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Acute Neuromuscular and Hormonal Responses and Long-term Adaptations to Hypertrophic Resistance Training

with Special Reference to Constant Versus Variable Resistance

JYVÄSKYLÄN YLIOPISTO

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"Beyond the very extremes of fatigue and distress, we may find amounts of ease and power we never dreamed ourselves to own; sources of strength never taxed at all because we never push through the obstruction"

Willam James

ABSTRACT

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Yhteenveto: Akuutit hermolihasjärjestelmän ja seerumin hormonivasteet sekä krooniset adaptaatiot vakio- ja muuttuvavastuslaitteilla toteutetussa voimaharjoittelussa

The aim of the present study was to investigate the effect of constant vs. variable external resistance on: 1) acute neuromuscular, hormonal, and molecular responses before and after a prolonged period of hypertrophic training, and 2) chronic adaptations in neuromuscular performance and muscle hypertrophy in young and older men. Sixty seven young (20–35 yrs) and 50 older (60–72 yrs) physically active men, but not experienced in resistance training, took part in the present study. Maximal strength (15 sets of 1 repetition maximum) and hypertrophic (5 sets of 10 repetition maximum) resistance loadings were performed before a 20-week hypertrophic training period using constant and variable resistance devices for the lower limbs. Variable external resistance caused greater force and muscle activity during single-repetition leg press actions compared to constant external resistance. During maximal strength loadings before training, variable resistance led to greater decreases in force production and muscle activation, and increases in serum growth hormone concentration. During hypertrophic loadings before training, variable resistance led to greater decreases in force production and muscle activation, and greater increases in serum hormone concentrations and phosphorylation of mitogen-activated protein kinases, particularly ERK 1/2. These differences were also observed during hypertrophic loadings after training with the exception of ERK 1/2 phosphorylation. The 20-week hypertrophic training program of the present study induced large improvements in maximum force production and muscle hypertrophy of the lower limbs in both constant and variable resistance training groups and in both young and older men. However, only the young and older men that trained using variable resistance improved fatigue-resistance performance, assessed by a repetition to failure test. The present study provides a broad evaluation of the effects of constant and variable resistance in both young and older men. The results suggest that variable resistance may be beneficial during periods of high volume, medium intensity training with a large number of repetitions per set, especially to improve fatigue-resistance.

Keywords: lower limbs, force production, fatigue-resistance, hypertrophy, muscle activation, serum hormones, muscle signalling

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To those who have gone before and showed us the way,
may we be worthy guides for those to come.

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The house is only as good as its foundations. I could not have wished for a better family than the one I have left behind on my world travels. You have made me what I am today, I love you all dearly. The person who has had the greatest influence on me is Mam. She is the epitome of parenthood. I have been encouraged to follow my dreams, supported to achieve my goals, taught how to deal with adversity, and shown the importance of helping others. My greatest achievement will be to match your level with my own son, Nooa.

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Jyväskylä, November 2012
Simon Walker

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following original articles, which are referred to in the text by their Roman numerals.

I Walker, S., Peltonen, H., Avela, J. & Häkkinen, K. 2011. Kinetic and electromyographic analysis of single repetition constant and variable leg press actions. *Journal of Electromyography and Kinesiology* 21 (2), 262-269.

II Walker, S., Taipale, R. S., Nyman, K., Kraemer, W. J. & Häkkinen, K. 2011. Neuromuscular and hormonal responses to constant and variable resistance loadings. *Medicine and Science in Sports and Exercise* 43 (1), 26-33.

III Walker, S., Peltonen, H., Avela, J. & Häkkinen, K. 2012. Neuromuscular fatigue in young and old men using constant or variable resistance. *European Journal of Applied Physiology* DOI:10.1007/s00421-012-2526-2

IV Walker, S., Hulmi, J. J., Wernbom, M., Nyman, K., Kraemer, W. J., Ahtiainen, J. P. & Häkkinen, K. Variable resistance training promotes greater fatigue-resistance but not hypertrophy vs. constant resistance training. (submitted for publication).

V Walker, S., Peltonen, H., Sautel, J., Scaramello, C., Kraemer, W. J., Avela, J. & Häkkinen, K. Neuromuscular adaptations to constant vs. variable resistance training in older men. (submitted for publication).

ABBREVIATIONS

rep	repetition
RM	repetition maximum
1RM	one repetition maximum
VAR or V	variable
CON or C	constant
Co	control
LP	leg press
BP	bench press
KE	knee extension
EF	elbow flexion
S	squat
CMJ	countermovement jump
FW	free weight
VL	vastus lateralis
VM	vastus medialis
RF	rectus femoris
CSA	cross-sectional area
DXA	dual-energy x-ray absorptiometry
MRI	magnetic resonance imaging
CT	computer tomography
kg	kilogram
N	newton
Nm	newton metre
EMG	electromyogram
rmsEMG	root mean square electromyogram
iEMG	integrated electromyogram
TT	total testosterone
GH	growth hormone
kDa	kilo dalton
mTOR	mechanistic target of rapamycin
Akt	protein kinase B
rpS6K	ribosomal protein S6
$p70^{S6K}$	ribosomal protein S6 kinase (size 70 kDa)
eEF2	eukaryotic elongation factor 2
MAPK	mitogen-activated protein kinase
ERK 1/2	extracellular signal-regulated kinase
MAPKAPK-2	MAPK activated protein kinase 2
CV%	coefficient of variation %
SD	standard deviation
SE	standard error
ANOVA/ANCOVA	analysis of variance/ analysis of covariance

CONTENTS

1 INTRODUCTION

Attempts to improve physical abilities and performance have been practiced throughout history. Resistance training is thought to have occurred in ancient Greece where the concept of progressive resistance training is credited to Milo of Crotona, a multi-Olympic champion, who carried a newborn calf on his back until it was fully grown (Atha 1981). The Romans adopted the Greek methods and applied them to more military aims and, although there appears to have been a void after the Roman Empire, 16th Century literature shows a resurgence of interest in resistance training where it is noted to have improved running and jumping ability - as well as a means of keeping men away from alcohol and women (Todd 1995).

Over the last century, resistance training has developed to comprise free weights, resistance devices, and of course using one's own body weight. Resistance training has also become an increasing subject of scientific study, and has resulted in training recommendations (Pollock et al. 1998). Furthermore, resistance training is no longer perceived as a method solely used by athletes. Scientific studies have shown the benefits of resistance training on increased strength and muscle mass after injury (e.g. Gerber et al. 2009), functional capacity in the elderly (e.g. Skelton et al. 1995) and patients with neuromuscular diseases (e.g. Dodd et al. 2003), and improved body composition in overweight and obese (e.g. McGuigan et al. 2009) subject groups. Consequently, a thorough understanding of the training strategies, biomechanical and physiological mechanisms, and potential performance/health outcomes is an essential scientific endeavour.

Perhaps as a consequence of scientific interest, investigators have sought to improve on current resistance training practices and optimise training-induced adaptations. One such example where scientific knowledge may be used to improve resistance training practices is the *in vivo* force-angle relationship. In other words, the maximum force that can be produced is dependent upon joint angle. Multi-joint exercises, such as the leg press, typically display a linearly increasing force-angle curve from more flexed to extended knee angles

whereas single-joint actions, such as knee extension, typically display an inverted U-shaped force-angle curve, as reviewed by Kulig et al. (1984).

Theoretically, training using free weights or any equipment that provide constant external resistance (i.e. the resistance remains the same throughout the range of motion) will require certain joint-angles to produce force closer to their maximum than others. Therefore, it may be hypothesised that training using variable external resistance (i.e. greater resistance during parts of the range of motion capable of producing larger force) may challenge the neuromuscular system to a greater extent and result in greater training-induced adaptations.

To the author's knowledge, the first scientifically documented variable-resistance device was produced in 1954 (Noland & Kuckhoff) for use during rehabilitation. This relatively crude device has been improved in commercially available resistance devices that utilise cams or pulleys to manipulate the lever arm distance. Early intervention studies have shown that constant resistance induced greater improvements in maximum strength (Stone et al. 1979), variable resistance induced greater improvements in maximum strength (Ariel 1976), and similar improvements in both groups (Coleman 1977, Silvester & Bryce 1981, Manning et al. 1990). Additionally, some studies have found that the greatest improvements occurred in the training-specific device (Pipes 1978, Boyer et al. 1990), in other words, the group that performed constant resistance training improved constant resistance force production more than the variable group and vice versa. However, scientific interest in this topic has somewhat faded in recent years, perhaps due to difficulties in matching the *in vivo* force-angle relationships of humans (Harman 1983, Johnson et al. 1990, Folland & Morris 2008) and the largely similar improvements in maximum strength observed in those early scientific studies. Therefore, training intervention studies using the latest scientific methodologies have not been performed. However, two studies have shown that acute fatigue is greater during resistance loading using variable resistance devices compared to constant resistance devices (Häkkinen et al. 1988a, Garcia-Lopez et al. 2010), which may lead to different magnitudes or types of adaptation when long-term training is performed with these devices.

The present study was designed to investigate the acute responses and long-term adaptations to resistance training using constant vs. variable external resistance devices. The present study was designed to obtain new scientific information of the effect of variable external resistance on; 1) single-repetition performance and muscle activation, 2) acute loading-induced neuromuscular fatigue, serum hormone concentration and intra-muscular protein kinase phosphorylation responses, and 3) chronic adaptations in neuromuscular performance, muscle activation, and muscle hypertrophy of the lower limbs. The obtained information can be applied to testing and designing training programs for athletes, as well as in healthy young and older individuals.

2 REVIEW OF THE LITERATURE

2.1 Background of modern resistance training

De Lorme's (1945) seminal paper on the use of resistance training during rehabilitation has shaped the ideas currently used today. Notably, De Lorme (1945) used a combination of methods emphasising "power-building" (the maximum load that can be lifted for one repetition - 1RM) and "endurance-building" (lifting a submaximal load for a total of 100 repetitions - 10 × 10) for the quadriceps muscles. Modern design of a single-session resistance training program (referred to in the present study as "resistance loading") is made up of several acute program variables identified by Fleck & Kraemer (1987). These variables are: choice of exercise, order of the exercises, intensity of the exercise, number of repetitions/sets, duration of rest between sets/exercises. As can be appreciated, there can be almost an infinite number of combinations that can make up resistance loading, which exert influence on, for example, muscular activation patterns, energy demand, magnitude and duration of fatigue etc.

The choice of exercise and order of exercises are outside of the scope and interest of the present study and, thus, will not be discussed. For further information on these variables, the reader is directed to a review by Kraemer & Ratamess (2004). Quantifying the load (i.e. intensity of the exercise) has generally been done in one of two ways. The first uses the same terminology as De Lorme (1945), in that intensity is the number of repetitions (reps) that the load can be lifted to failure (e.g. 6 repetition maximum or 6RM). The second describes the load as a percentage of 1RM (e.g. 75 % 1RM). In both cases, as intensity increases closer to 1RM, the number of repetitions decreases. In his review, Fry (2004) suggested that 18–35 % of the variance in hypertrophy was accounted for by intensity, and so this may be viewed as a particularly important variable to stimulate adaptation.

It has been proposed that a continuum exists whereby adaptations move from maximal strength and/or power using 1–6 reps per set towards strength endurance using more than 14 reps per set (Stone et al. 1982), while rep ranges

of 8–12 are considered to be primarily aimed to promote muscle hypertrophy. In addition to reps, training volume can be increased through the number of sets performed during resistance loading. Intervention studies have shown clear differences in improvements in force production (Schlumberger et al. 2001, Rhea et al. 2002) and/or hypertrophy (Ronnestad et al. 2007) between 1 set and 3 sets per exercise.

Rest between sets, and also exercises, is an important consideration in terms of the number of reps achieved in subsequent sets. Shorter rest periods (e.g. 60–90 s vs. > 180 s) can change the primary stimulus of the loading through inducing greater blood lactate and hormonal responses (Kraemer et al. 1990). Finally, training frequency for beginners is usually twice per week, increasing to 3–4 and then 4–5 times per week as training experience progresses (Fleck & Kraemer 1987). In experienced resistance trainers, additional benefit may be gained through performing 2 sessions per day during a short training period, although this probably requires the overall volume of each session to be greatly reduced to prevent over-reaching (Häkkinen & Kallinen 1994).

Many resistance training programs used in diverse subject populations have been designed to develop maximal strength and hypertrophy (e.g. De Lorme 1945, Skelton et al. 1995, Dodd et al. 2003, Gerber et al 2009), and so the focus of the present study is on these two main outcomes. Therefore, the following review of the literature includes studies with rep ranges of 1–12 per set and an intensity of 60–100 % 1RM.

2.2 Acute responses to resistance loading

2.2.1 Neuromuscular responses

Not only is it important to understand why a human cannot continue performing muscular actions to the same level of force or work (i.e. fatigue), from a training perspective, it is important to understand the mechanisms of fatigue during a specific condition (i.e. loading) in order to understand the specificity of training-induced adaptations (Enoka & Duchateau 2008). A great deal of scientific investigation has focussed on acute neuromuscular fatigue, however, only a limited number of studies have used isotonic resistance loading protocols (Häkkinen 1993, Häkkinen 1994, Ahtiainen & Häkkinen 2009, Izquierdo et al. 2009a, McCaulley et al. 2009, Gonzalez-Izal et al. 2010, Smilios et al. 2010, Walker et al. 2012). Within these studies, the most common resistance loading protocols may be categorised as medium intensity (quantified as 50–85 % 1RM, or 10–12RM if not defined relative to 1RM), high volume (total of 40–100 reps) with short inter-set rest intervals (1.5–2 min), otherwise known as "hypertrophic loading protocols". During a very strenuous 10 × 10 using 70 % 1RM squat loading protocol, a ~47 % reduction in maximum bilateral isometric leg extension force was observed in men with a resistance training (~8 years) background (Häkkinen 1994). Furthermore, electromyography (EMG) amplitude of

the vastus lateralis and vastus medialis muscles was significantly lower following loading. Blood lactate was significantly increased post-loading (~15 $mmol.L^{-1}$) and this was negatively related to isometric force decreases for men and women combined. A ~27 % reduction in maximum isometric squat force was observed following 4 × 10 using 75 % 1RM squats with an increase in blood lactate to ~13 $mmol.L^{-1}$ (McCaulley et al. 2009, Fig. 1), however, this was not accompanied by decreased vastus medialis EMG amplitude. In agreement with these findings, Smilios et al. (2010) observed no changes in EMG amplitude for the superficial vastii and rectus femoris muscles during isometric knee extension after 4 × 20 using 50 % 1RM squat loading despite a ~19 % decrease in isometric force.

One possible explanation for the discrepancy in muscle activity results may be the training status of the subjects, as Ahtiainen & Häkkinen (2009) showed that only strength athletes had decreased concentric EMG amplitude during the forced rep protocol. These findings may indicate that several years of training may lead to greater neural/central fatigue during acute resistance loadings. Indeed, even short-term training programs (7–11 weeks) have led to observations of greater neuromuscular fatigue following the same loading protocol after training (Izquierdo et al. 2009a, Walker et al. 2010).

Alternatively, the lack of change in EMG amplitude may be due to inherent features of the EMG signal. Some recent studies have assessed the concentric actions during hypertrophic loadings (Gonzalez-Izal et al. 2010, Smilios et al. 2010, Walker et al. 2012), in contrast with the aforementioned studies that primarily assessed changes in maximum isometric force production. As the set progresses from rep 1 towards the final reps (10 or 20 in these studies) there is an increase in EMG amplitude and a concomitant decrease in EMG median frequency. These observations led to the authors of these studies suggesting that increased drive to the agonists occurred (initial increases in EMG amplitude), but once the absolute load was reduced there would likely be no further possible increases. The combination of increasing EMG amplitude with decreasing EMG median frequency might suggest greater motor unit synchronisation (Gonzalez-Izal et al. 2010, Walker et al. 2012). Increased motor unit synchronisation would likely increase EMG amplitude through reduced signal cancellation thereby masking indications of reduced muscle activity (Yao et al. 2000). This seems a plausible phenomenon given the observed decrease in EMG median frequency (Walker et al. 2012) and typically maintained (Ahtiainen & Häkkinen 2009, McCaulley et al. 2009, Smilios et al. 2010) or even increased (Izquierdo et al. 2009a) EMG amplitude during post-loading isometric actions.

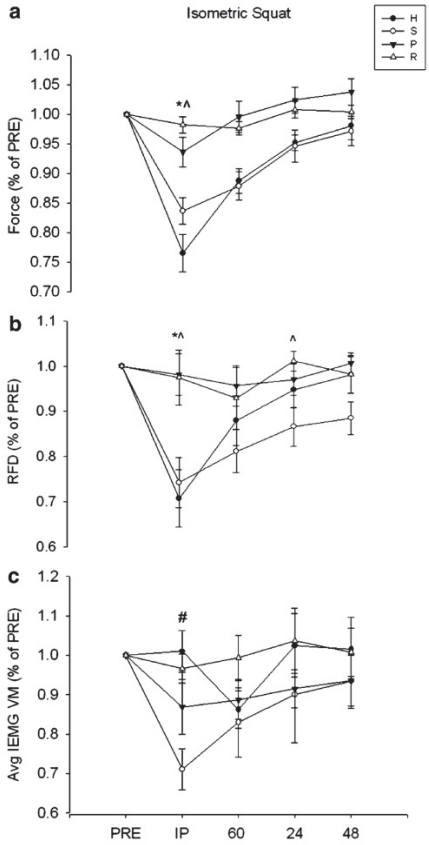

FIGURE 1 Acute decreases in maximal isometric squat force (a), maximal isometric squat rate of force development (b), and vastus medialis muscle activity (c) following hypertrophic (H), maximal strength (S), and power (P) loadings matched for total work and during a rest (R) condition (McCaulley et al. 2009). Copyright 2009 by Springer Publishing, reproduced with permission.

In comparison to hypertrophic loading protocols, three studies have investigated acute neuromuscular responses to loading protocols with high intensity (quantified as 90–100 % 1RM), low volume (total of 15–33 reps) with relatively long inter-set rest intervals (3–5 min), otherwise known as "maximal strength loadings". In men, Häkkinen (1993) observed a ~24 % reduction in bilateral isometric leg extension force following 20 × 1RM squats. Significant reductions in EMG amplitude of the quadriceps accompanied the loss in force production leading the author to suggest that neural fatigue had occurred. McCaulley and colleagues (2009) observed a ~17 % decrease in isometric squat force following 11 × 3 using 90 % 1RM squats (Fig. 1). Significant recovery took place 60 min post-loading and gradually returned to baseline over a 48-hour period in a similar manner to that observed by Häkkinen (1993). Another consistent finding was that EMG amplitude of the vastus medialis was significantly reduced immediately post-loading and recovered towards baseline over the recovery period. Following 15 × 1RM leg press loading, Walker and colleagues (2012) ob-

served a ~15 % decrease in bilateral isometric leg extension force and a ~12 % decrease in average vastus lateralis and vastus medialis (VL+VM/2) EMG amplitude. There were no changes in EMG median frequency during loading and the authors suggested that reduced firing frequency, rather than motor unit recruitment, may have accounted for the decrease in EMG amplitude. These previous studies observed statistically significant but moderate (4–7 $mmol.L^{-1}$) increases in blood lactate (Häkkinen 1994, McCaulley et al. 2009, Walker et al. 2012), which may explain part of the decreased neuromuscular efficiency (Walker et al. 2012) - calculated as the Force:EMG ratio.

2.2.1.1 Neuromuscular responses to constant and variable resistance during single-repetition actions

Quantification of single-repetition performance of constant and variable resistance actions has been studied for a variety of exercises (Harman 1983, Johnson et al. 1990, Cabell & Zebas 1999, Folland & Morris 2008). During single-joint knee extension actions, a variety of commercially available devices have been shown to create resistance at more extended knee angle positions that exceed the *in vivo* torque-angle relationship (Harman 1983, Johnson et al. 1990, Folland & Morris 2008). The practical implications of these studies would lead to subjects needing to use a lower load in order to complete full range of motion. However, the same may be said for constant resistance devices at the lowest and highest joint angles during single-joint actions. Cabell & Zebas (1999) investigated a reportedly variable resistance biceps curl device and observed that, not only did it produce little variation in resistance throughout the range of motion, but that at < 15° and > 105° of flexion the device produced greater resistance than the subjects could voluntarily produce torque (i.e. human torque capabilities).

In addition to resistance devices, free weight actions have been manipulated by the addition of either chains or rubber bands (Wallace et al. 2006, Baker & Newton 2009, Israetel et al. 2010, Stevenson et al. 2010). Naturally, different combinations of free weight-band tension relationships makes comparison between studies difficult, however, some general trends for the squat and bench press exercises may be summarised as follows; greater average force and power with the addition of rubber bands when using 85 % 1RM (Wallace et al. 2006), greater force and quadriceps EMG amplitude during phases of high rubber band tension (i.e. extended knee angles) (Israetel et al. 2010). Greater concentric velocity was observed when the free weight plus chain resistance was equivalent to free weight only (Baker & Newton 2009), however, concentric velocity was greater during free weight actions when the rubber band produced 20 % additional resistance (Stevenson et al. 2010). Therefore, the training stimulus may be very different depending on the distribution of free-weight load:rubber band resistance, and it should also be pointed out that this type of linearly increasing variable resistance would theoretically suit the *in vivo* force-angle relationship of multi-joint actions, such as the squat, deadlift, and bench press.

2.2.1.2 Neuromuscular responses to constant and variable resistance during repetition to failure tests

Given that the mechanisms of acute neuromuscular fatigue may indicate the specificity of training-induced adaptations (Enoka & Duchateau 2008), it is surprising that limited scientific investigation of constant vs. variable resistance loading has been performed. Häkkinen and colleagues (1988a) performed a repetition to failure test using 60 % 1RM with a constant and a variable resistance knee extension device. The authors observed that the strength trained subjects could perform significantly fewer reps with the variable compared to the constant resistance device (16.7 ± 3.5 vs. 20.5 ± 4.5 reps, respectively). Increases in EMG amplitude of the superficial vastii muscles was observed throughout the test using both devices, however, only testing using the variable resistance device led to significant increases in rectus femoris EMG amplitude. These results may suggest that variable resistance knee extension loading may fatigue the rectus femoris muscle to a greater extent than constant resistance and lead to impaired neuromuscular performance over fewer repetitions. Using a similar methodology, Garciz-Lopez and colleagues (2010) performed a repetition to failure test using 70 % 1RM with a pulley cable or a pulley cable with a rubber band attached. A significant difference was found for the number of repetitions performed and concentric acceleration was also lower using the rubber band attachment ($p < 0.05$) (Garcia-Lopez et al. 2010). The observed lower accelerations would arguably result in longer contractions times/time under tension, and this may have influenced the development of fatigue during the test. Finally, similar post-loading changes in isometric force production and markers of muscle damage were observed when comparing two types (linearly increasing vs. inverted-U shaped force-angle curve) of variable resistance during knee extension loadings (Aboodarda et al. 2011).

2.2.2 Hormonal responses

Endocrine hormones respond to resistance loading and act as acute signals, which are part of several interactive systems that cause/aid muscle hypertrophy (Spiering et al. 2008). Three of the most studied hormones are testosterone, 22kDa growth hormone, and cortisol. Testosterone has been shown to influence muscle hypertrophy through exerting an influence on protein synthesis (Ferrando et al. 1998) and satellite cells (Sinha-Hikim et al. 2003). Over 100 forms of growth hormone have been identified with the 22kDa isoform being the most common in blood (Baumann 1991). Growth hormone stimulates insulin-like growth factor-1 expression in circulation and in skeletal muscle (Florini et al. 1996), initiates phosphorylation of muscle protein kinases through Janus kinase 2 (Campbell 1997), and also influences tendon collagen synthesis rates (Doessing et al. 2010). Cortisol, a glucocorticoid hormone, increases protein breakdown in muscle cells and stimulates lipolysis in adipose cells (Hickson & Marone 1993), possibly to meet the metabolic demands of exercise (Viru et al. 1994). Cortisol also affects inflammation responses, observed in increased leu-

kocyte and cytokine concentrations, which is a characteristic of the recovery process after resistance loading (Paulsen et al. 2012). Consequently, it may be hypothesised that changes in acute serum hormone concentrations during resistance loading may aid chronic changes in muscle mass and, directly or indirectly, force production.

2.2.2.1 Resistance loading protocol affects the magnitude of acute hormone increase

Kraemer and colleagues (1990) were among the first to demonstrate that changes to the acute program variables of resistance loading can influence serum hormone responses. Total testosterone concentration was significantly increased following both high intensity (5RM) and high volume (10RM) loading protocols, whereas growth hormone and blood lactate responded to a greater extent following a high volume protocol with short inter-set rest interval (10RM with 1 min rest vs. 10RM with 3 min rest) (Kraemer et al. 1990, Fig. 2). This was also observed after performing 10 × 5 squats explosively using 70 % 1RM in resistance trained men (Fry & Lohnes 2010). There may be, however, a threshold on the volume required to increase testosterone concentration during high intensity resistance loadings as Häkkinen & Pakarinen (1993) observed no change during 20 × 1RM squats with 3 min inter-set rest interval. This was in stark contrast to the large responses observed following 10 × 10 using 70 % 1RM protocol (Fig. 2).

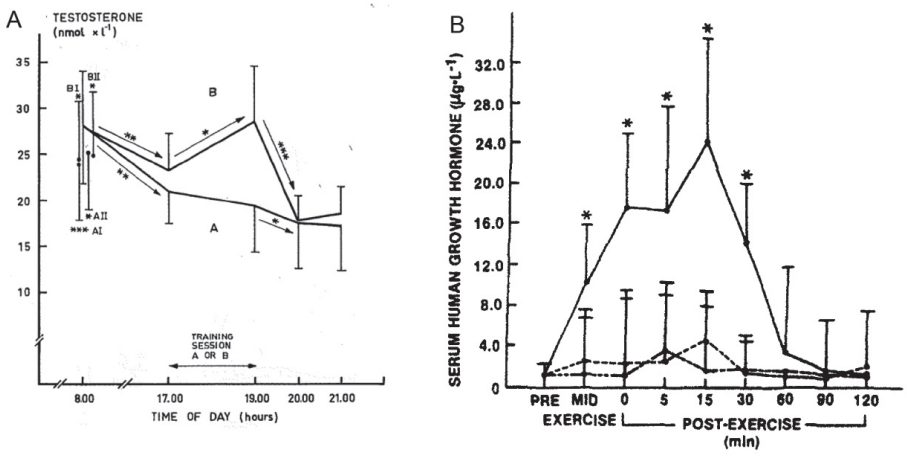

FIGURE 2 Acute loading-induced responses in serum total testosterone during 10 × 10RM vs. 20 × 1RM loading and recovery (A, Häkkinen & Pakarinen 1993) and 22 kDa growth hormone during 10RM with 1 min rest vs. 5RM with 1 min rest vs. 10RM with 3 min rest (B, Kraemer et al. 1990). Copyright 1993 and 1990 respectively by the American Physiological Society, reproduced with permission.

Acute increases in testosterone, growth hormone, and cortisol have been shown to be greater following 3 sets compared to 1 set during multi-exercise resistance loading (Gotshalk et al. 1997). Furthermore, the acute growth hormone response has been shown to increase when comparing 2 vs. 4 sets of 10RM, however, no additional increase was observed when comparing 4 vs. 6 sets (Smilios et al. 2003). The additional number of sets did not affect the acute cortisol response. A final confirmation that loadings consisting of medium intensity, high volume and short inter-set rest intervals produced the greatest acute serum hormone responses was provided by McCaulley et al. (2009). Matching loading protocols for total work, the 4 × 10 using 75 % 1RM squat protocol induced greater testosterone and cortisol responses compared to the 11 × 3 using 90 % 1RM protocol (McCaulley et al. 2009).

These acute elevations in serum hormones have been shown to last from 15 min to 2 hours in various hormones during recovery following medium intensity, high volume loading protocols. Increases in total testosterone dissipate quickly during recovery with most studies showing that concentrations return to baseline levels within 15 min (Kraemer et al. 1990, Häkkinen et al. 2002, Ahtiainen et al. 2003), although one study observed significantly increased total testosterone for up to 60 min post-loading (Gotshalk et al. 1997). Growth hormone appears to remain elevated for approx. 30–60 min post-loading (Kraemer et al. 1990, Häkkinen & Pakarinen 1993, Izquierdo et al. 2009b). Cortisol can be elevated during recovery for up to 2 hours post-loading (Häkkinen & Pakarinen 1993), which is usually longer than the testing period of most studies (Kraemer et al. 1990, Ahtiainen et al. 2003, Izquierdo et al. 2009). However, some studies observe a return to baseline within 60 min (e.g. McCaulley et al. 2009). The duration of elevated concentrations of these serum hormones may be related to the severity of the loading protocol, the training status and/or the age of the subjects (Häkkinen & Pakarinen 1995, Kraemer et al. 1999). In addition to immediate responses, it has also been shown that basal serum testosterone concentrations may be reduced for 2 days by very demanding resistance loading, even when force production capabilities have recovered (Häkkinen & Pakarinen 1993, Fig. 2).

2.2.2.2 Influence of age and training status on the magnitude of acute hormone increase

In addition to the effect of resistance loading protocol on acute serum hormone responses, studies have also demonstrated differences when examining the influence of age (Häkkinen & Pakarinen 1995, Kraemer et al. 1999) and training experience (Ahtiainen et al. 2003, Cadore et al. 2008). In previously untrained subjects, leg press loadings (5 × 10RM with 3 min inter-set rest interval) induced significant elevations in total testosterone and growth hormone in young and middle-aged men but not older men leading to statistically significant differences between the groups (Häkkinen & Pakarinen 1995). Similarly, Kraemer et al. (1999) showed that the testosterone and growth hormone response following

4 × 10RM squats in young men was greater than older men with significant between group differences observed in free testosterone.

Leg press loading (5 × 10RM) in strength athletes was shown to induce greater growth hormone, but not total testosterone or cortisol, responses compared to untrained subjects (Ahtiainen et al. 2003). Cadore and colleagues (2008) compared acute hormone responses of middle-aged trained and untrained subjects using a multi-exercise protocol of 65–75 % 1RM loads. The trained subjects demonstrated clearly attenuated total testosterone and cortisol responses, while response in free testosterone was similar between groups. However, to the author's knowledge, the evaluation of age/training status on acute hormone responses has not been separated from the possible influences of greater total work performed by the young and/or trained individuals, which makes comparisons difficult.

2.2.2.3 Role of acute hormone responses on chronic adaptation to resistance training

When examining the influence of acute increases in serum hormone concentrations and chronic adaptations to resistance training, elbow flexor force production has improved to a greater extent when training was performed with acutely elevated serum hormone concentrations (Hansen et al. 2001, Ronnestad et al. 2011). Specifically, cross-sectional area (CSA) significantly increased at distal parts of the elbow flexors when hormone concentration was elevated, but not in the group without prior elevation of serum hormone concentrations (Ronnestad et al. 2011). In support of these findings, some studies have observed associations between the magnitude of acute increases in growth hormone and testosterone and muscle hypertrophy (McCall et al. 1999, Ahtiainen et al. 2003, respectively). However, it must be acknowledged that muscle hypertrophy has also been observed from training programs that have not increased serum hormones acutely (Wilkinson et al. 2006, West et al. 2010). One possibility is that intra-muscular hormones, such as Insulin-like Growth Factor-1 (Bamman et al. 2001), acting in an autocrine/paracrine manner may contribute to muscle hypertrophy in the absence of acute elevations in serum concentrations. Therefore, it seems that other (perhaps intra-muscular) mechanisms, in addition to acute increases in serum hormone concentrations, contribute to improved strength/hypertrophy and should be investigated. Nevertheless, acute increases in serum hormone concentration may be important in potentiating training-induced adaptations.

In the context of the present study, greater serum hormone responses to resistance loading (constant vs. variable resistance) may indicate a greater potential for chronic adaptation. However, neither acute hormonal responses, nor their influence on training-induced adaptation, to constant and variable resistance has been previously investigated.

2.2.3 Molecular responses

The aim of this chapter is to provide an overview of resistance loading-induced phosphorylation of protein kinases of the mechanistic target of rapamycin (mTOR) and mitogen-activated protein kinase (MAPK) signalling pathways (Fig. 3), which have been identified to play an important role in protein synthesis and overall muscle hypertrophy (Baar & Esser 1999, Bodine et al. 2001, Haddad & Adams 2004, Norrby & Tågerud 2010). Detailed investigation on the many different intra-muscular effectors of skeletal muscle adaptation is beyond the scope of the present study, and the interested reader is directed to detailed reviews on these topics (Roux & Blenis 2004, Goldspink 2005, Bodine 2006, Burkholder 2008, Cuadrado & Nebreda 2010).

The mTOR and MAPK signalling pathways are made up of many proteins that are activated, or sometimes inactivated, via phosphorylation in a cascading manner. Figure 3 shows some of the frequently studied proteins in these signalling pathways and the potential effects of their activation. Following acute "hypertrophic" resistance loadings (consisting of 4–8 sets × 6–10 reps), studies have shown that several proteins of the mTOR and MAPK pathways have increased levels of phosphorylation lasting approx. 10−360 min post-loading.

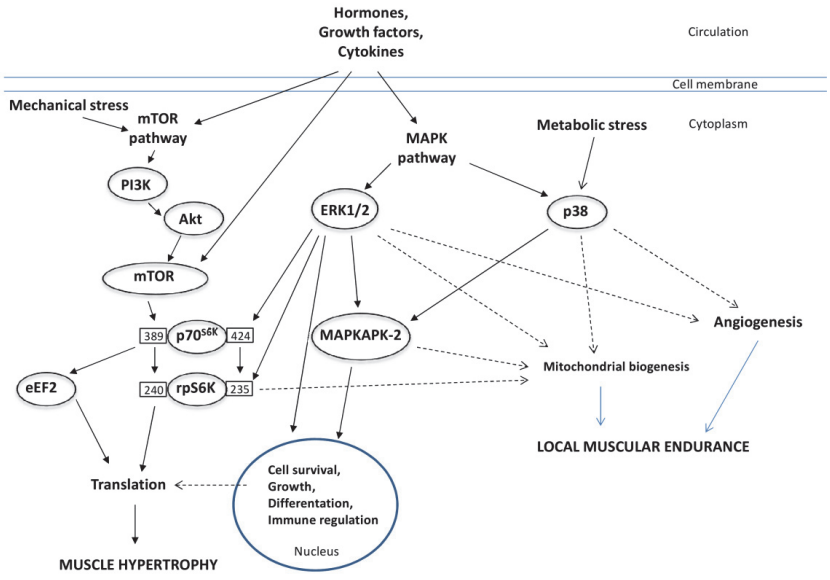

FIGURE 3 Cascading signalling of muscle protein kinases in the mTOR and MAPK pathways. Solid lines represent direct effects, dashed lines represent indirect effects.

2.2.3.1 Acute loading-induced responses in proteins of the mTOR pathway

Upstream to mTOR, protein kinase B (Akt) phosphorylation at Ser^{473} has been shown to initially decrease (Terzis et al. 2008a, Hulmi et al. 2009a) and then increase from 180−360 min post-loading (Dreyer et al. 2006, Drummond et al. 2008). Although there have been conflicting data in the early responses of Akt, one reason may be the use of combined resistance loading and nutrient intake as different responses have been observed when comparing protein supplementation with placebo (Hulmi et al. 2009a, Reitelseder et al. 2011). Conflicting findings have been observed in the phosphorylation of mTOR at Ser^{2448} and Ser^{2481} with increases 15−120 min (Dreyer et al. 2006, Mascher et al. 2008, Terzis et al. 2008a, Terzis et al. 2010) and no change 360 min (Glover et al. 2008) occurring after hypertrophic resistance loadings. Furthermore, increasing the number of sets during resistance loading from 1 to 5 did not influence the magnitude of mTOR phosphorylation at Ser^{2448} 30 min post-loading (Terzis et al. 2010). These mixed findings make interpretation of the importance of post-loading phosphorylation of Akt and mTOR on muscular adaptation difficult.

One protein that has been highlighted as playing an important role in muscle hypertrophy is $p70^{S6K}$. The magnitude of muscle hypertrophy has been shown to be positively related to phosphorylation of $p70^{S6K}$ in both rats (Baar & Esser 1999) and humans (Terzis et al. 2008a). Increased phosphorylation post-loading has been observed in a large number of studies (Dreyer et al. 2006, Drummond et al. 2008, Mascher et al. 2008, Terzis et al. 2008a, Hulmi et al, 2009a, West et al. 2009, Reitelseder et al. 2011, Hulmi et al. 2012). Quite interestingly, Hulmi and colleagues (2012) showed that $p70^{S6K}$ at Ser^{424}/Thr^{421} increased after both 15 × 1RM and 5 × 10RM leg press loadings, but $p70^{S6K}$ at Ser^{389} phosphorylation increased only following the 5 × 10RM loading protocol (Fig. 4). This suggests volume and/or metabolic demand influence phosphorylation of $p70^{S6K}$ at Ser^{389} and not intensity/muscle tension, at least immediately following resistance loading. Furthermore, Terzis et al. (2010) showed that the magnitude of phosphorylation at this binding site is highly dependent on total work performed during loading.

As can be seen from Figure 3, ribosomal protein S6 (rpS6) is downstream to $p70^{S6K}$. Increased phosphorylation of rpS6 at Ser^{235} is also dependent on the volume performed during resistance loading (Terzis et al. 2010, Hulmi et al. 2012). Another protein downstream to $p70^{S6K}$, Eukaryotic elongation factor 2 (eEF2), appears not to change in the early stages of recovery (Hulmi et al. 2009a) and is more active (decreased phosphorylation) 180−360 min post-loading (Drummond et al. 2008, West et al. 2009), which may indicate that it is important during the late recovery phase after resistance loading.

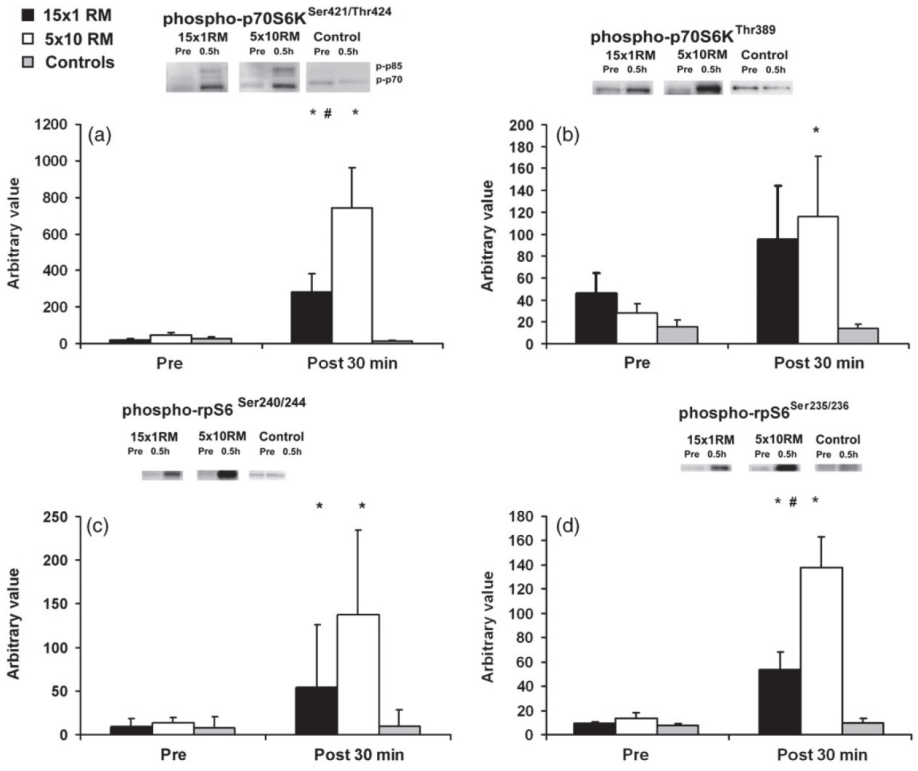

FIGURE 4 Acute loading-induced responses in $p70^{S6K}$ and rpS6 during maximal strength and hypertrophic leg press loadings (Hulmi et al. 2012). Copyright 2010 by John Wiley and Sons, reproduced with permission.

2.2.3.2 Acute loading-induced responses in proteins of the MAPK pathway

In addition to mTOR proteins, MAPKs have also been studied during acute resistance loadings. Presently, there is some debate as to the exact effects of MAPK proteins as results from animal studies have shown a vast range of influences on different tissues (Roux & Blenis 2004). However, it may be that phosphorylation of MAPK proteins induce adaptations in skeletal muscle that promote increased muscle mass and/or increased muscle endurance capacity.

ERK 1/2 phosphorylation at $Thr^{202/204}$ has been shown to increase immediately following 4–5 × 10RM leg press loading (Karlsson et al. 2004, Hulmi et al. 2012) and 8 × 10 knee extension loading in young men (Drummond et al. 2008). This response was clearly attenuated when performing 1 repetition per set (Hulmi et al. 2012) and no change in phosphorylation was observed with 6 reps per set (Terzis et al. 2010) suggesting that perhaps ERK 1/2 responds to the metabolic demand created by ~10 reps per set. However, it should be noted that increases have been observed following 15 × 3RM power clean pulls (Galpin et al. 2012). Therefore, a low number of reps per set may stimulate ERK 1/2 phosphorylation if performed with maximum velocity (i.e. explosively).

In general, loading protocols that induce increases in ERK 1/2 phosphorylation also increase p38 phosphorylation (Karlsson et al. 2004, Hulmi et al. 2012, Galpin et al. 2012). However, when separating the purported α/β and γ bands, Hulmi et al. (2012) observed increased phosphorylation of the α/β band following 15 × 1RM leg press loading. This suggests that high intensity/muscle tension may be necessary to stimulate p38 α/β phosphorylation. One protein that has not received much scientific attention is MAPK-activated protein kinase 2 (MAPKAPK-2). Its phosphorylation has been shown to increase following endurance exercise (Krook et al. 2000) possibly indicating that high metabolic demand stimulates MAPKAPK-2 through p38γ activation but, to the author's knowledge, this protein has yet to be investigated during resistance loading.

As noted for serum hormones, no scientific investigation has studied the phosphorylation responses of protein kinases in the context of constant vs. variable resistance loadings. However, evaluation of the acute responses in these, and other, protein kinases may improve our understanding of the impact of acute resistance loading protocols, and consequently potential mechanisms involved in muscular adaptations to resistance training.

2.3 Long-term adaptations to resistance training

2.3.1 Neural adaptations

Theoretically, neural adaptations could occur due to improved agonist and/or synergist activation, as well as reduced coactivation of antagonists. Increased agonist activation has been the focus of most scientific studies and will be discussed here. Agonist activation could improve through greater motor unit recruitment or firing frequency through greater descending drive from supraspinal centres, greater motor unit synchronisation, greater spinal motor neuron excitability, and/or reduced spinal inhibition of descending drive (Aagaard & Thorstensson 2003).

The classic study by Moritani & de Vries (1979) described that in previously untrained subjects the initial improvements in force production could be accounted for by neural adaptations and that hypertrophy would progressively account for improvements following approx. 4 weeks of training. Some studies have suggested that neural adaptations had occurred based on the observations of disproportionate increases in force production and muscle hypertrophy (Dons et al. 1979, Jones & Rutherford 1987, Sale et al. 1992). Other previous studies have attempted to more directly describe changes in muscle activation via measurements such as surface and intramuscular EMG (Häkkinen & Komi 1983, Keen et al. 1994, Häkkinen et al. 1998a, Häkkinen et al. 2001a, Aagaard et al. 2002b, Kamen & Knight 2004, Christie & Kamen 2010, Vila-Cha et al. 2010), superimposed twitch during maximum isometric contraction (Ramsay et al. 1990, Harridge et al. 1999, Knight & Kamen 2001), assessment of M-wave, V-wave and Hoffman (H)-reflex properties (Aagaard et al. 2002a, Fimland et al.

2010), and also transcranial magnetic stimulation (TMS) (Lee et al. 2009, Latella et al. 2012). Figure 5 shows early increases (4–8 weeks) in isometric force accompanied by increased quadriceps EMG activity with minor increases in muscle fibre cross-sectional area of the vastus lateralis muscle (Häkkinen et al. 1981, Häkkinen et al. 1983).

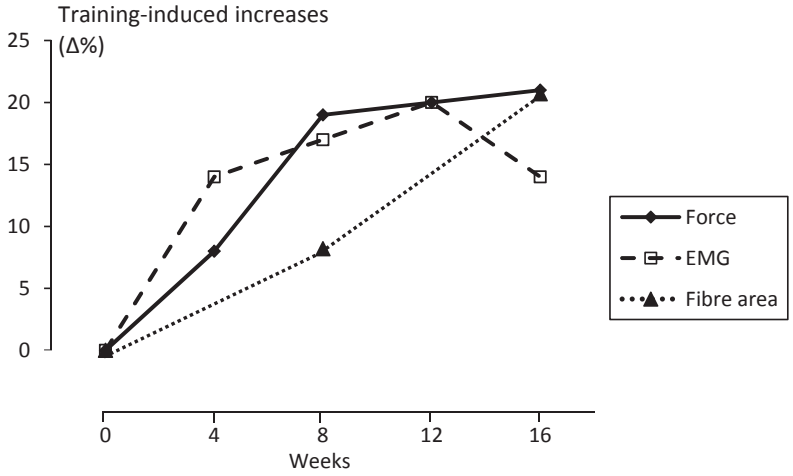

FIGURE 5 The effect of resistance training on maximal bilateral isometric leg extension force (Force), averaged quadriceps muscle activity (EMG), and averaged muscle fibre area of the vastus lateralis (Fibre area) in young men (modified from Häkkinen et al. 1981 and Häkkinen et al. 1983). Copyright 1981 and 1983 by John Wiley and Sons and Lippincott Williams and Wilkins respectively, reproduced with permission.

Increased surface EMG amplitude has been observed following resistance training in healthy young subjects (Häkkinen & Komi 1983, Narici et al. 1989, Aagaard et al. 2002b), and in middle-aged and older subjects (Häkkinen et al. 2001a, Suetta et al. 2004, Karavirta et al. 2011) following training periods of 8–21 weeks. Although interpretations of neural adaptation based solely on EMG amplitude should be made with caution due to methodological constraints and confounding factors (Farina et al. 2004), increased amplitude could be due to greater motor unit recruitment, firing frequency, or synchronisation. Studies on the tibialis anterior (Van Cutsem et al. 1997) and soleus (Oya et al. 2009) muscles have shown that recruitment of motor units occurs until approx. 90 % and 95 % of maximum isometric force respectively. Unfortunately, recruitment patterns of the quadriceps have not been quantified, nevertheless, based on these observations, it seems likely that greater motor unit recruitment does not account for neural adaptations (and increased EMG amplitude) following resistance training.

Kamen & Knight (2004) showed increased firing frequency of the vastus lateralis muscle following 6 weeks of knee extension training with 3 × 10 using 85 % 1RM in both young and older subjects. In this study, the increased firing frequency occurred largely in the early weeks of training, even in the control

period before the training intervention. Furthermore, the inclusion of 3 maximum isometric knee extensions during training does not allow the reader to assess the origin of the training-induced improvements. In another study from this laboratory (Christie & Kamen 2010) 5 weeks of isometric training of the dorsiflexor muscles showed significant training-induced increases in firing frequency during maximum isometric force in both young and older subjects. In addition to potentially influencing maximum force production, increased firing frequency has been shown to accompany improved rate of force development since the seminal findings of Van Cutsem and colleagues (1998). Finally, 6 weeks of strength training increased firing frequency, while no change was observed following endurance training (Vila-Cha et al. 2010).

Motor unit synchronisation has been shown to increase EMG amplitude (Yao et al. 2000, Arabadzhiev et al. 2010). Furthermore, increased synchronisation has been shown following 6 weeks of isometric training (Milner-Brown et al. 1975) and in strength-trained athletes compared to untrained controls (Milner-Brown et al. 1975, Semmler & Nordstrom 1998). However, data indicating that motor unit synchronisation does not aid force production has been shown (Yao et al. 2000, Kidgell et al. 2006).

Peripheral nerve stimulation has been used to quantify motor neuron excitability originally in upper limb muscles (Sale et al. 1983) and, thereafter, in the soleus muscle (Aagaard et al. 2002a, Fimland et al. 2010). The V wave is the voluntary contraction equivalent of the more commonly known H-reflex. When expressed relative to the M-wave, the V-wave gives information regarding changes in descending drive, motor neuron excitability, and/or pre-synaptic inhibition as voluntary action potentials collide with, and clear, the antidromic impulses (Aagaard & Thorstensson 2003). Aagaard et al. (2002a) observed increased V-wave amplitude after 14 weeks of seated calf raises using 4–5 sets of 3–10 reps. The authors attributed this increase to increased descending drive and/or increased motor neuron excitability, but specifically discussed the possibility of increased descending drive through greater firing frequency. These findings were also observed in multiple sclerosis patients following 3 weeks of 4 × 4 seated calf raises (Fimland et al. 2010).

Electrical stimulation has also been used to assess voluntary activation level (i.e. the proportion of "true maximum" activation during maximum voluntary effort). By superimposing a twitch during maximum isometric contraction (Merton 1954) comparison to a subsequent resting twitch (Bellemare & Bigland-Ritchie 1984) yields voluntary activation level as a percentage of maximum activation achieved. Increased voluntary activation level following training is purported to represent improved motor unit recruitment and/or firing frequency. Some studies have observed increased voluntary activation level in young and older subjects (Knight & Kamen 2001), while others have failed to demonstrate statistically significant increases (Ramsay et al. 1990, Harridge et al. 1999). This may be indicative of the methodology to detect changes of sufficient magnitude to reach statistical significance and it has been suggested that small increases represent a physiologically significant improvement in muscle activa-

tion (Herbert & Gandevia 1999). Furthermore, individual increases in voluntary activation level have been associated with improved force production (Harridge et al. 1999).

More recently, the use of TMS to describe training-induced neural adaptations has been used and showed mixed findings. Motor evoked potentials from TMS stimulation increased in parallel with improved force production (Kidgell et al. 2010), indicating increased descending drive. Lee et al. (2010) on the other hand observed no changes in either voluntary activation level or response to TMS stimulation following 4 weeks of 4 × 8 (70-85 % 1RM) wrist abduction training. This data suggests that increased descending drive did not account for the observed improved (~11 %) forced production. Support for this finding was provided by Latella and colleagues (2012). Subjects performed unilateral leg press actions 3 times per week for 8 weeks (3 sets of 4–8 reps) and demonstrated no changes in EMG amplitude. However, a reduced silent period observed in both the trained and untrained rectus femoris muscle suggests reduced corticospinal inhibition (Latella et al. 2012).

Taken together, the results of scientific investigation seem to suggest that neural adaptation does occur due to resistance training. However, due to a complex and interactive system of excitatory and inhibitory influences, as well as methodological constraints, it is very difficult to identify the exact mechanism of neural adaptation that leads to improved force production.

2.3.2 Muscular adaptations

Muscle fibres have been classified according to their histochemical staining properties, as well as twitch characteristics. Most studies focus on three types; Type I (slow twitch), Type IIa (Fast twitch, oxidative), and Type IIx (Fast twitch, glycolytic) - referred to as Type IIb in earlier studies. Previous studies have identified changes in muscle fibre subtype due to resistance training (Staron et al. 1994, Häkkinen et al. 1998b, Campos et al. 2002). It appears that, through maximal strength and hypertrophic resistance training, there is a shift in fibre type distribution away from Type IIx towards Type IIa (Staron et al. 1994, Häkkinen et al. 1998b, Andersen & Aagaard 2000, Campos et al. 2002), however, it seems that no exchange takes place between Type I and Type II fibres.

In addition to changes in muscle "quality", resistance training induces increases in muscle "quantity". Although hyperplasia (the increased number of muscle fibres) is theoretically possible, supported by evidence from animal studies, this seems to have been dismissed as a possibility of post-natal skeletal muscle hypertrophy in humans. Therefore, only muscle hypertrophy (the increase in size of existing muscle fibres) will be discussed. Early animal studies suggested that micro-trauma is a prerequisite for muscle hypertrophy (Goldspink 1971). However, little is known about the exact resistance training stimuli needed to induce hypertrophy, and several requirements have been proposed recently, such as muscle damage, mechanical tension, and metabolic stress (for review see Schoenfeld 2010).

Studies have analysed muscle hypertrophy by, for example, muscle fibre CSA from biopsy samples (Häkkinen et al. 1981, Aagaard et al. 2001, Campos et al. 2002, Häkkinen et al. 2002, Mero et al. 2012), as well as whole muscle volume and muscle CSA with magnetic resonance imaging (MRI) (Narici et al. 1989, Narici et al. 1996, Häkkinen et al. 1998b, Kraemer et al. 1999, Aagaard et al. 2001, Ahtiainen et al. 2003) or computer tomography (CT) scanning (Sale et al. 1992). These studies have observed robust increases in quadriceps muscle fibre and whole muscle size as a consequence of resistance training.

In previously untrained young men, the separation of training into low rep (3–5RM), intermediate rep (9–11RM), and high rep (20–28RM) training groups led to increases in cross-sectional area of Type I (~13 %), IIa (~20 %), and IIx (~26 %) fibres in the low and intermediate groups after 8 weeks of training (Campos et al. 2002). These results suggest that, when training is matched for total work, high or medium intensity is needed to induce hypertrophy in previously untrained subjects. In a study by Aagaard and colleagues (2001), significantly increased CSA of Type II (~18 %) but not Type I (~9 %) fibres was observed. Taken together, it appears that Type II fibres increase size more readily than Type I fibres, at least in young subjects.

At the whole muscle level, Narici et al. (1989) observed an ~8.5 % increase in quadriceps CSA following 60 days of isokinetic knee extension training. Slightly greater increases (~10–11 %) were observed following 19 weeks of leg press training with 7–20 reps per set (Sale et al. 1992) and 14 weeks of combined low (4–6) and intermediate (10–12) rep training of the lower limbs (Aagaard et al. 2001). It also appears that hypertrophy is non-uniform along the muscle length and that specific regions of the quadriceps are more susceptible to hypertrophy than others (Narici et al. 1996, Häkkinen et al. 2001b, Ahtiainen et al. 2003). Distal and proximal regions of the quadriceps increased CSA by ~19 % while the central region increased by ~7 % after 21 weeks using 6 × 8 with 80 % 1RM (Narici et al. 1996), although all regions increased significantly before vs. after training.

In older men, a 10 week resistance training period increased quadriceps CSA by ~8.5 %, which was similar to the increases in young men as assessed by MRI (Häkkinen et al. 1998b). Furthermore, large increases in VL fibre CSA was observed in Type I (~50 %), IIa (~48 %), and IIx (~46 %) fibres following 24 weeks of linearly periodised, progressive resistance training (Häkkinen et al. 2002). Conversely, in another study by Häkkinen et al. (1998a) of similar training duration, there were no changes observed for older men in whole muscle CSA (~2 ± 2 %) and modest, but significant, increases in middle-aged men (~5 ± 3 %). These results may be partly due to the accuracy/sensitivity to detect changes of the ultrasound measurements of that time. Alternatively, some studies have observed differences a lower magnitude of hypertrophy in older vs. young subjects (Kraemer et al. 1999, Mero et al. 2012), and one factor that has been identified as a possible explanation is a lower protein intake during training in the older subjects (Mero et al. 2012).

Finally, changes in pennation angle have been observed during to resistance training (e.g. Aagaard et al. 2001). This could increase muscle force production by allowing a greater fibres area per given volume of muscle. Interestingly, increased pennation angle and muscle thickness has been observed during hypertrophic resistance training, while decreased pennation angle has been accompanied by increased muscle thickness in the group performing plyometric training (Blazevich et al. 2003). These results suggest that training-specific adaptations in muscle architecture are in-line with proposed theory for improved force production or shortening velocity of muscle fascicles.

2.3.3 Hormonal and molecular adaptations

Basal hormone concentrations after resistance training have been shown to remain unchanged (Craig et al. 1989, McCall et al. 1999, Ahtiainen et al. 2003), increase (Häkkinen et al. 1985a, Sallinen et al. 2007, Sillanpää et al. 2010), or decrease (Fry et al. 1993, Rankin et al. 2004) following resistance training lasting 10–24 weeks. An increase in basal testosterone would seem to be advantageous in promoting training-induced adaptations (Häkkinen et al. 1985a, Häkkinen et al. 1988). However, it is difficult to attribute any observed change in basal testosterone concentrations to short-term training *per se*, as it has been shown that the seasonal variation (Svartberg et al. 2003) and dietary intake (Anderson et al. 1987, Bishop et al. 1988) influence androgen concentrations. Perhaps the strongest scientific evidence that resistance training can increase basal serum hormone concentrations comes from a study where weightlifters were assessed over 2 years (Häkkinen et al. 1988). The results of this study suggest that chronic and frequent high-intensity resistance training can influence the endocrine system, which may be important in promoting further adaptation once significant increases in strength and muscle mass have been achieved (Häkkinen et al. 1988).

Regarding adaptations in the responsiveness of serum hormones to acute resistance loading, short-term resistance training studies (7–12 weeks) in young subjects have shown mixed findings. Acute total testosterone (Kraemer et al. 1998) and growth hormone (Craig et al. 1989, Izquierdo et al. 2009b) response can be greater following a training period, although similar responses have also been observed for testosterone (Craig et al. 1989) and growth hormone (McCall et al. 1999). It is difficult to discern, based on these studies, whether greater responsiveness in growth hormone is due to alterations within the endocrine system or due to an greater total work performed during loading, as the magnitude of growth hormone response has been shown to be related to greater volume and intensity during loadings (Kraemer et al. 1990, Häkkinen & Pakarinen 1993, Smilios et al. 2003). However, a larger/longer growth hormone response seems to be observed in most short-term training studies. A lower magnitude of acute growth hormone response 30 min post-loading in young men has also been observed, which was accompanied by lower blood lactate response (Kraemer et al. 1999). As growth hormone response has been shown to be related to blood lactate response (Häkkinen & Pakarinen 1993, Gordon et al. 1994), it may be that training-induced adaptations led to a reduced reliance on anaerobic me-

tabolism in response to the same loading protocol. This interpretation is supported by the findings that acute cortisol response was lower in the same study (Kraemer et al. 1999).

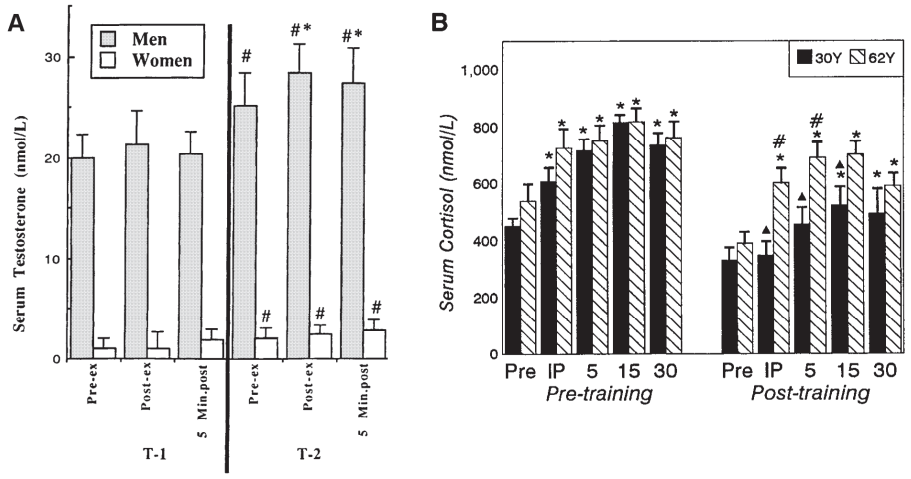

FIGURE 6 Serum total testosterone in young men (A, Kraemer et al. 1998) and cortisol in young and older men (B, Kraemer et al. 1999) during recovery from acute resistance loadings before and after a period of resistance training. Copyright 1998 by Springer Publishing and 1999 by the American Physiological Society respectively, reproduced with permission.

Acute cortisol response can be attenuated (Hickson et al. 1994, Kraemer et al. 1999) or remain similar (Kraemer et al. 1998, Izquierdo et al. 2009b) after a resistance training period. A reduction in serum cortisol response to resistance loading may be viewed as a marker of training-induced adaptation. As cortisol responds to psycho-physiological stress, it is possible that the subjects have become accustomed to the physical challenge of the resistance loading protocol due to training in addition to the potential for lower metabolic stress discussed above. Regarding those studies that observed no change in acute cortisol response (Kraemer et al. 1998, Izquierdo et al. 2009b), it may be that training needs to be longer than 8 weeks duration to induce these adaptations.

In older men, it appears that adaptations in the magnitude of acute endocrine responses due to resistance training may be clearly observed. In subjects demonstrating signs of andropause and somatopause, training-induced adaptations in acute hormone responses have been readily observed, despite fewer studies investigating this phenomenon. Greater acute total testosterone responses have been observed after 10 weeks (Kraemer et al. 1999) and 24 weeks (Häkkinen et al. 2002) of resistance training. Significant elevations in growth hormone have been observed after 24 weeks of training (Häkkinen et al. 2002) in older men and 21 weeks in older women (Häkkinen et al. 2001b). Furthermore, it appears that particularly low responders are able to increase their acute growth hormone response to resistance loading, as reduced inter-individual

variability led to statistically significant increases in older women following 24 weeks of training (Häkkinen et al. 2002).

One area of study that has received very little scientific attention is changes in acute molecular responses after a period of resistance training. Resting phosphorylation levels of Akt, eIF4E, FAK, and GSK3-β were significantly elevated after the training period (Wilkinson et al. 2008), which agreed with previous work by Leger et al. (2006). The authors proposed that higher resting levels indicate a "heightened state of responsiveness" and may lead to greater potential for muscle hypertrophy (Wilkinson et al. 2008).

Wilkinson and colleagues (2008) showed that, in response to 5 × 8–10 knee extension loading, phosphorylation of Akt at Ser^{473} and eIF4E at Ser^{209} immediately post-loading was greater than before the training period (10 weeks) suggesting greater responsiveness in anabolic signalling. However, phosphorylation of rpS6 at Ser^{235} was significantly lower 240 min post-loading compared to before training. Unfortunately, loadings were performed in the fed state and so the enhanced phosphorylation of some protein kinases, especially Akt, could be attributed to either the effect of loading or nutrition as discussed above (Hulmi et al. 2009a, Reitelseder et al. 2011). Mayhew and colleagues (2011) found indications that, at least in high responders to resistance training, the acute p70 and eIF2Bε responses were blunted after 16 weeks of 3 × 8–12 lower limb resistance training 3 times per week. This matches the lower rpS6 phosphorylation observed by Wilkinson et al. (2008) and perhaps seems logical that the same resistance loading stimulus would induce lower responses as training and training-induced adaptations progress.

2.4 Long-term gains in force production to constant vs. variable resistance training

Several studies have investigated training-induced adaptations to training using resistance devices that produce either constant or variable external resistance, the results of which are summarised in Table 1. These devices have manipulated the lever arm distance by the use of cams or pulleys. Ariel (1976) showed that training for 4 weeks (4 × 3−8RM) significantly improved force production by 4 % in the variable resistance group and 1 % in the constant resistance group. This indicates greater benefit from training with variable external resistance. However, the overall gains in both groups are low and this study has been criticised as the author helped to design the equipment. Alternatively, Stone et al. (1979) observed greater improvements in the group training with power cleans compared to the group training with variable resistance knee extension. The test in this study was non-specific (jump squat) and perhaps favoured the group training with a similar movement pattern. Similarly, Silvester & Bryce (1981) compared variable resistance devices for the lower limbs vs. free weight box squats. Both training modes were equally effective in improving

jump squat performance, an action not performed in training but more closely matching the movement pattern of box squat training of the constant group.

Two training studies have investigated the effect of testing on the training-specific device, which highlight the importance of test selection to make conclusions on the effectiveness of either training mode. Pipes (1978) used a multi-exercise 3 × 8 training program for 10 weeks. For the leg press exercise, greater improvements were observed in the constant group when testing was performed using a constant resistance device and greater improvements were observed in the variable group when testing was performed using a variable resistance device. Similar device-specific training improvements were found for the pull-down, military press, and biceps curl exercises (Pipes 1978). The study by Boyer (1990) corroborated these findings for the leg press exercise in that testing on the constant resistance device revealed ~16 % and ~11 % improvements in the constant and variable training groups, respectively. Testing on a variable resistance device, conversely, revealed ~17 % and ~29 % improvements in the constant and variable training groups, respectively.

Coleman and colleagues (1977) used the same resistance devices as Pipes (1978) and observed similar improvements in force production from both training modes. For the biceps curl exercise, Silvester & Bryce (1981) observed similar improvements in isometric force production from variable resistance device vs. free weights biceps curl training over 13 weeks with different training programs for the groups. In agreement, Manning and colleagues (1990) compared constant vs. variable resistance knee extension training (10 weeks, 2−3 days per week, 1 × 8−12) and observed equivalent improvements in isometric torque throughout the range of motion. Although the relative improvements in dynamic (device-specific) load used during training improved more in the variable group (~46 % vs. ~24 %), the authors dismissed this as evidence of greater improvements due to variable resistance training as the variable group was weaker than the constant training group at the beginning of training.

TABLE 1 Summary of training intervention studies comparing constant and variable external resistance.

Study	Training mode (n)	Training duration	Training program	Main findings
Ariel 1976	CON vs. VAR	4 wk	5d ·wk^{-1}, 4 × 3−8RM	1RM : 1 vs. 4 %
Coleman et al. 1977	LP, CON vs. VAR (total = 60), young men untrained	10 wk	3d ·wk^{-1}, 2 × 8−12RM	LP 1RM : 16.5 vs. 16 %
Pipes 1978	LP, CON vs. VAR (total = 36), young men untrained	10 wk	3d ·wk^{-1}, 3 × 8 using 75 % 1RM	CON LP 1RM:* 29 vs. 8 %, VAR LP 1RM:* 8 vs. 27 %, estimated lean body mass: 4 vs. 5 %
Stone et al. 1979	FW power clean (16) vs. VAR KE (16) trained men	5 wk	3d ·wk^{-1}, FW multiple sets vs. VAR 1 set to failure	jump height:* FW > VAR
Silvester & Bryce 1981	EF, FW vs. VAR, FW S vs VAR KE	EF 8 wk S 13 wk	3d ·wk^{-1}, FW multiple sets vs. VAR 1 set to failure	FW = VAR
Boyer 1990	LP, CON vs. VAR (total = 32) young women untrained	12 wk	3d ·wk^{-1}, 3 × 6−10RM	CON LP 1RM:* 16 vs. 11 %, VAR LP 1RM:* 17 vs. 29 %,
Manning et al. 1990	KE, CON (17) vs. VAR (17), young untrained	10 wk	2−3d ·wk^{-1}, 1 × 8−12RM	peak isometric torque: 16 vs. 17 %, training load: 24 vs. 46 %
Anderson et al. 2008	S and BP, FW vs. B (total = 39), young athletes	7 wk	3d ·wk^{-1}, 3−6 × 2−10 using 72–98 % 1RM	estimated S 1RM:* 6 vs. 16 %, estimated BP:* 1RM 4 vs. 8 %
Ghigiarelli et al. 2009	BP, FW (12) vs. B (12) vs. C (12), young athletes	7 wk	1d ·wk^{-1}, 6 × 3RM	estimated 1RM: 5 vs. 7 vs. 8 %
McCurdy et al. 2009	BP, FW vs. C (total = 27), young athletes	9 wk	2d ·wk^{-1}, 5−9 × 1−8 using 60–95 % 1RM	FW 1RM: 6 vs. 6 %, C 1RM: 7 vs. 15 %
Bellar et al. 2011	BP, cross-over FW vs. B (11), young untrained	3 wk vs. 3 wk	2d ·wk^{-1}, 5 × 5 using 85 % 1RM	1RM:* 7 vs. 10 %
Shoepe et al. 2011	S and BP, FW (10) vs. B (10), young active	24 wk	3d ·wk^{-1}, 67–95 % 1RM (sets × reps not specified)	S 1RM: 9 vs. 20%, BP 1RM: 32 vs. 33 %

LP = leg press, KE = knee extension, EF = elbow flexion, S = squat, BP = bench press, CMJ = coutermovement jump, CON = constant resistance device, VAR = variable resistance device, FW = free weight, B = rubber band + free weight, C = chain + free weight, wk = weeks. * = significant difference between groups.

Recently, studies have investigated training free weight exercises with the addition of either rubber bands or chains to provide linearly increasing resistance. Typical use of this equipment is focussed on the exercises used in powerlifting, namely the squat, bench press, and deadlift exercises. These multi-joint actions would theoretically be well-suited to this form of variable resistance, however, results of studies have also been mixed. Methodological considerations when evaluating these studies is that; 1) all testing was performed with free weights only (i.e. constant resistance), and 2) the free weight resistance has been substituted for the variable resistance (i.e. the resistance was equal between groups only at full extension).

Anderson et al. (2008) showed that college athletes improved maximum force production during dynamic bench press and squat exercises to a greater extent over 7 weeks using combined free weight and rubber bands than free weight resistance only. It should be noted, however, that the subjects performed 1−3RM during testing and the 1RM scores were calculated based on standardised conversion factors. Using a randomised cross-over design, Bellar and colleagues (2011) observed significantly greater improvements in the group training with combined free weight and rubber bands for 3 weeks with 5 × 5 using 85 % 1RM.

Conversely, estimated 1RM (5−7RM testing) bench press improved similarly by in rubber band + free weight, chain + free weight, and free weight only training groups, respectively, following low rep resistance training (3 reps per set) incorporated only once per week into a 7-week program (Ghigiarelli et al. 2009). In the longest training study of 24 weeks, Shoepe et al. (2011) observed no statistical differences in 1RM bench press and squat improvements when comparing combined rubber band + free weight vs. free weights only. However, it is noticeable that the improvements in the bench press were twice as great in the free weight only group (Table 1).

In the only study using training-specific, as well as non training-specific bench press tests, identical improvements in free weight bench press were observed between the groups but the group training with variable resistance improved combined chain and free weight bench press performance by ~15 % vs. ~6 % of the free weight only group (McCurdy et al. 2009). The authors did not observe statistically significant differences between the two training groups, although the training-specific improvements following chain + free weight training was more than twice that observed in the free weight only group.

It is noticeable that these studies have assessed only maximum force production, in which improvements in previously untrained subjects could be expected to similar. There is a clear gap in scientific research investigating other parameters, such as muscle hypertrophy, when comparing constant and variable resistance training. Collectively, the studies that have investigated constant and variable resistance have contained elements within their methodologies, such as test selection, lower resistance at small joint angles in the variable resistance mode, initial strength of the groups, and especially varying training program variables, which may either not allow accurate comparisons or bias

the results towards one training mode or the other. These considerations have perhaps led to inconsistent findings and, consequently, scientifically-supported practical application of these training modes has not been possible.

3 PURPOSE OF THE STUDY

Muscular contraction *in vivo* has been shown to produce distinct force-angle relationships. Single-joint contractions tend to produce inverted U-shaped force-angle curves with peak force produced during the mid range of motion, while multi-joint contractions produce either linearly increasing or decreasing force-angle curves. Typical resistance training is characterised by constant external resistance (i.e. the external resistance remains the same throughout the whole range of motion). Therefore, theoretically, the load that is lifted during resistance training is limited to the weakest parts of the range of motion. Variable external resistance gives potential for muscular contractions that more closely resemble their maximum force-angle capabilities by using. It is possible that training with variable external resistance may lead to greater improvements in neuromuscular performance, muscle activation, and/or muscle hypertrophy.

The specific aims of the present experiments were:

1) To describe the effects of cam-based variable external resistance devices on kinetic, kinematic, and muscle activation variables in comparison to constant external resistance in the lower limbs (original paper I).

2) To evaluate the acute effects of constant and variable external resistance loading on neuromuscular fatigue, blood lactate, serum hormone, and phosphorylation of muscle protein kinases before and after a period of resistance training (original papers II−IV).

3) To evaluate chronic adaptations to resistance training using either constant or variable external resistance devices in the lower limbs (original papers IV and V).

4) To determine whether similar acute and chronic responses to constant versus variable external resistance occur in young and older subjects (original papers III and V).

The primary hypothesis was that variable external resistance causes greater force during parts of the range of motion that are capable of producing larger force, which is accompanied by greater muscle activation compared to constant external resistance. This will lead to greater acute neuromuscular fatigue, increases in serum hormone concentration and protein kinase phosphorylation during loading, which will promote greater training-induced adaptations in neuromuscular performance, as well as muscle activation and/or hypertrophy when using variable external resistance.

4 METHODS

4.1 Subjects

A total of 125 subjects volunteered to participate in the present study, which included 73 young (age range 20–35 yrs) and 52 older men (age range 60–72 yrs). During the course of the study, 6 young men dropped out due to personal reasons, not completing all study criteria, and musculoskeletal injuries. Two older men dropped out due to pre-existing musculoskeletal injuries (1 in paper III and 1 in paper V). Therefore, a total of 117 subjects (67 young and 50 older men) completed all study requirements and were considered in analyses. All subjects were healthy and physically active, participating in low-intensity, endurance-type exercise, such as jogging, cycling, and cross-country skiing, however, none of the subjects had regularly performed resistance training at a frequency greater than once per week for the previous 12 months. Some of the young subject also participated in ball games (e.g. football, floorball, volleyball etc) at a frequency of 1–2 times per week. All subjects were instructed to continue wioth their habitual physical activity habits during the study. Exclusion criteria included cardiovascular diseases, diabetes, musculoskeletal dysfunctions, impaired endocrine function, or any other condition that may have hindered performing the training or testing protocols. All subjects were recruited through advertisement and email lists. Physical characteristics of the subjects that completed each part of the study are presented in Table 2.

TABLE 2 Physical characteristics of the subjects (mean ± SD).

Original paper	Subjects	Age (years)	Height (cm)	Body mass (kg)	Body fat (%)
I	Y, n = 9	29 ± 4	179 ± 5	79 ± 7	12 ± 3
II	Y, n = 13	28 ± 4	180 ± 4	79 ± 10	15 ± 3
III	Y, n = 12	28 ± 5	181 ± 4	79 ± 10	17 ± 6
	O, n = 13	65 ± 4	176 ± 5	79 ± 9	22 ± 6
IV	YV, n = 11	27 ± 5	177 ± 6	71 ± 8	19 ± 10
	YC, n = 12	29 ± 5	181 ± 6	79 ± 11	18 ± 7
	YCo, n = 10	30 ± 4	180 ± 6	84 ± 14	19 ± 6
V	OV, n = 13	65 ± 4	177 ± 6	82 ± 7	25 ± 8
	OC, n = 13	65 ± 4	176 ± 4	80 ± 8	24 ± 5
	OCo, n = 11	65 ± 3	178 ± 7	78 ± 13	22 ± 6

Y = young, O = older, V = variable resistance training, C = constant resistance training, Co = control

The subjects were carefully informed of the study design and all potential risks and discomfort before the commencement of the study, after which all subjects provided written consent. The older men were then examined by a physician, including electrocardiogram assessment and were proclaimed healthy to perform rigorous exercise. None of the subjects were taking medication that may influence the neuromuscular or endocrine systems. The study was conducted according to the Declaration of Helsinki, and was approved by the Ethics Committees of the University of Jyväskylä and the Central Hospital, Jyväskylä, Finland.

4.2 Experimental design

In order to study the effect of variable versus constant resistance training, the present study comprised evaluation of single-repetition performance, acute maximal strength and hypertrophic loadings, and long-term training (Fig. 7). Also, to examine whether the effects of variable versus constant resistance are similar in different groups, subjects in this study were young (20–35 yrs) and older (60–72 yrs) men. The experimental designs used in each of the original papers are summarised in Table 3 and Figure 7.

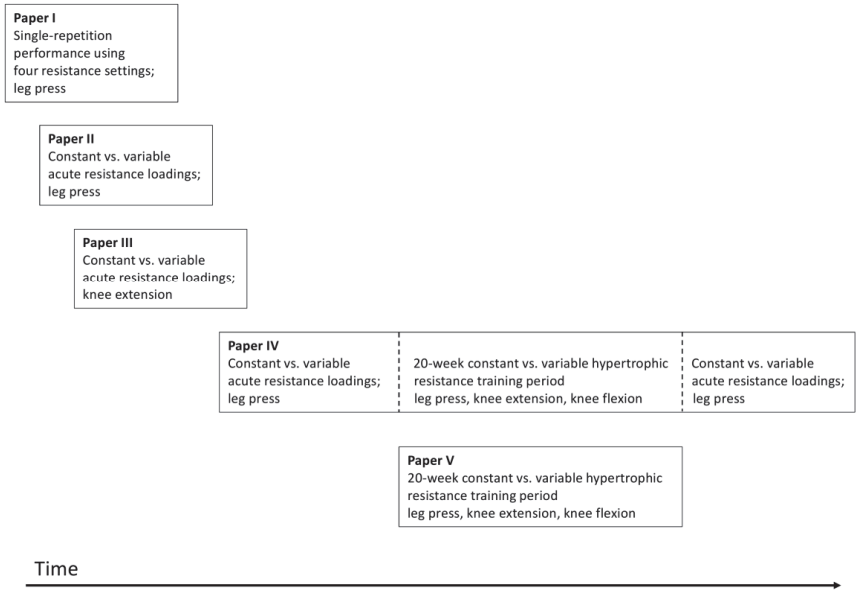

FIGURE 7 Overall study design, which includes three cross-sectional and two longitudinal experiments.

During the single-repetitions, concentric performance was evaluated during both steady-paced (paper I), and were assessed by kinetic variables and surface electromyography (EMG). Measurements pre-, immediately post-, and up to 30 min post- acute loading protocols assessed the impact of the constant and variable resistance loadings. Measurements included concentric force and EMG, as well as isometric force and EMG (II–IV), blood samples (II, IV) and muscle biopsy samples (IV). The effects of training with either constant or variable resistance were measured before, after 10 weeks of training ("mid"-training), and after 20 weeks of training (IV, V). Training was performed twice per week, and both the training and control groups were instructed to maintain their habitual physical activity throughout the training period. Non-training, age-matched control groups were examined during the longitudinal design before and after the 20-week period (IV, V). The testing sessions for individual subjects were performed at the same time of day during the study to control for diurnal variation (Sedliak et al. 2007).

TABLE 3 Summary of the experimental designs of each original paper and primary variables measured.

Original paper	Subjects	Experimental design	Primary variables
I	Young	Cross-sectional (single-repetition performance; leg press)	1) Concentric force and velocity 2) Concentric muscle activity
II	Young	Cross-sectional (acute loadings 15 × 1RM and 5 ×10RM; leg press)	1) Concentric and isometric leg extension force production 2) Concentric and isometric muscle activity 3) Serum hormone responses
III	Young and Older	Cross-sectional (acute loadings 15 × 1RM and 5 ×10RM; knee extension)	1) Concentric and isometric leg extension force production 2) Concentric and isometric muscle activity 3) Responses to electrical stimulation
IV	Young	Longitudinal (20-week hypertrophic training program with acute hypertrophic loadings before and after training; leg press)	1) Force production and fatigue-resistance performance 2) Muscle hypertrophy 3) Serum hormone responses 4) Muscle protein kinase responses
V	Older	Longitudinal (20-week hypertrophic training program)	1) Force production and fatigue-resistance performance 2) Muscle hypertrophy

4.3 Data collection and analyses

4.3.1 Anthropometric and muscle mass measurements

Body mass was measured by a calibrated scale during familiarisation testing (I–III) or after a 12 hour, overnight fast (IV, V). Height was measured by a wall-mounted scale. All anthropometric measurements were made after 48 hours abstinence from exercise.

4.3.1.1 Whole body composition and lean body mass

Bioelectrical impedance. Whole body fat percentage and total muscle mass was measured by an eight-polar bioelectrical impedance device (InBody 720 body composition analyzer, Biospace Co. Ltd, South Korea) and used to describe the

subjects' physical characteristics (Table 2). The subjects were upright with the arms abducted by approx. 20° to ensure that the arms and trunk were not in contact.

Dual-energy X-ray Absorptiometry (DXA). Whole body composition was measured by DXA (LUNAR Prodigy Advance, GE Medical Systems, Madison, USA), which was used to describe changes during the training period (IV, V). The device measures lean tissue, including muscle, as well as connective tissue, and excludes fat and bone. The legs and arms were isolated from the trunk using software generated regions (enCORE 2005, version 9.3). The automatic region for the legs was adjusted manually, so that the proximal region dissected the pelvis from the lateral portion of Ilium to the sacral promontory (Fig. 8), to ensure that the hamstrings and the gluteal muscles were included in the measurement. The legs were secured by non-elastic straps and the arms secured by rice bags to prevent movement during the measurement.

Before both bioelectrical impedance and DXA measurements, the subjects were advised to drink 2 dl (one cup) of water to standardise hydration status (Thompson et al. 1991). All metal objects were removed from the subject prior to measurement and the same investigator performed all measurements and a separate investigator performed all analyses (including region adjustments).

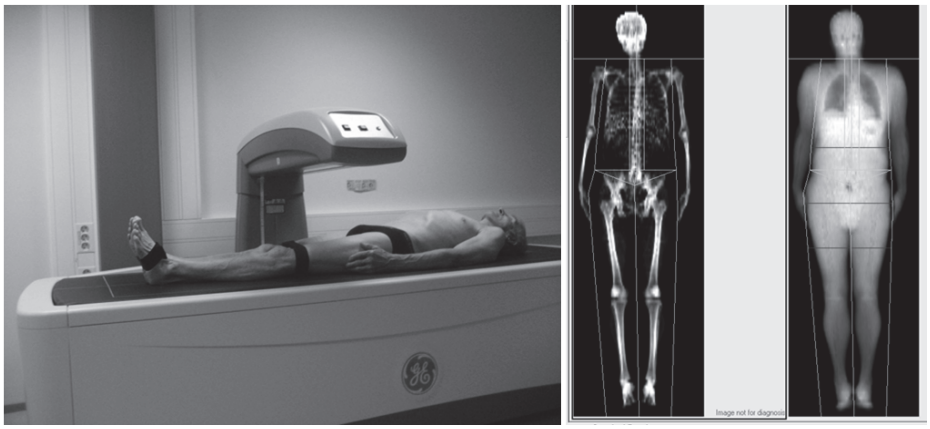

FIGURE 8 Assessment of whole body composition by DXA (left) and a software generated image with adjusted regions used in the analysis (right).

4.3.1.2 Muscle cross-sectional area

Cross-sectional area (CSA) of the vastus lateralis was assessed by B-mode axial-plane ultrasound (model SSD-α10, Aloka Co Ltd, Japan) using a 10 MHz linear-array probes (60 mm width) with the extended field of view mode. The validity (Ahtiainen et al. 2010) and reliability (Noorkoiv et al. 2010) of this method has been reported. Subjects lay supine with the legs strapped securely to polystyrene moulds. A specially crafted convex probe support was used to assure a perpendicular angle and divide pressure evenly on the skin. Oriented in the axial-plane, the probe was moved manually with a slow and continuous

movement from the lateral to medial along a marked line on the skin (Fig. 9). Great care was taken to diminish compression of the muscle tissue. Images are obtained throughout the movement and, due to a higher frame rate of the software, a large amount of overlap from one image to the next occurs. As the orientation of each image relative to adjacent images is known, the software builds a composite image. Three panoramic CSA images were taken at 50 % femur length, from the lateral aspect of the distal diaphysis to the greater trochanter, and 3 images were taken 2 cm distally of this point. CSA was determined by manually tracing along the border of the vastus lateralis muscle using Image-J software (version 1.37, National Institute of Health, USA). The mean of the two closest values were taken as the CSA result for each level (50 % femur length and 2 cm distally) and then the mean of the two levels was used in further analysis. The same investigator performed all measurements and analyses.

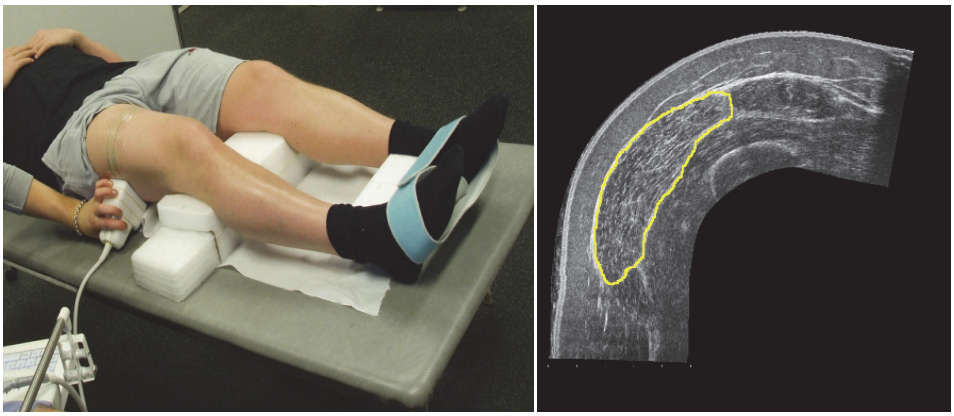

FIGURE 9 Assessment of cross-sectional area with axial plane ultrasound (left) and a composite image of the quadriceps muscles with the vastus lateralis borders highlighted (right).

4.3.2 Neuromuscular performance

4.3.2.1 Isometric performance

Leg extension. Maximal bilateral leg press (hip, knee, ankle extension) was measured on an electromechanical dynamometer (Department of Biology of Physical Activity, University of Jyväskylä, Finland) with a knee angle of 107° (180° = full extension) and a hip angle of 110°. The subjects were instructed to push "as fast and as hard as possible" and maintain their maximum force for approx. 3 sec. Three contractions were performed pre-loadings (II, IV) and before, mid-, and after the training period (IV, V), and 2 contractions were performed immediately post-loadings (II, IV) and also 15 min and 30 min post-loadings (II). Isometric leg extension contractions were sampled at 2000 Hz and filtered by a 10 Hz low-pass (4^{th} order Butterworth) filter. A customized script (Signal 4.04, CED, UK) was used to analyse force data from a time window of

500–1500 ms after the onset of contraction (defined as a 4 % increase in baseline force).

Knee extension. A modified David 200 knee extension device (David Health Solutions Ltd, Helsinki, Finland), with locking system and strain gauges (Häkkinen et al. 1987), allowed assessment of maximal unilateral isometric knee extension. Subjects were secured by a non-elastic strap at the hip and a pad across the knee to prevent extraneous movement with a knee angle of 107° and hip angle of 110°. Subjects were instructed to perform 3 maximal isometric contractions by gradually increasing force over a 3–5 s period. This was performed preloading (III) and before, mid-, and after training (V). A superimposed twitch (see Quadriceps muscle and femoral nerve electrical stimulation for details) was evoked at the peak force to assess voluntary activation. After loading (III), a further 3 knee extension contractions with superimposed twitch were performed. Maximal unilateral isometric torque (sampled at 2000 Hz, and filtered by a 20 Hz low-pass 4th order Butterworth filter) was considered as the greatest torque prior to the superimposed twitch. Verbal encouragement and visual feedback was provided during all contractions.

4.3.2.2 Dynamic performance

Maximal force production. Maximal bilateral concentric one repetition maximum (1RM) was measured during the leg press (David 210, David Health Solutions Ltd, Helsinki, Finland, papers II, IV, V: David M16, David Health Solutions Ltd, I) and knee extension (David 200, David Health Solutions Ltd, Helsinki, Finland, III) actions. Subjects were required to lift the load to a fully extended position (i.e. 180° knee angle) from a beginning knee angle of approx. 60°. Subjects performed sets of progressively increasing load (1 × 10 × 70 % estimated 1RM, 1 × 7 × 75 % estimated 1RM, 1 × 5 × 80 % estimated 1RM, 1 × 1 × 90 % estimated 1RM) in order to fully prepare for maximal contractions. Thereafter, single repetitions using 5 kg increments were performed until the subject could no longer lift the load to full extension. Three to four single repetitions were needed to determine each subject's 1RM. The 1RM load was used to calculate submaximal loads (I–IV) and also assess training-induced changes in maximal bilateral concentric 1RM (IV, V).

Repetition to failure test. Subjects were required to lift a load corresponding to 75 % of their 1RM for as many repetitions as possible until they could no longer voluntarily fully extend the legs (full extension = 180° knee angle). This test was performed on a David 210 leg press device (David Health Solutions Ltd, Helsinki, Finland), which increased the resistance by ~6 % between 120–180° knee angles. A lifting tempo of 2 s concentric and 2 s eccentric phase was encouraged and supervised by an experienced trainer to ensure that repetition speed did not change during the test or during training. The repetitions were counted and recorded, and the load was multiplied by the number of repetitions to give total work performed during the test (i.e. load × reps = volume

load). Subjects were verbally encouraged throughout the test, and especially as fatigue progressed, to give maximum effort.

Submaximal steady-paced contractions. Using a modified David M16 leg press device (David Health Solutions Ltd, Helsinki, Finland, Fig. 10), randomised single contractions of 40 % 1RM, 60 % 1RM, and 80 % 1RM were performed with 2 min between trials. The device was modified to provide either constant resistance (i.e. the same resistance throughout the range of motion) or variable resistance (i.e. the resistance changed with increasing knee angle). The contraction time was instructed to be 2 s and this tempo was encouraged by the researcher with the aid of a metronome, and the subject was given 2 attempts at each intensity for each of the 4 resistance settings.

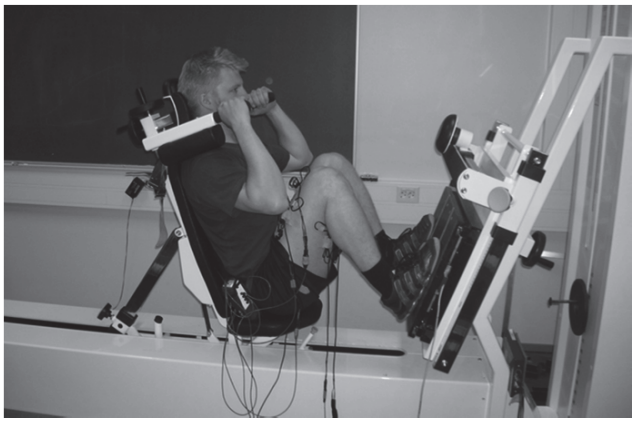

FIGURE 10 Modified M16 leg press device with mounted force plate and infra-red displacement sensor.

Raw concentric leg press data was recorded (2000 Hz sampling frequency), and then manually filtered and analysed (Signal 2.16, CED, UK). A 4th order Butterworth low-pass filter was used for force (20 Hz), seat displacement and angle data (75 Hz). Force was determined for each 20° knee angle segment and the whole concentric phase (~60°–180°). Concentric velocity was determined from the seat's linear displacement ($v = d/t$) for each 20° segment and whole concentric phase. Thereafter, concentric power was determined from force, linear displacement, and time ($P = F \times d/t$).

Two different resistance settings were tested during each session. The four resistance settings were; 1) Constant resistance, 2) Variable resistance with small increases in force (classified as conservative CAM), 3) Variable resistance with large increases in force (classified as exponential CAM) and 4) Variable resistance with decreases in force (classified as drop off CAM). Each test session was separated by at least 2 days of rest, but no more than 5 days passed between test sessions. Selection of resistance setting was randomized. Thirty min rest was given before the same single-repetition contraction procedures were repeated using the second resistance setting of the session.

4.3.2.3 Muscle activity and electrical stimulation measurements

Surface electromyography. Bipolar Ag/AgCl electrodes (5 mm diameter, 20 mm inter-electrode distance, common mode rejection ratio > 100 dB, input impedance > 100 MΩ, baseline noise < 1 μV rms; Department of Biology of Physical Activity, University of Jyväskylä, Finland) were positioned, following shaving and abrasion, on the vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF, I, II), and biceps femoris (BF) of the right leg according to SENIAM guidelines (Hermens et al. 1999). Raw signals were amplified (500 gain) at a bandwidth of 10–500 Hz (2000 Hz sampling frequency) and were passed from a transportable pack to the receiving box (Telemyo 2400R, Noraxon, Scottsdale, USA), which were then relayed to an AD converter (Micro1401, Cambridge Electronic Design, UK) and recorded by Signal 4.04 software (Cambridge Electronic Design, UK). The signal delay from the transportable pack to the receiving box was 150 ms and was accounted for during analysis (*signals were passed in real time in paper III*). After testing, EMG signals were band-pass filtered (20–350 Hz).

Bilateral dynamic concentric leg press action EMG signals were converted to root mean square (rms) for the whole range of motion (60°–180° knee angle), first half of the range of motion (60–120° knee angle), and also in 20° segments (e.g. 60°–80° etc). The rmsEMG of the 20° segments was also analysed by area under the curve for 60°–120°, and 120°–180°. This data was either normalized (I) based on each muscle's maximum rmsEMG (% of isometric max EMG) or remained as absolute values (II, IV). Data are presented for each muscle and averaged for the quadriceps muscles (e.g. VL+VM+RF/3). Median frequency was determined from 60° to 120° knee angle.

Bilateral isometric leg extension action EMG signals were analysed by a customized script with maximum values obtained from the contraction time period of 500–1500 ms (Signal 2.16, CED, UK). Data are presented for each muscle and averaged for the quadriceps muscles (e.g. VL+VM+RF/3). Median frequency was calculated from isometric iEMG over the force plateau's most stable 1 s time window by fast fourier transformation (Hanning windowing, 2048 data points).

Unilateral isometric knee extension EMG signals were converted to root mean square (rms) for EMG amplitude or analysed by fast fourier transformation (Hanning windowing, 1024 data points) for EMG median frequency over a 500 ms epoche immediately before the superimposed twitch.

Quadriceps muscle and femoral nerve electrical stimulation. Muscle stimulation was performed by placing four, galvanically paired, self-adhesive electrodes (6.98 cm V-trodes, Mettler Electronics Corp, USA) on the proximal and mid regions of the quadriceps muscle belly (Fig. 11). Single 1ms rectangular pulses were delivered by a constant-current stimulator (Model DS7AH, Digitimer Ltd, UK) until a torque plateau was observed. An additional 25 % of stimulation current was added to the current identified to produce maximum torque. During the unilateral maximum isometric knee extension trials, the same single-

pulse stimulation was delivered during the plateau of peak torque and then one more pulse 2 sec after contraction cessation to assess voluntary activation (Merton 1954). Voluntary activation was assessed from the additional torque produced by the superimposed twitch and the maximum torque of the subsequent resting twitch using the formula of Bellemare and Bigland-Ritchie (1984); activation % = [1 – (Pts/Pt)] × 100. Resting twitches were analysed for maximum torque, maximum rate of twitch torque production (10 ms epoche) and half-relaxation time. BF EMG showed that our methods did not stimulate antagonist muscles. These measurements were performed pre- and post-loadings (III) and before, mid, and after training (V).

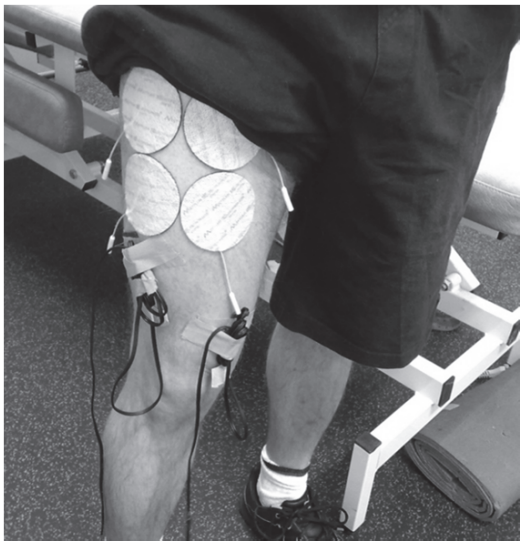

FIGURE 11 Direct muscle stimulation electrodes placed on the proximal and mid regions of the muscle belly and surface EMG electrodes placed on the vastus lateralis and medialis muscles.

M-wave properties of the VL and VM muscles were assessed by femoral nerve stimulation (III). Subjects were instructed to stand fully upright with their bodyweight balanced equally between both legs, feet hip width apart. A standing position was chosen to determine M-wave properties because, during pilot testing, our measurements in a seated position did not achieve an acceptable level of reliability (possibly due to changes in cathode pressure and position relative to the nerve). The stimulating cathode (1 cm diameter) was placed firmly into the femoral triangle at the point that gave the strongest response to a weak stimulation current, which was marked on the skin for replacement. The anode (6.98 cm V-trode) was placed on the greater trochanter. Current was increased in 10 mA stages (1ms single-pulse, 400 V) until there were clear plateaus in the M-wave amplitude of both VL and VM muscles. Thereafter, an additional 25 % of stimulation current was applied. Maximum M-wave properties were analysed for peak-to-peak amplitude and peak-to-peak duration.

4.3.3 Blood sampling and analyses

Venous blood samples were collected from an antecubital vein (Fig. 12) pre-, post-, 15 min post-, and 30 min post-loadings (II, IV) using sterile techniques with the blood transferred into serum tubes (Venosafe, Terumo, Belgium). In addition to the loading blood samples, resting serum blood samples (control condition) were obtained at the same time of day as the loadings (paper II). The samples were held for 15min at room temperature before being centrifuged for 10min at 3500 rpm (Megafuge 1.0R, Heraeus, Germany). Once the serum had been separated from red blood cells, it was pipetted into tubes and stored in the refrigerator (–80°C) for future analysis. Serum samples were analysed for total testosterone (TT), 22kDa growth hormone (GH), and cortisol (Analytical sensitivity; total testosterone = 0.5 nmol/L, growth hormone 22kDa = 0.01 µg/L, cortisol = 5.5 nmol/L) by immunomeric chemiluminescence techniques using the Immulite 1000 and hormone-specific immunoassay kits (Immulite, Siemens, Illinois, USA). Intra- and Inter-assay reliability were within acceptable limits, CV %; total testosterone = 5.7 and 8.3 %, 22kDa growth hormone = 5.8 and 3.6 %, cortisol = 4.6 and 6.1 %. Data presented are uncorrected for plasma volume changes. Greater plasma volume change (–15 ± 3 % vs. –8 ± 3 %, $P < 0.01$) was observed in the cross-sectional study (II) between variable and constant resistance loadings but not in the longitudinal training study (IV).

Fingertip blood lactate samples (20 µL) were collected immediately pre-, post-, and 15 min post-loadings (II–IV) into capillary tubes, which were placed in a 1 mL hemolyzing solution and analysed according to the manufacturer's instructions (EKF diagnostic, Biosen, Germany).

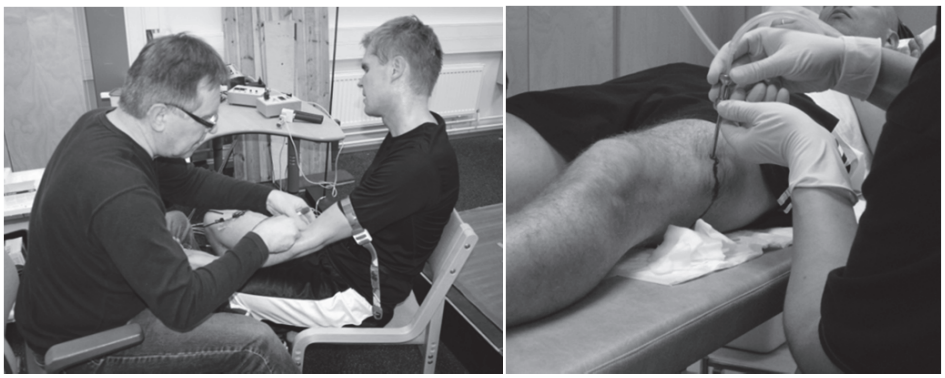

FIGURE 12 Blood draw from an antecubital vein (left) and vastus lateralis muscle biopsy sampling (right).

4.3.4 Muscle biopsy procedures and analyses

Muscle biopsies were obtained 30 min pre- and 30 min post-loading. Biopsies were taken from the VL with a 5 mm Bergström biopsy needle together with suction (Fig. 12), midway between the patella and greater trochanter. Muscle

depth was kept constant through markings on the needle. The pre-loading biopsy was always from the right leg and post-loading biopsy from the left leg. To avoid any residual effects of the previous biopsies, the biopsies during subsequent loadings were obtained ~2 cm from the previous biopsy location. The muscle sample was cleaned of any visible connective and adipose tissue as well as blood and frozen immediately in liquid nitrogen (–180°C) and stored at –80°C.

Biopsy specimens were hand-homogenised in ice-cold buffer (20 mM HEPES pH 7.4, 1 mM EDTA, 5 mM EGTA, 10 mM $MgCl_2$, 100 mM β-glycerophosphate, 1 mM Na_3VO_4, 2 mM DTT, 1 % Triton X-100, 0.2 % sodium deoxycholate, 30 µg/mL leupeptin, 30 µg/mL aprotinin, 60 µg/mL PMSF, and 1 % phosphatise inhibitor cocktail [P 2850; Sigma, St. Louis, Missouri, USA]) at a dilution of 15 µL/mg of wet weight muscle. Homogenates were rotated for 30 min at 4 °C, centrifuged at 10 000 *g* for 10 min at 4 °C to remove cell debris, and stored at –80 °C. Total protein content was determined using the biinchroninic acid protein assay (Pierce Biotechnology, Rockford, Illinois, USA).

Western immunoblot analyses. Aliquots of muscle lysate, containing 30 µg of total protein, were solubilised in Laemmli sample buffer and heated at 95 C° for 10 min, and were then separated by SDS-PAGE for 60–90 min at 200 V using 4–20 % gradient gels on Criterion electrophoresis cell (Bio-Rad Laboratories, Richmond, CA). All samples from each subject were run on the same 18-sample gel. Proteins were transferred to PVDF membranes at 350 mA constant current for 3h on ice at 4°C. Membranes were blocked in TBS with 0.1% Tween 20 (TBS-T) containing 5 % non-fat dry milk for 1h and then incubated overnight at 4°C with rabbit polyclonal primary antibodies. Antibodies recognized phosphorylated eEF2 at Thr^{56}, Akt at Ser^{473}, mTOR at Ser^{2481}, $p70^{S6K}$ at Thr^{389}, p38 MAPK at Thr^{180}/Tyr^{182}, ERK1/2 (p44/p42) at Thr^{202}/Tyr^{204}, and MAPKAPK-2 at Thr^{334}, and rpS6 at both $Ser^{235/236}$ and at $Ser^{240/244}$ (Cell Signaling Technology, Beverly, MA). Additionally, total proteins of mTOR, Akt, $p70^{S6K}$ (Santa Cruz Biotechnology, USA), ERK1/2 and rpS6 (Cell Signaling Technology) with respective antibodies were analysed to verify that the total protein content of part of the phosphospecific proteins analysed of signalling proteins does not significantly change during loading or due to training. The uniformity of protein loading was confirmed by staining the membrane with Ponceau S and by re-probing the membrane with an antibody against α-actin (Sigma, Saint Louis).

All the primary antibodies were diluted 1:2 000 in TBS-T containing 2.5 % non-fat dry milk except against α-actin which was diluted 1:20 000. Membranes were then washed (5 × 5 min) in TBS-T, incubated with secondary antibody (horseradish peroxidase-conjugated anti-rabbit IgG; Cell Signaling Technology, USA) diluted 1:25 000 in TBS-T with 2.5 % milk for 1h followed by washing in TBS-T. Phosphorylated proteins were visualized by ECL according to the manufacturer's protocol (SuperSignal west femto maximum sensitivity substrate, Pierce Biotechnology, Rockford, USA) and quantified (band intensity × volume) using a ChemiDoc XRS in combination with Quantity One software (version 4.6.3. Bio-Rad Laboratories, USA). Quantification of p38 was based on the aver-

age of two visible bands at 42 and 44 kDa, purportedly α/β and γ respectively, and the 47 kDa band was used to quantify MAPKAPK-2 (Ronkina et al. 2007).

4.4 Resistance loading procedures

Acute resistance loadings were performed using a leg press (M16, David Health Solutions Ltd, Helsinki, Finland, II, IV) and a knee extension (David 200, David Health Solutions, Helsinki, Finland, III) device. The specifically tailored M16 leg press device used a CAM to alter the resistance at large knee angles, and provided ~30 % (paper II) and ~70 % (paper IV) greater resistance at knee angles of 120–180°, whereas the David 200 knee extension device provided the greatest resistance at 100–140° (III). The starting knee angle for all loadings was approximately 60° and subjects were required to perform each contraction to full knee extension (180° knee angle). Concentric force was recorded during the loadings by a force plate (I, II, IV) installed onto the leg press (vertical force) and strain gauges (III) on the knee extension device (Department of Biology of Physical Activity, University of Jyväskylä, Finland).

To control for diurnal variation, individual subjects' loading tests took place at the same time of day (± 1 hour) throughout the study. Each loading test was separated by 7 days and subjects refrained from exercise and alcohol consumption for 48 hours, and caffeine products for 24 hours prior to loadings. Young and older subjects arrived at the laboratory in alternating fashion to ensure no between-group time differences occurred (III). To control for the effects of pre-loading nutrition (Hulmi et al. 2005, Hulmi et al. 2009a) and hydration status (Judelson et al. 2007, Judelson et al. 2008), subjects fasted for 3 hours and consumed 0.5 litres of water 1 hour before loading. Additionally, dietary intake was recorded in diaries for one day before and on the day of the first loading. The subjects were given a photocopy of this record and instructed to replicate their diet as closely as possible before the subsequent loading days.

A total of four loadings were completed in a randomized order: 1) Constant resistance maximal strength loading, 2) Variable resistance maximal strength loading, 3) Constant resistance hypertrophic loading, and 4) Variable resistance hypertrophic loading (The longitudinal study, IV, investigated constant and variable hypertrophic loadings before and after training). Subjects were verbally encouraged throughout the loadings to give maximum effort. Loadings were preceded and followed (0 min, 15 min, and 30 min post-loadings) by isometric contractions, blood collection, electrical stimulation, and muscle biopsy measurements.

4.4.1 Maximal strength loading protocol

Warm up consisted of 5 dynamic contractions using a 50 % 1RM load and several submaximal isometric contractions of increasing intensity at the subject's own discretion. Following the initial set up (e.g. electrode placement etc) and

testing (e.g. blood collection, isometric tests etc), subjects performed 15 sets of 1 repetition beginning with the pre-determined 1RM load. Each set was separated by 3 min of rest. If the load was successfully lifted to full knee extension, an attempt was made at a slightly (2.5–5 kg) higher load during the subsequent set. If the subject could not voluntarily perform the concentric phase to full knee extension, the subject was assisted by an experienced trainer so that the repetition was completed and the load was reduced for the subsequent set.

4.4.2 Hypertrophic loading protocol

Following initial set up and testing, subjects completed 5 sets of 10 repetitions to failure beginning with 80 % of the pre-determined 1RM load. Two minutes rest was given between sets. If the subjects could complete 10 repetitions without the need for assistance, then the load was increased for the next set. However, if the subjects could not voluntarily complete 10 repetitions, some assistance was provided and the load was reduced for the next set. Subjects were instructed to maintain a lifting tempo of 2 sec concentric and 2 sec eccentric contractions with the aid of a metronome and verbal feedback from the tester.

In the longitudinal training study (IV), during testing of acute fatigue responses, the subjects from the variable training group performed variable resistance loading on day 1 and constant resistance loading on day 2 following 7 days rest. The subjects from the constant training group performed constant resistance loading on day 1 and variable resistance loading on day 2 following 7 days rest. This order was maintained after the training intervention.

4.5 Resistance training program

Eleven young subjects performed training using variable resistance devices and 12 young subjects performed training using constant resistance devices for the lower limbs. In the older subjects, 13 performed training using variable resistance devices and 13 subjects performed training using constant resistance devices for the lower limbs. Lower limb exercises were leg press, knee extension and knee flexion. Both groups trained the upper limbs and torso with constant resistance devices for the following exercises: bench press, shoulder press, lat pulldown, seated row, bicep curl, triceps pushdown, abdominal crunches and back raises. Training was performed twice per week and all major muscle groups were performed in one training session using a combination of 8–9 exercises per session. Lower limb exercises were performed before other muscle groups and all limb exercises were performed bilaterally. Furthermore, the three lower limb exercises were performed in every training session. Training was split into two identical 10-week periods, where the relative intensity remained the same during the second 10-week period and absolute loads increased in-line with subjects' individual improvements in strength. The subjects performed 2–3 sets and 12–14 reps (60–70 % 1RM) per exercise in the first 4

weeks, then 2–3 sets and 10–12 reps (70–80 % 1RM) per exercise in the next 3 weeks, and 3–4 sets per exercise and 8–10 reps (75–85 % 1RM) per exercise for the final 3 weeks. One min rest was given between sets during the first 4 weeks and then 2 min rest was given between sets during the remaining 6 weeks. This was repeated in the second 10-week period. All subjects were required to complete 18/36 from a total of 20/40 training sessions prior to testing after 10 and 20 weeks respectively. Subjects were given nutritional counselling during the study to optimize the muscle hypertrophy response. Subjects in the age-matched control groups (young, n = 10, older, n = 11) were instructed to maintain their normal physical activity levels and refrain from resistance training throughout the intervention.

4.6 Statistical analyses

Conventional statistical methods were used to obtain means, standard deviations, standard error, area under the curve, and correlation coefficients. Normal distribution was determined through the Shapiro-Wilk test. Data that were not normally distributed were either log transformed before applying parametric tests (IV) or analysed using Friedman's test for multiple comparisons, and then Wilcoxon matched pairs were used as post hoc tests (I, II). Dependent variables were assessed by analysis of variance (ANOVA), or analysis of covariance (ANCOVA) where appropriate, with repeated measures with Bonferroni adjustments as post hoc tests. Area under the curve analysis was analysed using a paired t-test (II). Absolute EMG amplitude (III) was analysed by paired t-test (within group; pre- vs. post-loading). Changes in relative values over time (i.e. Δ %) were analysed using one way ANOVA. The alpha level was set at 0.05.

5 RESULTS

The main findings of the present series of experiments are presented below. For more details the original articles (I–V) should be consulted.

5.1 Effects of variable resistance on single-repetition characteristics (I)

5.1.1 Kinetic and kinematic variables

The CAM settings of the leg press device, that modify the lever arm distance and consequently the external resistance, took effect during more extended knee angles (Fig. 13). Beginning from the 100°–120° knee angle segment, force was significantly greater using the exponential CAM compared to all other resistance settings (Fig. 14A and 14B). However, during 80 % 1RM contractions, the change in velocity was clear between 100°–140° using exponential and drop off CAMs. This led to significant differences between the exponential CAM compared to drop off CAM and constant resistance setting using 80 % 1RM ($P < 0.01$, Fig. 14C), as well as drop off CAM compared to conservative and exponential CAMs using 40 % 1RM ($P < 0.05$, Fig. 14D) (similar observations were made during 60 % 1RM).

Despite no individual 20° knee angle differences, area under the curve analysis revealed that the force at larger knee angles (120°–180°) was significantly greater using the conservative CAM during 80 % and 40 % 1RM loads compared to constant resistance ($P < 0.001$ and $P < 0.05$ respectively). There were no differences in force at more flexed knee angles (60°–120°) between the conservative CAM and constant resistance settings.

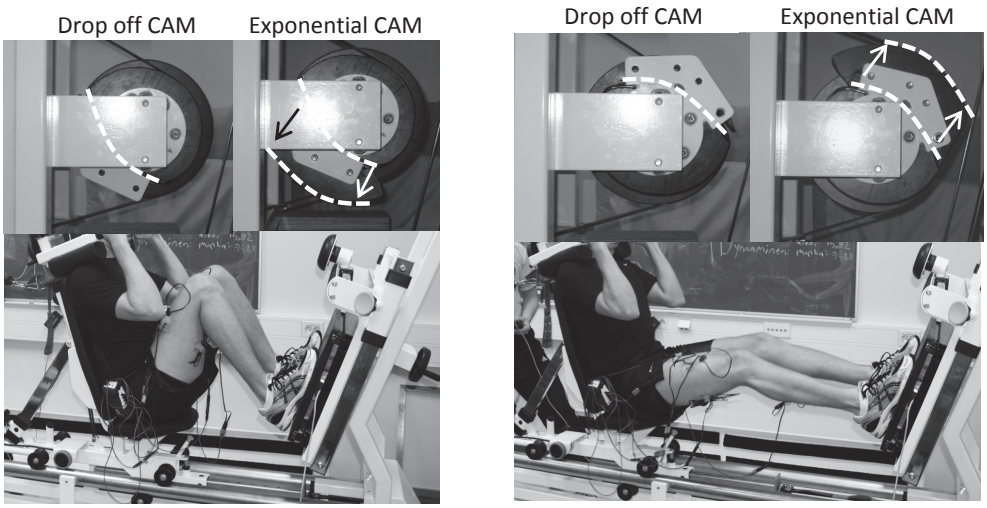

FIGURE 13 Experimental leg press set up at small and large knee angles showing the corresponding exponential and drop off CAM block positions. The dashed lines represent the path of the weight-stack belt. The arrows denote the difference in lever arm distance between these two CAMs. Note: Constant resistance used a wheel of equal radius distance, while conservative CAM used a smaller block compared to the exponential CAM.

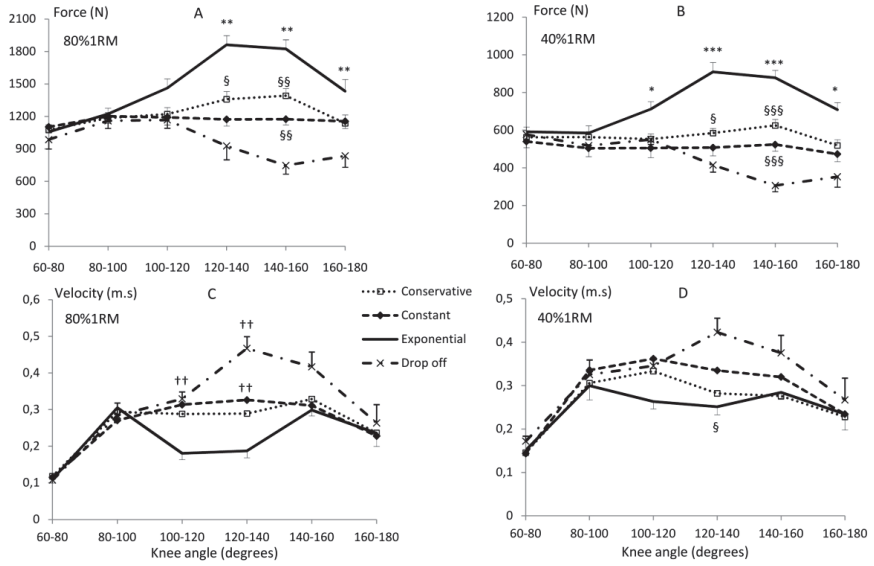

FIGURE 14 Mean (± SE) concentric force (A) and velocity (C) during 80 % 1RM, and concentric force (B) and velocity (D) during 40 % 1RM steady-paced contractions. * = P < 0.05 compared to all other resistance settings. † = P < 0.05 compared to exponential CAM only. § = P < 0.05 compared to drop off CAM only.

Table 4 shows that contraction time during the repetitions was approximately the intended 2 seconds for all resistance settings. However, the contraction time of the drop off CAM was significantly shorter than conservative CAM during 60 % and 40 % 1RM, and exponential CAM during 80 % and 40 % 1RM ($P < 0.05$).

TABLE 4 Mean contraction time (± SD) for each resistance setting from 60°–180° knee angle.

Resistance setting	**Contraction time (s)**		
	80 % 1RM	**60 % 1RM**	**40 % 1RM**
Constant resistance	2.04 ± 0.3	1.91 ± 0.3	1.8 ± 0.2
Conservative CAM	2.03 ± 0.4	2.14 ± 0.1*	1.99 ± 0.4*
Exponential CAM	2.45 ± 0.4*	2.14 ± 0.3	1.97 ± 0.3*
Drop off CAM	1.91 ± 0.3	1.85 ± 0.3	1.69 ± 0.3

* = $P < 0.05$ compared to drop off CAM only. N.B. Only comparisons between resistance settings are highlighted in this Table.

5.1.2 Muscle activity

Significant differences were observed in EMG amplitude between the different resistance settings (Fig. 15). During all loading intensities, there was a consistent difference in quadriceps EMG amplitude between exponential and drop off CAMs beginning from 100°–120° knee angle ($P < 0.05$). Also, at several knee angles, there were differences between the exponential CAM and constant resistance (Figure 15A–D). Additionally, area under the curve analysis revealed significantly greater VL and average knee extensor ((VL+VM)/2) EMG amplitude between conservative CAM and constant resistance using 80% 1RM ($P < 0.05$).

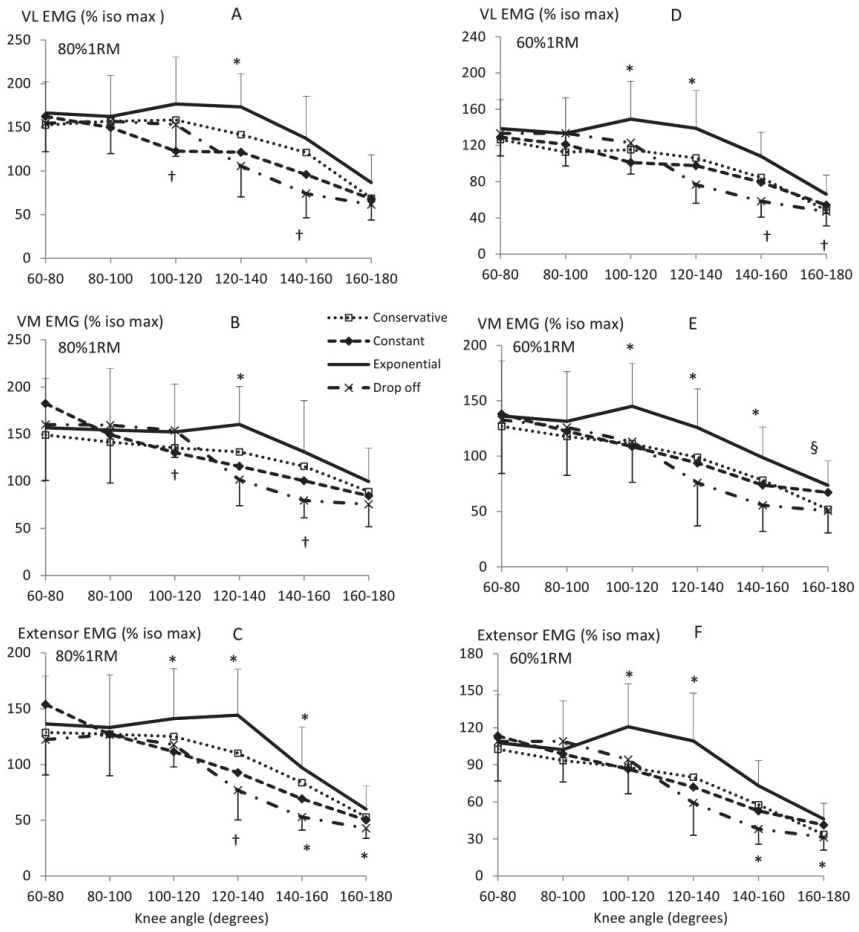

FIGURE 15 Normalised muscle activity (± SE) of the VL (A), VM (B), and averaged extensor (C) muscles during steady-paced 80 % 1RM contractions, and of the VL (D), VM (E), and averaged extensor (F) muscles during steady-paced 60 % 1RM contractions. * = $P < 0.05$ compared to all other resistance settings. † = $P < 0.05$ both constant resistance and drop off CAM compared to exponential CAM. § = $P < 0.05$ compared to drop off CAM only.

5.2 Total work performed during resistance loadings (II, IV)

Total work (assessed by repetitions × sets × average concentric force) was similar between variable and constant resistance loadings during both maximal strength (25625 ± 4041 N vs. 26155 ± 4529 N, respectively) and hypertrophic loadings (80154 ± 12882 N vs. 81953 ± 11666 N, respectively) when using the conservative CAM (II). However, total work during hypertrophic loadings was greater ($P < 0.01$) during variable vs. constant resistance loading both before

(73674 ± 15635 N vs. 64578 ± 12564 N, respectively) and after the training intervention (89101 ± 18281 N vs. 78310 ± 13063 N, respectively) when using the exponential CAM (IV).

5.3 Acute neuromuscular fatigue during loadings before and after training (II-IV)

5.3.1 Force production

5.3.1.1 Knee extension loadings

The relative change in concentric torque between variable vs. constant loading in young men was statistically significant during 15 × 1RM ($P < 0.05$, Table 5). Also, young men produced significantly greater concentric torque compared to older men during 15 × 1RM loadings ($P < 0.05$, Table 5).

TABLE 5 Average concentric torque (Nm) over 60°–180° knee angles during each loading session (mean ± SD).

Resistance setting		Young			Older	
	Baseline	Last set	Δ %	Baseline	Last set	Δ %
15 × 1RM constant	254 ± 19§	239 ± 21§	-6 ± 4 %*	195 ± 35	182 ± 29	-6 ± 4 %
15 × 1RM variable	292 ± 31§	262 ± 32§	-11 ± 7 %	212 ± 36	194 ± 32	-8 ± 6 %
5 × 10RM constant	191 ± 29	169 ± 23	-11 ± 13 %	145 ± 33	131 ± 20	-6 ± 25 %
5 × 10RM variable	205 ± 31	180 ± 44	-13 ± 12 %	159 ± 37	137 ± 33	-11 ± 16 %

* = $P < 0.05$ compared to variable resistance loading, § = $P < 0.05$ compared to older men.

Significant decreases in maximal isometric torque were observed after all four loadings ($P < 0.05$). Furthermore, there was a trend that hypertrophic variable resistance loading caused a greater decrease in isometric torque in young men (–44 ± 11 % vs. –50 ± 15 %, $P = 0.058$, Fig. 16). Age influenced the magnitude of loading-induced fatigue in that older men maintained a higher percentage of their pre-loading performance compared to the young men during all loadings ($P < 0.05$, Fig. 16).

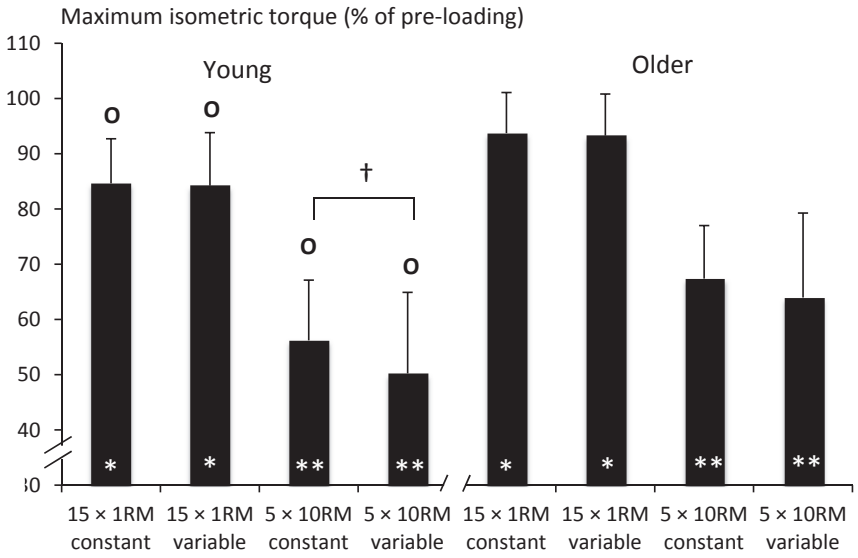

FIGURE 16 Relative changes (mean ± SD) pre- to post-loading in unilateral maximum isometric torque in young and older men. Symbols inside the bars depict significant within-group difference from pre-loading, * = $P < 0.05$, ** = $P < 0.01$. O depicts significant difference compared to older men, $P < 0.05$. † = trend between constant and variable resistance loading, $P = 0.058$.

5.3.1.2 Leg press loadings

In the untrained state (II), concentric load increased from set 1 to set 3 during both constant and variable resistance hypertrophic loadings ($P < 0.01$), and then plateaued from set 3 to 4 (Table 6). The load decreased from set 3 to set 5 during variable loading with the conservative CAM ($P < 0.05$). During constant resistance maximal strength loadings, the load increased from set 1 to set 3 ($P < 0.01$), and then decreased thereafter ($P < 0.05$, Table 6). Only decreases were observed from set 5 to set 15 during variable resistance maximal strength loadings ($P < 0.01$, Table 6). During variable resistance loading with the exponential CAM before training (IV), the load decreased from set 1 to set 5 ($P < 0.05$, Table 6). During constant resistance loading before training and both loadings after training, the load was maintained.

TABLE 6 Mean (± SD) concentric load (kg) during maximal strength and hypertrophic leg press loadings in the cross-sectional (II, n = 13) and longitudinal training (IV, n = 14) studies.

Resistance setting	Before Training				After Training		
	Set 1	**Set 3**	**Set 5**	**Set 15**	**Set 1**	**Set 3**	**Set 5**
(Study II) Constant 15 × 1RM	195 ± 31	202* ± 27	198§ ± 28	190§ ± 28			
Conserv. 15 × 1RM	192 ± 33	194 ± 33	191 ± 33	180*§ ± 29			
Constant 5 × 10RM	158 ± 25	173* ± 29	171* ± 32				
Conserv. 5 × 10RM	152 ± 25	162* ± 26	156§ ± 27				
(Study IV) Constant 5 × 10RM	135 ± 25	140 ± 33	130 ± 32		187† ± 32	197† ± 31	185† ± 37
Exponen. 5 × 10RM	130 ± 29	120 ± 25	108* ± 29		166† ± 33	171† ± 37	159† ± 40

Conserv. = Conservative CAM setting, Exponen. = Exponential CAM setting, * = $P < 0.05$ compared to set 1, § = $P < 0.05$ compared to previous time point, † = $P < 0.05$ compared to before training.

Large reductions in maximal bilateral isometric leg extension force were observed following all loadings ($P < 0.01$, Table 7). In the untrained state (II), reductions during hypertrophic loadings (constant resistance: –50 % and variable resistance: –52 %) were greater than maximal strength loadings (constant resistance: –27 % and variable resistance: –29 %) ($P < 0.01$, Table 7). Following both hypertrophic loadings, force recovered during 15 min. However, 15–30 min after constant resistance hypertrophic loading, maximum isometric force continued to recover ($P < 0.05$) whereas there were no further regains following variable resistance loading (Table 7). Following variable resistance loading after the training intervention (IV), reductions were greater than both constant resistance loading after training and variable resistance loading before training ($P < 0.05$, Table 7).

TABLE 7 Mean (± SD) maximal bilateral isometric leg extension force (N) pre- and post-loading, and during 30 min recovery during maximal strength and hypertrophic leg press loadings in the cross-sectional (II, n = 13) and longitudinal training (IV, n = 14) studies.

Resistance setting	Before Training				After Training	
	Pre	Post	15 min Post	30 min Post	Pre	Post
(Study II)						
Constant 15 × 1RM	2684 ± 544	1960** ± 370	2062**§ ± 370	2208** ± 528		
Conserv. 15 × 1RM	2703 ± 506	1947** ± 418	2123**§ ± 444	2109** ± 422		
Constant 5 × 10RM	2745 ± 482	1410** ± 390	1880**§ ± 359	2036**§ ± 434		
Conserv. 5 × 10RM	2772 ± 609	1406** ± 394	1946**§ ± 543	1990** ± 508		
(Study IV)						
Constant 5 × 10RM	2750 ± 948	1678** ± 601			2843 ± 1109	1850**‡ ± 817
Exponential 5 × 10RM	2709 ± 844	1712** ± 676			2789 ± 716	1501**† ± 535

Conserv. = Conservative CAM setting, ** = $P < 0.01$ compared to pre-loading, § = $P < 0.05$ compared to previous time point, † = $P < 0.05$ compared to before training, ‡ = $P < 0.05$ compared to variable resistance loading.

5.3.2 Changes in muscle activity

5.3.2.1 Knee extension loadings

During maximum unilateral isometric knee extension in older men, VM EMG amplitude was reduced (–20 ± 24 %, $P < 0.05$, Fig. 17A) following maximal strength variable resistance only. In young men (Fig. 17B), significant reductions in EMG amplitude were observed in both VL and VM muscles following maximal strength variable resistance ($P < 0.01$) and constant resistance loading ($P < 0.05$). Following hypertrophic variable resistance loading, EMG median frequency was reduced in older (VL: –14.1 ± 10.4 %, $P < 0.01$) and young men (VM: –11.8 ± 12.7 %, $P < 0.05$). Also, this significant difference was observed in both groups when the VL and VM muscles were combined and averaged ($P < 0.05$). There were no changes in EMG amplitude during hypertrophic knee extension loadings in either young or older men.

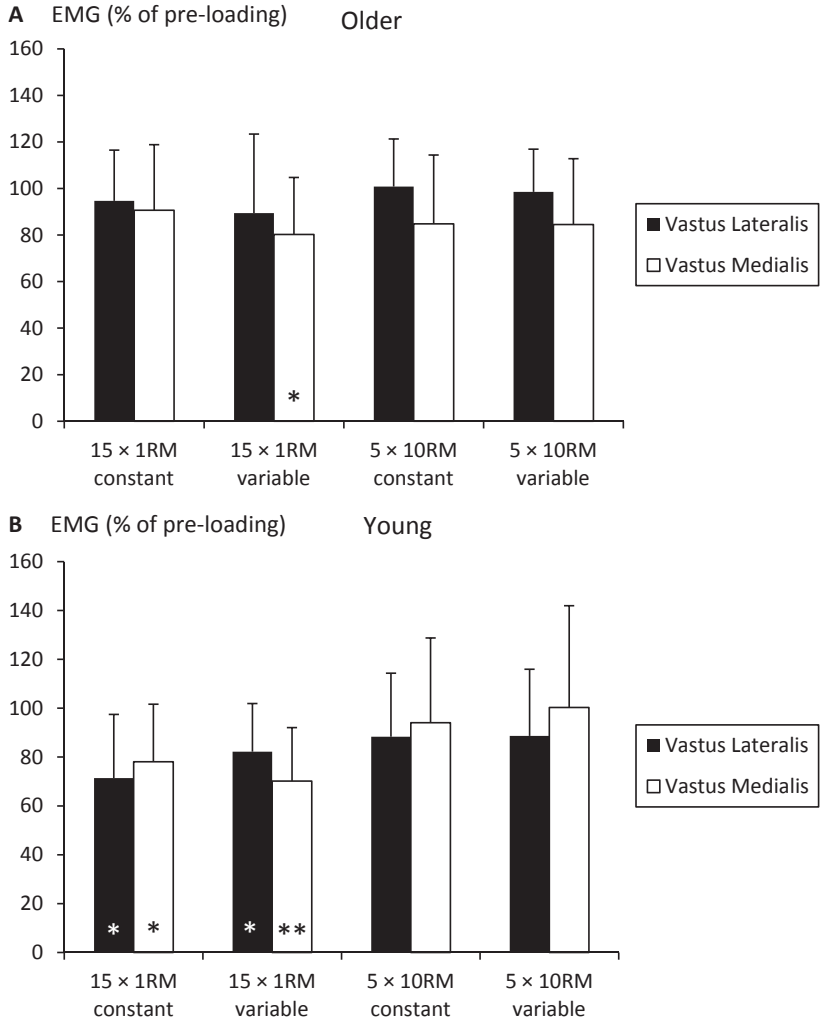

FIGURE 17 Relative changes (mean ± SD) pre- to post-loading in isometric EMG amplitude of the vastus lateralis and medialis muscles in the older (A) and young (B) men during hypertrophic loadings. Symbols inside the bars depict significant within-group difference from pre-loading, * = $P < 0.05$, ** = $P < 0.01$.

5.3.2.2 Leg press loadings

During variable resistance hypertrophic loadings (II), average knee extensor (VL+VM+RF/3) concentric EMG amplitude (60°–180° knee angle) increased significantly following repetition 2 in each set ($P < 0.05$). Furthermore, the magnitude of the EMG signal was greater for repetition 2 ($P < 0.05$) and repetition 8 ($P = 0.06$, Effect size = 0.49) during set 5 compared to set 4 despite decreased load ($P < 0.01$). During constant resistance hypertrophic loadings (II), increases in average extensor concentric EMG were observed in set 3–5. There was no

change in average extensor concentric EMG amplitude during maximal strength loadings using either constant or variable resistance. Reductions in vastus lateralis EMG median frequency between repetition 2 and 8 occurred in set 3 (57 ± 14 Hz vs. 47 ± 9 Hz, $P < 0.05$) and set 5 (53 ± 11 Hz vs. 47 ± 6 Hz, $P < 0.05$) during variable resistance loading before training only (IV). No changes were observed for the BF muscle during any loading.

In the untrained state (II), maximum isometric EMG amplitude (VL+VM+RF/3) decreased during both maximal strength loadings (–15 % pre- to post-loading during both loadings) and remained lower than pre-loading throughout recovery ($P < 0.05$). During both hypertrophic loadings, maximum isometric EMG amplitude decreased pre- to post-loading (constant resistance: –14 %, $P < 0.05$ and variable resistance: –19 %, $P < 0.01$), increased during 15min recovery and plateaued thereafter. However, during loadings of the longitudinal training study (IV), there were no changes observed in maximum isometric EMG amplitude.

During variable resistance hypertrophic loadings in the untrained state (II), as well as before and after training (IV), reduced vastus lateralis EMG median frequency occurred. Furthermore, the relative changes after training were significantly different compared to constant resistance loadings ($P < 0.05$, Table 8). No changes were observed for the BF muscle during any loading.

TABLE 8 Mean (± SD) pre- and post-loading median frequency (Hz) during hypertrophic leg press loadings in the cross-sectional (II, n = 13) and longitudinal training (IV, n = 14) studies.

Resistance setting	**Before Training**			**After Training**		
	Pre	**Post**	**Δ %**	**Pre**	**Post**	**Δ %**
(II)						
Constant	73 ± 9	67 ± 9	-7 ± 12			
Conservative	75 ± 13	66 ± 13*	-11 ± 11			
(IV)						
Constant	62 ± 16	59 ± 12	-3 ± 10	61 ± 11	57 ± 8	-6 ± 14‡
Exponential	64 ± 14	57 ± 10*	-9 ± 13	63 ± 12	52 ± 10*	-14 ± 12

* = $P < 0.01$ compared to pre-loading, ‡ = $P < 0.05$ compared to variable resistance loading.

5.3.3 Responses to electrical stimulation

In the untrained state (III), both maximal strength loadings caused decreased voluntary activation levels in young men (constant and variable resistance, Fig. 18A and 18B respectively). However, only variable resistance loading caused changes in older men (Fig. 18B). Following hypertrophic loadings, only young men showed significant decreases in voluntary activation level when using variable resistance (Fig. 18D, $P < 0.05$).

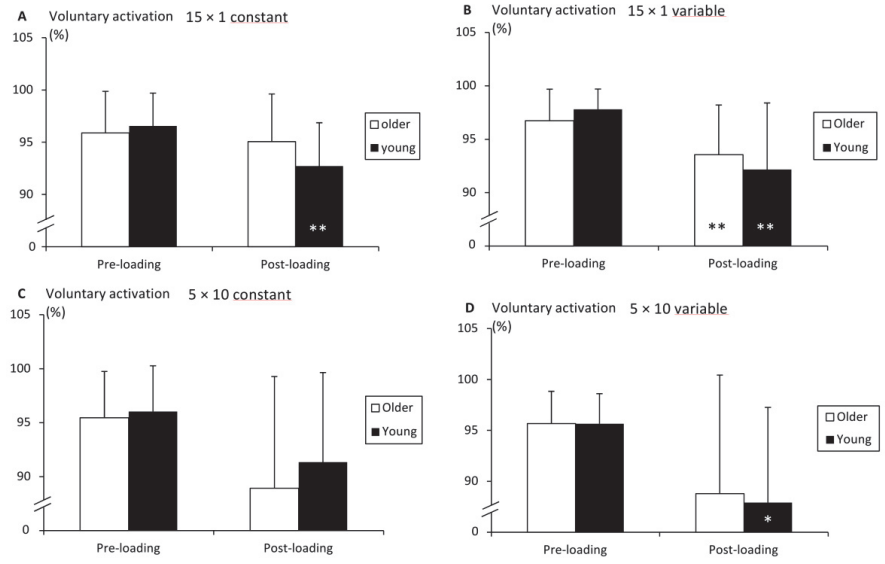

FIGURE 18 Voluntary activation level (mean ± SD) in young and older men during maximal strength loading with constant resistance (A), maximal strength loading with variable resistance (B), hypertrophic loading with constant resistance (C), and hypertrophic loading with variable resistance (D). Symbols inside the bars depict significant within-group difference from pre-loading, * = $P < 0.05$, ** = $P < 0.01$.

Maximum twitch torque was reduced in both young and older men following maximal strength variable resistance loading (young: –15 ± 15 %, $P < 0.01$, older: –11 ± 16 %, $P < 0.05$) and following both hypertrophic resistance settings (young variable: –69 ± 12 %, $P < 0.01$, older variable: –54 ± 19 %, $P < 0.01$, young constant: –65 ± 16 %, $P < 0.01$, older constant: –51 ± 26 %). Comparing young and older men, there were greater reductions in maximum twitch torque following hypertrophic variable resistance in the young men ($P < 0.05$). Results were similar for maximum rate of twitch torque development but no changes were observed for half-relaxation time.

A significant increase was observed in VL peak-to-peak M-wave duration in older men following hypertrophic variable resistance loading only (Fig. 19A). In young men, both the VL and VM muscles showed increased M-wave duration following hypertrophic variable resistance, while the VL muscle had increased M-wave duration following hypertrophic constant resistance loading (Fig. 19B). There were no loading-induced changes in M-wave amplitude for the VL and VM muscles.

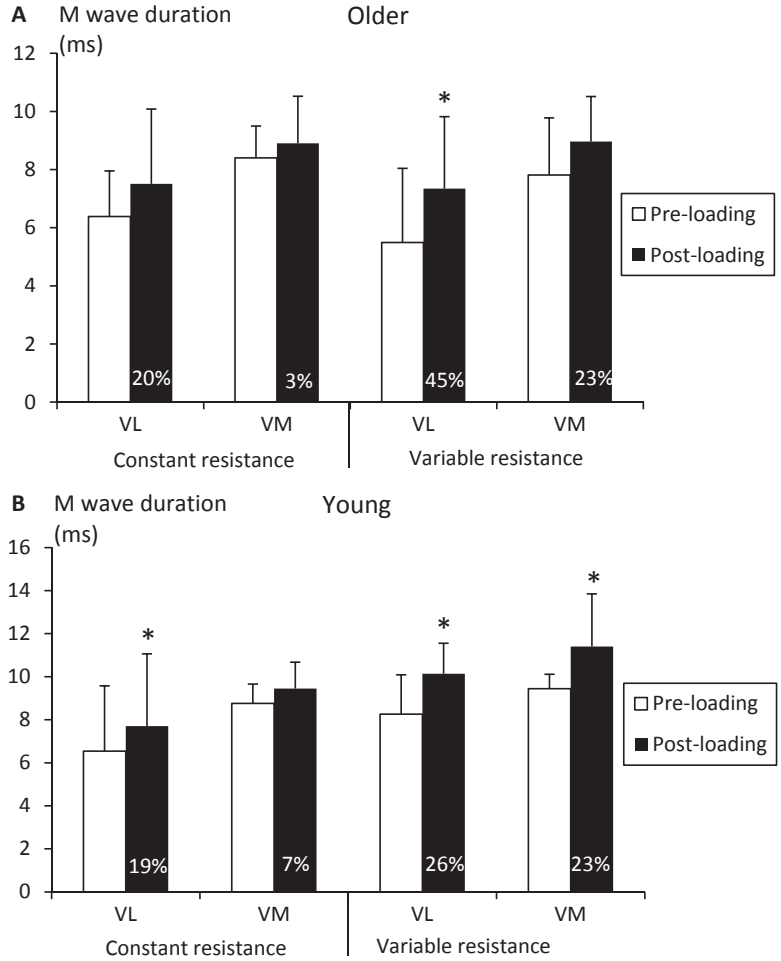

FIGURE 19 Peak-to-peak M-wave duration (mean ± SD) during hypertrophic loadings in older (A) and young (B) men. Symbols inside the bars depict significant within-group difference from pre-loading. Values within the bars depict the mean relative change from pre- to post-loading, * = $P < 0.05$.

5.4 Acute hormonal and molecular responses during loadings before and after training (II, IV)

5.4.1 Acute hormonal responses

During maximal strength variable resistance loading (II), GH concentration was increased immediately post-loading ($P < 0.05$) in young men. No changes were observed for TT or COR during either maximal strength loadings.

During all hypertrophic variable resistance loadings (II, IV), serum TT was significantly increased immediately post-loading ($P < 0.05$, Fig. 20). These eleva-

tions dissipated throughout recovery with the exception of 15 min post-loading after the training period. The difference in relative changes 15 min post-loading between variable and constant resistance was significant ($P < 0.05$). Significant increases in TT were observed immediately post-loading ($P < 0.05$, Fig. 20) during constant resistance loading after the training period only.

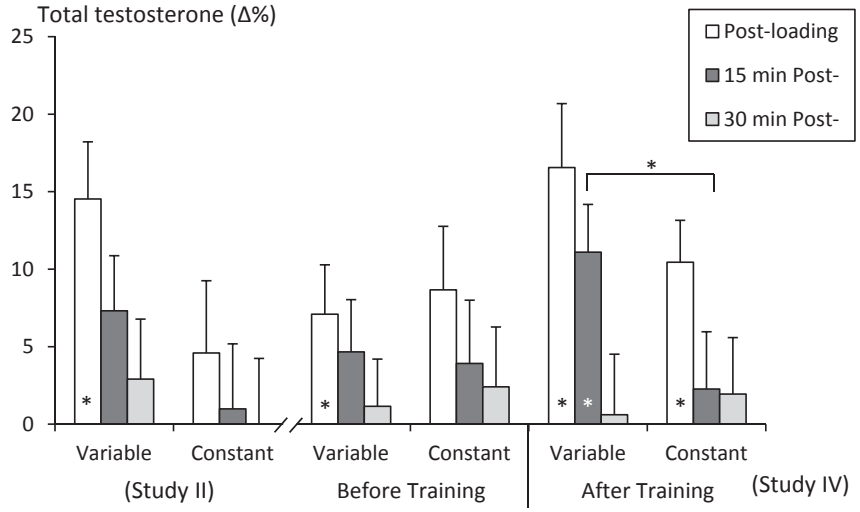

FIGURE 20 Relative loading-induced changes (mean ± SE) in serum total testosterone during the cross-sectional study (left, study II, n = 13) and longitudinal training study (right, study IV, n = 14). Values within the bars depict pre- to post-loading difference, * = $P < 0.05$.

Serum COR was increased at 15 and 30 min post-loading following all loadings, with the exception of constant resistance loading after training (Fig. 21, II, IV). However, in the cross-sectional study (II), COR was significantly increased immediately post-loading during variable resistance loading only ($P < 0.05$, Fig. 21). Also, in the training study (IV), area under the curve analysis showed that the before training COR response following variable resistance loading was significantly greater than constant resistance loading (1524 ± 271 nmolL ·30min^{-1} vs. 1369 ± 229 nmolL ·30min^{-1} respectively, $P < 0.05$).

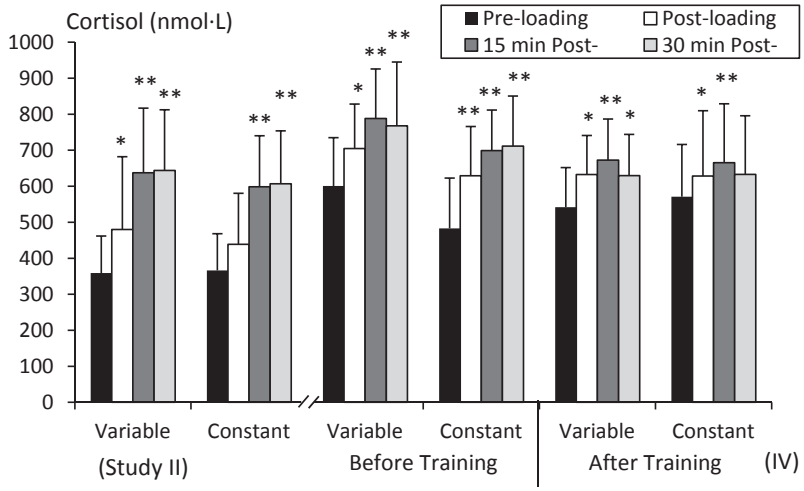

FIGURE 21 Mean (± SD) serum cortisol concentrations during the cross-sectional study (left, study II, n = 13) and the longitudinal training study (right, study IV, n = 14). * = P < 0.05 compared to pre-loading. ** = P < 0.01 compared to pre-loading.

Serum GH was significantly increased post-loading and throughout 30 min recovery to a similar magnitude following both variable and constant resistance loadings (II, IV). However, the increase immediately post-loading following constant resistance loading was at the level of a trend in the untrained state (P = 0.051, II).

5.4.2 Acute molecular responses

Following both variable and constant resistance hypertrophic loadings, phosphorylation of $p70^{S6K}$, rpS6 at both $Ser^{235/236}$ and at $Ser^{240/244}$, MAPKAPK-2, and p38 were increased (P < 0.05, Fig. 22). Increased phosphorylation of ERK1/2 occurred before training only, and the level of phosphorylation was significantly greater following variable resistance loading compared to constant resistance loading (P < 0.05, Fig. 22D). The level of phosphorylation of p38 was greater following variable resistance loading before training compared to after training (Fig. 22E).The phosphorylation of Akt decreased following both loadings before training and constant resistance loading after training (P < 0.05–0.01). There were no statistically significant changes in phosphorylation of mTOR or eEF2 (data not shown) following any loading. There were no changes in total protein or baseline phosphorylation values during loadings (apart from ERK 1/2 phosphorylation after the training intervention; P < 0.05, Fig. 22D).

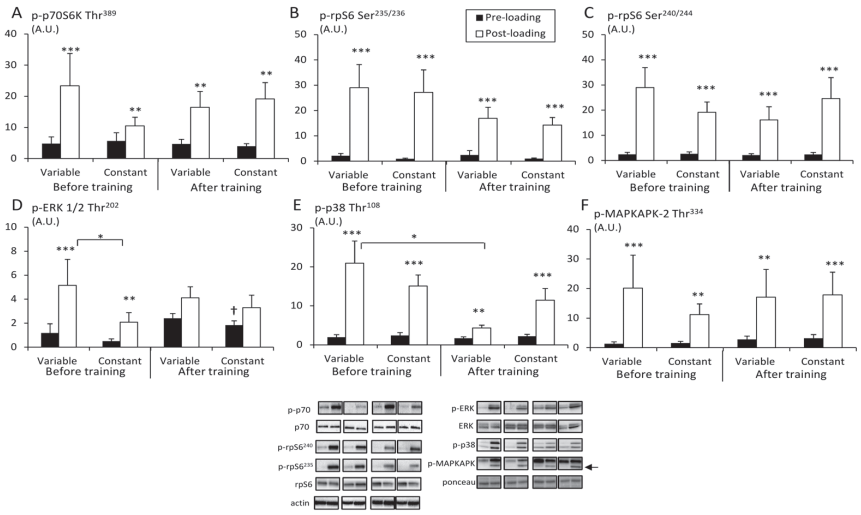

FIGURE 22 Mean (± SE) phosphorylation of p70S6K at Thr^{389} (A), rpS6 at Ser^{235} (B), rpS6 at Ser^{240} (C), ERK 1/2 at Thr^{202} (D), p38 at Thr^{108} (E), MAPKAPK-2 at Thr^{334} (F), in the combined training groups (n = 14). * = P < 0.05, ** = P < 0.01, *** = P < 0.001 compared to pre-loading. † = P< 0.05 compared to the same time-point before training. Representative western blot images for signaling proteins, phosphorylation sites, and α-actin and ponceau staining are shown following the same loading order as the bars in the figures. The two p38 bands (42 and 44 kDa) were averaged. The arrow depicts the MAPKAPK (47 kDa) band that was used for analysis.

Relative changes in post-loading ERK phosphorylation (Δ%) were associated with post-loading serum cortisol response (r = 0.36, P = 0.059, n = 28) and also increased volume load during the repetition to failure test (r = 0.35, P = 0.069, n = 28) at the level of a trend.

5.5 Blood lactate responses during loadings

During all leg press loadings, pre- to post-loading increases in blood lactate concentration were significant (P < 0.01), and blood lactate levels reduced following 15 min recovery (P < 0.05). Following hypertrophic loadings, blood lactate levels were greater than following maximal strength loadings (P < 0.01, II). Furthermore, post-loading blood lactate levels were significantly higher following hypertrophic variable resistance loading compared to constant resistance hypertrophic loading (P < 0.05) in the cross-sectional study only (II). Loading-induced blood lactate concentrations were higher (P < 0.05) after the training

intervention (variable = 15.2 ± 2.9 mmol·L^{-1}, constant = 14.9 ± 4.2 mmol·L^{-1}) compared to loadings before training (variable = 12.4 ± 2.9 mmol·L^{-1}, constant = 12.8 ± 2.4 mmol·L^{-1}) with no differences between variable vs. constant resistance loadings (IV). During knee extension loadings, blood lactate concentration was increased in both young and older men after both hypertrophic loadings only. There were no differences when comparing variable vs. constant resistance loadings. However, young men had higher blood lactate concentrations than older men post-loading ($P < 0.01$).

5.6 Long-term adaptations to constant versus variable resistance training (IV, V)

5.6.1 Neuromuscular performance

5.6.1.1 Maximum force production

Bilateral concentric force production of the leg extensors (1RM) increased ($P < 0.01$) in all training groups at mid-training and the increase was maintained after training (Fig. 23). The relative increases were significantly greater than in the age-matched control groups after the training period (young variable: 14 ± 5 % and constant: 20 ± 9 % vs. control: 6 ± 6 %, $P < 0.01$, older variable: 19 ± 14 % and constant: 24 ± 11 % vs. control: 2 ± 4 %, $P < 0.01$).

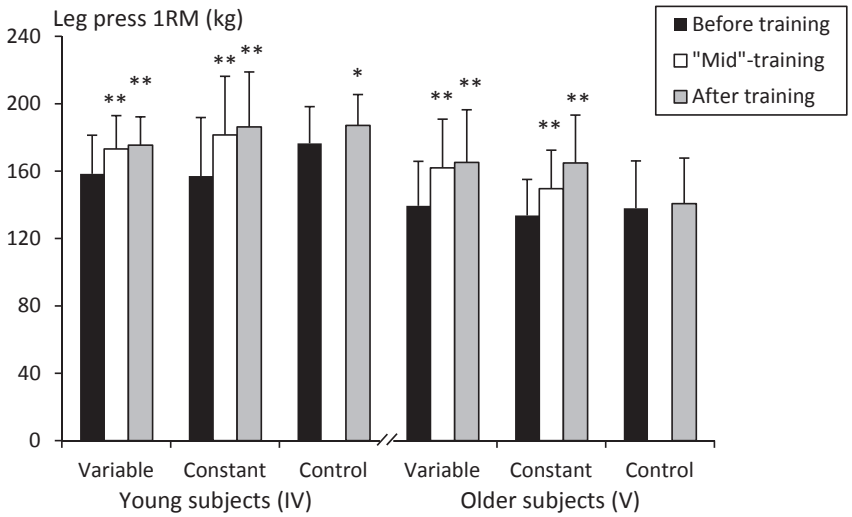

FIGURE 23 Mean (± SD) maximum bilateral concentric force production of the leg extensors (one repetition maximum) before, after 10 weeks ("Mid"-training), and after 20 weeks of training in young (left, study IV, n = 33) and older men (right, study V, n = 37). * = $P < 0.05$ compared to before training, ** = $P < 0.01$ compared to before training.

Similarly, maximum isometric force production of the leg extensors increased ($P < 0.05$) at mid-training except in young men using constant resistance (young variable: 19 ± 20 %, young constant: 16 ± 24 %, older variable: 19 ± 12 %, older constant: 15 ± 15 %), but the plateau and slight decrease thereafter led to non-significant improvements after training in all training groups.

5.6.1.2 Fatigue-resistance during a repetition to failure test

In young men (IV), significant improvements in the repetition to failure test were observed only in the variable resistance training group as assessed either by the total number of repetitions ($P < 0.05$, Fig. 24A) or volume load ($P < 0.05$, Fig. 24B). Furthermore, the relative changes in the number of repetitions and volume load were significantly greater in the variable compared to the control group (reps: 41 ± 46 % vs. –4 ± 40 %, volume load: 54 ± 37 % vs. 1 ± 40 %, $P < 0.05$).

In older men (V), only the variable resistance training group improved the volume load performed during the repetitions to failure test (variable before: 2977 ± 848 kg vs. after: 3681 ± 1068 kg, $P < 0.05$). Relative improvements in both training groups were greater than the control group after training (variable: 28 ± 39 % and constant: 33 ± 54 % vs. control: 1 ± 50 %, $P < 0.01$).

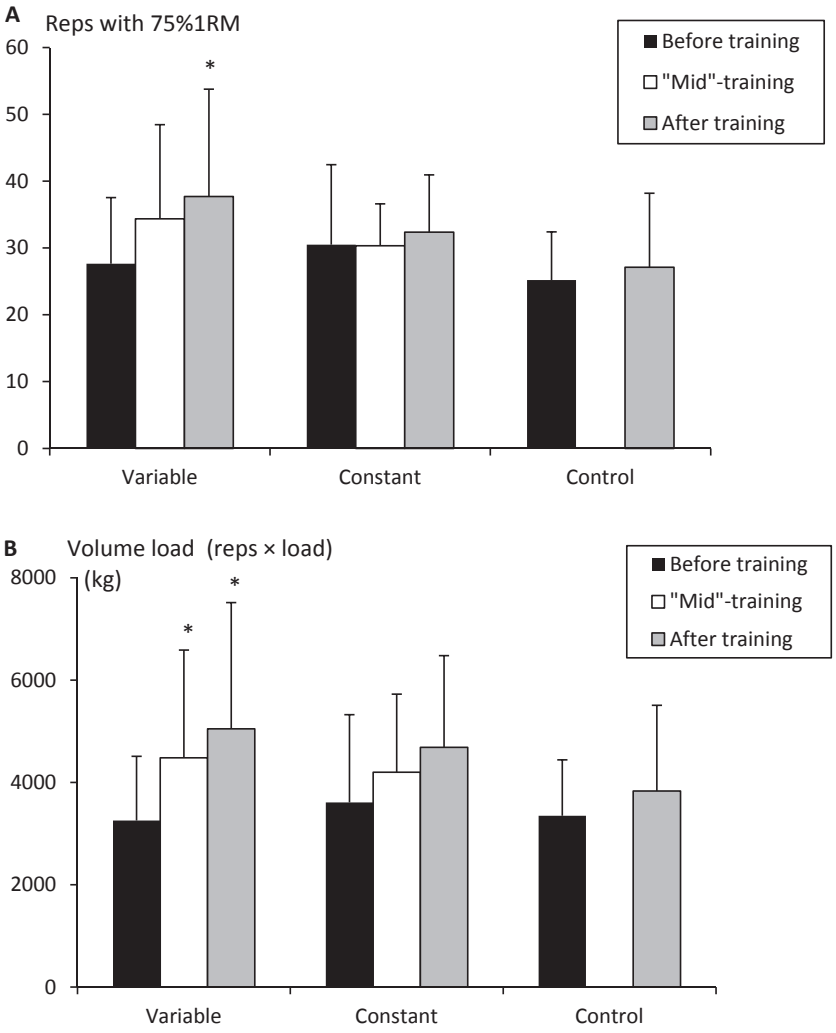

FIGURE 24 Mean (± SD) number of repetitions (A) and volume load (B) performed using 75 % 1RM in young men before, after 10 weeks ("Mid"-training), and after 20 weeks training. * = $P < 0.05$ compared to before training.

5.6.2 Changes in muscle activity and voluntary activation

In older men (V), there were no statistically significant changes in EMG amplitude during maximum bilateral concentric leg extension when the VL and VM muscles were assessed separately. However, when the VL and VM were averaged (VL+VM/2), increases were observed in the constant group ($P < 0.01$) at post-training and trends were observed in the variable group at mid-training ($P = 0.054$, Effect size = 0.39, power = 0.71) and post-training ($P = 0.057$, Effect size = 0.38, power = 0.70) during maximum concentric leg extension (Fig. 25). Also, during maximum bilateral isometric leg extension, EMG amplitude increased in

both training groups at mid-training and in the constant group at post-training. At mid-training, the relative changes in isometric leg extension force production and average VL + VM EMG amplitude were significantly related (r = 0.49, P = 0.016, n = 24). There were no changes in biceps femoris activity or co-activation ratio. In young men (IV), no significant changes were observed in surface EMG amplitude or voluntary activation over the training period.

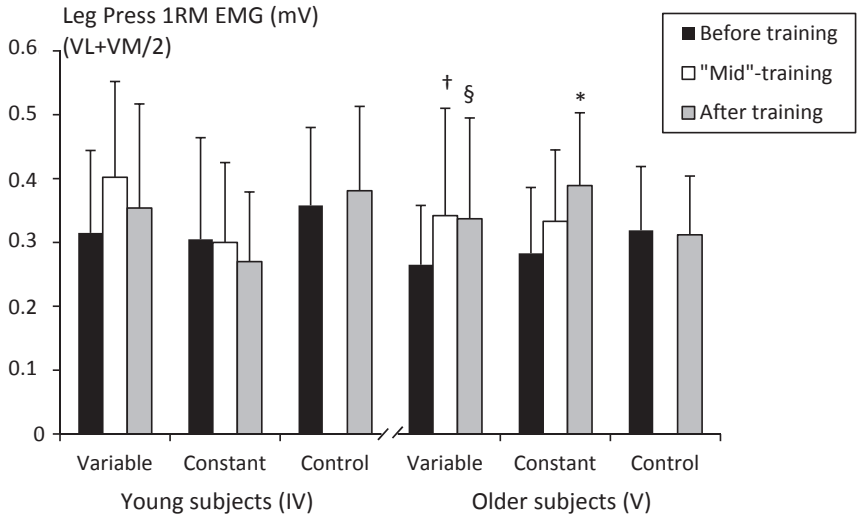

FIGURE 25 Mean (± SD) muscle activity of the vastus lateralis and vastus medialis during maximum bilateral concentric leg extension before, after 10 weeks ("Mid"-training), and after 20 weeks of training in young (left, study IV, n = 33) and older men (right, study V, n = 37). † = P = 0.054 compared to before training, § = P = 0.057 compared to before training, * = P < 0.05 compared to before training.

There were no changes in voluntary activation within individual groups. However, when the variable and constant resistance training groups were combined, voluntary activation was significantly increased at mid-training in older men only (from 90.9 ± 6.4 % to 93.1 ± 5.7 %, P < 0.01, Fig. 26).

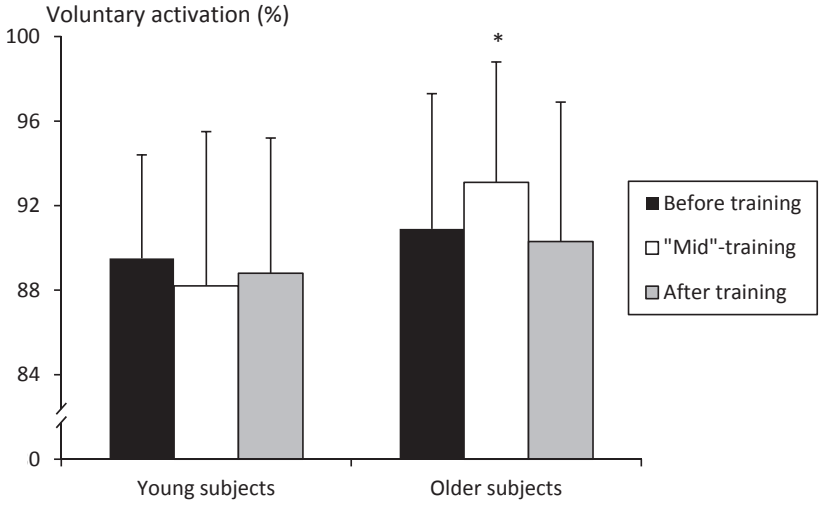

FIGURE 26 Mean (± SD) voluntary activation level of the knee extensors assessed by superimposed twitch before, after 10 weeks ("Mid"-training), and after 20 weeks of training in young (n = 23) and older men (n = 26) when the variable and constant training groups were combined. * = $P < 0.05$ compared to before training.

5.6.3 Changes in lean mass and muscle cross-sectional area

In young men (IV), VL cross-sectional area and lean mass of the legs increased in both training groups after 10 weeks of training and then plateued ($P < 0.05$, Fig. 27A and 27B, respectively). The relative changes in lean leg mass (variable: 3 ± 2.4 %, constant: 2.8 ± 1.8 %) and VL cross-sectional area (variable: 17.3 ± 16.6 %, constant: 17 ± 12.3 %) in both training groups were greater than in the control group (lean mass of the legs: -0.1 ± 2.6 %, VL CSA: 3.2 ± 5 %, $P < 0.05$) after training. In older men, whole body fat mass and fat percentage decreased in all groups over the study period ($P < 0.05$). There were no significant changes in lean mass of the legs (variable: 1.7 ± 2.5 %, constant: 0.9 ± 2.9 %) but VL CSA increased ($P < 0.05$, Fig. 27A) at mid-training (variable: 15.3 ± 16.2 %, constant: 16.9 ± 10.6 %) and after training in both training groups (variable: 9.8 ± 10.8 %, constant: 14.5 ± 11 %).

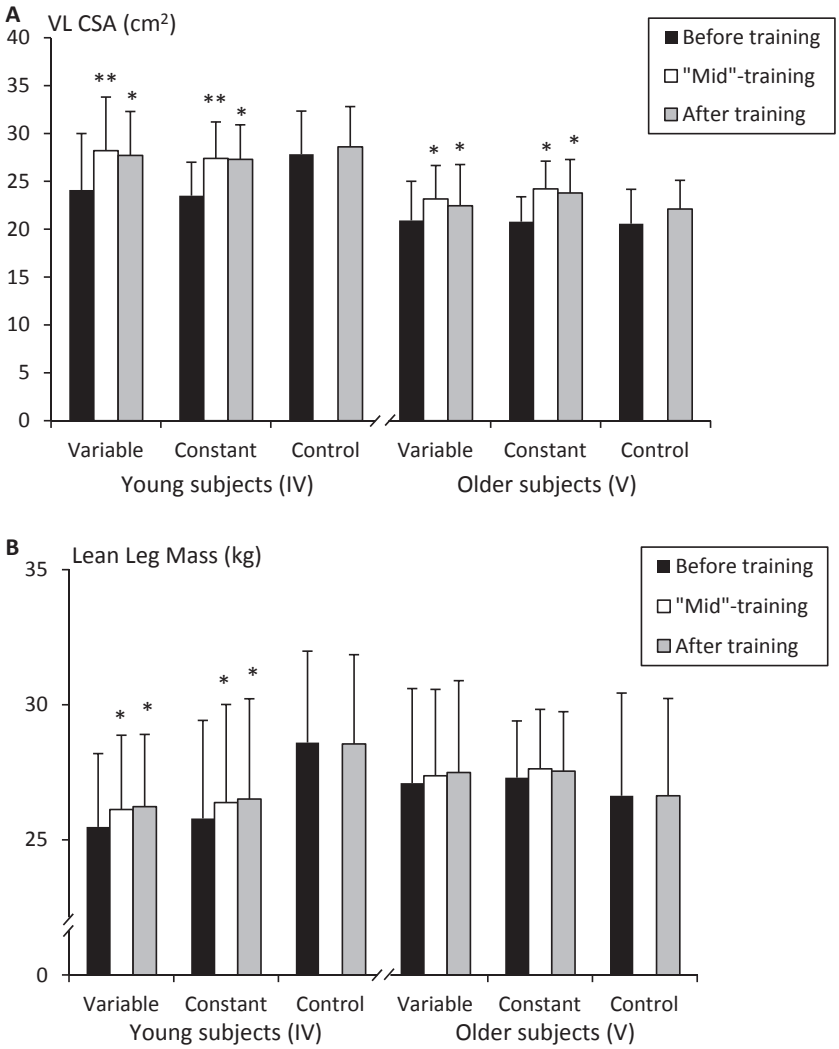

FIGURE 27 Mean (± SD) vastus lateralis cross-sectional area (A) and lean mass of the legs (B) in young (left, study IV, n = 33) and older men (right, study V, n = 37) before, after 10 weeks ("Mid"-training), and after 20 weeks of training. * = $P < 0.05$ compared to before training.

6 DISCUSSION

The present study investigated the effect of constant vs. variable resistance on acute responses and chronic training adaptations in young and older men. The results showed that increased resistance at specific joint angles, which more closely resembles the *in vivo* force-angle relationship, is accompanied by greater quadriceps muscle activity during single-repetition performance. Consequently, the greater need for force and muscle activation led to a greater magnitude of acute neuromuscular fatigue, greater acute serum testosterone and cortisol responses, and phosphorylation of mitogen-activated protein kinases (MAPKs) compared to constant external resistance loading. In both young and older men, training for 20 weeks using variable external resistance resulted in greater improvements in a repetition to failure test compared to groups training with constant external resistance. Maximum strength and muscle mass increased significantly during training but did not differ between constant and variable resistance training groups or between young and older men.

6.1 Acute responses during constant and variable resistance loadings (I–IV)

6.1.1 Neuromuscular responses

During single-repetition leg press actions (I, II), the variable resistance (i.e. CAM) settings used in the present study induced greater EMG amplitude at large knee angles (120°−180°). This is likely a direct consequence of greater resistance at those knee angles (Alkner et al. 2000) and suggests that the gross activation of the quadriceps is greater. However, multi-joint leg press actions have been shown to result in decreasing EMG amplitude from small to large knee angles (Eloranta & Komi 1980, Escamilla et al. 1998) and this pattern occurred in the present study using all resistance settings, despite variable resistance prolonging the level of muscle activity. It is currently unclear as to the cause of decreased quadriceps EMG activity during multi-joint leg press actions. Some au-

thors have proposed that the decrease in EMG amplitude is due to mechanical advantage (Eloranta & Komi 1980) or coordination of hip and knee extensor muscles (Escamilla 2001), whereas the influence of increased hip and knee joint angle *per se* has showed conflicting results (Maffiuletti & Lepers 2003, Azegami et al. 2007). Alternatively, changes in EMG amplitude throughout dynamic contractions may be a consequence of EMG methodology itself. For example, anatomical changes throughout the range of motion, such as electrode proximity to innervation zones and tendons (Rainoldi et al. 2000, Piitulainen et al. 2009), and changes in fascicle length (Mesin et al. 2006) and pennation angle (Farina et al. 2002) throughout the range of motion can affect EMG amplitude. Nevertheless, given that the same joint angles were analysed for all resistance settings, this is not likely to be the major cause of the observed differences between resistance settings.

Following all loadings, significant reductions in maximal isometric force production were observed in both young and older men. Hypertrophic loadings (5 × 10RM) caused greater decreases in force production than maximal strength loadings (15 × 1RM), as would be expected based on previous findings (Häkkinen 1993, Häkkinen 1994). In addition to a greater magnitude of fatigue, it may be expected that differing causes/sites of fatigue would exist between hypertrophic and maximal strength loadings (Cairns et al. 2005), as chronic training adaptations have been shown to be specific to the training protocol (Berger 1962, Campos et al. 2002). In regard to the specific aims of the study, reductions in isometric force production were greater and the rate of recovery was slower following variable vs. constant hypertrophic resistance loadings (II−IV).

Maximal strength loadings consistently showed decreased post-loading isometric EMG amplitude of the knee extensor muscles. However, reduced voluntary activation level was observed in young and older men following variable resistance loading only (III). These results suggest that central fatigue occurred during maximal strength loadings (Bigland-Ritchie et al. 1983, Woods et al. 1987, Häkkinen 1993, Todd et al. 2007), and was perhaps at a greater magnitude during variable resistance loadings. Given that no changes in EMG median frequency were observed, which represents average conduction velocity of the active motor units (Solomonow et al. 1990), it may be that the reduced ability to activate the muscles was related to impaired firing frequency (Woods et al. 1987, de Ruiter et al. 2005) rather than an inability to activate all motor units. This cannot be confirmed by the measurements of the present study, but support for this interpretation may be provided by findings of increased firing frequency following 2 weeks of training with maximum isometric contractions (Christie & Kamen 2010).

During hypertrophic loadings, large reductions in maximum resting twitch torque in response to both constant and variable resistance were observed representing peripheral fatigue (Nordlund et al. 2004, Babault et al. 2006). Large increases in blood lactate and partial recovery 15 min post-loading in both isometric force and blood lactate were observed, suggesting that lactate

accumulation/lower intra-muscular pH (Duchateau et al. 1987), and perhaps also depleted ATP-PC stores (Gorostiaga et al. 2010), affected muscular force following hypertrophic loadings to some extent. Similar increases in blood lactate were observed between constant and variable resistance loadings. These findings may indicate that greater decreases in post-loading maximum force production during variable resistance loadings were due to factors other than anaerobic metabolism and by-product accumulation.

As indicated by the M-wave duration data, action potential propagation was reduced more systematically and to a greater magnitude following variable resistance loading in both young and older men (III). Although lactate accumulation has been shown to reduce median frequency and conduction velocity (Brody et al. 1991), the present study observed similar increases in blood lactate between constant and variable resistance loadings. Recent studies have suggested that muscle damage may interfere with action potential propagation along the sarcolemma (Piitulainen et al. 2011), perhaps through changes in stretch-activated Na^+/K^+ pumps (McBride et al. 2000), and that this is more readily observed following eccentric rather than concentric actions where the force production/resistance is greater. Furthermore, the findings of Dartnell et al. (2008) suggested that muscle damage alters discharge behaviour leading to greater motor unit synchronisation. Therefore, it could be suggested that the observed decreases in median frequency and prolonged M-wave duration following variable but not constant resistance loadings may be due to greater muscle damage. The increased contraction force when using variable resistance gives the potential for greater muscle damage, and it has been suggested that microtrauma is a prerequisite for muscle hypertrophy (Goldspink 1971).

Concentric EMG amplitude during hypertrophic variable resistance loading increased from rep 2 to rep 8 already in set 1 (II), and may arguably be an indication of more increased muscle activation (i.e. activation of larger motor units/higher firing frequency of active motor units) due to fatigue of the active motor units developed within the set. This phenomenon was not observed until set 3 during constant resistance loadings. Reductions in concentric EMG median frequency were also observed in set 3–5 during variable resistance loadings only (IV). The absolute load was lower than in set 1 and, suggesting that the subjects were already maximally activating their quadriceps, and may indicate that motor unit synchronisation had developed during the loading. Motor unit synchronisation would increase EMG amplitude (Yao et al. 2000) and decrease EMG median frequency (Weytjens & van Steenberghe 1984). Although the effect of motor unit synchronisation on force production is debateable, trained individuals have shown greater synchronisation compared to untrained individuals (Milner-Brown et al. 1975).

The present study was in agreement with previous studies that have observed age-related differences in the magnitude of acute neuromuscular fatigue (Häkkinen & Pakarinen 1995, Hunter et al. 2008). It is possible that, as a consequence of this lower overall fatigue, differences between constant and variable resistance loading would be smaller in older subjects compared to young sub-

jects. However, it must be pointed out that older subjects demonstrated reduced EMG amplitude and voluntary activation following variable resistance loading only (III). It may be that a greater stimulus is needed to induce central fatigue in older subjects than 15 sets of 1 RM using constant resistance knee extension used in the present study.

6.1.2 Hormonal and molecular responses

The findings of Ju (1999) suggest that there is a neuro-humoral connection, which may induce growth hormone release. In this regard, it may be possible that the demand on the neural system during maximal strength variable resistance loading was sufficient to cause the observed increase in growth hormone concentration (II). In support of this, increased growth hormone concentration occurred in the absence of increased blood lactate concentration. These findings are in agreement with the observed greater neuromuscular fatigue during maximal strength loading in the young (III), and may support greater long-term adaptations (McCall et al. 1999, West and Phillips 2012). However, the training program of the present study did not focus on maximal strength training (i.e. high intensity, low volume, low number of repetitions per set), and may be one possible reason why differences in either maximum strength or muscle hypertrophy were not observed between groups training using constant vs. variable resistance.

All hypertrophic loadings caused large increases in serum growth hormone concentrations that remained elevated throughout 30 min of recovery. The magnitude of increases in growth hormone concentration has been shown to be influenced by the loading volume (Kraemer et al. 1990, Häkkinen & Pakarinen 1993, Gotshalk et al. 1997, Smilios et al. 2003). In the present study, similar growth hormone responses were observed following constant and variable resistance loadings, even though total work was greater during variable resistance loading (IV). It may be that the difference in total work was not of sufficient magnitude to cause further increases to growth hormone concentrations, or that there is a threshold whereby no further increases would be induced despite increased volume. Alternatively, as the magnitude of growth hormone has been associated with the magnitude of blood lactate response (Häkkinen & Pakarinen 1993, Gordon et al. 1994), this similarity may be explained by the finding of similar blood lactate responses following constant and variable resistance loadings. The only exception that was observed in the present study occurred immediately post-loading in the untrained state (II), which may be explained by a greater change in fluid volume.

These findings may be important indicators of potentially similar training-induced adaptations in muscle due to the influence of growth hormone on several anabolic signalling cascades through the activation of Janus kinase 2 (Campbell 1997). This may help to explain the previously observed positive association between acute growth hormone response and growth of type I and II muscle fibres (McCall et al. 1999, West and Phillips 2012). Alternatively, increased serum growth hormone concentration has been shown to influence

muscle collagen synthesis with no effect on protein synthesis rates (Doessing et al. 2010) indicating possible improvements to force transmission of contracting fibres. Nevertheless, caution should be used when interpreting the impact of 22 kDa GH concentrations, a single member of a much larger family of GH polypeptides, in addition to consideration of the pulsatile secretion of GH.

During hypertrophic leg press loadings (II, IV), significant increases in serum total testosterone (TT) concentration occurred in the untrained state following variable resistance loading only. After training, both constant and variable resistance loadings led to increased TT concentration immediately post-loading but the elevations remained 15 min into recovery following variable resistance loading (IV). Acute TT response has been shown to be influenced by muscle mass/exercise (Kraemer 1988, Volek et al. 1997), volume (Gotshalk et al. 1997), intensity (Jezova et al. 1985, Raastad et al. 2000), and inter-set rest interval (Kraemer et al. 1990), so that larger muscle group exercise, greater volume, greater intensity, and/or shorter rest interval lead to greater acute TT increase. Consequently, greater serum TT responses in the present study may be representative of the greater resistance/muscle activation and perhaps also greater total work during variable resistance loadings. Recent studies have questioned the importance of acute TT increases in mediating training adaptations (West et al. 2009, West et al. 2010), and this may be plausible given that androgen receptor content has been shown to be acutely down-regulated post-loading (Ratamess et al. 2005, Vingren et al. 2009). However, it should be noted that that the findings have been refuted when serum hormone concentrations were elevated prior to performing elbow flexion actions (Ronnestad et al. 2011). Therefore, greater serum TT responses during hypertrophic variable resistance loadings both before and after training may be physiologically meaningful in terms of long-term adaptation to resistance training.

As with TT, greater acute serum cortisol responses were observed following variable resistance loadings before and after training (II, IV). Although cortisol has been typically considered as a catabolic hormone, the magnitude of acute elevations has been related to increased lean body mass and growth of muscle fibre cross-sectional area (West & Phillips 2011). As discussed by Uchida et al. (2009), it may be that cortisol provides amino acids for remodelling processes in combination with muscle damage, and may explain the strong relationship between cortisol and creatine kinase responses (Kraemer et al. 1998) and the attenuating effect of energy drink supplementation on cortisol responses (Tarpenning et al. 2001, Baty et al. 2007). Therefore, it may be that muscle damage (perhaps indicated by the M-wave results of the present study) stimulated the greater cortisol response as part of cortisol's inflammatory function. Secondly, while cortisol has also been shown to respond to metabolic stress (Viru et al. 1994), similar blood lactate responses between constant and variable resistance loadings (III, IV) suggest that this was not the cause for greater cortisol response following variable resistance loading.

In addition to the growth hormone responses discussed above, support for a potentially similar magnitude of training-induced muscle hypertrophy was

also observed in the phosphorylation of protein kinases. The mechanistic target of rapamycin (mTOR) pathway has been widely studied in both animal and human experiments and shown to be a key regulator of protein synthesis (Baar & Esser 1999, Bodine et al. 2001, Drummond et al. 2009, Mayhew et al. 2009). Downstream targets of mTOR, including $p70^{S6K}$ and rpS6, have been shown to respond to resistance loading (Drummond et al. 2009, Hulmi et al. 2009, Mayhew et al. 2009). Indeed, positive associations have been observed between $p70^{S6K}$ and hypertrophy in both rats (Baar & Esser 1999) and humans (Terzis et al. 2008a). Furthermore, elongation factor 2 (eEF2) mediates the translocation step of elongation (Drummond et al. 2009). It should be noted that the results of the present study, and their interpretations, are limited to early responses (30 min post-loading). Nevertheless, in all of the studied mTOR pathway proteins, the magnitude of response was similar between constant and variable resistance loadings both before and after the 20-week training period.

The present study observed greater responses in proteins of the mitogen-activated protein kinase (MAPK) pathway during variable resistance loadings. Before training, in addition to the statistically greater ERK 1/2 phosphorylation, variable resistance loading resulted in approx. 100 % greater response in p38 and approx. 30 % greater response in MAPKAPK-2. These greater responses may have physiological significance to either muscle hypertrophy (e.g. Baar & Esser 1999, Terzis et al. 2008a) and/or muscle "endurance capacity" (e.g. Nader & Esser 2001, Pogozelski et al. 2009). In particular, it may be that the greater phosphorylation of MAPKs may help to explain the greater fatigue-resistance after training with variable external resistance in the present study.

6.2 Long-term adaptations to constant and variable resistance training (IV, V)

In the present study, improvements in maximum bilateral concentric leg extension performance (i.e. 1RM) were statistically significant in all training groups. Furthermore, improvements in young vs. older men and constant vs. variable resistance were of a similar magnitude (mean increases of 14–24 % in the training groups). Maximum bilateral isometric force also increase significantly after 10 weeks of training (mean increases of 15–19 %) in the training groups, but were no longer statistically significant after the training period due to larger inter-individual differences compared to dynamic force production. The training-induced improvements in maximum force production are in agreement with previous studies in young and older men over a similar duration of training (Häkkinen et al. 1998a, Aagaard et al. 2001, Ahtiainen et al. 2003, Karavirta et al. 2011). The training program used in the present study (i.e. high volume, medium intensity with short inter-set rest intervals) consisted of a large number of repetitions per set, which primarily aimed to promote muscle hypertrophy. This training program did not focus on improving maximum force production

compared to other training programs with higher intensity, lower number of repetitions per set, and longer inter-set rest intervals (Berger 1962, Campos et al. 2002). Also, the training frequency of twice per week was less than other studies that have not focussed solely on hypertrophic training, and was necessary based on the large magnitude of acute fatigue and longer recovery expected due to this type of resistance training. Nevertheless, the large training-induced improvements in maximum force production of the lower limbs, especially over the first 10 weeks of training, shows the robust responsiveness of previously untrained subjects to hypertrophic resistance training.

In the present study, no training-induced changes in maximum EMG amplitude occurred in young men during maximum concentric and isometric leg press actions. Despite general scientific acceptance that neural adaptations occur early upon initiation of resistance training (Moritani & de Vries 1979), this is not an unprecedented finding (Garfinkel & Cafarelli 1992, Narici et al. 1996, Aagaard et al. 2002b). There are many possible explanations for a lack of increased EMG amplitude; Rabita et al (2000) found increases in only the rectus femoris muscle after 4 weeks of knee extension training, therefore, it may be that muscle-specific adaptations have occurred. Alternatively, testing after 10 weeks of training may have missed possible increases in EMG amplitude, as some studies have observed an initial increase followed by a decrease in EMG amplitude (Häkkinen & Komi 1983, Keen et al 1994, Karavirta et al. 2011). Perhaps more likely, it may be that the present training program did not provide enough of a stimulus to increase muscle activation, for example, the present training program used medium intensity that did not exceed 85 % 1RM and did not include explosive contractions, as in some studies (Häkkinen et al. 1998b, Karavirta et al, 2011). In subjects accustomed to resistance training, Häkkinen et al. (1985b) observed reduced maximum muscle activity during training using medium loads of only 70–80 % 1RM and increased maximum muscle activity during training using high loads of 80–110 % 1RM. As the subjects of the present study were physical activity, taking part in ball sports including explosive actions (e.g. jumping), this may have reduced their responsiveness to training using 60–85 % 1RM.

In older men, on the other hand, significant increases in quadriceps EMG amplitude that have typically been observed (Moritani & deVries 1980, Häkkinen et al. 1998a, Häkkinen et al. 1998b, Häkkinen et al. 2001) during dynamic and isometric actions occurred in the present study. Furthermore, the present study observed significant increases in voluntary activation in the combined training groups using a method that is difficult to observe statistically significant changes (Herbert & Gandevia 1999, Harridge et al. 1999). The improved muscle activation was associated with improved maximum force production and suggests that the present study's training program is capable of improving central, as well as peripheral parts of the neuromuscular system in older subjects. It may be speculated that the older men in the present study had higher firing frequencies after the training intervention, as firing frequency has been associated with voluntary activation level (Knight & Kamen 2008) and that

short-term training had been shown to increase firing frequency especially in older individuals (Christie & Kamen 2010).

The present training program induced robust increases in muscle mass of the lower limbs in both young and older men. Of particular note is the magnitude of increase in VL CSA. When the constant and variable resistance training groups were combined, increases of ~17 % in young and ~15 % in older men were observed over the first 10 weeks of training. These are some of the largest improvements in muscle CSA reported (Wernbom et al. 2007). Although increases in muscle size were more readily observed in young men in the present study (i.e. in both DXA and ultrasound measurements), there were no significant differences found between the age groups. Discrepancies between the DXA and ultrasound data in the older men may be due to a difference in adaptability between the quadriceps and hamstring muscles in older subjects (Kraemer et al. 1999). The present findings are, therefore, in agreement with previous studies that show similar relative increases in quadriceps muscle mass between young and older men (Häkkinen et al. 1998b, Mayhew et al. 2009). Similarly, hypertrophy of the lower limbs was equivalent between groups performing constant resistance and groups performing variable resistance training.

In addition to the similar acute responses of several purported anabolic effectors discussed previously, one finding that may have influenced the magnitude of muscle hypertrophy relates to consistent muscle tension throughout the repetition. It is noteworthy that the point where force increased (100°–120° knee angle) coincided with decreased velocity when using the exponential CAM, which probably accounts for the prolonged contraction time with 80 % 1RM. As maintained/consistent muscle tension throughout the contraction has been associated with hypertrophy mechanisms (Martineau & Gardiner 2002, Frey et al. 2009), it is conceivable that too large increases in force - leading to changes in absolute/rate of muscle tension - may affect muscle hypertrophy.

However, it should be remembered that the training program of the present study consisted of two similar mesocycles of 10-week duration. Although the absolute loads used in training during the second 10-week period were greater than during the first period (due to increased strength), the relative intensity and number of reps/sets did not differ. This training program allowed the evaluation of a prolonged hypertrophic training period on the dependent variables. It is possible that, based on the results from maximal strength loadings, differences between groups may have begun to be realised during the second mesocycle if relative intensity had increased. Therefore, the question regarding the effect of constant vs. variable resistance training on maximum force production and hypertrophy during a linearly periodised training program remains open.

6.3 Possible mechanisms for greater fatigue-resistance after variable resistance training

The novel finding of the present study was that greater chronic improvements in fatigue-resistance during a leg press repetition to failure test were observed after training with variable external resistance only. Unfortunately, it was not practical to measure muscle activity, serum hormone, or protein phosphorylation responses during the repetition to failure test itself. In particular, muscle activity measures may have provided data concerning differing muscle activation patterns as fatigue develops between the constant and variable training groups. However, data from the resistance loadings may provide evidence that support this variable resistance training-induced adaptation.

Activation of the MAPK pathway may influence many different adaptive mechanisms in skeletal muscle (for review, see Roux & Blenis 2004 and Cuadrado & Nebreda 2010). The present study observed greater phosphorylation of muscle protein kinases of the MAPK pathway during variable resistance loading, especially before training. ERK 1/2, p38, and MAPKAPK-2 are responsive to both resistance and endurance exercise and are thought to be related to a stress response to exercise, as discussed by Nader & Esser (2001). This is supported by the association of acute ERK and cortisol responses to loading found in the present study, and also by the greater increases in serum testosterone during variable resistance loadings before and after training.

ERK 1/2 has been shown to (Echave et al. 2009) activate neuregulin, which is involved in mitochondrial biogenesis, and increase cytochrome c, a mitochondrial protein. Furthermore, phosphorylation of ERK 1/2 has been shown to be involved in angiogensis (Zhou et al. 2007). These adaptations would promote the "endurance capacity" of muscle and likely prolong fatigue in a repetition to failure test lasting approx. 2 min (2 s concentric and 2 s eccentric actions for ~30 reps in all groups). The present study's finding of a relationship, at the level of a trend ($r = 0.35$, $p = 0.069$), between acute ERK 1/2 response before training and training-induced improvement in a repetition to failure test may be indicative of the upstream/indirect influence of these MAPK proteins.

Another possible explanation is that ERK 1/2 has been shown to modify myosin heavy chain expression away from Type IIx towards more oxidative fibres- Type IIa and I (Murgia et al. 2000, Higginson et al. 2002), which may be suggested to influence fatigue-resistance properties. Fibre type conversions in this direction have been observed following resistance training (Staron et al. 1994, Andersen & Aagaard 2000, Campos et al. 2002). However, as there were no observable differences when comparing low repetition vs. high repetition training (Campos et al. 2002), it may be unlikely that this caused the group differences in fatigue-resistance in the present study. Support for this hypothesis comes from the finding of a strong association ($r = 0.7$, $p < 0.01$) between capillary density and number of repetitions to failure using 70 % 1RM, but no association with fibre type and performance (Terzis et al. 2008b).

It should be noted that long-term bodybuilding has been shown to increase muscle glycogen, ATP, phosphocreatine, and creatine concentrations (MacDougall et al. 1977), increase mitochondrial enzyme activity (Tang et al. 2006), improve buffering capacity (Tallon et al. 2005), and induce capillarisation (Campos et al. 2002). These collective findings suggest that the long-term outcome of medium intensity, high volume resistance training favoured by bodybuilders is improved fatigue-resistance (i.e. muscle "endurance capacity") in addition to muscle hypertrophy. The results of the present study suggest that training using variable external resistance provides additional benefit compared to traditional constant external resistance training in this component of neuromuscular performance.

6.4 Methodological considerations

6.4.1 Strengths of the study

Some variable external resistance devices increase the resistance beyond the natural force-angle curve of the exercise (Harman 1983, Johnson et al. 1990, Folland & Morris 2008). However, during the leg press exercise of the present study, the force increased by ~70 % and ~30 % using the exponential CAM and conservative CAM, respectively. Maximal force production during isometric leg press actions may increase force up to ~200 % during isokinetic (Eloranta 1989) and ~100 % during concentric actions from 80°–150° knee angle (Eloranta & Komi 1980). Therefore, the leg press settings used in the present study did not exceed the limits of the force-angle curve.

Subjects in the training study were randomised, all cross-sectional studies used a balanced, cross-over design and no physical training was performed 48 hours pre-loading. The effects of time-of-day (Sedliak et al. 2007) were controlled, and instructions and strong verbal encouragement to the subjects were standardised and maintained throughout the study. The same investigator performed all measurements and/or all analyses to eliminate differences in measurement/analysis technique between researchers.

All training sessions were supervised by researchers from the Department of Biology of Physical Activity. Supervised training ensured that exercise technique, inter-set rest interval, and completion of training goals (i.e. reps and sets) were standardised and adhered. Furthermore, the present study included strict loading and training adherence conditions (90 % completion rate).

Nutritional counselling was given to all subjects in an attempt to standardise nutritional habits, especially protein consumption, which contribute to long-term adaptations (Hulmi et al. 2009b). Furthermore, hydration status, which may influence acute loadings (Judelson et al. 2007) and body composition tests (Thompson et al. 1991), was accounted for through the consumption of a standard quantity of water and 12 hour fasting prior to body composition measurements.

Muscle hypertrophy was assessed by two different methods. DXA may be considered as the gold standard in body composition assessment (van der Ploeg et al. 2003). For more detailed evaluation of the vastus lateralis muscle CSA, the latest technological technique based on ultrasound was used (i.e. composite image by extended-field-of-view). The same site was used in the ultrasound and biopsy measurements. This is important for the evaluation of molecular responses and parallel assessment of training-induced muscle hypertrophy, as studies have shown that hypertrophy is non-uniform along the quadriceps muscle length (Narici et al. 1989).

The present study has examined the effects of constant and variable external resistance using a combined cross-sectional and longitudinal study design with a variety of methods related to neural, muscular, hormonal, and molecular mechanisms. The present study provides new information that can be used in the design and implementation of resistance training programs for different subject populations.

6.4.2 Weaknesses of the study

The subjects were selected by convenience sampling from the local area, which may have resulted in volunteers that are not representative of the entire population, particularly in the case of the older men in the present study. The physically active background of these subjects ensured that they were healthy and capable of strenuous training. However, their neuromuscular properties may not have deteriorated as would have been expected in this age group (Deschenes 2004). Consequently, the young and older men were likely to be more homogenous than may have been expected at the onset of the study.

The subjects were unaccustomed to resistance training. The untrained state likely diluted the effect of training with different forms of resistance on between-group differences. However, this may also be viewed as a strength of the study, in that differences were identified even though the power to detect between group differences was likely to be low.

Dynamic concentric performance before and after training was performed using a leg press that may be considered as a constant external resistance device (producing only ~6 % increase in force between 120°–180°). However, this would, if anything, bias the results in favour of constant resistance training.

All results and conclusions are specific to the loading and training protocols that were used, and differences between constant and variable resistance should not be generalised to all forms of resistance training. Also, the present study cannot determine the outcome had the training program been linearly periodised, as is common practice.

7 MAIN FINDINGS AND CONCLUSIONS

The present study showed that the resistance training program using both constant and variable external resistance was effective in increasing maximum force production and muscle hypertrophy of the lower limbs in young and older men. Furthermore, the changes in muscle activation observed in older men were similar between these resistance settings. However, the present results show that training using variable external resistance induced greater adaptations in fatigue-resistance in both young and older men, as assessed by a repetition to failure test. Results from the acute resistance loadings indicate that the observed adaptations to long-term training may have been due to greater acute neuromuscular fatigue and supported by greater serum hormone and muscle protein kinase phosphorylation responses following variable resistance loadings.

The specific findings and conclusions of the present study are as follows:

1) The greater force requirement beyond ~100° knee angle using the variable resistance settings led to prolonged high muscle activity level of the quadriceps. Although this did not change the typically observed decrease in muscle activity level from small to large knee angles during the leg press action, it may indicate a greater muscle activation requirement during each repetition with submaximal loads (I).

   It appears that variable resistance settings impact the level of muscle activation to a greater extent than constant resistance during submaximal single-repetition actions. This may have altered the acute responses during constant vs. variable resistance loadings.

2) Variable resistance loadings before and after training resulted in greater acute neuromuscular fatigue, serum total testosterone and cortisol responses, and phosphorylation of MAPK proteins, in particular ERK 1/2. These greater acute responses may help to explain the greater improve-

ment in fatigue-resistance during a repetition to failure test in both young and older men that trained using variable external resistance (IV, V).

Collectively, the neuromuscular, hormonal, and molecular data of the present study suggest that variable resistance loadings were more "stressful" than constant resistance loadings, which may have led to training-specific adaptations in performance of a repetition to failure test. The results of the present study suggest that it may be beneficial to train using variable external resistance during periods of high volume, medium intensity, with a large number of repetitions per set, especially if the aim is to improve fatigue-resistance performance.

3) Only the variable resistance training groups improved performance in a repetition to failure test as a consequence of training. Large increases in maximum force production and muscle hypertrophy occurred during the first 10 weeks of training in both young and older men. This was accompanied by similar acute loading-induced increases in serum growth hormone concentration and phosphorylation of purportedly anabolic protein kinases before and after training (IV, V).

   It appears that the training program of the present study did not differ sufficiently between constant and variable resistance to induce different magnitudes of adaptation in maximum force production and muscle hypertrophy of the lower limbs in previously untrained subjects. The reader should note that, while it was our intention to perform a prolonged period of hypertrophic resistance training, this is not typical practice within a linearly periodised training program. The results of the present study show the robust increases obtainable during the initial stages of resistance training. It is perhaps also important to properly periodise future intervention studies in order to distinguish between constant and variable resistance training in the development of maximum force production and hypertrophy.

4) Acute loading-induced reductions in force production were lower in older men compared to young men (III). This perhaps also reduced the effect of variable resistance loading to induce greater neuromuscular fatigue in older men, although differences in voluntary activation level and M-wave duration between constant and variable resistance loadings were observed, as was observed in young men. In addition, similar adaptations in maximum force production and hypertrophy to resistance training were observed in both age-groups (IV, V).

   Variable resistance loadings led to greater neuromuscular fatigue in older men, in-line with young men. However, the magnitude of the differ-

ences between constant and variable resistance loading was lower. Furthermore, the differences in training-induced improvement in fatigue-resistance between constant and variable resistance was not to the same extent as in young men. These findings perhaps indicate that the additional benefit of variable resistance training is lower in older men compared to young men.

YHTEENVETO (Finnish summary)

Akuutit hermolihasjärjestelmän ja seerumin hormonivasteet sekä krooniset adaptaatiot vakio- ja muuttuvavastuslaitteilla toteutetussa voimaharjoittelussa.

Aiemmat tutkimukset ovat osoittaneet, että voimaharjoittelusta on hyötyä muun muassa urheilusuorituksissa, voimantuotto- ja toimintakyvyn ylläpidossa ikääntyessä, lihasten koon kasvattamisessa sekä ikääntymisen aiheuttaman lihaskadon minimoimisessa. Lisäksi voimaharjoittelun avulla voidaan optimoida kehon koostumusta. Voimantuottokyvyn paraneminen johtuu muutoksista hermolihasjärjestelmässä kuten paremmasta lihasaktiivisuudesta tai suuremmasta lihasmassasta. Spesifiset akuutit vasteet voimakuormituksessa vaikuttavat näihin muutoksiin, ja seerumin hormonipitoisuuksien akuutit muutokset tukevat näitä muutosprosesseja. Perinteisessä voimaharjoittelussa vastus pysyy samana koko harjoitusliikkeen aikana, vaikka maksimivoimantuotto muuttuu nivelkulman mukaan. Tämän väitöskirjatutkimuksen tarkoituksena oli selvittää hermolihasjärjestelmän ja seerumin hormonipitoisuuksien akuutit vasteet sekä krooniset adaptaatiot vakio- ja muuttuvavastuslaitteilla toteutetussa voimaharjoittelussa eri-ikäisillä miehillä.

Tutkimuksen suoritti loppuun kuormitusten osalta 47 koehenkilöä (34 nuorta ja 13 vanhaa) sekä voimaharjoitusjakson osalta 70 koehenkilöä (33 nuorta ja 37 vanhaa), joilla ei ollut säännöllistä voimaharjoittelutaustaa. Voimakuormitukset sisälsivät kaksi erilaista protokollaa sekä jalkaprässi- että polvenojennuslaitteilla: maksimivoimakuormituksessa suoritettiin viisitoista sarjaa yhden toiston maksimipainolla ja lihaskasvukuormituksella koehenkilöt suorittivat viisi sarjaa kymmenen toistoina 80 %:lla yhden toiston maksimipainosta. Kuormituksen aikana seurattiin isometrista voimantuottoa, lihasaktiivisuutta (EMG:llä sekä sähköstimulaatiolla hermostoon ja lihaksiin), seerumin hormonipitoisuuksia (testosteroni, kasvuhormoni ja kortisoli), ja proteiinisynteesin säätelyreittien aktivoitumista fosforyloinnin avulla (Akt-mTOR ja MAPK reitit). Voimaharjoittelu painottui lihaskasvua edistäviin kuormituksiin, eli 2-5 sarjaa 8-14 toistoa lyhyellä palautuksella sarjojen välissä (1-2 min). Koehenkilöt satunnaistettiin neljään harjoitteluryhmään (nuori vakiovastus- ja muuttuvavastusryhmä, vanha vakiovastus- ja muuttuvavastusryhmä) ja kahteen kontrolliryhmään (nuori ja vanha kontrolliryhmä). Harjoitteluryhmät harjoittelivat kahdesti viikossa. Kontrolliryhmää ohjeistettiin säilyttämään fyysinen aktiivisuus tutkimusta edeltävällä tasolla. Tutkimusmittaukset (maksimivoimantuotto jalkaprässissä ja maksimitoistotesti 75 %:lla yhden toiston maksimipainosta, lihasaktiivisuus, reisilihaksen poikkipinta-alan mittaus ultraäänellä, alaraajojen lihasmassan mittaus DXA:lla) suoritettiin ennen 20 viikon harjoittelujaksoa, jakson puolivälissä sekä harjoittelujakson jälkeen.

Tutkimuksen päätulokset osoittavat, että muuttuvavastuslaitteet vaikuttavat enemmän sentraaliseen ja periferaaliseen väsymykseen kuin vakiovastuslaitteet lihaskasvukuormituksessa. Lisäksi akuutit seerumin hormonipitoisuusvasteet olivat suurempia (kortisoli) ja/tai pidempikestoisia (testosteroni, kas-

vuhormoni ja kortisoli) muuttuvalla vastuksella suoritetussa lihaskasvukuormituksessa nuorilla miehillä. ERK 1/2-proteiinin fosforylaatiota lisääntyi vain tässä kuormituksessa ennen voimaharjoittelujaksoa. Maksimivoimakuormituksessa akuutit hermolihasjärjestelmän vasteet olivat pienempiä vanhoilla kuin nuorilla miehillä. Maksimivoimantuotto jalkaprässissä parani merkitsevästi kahdesti viikossa toteutetulla vakio- ja muuttuvavastusvoimaharjoittelulla sekä nuorilla että vanhoilla miehillä. Voimantuoton muutosten lisäksi harjoittelu aiheutti reisilihaksen poikkipinta-alan sekä alaraajojen lihasmassan kasvun nuorilla miehillä ja lihasaktiivisuuden kasvun vanhoilla miehillä. Kuitenkin vain muuttuvavastusharjoitusryhmien koehenkilöt paransivat maksimitoistotestin tulostaan.

Tutkimuksen tulokset osoittavat, että voimaharjoituksissa käytettävillä muuttuvavastuslaiteilla on enemmän vaikutusta kuin vakiovastuslaiteilla akuuttiin hermolihasjärjestelmän väsymykseen, suurempiin akuuteihin seerumin hormonipitoisuuksiin ja ERK 1/2- fosforyloinnin vasteisiin. Kumpikin voimaharjoittelutapa aiheuttaa samanlaisen maksimivoimantuoton, lihasaktiivisuuden ja lihasmassan kasvun molemmissa ikäryhmissä. Muutuvavastusvoimaharjoittelu johti sen sijaan suurempaan muutokseen väsymyksen sietokyvyssä, mikä todettiin tämän tutkimuksen maksimitoistotestissä. Tämän tutkimuksen tuloksia voidaan hyödyntää käytännössä voimaharjoittelun ohjelmoinnissa spesifisten voimaharjoitustarpeiden suunnassa useilla eri kohderyhmillä.

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