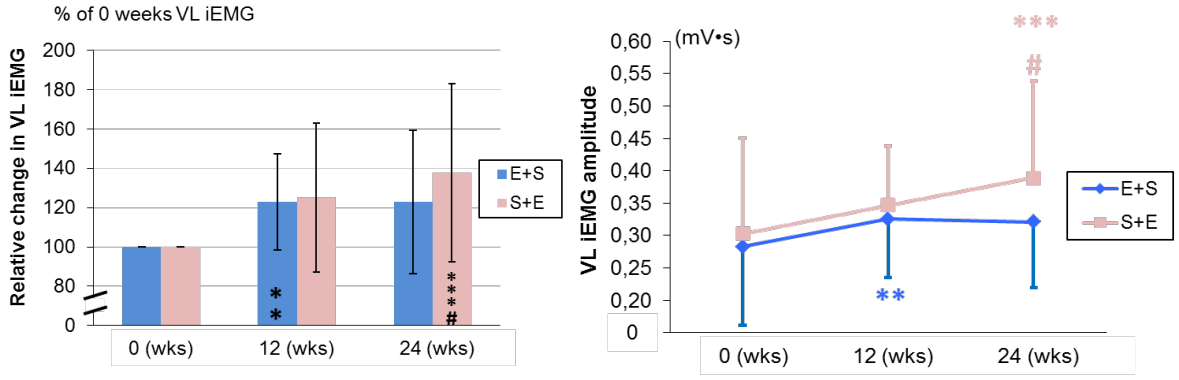

FIGURE 44. Mean (± SD) relative changes (*left*) in bilateral isometric leg press 500-1500 ms maximal iEMG amplitude and mean (± SD) absolute values (*right*) of the right VL muscle during the 24-week training period in E+S and S+E. Relative changes are presented in relation to 0 weeks values. * = significant from 0 weeks # = significant from 12 weeks. **p<0.01 ***p<0.001 and #p<0.05.

The maximal VL iEMG amplitude normalized to M_{max} (iEMG / M_{max}) during the peak force phase for bilateral isometric leg press displayed non-significant increases of 7% and 17% (p>0.05) over the 24-week training period for E+S [0.27 ± 0.08 to 0.29 ± 0.13] and S+E [0.28 ± 0.12 to 0.31 ± 0.13], respectively (figure 45).

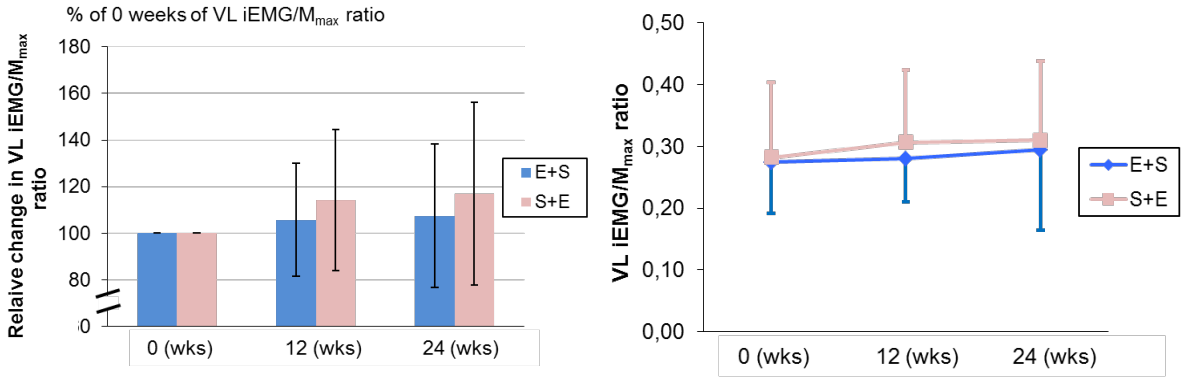

FIGURE 45. Mean (± SD) Relative changes (*left*) in maximal 500-1500 ms iEMG normalized to M_{max} and the iEMG / M_{max} ratios (*right*) of the right VL muscle during bilateral isometric leg press during the 24-week training period for E+S and S+E. Relative changes are presented in relation to 0 weeks values.

Bilateral isometric leg press VL iEMG 0-500 ms. E+S displayed a significant increase of 17% [0.13 ± 0.06 mV•s to 0.15 ± 0.05mV•s] (p<0.05) during weeks 0 to 12 and a non-significant increase of 23% [0.13 ± 0.06 mV•s to 0.15 ± 0.05mV•s] (p>0.05) during weeks 0 to 24 (figure 46). After the 24-week training period the S+E group significantly increased 0-500ms VL

iEMG amplitude by 39% [0.14 ± 0.06 mV•s to 0.15 ± 0.05mV•s] ($p<0.01$). There were no significant differences detected between E+S and S+E at any time during the training.

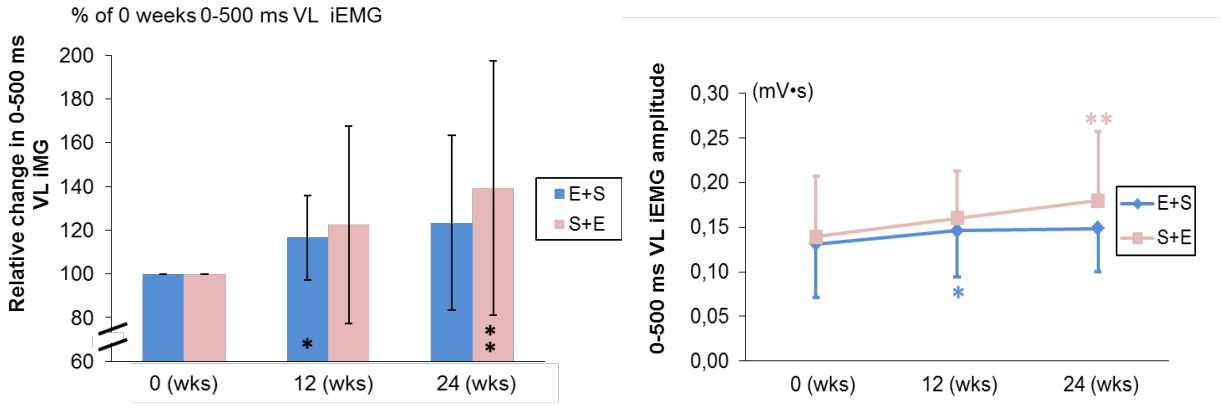

FIGURE 46. Mean (± SD) relatvie changes(*left*) for rapid 0-500 ms iEMG amplitude and absolute values (*right*) of VL during bilateral isometric leg press throughout the 24-week training priod for E+S and S+E. Relative changes are presented in relation to 0 weeks values. * = significant from 0 weeks. *p<0.05 and **p<0.01.

The 0-500 ms iEMG ampltiude of the VL muscle normalized to M_{max}, remained statistically unchanged ($p>0.05$) with increases of 6% [0.13 ± 0.06 to 0.13 ± 0.06] and 15% [0.13 ± 0.06 to 0.14 ± 0.07] in E+S and S+E, respectively (figure 47). No differences between E+S and S+E at any time point during the training period.

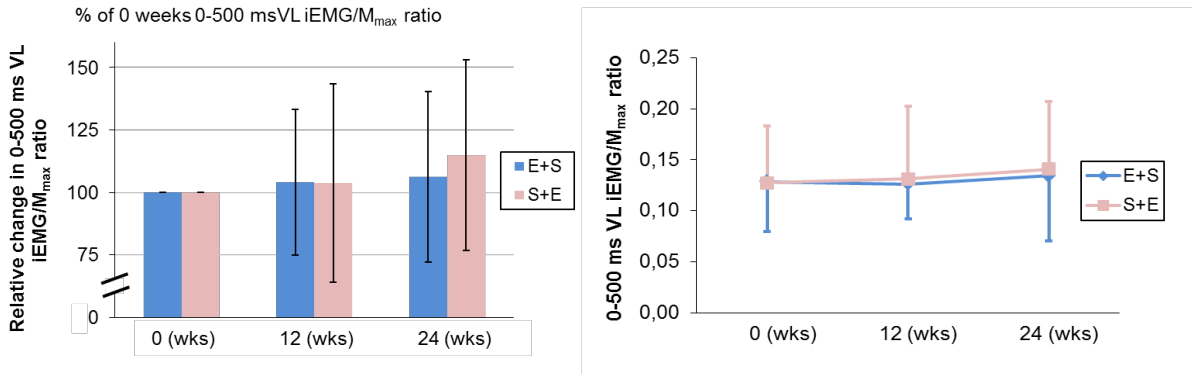

FIGURE 47. Mean (± SD) relative changes (*left*) in the rapid 0-500 ms iEMG normalized to M_{max} and iEMG / M_{max} ratios (*right*) of the right VL muscle during bilateral isometric leg press during the 24-week training period in E+S and S+E. Relative changes are presented in relation to 0 weeks values.

7.3.5 Unilateral isometric knee extension and flexion 500-1500 ms iEMG

Unilateral knee extension VL 500-1500 ms iEMG. Over the 24-week training period the maximal iEMG amplitude of VL during the peak force phase of 500-1500ms, S+E experienced significant increases of 22% [0.23 ± 0.09 mV•s to 0.29 ± 0.16mV•s] ($p<0.05$) and 39% [0.23 ± 0.09 mV•s to 0.32 ± 0.17mV•s] during weeks 0 to 12 weeks and 0 to 24, respectively (figure 48). There were non-significant ($p>0.05$) increases of 25% and 14% [0.24 ± 0.10 mV•s to 0.25 ± 0.07mV•s] for E+S during weeks 0 to 12 and 0 to 24, respectively. There was a significant difference between E+S and S+E in the change of maximal iEMG amplitudes of VL during weeks 12 to 24 weeks ($p<0.01$).

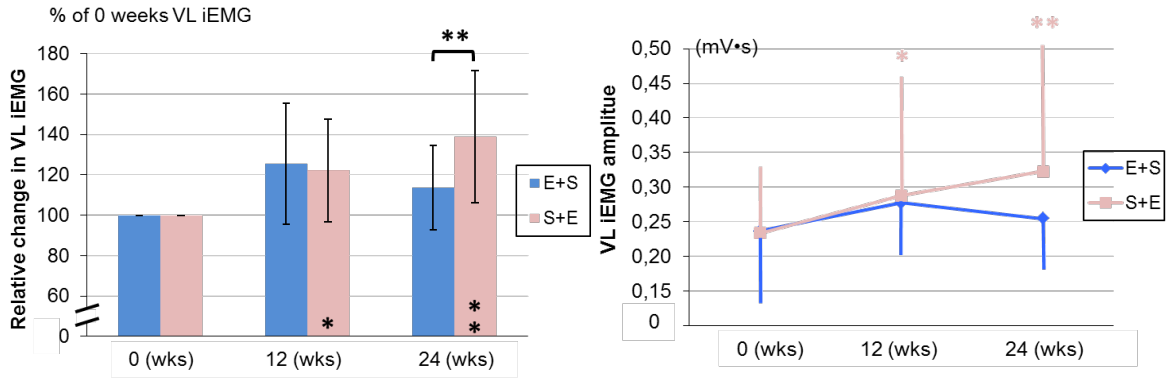

FIGURE 48. Mean (± SD) relative changes (*left*) in maximal 500-1500 ms iEMG amplitude and absolute values (*right*) of the right VL muscle during unilateral knee extension throughout the 24-week training period for E+S and S+E. Relative changes are presented in relation to 0 weeks values. * = significant from 0 weeks. *$p<0.05$ and **$p<0.01$.

When the maximal iEMG amplitude of VL was normalized to M_{max} (iEMG / M_{max}) the S+E group displayed no significant increases during the 24-week training period, however, during weeks 0-24 an increase in normalized iEMG amplitude of 21% [0.22 ± 0.09 to 0.26 ± 0.10] approached significance ($p=0.063$) (figure 49). The E+S group displayed non-significant ($p>0.05$) changes of 14% and 4% during weeks 0 to 12 weeks and 0 to 24 weeks, respectively. No significant differences were observed between E+S or S+E throughout the 24-week training period in changes to normalized maximal iEMG of the right VL muscle.

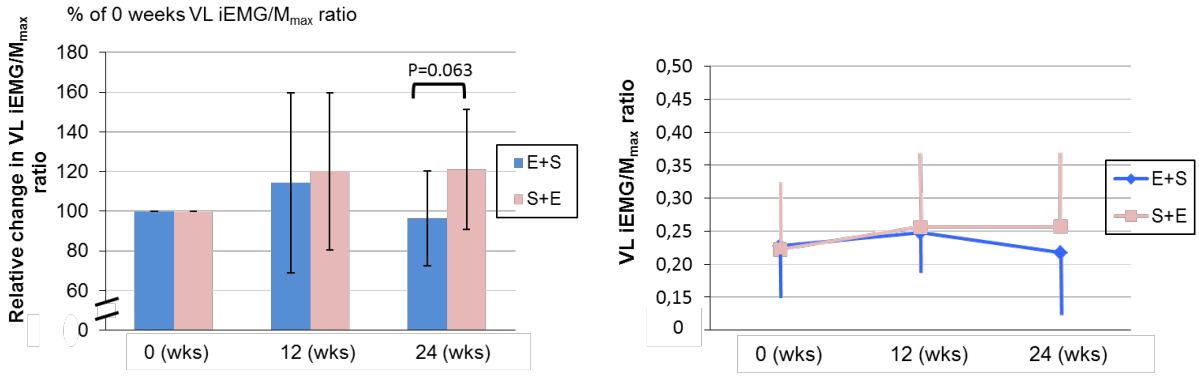

FIGURE 49. Mean (± SD) relative changes (*left*) for maximal 500-1500 ms iEMG normalized to M_{max} during unilateral knee extension and iEMG / M_{max} ratios (*right*) for the right VL muscle over the 24-week training period in E+S and S+E. Relative changes are presented in relation to 0 weeks values.

Unilateral knee flexion BF 500-1500 ms iEMG. During the 24-week training period, S+E significantly increased maximal iEMG amplitude of BF by 26% [0.20 ± 0.06 mV•s to 0.24 ± 0.06mV•s] ($p<0.05$) and 35% [0.20 ± 0.06 mV•s to 0.25 ± 0.06mV•s] ($p<0.01$) during weeks 0 to 12 and 0 to 24, respectively (figure 50). The E+S group displayed non-significant increases in maximal iEMG amplitude of the BF of 22% and 27% [0.20 ± 0.06 mV•s to 0.25 ± 0.06mV•s] during weeks 0 to 12 and 0 to 24 weeks ($p<0.05$). No significant differences were detected between E+S and S+E at any time point for changes in maximal iEMG amplitude of the BF.

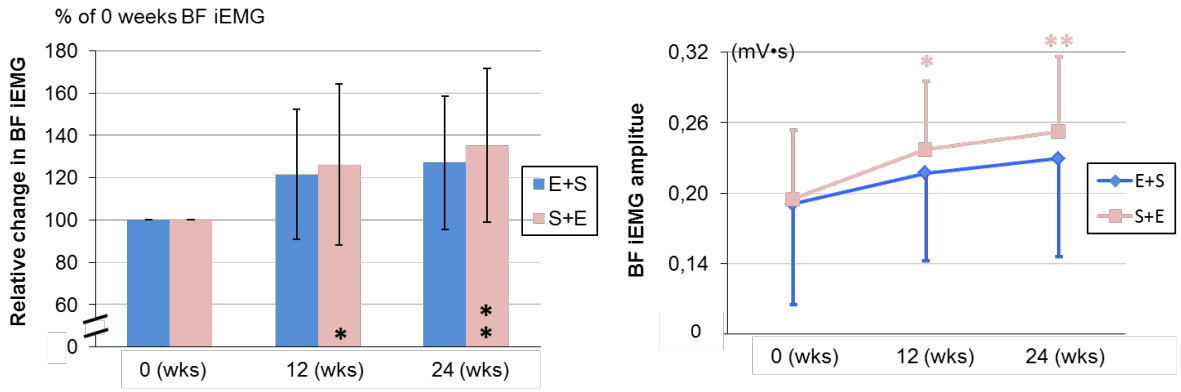

FIGURE 50. Mean (± SD) relative changes (*left*) in maximal 500-1500 ms iEMG amplitude and the absolute values (*right*) of the right BF muscle during unilateral isometric knee flexion over the 24-week training period for E+S and S+E. Relative changes are presented in relation to 0 weeks values. * = significant from 0 weeks. *$p<0.05$ and **$p<0.01$.

7.3.6 Antagonist co-activation ratio of unilateral isometric knee extension

Co-activation of the BF muscle as an antagonist during unilateral isometric knee extension in the S+E group displayed a non-significant decrease of 9% ($p>0.05$) during weeks 0 to 12 and 1% after 24 weeks [15.5 ± 9.2% to 13.4 ± 6.7%] ($p>0.05$) (figure 51). Antagonist co-activation in E+S also remained statistically unaltered during weeks 0 to 24 [16.9 ± 12.3% to 14.2 ± 10.5%] ($p<0.05$) although there was a significant decrease during weeks 12 to 24 [18.3 ± 16.0% to 14.2 ± 10.5%] ($p<0.05$). No significant differences between E+S and S+E were detected in changes to antagonist co-activation

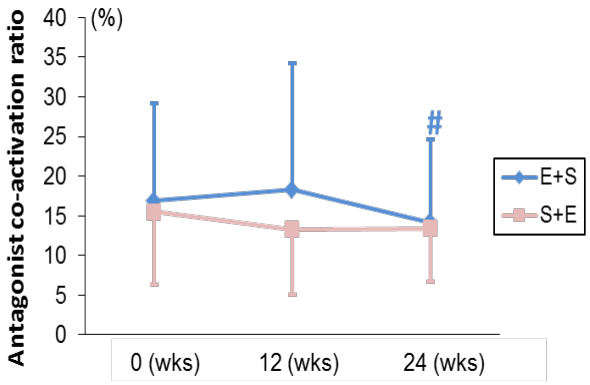

FIGURE 51. Mean (± SD) change in the antagonist co-activation ratio during unilateral isometric knee extension throughout the 24-week training period for E+S and S+E. # = significant from 12 weeks. #$p<0.05$.

7.4 Voluntary activation

During weeks 0 to 12 significant increases in maximum voluntary activation (VA) of QF were observed for both E+S [88.3 ± 6.5% to 92.5 ± 6.1%] ($p<0.05$) and S+E [87.7 ± 9% to 90.6 ± 6.9%] ($p<0.01$) (figure 52). However, over the entire 24-week training period only the S+E group displayed significant increases in VA of QF [87.7 ± 9% to 91.2 ± 6.8%] ($p<0.01$). The E+S groups displayed non-significant increases of QF VA [88.3 ± 6.5% to 90.8 ± 6.1%] after the 24-week training period. No significant differences between E+S and S+E were observed at any time point.

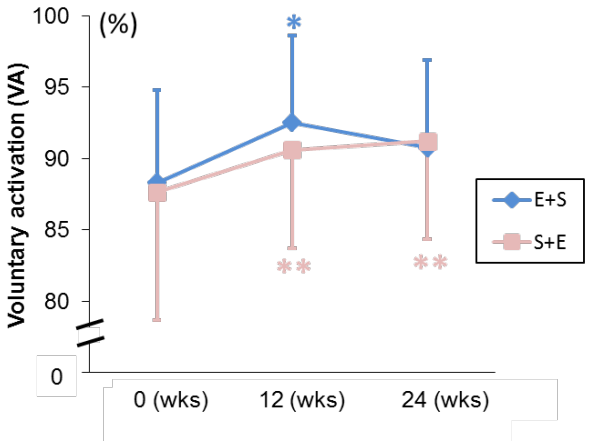

FIGURE 52. Changes in Mean (± SD) absolute VA of the QF muscles during unilateral isometric knee extension throughout the 24-week training period for E+S and S+E. * = significant from 0 weeks. *p<0.05 and **p<0.01.

There were significant correlations between the individual changes in VA of the QF muscles and the changes in MVC_{VA} during weeks 0 to 12 for both E+S (r = 0.657, p<0.05) and S+E (r = 0.524. p<0.05), respectively. During weeks 13 to 24 there was no significant correlation between the changes in MVC_{VA} and the changes in VA for S+E (r = 0.354, p<0.150). There was a significant correlation between the individual changes in VA (~ 2%) and changes in MVC_{VA} strength during weeks 13 to 24 in E+S (r = 0.848, p<0.001) (figure 53).

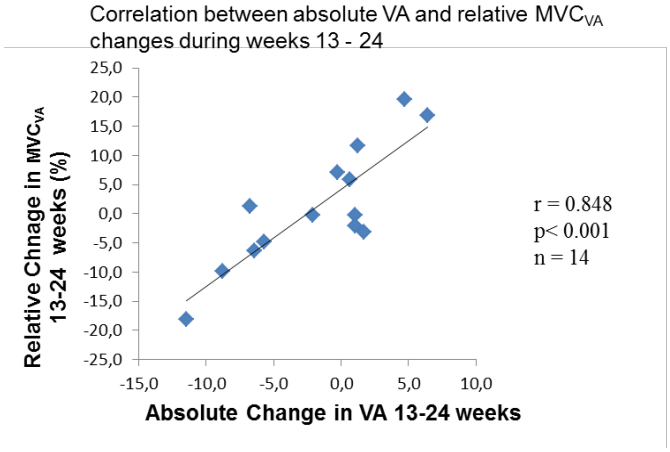

FIGURE 53. Correlation between the absolute changes in VA of the QF muscles and relative changes in MVC_{VA} in the E+S group during weeks 13 to 24.

8 DISCUSSION

The main findings of the present study were that training either E+S or S+E resulted in significant increases in both maximal and explosive strength after 24 weeks of training. Moreover, the degree of strength development was not influenced by the intra-session exercise order, as there were no statistical differences between E+S and S+E although the gains in S+E tended to be somewhat larger than in E+S, especially for the second 12-week training period. It was apparent that the exercise order of single-session combined training influenced adaptations to both maximal and rapid neural activation strategies of knee extensor muscles. An inhibition of both sEMG activity and VA were observed in the E+S training group during the second 12-week training period at 24 weeks whereas S+E training led to significant increases in these same variables.

8.1 Adaptations in voluntary activation, surface EMG and strength development

The 24-week single-session combined strength and endurance-training program of the present study with adult untrained men resulted in similar increases for E+S and S+E in both concentric and isometric maximal strength of the leg extensor muscles. The current findings indicate that performing the current cycling endurance exercise protocol prior to strength over a prolonged combined training period does not interfere with long-term maximal strength development. The present findings that there was no single-session combined training order effect is in agreement with a number of earlier single-session combined training studies for previously untrained young adult males and females (Sale et al. 1990a; Collins & Snow 1993; Gravelle & Blessing 2000). However, the current results are contrary to recent observations by Cadore et al. (2012), who observed an order effect with sedentary elderly individuals after finding that performing strength training immediately prior to endurance exercise for 12-weeks was more beneficial than the opposite training order in regard to maximal strength. Together, these findings may indicate that younger individuals may recover faster from either acute central or peripheral fatigue (Klein et al. 1988) caused by preceding cycling endurance training in single-session combined training regimens (Lepers et al. 2001; Kremenic et al. 2009). These fatigue characteristics in younger individuals may allow for long-term maximal strength gains while concurrently

training strength and endurance during a single session, independent of the training order. Therefore, the influence of intra-session exercise order of a combined training program on maximal strength seemed minor in the young adults of the present study as no significant difference between groups was observed, although S+E resulted in somewhat larger gains than E+S during the second 12-week training phase.

Recently, Cadore and colleagues (2012) suggested that an E+S training order would inhibit neural characteristics typically induced by pure-strength training. Although we observed that training order had only minimal influence on strength development, we did observe neural adaptations were influenced by the intra-session training order. After the 24-week intervention period both maximal vastus lateralis sEMG activity and voluntary neural activation of the quadriceps femoris remained unchanged from before training in E+S. Conversely, training in the S+E order led to significant increases in quadriceps femoris voluntary activation and increases in sEMG activity. These findings agree with previous suggestions of inhibited sEMG activity following 12 weeks training in an E+S order with elderly individuals (Cadore et al. 2010). Thus, in the present study, the resulting training-induced neural adaptations after 24 weeks seemed to reflect the specific neural adaptations of the training mode performed first in the intra-session order. The inhibited VA and sEMG activity in the E+S group are similar to endurance-training only whereas the increases in VA and sEMG reflect changes after pure strength-training (e.g. Häkkinen & Komi 1983; Knight & Kamen 2001; Vila-Chã et al. 2010).

In general, the magnitudes of the current increases in concentric leg press 1-RM load of 13% and 17% for E+S and S+E, respectively, after the 24-week training intervention are comparable to earlier studies (Sale et al. 1990b; Collins and Snow 1993). However, regarding the time-course of strength development, the current strength gains appear to have been diluted over the 24-week training period as similar or even larger increases have been reported following 7, 11 and 20 weeks of single-session combined training (Sale et al. 1990a; Collins & Snow 1993; Gravelle & Blessing 2000). Additionally, the present increases in maximal strength for E+S and S+E are considerably smaller than gains (> 20%) consistently reported by both pure-strength (Häkkinen et al.1998b; Häkkinen et al. 2000; Häkkinen et al. 2001) and separate-day combined training studies (Sale et al. 1990b; Häkkinen et al. 2003). Thus, this may suggest that there was some interference of strength for both groups in the present study. However, directly comparing the current results to those of earlier studies should be done with caution considering the individuality of separate studies, in terms of training program design, previous training

status of subjects, testing methods as well as the absence of a strength training only group in the present study. Nevertheless, we could speculate that there may still have been some type of strength interference (e.g. Hickson 1980) during the long duration of the current training program.

Interestingly, we observed that the majority of the current strength gains occurred during the first 12-weeks (weeks 0 to 12) whereas moderate increases occurred during weeks 13 to 24 in both E+S and S+E. Thus, the attenuation of strength following the initial 12 weeks of training may support our assumption of strength interference for both groups. The degree of combined training induced strength interference has been associated with training volume (Häkkinen et al. 2003; Docherty & Sporer 2000). The differences in relative training intensities of strength or endurance exercise as well as the frequency of training between weeks 0 to 12 and 13 to 24 may have contributed to the current changes in strength.

Notably, during weeks 0 to 12, when the majority of strength gains were achieved for both E+S and S+E, training volume was lower in relation to that of weeks 13 to 24. Training during the first 12 weeks consisted of periodized strength training combined with low-intensity continuous cycling endurance exercise. Several researchers have proposed that low-intensity endurance exercise does not interfere with strength development, regardless of whether endurance exercise is performance immediately prior to or following strength training (e.g. Docherty & Sporer 2000; De Souza et al. 2007). Moreover, the present increases in isometric knee extension strength during the initial 12 weeks occurred concomitantly with enhanced voluntary neural activation of the knee extensor muscles. The increases of 8% and 9% in isometric knee extension strength (MVC_{VA}) as well as the 4% and 3% increases in VA for E+S and S+E, respectively, were highly correlated suggesting that strength development was mainly the result of neural adaptations. The current increases in VA of 3% and 4% for E+S and S+E, respectively, are well within the range of values previously reported for changes in VA of quadriceps femoris muscle after short-term pure strength training (Knight & Kamen 2001; Reeves et al. 2004). The present increases in VA may indicate that preceding low-intensity cycling endurance training may not impede neural drive to exercised muscles in subsequent strength training. The present sEMG results over the first training period of both non-normalized and normalized support to some extent this trend. However, the problem with the present sEMG result may have been a result of only examining a single muscle from the quadriceps femoris (e.g. Rabita et al. 2000). Additionally, neither training order led to drastic changes in co-activation of the BF muscle

during knee extension, although, decreases in co-activation are not typically observed in younger individuals as opposed to older populations as strength increases (Häkkinen et al 1998b; Häkkinen et al. 2001). Therefore, it appears as that the strength increases for E+S and S+E during weeks 0 to 12 were primarily the result of increased agonist activation. Hence, the increases in descending neural drive to the trained quadriceps femoris muscles may have caused increases in either motor unit recruitment and / or motor unit firing rates (Häkkinen & Komi 1983; Kamen & Knight 2008). However, changes in muscle mass or architecture cannot be completely ruled out as a cause for the increased strength in both groups since these variables were not monitored in the present study.

High training intensities and training frequency / volume of combined training have regularly led to strength interference (e.g. Hickson 1980; Hunter et al. 1987; Hennessy & Watson 1994). Therefore, the increases in both of these acute training variables during weeks 13 to 24 may have accounted for the attenuation in strength gains at the end of the present 24-week study. Interference of strength development has been suggested to be the result of either alterations in the anabolic-to-catabolic hormone concentrations ratio, which is caused by overtraining and / overreaching syndromes, as well as alterations in motor unit recruitment and / or firing rate behavior (Chromiak & Mulvaney 1990; Leveritt et al. 1999a).

The apparent decrease in maximum voluntary neural activation of the knee extensor muscles for E+S during weeks 13 to 24, which was not observed in S+E, appears to be associated with the progression of the current cycling endurance exercise. Several studies have reported that high-intensity interval type endurance cycling, similar to the present study, acutely inhibits neural input to the knee extensors leading to reductions in acute strength development (Lepers et al. 2000; Kremenic et al. 2009). Moreover, these reductions may last up to 45 minutes post endurance exercise (Sidhu et al. 2009). Therefore, during last 12 weeks of the intervention the E+S group may have repeatedly strength trained while the nervous system was fatigued, thus, possibly leading to a decrease in maximum voluntary neural input to the knee extensors. Strength development was attenuated for both groups, but to a somewhat lesser magnitude in S+E, from weeks 13 to 24 although the phenomenon of decreased neural activation of knee extensors did not occur in the S+E group. Thus, alterations in motor unit recruitment or their behaviors may not be the cause of the present interference.

The present findings of attenuated strength gains during the last 12 weeks, as training frequency increased, could also be partly explained by an onset of overreaching and / or overtraining syndromes altering anabolic-to-catabolic hormone concentrations. Recent research has shown that after a single-session of combined training, with an intra-session loading order of E+S, optimal recovery periods may need to be as long as 48 hours or more before another optimal training session can be performed (Schumann et al. 2013). Schumann et al. (2013) reported that after training E+S recovery rates of anabolic endocrine function need at least 48 hours to recover while recovery of strength characteristics occurred after only 24 hours. Although the researchers reported an intra-session loading order of S+E recovery might be quicker after a single-session than E+S, responses over a prolonged training period in the S+E order are unknown. Because recovery variables were not investigated beyond 48 hours the demands for recovery may be altered after single-session combined training. Nonetheless, during the last 12 weeks of the present study it is hypothesized that the subjects may not have received adequate recovery time between training sessions. This may mean that participants continually trained in a more or less catabolic state. Thus, continual training without adequate recover may result in overreaching and / or overtraining syndromes causing attenuation in the development of strength (Häkkinen et al. 1985d; Fry & Kraemer 1997). However, the proposal of overreaching and / or overtraining occurring in the present study cannot be justified as these physiological variables were not examined and, therefore, are beyond the scope of this thesis.

The present explosive strength results during isometric leg press followed a similar pattern as maximal strength gains. Significant increases were observed in explosive strength, i.e. average force produced during the first 500 ms of maximal isometric contraction, during the first 12 weeks for E+S and S+E. However, during the second training phase, weeks 13 to 24, no further increases were observed for E+S, while S+E exhibited moderate increases that were non-significant. No significant changes in normalized sEMG from the first 500 ms of maximal isometric leg press were observed, while non-normalized sEMG indicated significant increases after the first 12 weeks for E+S and at 24 weeks for S+E. The significant increases in explosive strength for both E+S and S+E may be contributed in part by increased maximal strength and due to the mixed maximal and explosive strength-training program. On the other hand, increases in maximal strength have been shown to account for upwards of 50% of increases in explosive force production when examined at a time frame greater than 90 ms from the start of contraction (Andersen & Aagaard 2006). Therefore, the explosive strength gains in the present study appear to be the result of neural adaptations to maximum and / or explosive force produc-

tion. Moreover, the present explosive strength results may highlight the importance of training specificity for developing either explosive or maximal strength, and the underlying neural mechanisms (Häkkinen & Komi 1985a; Häkkinen & Komi 1985b).

8.2 Strengths and limitations of the present study

Strengths of the present study are featured in the careful planning, monitoring and execution of the study design in assessing the long-term neuromuscular adaptations. The extensive supervision of individual training sessions over the course of the 24-week study assured that proper adherence, techniques and training intensities of the prescribed training programs were followed. This careful supervision as well as the prolonged duration of the training allowed for the development of long-term adaptations. The assessment of both neural and strength adaptations were quite extensive, ensuring that multiple variables and movements were examined in order to get a larger picture of the overall changes.

A major limitation of the present study is the absence of a group training purely strength. As was seen in the maximal strength results a majority of the gains occurred within the first 12-weeks of training, while only minor increases occurred during the last 12-weeks for E+S and S+E. The addition of a pure strength-training group would have allowed us to examine whether or not the current combined training program resulted in some type of interference of strength development, similar to earlier investigations (Hickson 1980; Häkkinen et al. 2003).

Furthermore, there are potential limitations while assessing neural adaptations of the leg extensors over the course of the current 24-week study. Despite the use of indelible ink tattoos marking sEMG electrode positions in the present study, the assessment of sEMG activity during training studies has many potential sources of error that may confound measurements and interpretations of adaptations in voluntary neural activation. Problems in sEMG arise from possible inter-session errors such as changes in electrode placement, subcutaneous tissue properties, and underlying muscle fiber pennation angle. (De Luca 1997.) Additionally, sEMG activity was obtained from only one muscle, the VL of the right leg. This limits our understanding of the voluntary neural activation adaptations of the leg extensors to the current training program, as the leg and knee extension movements performed engage several muscles working together and they heterogeneously respond to training (Rabita et al. 2000). Monitoring sEMG activity of

other muscles simultaneously from the quadriceps femoris would allow a broader view of any neural activation adaptations of the leg extensor muscles. To limit the potential errors, sEMG activity was normalized to M_{max} responses that were taken during each measurement session (Gandevia 2001). However, M-wave responses have been shown to change to alterations in posture (Takahara et al. 2011). Since M_{max} responses were presently taken in a standing position, rather than in the seated testing positions, great care needs to be exercised regarding the interpretations of the normalized sEMG.

The current use of the SIT method to examine changes in VA, although our strongest measurement, may also limit interpretation underlying neural adaptations to the present 24-week combined training program. The use of SIT to measure VA can be confounded by methodological and quantification techniques (Herbert & Gandevia 1999; Folland & Williams 2007b). However, due to the low coefficient of variation measured during the control period we feel that the current methods and extrapolation techniques were reliable to assess VA. Nevertheless, the SIT method also limits the capability of specifying possible sites of neural adaptations as changes occur along the entire neuraxis following strength or endurance training. Therefore, in the future more specific measures, such as H-reflex and / or V-wave responses, should be utilized in addition to SIT.

8.3 Conclusions and practical applications

The present study provides moderate evidence for an order effect on training-induced neural adaptations after 24-weeks of single-session combined strength and endurance training, as we observed that adaptations were order-specific. There was no statistical difference between E+S and S+E after 24 weeks with regard to strength development. However, S+E tended to have somewhat larger strength gains than E+S indicating the possibility of an order effect on strength development. Thus, the present data suggest that long-term neural adaptations and strength development may be associated with the intra-session exercise order with the current progressive combined training program for previously untrained individuals, although there were no significant differences between groups in regard to strength. However, these findings may not apply to individuals with prior training experience, particularly endurance trained persons, as they may have higher tolerances for intense combined training exercise bouts. Furthermore, research is needed to investigate the differences in strength adaptations between un-

trained and trained individuals to the order effect of single-session combined strength and endurance training.

Training intensity and frequency may have affected both the neural adaptations and strength development in the present study. During the first 12 weeks when training intensity, specifically endurance exercise, was low and training frequency was only 2-combined sessions / week the majority of current strength increases for both E+S and S+E occurred as the result of what appeared to be mainly neural adaptations that increased agonist activation. As both endurance exercise intensity and training frequency increased during weeks 13 to 24 there appeared to be some attenuation of strength development in both groups, which was especially more pronounced for E+S. The reduced strength gains for E+S may have been a result of inhibited maximal neural activation adaptations caused by performing high-intensity cycling endurance training before strength exercises. It may be assumed that if the mode of endurance exercise was running both neural and strength adaptations may be similar to the present results. However, because endurance running is biomechanically dissimilar to strength training any neural or strength interference may be more pronounced than presently observed with cycling.

The current observations are significant because they highlight possible mechanisms involved in the interference of strength typically observed after prolonged concurrent training. Furthermore, they may assist in the development of strategies to optimize programming of single-session combined strength and endurance training. Therefore, in practical terms it seems that training strength immediately prior to endurance may be more beneficial regarding strength development. Additionally, for untrained individuals, low-intensity endurance exercise as well as reduced training frequencies (i.e. 2-combined sessions / week) may result in the greatest development of strength when strength and endurance are completed in the same session.

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