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The influence of external loading and speed of movement on muscle-tendon unit behaviour and its implications for training

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The Influence of External Loading and Speed of Movement on Muscle-Tendon Unit Behaviour and its Implications for Training

A PhD thesis by

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USE OF THESIS

The Use of Thesis statement is not included in this version of the thesis.

Summary of Thesis

In this thesis great emphasis has been placed on vastus lateralis (VL) muscle-tendon unit (MTU) structure, behaviour/movement and adaptation. Of particular interest was how external loading and movement speed influence these variables. In the first study (Chapter 3) we developed a new methodology by which electromyography (EMG) could be normalised during large range of motion knee extensions. This methodology was then used as part of a larger study, which investigated how external loading influenced the interaction of muscle and tendon (MTU behaviour) during stretch shortening cycle isoinertial knee extensions, and how muscle activity and intrinsic tendon force (F_t) influenced MTU behaviour (Chapter 4). In this study it was observed that as external loading increased the tendon strain decreased despite muscle activity and F_t increasing. It was concluded that the rapid rate of F_t development (RFDt) and speed of movement resulted in an increase in tendon stiffness that was neglected additional strain that is normally associated with increased load/force.

We then investigated how external loading influenced MTU behaviour during parallel depth jump squats (JS-P), which is a more complex but also more commonly performed movement (Chapter 5). Our findings in this study contrasted those of our previous study in that we observed tendon strain increased as external loading increased. Further investigation revealed that while peak F_t increased and movement velocity decreased with increased loading intensity, the RFDt through the tendon did not significantly increase with external loading. In addition, when comparing the results from this study to those of the previous study it was found that the peak RFDt observed during heavy squat jumps was a fraction of the value observed during heavy leg extensions. These results led us to the conclusion that the RFDt that is the primary determinate of MTU behaviour and the influence of loading on MTU behaviour varies between tasks.

In our next study we investigated how speed of movement influences MTU behaviour during parallel depth squatting-type movements (Chapter 6). In this study it was observed that the influence of speed of movement had on MTU behaviour differed between the eccentric and concentric phases. Specifically, it was observed that during initial tendon loading the tendon went through less strain when the movement was performed at faster speeds, however, late in the movement tendon strain increased with increased movement speed. Further investigation revealed that during initial tendon loading RFDt significantly increased with increasing movement speeds, which resulted in the viscoelastic properties of the tendon to predominate the movement. However, late in the movement when relative differences in RFDt were small the tendon behaved as a predominately elastic structure. The results from this study along with the studies prior highlighted that changing either the external load or the speed at which the load it lifted can vastly influence of the VL-MTU behaviour.

In the final study of this thesis we compared the training specific structural and mechanical adaptations to slow-speed, high-load (SHL) squat training to determine how this might differ to relatively fast-speed, light-load (FLL) jump squat training (Chapter 7). In this study we observed that both groups significantly increased their strength, the cross sectional area of their quadriceps muscles, and the fascicle length of their VL. However, only subjects in the SHL group were able to increase the stiffness of their quadriceps tendon and only subjects in the FLL group increased their VL fascicle angle. It is believed that the observed training specific adaptations resulted from previously observed differences in MTU behaviour, intrinsic forces, and muscle activity observed in the previous studies. Because of this it is concluded that intentional manipulation of external load and speed of movement are viable ways to target specific muscular and tendinous adaptations. The results of this thesis has potential practical applications for designing training programs for athletes and sets the stage for further investigation into how these variables can be manipulated for prevention and rehabilitation of musculotendinous injuries.

Declaration

I certify that this thesis does not, to the best of my knowledge and belief:

- i. incorporate without acknowledgement any material previously submitted for a degree or diploma in any institution of higher education*
- ii. contain any material previously published or written by another person except where due reference is made in the text; or*
- iii. contain any defamatory material.*

I also grant permission for the Library at Edith Cowan University to make duplicate copies of my thesis as required.

Dedication

This thesis is dedicated to my grandparents Loren and Frances Rademacher.

You have always been a source of love and inspiration to me.

I greatly cherish the wisdom you have shared with me and

I strive to live my life with the same love, compassion

and grace that you use to live your life.

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This research was completed in thanks to the financial support from the National Strength & Conditioning Association's Graduate Research Grant as well as the School of Exercise and Health Sciences at Edith Cowan University.

I would like to thank all those who have supported me throughout my academic career. I have been very fortunate to have had the privilege to work with so many wonderful people. In the words of my second favourite Newton (Sir Isaac), "If I see further it is by standing on the shoulders of giants."

To my primary supervisor Professor Robert Newton, I asked to study under you because of the vast respect I have for you as a researcher but also because of the way your positive outlook on life inspires all of those around you. After three years working with you I know I made the right decision and I can't express my gratitude for constant support you've given me. To Associate Professor Anthony Blazeovich and Dr. Prue Cormie, I greatly appreciate the trust, guidance and support you've given me during my time at Edith Cowan University. I have learned a great deal from all of you and I look forward to our future relationships and achievements. My progress as a sports scientist can also be attributed to all of those that have supported me in the past. I would especially like to thank Professor William Kraemer and all of those at the University of Connecticut who introduced me to world of high calibre research and instilled in me a passion that makes everyday a new exciting challenge.

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List of Abbreviations

1RM - One repetition maximum

1RM:BM - Parallel depth squat one repetition maximum to body mass ratio

2P, 3P, 4P – Polynomial curves of different complexities: 2nd, 3rd or 4th order respectively used to express the EMG-joint angle relationship

a_{Bar} - Acceleration of the bar ($\text{m}\cdot\text{s}^{-2}$)

A_f - Fascicle angle ($^{\circ}$)

ASIS - Anterior superior iliac spine

BM - Body mass

BF - Biceps femoris

C - Control group that performed no training during their intervention

CSA – Cross-sectional area of a muscle or muscle group (cm^2)

Dist - Distal (inferior) region of the quadriceps

EMG - Electromyography

EMG_p - Peak EMG amplitude that occurred during a movement

EMG_a - Average EMG signal over a period of time

EMG_i - The integrated EMG signal obtained during a movement

Eq - Equation

ES - Erector spinae

F_t - Force expressed through the patellar tendon (N)

FLL - Fast-speed light-load

GM - Gluteus maximus

GRF - Ground reaction force (N)

JS-P - Parallel depth jump squat

JS-V – Volitional depth jump squat

k_t - Stiffness of the quadriceps tendon ($\text{N}\cdot\text{cm}^{-1}$)

L_f - Length of the vastus lateralis fascicles (cm)

L_{MTU} - Length of the vastus lateralis muscle tendon unit (cm)

L_t - Length of the tendinous tissue of the vastus lateralis (cm)

L_{qt} - Length of the quadriceps tendon as measured by ultrasound (cm)

LIN - A linear fitted curve used to express the EMG-joint angle relationship

LPT - Linear position transducer

M - Joint moment (Nm)

$MA_{\text{Peak,Angle}}$ - Maximal EMG activity either across the entire range of motion (Peak) or occurring at a specific joint angle (Angle)

MA % - Percentage of maximal activation as recorded by EMG

MANOVA - Multiple analysis of variance assessments

MG - Medial gastrocnemius

MSE - Mean square error

MTJ - Myotendinous junction of the vastus lateralis

MTU - Muscle-tendon unit

P_{Bar} - Power of the system as measured by bar velocity and ground reaction forces (W)

Pos_{Bar} - Position of the bar as measured by the linear position transducer (cm)

prox - Proximal (superior) region of the quadriceps

QF - Quadriceps femoris

RF - Rectus femoris

RFD_t - The rate of force development in the patellar tendon ($\text{N}\cdot\text{s}^{-1}$)

ROM - Range of motion (degrees)

SENIAM - Surface electromyography for the non-invasive assessment of muscles

SHL - Slow-speed high-load

SO - Soleus

SQ-P - Parallel depth squat

SSC - Stretch-shortening cycle

T_{knee} - Torque of the knee (Nm)

T_{pt} - Thickness of the patellar tendon as measured by ultrasound (cm)

TA - Tibialis anterior

TS-P - Parallel depth squat performed at tempo: 2 seconds eccentric movement, 1 second pause then 2 seconds concentric movement

v_f - Velocity of the vastus lateralis fascicles ($\text{cm}\cdot\text{s}^{-1}$)

v_t - Velocity of the tendinous tissue of the vastus lateralis ($\text{cm}\cdot\text{s}^{-1}$)

v_{bar} - Velocity of the bar ($\text{m}\cdot\text{s}^{-1}$)

VI - Vastus intermedius

VL - Vastus lateralis

VM - Vastus medialis

VOL - Estimated volume of a muscle or muscle group (cm^3)

A - Angular acceleration ($^{\circ}\cdot\text{s}^{-2}$)

θ - Joint angle ($^{\circ}$)

ω - Angular velocity ($^{\circ}\cdot\text{s}^{-1}$)

Chapter 1

Introduction

Training specificity has long been considered a key to maximising task performance. However, the use of training exercises performed at similar speeds and intensities to the task may limit adaptations because the stimulus for adaptations may not surpass the threshold for structural adaptations to occur (13, 24, 109). While the use of training programs that closely match the force or velocity characteristics of the target task are effective for improving performance in that task (7, 58, 63, 65), research has shown that similar results may also arise from non-specific training (7, 58, 72, 113, 231, 239). For example, plyometric training has been shown to increase maximal isometric and dynamic force production in both trained and untrained subjects (231), whilst slow heavy-load (SHL) training has been linked to increases in vertical jump performance (7). Furthermore, both vertical jump and SHL training have been commonly observed to lead to increases in sprint running speed in both athletes and untrained individuals (58, 72, 113, 239). These results question the traditional concept of training specificity and are more consistent with the concept of specificity of adaptation; i.e. that specific adaptations resulting from one type of training may be beneficial to performance in other dissimilar tasks. While research has examined the performance outcomes that can arise from SHL (58, 110, 114, 155) and fast light-load (FLL) (109, 113, 239), much less is known about how muscle, tendon and the nervous system adaptations differ between these two types of training. A better understanding of these differences could potentially help practitioners to design resistance training programs that target the specific structural, neurological or performance adaptations.

TRAINING SPECIFICITY

Traditionally, SHL training has been used to increase peak strength, typically at lower movement speeds, whilst FLL training has been used to increase force production at higher movement speeds. This line of thinking has been developed and reinforced by research demonstrating velocity-specific adaptations (55, 142, 233). Kaneko et al. (143) trained the elbow extensors of previously untrained subjects with external loads of either 0, 30, 60 or 100% maximal isometric

strength. They found significant improvements in all training groups in maximal velocity, force and power. However, the magnitudes of the improvements differed between training groups such that subjects training at 0% had the greatest increase in maximal velocity, those training at 100% had the greatest increase in maximum force, and those training at 30% load had the greatest improvement in peak power production. Since this study, the loading that maximises peak power has been determined for a variety of exercises and populations, with optimal power production during jump squatting being found to occur with external loads between 0-30% of one repetition maximum load (24, 64, 195, 239).

Training at a particular velocity gives specific force producing advantages at that velocity (55). This has been shown particularly for isokinetic training at high velocities, although training at lower velocities has sometimes been shown to improve performance across a broad range of velocities [19]. This isokinetic research indicates that there may be a limited benefit of light-load, high-velocity training. However, a meta-analysis (231) of the influence of lower body plyometric training on strength performance determined that FLL training does increase performance in a variety of strength tests, regardless of the subjects' training histories. Because of the inconsistency of these findings, a better understanding of underlying structural and neuromuscular adaptations to training with different loads and velocities may lead to a more comprehensive understanding of the training response.

MUSCLE ADAPTATIONS AND FASCICLE MOVEMENT

SHL resistance training is widely accepted to be an effective way of increasing muscle size (volume and fibre size (110, 155)), whilst FLL training has been shown to result in a minimal increase in muscle size (109, 169, 233). Muscle architectural adaptations also appear to be training-specific. SHL training has been associated with increases in muscle pennation angle and fascicle length (37, 38, 40, 146). Increased pennation allows for an increased

physiological cross-sectional area, increased force-per cross-sectional area and increased joint excursion (21, 35). In contrast, pennation angle has been shown not to change, or to decrease, in response to FLL training (40), allowing for greater fascicle length within a given muscle volume (146). The increase in fascicle length from SHL training occurs in spite of the increased pennation, and instead is associated with an increase in muscle thickness (40). An increased fascicle length is thought to allow for greater fascicle shortening speeds and an increased ability to produce force during high-speed movements (35).

Using ultrasonography, the behaviour of human muscle fascicles during high-speed movements can now be recorded at rates >100 frames per second (fps) (87, 89, 135, 160). Such research has fostered a better understanding of fascicle shortening during isometric contractions (140, 206) and selective muscle shortening or lengthening during isokinetic contractions (88, 90, 132). Furthermore, research examining fascicle behaviour during jumping has demonstrated greater fascicle lengthening and shortening in sub-maximal compared to maximal vertical jumps, despite the joint going through the same range of motion and the entire muscle-tendon unit (MTU) shortening at a slower velocity (132). This research illustrates that the shortening and/or lengthening of the muscle fascicles or tendon does not necessarily match that of the muscle and tendon as a whole (i.e. the MTU). Because of this, the muscle performed more mechanical work in the sub-maximal jumps while the relatively compliant tendons contributed more to the MTU length change in the maximal jumps (178). In another study (89), increased eccentric loading during drop jumps was shown to result in less fascicle and greater tendon lengthening. While these studies have improved our knowledge of muscle and tendon behaviour during jumping and isokinetic movements, fascicle behaviour during SHL resistance training has received almost no attention. This distinction is necessary because both modelling [70] and isolated-specimen [71] studies have demonstrated that the tendon's resistance to stretch increases as external loading increases due to the tendon's viscoelastic properties. Developing an understanding of how muscles

and tendons interact during resistance training movements could potentially allow for better understanding of stimuli needed for certain muscle and tendon adaptations.

TENDON

All forces exerted by muscle are transmitted through tendons to produce movement. Tendons allow for energy to be stored during their lengthening and then reutilised during their recoil (14, 18, 80, 94, 153, 240). The amount of tendon deformation caused by a given force is dictated by the tendon's stiffness (stiffness = force / deformation). A stiffer tendon requires a greater force to be exerted on it to achieve the same deformation as a more compliant tendon (8, 13, 215), and undergoes less deformation at a given load (13). In addition, if a stiffer tendon is lengthened to the same extent as more compliant tendon the recoil force, and hence its velocity would be greater due to Hooke's Law. For these reasons the optimum stiffness required for optimal tendon lengthening and recoil can vary based on the task performed. During vertical jumping a more compliant tendon is sometimes considered to be better suited for performance (94, 162) because it allows greater tendon lengthening to occur during the countermovement phase thus allowing greater recoil (43, 45). Research has found that one adaptation to SHL and FLL training is an increase in eccentric velocity during the countermovement (63, 219, 223), which would be required to optimally load a stiffer tendon. Nonetheless, this hypothesis is yet to be explicitly examined. Tendon stiffness is dependent upon a variety of anatomical factors, two of the most being its length and cross-sectional area (154, 190, 215); a shorter, thicker tendon will be stiffer than a longer, thinner tendon. SHL training has been shown to significantly increase tendon thickness and cross-sectional area (154, 215) as well as stiffness (52, 164, 200, 215) while FLL training has tended to result in smaller increases or no change in tendon stiffness (52, 164). Additionally, tendon intrinsic properties can be affected by training, which results in a change in the stiffness without any observable changes in cross-sectional area (215). At present there is a limited understanding of how training-induced

changes in tendon structure or mechanical properties will influence movement kinetics and the muscle-tendon interaction during movement.

SUMMARY

SHL and FLL training are both viable methods of improving athletic performance. Both forms of training can elicit improvements in movement-specific tasks as well as well those with non-specific loads, velocities and kinetic patterns. To understand the differences in training-specific adaptations between SHL and FLL training an understanding of how the movements being performed during training differ in regards to MTU behaviour, movement kinetics and muscle activity is required. These differences might indicate the possible locations of the upstream regulators of training specific adaptations, such as differences in muscle size and architecture, tendon structure and mechanical properties, and muscle activation. Changes in any of these parameters are likely to influence movement kinetics as well as MTU behaviour and might help to explain why nonmovement-specific training adaptations occur. It is possible that training-specific adaptations, which develop different aspects of the neuromuscular or musculotendinous systems, will result in different pathways by which performance can be improved.

PURPOSES OF THE CURRENT RESEARCH

The primary purpose of this thesis was to investigate how applying different training loads influences muscle-tendon unit behaviour, movement kinetics, muscle activity and the training-specific adaptations. In this thesis focus is placed on the knee extensor muscles, in particular the vastus lateralis (VL) and the quadriceps tendon. This muscle tendon unit (MTU) was chosen because of the large muscular forces the tendon experiences during training and athletic movements, its importance in athletic and strength performance, it's ability to adapt to training stimuli and the quality of measurement that can be taken.

The specific purposes of this thesis were:

- (1) To develop a methodology by which quadriceps muscle activity could be assessed (i.e. normalised) during a large range of motion knee extension exercise (Chapter 3)
- (2) To determine the influence of external load on vastus lateralis MTU behaviour, force production and knee extensor muscle activation during a maximal, stretch-shortening cycle (SSC) knee extensions (Chapter 4).
- (3) To determine the relationship between eccentric and concentric force production and MTU behaviour during SSC knee extensions (Chapter 4).
- (4) To determine the influence of load on VL fascicular behaviour, force production and muscle activation during back squatting and jump squatting exercises (Chapter 5).
- (5) To determine how the speed of movement influences VL fascicular behaviour, force production and muscle activation during back squatting and jump squatting exercises (Chapter 6).
- (6) To compare training-specific adaptations in quadriceps muscle cross-sectional area, VL, fascicle length, fascicle angle, quadriceps tendon length and stiffness, and patellar tendon thickness between SHL back squat and FLL jump squat training (Chapter 7).
- (7) To compare training-specific adaptations to FLL jump squat training when the countermovement was performed using either a self-selected (~1/2 squat) depth versus full range of motion (parallel squat) depth (Chapter 7).

SIGNIFICANCE OF PROPOSED RESEARCH

Individuals taking part in both resistance training and sport typically subject their bodies to a variety of loads on a daily basis. However, to our

knowledge no previous research has investigated how loading and speed of movement affects MTU behaviour. Understanding this relationship provides valuable insight into the stress and strain stimulus imposed on the muscle-tendon system during training, which can then influence the adaptive process. Furthermore, there is currently a limited understanding of the differences in training specific-adaptations to SHL and FLL training. This thesis is the first to provide an in-depth comparison of these training-specific structural adaptations as well as link these adaptations to underlying MTU behaviour, joint forces and muscle activity. This thesis provides valuable insights into the training-specific adaptations of the neuromuscular and musculotendinous systems to SHL and FLL training, which can allow for better exercise prescription by clinical and coaching practitioners.

Chapter 2

Review of Literature

This review examines the impact of external loading and speed of movement on muscle and tendon interaction during movement and the adaptations to prolonged physical training. The structure and function of muscle and tendon in the human body, and how they interact during movement will be addressed. A special focus will be placed upon *in vivo* observations of muscle and tendon behaviour during movement using ultrasonography. How the manipulation of movement speed and external loading influences neuromuscular performance will then be discussed, and differences between two commonly utilised training modalities, slow-speed, high-load (SHL) and fast-speed, light-load (FLL) training will be highlighted. Lastly training specificity and the concept of specificity of adaptation will be discussed and an attempt will be made to link the neuromuscular stimuli and muscle-tendon unit (MTU) behaviour most likely responsible for such adaptations.

MUSCLE STRUCTURE

ORGANISATION

A great deal of information exists detailing the structure, function and plasticity of skeletal muscle. However, our knowledge of the importance of muscle structure and how the muscle operates during complex movements is still developing. To elicit movement a muscle receives an electrical signal from an alpha motor neuron, which initiates a cascade of physiological events that ultimately lead to muscle contraction (23). The contractile machinery includes the myofilaments actin and myosin which represent the smallest level of muscle structure that we currently understand in detail (23). These myofilaments are capable of generating great forces when active, which can result in forceful and/or high-speed joint rotations (32, 48). Without neurological activity the myofilaments disassociate and passive forces are developed by the cytoskeletal proteins (i.e. titan, alpha actinin, desin, etc.) after a considerable amount of muscle lengthening occurs (122, 198, 216). In addition to the excitability and passive properties of the myofilaments, muscles are organised in such a way that

greatly affects their force expression and ultimately how they underpin movement (76, 77, 87, 146).

Muscles are greatly compartmentalised. Several myofilaments are bundled together and encased into a single muscle fibre by a sheath of connective tissue called the endomysium (23). A number of muscle fibres share an alpha motor neuron, which is either active or silent according to the all-or-none principle (186). These muscle fibres are then bundled into muscle fascicles surrounded by the perimysium (23), which run in series and are the smallest visible muscular structure. The collation of the fascicles make up the muscle as a whole, which is encased by the epimysium (23). Additionally, aponeurotic sheaths and extra-muscular fascia help to separate muscles and further reinforce the epimysium (100). Given the complex arrangement and compartmentalisation of muscle, it is fair to assume that this arrangement has important functional significance, and that variations in this structure will influence muscle contractile properties and force production.

MUSCLE ARCHITECTURE

Unlike the muscle fibres, which run in parallel within the fascicles, the directionality of the fascicles themselves can be highly variable within the muscle as a whole (23, 146). This deviation in directionality is referred to as muscle pennation. The term 'fascicle angulation' (i.e. the angle of the fascicle relative to the aponeurosis) will be used synonymously with pennation (i.e. the angle relative to the tendon) in this thesis although it should be noted that this distinction can be functionally important (23, 35, 146). Pennate skeletal muscles possess a unique structure that provides a mechanical advantage during muscle contraction (35, 76, 77, 88, 146). One of the most common organisations of fascicles within a muscle is the unipennate structure, which can be found in the vasti muscles, gastrocnemius, soleus and triceps brachii, for example (76, 130, 145, 217). Fascicle angulation allows a greater amount of contractile tissue to attach to a given area of tendon, or aponeurosis, thus increasing the

physiological cross-sectional area of a muscle [(11, 27, 35, 39) Figure 1]. Angulation can also allow for greater tendon excursion for a given fascicular shortening which effectively diminishes the amount of muscle translocation relative to fascicle shortening, increasing the muscle shortening velocity for a given fascicle shortening velocity (42, 54). In addition, angulation increases the cross-sectional area of the connective tissue through which the muscle pulls, which may in turn reduce the risk of injury (76). Lastly, the indirect transfer of forces caused by angulation, may increase the muscle's ability to withstand high eccentric forces by transmitting them to the passive structures of the muscle (76). However, fascicle angulation also reduces the efficiency of force transfer since the fascicles pull at an angle to the tendon reducing force transfer is proportional to the cosine of the fascicle angle (42). Thus, fascicle angulation, and changes in it may significantly affect muscle function and injury propensity.

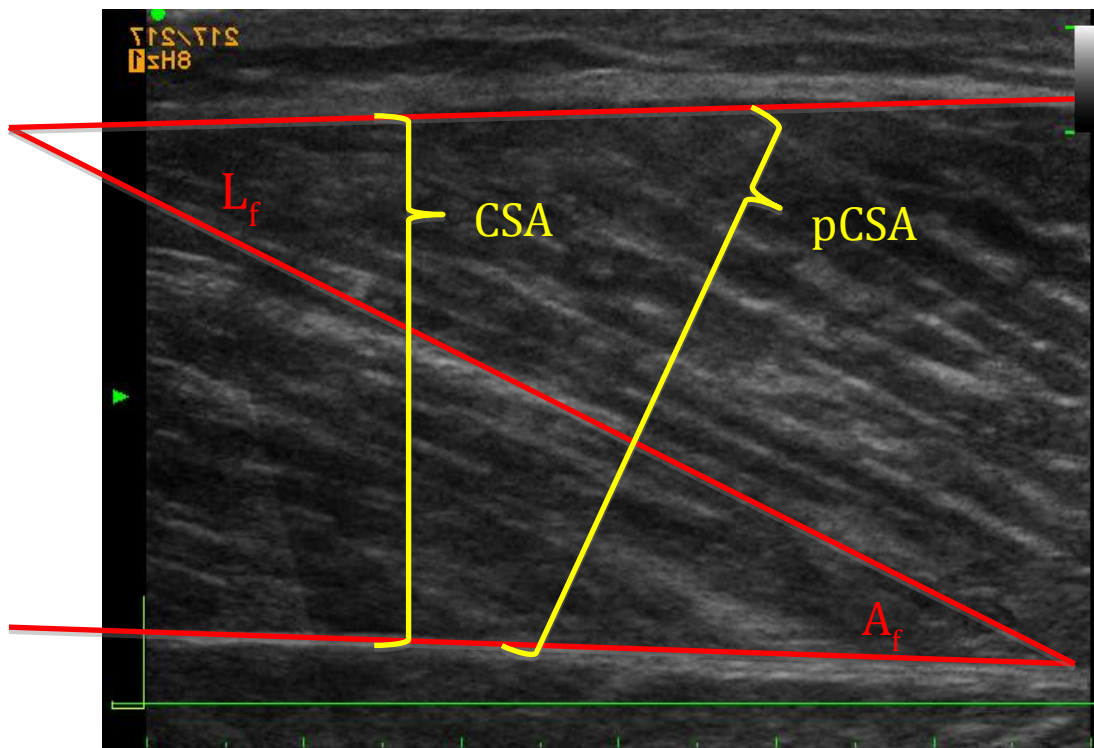


Figure 1: Longitudinal ultrasound image of the vastus lateralis. Fascicle length (L_f), fascicle angle (A_f) and the anatomical (CSA) and physiological (pCSA) cross-sectional area of the muscle.

Fascicle length is measured from the deep to the superficial aponeurosis (Figure 1) and is considered to provide information as to the number of sarcomeres in series (11, 35). Thus, long fascicles are likely to have more contractile elements and thus can produce greater range of motion and dynamic forces (35, 54). Furthermore, it has been hypothesised that sarcomeres within longer fascicles will go through relatively less shortening for a given amount of total muscle shortening (5, 11, 35, 39, 167). This should theoretically be beneficial when producing forces at fast movement speeds. However, this too comes at the cost of metabolic efficiency, as more contractile elements are active and thus the muscle uses more energy (5, 35).

As both fascicle angulation and length provide physiological advantages and disadvantages, optimum muscle architecture differs based on the force, length and velocity characteristics of the movement to be performed. During jumping and drop jumping, when eccentric loading is high, larger fascicle angulation could be considered preferable (76, 77). However, during sprinting when joint velocity is extremely fast but large muscle mass can be detrimental to performance, it is likely that smaller angulation is preferable (5, 167, 220). Similarly long fascicles are believed to be beneficial for tasks such as vertical jumping (76, 77) and sprinting (5, 167, 220), when the muscle works at relatively fast shortening speeds yet large forces need to be exerted, but seem less important in long distance running (5, 42), when movement economy is a more important factor. Nonetheless, there are probably not enough data as yet to confidently predict the optimum architecture for specific tasks.

Physical training can alter muscle architecture, and research suggests that the body can adapt its muscle architecture to better suit movements that are commonly performed (1, 12, 35, 37, 38, 40-42). For example, both fascicle length and angle have been found to increase in previously untrained men who performed slow-speed, high-load (SHL) resistance training, when high forces need to be exerted (1, 38). In opposition, increases in fascicle length have been found in response to sprint training, along with decreases in fascicle angle (5,

40). Interestingly, to our knowledge, only one study has examined changes in muscle architecture in response to fast-speed, light-load (FLL) jump training (40), with those authors reporting an increase in fascicle length, but a decrease in fascicle angle. However, in that study well-trained junior athletes performed a combination of jump and squat training and refrained from their usual resistance training during this time (40). So the influence of physical training at different movement speeds and loading intensities is yet to be fully explored.

MUSCLE STRUCTURE

While our understanding of the importance of muscle architecture is a relatively recent development, we have long understood the importance of muscle size (27, 39, 98). It is well established that larger muscles possess a greater quantity of contractile protein and can thus produce greater forces (98). Furthermore, the link between muscle cross-sectional area (Figure 2) or volume and its ability to produce force and develop power has been well established (246). For example, increasing muscle cross-sectional area at the mid-thigh has been shown in response to SHL training in both trained and untrained individuals (109, 128, 192, 213, 230). However, FLL training, such as plyometrics, has been shown to result in only marginal increases in mid-thigh cross-sectional area or no significant changes (109, 169, 233). Thus, the link between gross anatomical structure and functional capacity appears to be training specific.

An interesting area of research that is gaining increasing attention revolves around the concept of regional-specific hypertrophy (47, 124, 192, 193, 235). Regional-specific hypertrophy is the observation that increases in muscle size can occur at different locations within a muscle or muscle group. However, currently little is known of the cause or functional significance of these findings. In a landmark study by Narici et al. (192), regional-specific muscle hypertrophy (as measured by cross-sectional area) was found in the area of the quadriceps muscle that received the greatest neurological stimuli during leg extension training. Other studies have also reported regional-specific hypertrophy, but little

is presently understood about what stimulates such specificity and it is not possible to predict *a priori* where the hypertrophy will be (47, 124, 193, 235). The most common finding from these studies is that SHL knee extension training resulted in greater quadriceps cross-sectional area in the proximal region of the thigh when compared to other regions (47, 192, 193, 235). However, the author's knowledge, no research has examined the influence of FLL training on regional hypertrophy. Furthermore, it is not known whether training with different external loads or movement speeds will result in hypertrophy in different locations along a muscle. It is possible that such differences exist and that these differences influence how the muscle develops force.

If regional-specific hypertrophy does occur it could change the way muscle forces are produced and transferred to the tendon. As muscle is isovolumetric, hence muscle fibres are forced to rotate during contraction (87). The concept of variable gearing states that the way in which a muscle rotates will depend on the speed and force needed for a given movement (21). This means the muscle functions in a way in which the internal moment arm of the muscle changes; much like a bicycle changing gears. A muscle that needs greater force will function better if the mass of the muscle is further away from the load, resulting in the muscle acting in low gear by decreasing the moment arm of the muscle [Figure 3 (21)] . In contrast a muscle that needs speed rather than strength will function better if the muscle mass is closer to the knee, resulting in the muscle acting in high gear by increasing the internal moment arm [Figure 3 (21)]. However, observation of this theory in practice has not yet occurred *in vivo*.

MUSCLE-TENDON UNIT

Muscles transfer their forces to bone via elastic tendons. Therefore, it is important to understand how muscle-tendon units function and respond to training. The MTU is comprised of three sections each containing specific mechanical properties. Muscle itself is vastly more metabolically active than

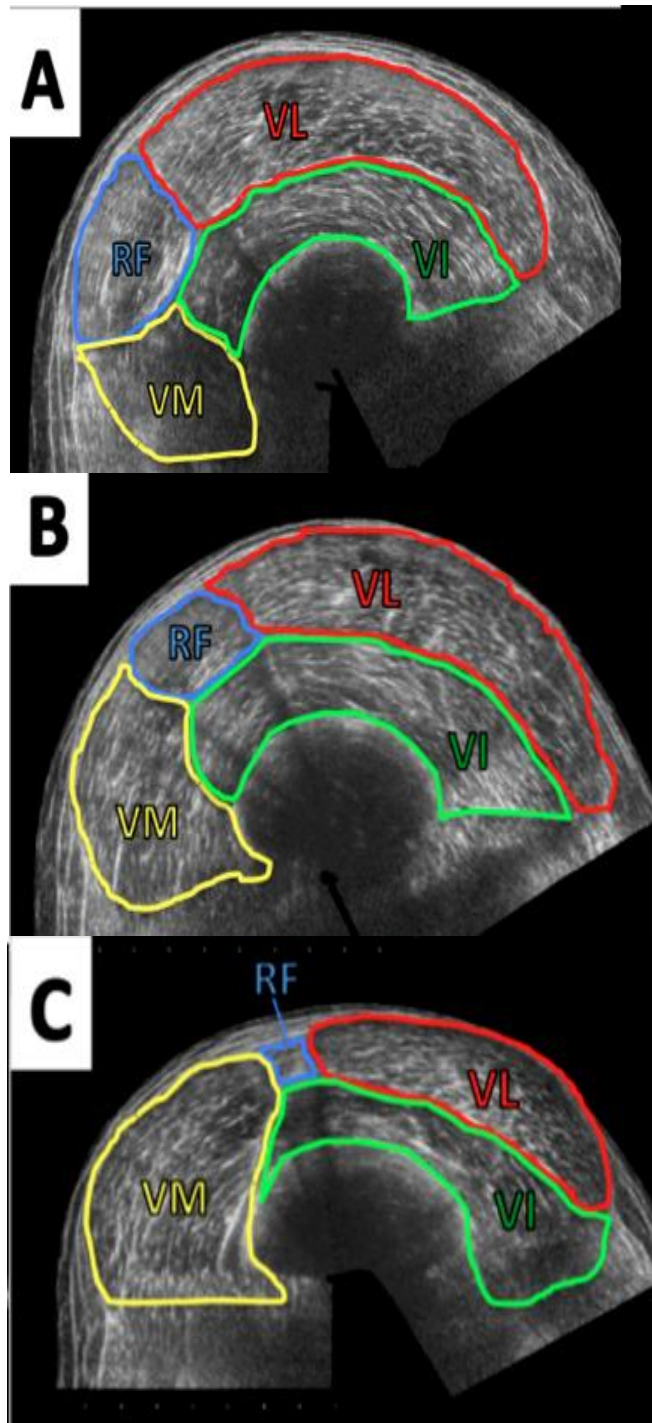


Figure 2: An example of extended field of view ultrasound images taken at the superior- (A), mid- (B) and distal-thigh (C). Cross-sectional area of the vastus lateralis (VL), medialis (VM) and intermedius (VM) and the rectus femoris (RF) are highlighted at each region.

tendon and possesses the ability to shorten when excited; thus the muscle is often referred to as the contractile element (45). The tendon to which the muscle attaches acts as a passive link and has its own unique structure and mechanical properties (45, 79, 117). Because tendons are passive, their function is dependent upon the forces exerted by the muscle; thus the tendon is referred to as a series elastic element (45). The muscle itself possesses cytoskeletal proteins (i.e. titin, alpha actinin, desmin, etc.) and connective tissue (fascia and epimysium, peri- and endomysium) that possesses elastic properties, and is referred to as the parallel elastic element of the MTU (45, 125, 177). However, cytoskeletal proteins, actin-myosin cross-bridges, and the titin protein within the muscle form part of the series elastic element, thus the muscle contributes to both series and parallel elastic components. Because muscle contraction cannot produce movement without these elastic elements, it is important to develop a comprehensive understanding of them and their functional importance.

TENDON

TENDON STRUCTURE

Tendon, much like muscle, is compartmentally organised. However, tendon is comprised of primarily type-1 collagen, although it also contains significant proportions of elastin (~2%) and proteoglycans (1-5%) (180). Small collagen fibrils are packaged into fibres, which are then bundled and packaged into sub-fascicles, fascicles and finally tertiary fibre bundles. Each of these is encased by their own endotenon (144). These structures make up the tendon as a whole, which is encased by the epitendon (144). It is on the fascicle level that fibroblasts, which are responsible for tendon growth as well as a crimp-like structural organisation, are located (92, 144, 188). Crimp is a description of the waviness that a tendon possesses when it is not stretched (92). Because of crimp, the collagen structures are not stretched directly during initial tendon lengthening (i.e. strain), rather the tendon fascicles are reorganised to become parallel with the line of action of the tendon (92, 188). This results in very little

force being needed to stretch the tendon (i.e. a low stiffness) during initial lengthening. On a stress-strain curve of a tendon this initial compliant lengthening is known as the toe region [Figure 4 (19)]. In the patellar and quadriceps tendon it is not until approximately 50% of maximal voluntary contraction force is produced that this toe region ends and stiffness rises rapidly but the rate of stiffness increase starts to plateau (205). In most research it is the stiffness at these force levels that is typically used to describe the inherent stiffness/mechanical properties of the tendon (205).

The inherent stiffness of a tendon is dependent upon several factors. However, the gross structure (i.e. the cross-sectional area and length) of the tendon is likely to be the predominant factor influencing stiffness. Tendons with greater cross-sectional area typically possess a greater amount of collagen material arranged in parallel, so stiffness is usually greater. However, increases in tendon length reduce stiffness, as less proportional elongation of collagen fibres is required for a given absolute tendon length change. Both tendon length and cross-sectional area have been shown to differ between individuals and muscles (160, 190). Tendon cross-sectional area and stiffness have also been shown to increase in response to eccentric and SHL resistance training (13, 52, 68, 154, 164, 166, 215). However, it should be noted that some studies have found no significant changes in tendon cross-sectional area in response to similar training protocols, despite increases in stiffness being reported (161, 204). Differences between studies may be attributed to several factors. First, relatively small changes in cross-sectional area may occur that are outside of the range of sensitivity for the equipment used for measurement (49). Second, tendons may possess a relatively slow time course for adaptation, so hypertrophy may occur over longer training periods than those studied (157, 158). In these cases other factors such as fibre cross-linking may be responsible for the observed increase in stiffness (67, 112). Third, a recent study has suggested that tendon hypertrophy is region-specific, so tendon hypertrophy may be missed if measurements are not made along the entire length of the tendon (154).

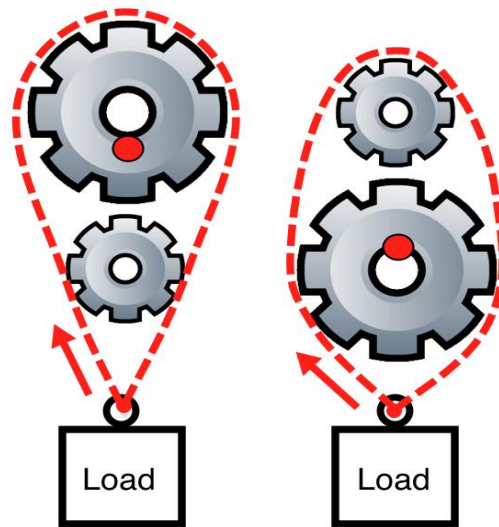


Figure 3: An example of how changes in muscle structure influence joint moment through the process called variable gearing. The red circle indicates the centre of mass or the internal moment arm of the muscle, while the arrow indicates the direction of pull on the load.

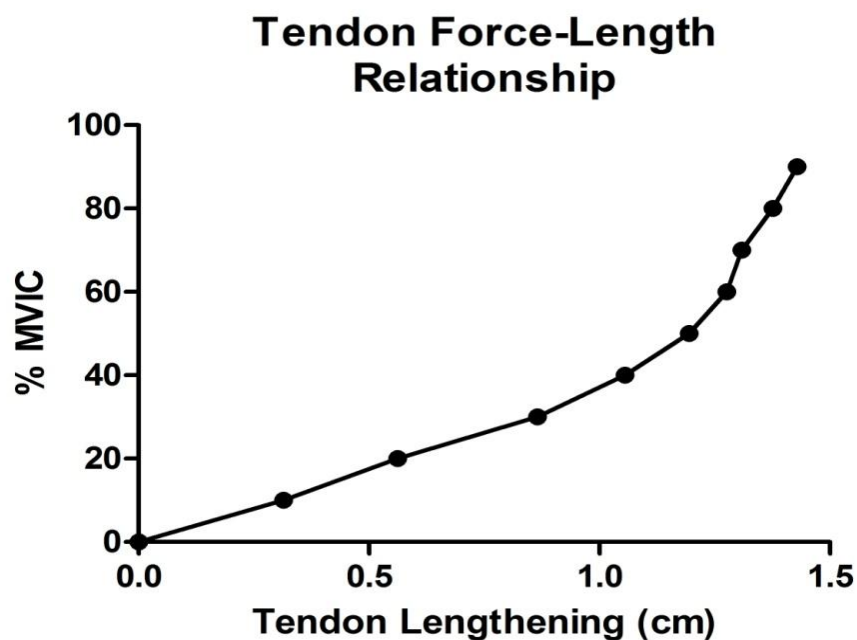


Figure 4: An example of the stress strain relationship from data obtained from the quadriceps tendon during a maximal voluntary isometric contraction (MVIC).

Several studies have examined the effects of FLL training, such as plyometrics, on tendon structure and mechanical properties, but so far no changes have been reported (52, 91, 105, 164). This has led researchers to believe that there is a threshold or particular stimuli necessary for tendon adaptations to occur (164). Arampatzis, in two landmark studies (16, 17), investigated how strain magnitude and frequency influenced the mechanical properties of tendon during an isolated movement and found that at greater magnitude and lower stretch frequencies induced greater increases in tendon stiffness. However, similar evidence in humans during complex multi-joint movements is currently lacking.

In contrast to cross-sectional area, tendon length has not been investigated in such detail as a location of potential training adaptation, as it is generally believed to be genetically determined (190). However, theoretically, lengthening of the tendon could occur in much the same way that lengthening of the muscle fascicles occurs. It is also possible for resting tendon length to change in response to changing muscle length or intramuscular pressure (9, 71, 202, 207). An increase in muscle length in response to training could decrease resting tendon length, while an increase in intramuscular pressure in response to increased protein content or change in fascicle angle could result in an increase in resting tendon length. However, in such scenarios the maximal strain of the tendon would most likely not be significantly altered, but the tendon would operate over a different length range on its length-stiffness continuum. Because of the functional significance that tendon structure has on its mechanical properties and the many potential locations for such adaptations to occur this is a rapidly expanding and intriguing area of research with many possible future implications.

VISCOELASTICITY

Tendons are a viscoelastic material; containing both elastic and viscous properties. Because of the viscous properties of tendons, their behaviour is

dependent upon the speed at which they are lengthened and the rate at which force is exerted upon them (116, 194, 199). Tendons will resist deformation the faster they are lengthened (116) and the greater the rate of force increase that is transmitted through them (199). These properties can be observed during a process called creep (199, 214). Creep can be characterised by gradual tendon lengthening after a force is applied and a gradual return to its original length after a force is maintained reduced (Figure 5). This viscous behaviour has been found in studies using isolated tendons stretched at increasing speeds (116). However to our knowledge, Pearson et al. (199) published the only paper that has directly observed these properties *in vivo*. Pearson et al. had subjects perform ramped force maximal isometric knee extensions at different rates, during which tendon lengthening was observed using ultrasonography. Results from this study demonstrated that the shorter the duration of the contraction, and thus the faster the rate of force development, the stiffer the tendon had become and the less the tendon lengthened. However, similar findings have not been made in humans during active or passive movement (89, 90, 132, 133, 222).

MUSCLE TENDON UNIT BEHAVIOUR

MUSCLE ACTIVATION

As previously noted the muscle is vastly more metabolically active than tendon and thus movement of the tendon is entirely dependent upon force developed by the muscle. Therefore muscle, unlike tendon, can modulate its mechanical properties by activation from neurological stimulation (180). In general, a maximally activated muscle is significantly stiffer than its tendon and thus the tendon will lengthen as a muscle shortens (18, 20, 82). This MTU behaviour was originally observed by Ito et al. (140) during maximal intensity isometric contractions. However, when a muscle is inactive the tendon often becomes the stiffer element resulting in the muscle lengthening prior to the tendon when the MTU is stretched (6, 222). This MTU behaviour can be

observed during passive movements such as static stretching (6). Thus, muscle activation is a key to MTU behaviour.

While the importance of muscle activation to joint movement is well established, our ability to observe muscle activation is limited (186). Unless radical and/or invasive methods are used, we can only observe muscle activity by the means of skin surface electromyography (EMG) rather than true muscle activation (186). Recorded EMG signals reveal information as to the electrical activity that is directly between two electrodes, and signals are dependent on the directionality in which the signals run (186, 241). Because of the methodological constraints of EMG when a joint moves through a range of motion the muscle underneath the electrodes moves and thus different muscle fibres are recorded (84, 85, 186, 203). Furthermore, as a muscle contracts its cross-sectional area can increase the amount of muscle tissue beneath the electrodes and thus can increase the number of motor units recorded (241). During muscle contraction the fascicles will also rotate and fascicle angle in relation to the skin increases, this changes the directionality of the signals and thus changes the EMG frequency and amplitude (84, 85, 203). To complicate this even further as a muscle is activated at shorter muscle lengths neurological inhibition occurs which can reduce EMG signals and therefore influence the EMG-muscle length relationship (107, 148, 245). For these reasons it is difficult to use surface EMG signals to determine when and how a muscle is activated during movements across a large range of motion. Nonetheless, Kellis et al. (151) tried to take this into by using a method by which EMG signals could be normalised in relation to the relative maximal muscle activity (EMG) at a given joint angle. The researchers had their subjects perform maximal isokinetic contractions during which EMG signals and joint angle were simultaneously recorded. They then divided the movement into several windows, each encompassing 10° of knee extension, and EMG signals were averaged and recorded during these windows. The researchers then considered these recorded values to be the maximal EMG

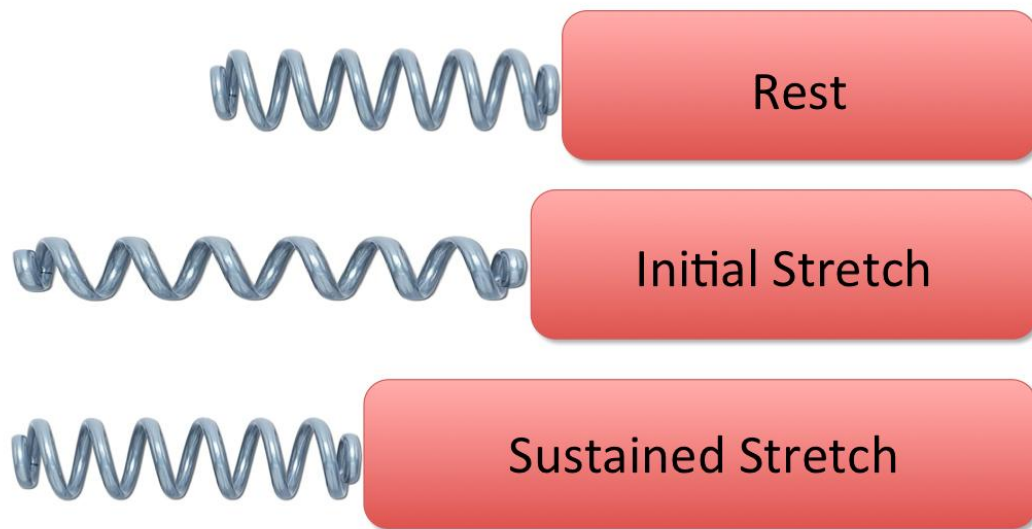


Figure 5: A depiction of tendon creep during a rapid, but sustained stretch. The red box represents a muscle while the spring represents a tendon.

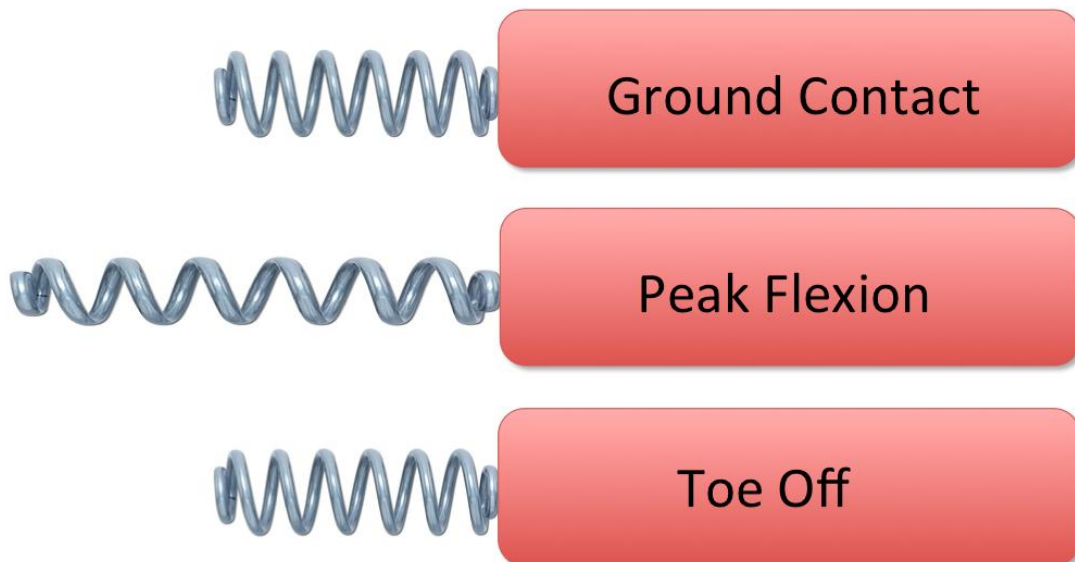


Figure 6: A depiction of quasi-isometric muscle-tendon unit behaviour during a stretch shortening cycle movement. The red boxes represent a muscle while the springs represent a tendon.

possible relative to those joint positions and then compared all EMG signals subsequently recorded at similar joint angles to these values (151). While the process increased the ability to see relative joint activation during a large range of motion, the process of using 10° windows may limit the ability to quantitatively assess muscle activation using EMG-time curves because the referenced EMG values may drastically change between the 10° epochs, and thus values in an EMG-time curve may result in considerable shifts in values between these windows. Thus, a new methodology may be needed to make such assessments. Being able to better understand muscle activation is important when we investigate muscle and tendon interaction because tendon movement will be directly influenced by muscle activity and thus force production.

FUNCTIONAL SIGNIFICANCE OF THE MUSCLE-TENDON UNIT

As muscle supplies the driving force underpinning all movement, whilst tendon can only passively redistribute energy from the muscle, it becomes easy to question the functional significance of tendon. However, tendons serve to impact performance in several important ways. By incorporating a tendon into a MTU the maximum MTU shortening velocity and power as well as the movement efficiency can be substantially increased (43, 79-81, 94, 227-229). As stated previously, tendons are viscoelastic and will thus store and return energy. In this facet alone tendons are superior to muscle as they are able to return a greater proportion of stored elastic energy than muscle; i.e. tendons have less hysteresis than muscles (126, 159). However, this alone does relatively little to increase performance, rather it is the interaction of the muscle and tendon, which serves this important function (43, 80, 81, 172, 190, 227, 228). During a muscle contraction the tendon actually delays the transfer of forces to the bone as the tendon stretches. By delaying this movement it actually allows the muscle more time to be active and reach its maximal activity. By delaying the movement tendons also allow the muscle to work at a speed slower than the MTU as a

whole. This is beneficial to performance as it allows the muscle to work at a more optimal velocity, as dictated by the force-velocity relationship of muscle contraction (99, 238). Furthermore, during a stretch shortening cycle (SSC: or a movement with both an eccentric and subsequent concentric phase) movement the tendon can take up more relative elongation than the muscle because the tendon is more compliant than active muscle (132, 159, 205, 208, 209, 236). This allows the muscle to spend more time functioning at an optimal muscle length, as explained by the force-length relationship of muscle. Lastly, tendons serve as a redistributor of energy, much like a catapult that allows energy to be stored up slowly and released at faster speeds (79, 138, 208). This allows the MTU to shorten at speeds that would be otherwise impossible for a muscle in isolation.

MUSCLE-TENDON UNIT BEHAVIOUR

Recent advances in technology have made it possible to observe muscle and tendon lengthening and shortening non-invasively in humans using ultrasonography (96). Since its inception a great deal of knowledge has accrued in regards to how muscle and tendon interact during movement. Possibly the movements which have been researched the most using these variables are jumping-type movements and gait. Finni, Ishikawa and other researchers at the University of Jyväskylä in Finland developed an angled sledge apparatus that they then used in a series of papers to investigate MTU behaviour during jumping and drop jumping (88, 89, 132, 218). In 2003 Ishikawa et al. (132) investigated how performing sledge drop jumps to different rebound heights influenced vastus lateralis MTU behaviour. In this study it was observed that forces through the tendon and movement velocity increased and the tendon went through greater lengthening but the muscle went through less lengthening as jump height increased. This MTU behaviour demonstrated that the tendon acted as a predominately elastic structure by amplifying joint power. During a similar experiment investigating vastus lateralis MTU behaviour during drop jumps with different rebound heights, similar results were found (133). Finni et al. (90)

compared vastus lateralis MTU behaviour during countermovement and drop jumps and found similar results, suggesting that greater pre-activity of the muscle, as measured by EMG, caused the muscle to stiffen and thus the muscle went through less lengthening during the drop jump than the countermovement jump despite greater forces being developed at higher speeds. These studies, along with several others, have led researchers to believe that tendon elasticity allows the muscle to work in a quasi-isometric state during which maximal forces can be developed with minimal metabolic demands and greatest force output [Figure 6 (90, 136, 163, 205, 218, 236)].

In these studies the function of tendon was that of an elastic structure, going through increased lengthening when greater forces were exerted. However, these results do not depict the tendons acting as a viscous structure, as a viscous structure would significantly increase its stiffness as the speed and rate of force development increases and should therefore stretch less (116, 194, 199). While it is possible that the viscous properties of tendon might influence movement to some degree, these observations have not yet been made. It is possible that the changes in force between the different jumps of increasing intensities were too great and the differences in speed and rate of force development were not great enough for these properties to be observed. However, in another study by Ishikawa et al (138), that examined at high-intensity drop jumps performed at an optimal drop height (the drop height at which the subject could jump the highest) and at 10 cm above and below this height, they found that from supra-optimal drop height the gastrocnemius went through a phase of uncontrolled lengthening during which the muscle activity decreased and the fascicle quickly lengthened. During this uncontrolled fascicle lengthening the tendon did not lengthen. This could be a demonstration of the viscous properties of tendon resulting in increased stiffness as high forces are produced at very fast rates. However, the increase in fascicle length could also be an effect the efferent drive due to increased neural inhibition by which the high

forces caused the muscles to relax and thus the tendon did not lengthen because the joint forces were reduced (53, 56).

Besides jumping movements, MTU behaviour has also been observed during walking, jogging and running (139, 171, 173). In these studies subjects would walk, jog or run at different speeds and gastrocnemius and vastus lateralis MTU behaviour were observed. In these studies as movement speed or intensity increased the muscles experienced greater pre-activity and stiffness while the tendons experienced greater forces and went through greater strain (139, 171, 173). These results once again showed the tendon acting as an elastic structure despite the large changes in speed and most likely the rate of force development through the tendon.

While *in vivo* observation has shown the predominance of the elastic properties of tendons during jumping and gait movements little is known about the MTU behaviour during many other commonly performed movements. Of particular interest is the MTU behaviour during commonly performed training movements such as SHL, e.g. squats and FLL, e.g. loaded jump squats. This could be of interest because these are movements that commonly provide the training stimuli for adaptation (23, 185). Understanding the MTU behaviour of different movements and how tendons adapt to a specific MTU behaviour may provide information as to the exact stimuli responsible for many of the previously observed training specific adaptation (13, 16, 17). Furthermore, once this link is established we can work to maximise the stimuli responsible for adaptations by manipulating acute programme variables such as speed of movement and external load.

PRINCIPLES OF RESISTANCE TRAINING

The purpose of exercise is to provide the stimuli necessary for beneficial adaptations. Thus, resistance training, and in particular SHL resistance training, has proven effective in eliciting a multitude of desired adaptations such as:

increased strength (3, 23, 55, 62, 205), muscle and tendon hypertrophy (68, 154, 215, 235), changes in muscle architecture (1, 12, 37, 38, 40) and increases in tendon stiffness (13, 52, 68, 165, 166, 204, 215). However, even when prescribing the same exercise there are several acute programme variables that can influence adaptations. Two commonly manipulated acute programme variables are movement intensity, in the form of external loading, and speed of movement (23, 184). As both loading and movement speed are believed to influence MTU behaviour it is likely that manipulating these variables by even a small degree may alter the potency of the mechanical stimuli for adaptation (16, 17). However, load and speed are entirely independent variables and they may influence adaptation separately and differentially. (discussed below).

LOAD-SPEED RELATIONSHIP

The force-velocity relationship of muscle fibres can be expanded beyond the fibre level to that of the entire MTU in which case it is referred to as the load-speed relationship. This principle states that during concentric movement less force can be produced as joint speed increases (238). However, for the most part, the opposite holds true for eccentric contractions in that the faster the speed during an eccentric contraction the greater force that can be produced, although, this can be a point of debate as the benefits of increasing eccentric speed appear to reach a point of plateau or deflection (90).

However, in terms of resistance training arguably the greatest impact this load-speed relationship has on training is in the concentric domain. The reason for this is that most resistance training exercises have both an eccentric and concentric phase (SSC) and since less force can be developed concentrically this phase is the limiting factor in how much load can be successfully lifted. For this reason when a one repetition maximum (1RM) load is lifted the movement speed is usually relatively slow despite full effort by the lifter (238). In this scenario the eccentric phase is performed primarily to potentiate the concentric phase and to maintain positioning for a successful concentric lift (119). For these

reasons during high force scenarios it is believed that the tendon's role is to function as a transducer of force (212, 229). This concept has been put forward in modelling studies and isometric movements, but has yet to be observed during a SHL resistance training movement.

In contrast to SHL movements, during FLL ballistic movements such as vertical jumping, the person performing the jump now works further to the right on the load-speed relationship. In this scenario the role of the eccentric phase changes from that of a force transducer to that of a power amplifier (43, 88, 190, 229). Bobbert et al. (43) modelled the benefits to this MTU behaviour in a squat jump and others have found further evidence to support this concept *in vivo* (89, 90, 132, 133, 136). However, for the tendon to serve as an efficient power amplifier a great enough force needs to be exerted in the tendon to sufficiently stretch it (70, 190). It is likely for this reason that it has been observed that individuals with stiffer tendons perform worse at vertical jumping than those with more compliant tendons (163). However, to our knowledge this has not been observed after resistance training ended increases in tendon stiffness. Rather, resistance training, which has been shown to cause tendon stiffening, has also been shown to increase vertical jump height (7, 24, 164, 166). While it is possible that the increase in jump height comes in spite of an increase in tendon stiffness and instead from increases in muscle hypertrophy and other beneficial adaptations, another possibility is that tendon stiffening directly increases jump performance because a stiffer tendon stretched to the same length stores more energy and will then recoil at a greater speed (36). While this concept has not been explicitly examined as of yet, several studies have reported an increase in eccentric velocity after resistance training (62, 63, 66), and since an increased eccentric velocity would allow the muscles to produce greater forces and provide a greater downward momentum to be stored as elastic energy, there may be merit to this hypothesis.

SLOW-SPEED HIGH-LOAD TRAINING

As stated in the last section an exercise can only be executed at relatively slow speeds with a 1RM load. However, a variety of loads are often used to elicit different training specific adaptations in resistance training programmes. For example, loads between 75-80% of 1RM, which can be lifted 8-10 times, are often used so that a greater volume of repetitions can be performed (23). However, when lifting such loads it is not a prerequisite to perform the exercises as fast as possible, as doing so would result in the load being projected into the air. Rather, a movement speed that is less than the maximal speed, as dictated by the load-speed relationship, is utilised. For this reason SHL training is considered any training during which loads less than 1RM (but at least 60% of 1RM) are used and the load is not projected into the air, i.e. non-ballistic in the present thesis.

While SHL training is performed at submaximal speeds, the actual speed used can influence several important aspects of the movement and can result in different training adaptations (23, 184). It should be noted that distance the total amount of work done in a movement remains constant regardless of the speed at which it is lifted when lifting a given load a set (36, 244). However, it has been shown that the faster a load is lifted the greater is the peak ground reaction force during the movement (115, 244). In fact it has been shown that adaptations in rate of force development and several other variables are greater when a movement is performed at faster volitional speeds (31). In contrast to these findings, some practitioners recommend that their clients perform exercises at slower speeds to allow for greater control of the load. This is believed to allow their clients to focus on technique and thus reduce the likelihood of injury (184). Furthermore, performing an exercise at a slower speed can actually increase the metabolic demands and increase a muscle's time-under-tension which has been linked to greater increases in hypertrophy (101, 102, 224). However, it should be noted that using extremely slow speeds can also reduce the load that can be lifted and the number of repetitions a person can perform, thus it is possible that

such training can result in insufficient stimuli for certain adaptations. For these reasons exercises can be performed with slightly reduced speeds or at faster volitional speeds to elicit different training adaptations (31, 102, 244). However, more research is needed to understand exactly how manipulating speed influences MTU behaviour and tendon stress, strain and adaptations.

FAST-SPEED LIGHT-LOAD TRAINING

SHL, strength based training is not the only training modality commonly used to elicit preferential training adaptations. FLL power based training is also commonly performed for rehabilitation, personal training and athletic development (23). FLL training encompasses a variety of ballistic exercises, possibly the most common being the jump squat. During FLL movements, unlike SHL movements, exercises are performed at maximal speeds with the goal to project a load as fast as possible. Because of this varying the load will also influence the speed of movement (61, 238, 247). In sport it is rarely absolute speed or strength that dictates athletic success and instead is a combination of the two factors. Because of this a developing area of research is determination of then and training with loads at which optimal concentric power can be attained (25, 64, 75, 239). Power is the product of force and velocity. Movement velocity decreases with increasing loads, but the force produced increases, however power has a parabolic relationship with load and thus there is a load at which maximal power can be observed (64, 239, 247)). This load can differ between movements and individuals, but the majority of research has shown that optimal power in the squat jump usually occurs with loads around 30% of 1RM (239). However, while it has been shown that the force production during a jump squat can change as loading increases, no research has investigated how MTU behaviour changes along with this.

Training Specificity vs Specificity of Training Adaptations

Both SHL and FLL training are commonly prescribed training modalities, however they are often prescribed to elicit different performance adaptations (7, 23, 63, 113, 164). The principle of training specificity states that to increase performance at a given task the correct training stimulus has to be given to match the demands of that task. This principle is often taken further to recommend that similar movement patterns, forces and speeds should be used for training as is observed during the task (60). A classic example of this principle is that vertical jump training will increase vertical jump height. However, it has been observed that performance can be improved with training using 'non-specific' loads and movement speeds (24, 58, 63, 166, 231). For example, it has been shown that FLL training can increase isometric strength (231) and SHL training can increase vertical jump height (24, 58, 63, 164). In such cases seemingly non-specific movement patterns resulted in training specific adaptations that benefited performance across a variety of movements. This concept has been explored by several researches by having subjects train using isokinetic leg extensions at a particular velocity and then tested across a spectrum of velocities (83, 142). In these studies, the greatest increases in performance were observed at velocities similar to those used for training, however a crossover effect, where increases at non-specific velocities was also often observed.

Because of the variety of adaptations observed in these studies and the non-specific adaptations previously mentioned in regards to SHL and FLL training, it is apparent that performance is affected by underlying training specific adaptations, not simply by rehearsing movement patterns. In the cases of SHL and FLL training specific adaptations, it is very likely that both forms of training share some training specific adaptations, but as we have explored earlier in this review some key training specific muscular and tendinous adaptations can differ

between training modalities. These differences are likely due differing neuromuscular and musculotendinous demands between these modalities.

NEUROMUSCULAR DEMANDS OF TRAINING

As previously discussed, the recorded EMG signals, which are indicative to muscle activation, during a movement vary based on the movement's intensity. However, when discussing muscle activation during a movement it is important to understand two fundamental concepts: the all-or-none principle and size principle (180, 186). The former states that a motor unit (an alpha motor neuron and all of its associated muscle fibres) is either maximally activated or inactive, while the latter states that the lowest threshold motor units are activated first and as intensity increases higher threshold motor units are concurrently activated. This means when lesser forces are needed during a movement only parts of the muscle are activated, however, when greater forces are needed more muscle mass is activated. When comparing FLL and SHL movements during SHL movements greater forces can be produced and thus more muscle mass is activated. This is significant when the difference in low and high threshold motor units are further explored. Low threshold motor units are believed to be predominately made up of type-I muscles fibres and as recruitment increases fibre type changes to type-IIa and ultimately type-IIx muscle fibres (180). This distinction is important because type-II muscle fibres have proven to be more responsive to hypertrophy than type-I fibres and thus a greater stimulus for hypertrophy is present during SHL than FLL training (111).

However, several studies have reported muscle activation patterns that do not follow the pattern set forth by the size principle. The first study to find this behaviour was conducted by Nardone (191), who found that, the gastrocnemius (which is predominately, composed of type-II fibres) was active prior to the soleus (which is composed of type-I fibres) during high-speed plantarflexion in mice. While this was the first observation of selective motor unit recruitment it did suffer from two methodological limitations. First the gastrocnemius is a

biarticular muscle while the soleus is a monoarticular muscle and thus will be activated differently based on joint position of the knee (73, 103, 141), and second, no studies have shown that these two muscles share upstream afferent pathways. Since this publication, several studies have tried to replicate these results, with mixed results (57, 174); thus no consensus on this topic has yet been made. However, if selective recruitment does occur at high speeds, then type-II fibres may be selectively activated during FLL movements. Other differences may also exist in intramuscular motor unit synchronisation, firing frequency modulation and intermuscular coordination (186), however, it is beyond the scope of this review to address these topics as little is known about how these respond to different training stimuli and they will not be quantitatively measured in the research reported in the current thesis.

STIMULI FOR ADAPTATION

In addition to muscle activity, differences in metabolic demands and the stresses and strain in the muscle and tendon can also be sources of differing training-specific adaptations. The metabolic demands of a movement are largely determined by the amount of work (the product of force and displacement: (23)) performed during a movement and thus it is highly dependent on the volume of exercise i.e. the total number of repetitions performed or the volume-load lifted (156). However, as previously discussed, performing an exercise at a reduced speed can also increase the metabolic demands of the movement. However, when comparing SHL and FLL movements, comparisons in work are difficult as both the displacement and load can greater differ (61).

While the metabolic demands of a training session may constitute a potent stimulus for adaptation, when comparing two types of resistance exercises like SHL squat and FLL jump squats possibly the greatest stimuli for training specific adaptation is the direct mechanical stimulus of the exercise. Muscle and tendon cells are both believed to be highly responsive to mechanotransduction, i.e. a mechanical stimulus is directly responsible for chemical signalling (180). For

mechanotransduction to occur a cell can go through strain (i.e. pulled apart), compression (i.e. pushed together) or sheer (i.e. experiences multiple forces in opposing directions). While it has been observed that cells are responsive to mechanotransduction it also appears that the magnitude of force and the strain of the tissue may also be directly responsible for training specific adaptations (13, 16, 17). For example, chronic static stretching can increase resting muscle length by adding proteins in series, but at the same time no changes in cross-sectional area are observed (207, 226). In contrast, when a muscle is active at short muscle lengths proteins are added across the muscle belly increasing the cross-sectional area but not length (111). Because of these differences in muscle adaptation it is likely that MTU behaviour can influence the structural adaptations of a muscle. For example, if muscle strain decreases and tendon strain increases during a movement, as was observed during drop jumps of increasing intensity we may expect to see differential structural muscular adaptations. However, as of yet this hypothesis has not yet been substantiated.

Unfortunately, our current understanding of tendinous adaptation is much less than that of muscle. Tendons have reduced blood flow compared to muscle and thus are likely less affected by metabolic stimuli (180). Furthermore, changes in the properties of tendon have been observed in response to eccentric exercise (and SSC exercise) but are lacking or non-existent in concentric only exercise (104, 118). Furthermore, adaptations are believed to be greater in response to high magnitude and low frequency strain. By applying this information we suspect that an active muscle and high forces are needed to cause the active tendon strain necessary to provide a stimulus for adaptation. Thus, exercises, which demonstrate this type of MTU behaviour, are likely to be the optimal stimuli for tendon adaptations.

CONCLUSION AND IMPLICATIONS

MTU behaviour is highly movement specific and is likely to be influenced by the load and speed of movement. In addition, tendon strain is positively

influenced by the magnitude of force it encounters, but inversely influenced by the rate at which that force is expressed thought it and the speed at which it is lengthened. Furthermore, changes in MTU behaviour as loading or speed are varied are likely responsible for a plethora of underlying training-specific adaptations. However, because of the complex mechanical properties of tendon, inferences cannot be made of MTU behaviour during commonly used resistance training movements. It is thus imperative that an understanding of how manipulation of the acute programme variables such as load and speed influence MTU behaviour is developed. This information may be important in order to better understand training-specific adaptations. Such an understanding will increase our ability to prescribe movements that maximise adaptations in muscle and tendon.

Chapter 3

Experiment 1

**Knee angle-specific EMG
normalization: the use of polynomial
based EMG-angle relationships**

Abstract

Knee angle-specific EMG normalisation: the use of polynomial based EMG-angle relationships

The normalisation of EMG signals to those recorded during a maximal voluntary contraction provides a valid construct for comparisons of relative muscle activity. However, the length dependence of muscle activation and purported, substantial, muscle translocation and changes in muscle architecture during dynamic movements presents a need for joint angle-dependent normalisation processes. The purposes of the present study were to: 1) quantify variations in muscle activity across a large ROM, 2) determine the accuracy with which fitted EMG-joint angle curves accurately characterised these variations, and 3) compare peak (EMG_p) and average (EMG_a) EMG amplitudes obtained during a countermovement leg extension when normalised to both absolute peak and joint angle-specific muscle activity. Fifteen subjects performed a large ROM (110°) isokinetic ($30^\circ \cdot s^{-1}$) leg extension from which EMG-joint angle relationships were derived using polynomial fitting of different complexities. Ten subjects also performed loaded countermovement leg extensions from which EMG signals were normalised using peak muscle activity and EMG-angle curves. Ultrasonography revealed significant movement of the muscle in relation to the skin, as well as changes in fascicle angle, fascicle length and muscle thickness. EMG amplitude varied significantly over the ROM and the use of EMG-angle curves for signal normalisation resulted in significantly greater EMG-P and EMG-A than those normalised using the absolute peak EMG. Higher-order polynomial fitting better matched the filtered EMG amplitudes. Thus, there is a strong rationale for using EMG-angle polynomial fits to normalise EMG signals for large ROM movements.

INTRODUCTION

Surface electromyography (EMG) is often used to quantify the relative level of muscle activity during movement. Recorded EMG signals provide voltages that are reflective of the speed and number of depolarization waves between two electrodes (186). Whilst a vast number of variables have been calculated from EMG signals, two of those most commonly used in exercise and gait research are peak (EMG_p) and average (EMG_a) EMG (69, 107, 108, 152, 183). Treated EMG signals, whether by rectification and integration, root mean square (RMS) or more complex filtering processes that are expressed as voltages provide limited information to researchers. Such data cannot be used to make comparisons between subjects or with the same subject between testing sessions because variations in electrode position and tissue structure can influence the signal amplitude even if the level of muscle activation were constant (69). Thus, EMG signals are often normalised to the amplitude obtained during a reference contraction to allow such comparisons (10, 50, 51).

Maximal voluntary contractions (MVCs) are commonly used to obtain a reference amplitude because they then allow for signals to be expressed as a percentage of the assumed maximal muscle activity of the MVC (% MA); although sub-maximal isometric contractions performed at a predetermined force or torque have been found to be slightly more reliable than MVCs (150), such contractions do not allow an estimate of the level of muscle activation and are not sensitive to joint-specific changes in activation. If referenced values are not representative of maximal muscle activity under the specific movement conditions, such when as the movement being assessed is referenced to a contraction in which EMG activity is obtained at a different joint angle (or muscle length) the validity of such comparisons becomes questionable.

Muscle length, and therefore joint position, has been shown to influence EMG amplitudes (44, 107, 108, 152, 201, 203) however this relationship is complex and highly individualised (44, 151, 152, 201). Several factors are

believed to contribute to this variation in EMG voltages, including differences in the distance or orientation of the previously recorded motor units (85, 203), movement of the muscle in relation to the skin (85), changes in muscle pennation (84, 187) and changes in quantity of muscle or fat underneath the electrodes (85, 203). One method to counteract these issues is to determine the EMG-joint angle relationship and normalise EMG values according to maximal muscle activity at each represented joint angle (MA_{Angle}), although this is rarely done. This can be achieved by performing multiple isometric contractions at specific intervals across the entire ROM (28, 237, 245). Such a method is time consuming and can be influenced by either potentiation or fatigue affects (175). Another proposed method (151) uses an isokinetic contraction from which averaged RMS windows are calculated for each 10° interval. Both of these methods would significantly improve estimates of muscle activation, but have relatively weak resolution and can result in data shifts as values pass between the set intervals. Thus, there is currently a need for a valid, high resolution and easy-to-implement joint-derived normalisation procedure. The use of EMG-joint angle relationships obtained during slow isokinetic contractions may provide such a solution.

If EMG_p or EMG_a are to be calculated or a qualitative assessment of relative muscle activity over the ROM is performed, then collected signals should be normalised to a large ROM, MVC and reported as % MA_{Angle} (44, 107, 108, 152, 203). This need is increased when a large ROM is used or when peak muscle activation is expected to occur at different joint angles, as is the case when comparing different movements or when looking at the same movement with different intensities or external loads. Because of this, the purposes of the present study were to: 1) quantify muscle translocation and variations in both muscle architecture and muscle activity across a large range of motion, 2) determine if fitted joint EMG-angle curves accurately characterise variations in muscle activity across this ROM and, lastly 3) compare peak (EMG_p) and average (EMG_a) EMG during a dynamic leg extension between when signals are normalised to either absolute peak muscle activity across the entire ROM

(MA_{Peak}) or joint angle-specific maximal muscle activity (MA_{Angle}) from an isokinetic reference contraction. It was hypothesised that: 1) muscle activity would differ significantly across the ROM, 2) fitted EMG-joint angle curves would closely match the filtered signal when determined using higher order polynomials (>2nd order) and 3) during a countermovement knee extension, EMG_p and EMG_a values calculated by normalising MA_{Peak} would be significantly different than MA_{Angle}.

METHODOLOGY

SUBJECTS

Fifteen healthy, physically active men (n=8) and women (n=7) (age: 26.0 ± 3.1 yrs, height: 174.7 ± 6.4 cm, mass: 75.3 ± 9.8 kg) participated in this study after signing an informed consent document. Subjects were excluded from the study if they had a history of lower body musculoskeletal injuries. The study was reviewed and approved by the Human Research Ethics Committee of the University.

EXPERIMENTAL DESIGN

All subjects were familiarised to the procedures prior to testing. To determine each subject's EMG-angle relationship, surface EMG was recorded from vastus lateralis (VL), vastus medialis (VM) and rectus femoris (RF) simultaneously with joint angle data during two isokinetic (30°·s⁻¹) unilateral leg extensions. Each leg extension repetition was performed at maximal intensity through a full ROM (115-0°) with the subjects' self reported dominant leg. From the contraction with the greatest peak torque, the EMG-angle relationship was determined using polynomial functions of orders 1 – 4 [Linear (Lin), and 2nd (2P), 3rd (3P) and 4th (4P) order, respectively] (Figure 7).

VL, VM and RF EMG were recorded synchronously with joint angle data. Signals were filtered and smoothed (see EMG-Angle Relationship) and then

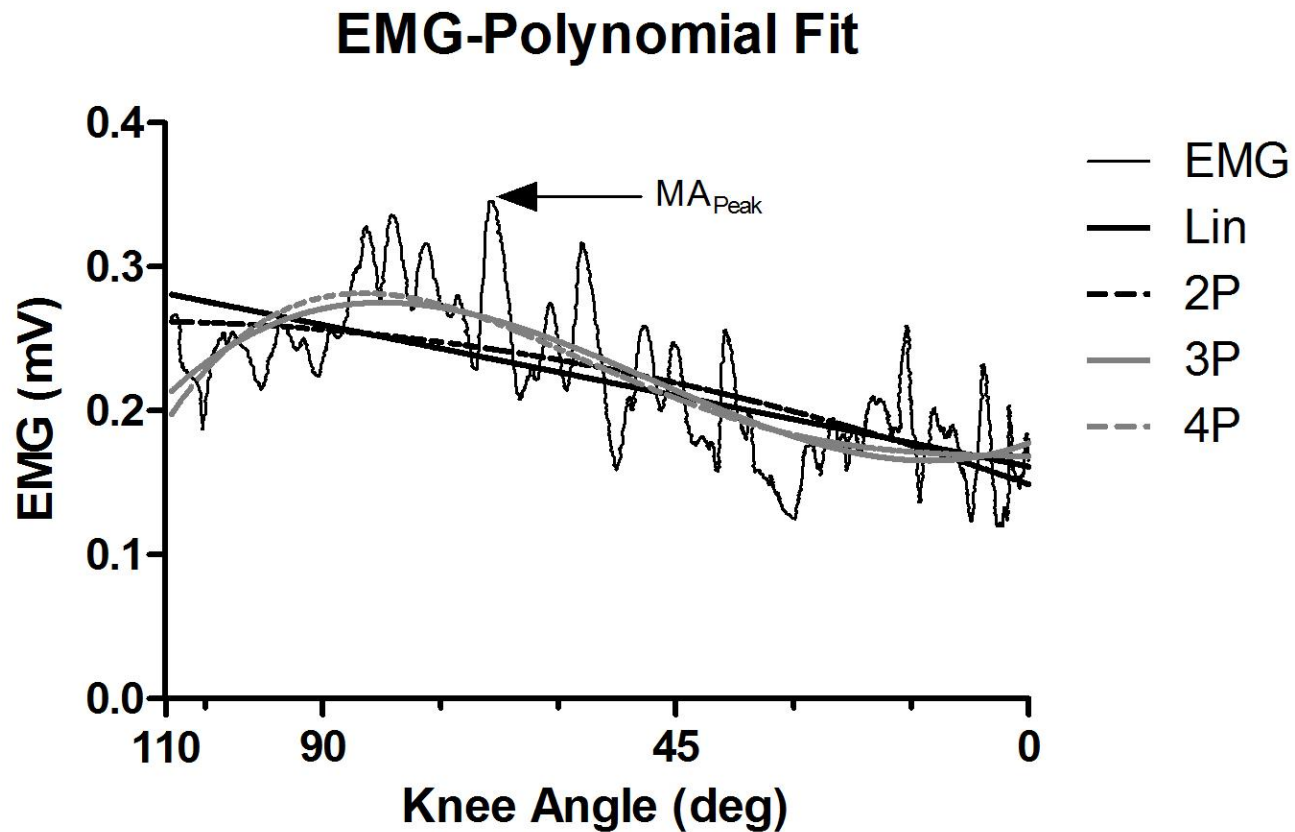


Figure 7: Example of polynomial fits of different orders [linear (Lin), 2nd (2P), 3rd (3P) or 4th (4P)] to determine the EMG-joint angle relationship of the vastus lateralis during an isokinetic (30°s⁻¹) knee extension. The mean square error between the recorded EMG signals (EMG), after being passed through a linear envelope, and the polynomial fits are: Lin: 1.348×10^{-3} , 2P: 1.290×10^{-3} , 3P: 1.008×10^{-3} , 4P: 0.981×10^{-3} . The arrow indicates the location of maximal muscle activation, which is later, used for normalisation procedures.

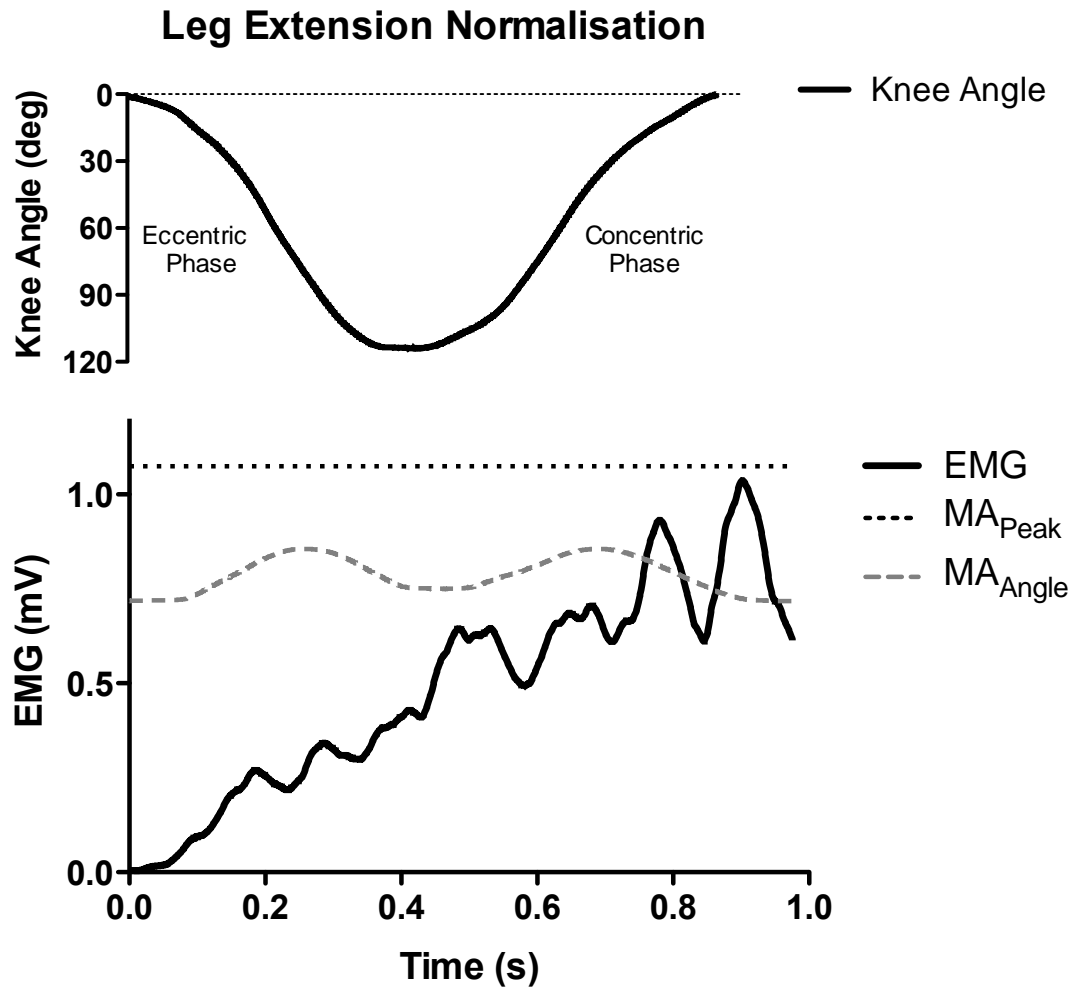


Figure 8: The process of normalisation of EMG signals obtained during a countermovement leg extension. Knee angle and filtered EMG signals (EMG) of the vastus lateralis obtained are shown along with reference values obtained during an isokinetic leg extension. Isokinetic maximal muscle activity (MA_{Peak}) over the entire range of motion and joint angle-relative muscle activity (MA_{Angle}) obtained using a 3rd order polynomial fit are shown.

Peak vs Knee Angle Normalisation

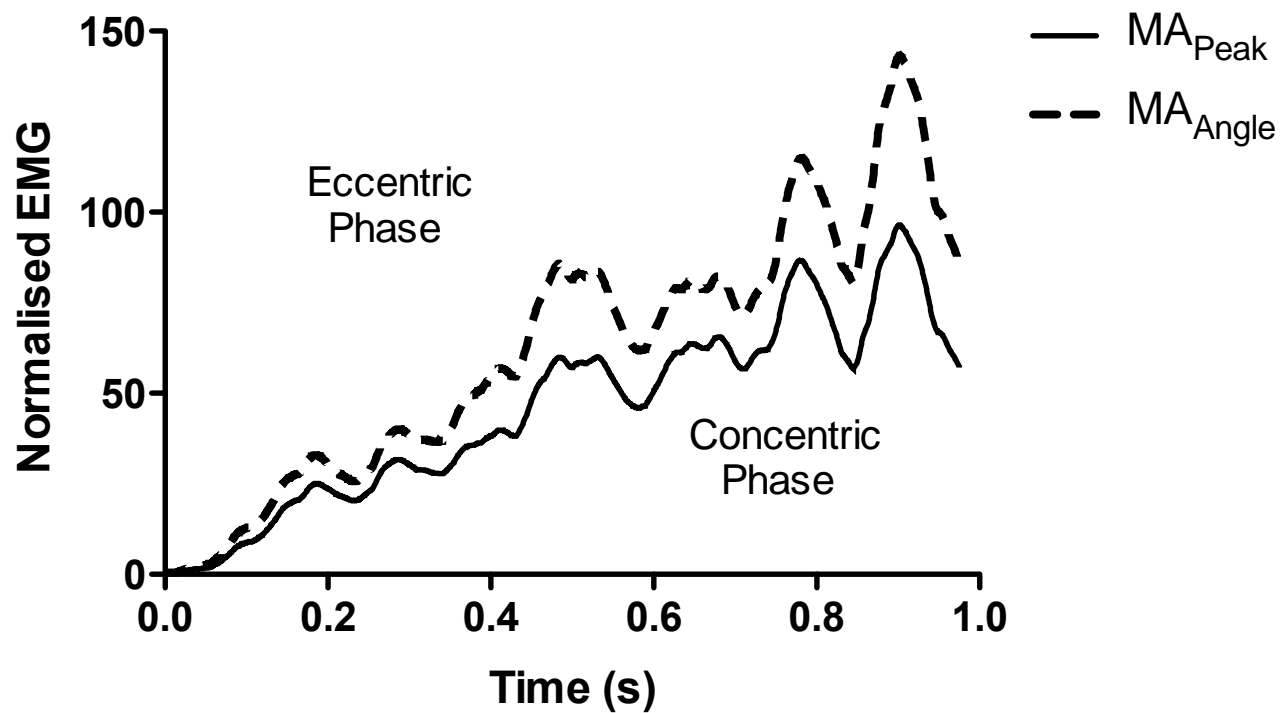


Figure 9: Vastus lateralis EMG amplitudes from a countermovement leg extension when normalised to either the absolute maximal muscle activation (MA_{Peak}) or joint angle relative (MA_{Angle}) values obtained from a referenced isokinetic contraction.

normalised (see EMG Normalisation) to values obtained during the previously performed isokinetic contraction, which allowed the signals to be reported as a percentage of MA (Figure 8). Normalisation was performed using both knee angle independent (maximal filtered EMG value) and angle relative (Lin, 2P, 3P and 4P) processes and this allowed for values to be reported as either % MA_{Peak} or % MA_{Angle}, respectively (Figure 9). EMG_p and EMG_a were then compared between the different normalisation procedures.

ISOKINETIC REFERENCE CONTRACTION

Before the testing, subjects performed a standardised warm-up consisting of five minutes of low intensity (1.5 kP, 60 rpm) stationary cycling as well as two isokinetic leg extensions at 50% and 80% of perceived maximal intensity. Subjects were then seated and strapped into an isokinetic dynamometer (Biodex 3, Biodex Medical System, USA) and performed two maximal isokinetic knee extensions through a 115° ROM at an angular velocity of 30°·s⁻¹. Each trial began by subjects producing a ramped (3 s) isometric contraction to maximum whilst in the starting position (115° flexion) before the lever arm of the dynamometer was allowed to move. Thus, a maximum level of muscle activation was obtained prior to commencement of the isokinetic movement. During subsequent analysis, data from the initial 5° were discarded in order to eliminate the period of isometric-to-concentric transition, which can contain variable EMG signals due to sudden change in joint acceleration. The angular velocity of the isokinetic leg extensions was chosen as pilot testing showed that this speed resulted in consistent force-angle relationships between trials with minimal data removal at the isometric-to-concentric transition point.

EMG-ANGLE RELATIONSHIP

Surface EMG signals were collected from each subject's dominant leg for the VL (67% of the distance between the anterior superior iliac spine (ASIS) and the patella), VM (80% of the distance between the ASIS and the patella) and RF (50% of the distance between the ASIS and the patella) as per SENIAM

guidelines (121). Two self-adhesive surface electrodes (Meditrace, Tyco Healthcare, Australia) with a 0.5 cm diameter were placed in a bipolar configuration. Inter-electrode distance was set at 2 cm and all signals were checked to ensure interelectrode impedance was $< 5 \text{ k}\Omega$. Raw EMG signals were recorded using a wireless EMG system (ZeroWire, Aurion, Milan Italy) at an analogue-to-digital conversion rate of 2000 Hz at 16 bit resolution after being amplified (1000x). Recorded signals were filtered using a dual-pass, sixth-order, 10-500 Hz band-pass Butterworth filter and full-wave rectified, then a linear envelope was created using a low-pass, fourth-order Butterworth filter with a cut-off frequency of 6 Hz (61). The 10-500 Hz band-pass filter was chosen to allow only recorded signals at physiologically relevant frequencies to be preserved for analysis while the 6 Hz linear envelope was deemed an appropriate method to smooth EMG data but retain enough sampling resolution as determined by the Nyquist Sampling Theorem.

Knee joint angle data were recorded using an electronic goniometer (MLTS700, AD Instruments USA) at a sampling rate of 1000 Hz simultaneously with the EMG data (LabChart 7.2 AD Instruments, USA). Joint angle data were filtered using a low-pass, 3rd order Butterworth filter with a cut-off frequency of 5 Hz, which was an appropriate rate by a residual analysis. All signal manipulation and analysis was performed using a custom LabView program (Labview 8.2, National Instruments, Texas USA). Filtered EMG values at four joint positions (110, 90, 45 and 0° leg flexion) were compared to examine differences across the ROM.

The EMG-angle relationship for each muscle was determined using polynomial curve fitting procedures of orders 1 – 4 (Lin, 2P, 3P and 4P) for data obtained between 110 and 0° knee flexion using a custom LabView program (Figure 10). In order to determine the characteristics of the polynomial fits in relation to the raw filtered signal of the reference contraction, the mean square error (MSE) of the fitted curve and the relative range $[(\text{maximum} - \text{minimum}) / \text{maximal value} \times 100]$ of the signals were compared between polynomial fits.

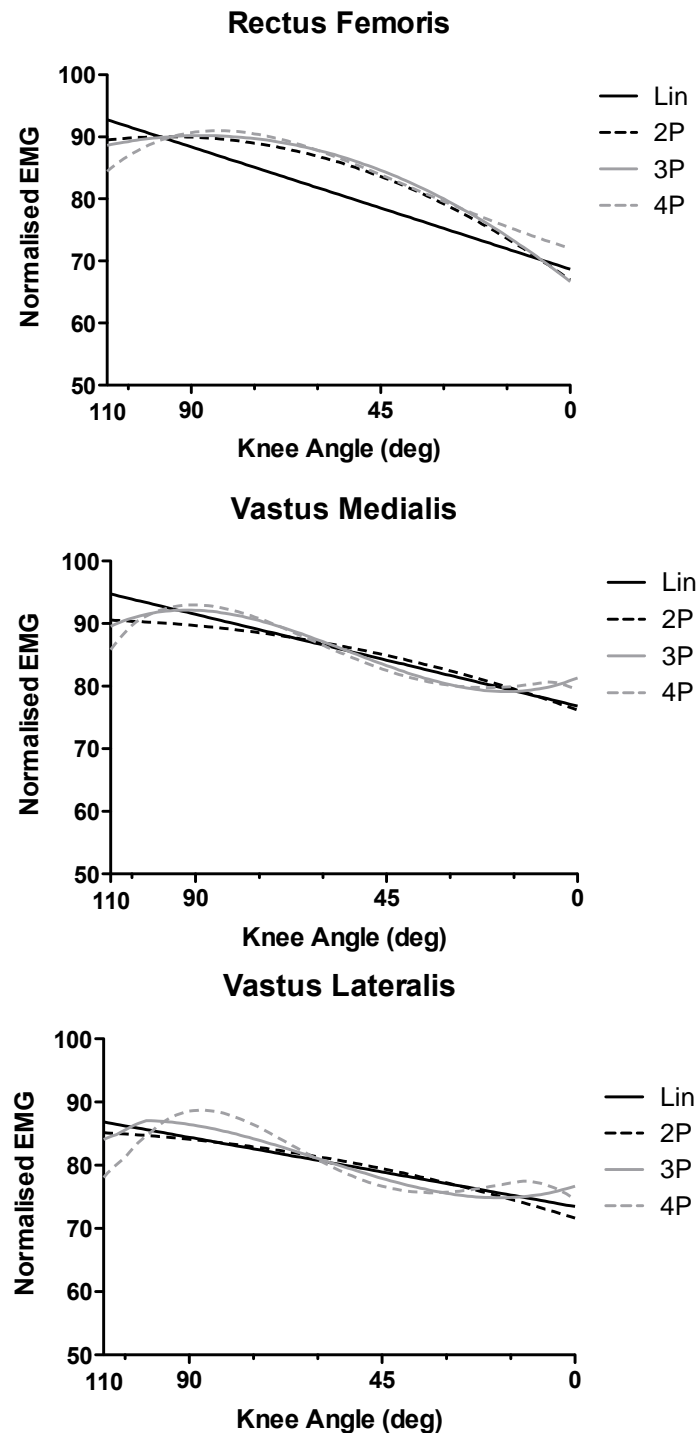


Figure 10: Average ($n=15$) muscle-specific EMG-joint angle relationships from polynomial fits of different complexities: Linear (Lin) 2nd (2P) 3rd (3P) or (4th) order. Values are reported as a percentage of peak muscle activation within the contraction using the 3P method.

ISOINERTIAL KNEE EXTENSIONS

Ten subjects subsequently took part in isoinertial knee extension testing after performing the isokinetic contractions. Subjects allocated to do the isoinertial testing had their one-repetition maximum (1RM) determined between 3-7 days prior to any other testing. Testing was done in a custom modified plate loaded leg extension machine (Figure 11). For each repetition the subject started with their leg fully extended and unloaded. Then, upon instruction, the load was released onto the subject's leg and immediately the subject performed an eccentric-concentric leg extension with the goal of projecting the load into a catching mechanism at the end of the movement. The countermovement was performed at a self-selected speed. Each subject performed three leg extensions at five different loads (20, 40, 60, 80 and 90% of 1RM) and the leg extension at each load with the highest concentric velocity was then further analysed. During each extension EMG, knee-angle and ultrasound images were recorded.

EMG NORMALISATION PROCEDURES

EMG signals collected during isoinertial leg extensions were normalised to values obtained during the isokinetic contraction. Signals were normalised two ways; 1) to the absolute peak EMG value or 2) to the instantaneous joint position-specific EMG amplitude using the predetermined EMG-angle relationships. Normalisation to the absolute peak was performed by dividing each EMG data point collected during the isoinertial leg extension by the greatest filtered EMG value from the reference contraction prior to polynomial fitting. This normalisation allowed for EMG signals from the isoinertial leg extension to be reported as a percentage of the peak activation from the entire isokinetic leg extension (MA_{Peak}).

EMG from the isoinertial leg extensions were also normalised based on the EMG-angle relationship that was determined during the isokinetic leg

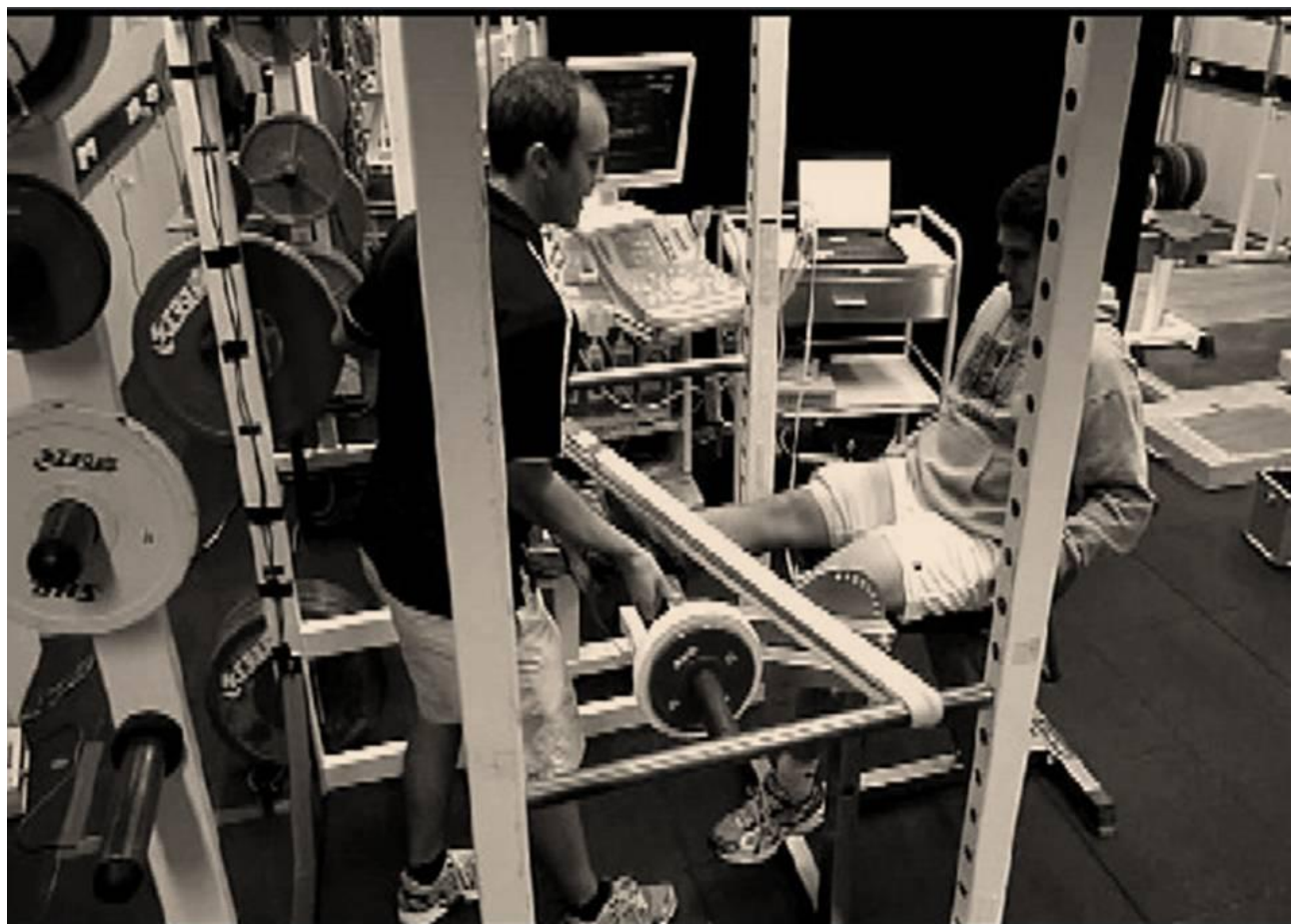


Figure 11: Experimental set-up of isoinertial countermovement knee extensions using a modified plate loaded machine.

extension. The four previously calculated joint EMG-angle polynomials (Lin, 2P, 3p and 4P) from the isokinetic reference contraction, were used by matching instantaneously recorded joint position to the relative EMG at that concurrent joint position (MA_{Angle}). This was done by using interpolation of the two signals (Figure 10). Lastly, the recorded EMG signals at each instantaneous joint position were divided by the joint relative muscle activation from the interpolated signal. This procedure allowed for calculation of the relative muscle activation throughout the movement by taking into account differences in muscle activity that arose across the ROM. For each normalised signal, EMG_p was taken as the highest value reported and EMG_a was determined from the start of the countermovement (the leg flexed 2° from starting position) until the leg extended to within 2° of full extension.

ULTRASONOGRAPHY

During isoinertial knee extensions, B-mode ultrasonography (Alpha 10, Aloka, Co., Ltd., Tokyo, Japan) was used to determine movement of the muscle in relation to the skin as well as changes in muscle fascicle length and fascicle (pennation) angle. A flat 6 cm T-head transducer (UST 5713, Aloka, Co., Ltd., Tokyo, Japan) with a 10 MHz sampling array was used to collect images at 104 images per second. The transducer was placed half way between the greater trochanter and the lateral condyle of the femur and aligned with the fibres of VL so that a single fascicle could be tracked throughout the entire range of motion of the knee. A thin echo-absorbent reference strip was fixed to the subject to correct for any probe movement that occurred during testing. The transducer head was fixed to the subject using a custom-made thermoplastic cast and taped into place. Recorded ultrasound images were analysed using DartFish (Prosuite 5.0, DartFish, Sydney, Australia). Movement of the muscle in relation to the skin was defined as the summed movement of both the superficial and deep aponeurosis. Fascicle length was determined by tracking the length of an individual fascicle from the deep aponeurosis to its insertion onto the superficial aponeurosis. Muscle thickness was defined as the distance between the deep

and superficial aponeurosis. In positions where the entire fascicle was not visible within a given frame, the fascicle and aponeurosis was extrapolated to their intersect point (37).

STATISTICAL ANALYSIS

Primary comparisons were made to determine whether EMG signals varied across the ROM during an isokinetic leg extension, as well as whether fitted polynomials accurately represented the joint specific muscle activity. For this purpose, repeated measures MANOVAs with Bonferroni *post hoc* tests were used to determine differences in muscle specific muscle activity at four distinct joint angles as well as differences in the MSE and relative range between data sets normalised to polynomials of different orders. To determine the effect of the normalisation method on EMG-P and EMG-A measured during the isoinertial leg extension a second repeated measures MANOVA with Bonferroni *post hoc* tests was used. Results are presented as mean \pm SD unless otherwise stated. All statistical analyses were conducted using PASW 18.0.1 (IBM, New York, USA) and statistical significance was accepted at an α level of $p < 0.05$.

RESULTS

Muscle activity varied across the ROM for all three muscles examined. Across the four joint angles of interest (110°, 90°, 45° and 0°) there were significant differences in the filtered EMG values (Figure 12). The relationship between joint angle and muscle activity was non-linear, with the highest filtered EMG amplitude recorded at 90° flexion and the lowest recorded at full extension (0°). EMG relative ranges (i.e. difference between the peak and minimum EMG amplitudes divided by the peak value \times 100) across these four positions were 24.5%, 17.2% and 9.7% for RF, VM and VL, respectively, which shows a substantial change across the ROM (Figure 10).

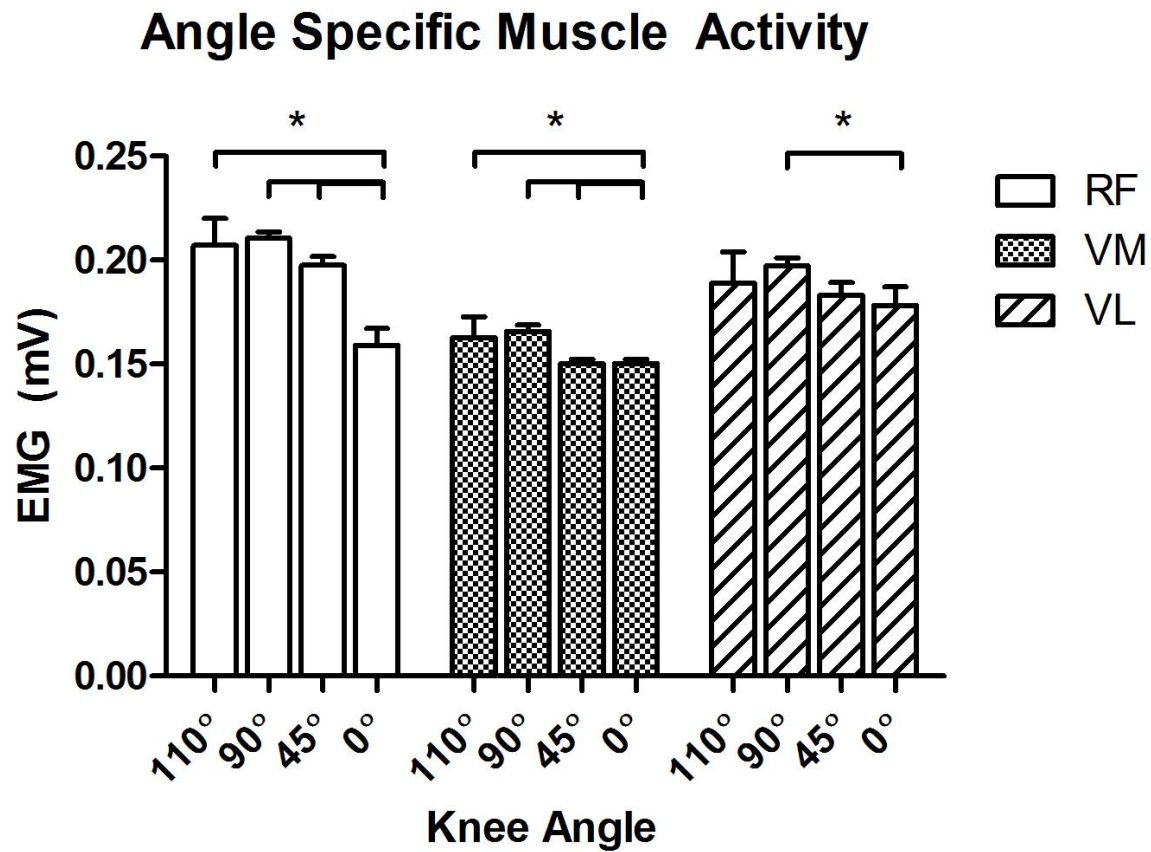


Figure 12: Muscle activity as expressed by filtered surface EMG (mV) of the rectus femoris (RF), vastus medialis (VM) and vastus lateralis (VL) at: (a) 110° (b), 90° (c), 45° (d) and 0° knee flexion. Mean values (\pm SD) and significant differences between angles are reported ($p < 0.05$).

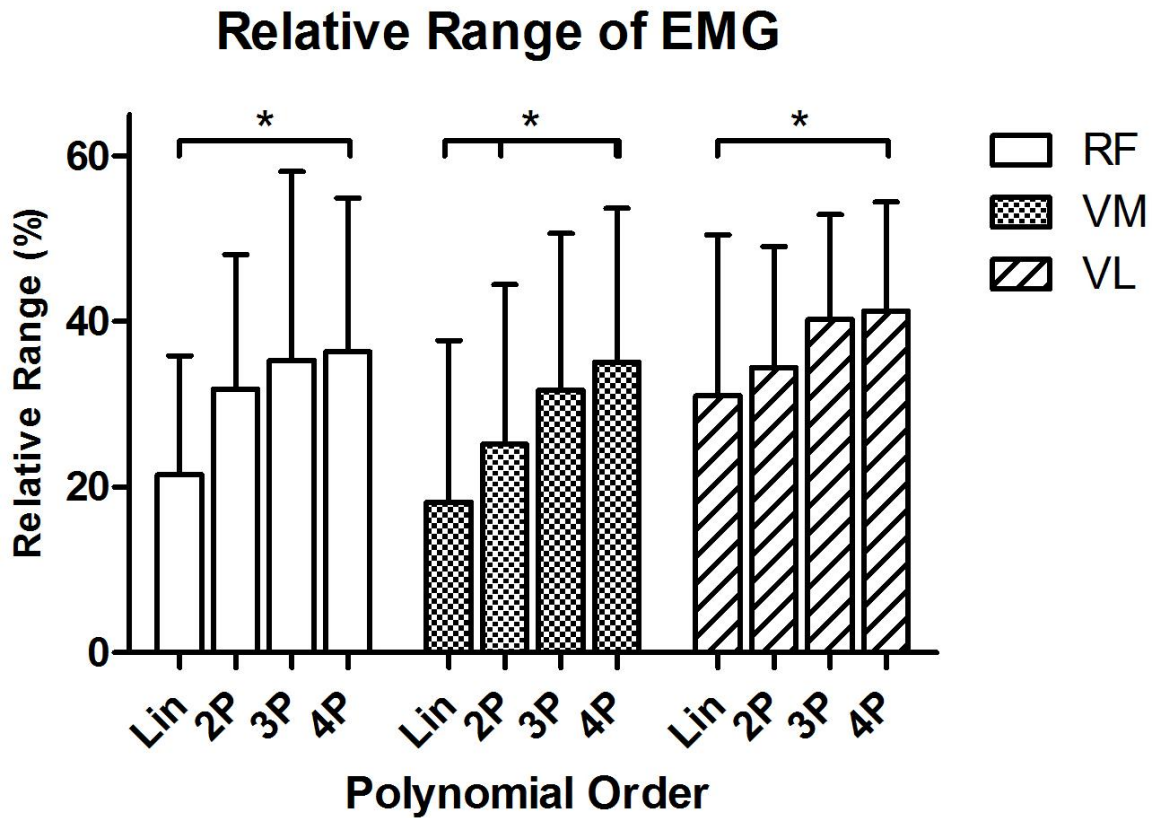


Figure 13: Relative range (range / maximum $\times 100$) of EMG signals obtained from a large range of motion (110°) isokinetic leg extension. Values given are for the rectus femoris (RF), vastus medialis (VM) and vastus lateralis (VL) with the signal normalised using fitted polynomials of different complexities. Mean normalised EMG (\pm SD) are shown for linear (Lin), 2nd (2P), 3rd (3P) and 4th (4P) order polynomials. * Indicates a significant difference from Lin and # indicates significant difference from 2P ($p < 0.05$).

During the isokinetic contractions, when polynomial curves were fitted to determine the EMG-angle relationship for each muscle, the EMG relative range was seen to increase as the polynomial order increased (Lin < 2P < 3P < 4P; Figure 13). For RF (21.5, 31.8, 35.3, and 36.3%) and VL (31.0, 34.4, 40.2 and 41.2%) the mean relative range across the ROM was statistically different between Lin and 4P, but there were no significant differences between 2P, 3P and 4P. However, the relative range for VM (18.2, 25.2, 31.7 and 35.1%) was significantly different between Lin and 4P and between 2P and 4P.

As higher order polynomial fits were used to determine EMG-angle relationships, the mean square error (MSE) of the curve (relative to the actual filtered signal) decreased (Figure 14). Thus, the higher order polynomial fits provided a better representation of the filtered EMG signal over the entire ROM. However, while there was a significant effect of polynomial order on the MSE there were no significant differences between 3P and 4P.

For the isoinertial leg extensions, analysis of ultrasound images showed an 8.50 ± 3.25 cm average movement of the aponeurosis-fascicle intersection point (i.e. the muscle) in relation to the skin. In addition the changes in muscle fascicle length, fascicle angle and thickness were 9.65 ± 3.47 cm $10.4 \pm 2.9^\circ$ and 0.54 ± 0.24 cm respectively over the entire ROM.

EMG_p and EMG_a were significantly influenced by the method used for normalisation (Figure 15). Normalising the EMG collected during the isoinertial leg extension to values obtained from the EMG-angle relationships (MA_{Angle}), regardless of the order of polynomial, resulted in significantly greater EMG_p and EMG_a values than when normalised to the absolute peak value (MA_{Peak}). When normalised to the maximum value obtained at a specific joint position, significant differences were found when using different polynomial fittings (Figure 15).

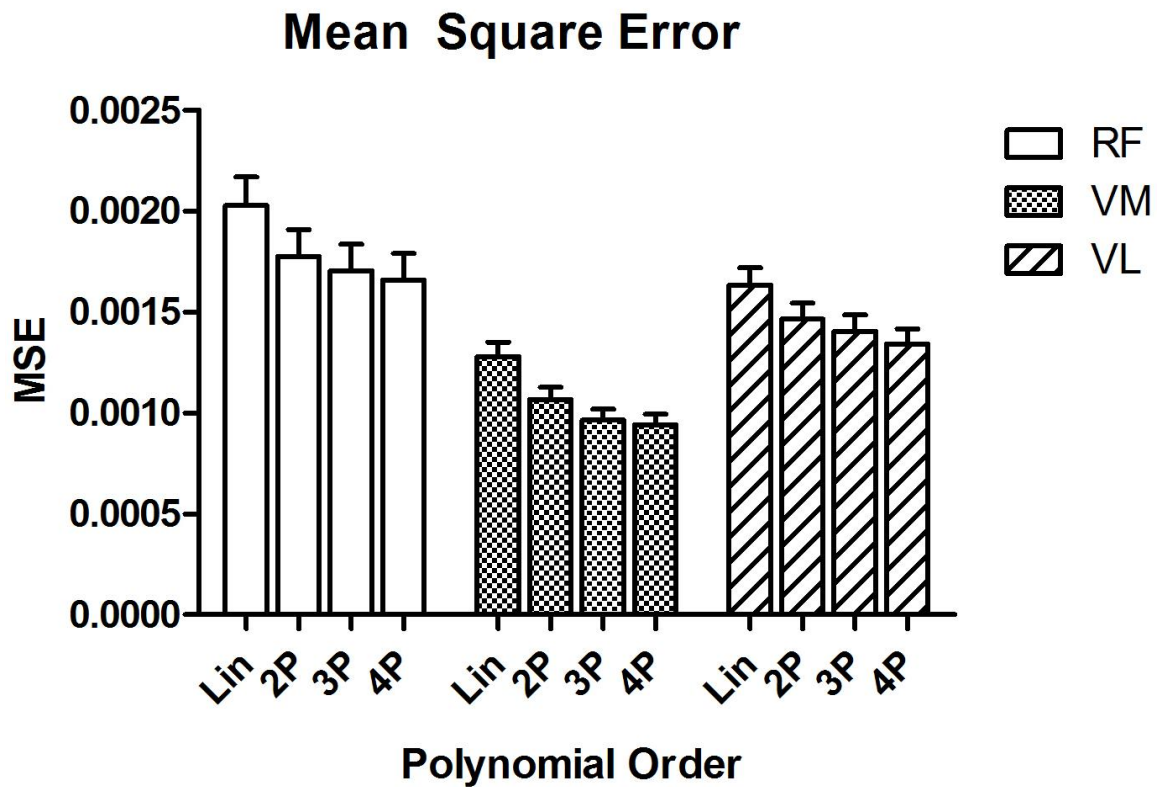


Figure 14: Mean square errors (MSE) for linear (Lin) and 2nd (2P), 3rd (3P) and 4th (4P) order polynomial fits to the filtered EMG signal. Values were collected during a large range of motion (110°) isokinetic leg extension. Means (\pm SD) for the rectus femoris (RF), vastus medialis (VM) and vastus lateralis (VL) are shown.

DISCUSSION

The major finding of the present study was that significantly different EMG_p and EMG_a values were found when signals were normalised using EMG-angle curves compared to the more conventional absolute peak EMG value. In addition, during a large ROM knee extension, maximal volitional muscle activity varied over the ROM and polynomial fits were able to provide accurate representation of the variance in the EMG, as depicted by the low MSE. These muscle activity variations would partly have resulted from significant muscle translocation (~8.5 cm) and changes in fascicle pennation (~10.5°), fascicle length (~9.7 cm) and muscle thickness (~0.5 cm). These findings support the efficacy of using joint angle-relative normalisation processes.

Results from the current study support those of Kellis & Baltzopoulos (148, 151) and Pincivero et al. (201) who found that the EMG-angle relationships for RF, VM and VL followed a bell-like pattern with peak values occurring between 60-90° knee flexion. Kellis & Baltzopoulos (148) determined the EMG-angle relationship by calculating the average EMG amplitude in 10° windows and then matching phases of the normalised contraction into these angle specific intervals. Such a method is a vast improvement upon non-joint relative normalisation procedures, however the use of angle-derived intervals can result in shifts in the normalised values when joint angle passes from one window to the next. Such a shift could interfere with signal interpretation if time sensitive EMG measurements are needed. When normalising to the predicted peak EMG amplitude derived from polynomial fits of the EMG-angle relationship, there is no shift in the reference values, thus it is more appropriate when calculating time-sensitive measurements. A major strength of the current methodology is that complex normalisation can be done by performing only a few isokinetic contractions, prior to the trial that is to be normalised. This is in contrast to previous knee angle normalisation methods that require multiple isometric contractions across an array of joint angles, which could result in a potentiation or fatigue effect and also requires a much longer testing duration (176).

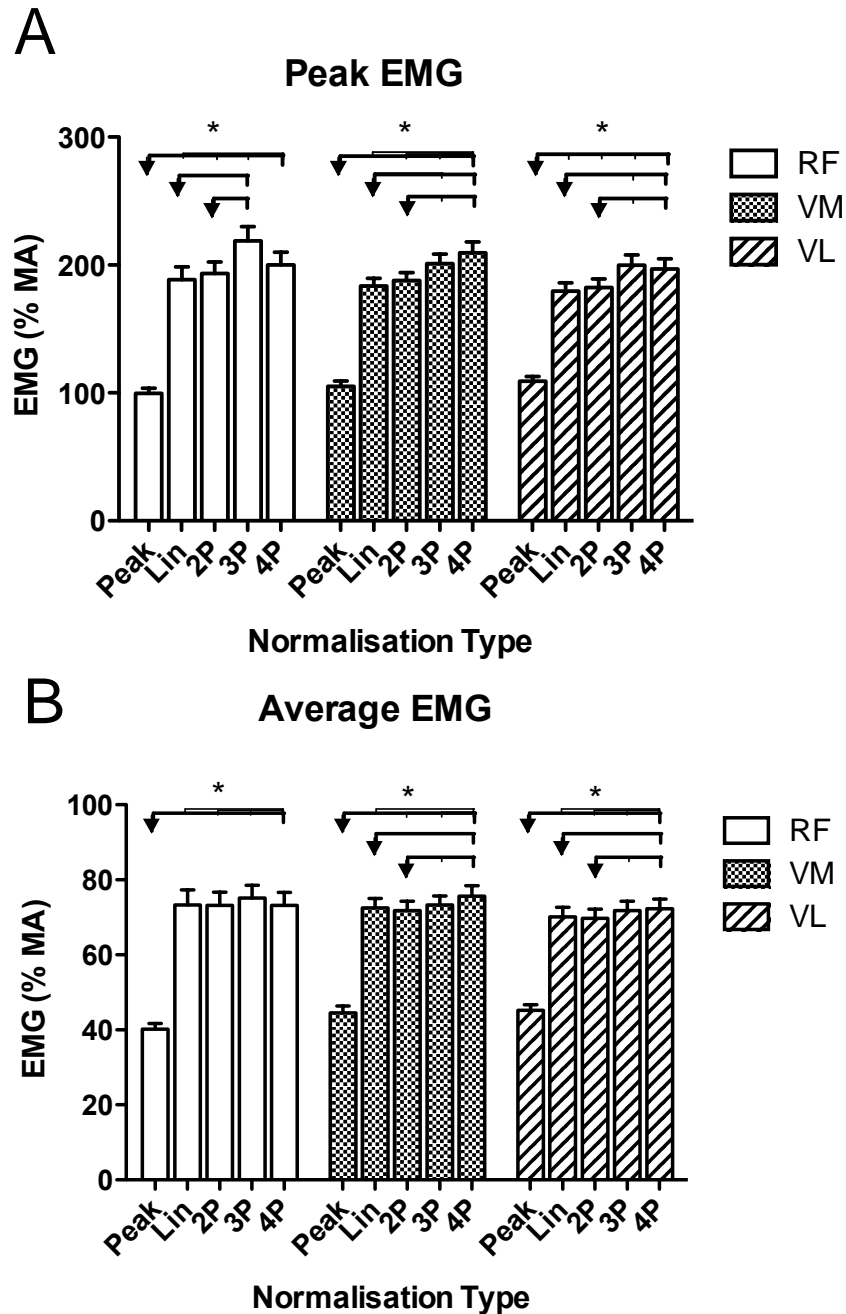


Figure 15: The influence of normalisation method on peak (A) and average (B) EMG amplitude for rectus femoris (RF), vastus medialis (VM) and vastus lateralis (VL). Signals were normalised using either absolute or joint-angle relative methods and presented as a percentage of maximal activity (% MA); using either the absolute peak EMG signal the entire range of motion (Peak), or linear (Lin), 2nd (2P), 3rd (3P) or 4th (4P) order polynomial fitted EMG-joint angle curves. Means and standard errors are shown, significant differences from each normalisation method are marked ($p < 0.05$).

As expected, joint angle-dependent normalisation processes resulted in greater EMG values than those obtained by normalising to the absolute peak. This is because EMG signals collected at joint angles other than the angle at which peak activation occurred were normalised to a smaller reference value. The isoinertial leg extensions were performed with a countermovement and at maximal volitional velocity ($300\text{-}400^\circ\text{s}^{-1}$), which most likely contributed to the high EMG_p and EMG_a values. Pilot data, which investigated the influence of velocity of movement on EMG using six subjects, showed that the EMG-angle relationship remains fairly consistent as velocity changes, but the amplitude of the EMG increases (Figure 16). It is often recommended that referenced contractions be performed at velocities similar to the normalised contractions to avoid this inflation. However, issues around reliability and the impact of elastic recoil on muscle length the EMG-angle relationship may discredit the use of high velocity isokinetic reference contractions, therefore more research is needed to explore this potential.

EMG estimates of muscle activity are influenced by changes in the position of the muscle in relation to the skin. This results in different motor units being recorded because of muscle translocation (85), changes in the directionality of the depolarization waves due to changes in muscle pennation (187) and changes in the amount of muscle tissue from the collection site (203). Ultrasound images of the VL were recorded during all isoinertial leg extensions, to determine if these changes occurred in the present experiment. We found that there was significant movement of the muscle in relation to the skin ($\sim 8.5\text{ cm}$) as well as changes in muscle fascicle angle (pennation; $\sim 10.4^\circ$), fascicle length ($\sim 9.7\text{ cm}$) and muscle thickness ($\sim 0.5\text{ cm}$). These data indicate that substantial changes in muscle fascicle angle and length, and location of the muscle in relation to the skin, can occur during a large ROM knee extension and support the hypothesis that structural changes in the muscle can influence the amplitude of EMG signals during movement (84).

Influence of Velocity on EMG

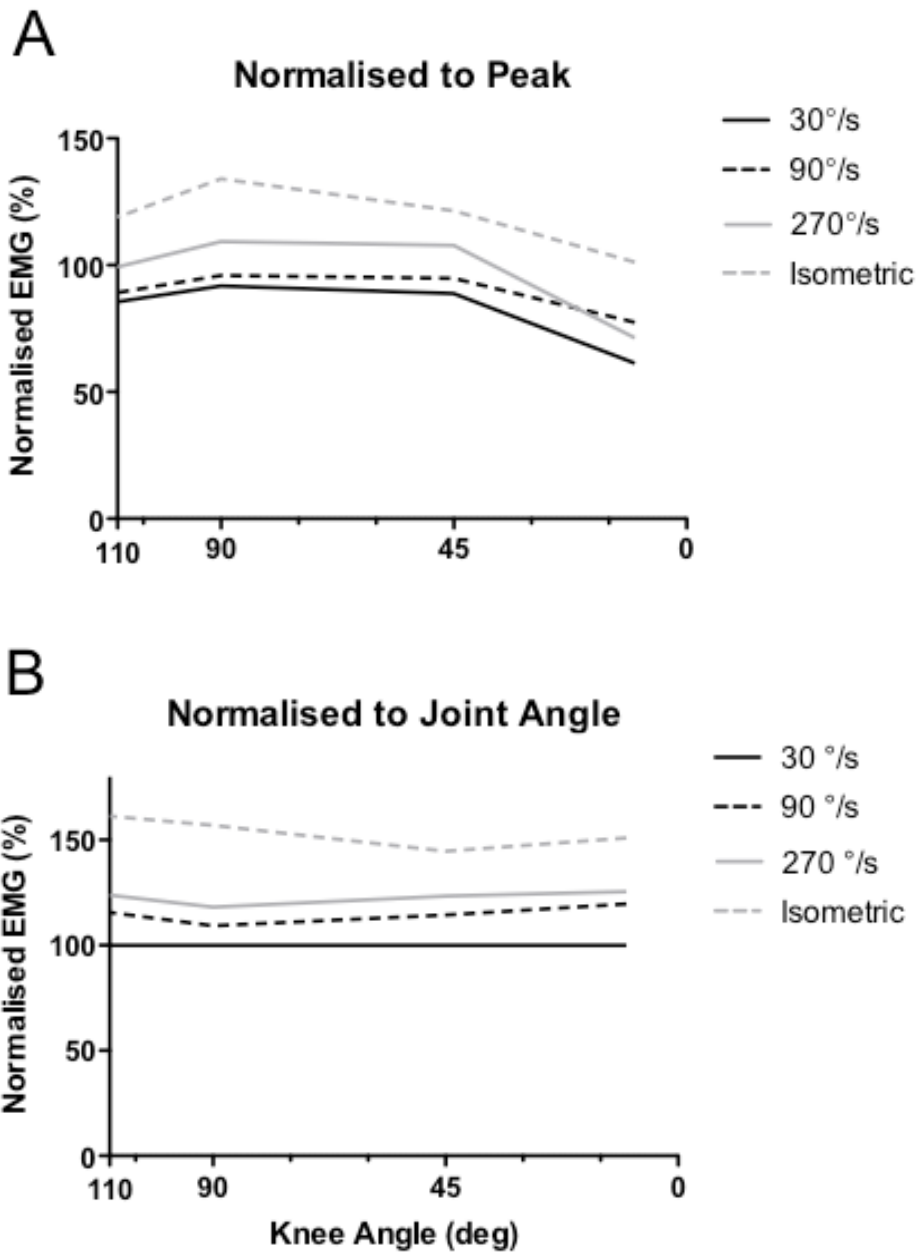


Figure 16: The influence of movement velocity on joint specific muscle activity of the vastus lateralis during isometric and isokinetic knee extensions at 30°s⁻¹, 90°s⁻¹ and 270°s⁻¹. Mean EMG values at 6 joint positions (110°, 90°, 45° and 10° knee flexion) for six subjects are shown and reported as a percentage of peak muscle activity at 30°s⁻¹ (A) and muscle activity at 30°s⁻¹ at each respective joint angle (B).

Unlike EMG-force and EMG-velocity relationships, which are in large part uniform across subjects (69), the EMG-angle relationship can be both highly variable and subject specific (148, 151, 201). The smallest observed relative ranges (range / maximal value \times 100) from the EMG-angle relationship were 15% (VL), 11% (RF) and 12% (VM), and the largest were 59% (VL), 67% (RF) and 61% (VM). This observation of subject and muscle specificity is a unique observation of the current study. While the underlying cause of this variance is unknown it is possible that the large variance may have several causes. Two possible explanations are that: 1) some subjects experience much greater muscular inhibition at short muscle lengths, this is supported by the finding that the fascicle length of the VL went through \sim 9.7 cm of movement. 2) Translocation of probes in relation to the muscle likely results in different motor units being sampled at different joint positions, this is supported by the \sim 8.5 cm of translocation observed in the VL. It is possible that this translocation results in more Type II fibers being recorded in some individuals as the knee extends but more Type I fibers being recorded in others. Whatever the underlying cause, these findings suggest that it is impractical to use a global correction factor to take into account relative muscle activation at different joint positions and that individual normalisation is necessary. Because of this, the calculated equations for joint angle normalisation are not reported here.

Polynomial fits of greater complexity better represented the recorded EMG signal. The differences between the different curve fits were more evident at the extremes of the ROM (110 and 0° knee flexion). However, there was no significant difference between either the MSE or the relative range between 3P and 4P curves. Thus, we propose that at least a 3P should be used when normalising EMG. The use of more complex curves than those studied is not recommended because the curves vulnerability to the commonly observed fluctuations in muscle force and activation during an isokinetic contraction increases as the complexity of the curves increases.

One drawback to using the curve fitting method is that large spikes or drop offs in EMG activity, such as those that can occur due to stretch reflexes at the beginning of a contraction or when the contraction mode (i.e. isometric eccentric or concentric) changes rapidly, can result in a large change in the shape of the curve. Because of this we consider it important to exclude data at the beginning of the reference contraction that could be influenced by the initiation of the concentric contraction. From pilot research it was determined that a 5° buffer (which lasted 0.17 s) was sufficient to exclude any confounding neurological events such as stretch reflexes. However this buffer may have to increase if a faster isokinetic velocity is used. Additionally, it is important that the useable ROM of the reference contraction is greater than the ROM of the movement to be normalised when using an interpolated normalisation methodology, otherwise errors will occur due to the limits of polynomial algorithms.

In conclusion, EMG amplitude varied significantly across the ROM during knee extension, but this variation appeared to be subject specific. Using joint angle-dependant normalisation results in significantly different values than normalising to the peak value obtained in a reference contraction. These data support the need for taking joint angle into account when reporting EMP-P or EMG-A in large ROM movements or in movements where EMP-P is believed to occur at different joint positions (i.e. in different movements or in the same movement but at different intensities). Our ultrasound data support the hypothesis that substantial translocation of the electrodes across the muscle, changes in fascicle length and changes in fascicle angle occur during knee extension, which will influence the signal recorded at the surface electrodes. The use of polynomial fitting procedures has been shown to be practical in application, and that the EMG-joint angle curves calculated can accurately match the changes in EMG recorded during the isokinetic reference contraction. From the present data, the use of a third order polynomial is recommended when analysing EMG data obtained from the quadriceps group because curves of less

complexity may result in significantly different values at more extreme joint positions.

Chapter 4

Experiment 2

**The influence of loading intensity on
muscle-tendon unit behaviour during
maximal knee extensor stretch
shortening cycle exercise**

Abstract

The influence of loading intensity on muscle-tendon unit behaviour during maximal knee extensor stretch shortening cycle exercise

Tendon stiffness increases as the magnitude and rate of loading increases, according to the tendon's viscoelastic properties. Thus, under some loading conditions tendons should become exceptionally stiff and act as rigid force transducers. Nonetheless, observations of tendon behaviour during multi-joint sprinting and jumping tasks have shown that increases in tendon strain increase whilst muscle strain decreases as the loading intensity increases. The purpose of the current study was to examine the influence of external loading intensity on muscle-tendon unit (MTU) behaviour during a high-speed single joint, stretch shortening cycle knee extension task. Eighteen men ($n=9$) and women ($n=9$) performed single-leg, maximum intensity stretch shortening cycle leg extensions with a full countermovement at loads of 20, 60 and 90% of their one repetition maximum (1RM). Vastus lateralis fascicle length (L_f) and velocity (v_f) as well as length of the MTU (L_{MTU}) and tendinous tissue (L_t) were measured using high-speed ultrasonography (96 Hz). Patellar tendon force (F_t) and rate of force development (RFD_t) were estimated using inverse dynamics. Results showed that concentric joint velocity and shortening v_f decreased whilst F_t and RFD_t increased, but no significant differences were observed in eccentric joint velocity or peak L_{MTU} or L_f . Also, the tendon lengthened significantly less at the end of the eccentric phase and tendon lengthening velocity tended to decrease at heavier loads. This is the first observation that during a SSC movement tendon stiffness increases significantly as loading intensity increases *in vivo*, resulting in a shift in the tendon acting as a power amplifier at light loads to a rigid force transducer at heavy loads.

INTRODUCTION

Tendons transfer forces to bones via elastic tendons. The temporal strain patterns of muscle and tendon during muscle contraction are often complex, but appear to function with appropriate synchronicity to maximise movement performance and minimise energy expenditure and risk of injury (87, 97, 140, 178). During ballistic stretch-shortening cycle (SSC) movements, in which muscle-tendon unit (MTU) shortening (concentric movement) is immediately preceded by active MTU lengthening (eccentric movement), significantly greater work is performed than during kinetically similar concentric-only movements. It is believed that the complex muscle and tendon interaction allows for (1) substantial storage and release of elastic energy, (2) the muscle to work at a more favourable length and velocity and (3) an increase in the duration of muscle activity and thus greater force potential (45, 227). However, while a significant volume of research has examined MTU behaviour during human movement, there is a lack of research examining how external loading intensities influence this relationship. The lack of such knowledge has contributed to an incomplete understanding of MTU behaviour and often an oversimplification of the complex nature of viscoelastic tendons.

Because tendon is a viscoelastic material, its mechanical properties (e.g. stiffness) are influenced greatly by both magnitude and rate of force acting on it (29, 82, 159, 162, 163, 194, 212). Tendon stiffness increases curvilinearly as the force acting on the tendon increases, resulting in a decreased tendon lengthening for a given force at high force levels (140, 212, 227). This relationship is further influenced by the rate of tendon loading, theoretically allowing the tendon to become a completely rigid structure when very high forces are developed rapidly (29, 212, 229). In this scenario the tendon would serve as a rigid force transducer and possibly serve to increase joint integrity (29, 190, 212). Nonetheless, to our knowledge, this behaviour has never been observed in humans during SSC contractions.

Whilst knowledge of the properties of tendons may allow for accurate predictions of how external loading influences MTU behaviour, *in vivo* measurements obtained during SSC movements have shown these interactions to be highly complex. The use of real-time ultrasonography has allowed for MTU behaviour particularly of the gastrocnemius and vastus lateralis (VL) muscles, to be non-invasively observed in humans during a variety of SSC movements, including running (134), jumping and drop jumping (89, 90, 136, 139, 206, 218). However, these studies have consistently found that the relative lengthening of the muscle decreases and the tendon increases as the movement intensity increases. In fact, during high velocity movements performed through a limited range of motion, such as during the ground contact phase in sprinting and drop jumping, the muscle has been shown to lengthen only marginally, if at all, during the eccentric phase (89, 90, 132). Thus, the muscle is considered to work quasi-isometrically, allowing for greater tendon lengthening as loading intensity increases (206) and for the tendon to act as a power amplifier as it recoils at high speeds (80, 190). Qualitatively, these observations are at odds with the prediction that the tendon should become more rigid during very high intensity movements. A possible explanation is that the movement ranges of motion and the magnitude and rate of tendon loading were insufficient to promote rigidity in the tendon, but it is not yet known whether increasing these parameters within normal physiological limits could promote such a significant change in the tendon behaviour. Therefore, the purpose of the present study was to examine the influence of loading intensity on MTU behaviour during a large range of motion, high-velocity SSC knee extension task. We used the knee extension exercise as the maximal force produced within the muscle is substantial, and the simple, single-joint movement pattern would allow for subjects to easily produce large forces at high rates of force development. Thus, the exercise provided the ideal conditions in which to test our hypothesis.

METHODOLOGY

SUBJECTS

Eighteen healthy, physically active men (n=9) and women (n=9) (age: 25.8 ± 2.8 yr, height: 1.76 ± 0.05 m, body mass: 73.4 ± 10.1 kg, knee extension 1RM: 38.9 ± 14.0 kg) participated in the study after signing an informed consent document. Subjects were excluded from the study if they had any history of lower body musculoskeletal injuries. The study was reviewed and approved by the Human Research Ethics Committee of the University.

EXPERIMENTAL DESIGN

Because of the novelty of the SSC knee extension movement, the subjects completed two familiarisation sessions and then had their one repetition maximum (1RM) determined prior to the experimental session. All testing was performed on the subjects' self-reported dominant legs.

During the experimental session, subjects performed a standardised warm-up consisting of five minutes of low intensity (14.7N, 60 rpm) stationary cycling and isokinetic leg extensions at 50% and 80% of perceived maximum intensity. The subjects then performed a series of isokinetic knee extensions during which EMG was recorded and used for normalisation of the EMG signals obtained during subsequent SSC leg extensions.

After 20-minutes of passive recovery, the subjects completed a second warm-up on a custom-modified isoinertial leg extension machine consisting of submaximal leg extensions at 50, 80 and 90% of estimated 1RM. Subsequently, isoinertial SSC knee extensions were performed with loads of 20, 60 and 90% of 1RM from which MTU behaviour, kinetics and muscle activity were measured. Ultrasonography was used to determine VL fascicle length (L_f) and MTU length (L_{MTU}) and quadriceps tendon length (L_t) were calculated by combining L_f and joint position into known equations (117). Electronic goniometer-derived joint

angles were used in the calculation of movement kinetics and muscle activity of the quadriceps femoris was recorded using surface EMG. Comparisons of MTU behaviour, muscle activity and movement kinetics were thus made between the different loading conditions.

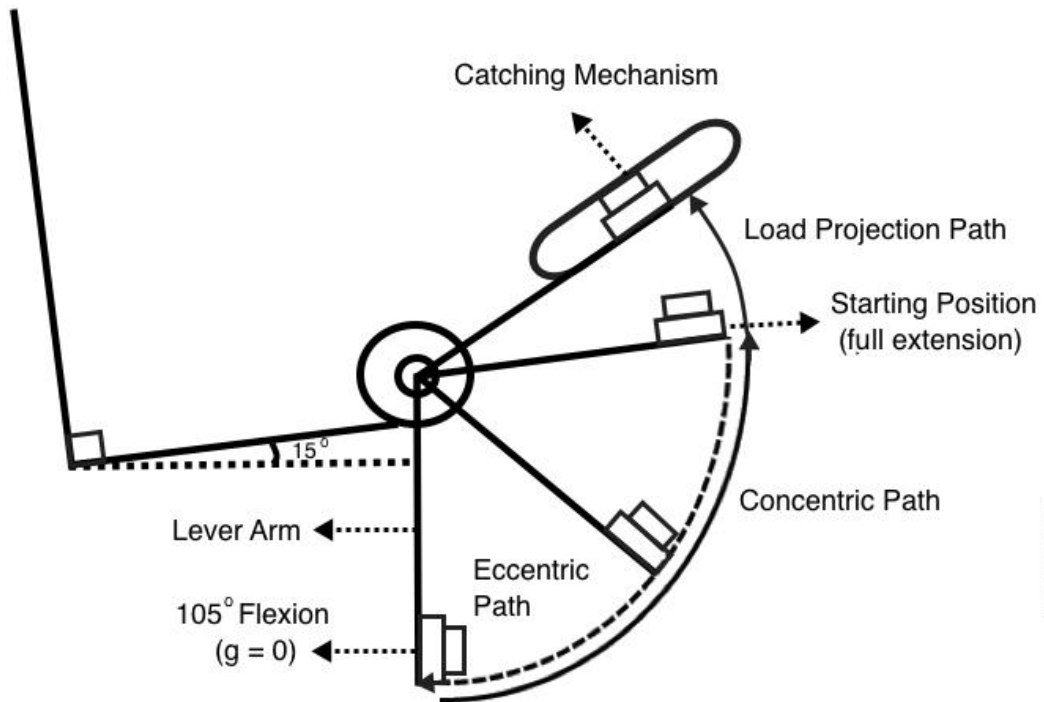
EXPERIMENTAL PROTOCOL

Testing was performed on a modified, plate loaded leg extension machine (Figure 17). For each repetition the subject started with their leg fully extended and unloaded. Then, upon instruction, a specific load was released onto the subject's leg and they immediately performed a SSC movement about the knee with the load projected into a catching mechanism at the end of the concentric phase. In order to ensure maximal performance, the subjects were instructed to "kick the load as high and fast as possible"; countermovements were performed at a self-selected speed and depth. Each subject performed three leg extensions at each load (20, 60 and 90% of 1RM) and the leg extension at each load with the fastest concentric joint velocity was selected for analysis. During each trial, EMG data, knee-angle data and ultrasound images were recorded for comparison.

MTU BEHAVIOUR

During the isoinertial SSC knee extensions, B-mode ultrasonography (Alpha 10, Aloka, Co Ltd, Tokyo, Japan) was used to obtain images of the VL fascicles for determination of L_f and fascicle angle (A_f) throughout the movement. A 6-cm linear array, 10 MHz T-head transducer (UST 5713, Aloka Co Ltd, Tokyo, Japan) was used to collect images at a rate of 96 images per second. The transducer was placed at 50% of the distance between the greater trochanter and the lateral epicondyle of the femur and aligned with the direction of the VL fascicles so that the echoes delineating a single fascicle could be tracked throughout the entire range of motion of the knee. A thin echo-absorbent reference strip was fixed to the subject to allow for correction of any probe

Side View of Chair



Front View of Lever Arm

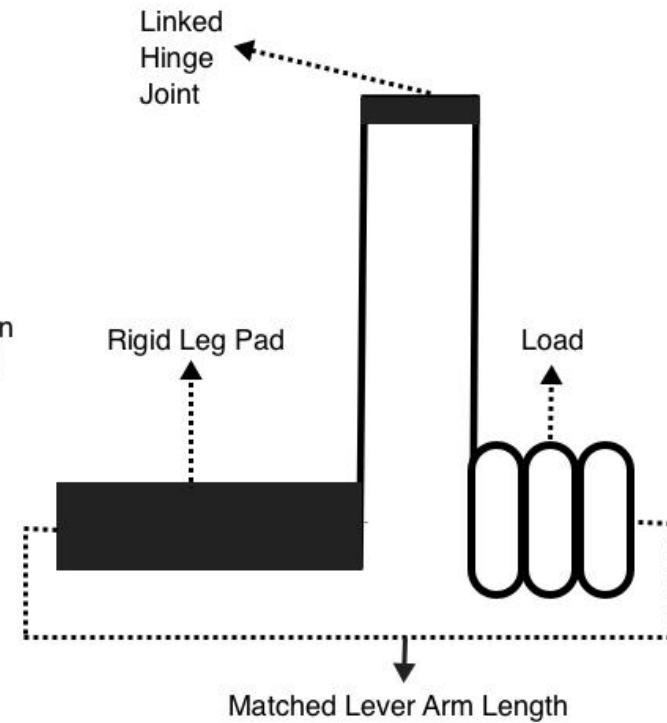


Figure 17: Graphic of the isoinertial knee extension machine and experimental set-up.

movement that occurred during the testing. The transducer head was fixed to the subject using a custom-made thermoplastic cast and taped into place.

Ultrasound images were analysed using DartFish (Prosuit 5.0, DartFish, Sydney, Australia) video analysis software. An individual fascicle was tracked throughout the movement and the L_f of an individual muscle fascicle and A_f from the deep aponeurosis were recorded for each image. In positions where the entire fascicle was not visible in the image, the fascicle and aponeurosis were linearly extrapolated to their intersect point using Eq. 1, where MT represents the cross-sectional thickness of the VL. Measurements were made three times, non-consecutively, and the average of the three trials was recorded.

$$L_f = MT \times \cos (A_f) \quad [\text{Eq. 1}]$$

MTU length (L_{MTU}) was estimated using previously derived models based on the joint position and limb length of each subject (117) and the length of the tendinous tissue (L_t) was calculated as the longitudinal length of the recorded fascicle subtracted from L_{MTU} (see Eq. 2 and 3).

$$L_t = L_t (prox) + L_t (dist) \quad [\text{Eq. 2}]$$

$$L_{MTU} = L_t + L_f \times \cos (A_f) \quad [\text{Eq. 3}]$$

It should be noted that L_t calculated this way includes the distal (dist) and proximal (prox) tendon components (6, 132, 168). Shortening and lengthening velocities of the fascicle (v_f) and tendon (v_t) were calculated as the change in length over time during both the concentric and eccentric phases of movement (Figure.18).

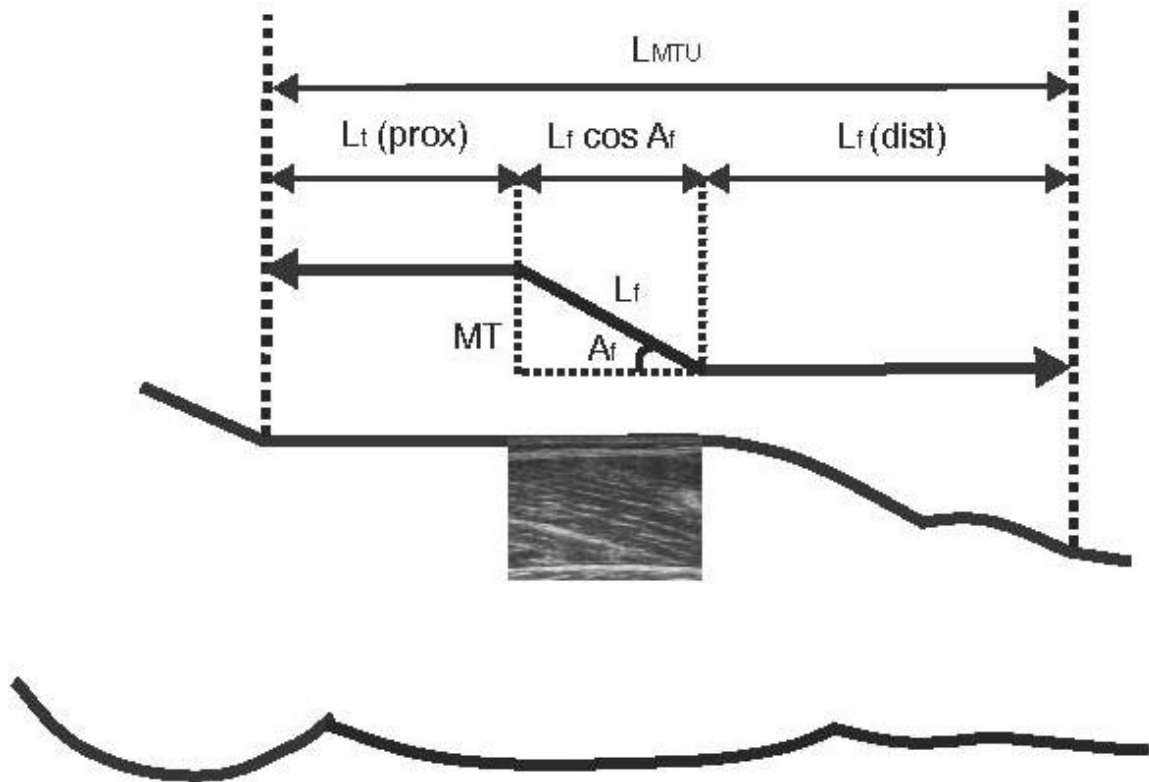


Figure 18: Model showing how length of the fascicle (L_f), muscle-tendon unit (L_{MTU}) and tendon (L_t), as well as fascicle angle (A_f) and muscle thickness (MT), were defined. The longitudinal component of L_f was defined as: $L_f \cdot \cos(A_f)$, L_t was defined as the sum of both the proximal [$L_t(\text{prox})$] and distal [$L_t(\text{dist})$] lengths of the tendon, and L_{MTU} was defined as the sum of longitudinal component L_f and L_t .

MOVEMENT KINETICS

Smoothed goniometer-derived (MLTS700, AD Instruments USA) knee angle-time curves were integrated to calculate angular velocity and acceleration. Joint torque (T_{knee}) was calculated using inverse dynamics by applying the impulse-momentum relationship and values were corrected for the effect of gravity (see Eq. 4),

$$T_{knee} = (M_{limb} \times \cos \theta + 15) + (m_{load} \times g \times \cos(\theta - 15) \times r_{load}) + (M_{limb} \div g \times r_{limb}^2 \times \alpha) + (m_{load} \times r_{load}^2 \times \alpha)$$

[Eq. 4]

where M_{limb} is the moment of the leg and shod foot as recorded by an isokinetic dynamometer with leg flexed to 20° (i.e. weight of the limb), θ is the knee angle, m_{load} is the mass of the load (i.e. 20, 60 or 90% of 1RM), g is gravitational acceleration, r_{load} is the moment arm of the leg extension machine, α is angular acceleration and r_{limb} is the estimated distance from the femoral condyles to the centre of mass of the lower limb (241).

Angular power (Eq. 5) and both the force (F_t ; Eq. 6) and rate of force development (RFD_t; Eq. 7) in the tendon were also estimated:

$$Power = T_{knee} \times \omega$$

[Eq. 5]

$$F_t = Torque \div MA_p$$

[Eq. 6]

$$RFD_t = F_{ti+1} - F_{ti}$$

[Eq. 7]

where ω is angular velocity of the knee, MA_p is the joint derived moment arm length of the patella (232), and F_{ti} and F_{ti+1} are the time derivatives of tendon force around the instant in question (sampled at 1000 Hz).

EMG COLLECTION AND NORMALISATION

Details of EMG collection and normalisation are explained in full detail in Chapter 3. During isoinertial SSC knee extensions EMG signals were collected from VL, vastus medialis (VM) and rectus femoris (RF) using a wireless EMG system (ZeroWire, Aurion, Milan Italy) simultaneously with knee joint angles. For analysis EMG signals obtained during SSC knee extensions were normalised to the joint angle relative muscle activity at each position using the calculated relationships (see Chapter 3) and reported as a percentage of the predicted maximal activity (% MA).

DATA COLLECTION AND PROCESSING

EMG and goniometer derived data were simultaneously recorded using data acquisition software (LabChart 7.2, AD Instruments, Bella Vista Australia) and ultrasound images were synchronised using an output pulse triggered by the computer to the ultrasound system. All signal manipulation and analysis was performed using custom-written LabView programs (Labview 8.2, NI Instruments, Texas USA). To allow for comparison between movements with different durations, signals were time-normalised and represented as a percentage of the movement between the start of the eccentric phase of the movement (leg flexed 2° from starting position) to the completion of the concentric phase of the movement (leg extended to within 2° of full extension) (61).

STATISTICAL ANALYSIS

Repeated measures MANOVAs with Bonferroni *post hoc* tests were used to examine differences in MTU, fascicle and tendon measurements, movement kinetics and muscle activity between the three loading conditions as well as the differences in time normalised L_t between the 20% and 90% loads. Results are presented as mean \pm SD. All statistical analyses were conducted using PASW 18.0.1 (IBM, New York, USA) and statistical significance was accepted at an α level of 0.05.

RESULTS

Differences in MTU behaviour, movement kinetics and muscle activity were observed between the three loads. Kinetic and kinematic variables are presented in Table 1. Despite subjects performing the leg extensions using a self selected depth there were no differences in peak knee flexion angle between conditions. Nonetheless, movement duration increased and the relative duration spent in the eccentric versus the concentric phase of the movement decreased as the load was increased. These changes coincided with significant decreases in concentric joint angular velocity and acceleration (Figure 19). However, no differences were found for eccentric joint angular velocity or acceleration between conditions (Figure 19). Greater loading also resulted in significant increases in peak knee torque, F_t , and RFD_t (Figure 20).

Data describing the structure of the MTU and MTU behaviour at the three loads are presented in Table 2. Throughout each SSC leg extension the MTU went through both lengthening and shortening. However, there were no significant differences in L_f or L_t at their longest or shortest lengths, or A_f at its smallest angles, between loading conditions.

The repeated measures MANOVA revealed that shortening v_f was significantly faster at 20% than 60% or 90% (Figure 21), however, there were no significant differences between loads for lengthening v_f . The maximal lengthening and shortening v_t did not significantly change as loading increased, despite a marginal mean decrease being evident (Figure 21).

After values were time normalised (i.e. reported as a % of total movement), L_t was compared between the 20% and 90% loads throughout the movement (Figure 22). This analysis showed that the tendon went through significantly greater lengthening under the 20% versus the 90% load at the end of the eccentric phase (42-45% and 46-48% of movement duration, respectively).

| | Load | | |
|--|-----------------------------|-----------------------------|-----------------------------|
| | 20% | 60% | 90% |
| Duration (s) | 0.748 ± 0.079 _{bc} | 0.855 ± 0.088 _{ac} | 0.919 ± 0.131 _{ab} |
| Eccentric Duration (%) | 59.4 ± 4.0 _{bc} | 54.2 ± 3.7 _{ac} | 52.5 ± 5.4 _{ab} |
| Knee Flexion (°) | 92.9 ± 9.9 | 94.4 ± 8.0 | 94.3 ± 9.4 |
| ω Eccentric (°·s ⁻¹) | 397 ± 68 | 405 ± 39 | 395 ± 73 |
| ω Concentric (°·s ⁻¹) | 593 ± 86 _{bc} | 473 ± 60 _{ac} | 443 ± 60 _{ab} |
| α Eccentric (°·s ⁻²) | 2195 ± 739 | 2516 ± 688 | 2396 ± 808 |
| α Concentric (°·s ⁻²) | 555 ± 889 _{bc} | 4351 ± 1192 _{ac} | 3824 ± 1009 _{ab} |
| Power (W) | 1435 ± 621 _{bc} | 2426 ± 1176 _{ac} | 3317 ± 1757 _{ab} |
| Torque (Nm) | 170.6 ± 75.5 _{bc} | 334.8 ± 128.1 _{ac} | 465.2 ± 223.2 _{ab} |
| F _T (kN) | 3.45 ± 1.45 _{bc} | 7.64 ± 2.35 _{ac} | 9.137 ± 4.175 _{ab} |
| RFD _T (kN·s ⁻¹) Maximum | 4.53 ± 1.93 _{bc} | 11.50 ± 5.22 _{ac} | 16.45 ± 5.90 _{ab} |
| RFD _T (kN·s ⁻¹) Minimum | -5.34 ± 2.20 _{bc} | -11.02 ± 5.11 _{ac} | -14.49 ± 6.64 _{ab} |

Table 1: Kinetics and kinematics descriptors during a stretch shortening cycle knee extension. Eccentric duration is reported as a percentage of the total movement duration. Significant differences between loads are depicted; 20 (a), 60 (b) and 90% (c).

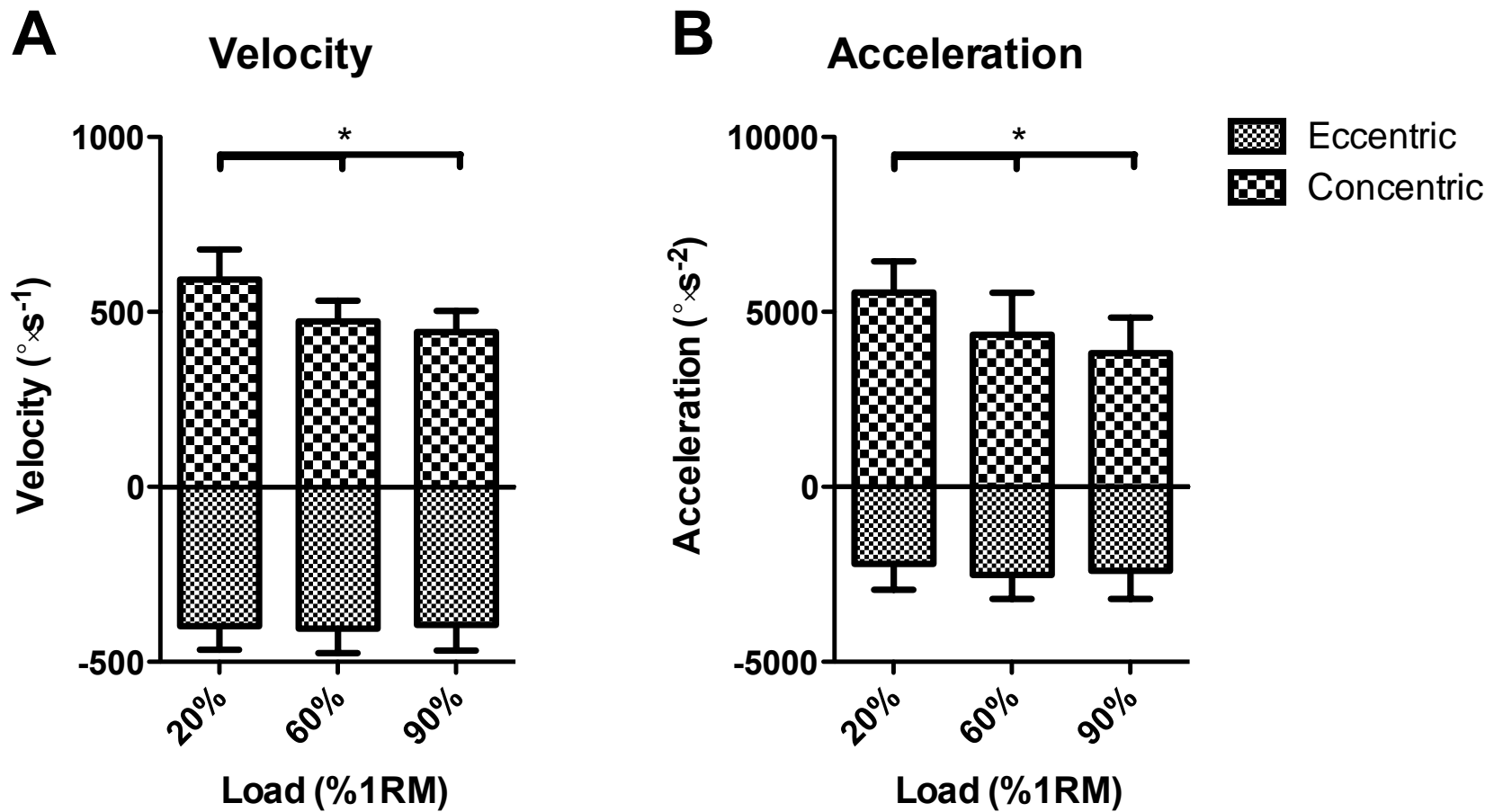


Figure 19: Peak eccentric and concentric joint angular velocity (A) and acceleration (B) during stretch shortening cycle knee extensions. * Indicates significant differences between loads [20, 60 or 90% of one repetition maximum (1RM)].

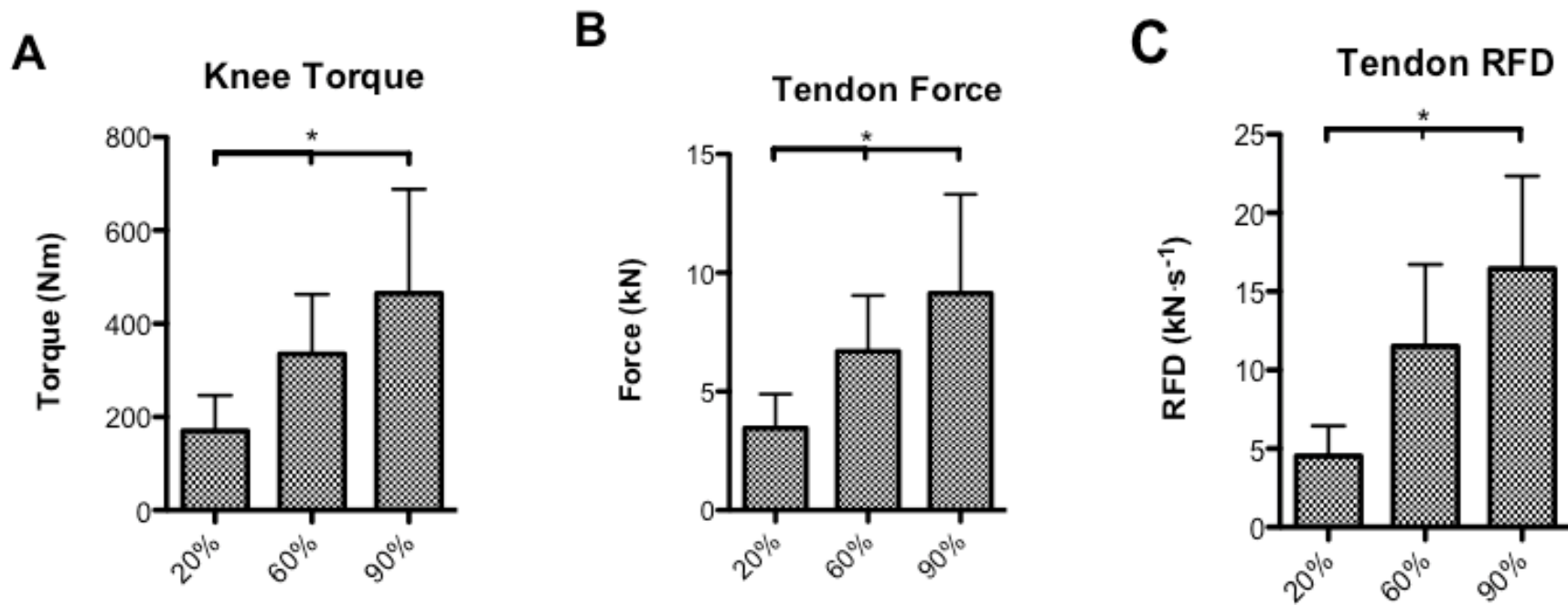


Figure 20: Peak torque, patellar tendon force (F_t) and rate of force development (RFD_t) during stretch shortening cycle knee extensions. * Indicates significant differences between loads [20, 60 or 90% of one repetition maximum (1RM)].

| | Load | | |
|---|----------------------|------------------|------------------|
| | 20% | 60% | 90% |
| L_t Max (cm) | 38.2 ± 3.1 | 38.2 ± 2.9 | 38.4 ± 3.2 |
| L_t Min (cm) | 31.9 ± 4.7 | 32.2 ± 4.4 | 32.1 ± 4.7 |
| L_f Max (cm) | 16.2 ± 4.5 | 15.7 ± 4.6 | 15.7 ± 4.9 |
| L_f Min (cm) | 6.8 ± 1.5 | 7.0 ± 1.4 | 6.9 ± 1.6 |
| A_f Max ($^\circ$) | 19.0 ± 3.5 | 19.4 ± 3.1 | 19.4 ± 3.1 |
| A_f Min ($^\circ$) | 8.2 ± 2.3 | 8.6 ± 2.6 | 8.8 ± 2.7 |
| v_t Lengthening ($\text{cm}\cdot\text{s}^{-1}$) | 60.7 ± 23.1 | 62.2 ± 31.9 | 48.6 ± 18.3 |
| v_t Shortening ($\text{cm}\cdot\text{s}^{-1}$) | 64.6 ± 27.8 | 59.7 ± 35.0 | 57.1 ± 26.4 |
| v_f Lengthening ($\text{cm}\cdot\text{s}^{-1}$) | 19.7 ± 6.7 | 24.0 ± 8.4 | 21.8 ± 10.2 |
| v_f Shortening ($\text{cm}\cdot\text{s}^{-1}$) | $38.1 \pm 13.7_{bc}$ | $21.0 \pm 9.1_a$ | $18.5 \pm 8.3_a$ |

Table 2: MTU structure and behaviour by loading intensity during a stretch shortening cycle knee extension. Significant differences between loads are depicted; 20 (a), 60 (b) and 90% (c).

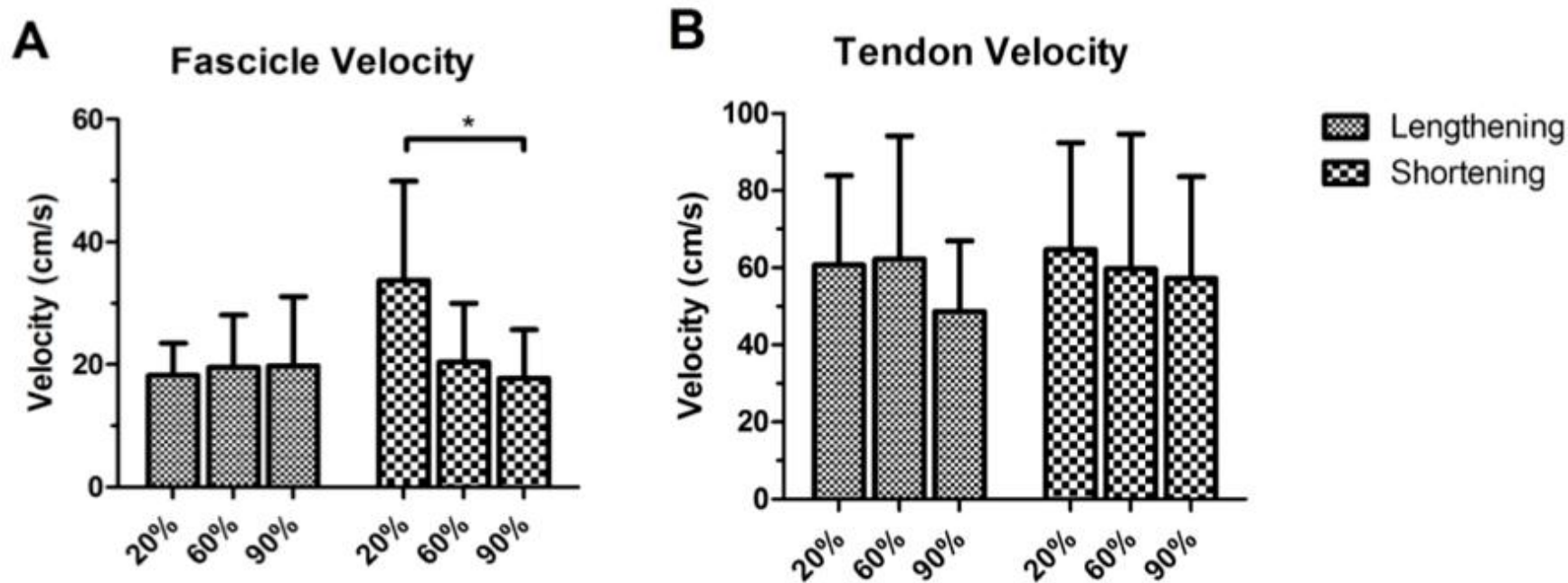


Figure 21: Peak lengthening and shortening velocities of the fascicles of the vastus lateralis and the tendinous tissue of the quadriceps tendon between during stretch shortening cycle knee extensions. * Indicates significant differences between loads [20, 60 or 90% of one repetition maximum (1RM)].

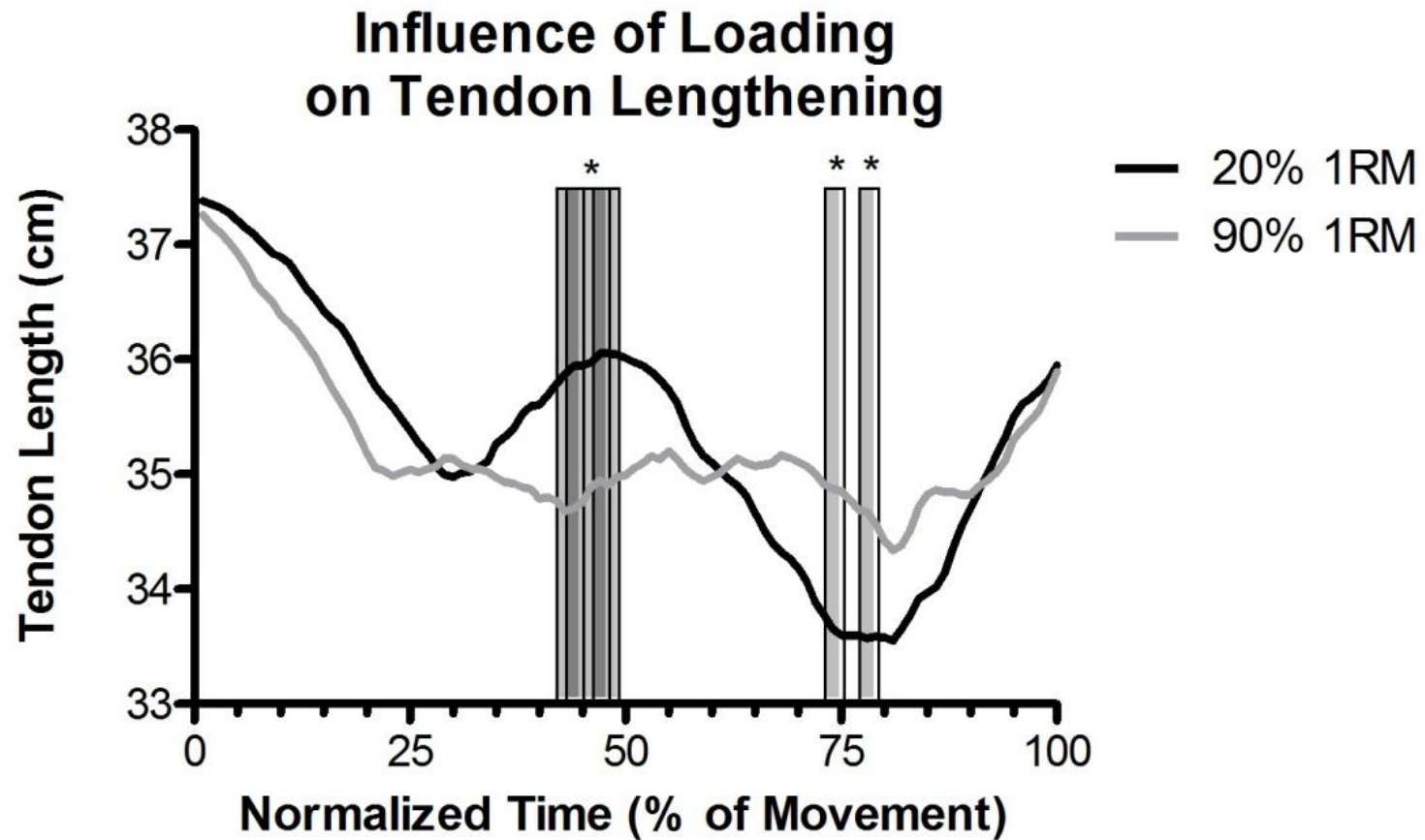


Figure 22: Influence of loading on tendon length (L_t) throughout a stretch shortening cycle knee extension. Time is depicted as relative to the completion of the movement. Significant differences between loads ($p < 0.05$) are depicted by dark shading and non-significant trends ($p = 0.053-0.075$) are depicted by light shading.

There was also a non-significant trend ($p = 0.053-0.075$) for the tendon to recoil to a shorter length during the concentric phase of the movement under the 20% versus the 90% load (73-75% and 77-79% of movement duration).

Differences in EMG activity between loads are reported in Table 3. The average of VL, VM and RF EMG amplitudes (i.e. quadriceps activity) increased significantly as the load increased. Peak VL EMG amplitude was found to be significantly greater under the 90% compared to the 20% load, but values under the 60% load were not different from those recorded under the 20 or 90% loads. However, there were no differences in peak VM or RF EMG amplitude between loads. Thus, increases in whole quadriceps muscle activity largely resulted from differences recorded in VL.

Time normalised curves showing joint displacement, angular velocity and acceleration, L_{MTU} , L_f , and A_f are shown in Figure 24. These figures clearly show differences in movement kinematics as well as MTU and fascicle dynamics between the loading conditions. Fascicular lengthening (ICC: 0.926, CI: 0.886 - 0.952) and shortening (ICC: 0.946, CI: 0.917 - 0.965) velocities were reliably obtained using the present methodologies, and no gender differences were observed in tendon or fascicular lengthening or shortening velocities. Quadriceps femoris muscle activity (i.e. EMG amplitude) is presented in Figure 25, which shows that muscle activity increased markedly from ~30% of movement time and was maximal during the concentric phase. The earliest and most rapid increase in EMG activity was observed in the heaviest (90%) loading condition in all muscles.

DISCUSSION

The major finding of the present study was that MTU behaviour changed as the external loading was increased in SSC knee extensions such that the tendon went through less lengthening during the eccentric phase of the movement. This occurred despite there being a lack of change in the MTU

| | Load | | |
|--------------------|-----------------------|-----------------------|-----------------------|
| | 20% | 60% | 90% |
| VL _{Peak} | 172 ± 55 _c | 213 ± 81 | 220 ± 93 _a |
| VL _{Avg} | 59 ± 15 _{bc} | 75 ± 19 _{ac} | 88 ± 27 _{ab} |
| VM _{Peak} | 193 ± 80 | 216 ± 117 | 224 ± 93 |
| VM _{Avg} | 65 ± 19 _{bc} | 79 ± 21 _{ac} | 93 ± 30 _{ab} |
| RF _{Peak} | 189 ± 73 | 216 ± 75 | 226 ± 131 |
| RF _{Avg} | 63 ± 25 _{bc} | 79 ± 25 _{ac} | 87 ± 30 _{ab} |

Table 3: Peak and average EMG amplitudes (muscle activity) of the vastus lateralis (VL) vastus medialis (VM) and rectus femoris (RF) during a stretch shortening cycle knee extension. Significant differences between loads are depicted; 20 (a), 60 (b) and 90% (c).

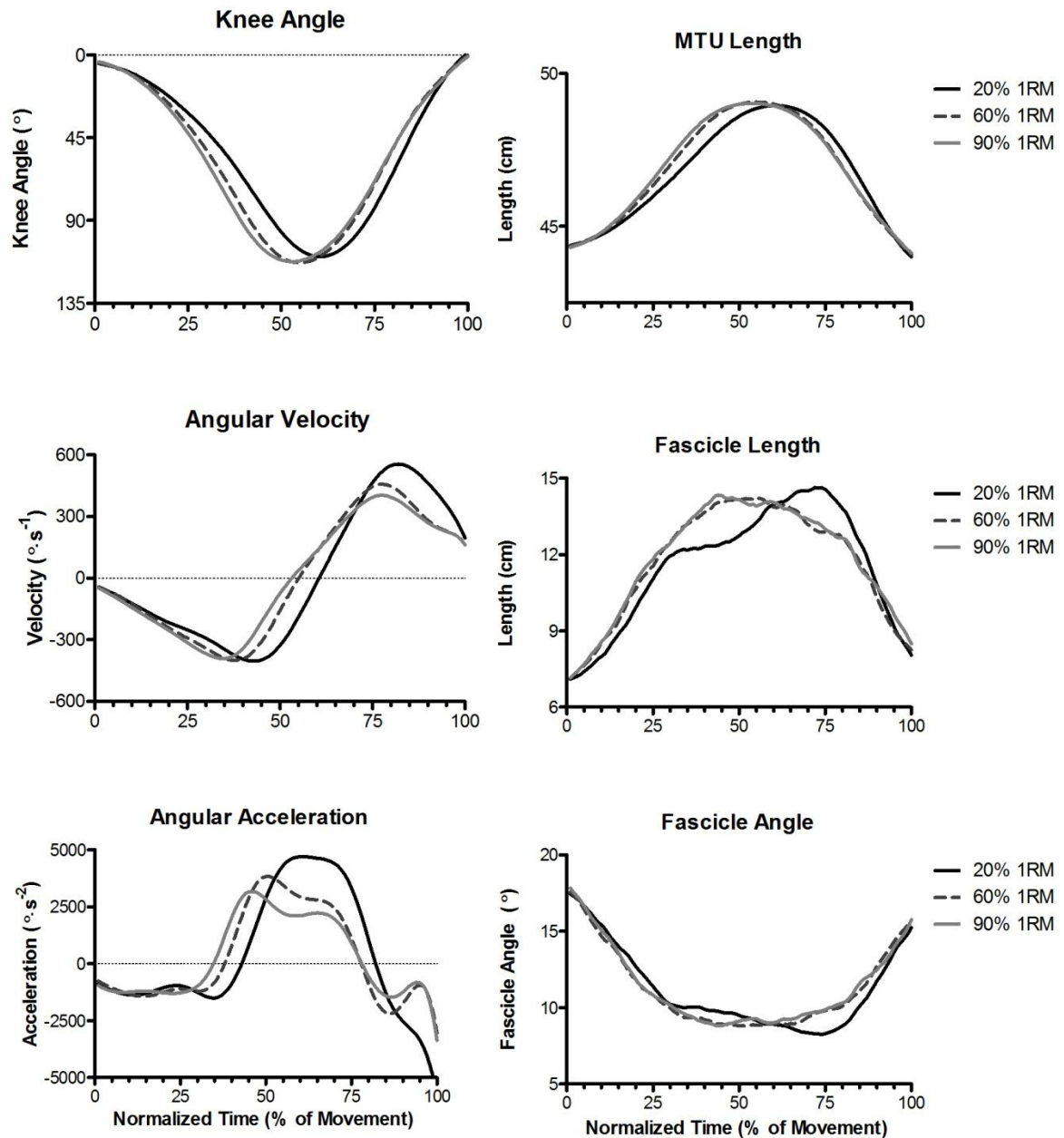


Figure 23: Changes in knee angle and angular velocity and acceleration and (1st column) as well as change in MTU (L_{MTU}), fascicle (L_f), and tendon (L_t) length (2nd column) over time during a stretch shortening cycle knee extension. Time is normalized to a percentage of total movement duration.

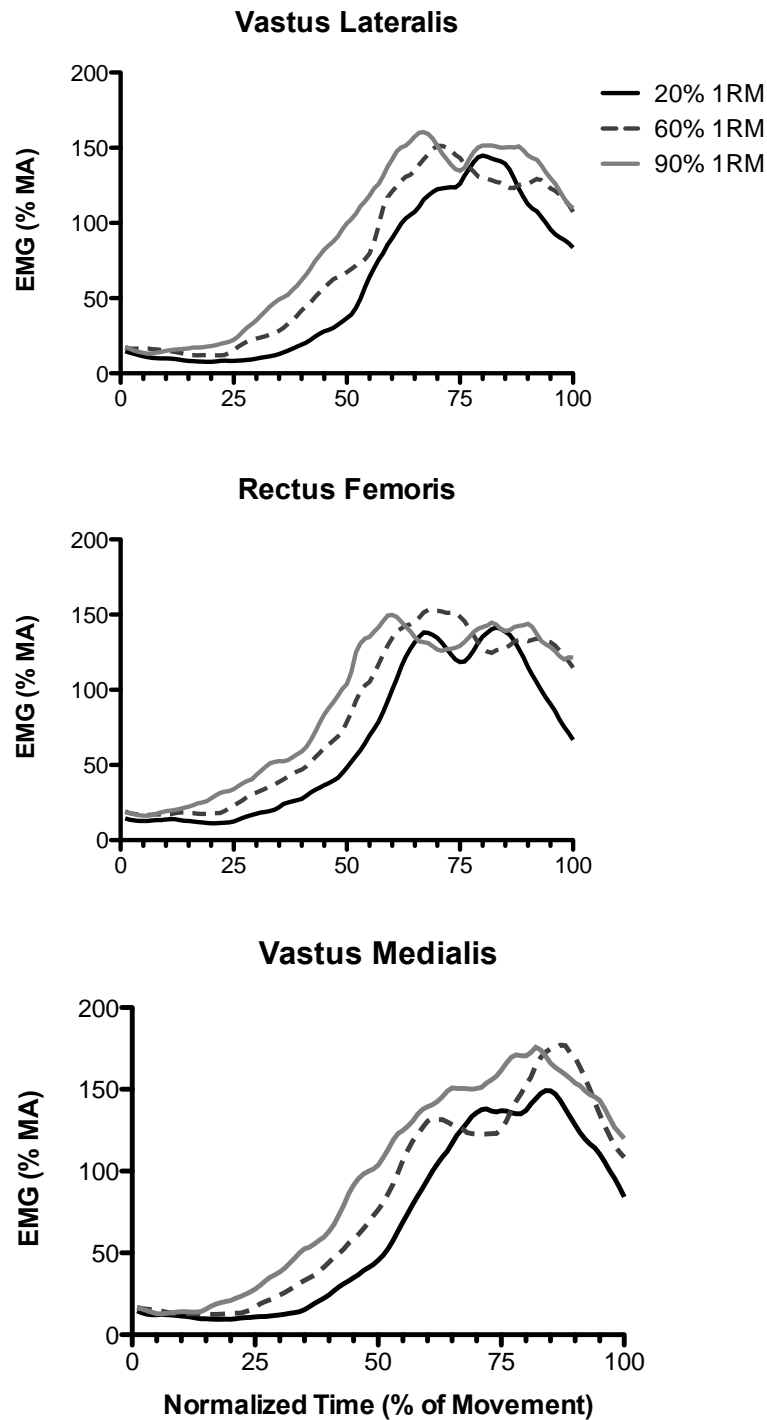


Figure 24: Changes in muscle activity of the VL, VM and RF over time during a stretch shortening cycle knee extension. Time is normalized to a percentage of total movement duration.

length (L_{MTU}), fascicle length (L_f) or eccentric angular velocity and acceleration. The finding is suggestive of a shift in the role of the quadriceps tendon from functioning as a power amplifier at light loads to a rigid force transducer at heavy loads. To our knowledge this is the first time such a phenomenon has been shown *in vivo* in humans.

Complex MTU behavioural strategies are often utilised during SSC movements. It has previously been hypothesised that these subconscious strategies are selected to maximise performance whilst minimising energetic costs (87, 178). While research has focused on the relative contribution of tendon lengthening (compared to muscle) during movement, tendon behaviour is clearly influenced by the force production of the active muscle to which it is attached. In the present study average muscle activity (EMG amplitude) of the quadriceps (VL, VM and RF) and peak muscle activity of the VL were significantly increased under the 90% load compared to the 20% load, which occurred through an earlier and more rapid rate of activation of the muscles (Figure 24). It is widely accepted that greater EMG activity is reflective of a greater activation of the muscles, which resulted in greater F_t and RFD_t . This would have underpinned the change in the role of the tendon during the SSC movement and occurred despite subjects not volitionally changing their approach to the performance of the movement.

It is of interest that specific differences in movement kinetics and MTU behaviour were found between the eccentric and concentric phases of the movement between loading conditions. In particular, load-dependent differences were found in joint angular velocity, angular acceleration and fascicle velocity during the eccentric phase of the movement, however tendon lengthening velocity did not significantly differ between loads. In addition, the tendon went through greater lengthening in the lighter loading condition (20%), which would have allowed the tendon to store more energy and perform more concentric work and thus act like a catapult (80, 208). In addition, the greater tendon compliance in the lighter load condition may have allowed for an increased eccentric phase

duration and thus allowed the muscle more time to reach a high level of activation and consequently perform more work (43). In support of this claim, a greater percentage of the total movement took place during the eccentric phase at the lighter load despite no significant difference in peak L_f or L_{MTU} . In the 90% loading condition the tendon underwent minimal lengthening during the eccentric phase, despite there being a substantial increase in both the peak force and RFD in the patellar tendon. This supports hypotheses developed from findings in isometric contractions (29, 82, 159, 212) as well as results calculated using musculoskeletal models (190, 229), which found that the stiffness of the tendon increases substantially as the peak force and/or RFD increases.

The findings of the current study are significant in that, for the first time, it has been clearly observed that increasing intensity caused a decrease in tendon lengthening during a complex SSC movement in humans. Our findings contrast those obtained during drop jumping and sledge jumping exercises (89, 90, 132, 133, 138, 206, 218) where increased tendon lengthening and decreased muscle lengthening were observed as loading intensity increased. Differences between present and previously published results might be explicable by the peak forces and RFDs generated at joints during jumping being insufficient to cause substantial tendon stiffening, and thus fascicle lengthening. Finni et al. (90) estimated F_t during maximal voluntary isometric contractions (6.65 ± 2.50 kN) as well as during unilateral countermovement jumps (~ 2 kN) and drop jumps (from optimal rebound height; ~ 3.6 kN) when performed on a custom-designed sledge apparatus. Ishikawa et al. (132) using the same apparatus and reported greater F_t values during drop jumps when subjects were dropped from 80% of their squat jump height (~ 5.5 kN). These force values are significantly less than those transferred through the tendon in the current study at the 90% 1RM load (9.13 ± 4.18 kN). Unfortunately, RFD_t was not reported for the jumping movements in previous studies, but it is likely that differences in these values also exist when compared to the present study. It is also possible that the range of motion utilised presently ($>90^\circ$), which exceeds those that are typically achieved in

jumping movements, was a factor in the differences in tendon behaviour because it allowed a greater momentum to be developed during the eccentric phase, and thus for the greater force levels to be obtained early in the concentric phase. Further research is required to more specifically address the influence of knee joint range of motion, as compared to the influence of the peak force and RFD per se, on MTU behaviour in SSC movements.

During the concentric phase of movement the lighter load elicited a significantly faster joint angular velocity and acceleration, as well as a faster muscle fascicle shortening velocity. Nevertheless, there was no significant difference in tendon shortening velocity, although a tendency for the tendon to recoil to a shorten length was observed ($p < 0.053-0.075$) with the lighter load. A visual assessment of individual tendon lengthening patterns showed that those subjects who exhibited less tendon lengthening also tended to exhibit the least shortening. The lack of statistical significance most likely resulted from the fact that while stiffer tendons undergo less deformation for a given force they also recoil at a faster velocity (190). Thus tendon recoil velocity is more likely to be dictated by the rate of unloading at the end of the concentric phase of the movement rather than the stiffness (and therefore recoil force, according to Hooke's Law) of the tendon (190).

An interesting aspect of this study is that both men and women participated as subjects. This is a unique aspect of this study because women are often not included in similar research because menstruation related changes in hormone levels have previously been shown to influence the mechanical properties of tendons and ligaments. However, as this study has a within subject design and all testing is performed in the same day it was determined that the influence of gender on MTU behaviour would not adversely influence our results. In support of this we found no significant differences in MTU behaviour between genders.

An important aspect of the methodology used in the present study is that time-normalisation was used to compare tendon length lengthening and shortening throughout the movement. Time-normalised comparisons were necessary because the movement duration significantly increased as the load increased, which made it impossible to compare phases of movement using non-time normalised values. However, it should be noted that the amount of normalised time spent in the eccentric phase was greater in the lighter load condition, thus there is some negative skewing of the time-normalised graphs at lighter loads, which did not allow for time-sensitive measures, such as fascicle velocity, to be compared between conditions.

In conclusion, loading intensity was found to clearly influence MTU behaviour. These changes most likely resulted from a modification in the dynamic stiffness of the tendon and distal aponeurosis, and activation patterns of the muscle. Furthermore, these changes occurred despite no differences in peak L_{MTU} or L_f being observed. Rather, a loading based dichotomy in the role of the tendon occurred: at lighter loads the tendon served as a power amplifier and increased the relative duration of the eccentric phase of the movement, whilst at heavy loads the tendon acted as a rigid force transducer and allowed efficient transfer of large muscular forces.

Chapter 5

Experiment 3

**The Influence of External Loading on
MTU Behaviour During the Jump
Squat Exercise**

Abstract

The influence of external loading on muscle-tendon unit behaviour during squat jumping exercise

Loads used during exercise are often manipulated to elicit specific training adaptations. However, little is currently known about how load manipulation influences muscle-tendon unit (MTU) behaviour. Such a lack of understanding arises from the fact that tendons are viscoelastic and thus can act as either an elastic or a viscous structure, depending on the tendon force (F_t) and rate of force development (RFD_t). The purpose of the current study was to examine the effect of external load variation on MTU behaviour during the jump squat exercise. Ten resistance trained men (one repetition maximum (1RM) $> 1.5 \times$ body mass) performed a series of jump squats to a constant depth (thigh parallel to the ground) with external loads of 0, 30, 60 and 90% of 1RM. Vastus lateralis fascicle (L_f), MTU (L_{MTU}) and tendinous tissue (L_t) lengths were measured using high-speed ultrasonography (96 Hz sampling rate). F_t and RFD_t were calculated using inverse dynamics by combining force platform-derived ground reaction force data and kinematic data obtained by high-speed motion analysis. F_t increased as loading increased but no significant differences were found in RFD_t , however jump height and movement velocity decreased with increasing load. Analysis of MTU behaviour revealed that the tendon went through two distinct lengthening and shortening phases, with one each in the eccentric and concentric movement phases. L_t increased as loading increased during the eccentric phase (14-20% of movement duration), but this was significantly less during the 0% loading condition than the heavier loads. These results show that the tendon functioned as a predominately compliant and elastic structure, showing greater lengthening and shortening as loading increased, which is in contrast to previous findings for the leg extension exercise (Chapter 4). Differences in tendon function between these movements most likely resulted from the smaller F_t and RFD_t in the jump squat movement compared to the leg

extensions. Since tendon strain and stress are believed to influence tendon mechanical adaptations, the results from the current study suggest that heavy external loads would be superior to light loads for stimulating tendon adaptation.

INTRODUCTION

External load is arguably the most commonly manipulated variable in resistance training programmes (23). In chapter 4 the effect of external loading on MTU behaviour during an open-chain, isoinertial SSC leg extension was examined. However, resistance training programmes incorporate numerous other movement types, predominately requiring multi-joint isotonic movements. No research, to our knowledge, has investigated how external loading influences MTU behaviour during a multi-joint isotonic movement such as the jump squat exercise, which is commonly used to enhance high-speed force production (63, 113).

It has been well documented that the force developed in a muscle increases as the muscle activity (often assessed using electromyography; EMG) increases (61, 70, 183). However, Cormie et al. (61) found that the rate of rise of EMG was slower when heavier loads were imposed during jump squat movements. As external loading increases the amount of work needed to move a load will increase, along with the amount of force needed to overcome the greater inertia (36, 241). Furthermore, the maximal velocity at which that load can be lifted will decrease as the load increases, according to the force-velocity relationship (36, 241). During a maximal intensity exercise with increasing external loading, peak (EMG_p) and integrated activity (EMG_i) recorded from agonist muscles would be expected to increase substantially, allowing for large forces to be produced over a long period of time. Differences in movement kinetics and muscle activity, such as those previously mentioned, will most likely be associated with a change in MTU behaviour.

While it has been observed that ground reaction force (GRF) increases as loading increases during squat and jump squatting movements (61, 78, 93, 115, 211, 247), the relative changes in joint moments that occur to provide these extra forces has received relatively little attention (93, 115, 211). Previous research has found that both knee and hip extensor moments increase as loading

increases in the squat exercise (115, 147). In contrast, ankle plantar flexor moment decreases and knee extensor moment increases during drop jumps of increasing intensity (90, 133). To our knowledge, however, joint moments have not been measured during jump squats under different loading conditions. During movements such as the jump squat, which utilises a large ranges of motion, knee extensor joint moment can be strongly influenced by the degree of knee flexion (22, 106, 147) and the movement of the centre of pressure at the feet which dictates the moment arm length through which GRF is exerted (36, 210, 211, 241). Thus, it is of interest to determine the specific joint kinetics and muscle activity that occur during jump squats performed with different loads, as these variables are important determinates of MTU behaviour.

MTU behaviour is strongly influenced by the mechanical properties of its respective muscles and tendons (29, 45, 79, 194, 212, 229). Inactive muscles are relatively compliant compared to tendons (6), but they may be stiffer when active during high intensity movements (132, 133). In contrast to muscles, tendons have lower metabolic activity and their mechanical properties are not actively controlled. However, tendons are viscoelastic and thus their mechanical properties vary in response to amplitude and temporal changes in stress applied to them by the muscle (19, 29, 45, 79, 159, 212, 229). Tendon strain increases as muscle force increases (29, 45, 79, 194, 212), however the non-linear relationship between force and elongation also predicts that continued increases in force results in progressively less deformation (162, 165, 212). Furthermore, due to the tendon's viscous properties, elongation is reduced as the rate of loading, and thus tendon stiffness, increases (29, 95, 212, 229). These complex relationships make prediction of muscle-tendon unit behaviour difficult during complex movements, and ensues that prediction of MTU behaviour is difficult to model in complex, multi-joint movements such as the jump squat.

In the previous chapter (Chapter 4) it was shown that the strain of the tendon decreased as external loading increased during an isoinertial SSC leg extension, resulting in the tendon functioning as a relatively rigid structure by

which force was transferred. However, these results contrast those found during jumping and drop jumping using a sledge apparatus (133, 136, 138). Muscle strain decreased as either the drop or rebound height was increased, which allowed the tendon to contribute more to the overall lengthening and shortening of the MTU (80, 133, 136, 138, 206). In these studies it was found that the muscle worked quasi-isometrically and the tendons served as power amplifiers by functioning in a catapult-like manner. The disparities between the MTU behaviour observed in the previous chapter and those observed in other studies was attributed to the substantially greater tendon forces (F_t) elicited during the knee extension; the greatest load during the knee extensor study resulted in approximately three times the estimated F_t observed during previous jumping studies. An alternative or complimentary explanation was that the rate of force development (RFD_t) also influenced tendon stiffness, and its behaviour. However, the specific effect of RFD_t could not be determined because RFD_t was not measured in previous jumping/sledge jumping studies (132, 133, 136).

The purpose of the current study was to determine how MTU behaviour is influenced by external loading during maximal intensity jump squats. In this specific study, the monoarticular vastus lateralis (VL) was examined, and assumed to be indicative of the other vastii muscles. A parallel-depth (i.e. large range of motion) jump squat exercise was used to ensure the knee range of motion was greater than used in previous jump and sledge jump studies (132, 133, 138). This information will provide a better understanding of how the vastii muscles and their tendon interact during exercises similar to those commonly performed in resistance training programmes. A secondary purpose was to determine how loading influences joint kinetics and muscle activity during squat jumps. This information, along with knowledge of MTU behaviour, will lead to a better understanding of the physical stresses on the body during resistance training and may allow us to better understand the stresses responsible for commonly observed load-specific training adaptations.

METHODOLOGY

The methodology described below pertains to the experiments detailed in both chapters 5 and 6. Testing for both chapters was done simultaneously using the same subjects but with different exercises/loads being used for comparison.

SUBJECTS

Ten healthy, resistance-trained men, who habitually performed squat and jump exercises [age: 25.8 ± 2.8 yr, height: 1.77 ± 0.06 m, body mass (BM): 83.8 ± 9.4 kg] participated in the study after signing an informed consent document. The subjects were screened to ensure that their one-repetition maximum (1RM) for the parallel squat was at least 1.5 times their BM (1RM: 138 ± 16 kg, 1RM:BM: 1.65 ± 0.12) and that they did not have a history of lower body musculoskeletal injuries or tendinopathy. This study was reviewed and approved by the Human Research Ethics Committee of the University and subject gave their written informed consent prior to participation.

EXPERIMENTAL DESIGN

Participation in this study involved three sessions, a familiarisation session, 1RM testing and the experimental session during which all the data reported was collected. The subjects were familiarised with the experimental protocol and had their 1RM determined on two separate days prior to the experimental session. The subjects were required to refrain from any exercise for at least 48 hours and refrain from alcohol for at least 24 hours prior to the experimental session. During the experimental session, the subjects performed parallel-depth slow-tempo traditional squats (TS-P), volitional speed squats (VS-P), and jump squats (JS-P), with external loads of 0 (body weight), 30, 60 and 90% of 1RM. Movement kinetics, prime mover (knee, hip and back extensors and plantar flexors) muscle activity and vastus lateralis (VL) MTU behaviour were assessed during each repetition. Comparisons of MTU behaviour, muscle activity and movement kinetics were then made between the different loads for

the maximal speed JS-P (Chapter 5) as well as between the three movements with varying speeds (TS-P, VS-P and JS-P) with the 60% load (Chapter 6)

MOVEMENT TECHNIQUE

Squat and jump squat movement technique was closely monitored and controlled throughout all sessions as subjects recruited for this study came from a variety of sporting backgrounds (weightlifting, powerlifting, basketball, etc.) and exhibited a variety of squat and jump squat techniques. Subjects were required to perform all squats and jump squats to a parallel depth (monitored in real time, as described below), as determined by the femoral line (line between the greater trochanter and the lateral epicondyle) being parallel to the ground. Prior to initial testing, subjects performed a parallel depth squat during which bar displacement was measured using a linear position transducer ([LPT] PT5A-150, Celesco Transducer Products, Chatsworth, CA) and the right knee joint angle was continuously monitored using an electronic goniometer (MLTS700, AD Instruments USA) at 1000 Hz. The maximal knee flexion angle and minimum bar displacement achieved during this squat was then used as the standard depth for all squats and jump squats performed during the experimental testing session. During the experimental testing session, the subjects were required to flex the knees to within $\pm 2.5^\circ$ and provide a bar displacement within ± 1.25 cm of that used during their 1RM test for all squat and jump squat conditions. These values were monitored in real-time and verbal and/or visual feedback was given to the subjects after each repetition.

ONE REPETITION MAXIMUM

The 1RM testing session was initiated with a standardised warm-up. The warm-up consisted of five minutes of low intensity cycling (5 kP, 60 rpm) on a cycle ergometer (Erogonomic 839, Monark, Sweden) as well as 4 sets of submaximal squats with two minutes rest between sets and loads based on estimated 1RM (10 repetitions at 0%-1RM, 8-repetitions at 50%-1RM, 3-repetitions at 80%-1RM and 1-repetition at 90%-1RM). Subjects were given

three minutes rest between 1RM attempts and all subjects obtained their 1RM within six attempts (23).

SQUAT AND JUMP SQUAT TESTING

During the experimental session subjects were required to perform jumps (JS-P) and squats (TS-P and VS-P) with different loads based on percentages of their 1RM. Subjects performed the same standardised warm-up as the 1RM testing session with the addition of one set of three total unloaded submaximal jump squats at 30, 60 and 90% of perceived maximal intensity. After completing the warm-up, the subjects performed the three test exercises: TS-P, VS-P and JS-P. The subjects were required to squat at a constant slow, controlled speed (2 seconds eccentric phase-1 second pause-2 seconds concentric phase) during TS-P. Movement speed was controlled using a metronome and repetitions not matching these criteria were discarded and the repetition repeated. During VS-P, subjects squatted using a self-selected (i.e. volitional) speed but were instructed not to pause during the amortization phase (i.e. the transition from eccentric to concentric phases). During JS-P, the subjects were instructed to jump as high as possible whilst keeping the load in constant contact with their shoulders, but no other instruction was given. Subjects performed each exercise using four loads: 0 (body weight), 30, 60 and 90% of their previously determined 1RM. Subjects performed all four loads of each exercise before performing a different exercise, and the exercise and load orders were randomised and counterbalanced between the subjects to minimise order effects. For each exercise and load combination the subjects performed at least two repetitions, each separated by one minute of rest. Between different loads and/or exercises the subjects were given two minutes of rest; additional repetitions were performed if the knee angle or bar displacement did not match the testing criteria. For each load and lift combination the repetition that most closely matched the knee angle and bar displacement achieved during their 1RM test was then used for analysis.

EMG COLLECTION AND ANALYSIS

EMG signals were recorded from VL, vastus medialis (VM), rectus femoris (RF), biceps femoris (BF), gluteus maximus (GM), erector spinae (ES), medial gastrocnemius (MG), soleus (SO) and tibialis anterior (TA) as per SENIAM guidelines (121) using two self-adhesive surface electrodes (Meditrace, Tyco Healthcare, Australia) placed in a bipolar configuration over their respective muscles (241) on the right side of the body. Inter-electrode distance was set at 2 cm and all signals were checked to ensure inter-electrode impedance was $< 5 \text{ k}\Omega$. Raw EMG signals were recorded using a wireless EMG system (ZeroWire, Aurion, Milan Italy) at an analogue-to-digital conversion rate of 2000 Hz and 16-bit resolution after being amplified (1000 \times). Recorded signals were full-wave rectified and filtered using a dual-pass, sixth-order, 10-500 Hz band-pass Butterworth filter, and then a linear envelope was created using a low-pass, second-order Butterworth filter with a cut-off frequency of 6 Hz.

EMG signals recorded during each repetition were normalised to the peak muscle activity recorded during a 0% (body weight) jump squat to volitional depth. This allowed signals to be reported as a percentage of the maximal activity observed during a bodyweight countermovement jump. This normalisation procedure was implemented because pilot testing showed that all muscles were active with repeatable amplitudes, and the large number of muscles and subjects tested precluded the normalisation methodology described in Chapter 3.

For each muscle, the EMG signals collected from the start of the movement until the movement's completion were reported in three ways to describe muscle activity. Firstly, the greatest EMG value was reported as the peak muscle activity (EMG_p). Next the integrated EMG signals (EMG_i) obtained throughout the movement were used to describe the total muscle activity of the movement. Lastly, the average of recorded muscle activity (EMG_a) was used to

express the changes in total muscle activity without the influence of changes in movement duration.

MOVEMENT KINETICS

During the experimental session the subjects started all movements standing on a tri-axial force platform sampling at 1000 Hz (9290AD, Kistler Instruments, Winterhur Switzerland) holding a bar with a ceiling-mounted linear position transducer (LPT) attached 10 cm from its centre. The peak resultant GRF, as recorded from the force platform, was defined as the magnitude of the resultant X, Y and Z vectors. Minimum bar position (i.e. depth) during all movements and maximum bar height (i.e. jump height) during JS-P were directly measured using the LPT while eccentric and concentric bar velocity (v_{Bar}) and acceleration (a_{Bar}) were calculated as the first and second derivatives of the displacement-time data. Whenever a time derivative was calculated the signal was smoothed using a 6 Hz, 3rd order Butterworth filter prior to its use in any calculations. Total system power exerted on the bar (P_{Bar}) was calculated by integration of vertical GRF and bar velocity data as:

$$P_{Bar} = GRF_z \times v_{Bar} \quad [Eq\ 8]$$

A high-speed camera (Sony HDV CRX 4100, USA) recording 100 frames per second with a shutter speed of 2000 Hz was placed 2.5 m sagittal to the centre of the bar, and used to record videos of all movements. Reflective markers were placed on the subjects' left sides on the 5th metatarsal head, lateral border of the calcaneus, lateral malleolus of the tibia, distal lateral epicondyle and greater trochanter of the femur, and the side of the neck at the level of the 5th cervical vertebrae. A 4-segment model was created using the X-Y (equivalent of the force plate Y-Z axes) coordinates of each marker. Joint position of the ankle (a: lateral malleolus), knee (k: lateral epicondyle) and hip (h: greater trochanter) throughout the movement and the minimum and maximum joint angle (α), velocity (ω) and acceleration (α) were calculated.

The relative joint moments were estimated by combining force plate and video data using previously published inverse dynamics equations (210), and segmental masses were estimated using cadaver derived equations provided by Dempster (241). Lateral forces and movement were assumed to be insignificant and thus excluded and joint movement were assumed to be identical between the sides of the body (210). To calculate the force and moments (M) acting on and about the ankle (Eq 9, 10 and 11), knee (Eq 12, 13 and 14) and hip (Eq 15, 16 and 17) the following equations were used:

$$A_y = (-GRF_y - m_f \times \alpha_f) \quad [\text{Eq 9}]$$

$$A_z = (-GRF_z + m_f \times g) \quad [\text{Eq 10}]$$

$$M_f = A_y \times (CO_{f,com,z} - CO_{mt,z}) + A_z \times (CO_{f,com,y} - CO_{mt,y}) - GRF_y \times (CO_{f,cm,z} - CO_{cop,z}) + GRF_z \times (CO_{f,com,y} - CO_{cop,y}) + (I_f \times \alpha_f) \quad [\text{Eq 11}]$$

$$K_y = A_y + m_l \times \alpha_k \quad [\text{Eq 12}]$$

$$K_z = A_z + m_l \times g + m_l \times \alpha_k \quad [\text{Eq 13}]$$

$$M_k = M_f + K_y \times (CO_{k,z} - CO_{l,com,z}) + K_z \times (CO_{k,y} - CO_{l,com,y}) + A_y \times (CO_{l,com,z} - CO_{a,z}) + A_z \times (CO_{l,com,y} - CO_{a,y}) + (I_l \times \alpha_k) \quad [\text{Eq 14}]$$

$$H_y = K_y + m_t \times \alpha_h \quad [\text{Eq 15}]$$

$$H_z = K_z + m_t \times g + m_t \times \alpha_h \quad [\text{Eq 16}]$$

$$M_h = M_k + H_y \div (CO_{h,z} - CO_{t,com,z}) + H_z \div (CO_{h,y} - CO_{t,com,y}) + K_y \div (CO_{t,com,z} - CO_{k,z}) + K_z \div (CO_{t,com,y} - CO_{k,y}) + (I_t \times \alpha_h) \quad [\text{Eq 17}]$$

Where A , K and H are the forces acting upon each joint, M is the joint moment, m is segmental mass, g is gravitational acceleration and I is the moment of inertia. Two dimensional Cartesian coordinates (CO) are given for 5th metatarsal (mt), ankle (a), knee (k) and hip (h) as well as the centre of mass (com) of the foot (f), lower leg (l) and thigh (t). The vertical (z) and fore/aft (y) values are given.

Relative joint moments (M_r) were calculated by dividing the joint moment by the subject's body mass (Eq 18) and joint power (P) was calculated by multiplying the torque by the angular velocity of the joint (Eq 19):

$$M_r = M / BM \quad [\text{Eq 18}]$$

$$P = M \times \alpha \quad [\text{Eq 19}]$$

Patellar tendon forces (F_t ; Eq 19) were estimated using the joint-derived moment arm length of the patella (MA_p) as determined using a previously published model (232):

$$F_t = M_k \times MA_p \quad [\text{Eq 19}]$$

The rate of force development in the tendon (RFD_t ; Eq 20) was calculated using the change in force at a given instant in time (t_i) of the F_t , after it was smoothed with a 5 Hz low-pass, 3rd order Butterworth filter:

$$RFD_t = (F_{ti-1} - F_{ti}) \div (t_i - t_{i-1}) \quad [\text{Eq 20}]$$

MTU BEHAVIOUR

During TS-P, VS-P and JS-P, B-mode ultrasonography (Alpha 10, Aloka, Co Ltd, Tokyo, Japan) was used to obtain images of the VL fascicles for determination of fascicle length (L_f) and fascicle angle (A_f) throughout the movement. A 6-cm linear array, 10-MHz T-head transducer (UST 5713, Aloka Co Ltd, Tokyo, Japan) was used to collect images at 96 Hz. The transducer was placed at 50% of the distance between the greater trochanter and the lateral condyle of the femur and aligned with the direction of the VL fascicles so that the echoes delineating a single fascicle could be tracked throughout the entire range of motion of the knee. A thin echo-absorbent reference strip was fixed to the subject to allow for correction of any probe movement that occurred during the testing. The transducer head was fixed to the subject using a custom-made thermoplastic cast and taped into place.

Ultrasound images were analysed using DartFish video analysis software (Prosuit 5.0, DartFish, Sydney, Australia). An individual fascicle was tracked throughout the movement and the L_f of that fascicle and A_f from the deep aponeurosis were recorded for each image. In positions where the entire fascicle was not visible in the image (132), the fascicle and aponeurosis were linearly extrapolated to their intersect point using a parallelogram model using Eq 21, where F_{TM} is the measured portion of the fascicle, MT is the cross-sectional distance between the most superficial part of the measured fascicle to the superficial aponeurosis. This method has been shown to be both valid and reliable (168).

$$L_f = L_{fM} + [MT \times \cos (A_f)] \quad [\text{Eq 21}]$$

MTU length (L_{MTU}) was estimated using previously derived models based on the joint position and limb length of each subject (117) (Eq 22) and the length of the tendinous tissue (L_t) was calculated as the longitudinal length of the recorded fascicle subtracted from L_{MTU} (Eq 23).

$$L_t = L_t (prox) + L_t (dist) \quad [Eq\ 22]$$

$$L_{MTU} = L_t + L_f \times \cos (A_f) \quad [Eq\ 23]$$

It should be noted that L_t calculated with this method includes the distal and proximal tendon components (6, 132, 168). Shortening and lengthening velocities of the fascicle (v_f) were calculated as the change in length over time during both the concentric and eccentric phases of movement.

DATA COLLECTION AND PROCESSING

LPT and EMG data were simultaneously recorded using a data acquisition system and its associated software (PowerLab 16/35 and LabChart 7.2, AD Instruments, Bella Vista Australia). Ultrasound images were synchronized using a 5-volt output pulse triggered by the data acquisition software, sent to the ultrasound system that was also used to initiate recording of the force plate. The high speed video was synchronised with the data acquisition system using a custom-made one-way light switch.

All signal filtering and analysis were performed using custom-written LabView programs (Labview 8.2, NI Instruments, Texas USA). To allow for comparison between movements with different durations, signals were time-normalized and represented as a percentage of the movement between the start of the eccentric phase of the movement to the completion of the concentric phase of the movement (or when the foot left the force plate during the JS-P condition) (61).

STATISTICAL ANALYSIS

Repeated measures MANOVAs with Bonferroni *post hoc* tests were used to examine differences in MTU, fascicle and tendon measurements, movement kinetics and muscle activity between the four loading conditions during the JS-P movement (Chapter 5) as well as differences between the TS-P, VS-P and JS-P

movements with the 60% loads (Chapter 6). A second repeated measures MANOVA was also used to determine differences in the tendon length through the duration of the movement using the time-normalised tendon length curves. Results are presented as mean \pm SD. All statistical analyses were conducted using PASW 18.0.1 (IBM, New York, USA) and statistical significance was accepted at an α -level of $p \leq 0.05$.

RESULTS

Varying the external load during jump squats significantly influenced VL MTU behaviour, movement kinetics and muscle activity. Temporal examination of L_t revealed that the tendon went through significantly less lengthening during loading (when the muscles were active) in the eccentric phase under the 0% load than either the 60% (19-20% normalised time) or 90% (14-17% normalised time) loads (Figure 25). However, during the end of the concentric phase of the movement, when the tendon went through a second loading and then an unloading phase, no significant differences in L_t were found between the loads.

Total body and joint kinetic data are presented in Tables 4 and 5. The differences in tendon lengthening occurred despite there being no significant difference in squat depth (Table 4), knee flexion or dorsiflexion magnitude (Table 5). However, there was significantly greater hip flexion in the 0% loading condition than all other loads (Table 5). Thus, across the loading, kinetically similar movement patterns were exhibited, although they were not identical.

GRF increased as external loading was increased, whilst jump height, power, and both eccentric and concentric v_{bar} and a_{bar} decreased (Figure 28 and Table 4). Knee and hip joint kinetics showed similar results, with extension (concentric) angular velocity (ω) decreasing across all loads (Table 5) whilst there was a significant effect of loading on ω_k and ω_h during flexion (i.e. the eccentric phase, differences were not found across all loads). No significant

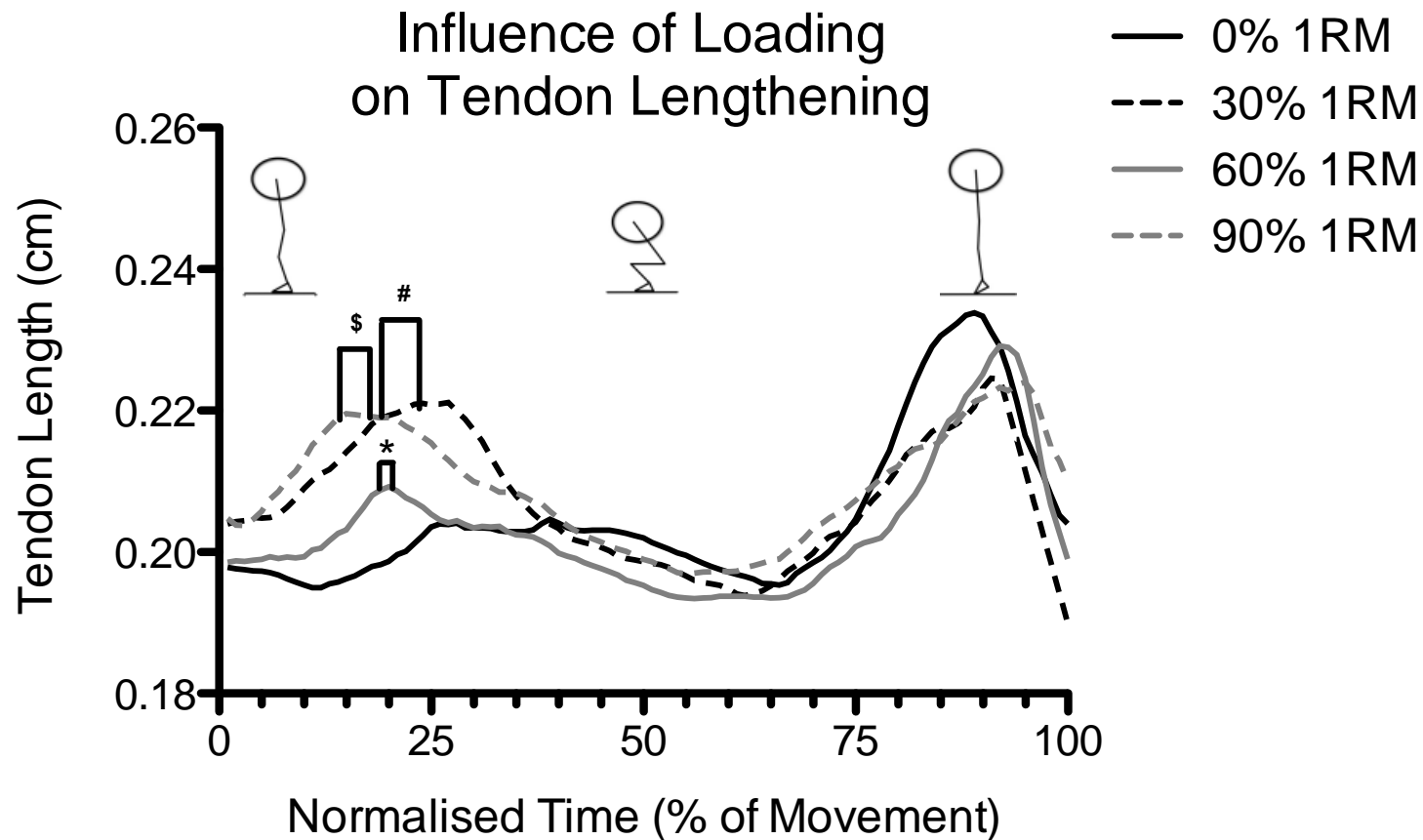


Figure 25: The influence of loading on tendon lengthening. External loads of, 0, 30, 60 and 90% of one repetition maximum (1RM) were compared during a jump squat movement across the movement duration. Time is normalised and represents a percentage of the total movement duration. Significant differences in between 0% load and other loads are indicated by *'s.

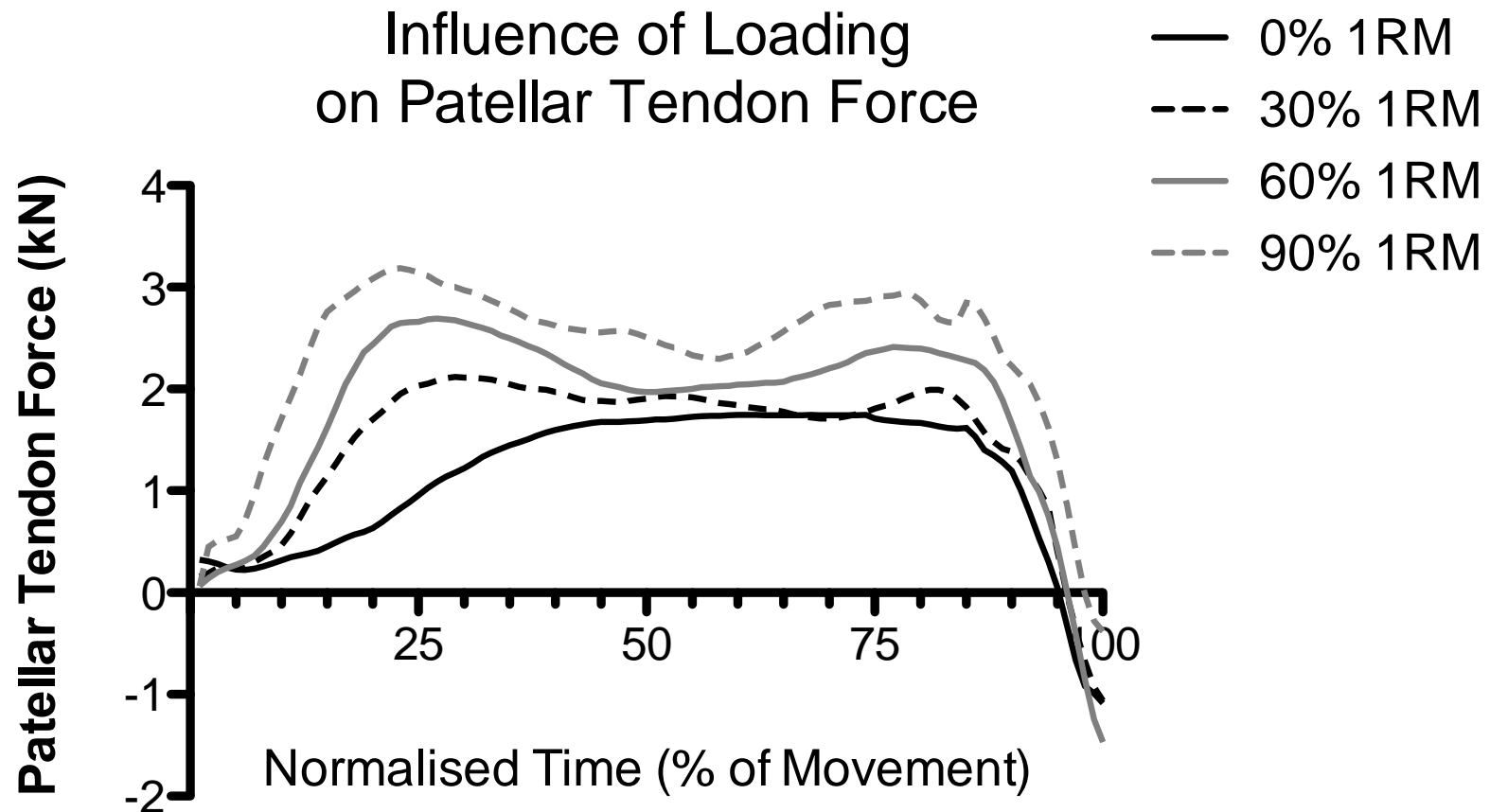


Figure 26: The influence of external loading on patellar tendon force (F_t). External loads of, 0, 30, 60 and 90% of one repetition maximum (1RM) were compared during a jump squat movement across the movement duration. Time is normalised and represents a percentage of the total movement duration.

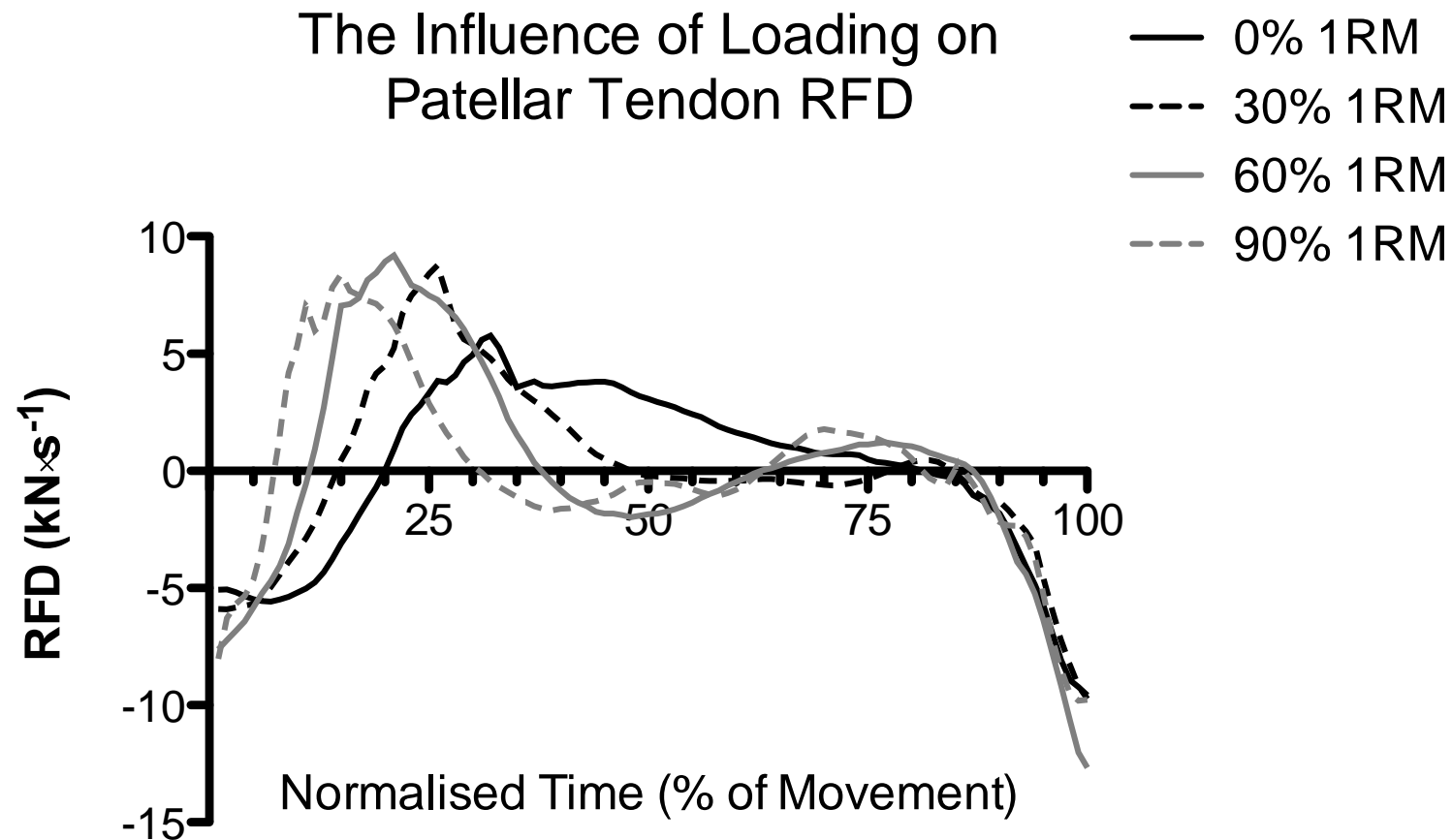


Figure 27: The influence of external loading on patellar tendon rate force development (RFD_t). Positive values represent tendon loading, while negative values represent unloading. External loads of 0, 30, 60 and 90% of one repetition maximum (1RM) were compared during a jump squat movement across the movement duration. Time is normalised and represents a percentage of the total movement duration.

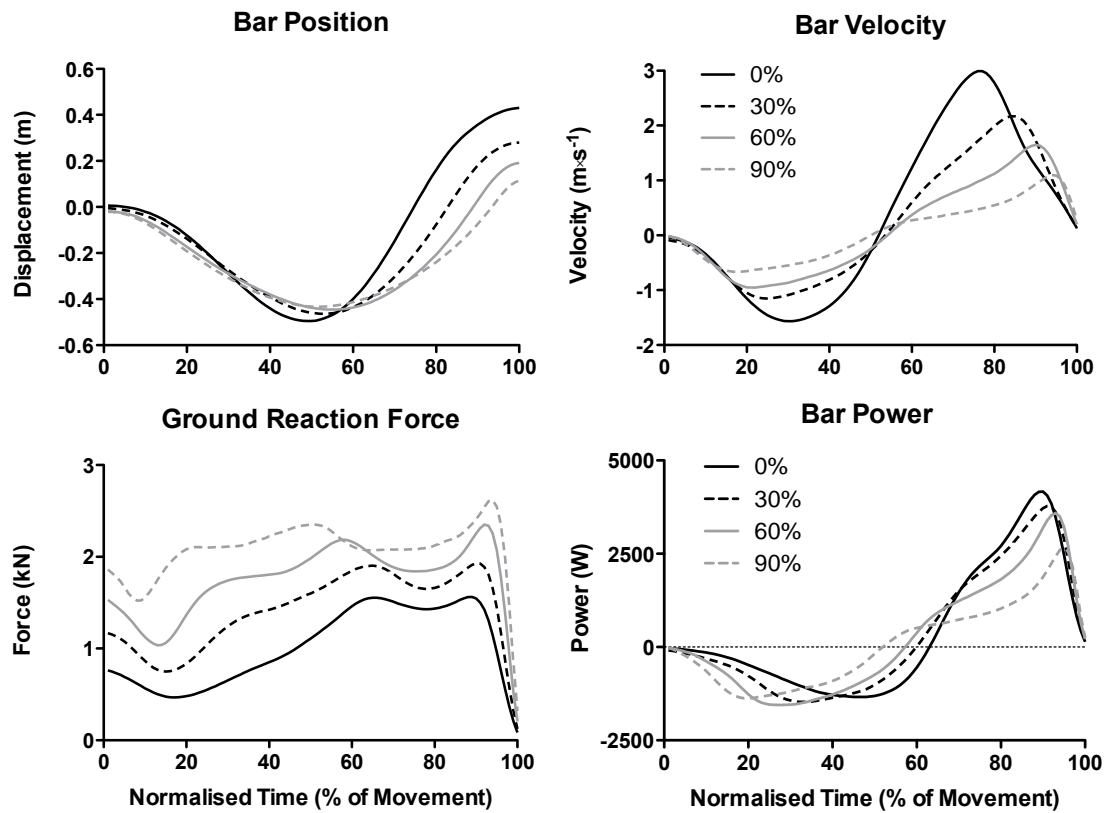


Figure 28: The influence of loading bar position (A), bar velocity (B), ground reaction force (C) and power exerted on the bar (D). External loads of, 0, 30, 60 and 90% of one repetition maximum (1RM) were compared during a jump squat movement across the movement duration. Time is normalised and represents a percentage of the total movement duration.

| Variable | Load | Mean \pm SD |
|--|------|----------------------------------|
| Ground Reaction Force-Z (kN) | 0 | 1.65 \pm 0.24 _{bcd} |
| | 30 | 2.08 \pm 0.35 _{acd} |
| | 60 | 2.37 \pm 0.32 _{abd} |
| | 90 | 2.66 \pm 0.40 _{abc} |
| Jump Height (m) | 0 | 0.439 \pm 0.054 _{bcd} |
| | 30 | 0.282 \pm 0.039 _{acd} |
| | 60 | 0.187 \pm 0.027 |
| | 90 | 0.112 \pm 0.029 _{abc} |
| Bar Velocity-Eccentric (m·s ⁻¹) | 0 | 1.61 \pm 0.25 _{bcd} |
| | 30 | 1.20 \pm 0.29 _{acd} |
| | 60 | 0.97 \pm 0.25 _{abd} |
| | 90 | 0.71 \pm 0.22 _{abc} |
| Bar Velocity-Concentric (m·s ⁻¹) | 0 | 3.08 \pm 0.22 _{bcd} |
| | 30 | 2.28 \pm 0.21 _{acd} |
| | 60 | 1.67 \pm 0.17 _{abd} |
| | 90 | 1.16 \pm 0.18 _{abc} |
| Bar Acceleration-Eccentric (m·s ⁻²) | 0 | 12.62 \pm 5.24 _{bcd} |
| | 30 | 8.26 \pm 2.69 _{acd} |
| | 60 | 7.54 \pm 2.91 _{abd} |
| | 90 | 5.21 \pm 1.90 _{abc} |
| Bar Acceleration-Concentric (m·s ⁻²) | 0 | 14.38 \pm 2.65 _{bcd} |
| | 30 | 7.90 \pm 1.78 _{acd} |
| | 60 | 5.04 \pm 1.48 _{abd} |
| | 90 | 3.40 \pm 1.23 _{abc} |

Table 4: Movement kinetics: the influence of load. Absolute and peak values obtained during the eccentric (Ecc) and concentric (Con) phases are given. Significant differences between 0 (a), 30 (b), 60 (c) and 90% (d) are shown.

| Variable | Ankle | | Knee | | Hip | |
|--|-------|--------------------------------|------|-------------------------------|------|--------------------------------|
| | Load | Mean \pm SD | Load | Mean \pm SD | Load | Mean \pm SD |
| Peak Flexion ($^{\circ}$) | 0 | 85 \pm 5 | 0 | 78 \pm 18 | 0 | 64 \pm 17 _{bcd} |
| | 30 | 84 \pm 6 | 30 | 78 \pm 18 | 30 | 77 \pm 15 _a |
| | 60 | 84 \pm 7 | 60 | 76 \pm 17 | 60 | 78 \pm 17 _a |
| | 90 | 85 \pm 5 | 90 | 80 \pm 21 | 90 | 80 \pm 17 _a |
| Angular Velocity-Eccentric ($^{\circ}\cdot s^{-1}$) | 0 | 95 \pm 32 | 0 | 226 \pm 17 _d | 0 | 241 \pm 20 _{bd} |
| | 30 | 80 \pm 21 | 30 | 209 \pm 38 | 30 | 187 \pm 34 _{ad} |
| | 60 | 71 \pm 25 | 60 | 192 \pm 43 | 60 | 196 \pm 75 |
| | 90 | 76 \pm 36 | 90 | 167 \pm 42 _a | 90 | 144 \pm 25 _{ab} |
| Angular Velocity-Concentric ($^{\circ}\cdot s^{-1}$) | 0 | 361 \pm 53 _d | 0 | 592 \pm 85 _{bcd} | 0 | 457 \pm 60 _{bcd} |
| | 30 | 333 \pm 49 _d | 30 | 509 \pm 62 _{acd} | 30 | 357 \pm 50 _{acd} |
| | 60 | 335 \pm 85 | 60 | 430 \pm 54 _{abd} | 60 | 301 \pm 51 _{abd} |
| | 90 | 248 \pm 56 _{ab} | 90 | 327 \pm 61 _{abc} | 90 | 227 \pm 38 _{abc} |
| Relative Moment (N \cdot kg $^{-1}$) | 0 | 1.03 \pm 0.45 _{bcd} | 0 | 1.68 \pm 0.56 _d | 0 | 1.54 \pm 0.56 _{bcd} |
| | 30 | 1.56 \pm 0.66 _a | 30 | 1.82 \pm 0.90 _d | 30 | 2.10 \pm 0.80 _{ad} |
| | 60 | 1.73 \pm 0.72 _a | 60 | 2.07 \pm 0.95 | 60 | 2.52 \pm 0.93 _a |
| | 90 | 1.84 \pm 0.87 _a | 90 | 2.28 \pm 1.00 _{ab} | 90 | 2.69 \pm 0.74 _{ab} |
| Relative Power (W \cdot kg $^{-1}$) | 0 | 2.27 \pm 1.68 | 0 | 5.33 \pm 3.88 | 0 | 7.10 \pm 3.34 |
| | 30 | 3.78 \pm 3.22 | 30 | 5.08 \pm 3.24 | 30 | 6.57 \pm 3.07 |
| | 60 | 4.29 \pm 3.86 | 60 | 4.91 \pm 3.46 | 60 | 7.16 \pm 2.70 |
| | 90 | 4.06 \pm 3.32 | 90 | 4.37 \pm 3.50 | 90 | 5.38 \pm 2.67 |

Table 5: Joint kinetics: the influence of load. Absolute and peak values obtained during the eccentric (Ecc) and concentric (Con) phases are given. Significant differences between 0 (a), 30 (b), 60 (c) and 90% (d) are shown.

differences were found in eccentric ω_a , however, concentric ω_a was significantly faster in the 0% and 30% loading conditions than the 90% condition. Ankle, knee and hip moments (M) varied significantly with load (Table 5). M_a was significantly less under the 0% load than the other loads. M_k was significantly less under the 0% and 30% loads than at 90%, and M_h increased significantly with load (although M_h was not significantly different between the 60% and the 30 or 90% loads: Table 5).

Estimated patellar tendon forces, and F_t - and RFD_t -time curves are presented in Figures 26 and 27. F_t significantly increased as loading increased, and was greater under the 60% and 90% loads than 0%, and greater under the 90% load than 30% (Figure 29). However, no significant differences in tendon loading rate (+ RFD_t) or unloading rate (- RFD_t) were found, despite mean values tending to increase in magnitude as the load was increased (Figure 29). MTU structural data are presented in Table 6. No between-condition differences in maximal or minimal L_{mtu} , L_t , L_f , A_f . v_f measured during lengthening did not differ across loading conditions was not significantly influenced by loading, despite a mean decrease of 47% between the 0% and 90% loads. However, shortening v_f decreased significantly as the load was increased.

Muscle activity was significantly influenced by the external load used (Table 7 and Figure 30). Knee extensor (VL, VM and RF), plantar flexor (MG and SO), GM and ES EMG_i significantly increased as the loading was increased. However, a significant difference between all loads was found only in the knee extensors. No significant differences were found in TA or BF EMG_i . EMG_a was only significantly different between loads for VL and SO, and these differences were not found across all loads. Lastly, EMG_p was not significantly different between loads for any of the recorded muscles. However, the increase in VL EMG_p as loading increased approached significance ($p=0.061$) when comparing 0% load to the 90% load.

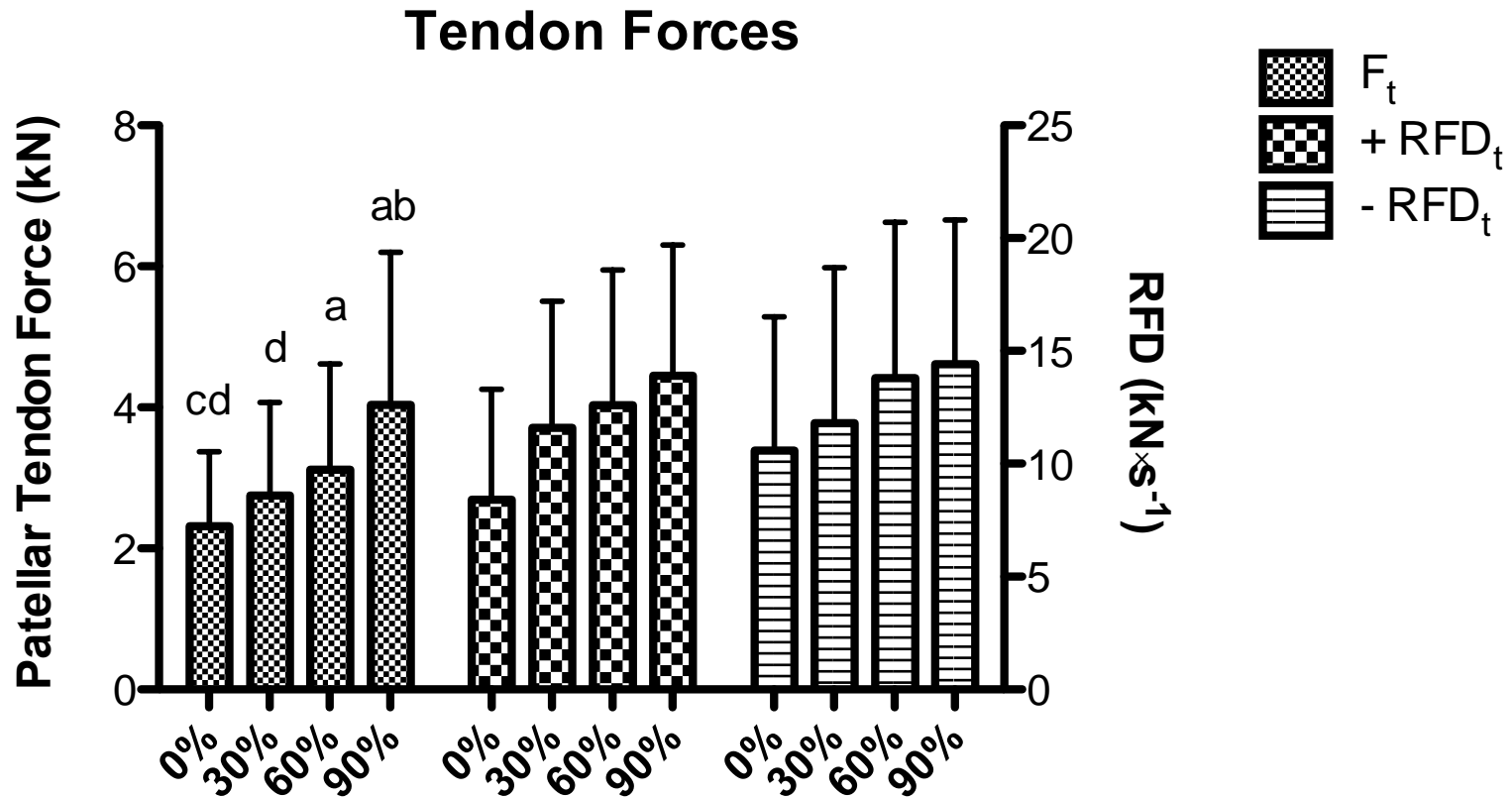


Figure 29: The influence of loading the forces acting on the patellar tendon. The patellar tendon force (F_t) and the rate of loading ($+RFD_t$) and unloading ($-RFD_t$) on the tendon are presented and significant differences between loads of 0 (a), 30 (b), 60 (c) and 90% (d) of one repetition maximum (1RM) are shown.

| Variable | Load | Minimum Mean \pm SD | Maximum Mean \pm SD |
|---|-------------|---|---|
| MTU Length (cm) | 0 | 26.1 \pm 2.5 | 33.3 \pm 2.8 |
| | 30 | 25.7 \pm 2.3 | 33.3 \pm 2.8 |
| | 60 | 25.9 \pm 2.3 | 33.3 \pm 2.8 |
| | 90 | 26.0 \pm 2.0 | 33.3 \pm 2.8 |
| Tendon Length (cm) | 0 | 18.0 \pm 3.1 | 24.0 \pm 3.0 |
| | 30 | 17.6 \pm 5.4 | 24.2 \pm 3.6 |
| | 60 | 17.4 \pm 3.8 | 23.7 \pm 3.7 |
| | 90 | 16.2 \pm 3.9 | 23.8 \pm 3.5 |
| Fascicle Length (cm) | 0 | 6.2 \pm 1.3 | 14.1 \pm 2.1 |
| | 30 | 5.8 \pm 1.5 | 14.5 \pm 3.9 |
| | 60 | 5.8 \pm 1.1 | 14.9 \pm 2.6 |
| | 90 | 5.7 \pm 0.9 | 15.2 \pm 2.8 |
| Fascicle Angle ($^{\circ}$) | 0 | 11.1 \pm 1.8 | 22.6 \pm 3.3 |
| | 30 | 10.7 \pm 1.9 | 22.7 \pm 4.1 |
| | 60 | 10.5 \pm 1.9 | 23.2 \pm 3.5 |
| | 90 | 10.4 \pm 1.9 | 23.7 \pm 3.9 |
| Fascicle Velocity ($\text{cm}\cdot\text{s}^{-1}$) | 0 | -11.6 \pm 4.4 | 20.5 \pm 7.5 _d |
| | 30 | -9.3 \pm 2.2 | 20.5 \pm 2.2 _d |
| | 60 | -9.2 \pm 4.0 | 14.1 \pm 7.2 _d |
| | 90 | -7.6 \pm 3.5 | 8.3 \pm 4.4 _{abc} |

Table 6: Muscle-tendon unit (MTU) structure and behaviour: the influence of load. Length of the vastus lateralis MTU (L_{mtu}), fascicle (L_f), and tendon (L_t), the fascicle angle (A_p) and velocity of the fascicle (V_f) are reported. Significant differences between 0 (a), 30 (b), 60 (c) and 90% (d) are shown.

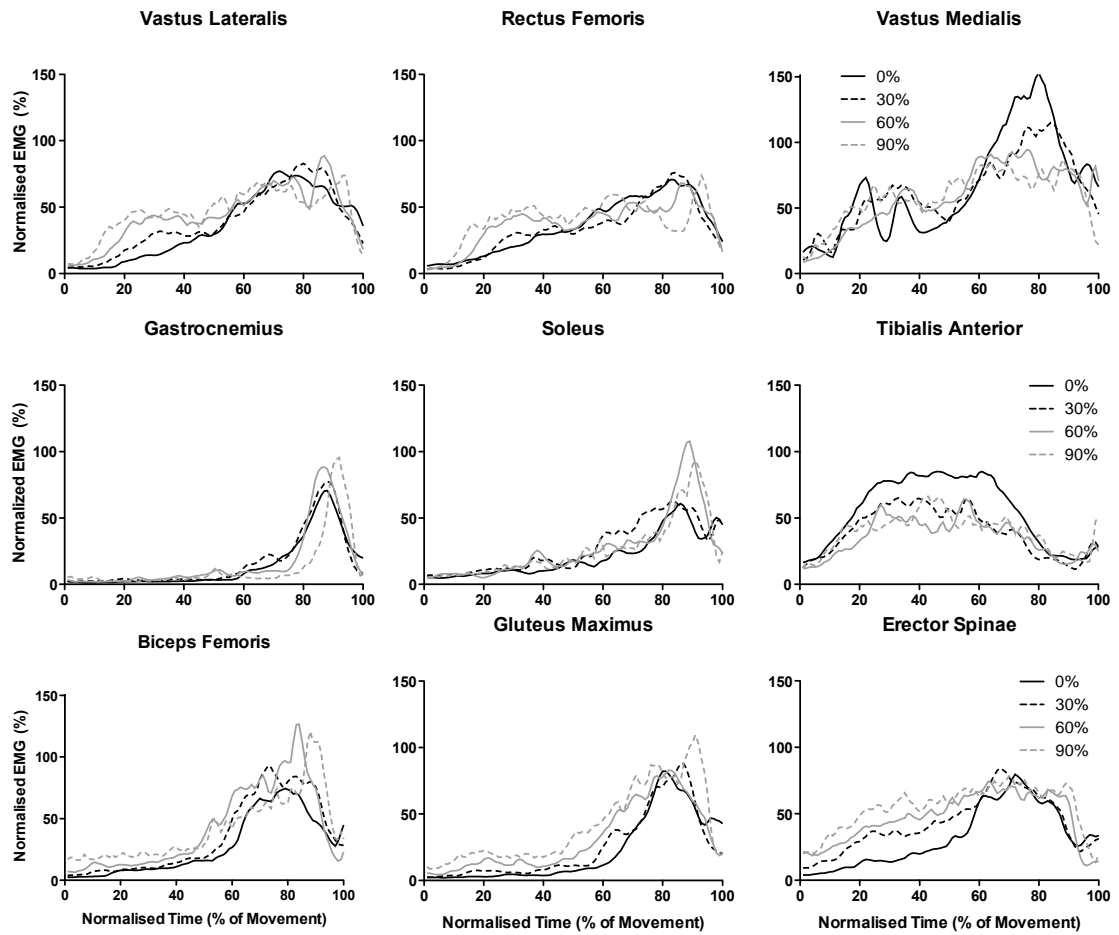


Figure 30: The influence of loading bar on muscle activity of the knee extensors (VL, RF, VM: top row), the plantar- and doris-flexors (MG, SO, TA: middle row) and the hip and lower back extensors (BF, GM and ES: bottom row). External loads of, 0, 30, 60 and 90% of one repetition maximum (1RM) were compared during a jump squat movement across the movement duration. Time is normalised and represents a percentage of the total movement duration.

| Muscle | Load | EMG-Peak Mean \pm SD | EMG-Average Mean \pmSD | EMG-Integrated Mean \pm SD |
|---------------|-------------|--|--|--|
| VL | 0 | 92.1 \pm 20.9 | 36.1 \pm 10.0 _{cd} | 38.9 \pm 10.5 _{bcd} |
| | 30 | 111.4 \pm 39.9 | 38.9 \pm 10.3 _d | 52.4 \pm 13.7 _{acd} |
| | 60 | 115.7 \pm 35.7 | 43.9 \pm 8.7 _a | 76.1 \pm 21.5 _{abd} |
| | 90 | 116.6 \pm 37.3 | 47.3 \pm 9.3 _{ab} | 118.6 \pm 41.0 _{acb} |
| RF | 0 | 101.5 \pm 38.1 | 35.7 \pm 10.5 | 38.3 \pm 10.6 _{bcd} |
| | 30 | 104.4 \pm 23.1 | 33.9 \pm 11.2 | 45.3 \pm 13.9 _{acd} |
| | 60 | 95.9 \pm 26.0 | 37.3 \pm 9.8 | 63.3 \pm 15.5 _{abd} |
| | 90 | 102.2 \pm 26.7 | 40.6 \pm 13.3 | 101.6 \pm 36.0 _{abc} |
| VM | 0 | 99.4 \pm 44.9 | 38.6 \pm 17.1 | 44.2 \pm 6.9 _{bcd} |
| | 30 | 91.3 \pm 37.7 | 40.4 \pm 17.8 | 58.5 \pm 9.8 _{acd} |
| | 60 | 117.8 \pm 50.4 | 48.6 \pm 19.7 | 92.3 \pm 17.2 _{abd} |
| | 90 | 105.8 \pm 45.8 | 50.7 \pm 19.3 | 136.6 \pm 36.0 _{abc} |
| BF | 0 | 103.5 \pm 55.6 | 28.4 \pm 13.4 | 29.1 \pm 11.3 |
| | 30 | 130.3 \pm 70.9 | 35.7 \pm 23.6 | 45.1 \pm 24.0 |
| | 60 | 151.7 \pm 102.2 | 42.0 \pm 34.0 | 69.7 \pm 49.3 |
| | 90 | 139.6 \pm 51.8 | 42.0 \pm 22.0 | 104.7 \pm 62.7 |
| GM | 0 | 96.9 \pm 29.3 | 22.6 \pm 5.3 | 22.9 \pm 5.6 _{cd} |
| | 30 | 99.2 \pm 28.8 | 25.3 \pm 6.6 | 31.6 \pm 8.2 _{cd} |
| | 60 | 113.3 \pm 33.7 | 31.4 \pm 7.4 | 52.1 \pm 8.5 _{abd} |
| | 90 | 150.6 \pm 47.2 | 41.2 \pm 7.5 | 97.5 \pm 17.8 _{abc} |
| ES | 0 | 97.4 \pm 52.0 | 35.3 \pm 17.4 | 40.0 \pm 18.8 _d |
| | 30 | 97.1 \pm 51.5 | 42.7 \pm 20.1 | 57.5 \pm 23.5 _d |
| | 60 | 103.0 \pm 42.3 | 47.1 \pm 19.6 | 82.1 \pm 32.2 _d |
| | 90 | 104.3 \pm 43.0 | 54.7 \pm 24.0 | 147.2 \pm 56.2 _{abc} |
| MG | 0 | 88.0 \pm 18.2 | 14.6 \pm 4.6 | 15.5 \pm 4.8 _{bcd} |
| | 30 | 88.9 \pm 32.6 | 16.3 \pm 5.0 | 21.4 \pm 5.4 _{ad} |
| | 60 | 105.4 \pm 36.0 | 16.4 \pm 4.2 | 27.8 \pm 7.6 _a |
| | 90 | 106.8 \pm 35.7 | 13.3 \pm 3.7 | 33.7 \pm 11.1 _{ab} |
| SO | 0 | 95.1 \pm 48.5 | 18.7 \pm 9.1 | 23.0 \pm 7.5 _{bcd} |
| | 30 | 111.2 \pm 49.4 | 24.5 \pm 13.3 | 36.9 \pm 13.5 _{acd} |
| | 60 | 126.1 \pm 65.3 | 24.9 \pm 12.3 | 48.5 \pm 13.3 _{ab} |
| | 90 | 98.1 \pm 52.4 | 23.9 \pm 12.2 | 74.9 \pm 31.6 _{ab} |
| TA | 0 | 126.9 \pm 60.3 | 55.2 \pm 28.5 | 58.8 \pm 30.5 |
| | 30 | 109.7 \pm 51.4 | 40.0 \pm 20.9 | 53.3 \pm 28.5 |
| | 60 | 101.0 \pm 43.4 | 35.7 \pm 15.2 | 60.0 \pm 24.3 |
| | 90 | 105.3 \pm 49.9 | 39.8 \pm 19.5 | 96.1 \pm 41.8 |

Table 7: Muscle activity: influence of load. The peak (EMG_p), average (EMG_a) and integrate (EMG_i) of muscle activity in the vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF), biceps femoris (BF), gluteus maximus (GM), erector spinae (ES), medial gastrocnemius (MG), soleus (SO) and tibialis anterior are given and significant differences between 0 (a), 30 (b), 60 (c) and 90% (d) are shown.

DISCUSSION

Significant changes in MTU behaviour, kinetics and muscle activity were found as external loading was varied during the jump squat exercise. A major finding of the current study was that greater lengthening of the tendon occurred during the eccentric (loading) phase of the movement as the load was increased. This most likely resulted from the greater muscle activity leading to greater tendon forces (F_t) during the higher load, slower speed movements.

An important strength of the current study was that movement patterns were closely mimicked when jumping with different loads. The subjects were required to perform their countermovements to the same bar depths (± 1.25 cm) and knee angle ($\pm 2.5^\circ$), with real-time feedback being given by the linear position transducer and electronic goniometer. The subjects were resistance-trained ($1RM:BM > 1.5$) and accustomed to training with the jump squat and squat exercises, so this standard was not difficult to maintain. The knee angle at the end of the eccentric phase was chosen as the control variable because L_{mtu} was calculated using a joint angle-derived equation. In contrast, hip and ankle joint angle information was not given to the subjects after each repetition. These criteria seemed effective as no differences in maximum bar depth or knee or ankle flexion were found between loads. However, it must be noted that the subjects exhibited significantly less hip flexion under the 0% load than the other loads. The increased hip flexion under greater loads is most likely a result of a posterior shift in the location of the centre of mass, which occurs when a loaded bar is placed on the subject's shoulders. Because of this difference the subjects performed the jumps under different loads with kinetically similar, but not identical, movement patterns. Such controls have not previously been used during investigations of MTU behaviour during jumping movements (132, 133, 138).

The kinetic data obtained in the current study are consistent with that obtained in previous studies, which demonstrate that the peak forces produced

increase as external loading increases, while jump height, bar velocity and bar acceleration decrease (61, 64, 147, 247). Interestingly, knee angular velocity tended to decrease with increased loading in both the concentric and eccentric phases (significant difference only between the 0% and 90% conditions in the eccentric phase). In all loading conditions bar and knee angular velocities were slower than those measured in the concentric phase, possibly suggesting that subjects adopted a 'controlled' eccentric loading phase followed by a maximum velocity concentric phase. The changing kinetics, which are directly a result of changing external load and possible changes in movement patterns incorporated to optimised performance, are likely to influence MTU behaviour (16, 17).

Whilst there was an overall decrease in movement speed as the load increased, the eccentric velocity expressed as a ratio of the concentric velocity increased as loading intensity increased (38%, 41%, 44% and 51% for the 0, 30, 60 and 90% loads, respectively; $p < 0.05$). Possible explanations for this are that the subjects were less able to control their eccentric velocity as the loading increased, or that increases in load had a greater negative effect on concentric than eccentric force production, as would be predicted from the force-velocity relationship of muscle (238). Importantly, working at a relatively greater eccentric velocity yet slower concentric velocity may have allowed the muscles to operate at velocities which are more favourable for force production (43, 238). However, the 45% decrease in lengthening fascicle velocity as loads were increased from 0 to 90% did not reach statistical significance ($p = 0.15$; $ES = 1.42$) and was only significantly different between the 0 and 90% loads during muscle shortening. Thus, these data suggest, in fact, that changes in muscle shortening velocity were not altered substantially between the loads (Table 4). This resulted from a relatively large inter-subject variability in the effects of load on fascicle velocity. The tendency toward slower fascicle lengthening might have resulted from the quadriceps being used to braking the decent of the body and to ensure that large changes in momentum are not required between the eccentric and concentric phases. Large momentum changes might induce significant reflex inhibition

through Ib, II and IV afferent loops, which would have impacted negatively on concentric movement speed and potentially increase the risk of injury (2, 56, 221). The slower eccentric speed would then also have affected concentric movement performance because less elastic potential energy would have been stored in the eccentric phase (129, 223).

Interestingly, the peak knee extensor (VL, RF and VM) EMG amplitude did not change significantly as the load was increased, although the integrated EMG significantly increased across all loads in all muscles and the mean VL EMG amplitude increased from the 0% to the 60% and 90% loads, and from the 30% to the 90% load. These results suggest that a greater knee extensor muscle activity is present at greater loads through the movement, which is most likely a result of an earlier and more prolonged muscle activation during the eccentric phase (Figure 30). The result of this activity was an increase in F_t and RFD_t [Figures 26 and 27 (45)]. As loading increased, F_t rose earlier in the movement and to a higher value, and the differences in the peak F_t attained were significant when comparing the 0% to the 60% and 90% loads and the 30% to the 90% load (Figure 29). These increases in peak force were not concurrent with increases in the RFD, which had a mean increase from 0 to 90% load of 26% [$p = 0.159$, effect size (ES) = 1.45], although the peak rate of loading occurred earlier in the movement (Figure 29).

As previously stated, a major finding of the current study was that tendon lengthening increased as external loading increased. Tendons serve as a passive structure whose behaviour is dictated by the forces imposed by the muscles as well as the velocity at which they are stretched. Tendons are viscoelastic structures that will stiffen to resist deformation (116, 199, 212, 229) when they encounter greater or more rapidly applied forces. In the present study, the tendon went through greater lengthening as the force expressed through the tendon increased. This behaviour has been previously observed using a custom-designed sledge apparatus when jumping to different heights and drop jumping from different drop heights (90, 132, 133, 206). The maximum F_t we observed

during JS-P with 0% load (2.32 ± 1.05 kN) was similar to those reported by Finni et al. (90) (~ 2 kN) during a unilateral sledge jump while those found during the 90% 1RM jump squat (4.04 ± 2.16 kN) were close to those reported by Ishikawa et al. (133) during drop jumps from 80% of maximum jump height (~ 5.5 kN) and Finni et al. (89) during a sledge drop jump from the optimal jump height (3.6 kN). However, while it is tempting to make comparisons between tendon forces observed in this study and those previously published caution must be taken as the method of force calculation differs between studies. In these studies, tendon lengthening was shown to increase as loading increased, which supports the current findings and demonstrates that the tendon lengthens less under the 0% load than the 60% and 90% loads due to lower forces acting on the tendon. These results contrast those found in the previous study (Chapter 4), where tendon lengthening decreased as both F_t and RFD_t increased. These results suggest that the patella tendon is likely to stretch further under loading as forces are increased in relatively low-load conditions but are likely to stretch less when loads are much greater. Such changes in behaviour could be expected to have significant consequences for movement efficiency and capacity.

A comparison of knee joint kinematics between the leg extension and the JS-P movements revealed that the concentric joint velocities during the lightest loads were similar (0% 1RM jump squat = $592 \pm 85^\circ\text{s}^{-1}$; 20% 1RM leg extension = $593 \pm 86^\circ\text{s}^{-1}$) and at the heavier loads (90%) differed by only 26% (90% 1RM jump squat = $327 \pm 60.8^\circ\text{s}^{-1}$; 90% 1RM leg extension = $443 \pm 60^\circ\text{s}^{-1}$). However, eccentric velocity was approximately 40% slower in the jump squat compared to the knee extension exercise under light loads (0% jump squat = $226 \pm 17^\circ\text{s}^{-1}$ versus 20% leg extension = $397 \pm 68^\circ\text{s}^{-1}$) and 58% slower under the heavy load compared to the knee extension at the greatest load (90% 1RM jump squat = $167 \pm 42^\circ\text{s}^{-1}$ versus 90% 1RM leg extension = $395 \pm 73^\circ\text{s}^{-1}$). With respect to kinetics, the RFD_t values obtained in the current study during JS-P movements were significantly less than those obtained during leg extensions in the previous study. Thus, it appears that both F_t and RFD_t both directly influence the function

of tendon. Under lighter load conditions the tendon functioned increasingly as a compliant-elastic element as RFD_t increased. However, during heavier loading conditions, the tendon functioned as a more rigid structure when RFD_t was increased.

The isoinertial countermovement leg extension used in the previous chapter was chosen in order to isolate the knee extensor muscles during a highly restrictive movement. In contrast, the JS-P movement performed in the current study is a very common movement that is often performed with a wide range of loads. However, difficulties exist in assessing complex (multi-joint) movements during which joint contributions and the locations at which force is exerted (the centre of pressure) can vary greatly. While it was found that tendon lengthening increased as external loading increased in the current study, it is possible that different MTU behaviours are exhibited in other commonly performed training exercises. The parallel-depth jump squat is a relatively slow stretch-shortening cycle movement with durations ranging from <1.5 s (0% load) to >3.5 s (90% load). Since fast eccentric joint velocities and rapid force development seems to elicit dynamic stiffening of the tendon, it is possible that faster, more intense movements, such as drop jumps from a supramaximal drop height or performed with load, could result in increased loading and thereby reduce the tendon strain. However, more research is required to investigate the influence of loading in movements other than the parallel-depth jump squat. As different MTU behaviours may be associated with different training specific adaptations, understanding how acute training variables such as external loading influences MTU behaviour has the potential to increase our understanding of how to maximise the desired adaptations.

Chapter 6

Experiment 4

**The Influence of Speed of Movement
on MTU Behaviour during Squatting
Movements**

Abstract

The influence of speed of movement on MTU behaviour during squatting movements

Since tendons are viscoelastic they should, theoretically, resist deformation more as the rate of force expressed through them increases. Thus tendons should act as a relatively rigid structure during high-speed movements. However, researchers who have observed muscle tendon unit (MTU) behaviour during running and jumping *in vivo* have found the opposite behaviour. This disparity in theoretical prediction versus practice is likely results from the propensity for load-induced tendon stretch to predominate over the increase in stiffness that should reduce tendon stretch. However, it is not known whether volitional movement speed manipulation influences MTU behaviour during a loaded resistance training exercise. Thus, the purpose of the current study was to examine how movement speed manipulation influences MTU behaviour during squat exercises (squats and jump squats). Ten resistance trained men [one repetition maximum (1RM) > 1.5× body mass] performed parallel-depth set tempo (2 s eccentric-1 s pause-2 s concentric: TS-P) and volitional speed squats (VS-P) as well as parallel-depth jump squats (JS-P) with 60% of 1RM. During each lift the vastus lateralis fascicle (L_f), MTU (L_{MTU}), and tendinous tissue (L_t) lengths were measured using high-speed ultrasonography (96 Hz). Patellar tendon force (F_t) and rate of force development (RFD_t) were estimated using inverse dynamics from data collected at high-speed by video camera and force platform. Results indicate that ground reaction forces, F_t and RFD_t increased when the same load was lifted at increasing speeds (TS-P < VS-P < JS-P). As seen in the previous chapter the tendon went through two distinct lengthening and shortening phases; one in the eccentric and one during the concentric phase of the movement. However, the influence of movement speed on MTU behaviour differed between these phases. During the eccentric phase the tendon lengthening decreased as movement speed increased, while during the concentric phase the lengthening

increased as movement speed increased. Differences in tendon behaviour were attributed to high RFD_t measured in the eccentric phase compared to the relatively low RFD_t measured during the concentric phase. These results show that the tendon functioned predominately as a rigid structure during the eccentric phase of the movement when the RFD_t was high, but as a compliant but elastic structure in the concentric phase when RFD_t was relatively low. These results highlight the complexity of MTU behaviour, demonstrating that the function of the tendon as a viscoelastic structure is sensitive to both the F_t and RFD_t exerted through it.

INTRODUCTION

The performance of resistance training exercises at different movement speeds can result in a vastly different mechanical and neurological stimulus being applied to the neuromuscular and musculo-tendinous system and thus in significantly different training-specific adaptations (4, 31, 40, 62, 72, 83, 131, 142, 149, 184, 189). While the role movement speed on muscle activity and force expression has received a great deal of attention, relatively few studies have investigated how movement speed can influence muscle-tendon unit (MTU) behaviour (59, 90). A more complete understanding of the influence of movement speed on MTU behaviour is important in order to determine what mechanical stimulus is applied to the neuromuscular and musculo-tendinous systems during training.

Movement speed greatly influences both the maximal force development (force-velocity relationship) and muscle activity (EMG-velocity relationship) of a movement (23, 241), and can result in vastly different long-term training adaptations (4, 31, 40, 62, 72, 83, 131, 142, 149, 184, 189). Clinicians prescribe exercises with a broad range of movement speeds in order to achieve varying aims (23, 184). It has been claimed that performing exercises with long eccentric and concentric phase durations or incorporating a pause during the amortization phase (i.e. the point of transition from eccentric to concentric phases), allows an individual the time to adjust body position in response to afferent feedback and thus minimise injury risk (23, 184). For these reasons, slow-speed (controlled) movements with a pronounced amortization phase are often used in training programmes. Increasing the movement duration also increases the time under tension of the muscles, which is thought to increase metabolic demand and potentially induce significant hypertrophic adaptations for a given amount of muscle work (26, 33, 224). Of course, only very light loads can be lifted when exceptionally slow movements are performed so muscle size and strength adaptation would be minimal, so there is not probably a benefit in such extreme cases (184).

Movements may also be performed at high speeds in order to improve force production at high rates of muscle shortening (24, 41, 142, 247). However, when the impulse provided to the load during a squatting movement is sufficient, the load will be projected into the air at the end of the concentric phase (i.e. a jump squat) (36). Newton et al. (195) found that when a light load is lifted at its greatest speed without being projected, braking rather than propulsive forces are produced for a significant proportion of the movement. Thus, the agonist muscles do not work for the entire concentric movement phase. This reduction in agonist muscle work may impact on the strength and hypertrophic adaptations elicited by training (195). In addition, high-speed ballistic movements (such as the JS-P) can result in greater forces, velocities and power production than their non-ballistic counterparts (7, 63). For these reasons faster-speed exercises performed without a deceleration of the load toward the end of the concentric movement phase are often shown to be superior to slower-speed exercises for increasing power production, movement speed and high-speed force production after a period of training (7, 63, 113, 164, 182).

While both slow- and fast-speed movements are often performed in training, little is known about the effects that manipulating speed has on MTU behaviour. Finni et al. (90) found no significant differences in fascicle length or angle during isokinetic knee extensions when velocity was varied from 60-180°s⁻¹, but tendon length change was not examined. Tendon stiffness increases as tendon stretch velocity increases, resulting in greater forces being required to cause tendon deformation (116, 194); such behaviour has been credited to the viscous properties of tendons (29, 120, 194, 199). However, at present no known studies have found an increase in dynamic tendon stiffness when speed of movement has been manipulated *in vivo*. In fact, the opposite has been found when speed, and incidentally tendon forces, has been increased during movements such as walking, running, hopping and jumping (90, 134, 138, 171, 205).

MTU behaviour has previously been described for movements when speeds have been either directly or indirectly manipulated. For example, Farley et al. (86) examined the influence of hopping cadence on gastrocnemius MTU behaviour. In this study, the Achilles tendon lengthened less, but the gastrocnemius more during ground contact in bilateral hopping, when hopping frequency was shorter than “optimum”. Studies of walking and running have described similar MTU behaviour in the gastrocnemius when walking velocity was increased (134, 137, 172, 173). However, in these studies it is likely that the forces exerted upon the relatively compliant Achilles tendon were not substantial enough to cause a drastic stiffening of the tendon, since such stiffening would result in reduced tendon lengthening at faster speeds. Additionally, the speed of movement has been indirectly manipulated by changing both the jump and the drop heights during drop jumps (90, 132). In these studies muscle fascicle lengthening decreased and the contribution of the tendon to MTU lengthening increased as movement speed increased (90, 132). However, the difference in speeds was relatively small and the range of motion used with the different speeds was not controlled in these studies, which may account for why an increase in dynamic stiffness was not observed as speed increased. In terms of understanding how movement speed influences MTU behaviour during a complex SSC movement, it is difficult to interpret the results of these previous studies, because the results may have been influenced by the substantial variation in tendon forces, relatively little difference in the movement speeds examined and lack of standardised ranges of motion in the movements investigated. Given the above, the primary purpose of the current study was to examine the influence of movement speed on MTU behaviour during a complex SSC movement (the squat), with a constant external load. A secondary purpose was to investigate the influence of speed of movement on the force expression and muscle activity during the same movement.

METHODOLOGY

Subject characteristics, control variables and methodology for this chapter was been previously explained in detail in chapter 5. Data collection for chapters 5 and 6 was done simultaneously and with the same subjects.

EXPERIMENTAL DESIGN

Participation in this study involved three sessions, a familiarisation session, 1RM testing and the experimental session during which all the data reported was collected. During the experimental session, the subjects performed the following exercises to parallel-depth: slow-tempo squats with a two second eccentric phase followed by a one second static pause prior to a two second concentric phase (TS-P), volitional-speed squat performed at a self-selected (volitional) speed (VS-P) and a jump squat (JS-P) performed with the intent to jump as high as possible and thus, attain the greatest possible concentric movement speed. All movements were performed with external loads of 0 (body weight), 30, 60 and 90% of 1RM. However, only those repetitions performed with the 60% load we used for comparisons in this study. These movements and speeds were chosen because they are commonly prescribed in resistance training programmes (23, 184). Movement kinetics, prime mover (knee, hip and back extensors and plantar flexors) muscle activity and vastus lateralis (VL) MTU behaviour were assessed during each repetition. Comparisons of MTU behaviour, muscle activity and movement kinetics were then made between the three movements with varying speeds (TS-P, VS-P and JS-P) with the 60% load.

RESULTS

Varying movement speed during the squat exercise significantly influenced VL-MTU behaviour, movement kinetics and muscle activation. The tendon went through significantly greater lengthening as the MTU was actively loaded (during the eccentric phase) during the TS-P than during either the VS-P (9-10% and 28-34% normalised time) or the JS-P (8-12% normalised time:

Figure 31) as the MTU was actively loaded (during the eccentric phase). In the JS-P, the tendon went through a distinct lengthening phase prior to its rapid shortening during the concentric phase of the movement, resulting in the tendon being at a significantly longer length than in the VS-P (91-94% normalised time) and TS-P (93-95% normalised time).

Movement and joint kinetics are reported in Tables 8 and 9. The differences in tendon lengthening occurred despite no differences in squat depth (Table 8) or knee, hip or ankle flexion range of motion (Table 9). We successfully manipulated speed of movement between the TS-P, VS-P and JS-P movements as supported by hierarchical differences (TS-P < VS-P < JS-P) in eccentric and concentric v_{bar} and a_{bar} . Concentric angular velocity at the knee and hip (ω_k and ω_h respectively) significantly increased as movement speed increased, however in the eccentric phase ω_k was only significantly different when comparing the JS-P to either the TS-P or VS-P, and eccentric ω_h was not significantly different between the TS-P and JS-P (Figure 34). Eccentric and concentric ω_a were only significantly different between the JS-P and both the TS-P and VS-P.

Peak ground reaction force significantly increased as movement speed increased (Table 8). However, similar system work was performed between the TS-P and VS-P movements, as indicated by the similar displacement with an identical load. In contrast, significantly greater work was produced during JS-P than either the VS-P or TS-P movements, as indicated by greater bar displacement (Table 8). M_a , M_k and M_h significantly increased as speed increased (Table 9). However, M_k and M_h differences were only present when comparing the TS-P to the JS-P movements and M_a was only significantly different when comparing the TS-P to either the VS-P or JS-P.

The estimated tendon forces (F_t) and rate of force development (RFD_t) are presented in Figures 32, 33, and 35. F_t was significantly greater in JS-P than TS-P. However, no significant differences were found between the VS-P and the

other two movement conditions (Figures 35). The rate of tendon loading (positive RFD_t) did not significantly change as movement speed increased, despite a moderate increase in mean values (Figure 35). The rate of unloading (negative RFD_t) significantly increased between the TS-P and JS-P, however no significant differences were found between VS-P and the other two loading conditions (Figure 35). MTU structural data is presented in Table 10. No significant differences in MTU structure were found in maximum or minimum values of L_{mtu} , L_t , L_f , or A_p . Both lengthening and shortening v_f were significantly greater in the JS-P than the TS-P, however no significant differences were found between VS-P and either TS-P or JS-P.

The influence of movement speed manipulation on muscle activity was found to be largely muscle specific (Table 11 and Figure 36). No significant differences were found in EMG_p or EMG_a between the TS-P and VS-P movements for any of the muscles assessed. However, EMG_p was significantly greater in JS-P than the TS-P and VS-P conditions for the VL, VM, MG and SO and same pattern was found in EMG_a values in the VL, VM, RF, MG and SO. Analysis of the integrated EMG (EMG_i), which is positively influenced by muscle activity and movement duration, resulted in complex findings. EMG_i was significantly lower in the VS-P than the TS-P movement for VL, RF, VM and BF. EMG_i was also significantly greater in the TS-P than the JS-P movements for the knee extensors (VL, RF and VM) but lower in the plantar flexors (MG and SO). Lastly, EMG_i was significantly lower during VS-P than the JS-P for the RF, VM, MG, SO and GM.

DISCUSSION

The major finding of the current study was that manipulation of the movement speed (i.e. TS-P < VS-P < JS-P) during a squat-type exercise significantly influenced VL-MTU behaviour. During the initial loading of the tendon lengthening occurred later in the eccentric movement phase and to a lesser

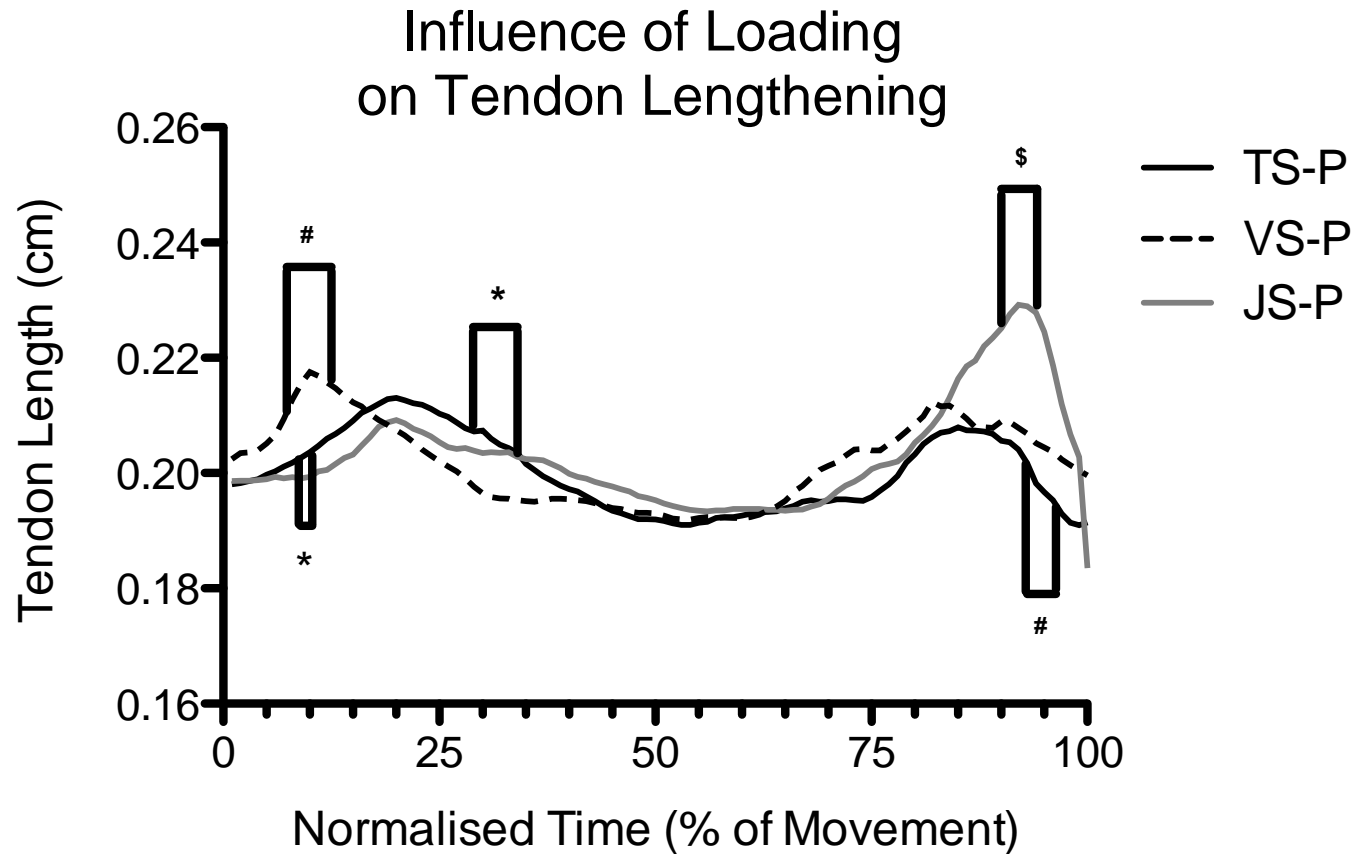


Figure 31: The influence of movement speed on tendon lengthening. Tempo squat (TS-P), volitional speed squat (SQ-P) and jump squat (JS-P) were compared across the movement duration. Time is normalised and represents a percentage of the total movement duration. Significant differences in between 0% load and other speeds are indicated by *'s.

Influence of Movement Speed on Patellar Tendon Force

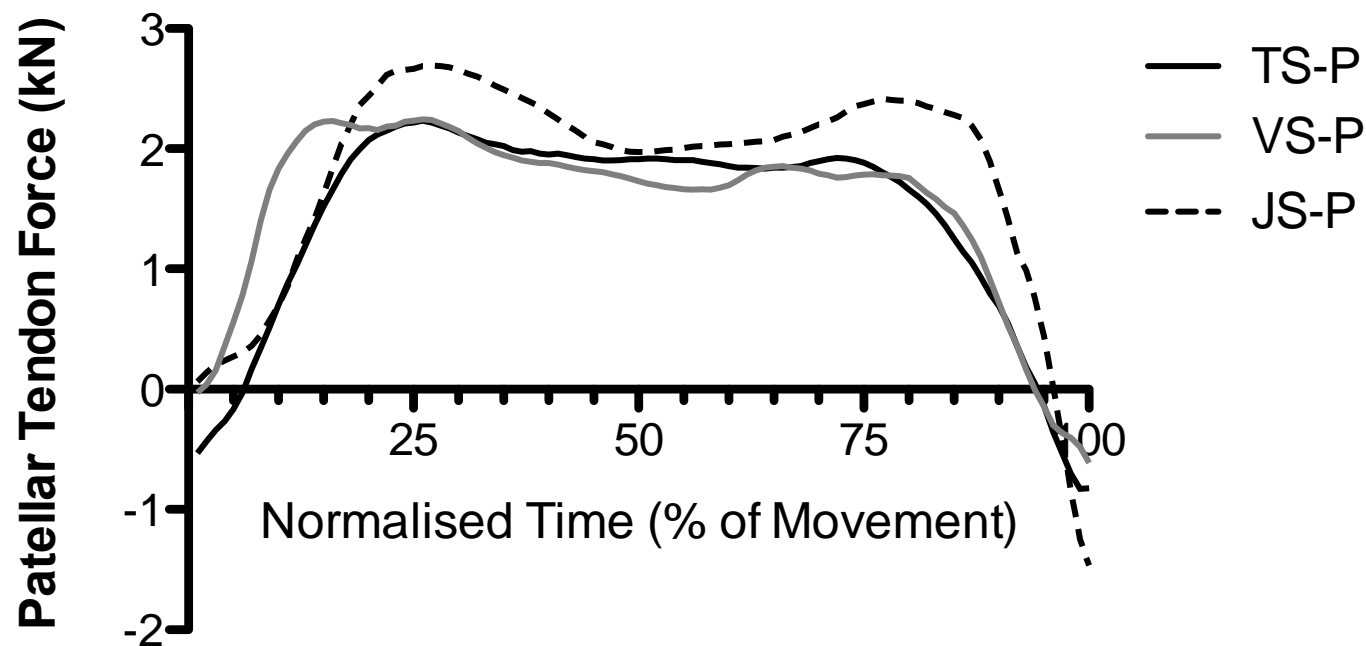


Figure 32: The influence of movement speed on patellar tendon force (F_t). Tempo squat (TS-P), volitional speed squat (VS-P) and jump squat (JS-P) were compared across the movement duration. Time is normalised and represents a percentage of the total movement duration.

Influence of Movement Speeds on Patellar Tendon RFD

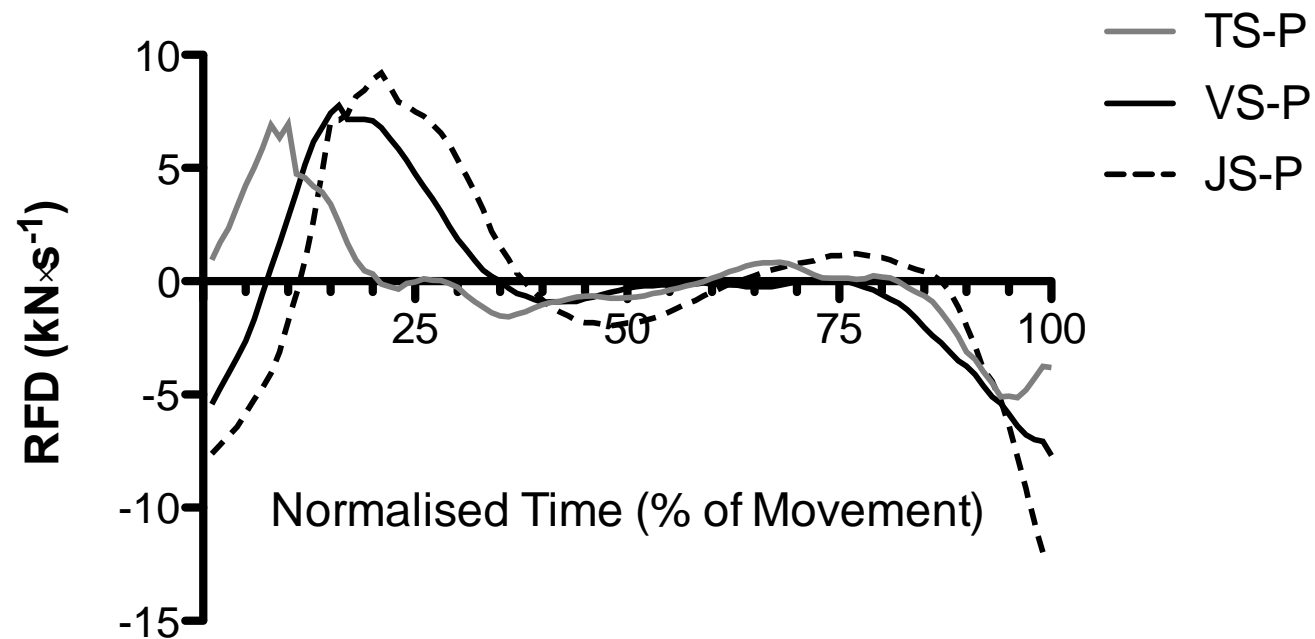


Figure 33: The influence of movement speed on patellar tendon rate force development (RFD_t). Positive values represent tendon loading, while negative values represent unloading. Tempo squat (TS-P), volitional speed squat (VS-P) and jump squat (JS-P) were compared across the movement duration. Time is normalised and represents a percentage of the total movement duration.

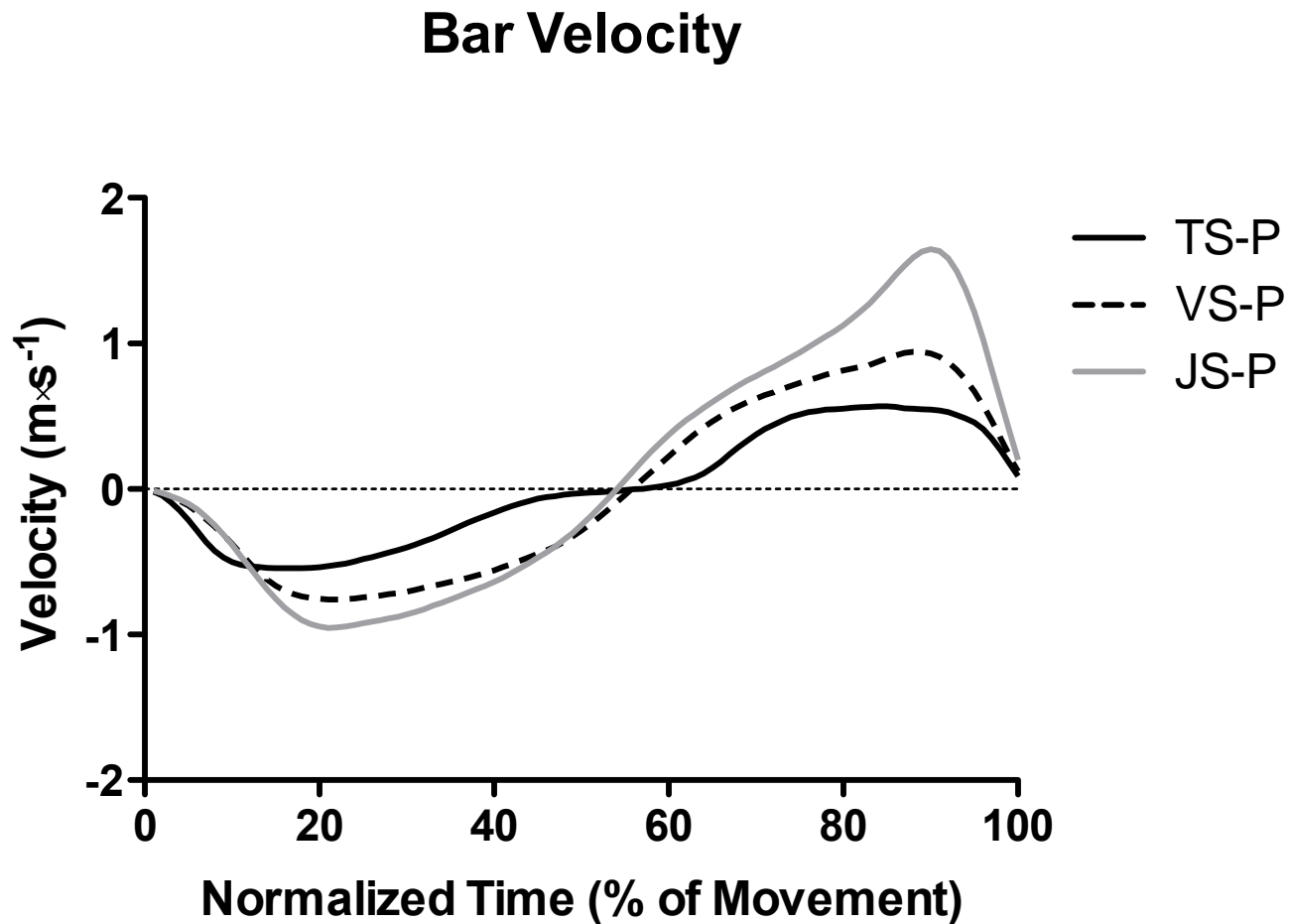


Figure 34: The influence of movement speed on bar velocity. Tempo squat (TS-P), volitional speed squat (SQ-P) and jump squat (JS-P) were across the movement duration. Time is normalised and represents a percentage of the total movement duration.

| Variable | Movement | Mean \pm SD |
|---|----------|--------------------------------|
| Ground Reaction Force-Z (kN) | TS-P | 1.84 \pm 0.22 _{bc} |
| | VS-P | 2.09 \pm 0.32 _{ac} |
| | JS-P | 2.37 \pm 0.32 _{ab} |
| Jump Height (m) | TS-P | 1.64 \pm 0.06 |
| | VS-P | 1.64 \pm 0.07 |
| | JS-P | 1.83 \pm 0.06 _{ab} |
| Bar Velocity Ecc (m·s ⁻¹) | TS-P | 0.57 \pm 0.10 _{bc} |
| | VS-P | 0.81 \pm 0.22 _{ac} |
| | JS-P | 1.14 \pm 0.38 _{bc} |
| Bar Velocity Con (m·s ⁻¹) | TS-P | 0.63 \pm 0.11 _{bc} |
| | VS-P | 0.99 \pm 0.26 _{ac} |
| | JS-P | 2.31 \pm 0.78 _{ab} |
| Bar Acceleration Ecc (m·s ⁻²) | TS-P | 2.54 \pm 0.71 _{bc} |
| | VS-P | 3.71 \pm 1.25 _{ac} |
| | JS-P | 5.83 \pm 1.98 _{ab} |
| Bar Acceleration Con (m·s ⁻²) | TS-P | 1.88 \pm 0.60 _{bc} |
| | VS-P | 3.43 \pm 1.31 _{ac} |
| | JS-P | 10.18 \pm 5.90 _{ab} |

Table 8: Movement kinetics: the influence of speed. Absolute and peak values obtained. Ground reaction force (GRF), jump height and bar velocity (v) and acceleration (a) are given and significant differences between tempo squat (TS-P: a), volitional speed squat (VS-P: b) and jump squat (JS-P: c) are shown.

| Variable | Movement | Ankle Mean \pm SD | Knee Mean \pm SD | Hip Mean \pm SD |
|---|----------|-------------------------------|-------------------------------|-------------------------------|
| Flexion ($^{\circ}$) | TS-P | 86 \pm 5 | 80 \pm 17 | 82 \pm 15 |
| | VS-P | 86 \pm 8 | 80 \pm 17 | 80 \pm 15 |
| | JS-P | 84 \pm 7 | 76 \pm 17 | 78 \pm 16 |
| Angular Velocity-Ecc ($^{\circ}\cdot s^{-1}$) | TS-P | 45 \pm 12 _c | 120 \pm 32 _c | 109 \pm 21 _c |
| | VS-P | 54 \pm 25 _c | 150 \pm 49 _c | 143 \pm 29 |
| | JS-P | 71 \pm 25 _{ab} | 192 \pm 43 _{ab} | 196 \pm 76 _a |
| Angular Velocity Con ($^{\circ}\cdot s^{-1}$) | TS-P | 46 \pm 9 _c | 125 \pm 26 _{bc} | 115 \pm 28 _{bc} |
| | VS-P | 68 \pm 28 _c | 185 \pm 55 _{ac} | 172 \pm 39 _{ac} |
| | JS-P | 335 \pm 85 _{ab} | 431 \pm 54 _{ab} | 301 \pm 51 _{ab} |
| Relative Moment (N \cdot kg $^{-1}$) | TS-P | 0.96 \pm 0.54 _{bc} | 1.56 \pm 0.71 _c | 2.00 \pm 0.69 _c |
| | VS-P | 1.23 \pm 0.61 _a | 1.59 \pm 0.84 | 2.39 \pm 1.08 |
| | JS-P | 1.73 \pm 0.72 _a | 2.07 \pm 0.95 _a | 2.52 \pm 0.93 _a |
| Relative Power (W \cdot kg $^{-1}$) | TS-P | 0.56 \pm 0.38 _c | 1.67 \pm 1.13 _{bc} | 2.59 \pm 1.17 _c |
| | VS-P | 0.81 \pm 0.57 _c | 2.25 \pm 1.42 _a | 3.93 \pm 2.19 _c |
| | JS-P | 4.29 \pm 3.86 _{ab} | 4.91 \pm 3.46 _a | 7.16 \pm 2.70 _{ab} |

Table 9: Joint kinetics: the influence of speed. Peak flexion, joint velocity (ω), relative joint Moments (M) and power (P) are given and significant differences between tempo squat (TS-P: a), volitional speed squat (VS-P: b) and jump squat (JS-P: c) are shown.

| Variable | Movement | Minimum Mean \pm SD | Maximum Mean \pm SD |
|---|----------|-----------------------------|-----------------------------|
| MTU Length (cm) | TS-P | 25.8 \pm 2.0 | 33.3 \pm 2.8 |
| | VS-P | 25.5 \pm 2.0 | 33.3 \pm 3.0 |
| | JS-P | 25.9 \pm 2.3 | 33.3 \pm 2.8 |
| Tendon Length (cm) | TS-P | 17.3 \pm 3.9 | 23.3 \pm 2.8 |
| | VS-P | 17.1 \pm 3.8 | 22.6 \pm 3.2 |
| | JS-P | 17.4 \pm 3.8 | 23.7 \pm 3.7 |
| Fascicle Length (cm) | TS-P | 5.8 \pm 0.9 | 15.0 \pm 2.5 |
| | VS-P | 5.9 \pm 1.3 | 14.6 \pm 1.4 |
| | JS-P | 5.8 \pm 1.1 | 14.9 \pm 2.6 |
| Fascicle Angle ($^{\circ}$) | TS-P | 10.5 \pm 1.9 | 24.4 \pm 5.2 |
| | VS-P | 10.8 \pm 1.8 | 23.5 \pm 5.3 |
| | JS-P | 10.5 \pm 1.9 | 23.2 \pm 3.5 |
| Fascicle Velocity (cm \cdot s $^{-1}$) | TS-P | -6.2 \pm 3.2 _c | 6.4 \pm 2.4 _c |
| | VS-P | -6.7 \pm 2.4 | 9.8 \pm 3.6 |
| | JS-P | -9.2 \pm 4.0 _a | 15.1 \pm 7.4 _a |

Table 10: Muscle-tendon unit (MTU) structure and behaviour: the influence of speed. Length of the vastus lateralis MTU (L_{mtu}), fascicle (L_f), and tendon (L_t), the fascicle angle (A_p) and velocity of the fascicle (v_f) are reported and significant differences between tempo squat (TS-P: a), volitional speed squat (VS-P: b) and jump squat (JS-P: c) are shown.

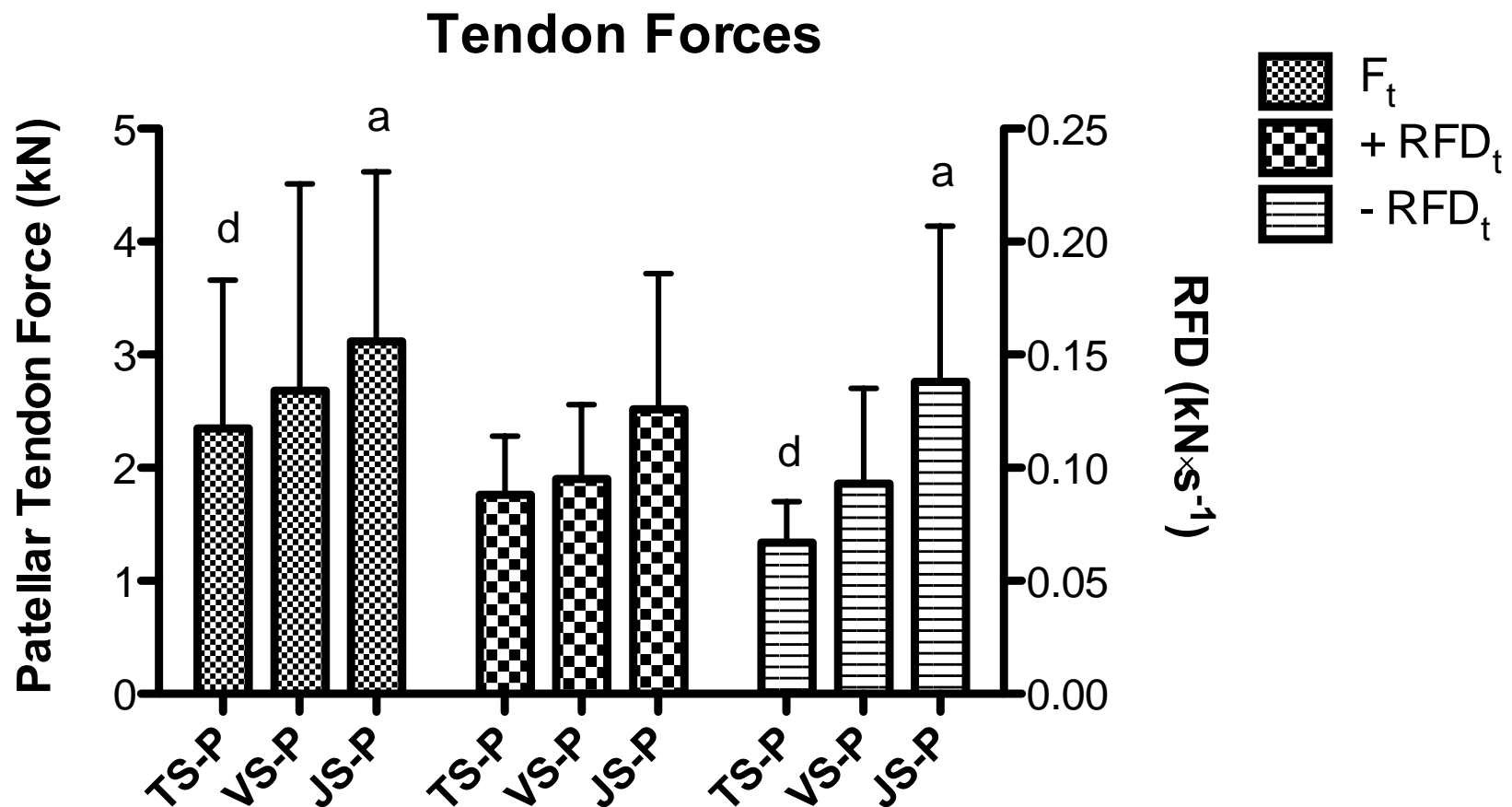


Figure 35: The influence of movement speed on the forces acting on the patellar tendon. The patellar tendon force (F_t) and the rate of loading ($+RFD_t$) and unloading ($-RFD_t$) on the tendon are presented and significant differences between tempo squat (TS-P: a), volitional speed squat (SQT-P: b) and jump squat (JS-P: c) are shown.

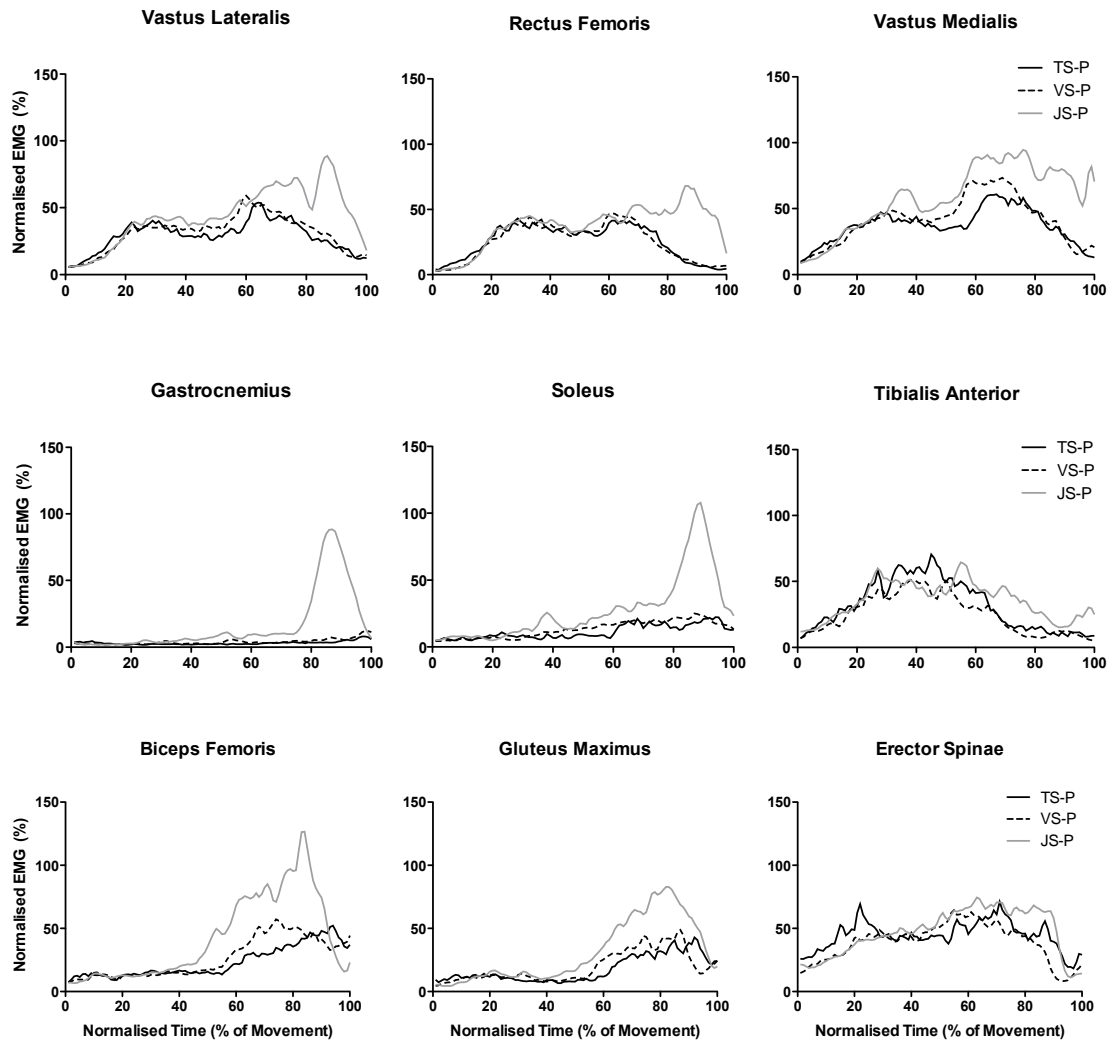


Figure 36: The influence of movement speed on muscle activity of the knee extensors (VL, RF, VM: top row), the plantar- and doris-flexors (MG, SO, TA: middle row) and the hip and lower back extensors (BF, GM and ES: bottom row). Tempo squat (TS-P), volitional speed squat (SQ-P) and jump squat (JS-P) were compared across the movement duration. Time is normalised and represents a percentage of the total movement duration.

| Muscle | Movement | EMG-Peak Mean \pm SD | EMG-Average Mean \pm SD | EMG-Integrated Mean \pm SD |
|--------|----------|--------------------------------|-------------------------------|---------------------------------|
| VL | TS-P | 76.7 \pm 19.2 _c | 29.2 \pm 6.1 _c | 98.1 \pm 25.8 _{bc} |
| | VS-P | 73.2 \pm 19.2 _c | 31.2 \pm 7.4 _c | 63.1 \pm 12.7 _a |
| | JS-P | 115.7 \pm 35.7 _{ab} | 43.9 \pm 8.7 _{ab} | 76.1 \pm 21.5 _a |
| RF | TS-P | 73.5 \pm 27.9 | 25.5 \pm 10.6 _c | 85.2 \pm 33.5 _{bc} |
| | VS-P | 70.2 \pm 30.7 | 25.1 \pm 10.9 _c | 50.3 \pm 20.2 _{ac} |
| | JS-P | 95.9 \pm 26.0 | 37.3 \pm 9.8 _{ab} | 63.3 \pm 15.5 _{ab} |
| VM | TS-P | 84.6 \pm 17.1 _c | 37.3 \pm 7.6 _c | 124.3 \pm 21.9 _{bc} |
| | VS-P | 95.3 \pm 29.9 _c | 41.5 \pm 12.0 _c | 83.1 \pm 22.0 _{ac} |
| | JS-P | 117.8 \pm 50.4 _{ab} | 48.6 \pm 19.7 _{ab} | 92.3 \pm 17.2 _{bc} |
| BF | TS-P | 69.0 \pm 42.0 | 23.4 \pm 13.4 | 75.2 \pm 39.0 _b |
| | VS-P | 81.6 \pm 52.7 | 26.7 \pm 15.4 | 52.7 \pm 27.0 _a |
| | JS-P | 151.7 \pm 102.2 | 42.0 \pm 34.0 | 69.7 \pm 49.3 |
| GM | TS-P | 59.5 \pm 18.3 _c | 17.7 \pm 3.3 | 58.1 \pm 9.4 |
| | VS-P | 63.6 \pm 37.6 _c | 19.7 \pm 5.0 _c | 40.0 \pm 9.0 _c |
| | JS-P | 113.3 \pm 33.7 _{ab} | 31.4 \pm 7.4 _b | 52.1 \pm 8.5 _b |
| ES | TS-P | 99.7 \pm 51.7 | 39.2 \pm 17.1 | 153.5 \pm 80.0 |
| | VS-P | 75.5 \pm 35.3 _c | 44.5 \pm 20.2 _c | 79.9 \pm 34.0 |
| | JS-P | 103.0 \pm 42.3 _b | 47.1 \pm 19.6 _b | 82.1 \pm 32.2 |
| MG | TS-P | 14.2 \pm 4.1 _c | 3.3 \pm 1.3 _c | 11.0 \pm 4.4 _c |
| | VS-P | 19.8 \pm 15.3 _c | 4.1 \pm 1.6 _c | 8.2 \pm 3.0 _c |
| | JS-P | 105.4 \pm 36.0 _{ab} | 16.4 \pm 4.2 _{ab} | 27.8 \pm 7.6 _{ab} |
| SO | TS-P | 43.8 \pm 26.2 _c | 9.7 \pm 5.9 _c | 31.6 \pm 18.2 _c |
| | VS-P | 37.5 \pm 19.8 _c | 13.4 \pm 6.7 _c | 26.7 \pm 12.8 _c |
| | JS-P | 126.1 \pm 65.3 _{ab} | 24.9 \pm 12.3 _{ab} | 48.5 \pm 13.3 _{ab} |
| TA | TS-P | 97.3 \pm 66.8 | 28.2 \pm 21.5 | 93.1 \pm 4.5 |
| | VS-P | 77.7 \pm 37.7 | 25.4 \pm 10.5 | 50.5 \pm 19.9 |
| | JS-P | 101.0 \pm 43.4 | 35.7 \pm 15.2 | 60.0 \pm 24.3 |

Table 11: Muscle activity: influence of speed. The peak (EMG_p), average (EMG_a) and integrate (EMG_i) of muscle activity in the vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF), biceps femoris (BF), gluteus maximus (GM), erector spinae (ES), medial gastrocnemius (MG), soleus (SO) and tibialis anterior are given and significant differences between tempo squat (TS-P: a), volitional speed squat (SQ-P: b) and jump squat (JS-P: c) are shown. All EMG values are reported as a percentage of muscle observed during a volitional depth jump squat performed with no external load.

magnitude as movement speed increased. This change occurred despite a greater F_t and RFD_t being observed in these faster movements, which demonstrates that MTU behaviour was predominated by the viscous properties of the tendon. Further, investigation revealed that a second SSC (i.e. tendon lengthening/shortening) occurred in the tendon during the concentric phase. This SSC pattern was characterised by faster joint velocities, moderate or high F_t , and relatively low RFD_t . However, in the second SSC, the tendon behaved as a predominately elastic structure as it went through significantly greater lengthening and loading in the parallel depth jump squats (JS-P) than either the set-tempo (TS-P) or volitional speed (VS-P) squats. When comparing the second SSC to the first, F_t was similar but the RFD_t was a fraction of its previous value. These findings suggest that the RFD_t strongly influences the behaviour of the quadriceps tendons during squatting-type movements. Furthermore, as RFD_t was relatively slow, the tendon behaved as a predominately compliant but elastic structure, however, the tendon's viscoelastic properties became apparent under fast RFD_t . A secondary finding of the current study was that, differences in movement and joint kinetics and muscle activity resulted from the change in movement speed. However, these differences were most apparent when comparing the TS-P to the JS-P and relatively few differences were present when comparing TS-P to VS-P.

A major strength of the current study was that all differences between the movement speeds were observed despite the conditions requiring very similar movement patterns (i.e. joint ranges of motion). The subjects were given immediate feedback of their knee angle and bar displacement during the previous repetition, and only repetitions that had a knee angle within $\pm 2.5^\circ$ and a bar depth within ± 1.25 cm of their pre-determined parallel squat position were used. Because subjects were experienced in resistance training there were no difficulties when attempting to meet these standards. To further check for differences in movement patterns between the three movements, maximum bar depth as well as knee, hip and ankle flexion were compared *post hoc* between

movements, and no differences were found. However, it should be noted that subjects used a greater plantar flexion angle at the end of the concentric phase in the JS-P movement which was expected given that the goal was to jump as high as possible.

No previous research has examined MTU behaviour during parallel-depth squatting movements. It was found that the tendon went through two distinct SSCs (Figure 31). The first occurred during the eccentric phase of the movement (during knee flexion), while the quadriceps actively lengthened. As flexion was initiated, the force through the tendon rapidly increased. It is during this initial tendon lengthening that the greatest F_t and RFD_t occurred (Figures 32 and 33). Next, as the knee continued to flex, F_t dropped but remained at a reasonably high level through the rest of the eccentric phase and into the early concentric phase (Figure 32). However, comparisons of L_t during the initial tendon SSC revealed that the tendon went through significantly greater lengthening in the TS-P than the VS-P or JS-P movements. Thus, the tendon lengthened more despite less force being present in the tendon in the TS-P compared to the JS-P. This demonstrates a stiffening of the tendon in the faster movements. Because tendons are viscoelastic, they will stiffen as the rate of loading increase (29, 199). Such an influence of the rate of loading on tendon stiffness has been shown in isolated tendon studies (116), and has been found during isometric (199) and SSC isoinertial knee extensions (Chapter 4). However, the results of the current study, obtained during loaded squat-type exercises are in contrast to those obtained during unloaded studies which movement speed was directly (walking, running, hopping) or indirectly (jumping and drop jumping) manipulated (90, 132-134, 173). There are several possible explanations for these differences. First, without an external load the relative forces (and RFD) in the tendon were insufficient to result in significant tendon stiffening. Second, differences in joint kinetics can occur as movement speed is changed during tasks such as jumping or running (132), which can result in a change in movement patterns (e.g. decreased joint flexion). Third, the knee went

through a relatively large amount of flexion in the current study compared to those reported in previous studies, so it is possible that the magnitude of tendon strain was greater.

The tendon underwent a second distinct SSC during the concentric phase of the movement in all conditions. As with the first SSC, the temporal pattern of L_t (Figure 31) closely matched that of F_t (Figure 32). While peak F_t usually occurred during eccentric phase, F_t was maintained relatively high compared to these values during the concentric phase. However, this was not the case with RFD_t , which was significantly less during the concentric compared to the eccentric phase because of the increased tension in the tendon that was maintained throughout the movement after initial force development (Figure 33). Similar to that observed in the first SSC in the tendon, when RFD_t was positive (i.e. the tendon was loaded) the tendon went through significant lengthening, however the tendon recoiled when RFD_t was negative (i.e. the tendon was unloaded). Unlike that seen in the initial SSC, the amount of lengthening of the tendon was greater in JS-P compared to the slower movements (TS-P and VS-P) during the concentric SSC. However, it should be noted that when comparing VS-P to TS-P, no significant differences in MTU behaviour, F_t , or RFD_t were found.

During the concentric phase, greater tendon lengthening occurred in the JS-P, which had the fastest speed and the greatest forces. These results suggest that the tendon functioned predominately as a compliant, elastic structure during the concentric phase of the movement. However, these results show also that MTU behaviour was different in the concentric than the eccentric phase. Thus, the viscoelastic properties of the tendon appear to significantly influence the MTU behaviour resulting in a decreased strain at fast speeds when the RFD_t is greater. However, the tendon will behave largely as a compliant but elastic structure when the RFD_t is relatively slow, resulting in greater tendon lengthening as greater forces are exerted upon it.

In addition to changes in MTU behaviour, we found significant changes in joint and movement kinetics and muscle activity as speed of movement was manipulated. First, as movement speed increased, peak GRF increased. Second, joint moments about the ankle, knee and hip increased as the speed of movement increased (these differences were not statistically significant in the ankle between VS-P and JS-P or the knee and hip between TS-P and VS-P). Muscle activity was also influenced by movement speed, although how activation was influenced varied by the variable assessed, the muscle in question and the movement performed. There were no differences in peak (EMG_p) or average (EMG_a) EMG amplitude between the TS-P and VS-P conditions. However, there was greater EMG_p and EMG_a in the knee extensor and plantar flexor muscles in the JS-P (Table 11). This finding was expected given that a maximum force was produced through the entire concentric phase without a deceleration at the end of the concentric phase (195). In contrast EMG_i , which has been previously used to estimate the amount of work done by the muscle and is largely dependent on both the magnitude of activity and the movement duration, showed a different pattern of results. For example, knee extensors EMG_i did not increase with increasing movement speed (i.e. TS-P > JS-P > VS-P was observed), and was greatest in the exercise with the longest force application duration (TS-P), followed by the movement with the greatest EMG_p and EMG_a (JS-P). However, in the plantar flexors, EMG_i was greatest in the JS-P possibly because of the requirement for maximal plantar flexion at the end of the concentric phase. This is interesting in that the previously reported differences in training-specific adaptations for exercises of different duration are often attributed to such differences in joint kinetics and muscle activity (235, 239). However, it is beyond the scope of the current study to speculate further on the underlying causes of training specific adaptations because of the cross-sectional design of the present study.

In conclusion, the primary purpose of the current study was to determine how speed of movement influences the VL-MTU behaviour during squatting-type

movements. It was found that even within a single squatting movement, during which the whole MTU went through a single SSC, the tendon went through two distinct SSCs (one in the eccentric and one in the concentric phase). Furthermore, the influence of movement speed on MTU behaviour differed between these SSCs. During the eccentric phase, which is characterised by a fast RFD_t and high F_t , the tendon was more compliant and went through greater lengthening during the slowest movement (TS-P) than during faster movements. However, during the concentric phase, which is characterised by low RFD_t but a relatively high F_t , the tendon went through its greatest lengthening in the fastest movement (JS-P). These results suggest that the tendon's viscous properties will dominate the MTU behaviour when RFD_t is large, but the elastic properties of the tendon will dominate when RFD_t is smaller. These findings are novel in that this dichotomous tendon behaviour has not previously been reported in human movements. As increased tendon stress and strain have been suggested to be the stimuli responsible for tendon adaptation, understanding how an acute programme variable such as movement speed influences tendon stress and strain has the potential to increase our ability to prescribe exercises that maximise desired training specific adaptations. Of particular interest is the role that speed of movement has on the eccentric phase of the movement. This is of interest because eccentric exercises are often performed for rehabilitation of various tendinopathies. However, further research is needed to explore how performing exercises with different movement speeds can result in differing training specific adaptations of the tendons. But the measured differences in MTU behaviour and stresses upon the tendon suggest that such differences may exist.

Chapter 7

Experiment 5

**Differential quadriceps femoris
musculotendinous adaptations in
response to slow-speed, high-load
and fast-speed, light-load squat lift
training**

Abstract

Differential quadriceps femoris musculotendinous adaptations in response to slow-speed, high-load and fast-speed, light-load squat lift training

Both slow-speed, high-load and fast-speed, light-load training have been shown to be effective for increasing performance in both kinetically similar and dissimilar movements, suggesting that some underlying adaptations are responsible for increasing performance across an array of tasks. In the previous chapters muscle tendon unit (MTU) behaviour, movement kinetics and muscle activity were found to differ as movement speed and external load were systematically varied. The primary purpose of the current study was to compare the training-specific adaptations to high-load, slow-speed and low-load, fast-speed squat lift training. A secondary purpose was to determine if the range of motion adopted during the training influenced the observed differences in adaptation. Thus, volitional-depth (JS-V) and parallel-depth (JS-P) jump squat exercises were compared to a parallel-depth, heavy load squat lift (SQ-P). Thirty-six healthy, physically active but non-strength trained men underwent MTU structural assessments during which their quadriceps tendon stiffness (k_t) and length (L_{qt}), patellar tendon thickness (T_{pt}), vastus lateralis fascicle length (L_f) and angle (A_f), and cross-sectional area (CSA) of the four quadriceps femoris (QF) components at distal-, mid- and proximal-thigh regions were assessed. Using the CSA measurements, QF and muscle-specific volume (VOL) within the regions of interest were also estimated. Lastly, one-repetition maximum (1RM) was determined for the parallel-depth squat lift. Subjects were stratified according to their 1RM to body-mass ratio (1RM:BM) and then allocated randomly into one of four groups. Three training groups completed 8 weeks of training, whilst a control group performed continued their normal daily activities. After the intervention, muscle CSA and volume, fascicle length and angle, k_t and 1RM

were reassessed. No changes were detected in the control group. 1RM:BM, VOL_{QF} , mid- CSA_{QF} and L_f increased in all training groups, but changes were not different between the training groups. However k_t increased only in SQ-P ($p \leq 0.05$) and A_f increased in both JS-V and JS-P ($p \leq 0.05$) whilst there was no change in SQ-P. The results from the current study along with those of previous chapters are suggestive that differences in adaptation are resultant of differing tendon strain, movement kinetics and muscle activation patterns when load and speed are manipulated. The finding of differing training-specific MTU structural and mechanical adaptations suggests that both slow-speed, heavy load and fast-speed, light load training should be incorporated into a training regimen in order to elicit all of the desired training specific adaptations.

INTRODUCTION

Exercises are often performed with different loads and speeds in order to elicit training-specific adaptations in kinematically similar movements (23, 184). However, training-related performance adaptations are often found in both movements with both similar and dissimilar load and speed conditions. These findings suggest that different training stimuli can result in different underlying training-specific adaptations, but may influence performance across a broad spectrum of movements. Thus, rather than prescribing exercises that mimic specific movement pattern, load and speed conditions (i.e. movement-specific training) practitioners might consider prescribing exercises that elicit specific adaptations that then impact movement performance more broadly (i.e. adaptation-specific training).

Slow-speed, heavy-load resistance training (SHL) and fast-speed, light-load (FLL) training are two commonly prescribed exercise types (23). SHL exercises are often prescribed with the goal of eliciting increases in slow speed strength, while FLL training targets performance increases during faster, light-load movements. While the use of training programs that closely match a task's force or velocity characteristics has been found to be effective for improving performance in that task (55, 127, 142, 233), research has shown that similar results may also arise from non-specific training. For example, FLL training, such as plyometrics, has been shown to increase maximal isometric and dynamic force production in both trained and untrained subjects (13, 231), whilst SHL training has been linked to increases in vertical jump and sprint performance (7, 58). Furthermore, both FLL and SHL training have resulted in increases in sprint running speed (41, 58, 72, 113, 239). These results are not consistent with the traditional concept of training specificity, but are more consistent with the concept of adaptation specificity; i.e. that specific adaptations resulting from one type of training may benefit performance in dissimilar tasks. While researchers have examined the performance outcomes that can arise from SHL (58, 110, 114, 155) and FLL (109, 113, 239) training, much less is known about how the

structure and mechanical properties of muscles and tendons adapt to these two types of training. A better understanding of how these adaptations differ could potentially help practitioners to design resistance training programs that target the specific desired structural adaptations.

During movement, forces derived from muscle contraction are transmitted through tendons. Both muscle and tendon are plastic tissues that can respond differently to different loading patterns. SHL resistance training is widely accepted to be an effective way of inducing muscle hypertrophy, whilst FLL is credited with little, if any, increases in muscle size (109, 169, 233). Muscle architectural adaptations also appear to be training-specific. SHL training has been associated with increases in muscle fascicle angle and length (37, 38, 40, 146). Increased physiological cross-sectional area theoretically allows for increased fascicle angle and increased joint excursion at low fascicle velocities (21, 35). The only study which has investigated changes in A_f in response to FLL training, prescribed both jumping and sprinting exercises to well-trained athletes and observed a decrease in A_f (40). The increase in fascicle length from SHL training occurs in spite of the increased fascicle angle, and instead is driven by the increase in muscle thickness (40). Increased fascicle length allows for greater fascicle shortening speeds and increased ability to produce force during high-speed movements (35).

A limited number of studies have investigated the regional-specific adaptations to training (47, 154, 181, 193, 235). Of these studies, regional-specific hypertrophy has been shown in specific areas of the muscle where muscle activity and anticipated forces are greatest (235). However, as muscle activity and joint moments are known to differ between FLL and SHL movements such as the parallel depth jump squat (JS-P) and back squat (SQ-P: see Chapters 5 and 6), to our knowledge no research to date has investigated how regional and muscle specific adaptations may differ between them.

Wakahara et al. (235) found that the region of greatest muscle activity during a training movement responded with the greatest hypertrophy. Arampatzis et al. (19) found that strain and forces in the tendon and the aponeurosis can differ along the length of the MTU in an individual muscle thus differing mechanical stimuli for adaptations may be present. Furthermore, the strain and muscle activity of biarticular muscles [i.e. gastrocnemius or rectus femoris (RF)] and monoarticular muscles (i.e. soleus or vasti group) that share a tendon have been shown to differ within a given movement at different joint angles or when a movement is performed at different speeds. In the previous chapters (Chapters 5 and 6) we found that the JS-P had different quadriceps muscle activity than the SQ-P. Muscle activity of the vastus lateralis (VL), vastus medialis (VM) and RF during an unloaded JS-P (a FLL movement) and SQ-P (a SHL movement) performed with 90% of 1RM (see chapters 5 and 6) is depicted in Figure 37. The results from these curves suggest that differences in muscle activity are present when performing SQ-P and JS-P. Previously, Newton et al. (195) found similar results with chest-press movement and came to the conclusion that the intent to project a load can diminish deceleration (or braking) forces at the end of the concentric phase of the movement.

Observations in previous studies and results from the study by Newton et al (195) suggest that differences in regional-specific and muscle specific adaptation may occur from SQ-P and JS-P, even when movements are performed to the same depth. Tendons allow for energy to be stored during their lengthening and then re-utilised during their recoil (14, 18, 80, 94, 153, 240). The amount of tendon deformation caused by a given force is called the tendon's stiffness (stiffness = force / deformation). A stiffer tendon requires a greater force to be exerted on it to achieve the same deformation (8, 13, 215) but undergoes less deformation at a given load (13). Tendon stiffness is dependent on a variety of anatomical factors, two of the most important being tendon length and tendon

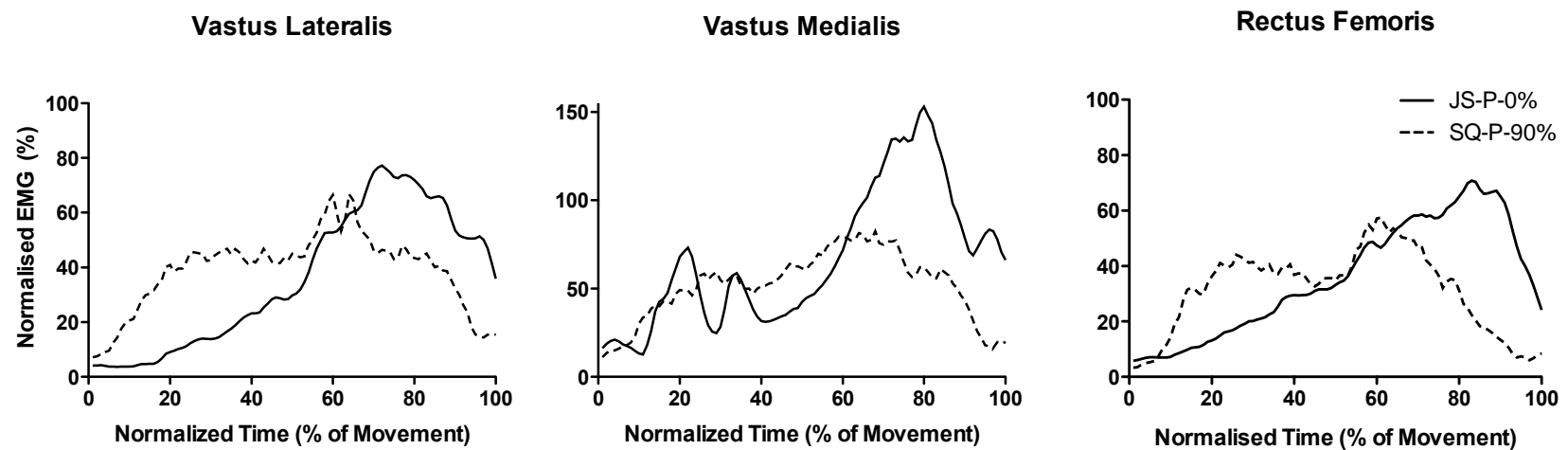


Figure 37: Average muscle activity of ten well trained men, recorded during an unloaded jump squat (JS-P-0%) and volitional speed squats performed with 90% of one repetition maximum (SQ-P-90%).

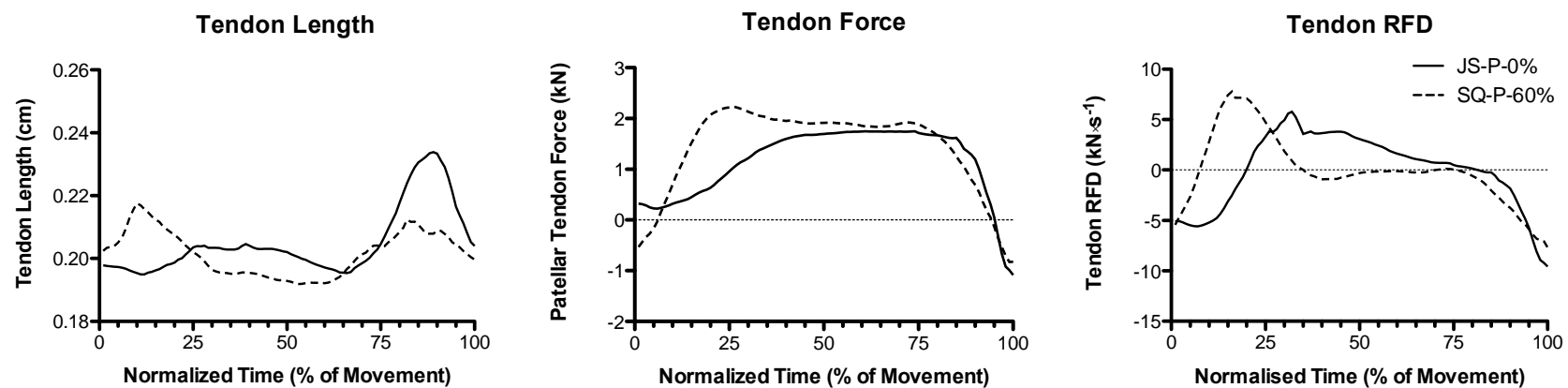


Figure 38: Average tendon length, force and rate force development of ten well trained men, recorded during an unloaded jump squat (JS-P-0%) and volitional speed squats performed with 60% of one repetition maximum (SQ-P-60%).

thickness (154, 190, 215); a shorter or thicker tendon will be stiffer than a longer or thinner tendon. SHL training has been shown to significantly increase tendon thickness and cross-sectional area (154, 215) as well as stiffness (52, 164, 200, 215) while FLL training has shown smaller increases or no change in tendon stiffness (52, 164). These results have led researchers to suggest that a threshold for adaptation in tendon strain and/or forces has to be met to induce changes in tendon structure or its mechanical properties (14). However, of these studies no research has directly investigated performing jump squats and squats using similar movement depths or when loaded jumps are performed. In the previous chapters (see Chapters 5 and 6) we observed that tendon strain and force differ as movement speed is manipulated (see Figure 38 as an example) providing rationale for such research.

Understanding the stimuli best suited for muscle and tendon adaptations is important for clinical populations and has implications for stretch shortening cycle performance as changes in structure are likely to result in differing movement specific and non-specific adaptations. Thus, the purpose of the current study was to investigate the structural adaptations of the MTU from SHL-SQ-P and FLL-JS-V training. Of particular interest are differences in tendon structure and mechanical properties, muscle architecture and both regional and muscle specific adaptations to training. A secondary purpose of the current study was to investigate if the observed differences in training specific adaptations are a result of load and speed being used or the range of motion (ROM) with which the movement is performed.

METHODOLOGY

SUBJECTS

Thirty-six healthy male subjects between the ages of 18 and 35 years were recruited for this study (Table 12). Subjects were physically active but had not been involved in a structured lower body resistance training program over the

| | SQ-P | | JS-V | | JS-P | | C | | Intraday | Interday |
|--|-------------|--------------|-------------|--------------|-------------|--------------|-------------|-------------|----------|----------|
| | Pre | Post | Pre | Post | Pre | Post | Pre | Post | ICC | ICC |
| Height (cm) | 178 ± 5 | 179 ± 5 | 177 ± 6 | 178 ± 6 | 175 ± 5 | 176 ± 5 | 178 ± 7 | 179 ± 7 | na | 1.00 |
| Body Mass (kg) | 88 ± 18 | 88 ± 18 | 79 ± 9 | 81 ± 10 | 69 ± 9 | 70 ± 9 | 81 ± 15 | 82 ± 15 | na | 1.00 |
| 1RM (kg) | 88 ± 18 | 128 ± 29* | 81 ± 10 | 101 ± 9* | 81 ± 12 | 98 ± 21* | 83 ± 24 | 88 ± 23 | na | 0.98 |
| K _t (n·cm ²) | 899 ± 300 | 1391 ± 536* | 951 ± 214 | 957 ± 209 | 838 ± 266 | 934 ± 340 | 763 ± 242 | 853 ± 287 | na | 0.83 |
| T _{pt} (cm) | 0.35 ± 0.04 | 0.36 ± 0.04 | 0.34 ± 0.04 | 0.35 ± 0.03 | 0.34 ± 0.02 | 0.35 ± 0.02 | 0.36 ± 0.03 | 0.35 ± 0.03 | 0.74 | 0.96 |
| L _{qt} (cm) | 5.70 ± 1.05 | 5.60 ± 0.84 | 5.62 ± 1.06 | 5.62 ± 1.08 | 5.17 ± 1.05 | 4.94 ± 1.43 | 5.75 ± 1.50 | 5.77 ± 1.62 | 0.93 | 0.99 |
| L _f (cm) | 7.98 ± 0.61 | 8.43 ± 0.78* | 7.60 ± 0.89 | 8.09 ± 0.98* | 7.12 ± 0.58 | 7.71 ± 0.55* | 8.09 ± 0.97 | 8.13 ± 0.95 | 0.90 | 0.94 |
| A _f (°) | 18.4 ± 3.0 | 18.9 ± 2.2 | 17.0 ± 2.2 | 19.1 ± 3.2* | 17.3 ± 3.2 | 19.5 ± 3.8* | 17.4 ± 2.3 | 17.6 ± 2.7 | 0.88 | 0.93 |
| CSA _{prox} (cm ²) | 60.4 ± 13.3 | 70.2 ± 13.8* | 57.6 ± 6.3 | 64.8 ± 4.6* | 52.2 ± 11.6 | 62.0 ± 14.8 | 60.4 ± 13.3 | 59.4 ± 13.8 | 0.96 | 0.98 |
| CSA _{mid} (cm ²) | 80.3 ± 13.0 | 91.0 ± 12.1* | 75.2 ± 8.7 | 83.5 ± 8.2* | 66.4 ± 15.5 | 75.4 ± 16.0 | 78.8 ± 13.3 | 7.77 ± 13.9 | 0.97 | 0.99 |
| CSA _{dis} (cm ²) | 79.0 ± 8.4 | 91.2 ± 11.8* | 74.7 ± 8.0 | 82.4 ± 7.6* | 67.9 ± 15.6 | 75.7 ± 15.6 | 74.3 ± 11.9 | 74.8 ± 12.5 | 0.96 | 0.98 |
| VOL _{QF} (cm ³) | 2135 ± 337 | 2441 ± 358* | 1966 ± 235 | 2185 ± 230* | 1720 ± 408 | 1965 ± 462* | 2020 ± 303 | 2001 ± 322 | 0.93 | 1.00 |
| VOL _{VL} (cm ³) | 715 ± 109 | 803 ± 111* | 624 ± 82 | 704 ± 94* | 541 ± 146 | 639 ± 183* | 675 ± 113 | 648 ± 100 | 0.97 | 0.94 |
| VOL _{VI} (cm ³) | 710 ± 144 | 837 ± 177* | 679 ± 89 | 754 ± 108* | 586 ± 147 | 659 ± 163* | 667 ± 80 | 652 ± 90 | 0.96 | 0.96 |
| VOL _{VM} (cm ³) | 510 ± 83 | 602 ± 68* | 462 ± 78 | 521 ± 51* | 424 ± 111 | 482 ± 111* | 488 ± 107 | 499 ± 116 | 0.94 | 0.96 |
| VOL _{RF} (cm ³) | 200 ± 73 | 200 ± 67 | 202 ± 50 | 206 ± 47 | 168 ± 45 | 184.6 ± 32* | 191 ± 36 | 186 ± 29 | 0.96 | 0.83 |

Table 12: Subject data and raw testing values before (pre) and after (post) 8-weeks of parallel depth squat training (SQ-P), jump squat training performed with volitional depth (JS-V) and parallel depth (JS-P) or no training (C). * indicates a significant increase in response to training.

last six months. All subjects were required to show proficient squat and jump technique prior to enrolment in the study and subjects were excluded if they had any history of lower body muscle or tendon injury that would interfere with any of the measurements taken throughout the study. The study was reviewed and approved by the Human Research Ethics Committee of the University and all subjects gave their written consent prior to participation.

EXPERIMENTAL DESIGN

Subjects were familiarised to all testing protocols and showed proficiency in squat and ramp isometric knee extension tests prior to testing. At least 48 hours later subjects went through a series of tests to determine the structure and mechanical properties of the quadriceps MTU and then had their 1RM determined for the back squat. MTU testing included resting ultrasonography measures to determine patellar tendon thickness (T_{pt}), quadriceps tendon length (L_{qt}), vastus lateralis (VL) fascicle length (L_f) and angle (A_f) and muscle and regional-specific cross-sectional area of the quadriceps femoris (QF), and isometric knee extensions were used to determine quadriceps tendon stiffness (k_t). Subjects were then assigned to one of four groups: heavy parallel squat training group (SQ-P; $n=9$), jump squat training group which performed jumps to volitional depth (JS-V; $n=9$), jump squat training group which performed jumps from a parallel squat depth (JS-P; $n=9$) and a control group (C; $n=9$). Subject group assignment was made by stratifying subjects based on their 1RM to body mass ratio (1RM:BM) and then randomly assigning the stratified subjects into one of the training groups. After 1RM testing all subjects went through a two-week washout period to dissipate any possible residual effects from the 1RM testing. Subjects assigned to SQ-P, JS-V and JS-P then trained three times per week for eight weeks while subjects in the C group were required to maintain their normal physical activities, but to avoid any form of resistance training for the duration of the study. Between 48-72 hours after the subject's final training

session, subjects repeated their pre-intervention testing. Comparisons were then made to determine training effects and differences between groups. Prior to all testing, subjects refrained from any exercise for at least 48 hours and were instructed to remain euhydrated and avoid alcohol for at least 24 hours.

RESTING MUSCLE AND TENDON MEASURES

B-mode ultrasonography (Alpha 10, Aloka, Co., Ltd., Tokyo, Japan) was used to determine T_{pt} and A_f at rest. While extended field of view (EFOV) images were taken to determine L_{qt} , L_f and proximal-, mid- and distal-thigh cross-sectional area (CSA) of the QF [VL, rectus femoris (RF), vastus medialis (VM) and vastus intermedius (VI)]. A 6 cm probe (UST 5713, Aloka, Co., Ltd., Tokyo Japan) with a 10 MHz sampling array was used for these measurements. All ultrasonography measurements were made on three separate images and measured three times for a total of nine measurements per variable. The lowest and highest measurements were discarded and the remaining seven measurements were averaged (76). To account for fluid shift after activity, subjects were asked to lay supine on a testing table for 20 minutes prior to their first images being taken (34).

To determine T_{pt} , subjects laid relaxed in a supine position with their hip and knee both flexed to 90° while mid-sagittal images are taken so that the patella and tibia were visible simultaneously (Figure 39). To determine L_{qt} the subjects laid supine with their leg and hip fully extended and relaxed, then the tendon was tracked using EFOV ultrasonography (74). To do this, the muscle belly of VL was identified using ultrasonography and this location marked on the skin. Next, a line was traced between the most superior border of the patella to the muscle belly of VL. Finally, an EFOV image was taken from the most superior point of the patella at which the tendon inserted, to the muscle belly of the VL so that the patella and MTJ could clearly be distinguished on the same image, this length was considered the L_{qt} (Figure 40) (74).

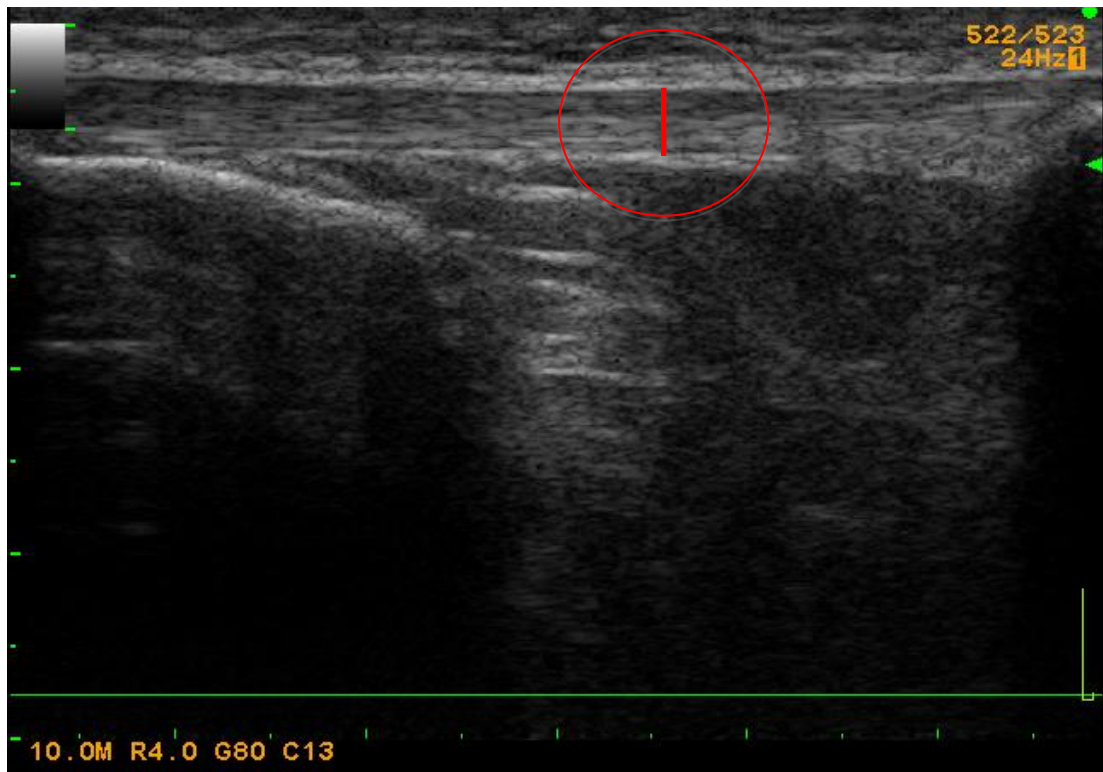


Figure 39: Example of a typical mid-sagittal B-mode ultrasound image of patellar tendon. The location of measurement is highlighted in red.

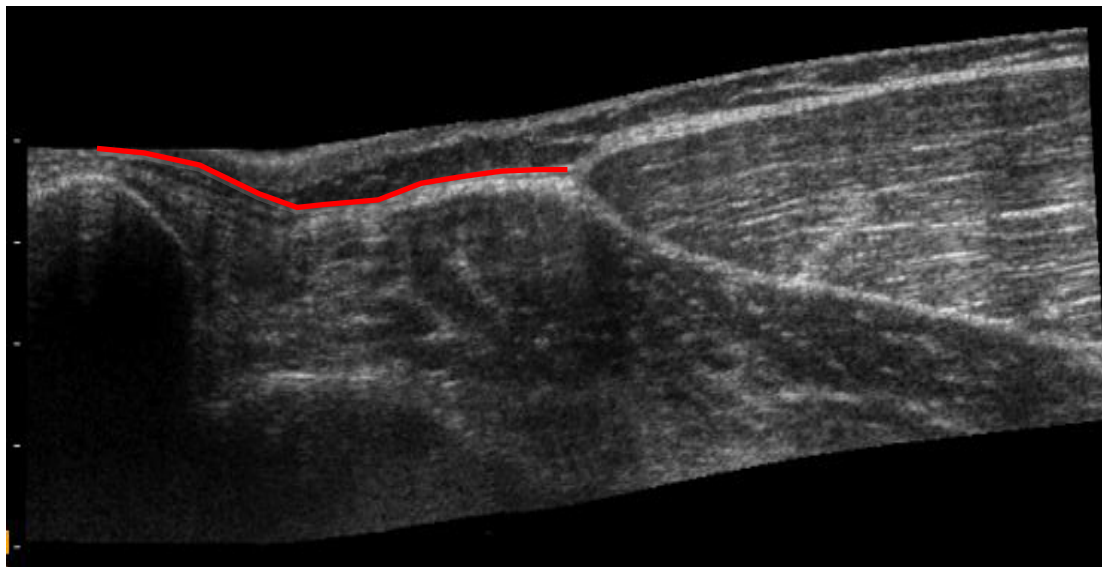


Figure 40: Example of an extended field of view ultrasound image of the quadriceps tendon. The tendon is traced from the myotendinous junction of the vastus lateralis to the patella.

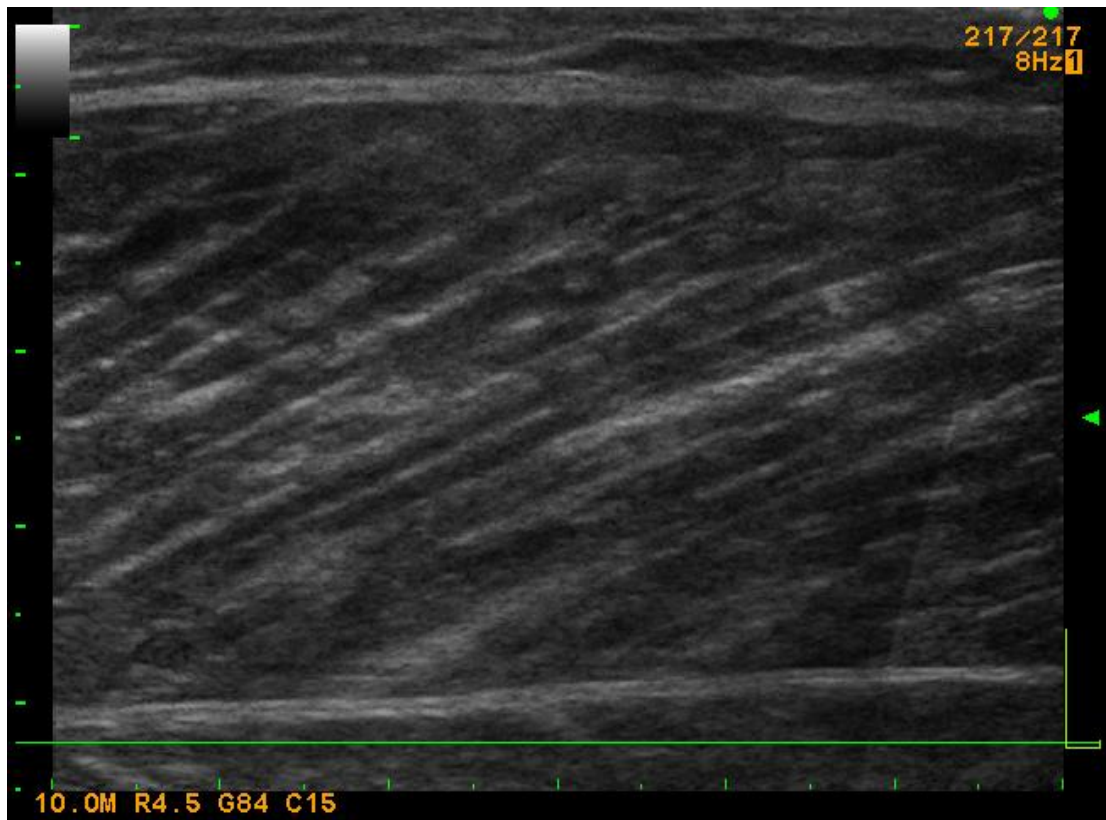


Figure 41: Example of a typical B-mode ultrasound image of the vastus lateralis.

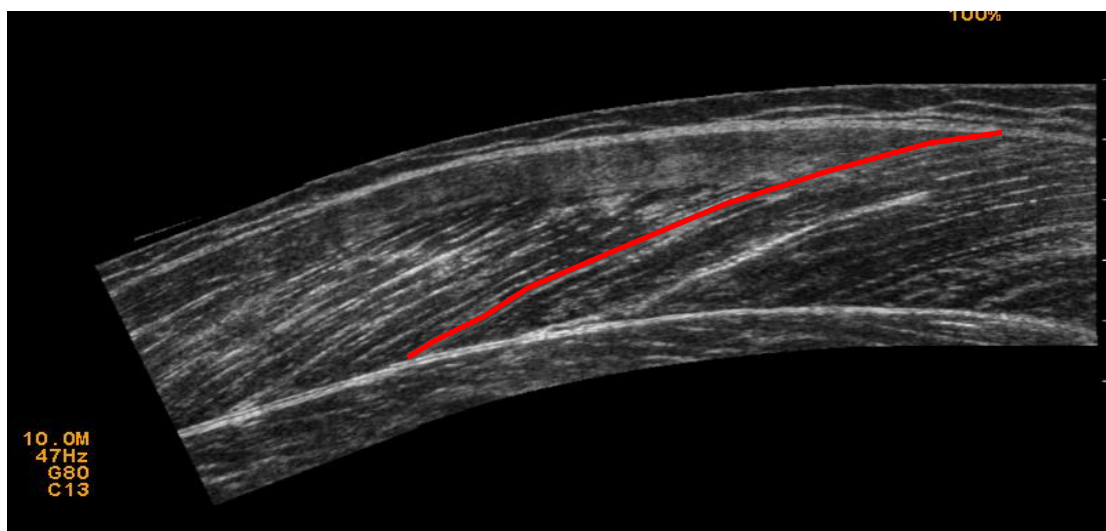


Figure 42: Example of a typical extended field of view ultrasound image of the vastus lateralis. An individual fascicle is traced in red.

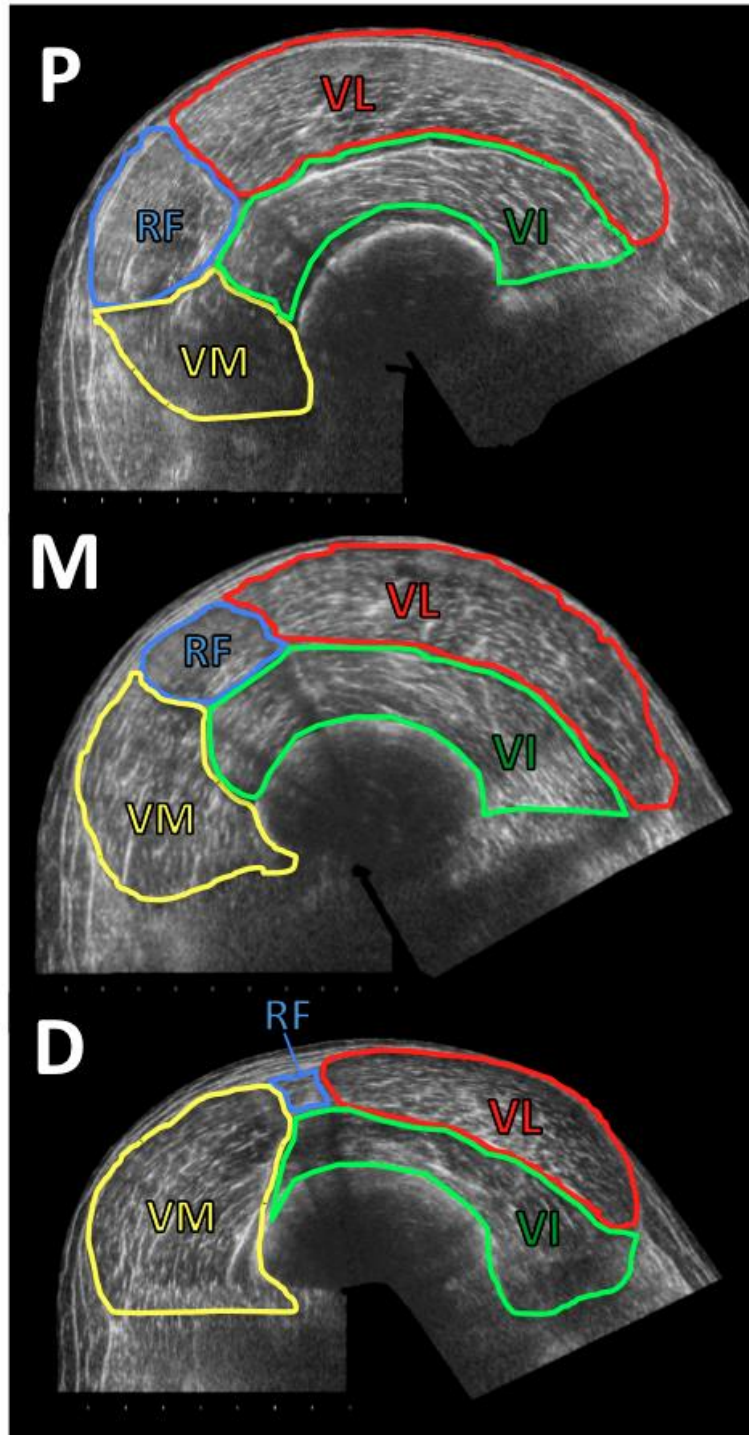


Figure 43: An example of transverse extended field of view ultrasound images of the quadriceps femoris. Images are taken at the distal- (D), mid- (M) and proximal- (P) thigh. The vastus lateralis (VL: red), vastus medialis (VM: yellow), vastus intermedius (VI: green) and rectus femoris (RF: blue) are traced to measure the cross-sectional area.

Muscle architecture of the VL was assessed at half the distance between the base of the lateral epicondyle and the peak of the greater trochanter of the femur. Longitudinal images were taken with the probe orientated in-line with the muscle fascicles. A_f was defined as the angle between the deep aponeurosis of the VL and muscle fascicles (Figure 41) (89). L_f was measured using an EFOV image in which the entirety of an individual fascicle could be viewed in the same image (Figure 42) (197).

To assess regional and muscle specific CSA, the subject laid supine with their leg straight and relaxed but their thigh suspended horizontally over the edge of a table and their foot supported. In this position CSA of the VL, VM, VI, RF and the QF (sum of all four quadriceps) were determined using transverse EFOV images taken at 33 (proximal), 50 (mid) and 66% (distal) of thigh length (196). This technique has been observed to be a valid alternative to magnetic resonance imaging (196). Using the location of the scans and the measured CSA of the muscles, an estimate of the muscle volume (VOL) between 33-66% of thigh length was performed. All MTU assessments were made on the subject's right side, regardless of dominance and analysis of resting ultrasonography images was performed using image analysis software (OsiriX, Pixmeo, Geneva, Switzerland).

TENDON STIFFNESS

Subjects were seated in a custom made rigid chair with a hip and knee angle of 90° and a strain gauge placed in-series with a 10 cm Velcro strap. Subjects had previously been familiarised to this testing and performed a standardised warm-up prior to commencement of testing. This warm-up consisted of five minutes of low intensity cycling (2.5 kP at 60 rpm: Monark Ergomedic 828E, Monark, Scandinavia) followed by submaximal isometric contractions at 50 and 80% of the subjects perceived maximal effort, each separated by one minute rest. To determine k_t , an ultrasound probe was secured to the knee at the myotendinous junction of the VL and images (47 images per second) were taken while subjects

performed 4-5 ramp isometric knee extensions. External force signals were recorded using a data acquisition system and its associated software (PowerLab 4/8 and LabChart 7.2, AD Instruments, Bella Vista Australia) and used to estimate tendon force via equation 24, where $F_{Machine}$ is the recorded external force, $MA_{Machine}$ is the distance between the axis of rotation of the rigid chair and location of the strap that is placed on the ankle, and MA_t is the estimated moment arm of the quadriceps tendon as determined using a previously published model (232). Ultrasound images were synchronized to force data using a 5-Volt output pulse triggered by the data acquisition software and sent to the ultrasound system. One isometric contraction was performed at a time followed by one minute rest prior to the next contraction. Subjects were required to have two successful contractions which were used for subsequent analysis, while those that did not fall in this time frame, which had a non-uniform increase in force or had a peak force that was not within 10% of the previous repetition, were discarded and repeated (205).

$$F_t = F_{Machine} \times MA_{Machine} \div MA_t \quad [Eq\ 24]$$

The longitudinal movement of the myotendinous junction, measured from resting position, was assessed using video analysis software (Prosuit 5.0, DartFish, Sydney, Australia). The tendon displacement and the force at each corresponding tendon length was then assessed between 50-100% peak force (162). k_t was defined as the change in force divided by the change in length. To calculate these changes, the relationship between knee force and tendon displacement was determined using a line of best fit equation between 50-100% peak force (162). The average of the two contractions was then used for comparison.

ONE-REPETITION MAXIMUM

After subjects completed their stiffness testing they were given a 15-min recovery and then started a squat specific warm-up for their 1RM testing. The warm up

consisted of 10 bodyweight squats followed by 60 s recovery, then 8-10 squats performed with 50% of estimated 1RM followed by 2 min recovery, then 3-5 repetitions performed with 80% of 1RM followed by two minutes recovery and lastly one repetition performed with 90% of 1-RM (23) followed by 3 min of recovery. Subjects were then permitted up to six attempts to find their 1-RM with a 3-min recovery between each attempt. The 1RM was defined as the greatest load that could be successfully lowered to and raised from parallel depth whilst maintaining correct technique.

To ensure consistency during testing and training, subjects had their knee angle recorded using an electronic goniometer (MLTS700, AD Instruments USA) and bar depth recorded using a linear position transducer (PT5A-150, Celesco Transducer Products, Chatsworth, CA) sampling at 1000 Hz. Prior to 1RM testing subjects performed a parallel depth squat during which knee angle and bar depth were recorded. These values were then used as the criteria for performing an acceptable parallel depth squat. It was required that knee angle was within 2.5° and bar depth was within 1.25 cm of the criterion values for the repetition to be retained and used in subsequent analysis.

TRAINING PROGRAMME

The subjects assigned to the three training groups (SQ-P, JS-V, JS-P) trained three times a week for 8 weeks. Subjects in the SQ-P group performed squats to a parallel depth, as determined by the femoral line (line between the greater trochanter and the lateral epicondyle being parallel to the ground). Because of the short length of the training programme (8-weeks) the prescribed programme was non-linear so as to encompass set, repetition and loading schemes commonly used for both hypertrophy and strength development (23). SQ-P was performed with loads between 75-90% of 1RM load (Day 1: 3 sets x 3 repetitions at 90%, Day 2: 3 sets of 8 repetitions at 75%, Day 3: 3 sets of 6 repetitions at 80%). Subjects in the JS-V and JS-P groups performed jump squats with loads between 0-30% of their 1RM load (Day 1: 7 sets of 6 repetitions at 0%, Day 2: 5

sets of 5 repetitions at 30%, Day 3: 7 sets of 6 repetitions at 0%). However, subjects in the JS-V group performed jumps with a natural countermovement (approximately between half and quarter parallel squat depth) while subjects in the JS-P group performed jumps with a countermovement in which subjects reached parallel depth using the criteria previously described. For SQ-P, loads progressed throughout the training programme as the subject increased their strength. After four weeks of training subjects in all the training groups went through a 1RM reassessment to track their progress in strength. At this time new loads were prescribed for the JS groups. Subjects were required to attend 90% of training sessions on time and complete all 24 training sessions prior to post testing. Details of the training programmes are presented in table 13.

| Training Program | | | | | | | | | |
|------------------|-------|------|---------|-------|------|---------|-------|------|---------|
| | Day 1 | | | Day 2 | | | Day 3 | | |
| | Sets | Reps | Load | Sets | Reps | Load | Sets | Reps | Load |
| SQ-P | 6 | 3 | 90%-1RM | 3 | 10 | 75%-1RM | 4 | 6 | 85%-1RM |
| JS-V & JS-P | 7 | 6 | 0%-1RM | 5 | 5 | 30%-1RM | 7 | 6 | 0%-1RM |

Table 13: Training programmes details. Set, rep and load configuration used during parallel depth squat (SQ-P) and jump squat (JS-V and JS-P) training.

STATISTICAL ANALYSIS

A two-way MANOVA with repeated measures with Bonferroni *post hoc* tests were used to examine the changes in variables before and after the training intervention and differences between groups before or after the intervention. Means, standard deviations and percentage change from baseline are reported. All statistical analyses were conducted using PASW 18.0.1 (IBM, New York, USA) and statistical significance was accepted at an α level of $p < 0.05$.

RESULTS

Subject data, pre and post intervention testing values and intraday and interday reliability of the tests are reported in Table 12. Every subject allocated into a training group was required to complete all 24 training sessions. To ensure identical training volumes, if a subject missed a training session for any reason an additional training session was added to the end of their training programme. However, subjects who missed more than 2 training sessions over the 8-week period were automatically withdrawn from the study. Using these strict criteria the attrition rate for the present study was 17.5%. Prior to the intervention no significant differences were found between any of the groups in any of the variables measured.

Results from the current study were that training specific adaptations occur in MTU structure and the mechanical properties when the speed and load are varied. We found that as training progressed all three training groups significantly increased their strength according to their 1RM:BM (SQ-P: $45.3 \pm 17.4\%$, JS-V: $22.0 \pm 11.4\%$, JS-P: $21.8 \pm 13.0\%$), while no significant difference was found in C ($1.6 \pm 4.8\%$; Figure 44). k_t significantly increased in the SQ-P, but did not change in any other group (Figure 45). The tendon force-length relationship obtained during isometric knee extension is presented in Figure 46. No significant differences were found in either L_{qt} (SQ-P: $-1.00 \pm 6.8\%$, JS-V: $1.8 \pm 5.7\%$, JS-P: $-1.75 \pm 6.95\%$, C: $-0.09 \pm 4.14\%$) or T_{pt} (SQ-P: $2.57 \pm 7.18\%$, JS-V: $1.91 \pm 7.14\%$, JS-P: $2.10 \pm 6.74\%$, C: $0.07 \pm 4.35\%$) despite a non-significant trend towards increases T_{pt} for all of the training groups (Figure 47). A_f was found to significantly increase in the JS-V ($11.8 \pm 9.1\%$) and JS-P ($13.2 \pm 10.8\%$) groups after training, while no significant differences were found in either SQ-P ($3.8 \pm 9.6\%$) or C ($1.0 \pm 6.0\%$; Figure 48). L_f significantly increased in all training groups (SQ-P: $5.65 \pm 5.86\%$, JS-V: 6.62 ± 7.10 , JS-P: 8.76 ± 9.98) but did not change in the C ($0.63 \pm 6.01\%$; Figure 48).

Changes in QF regional-specific CSA and VOL are depicted in Figure 49, changes in VOL of the VL, VM, VI and RF are depicted in Figure 50. The CSA and VOL of the C group did not change in any of the recorded muscles at any of the regions of interest. All training groups increased VOL_{QF} to a similar extent (Figure 49). While all three training groups increased their CSA_{QF} in the three regions of interest, training specific adaptations were present. Proximally SQ-P had significantly greater increase than the JS-V group, while distally the JS-P group reported the greatest increase (Figure 49). All training groups significantly increased VOL of the VL, VI and VM; however, the increases in VI were significantly greater in the SQ-P group than other groups (Figure 50). In addition, VOL_{RF} significantly increased only in the JS-P group (Figure 50).

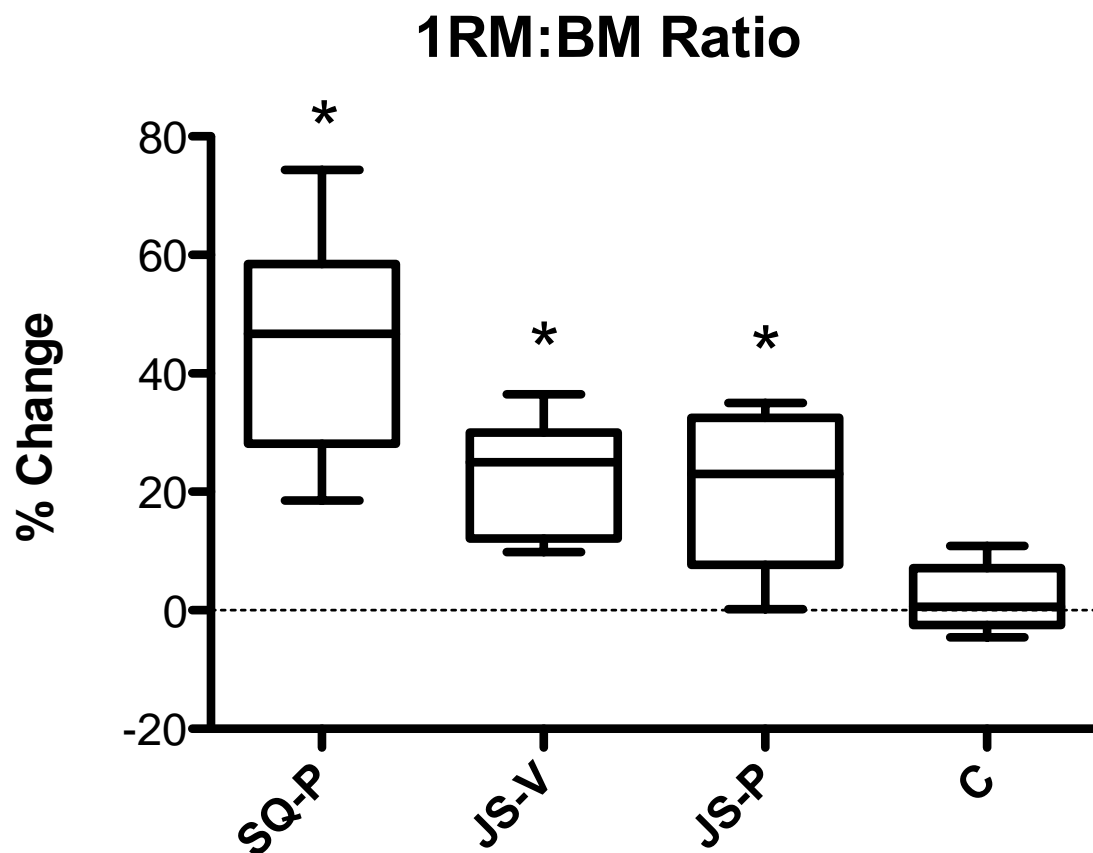


Figure 44: One repetition maximum to body mass ratio (1RM:BM) adaptations in response to 8-weeks of parallel depth squat training (SQ-P), jump squat training performed with volitional depth (JS-V) and parallel depth (JS-P) or no training (C). * indicates a significant increase in response to training.

Tendon Stiffness

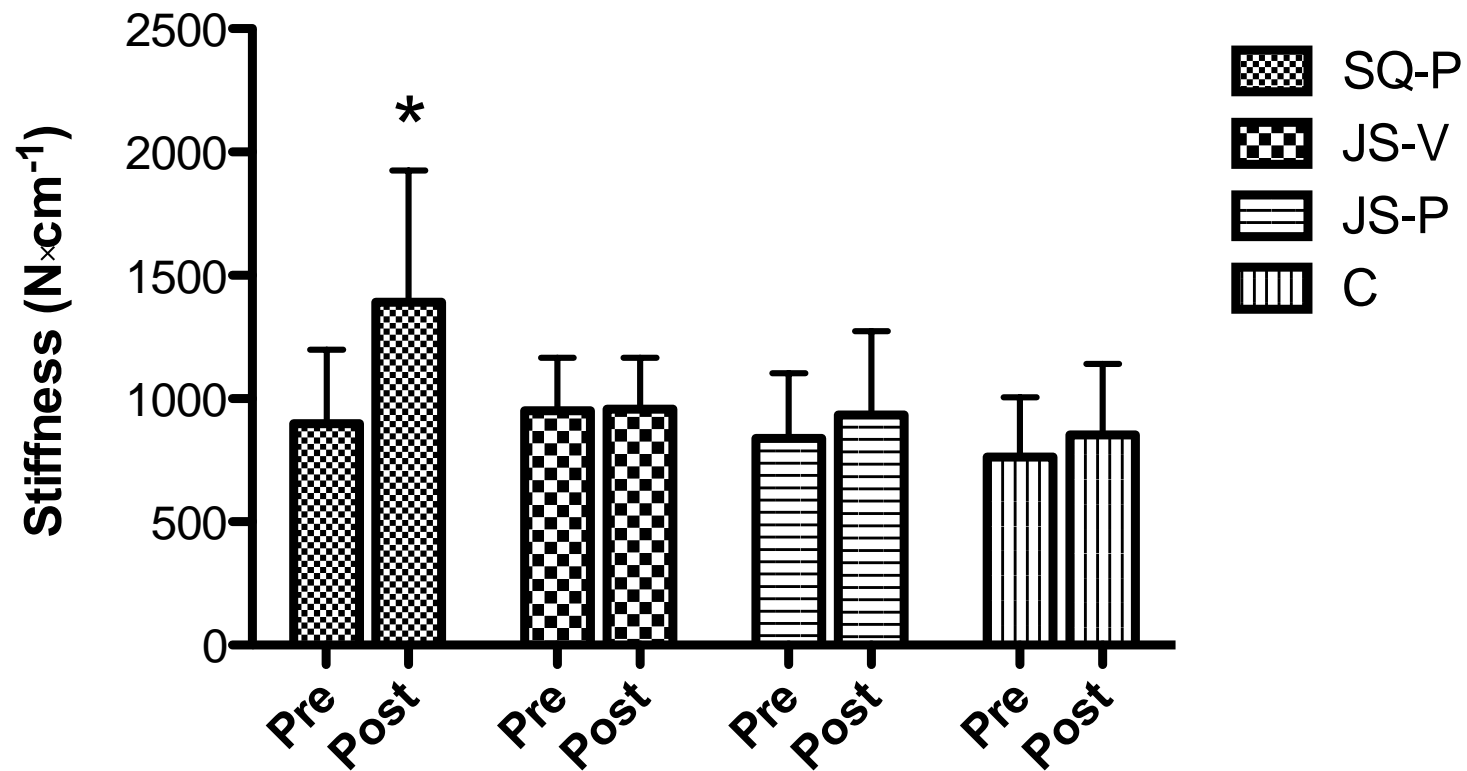


Figure 45: Quadriceps tendon stiffness adaptations in response to 8-weeks of parallel depth squat training (SQ-P), jump squat training performed with volitional depth (JS-V) and parallel depth (JS-P) or no training (C). * indicates a significant increase in response to training.

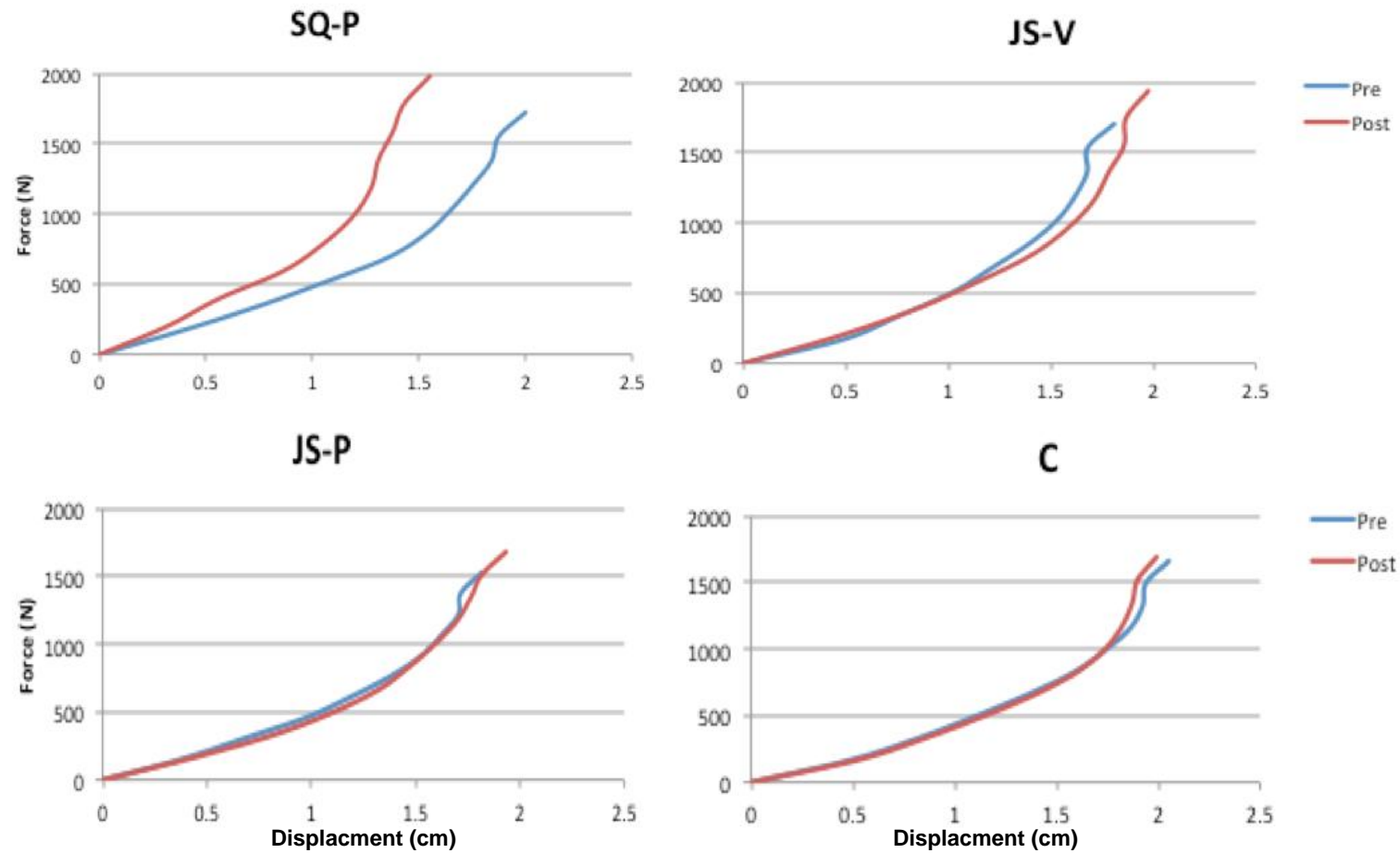


Figure 46: Training induced changes in the force-length response of the quadriceps tendon obtained during isometric knee extensions. The average Pre- (blue) and post-intervention measurements recorded after 8-weeks of parallel depth squat training (SQ-P), jump squat training performed with volitional depth (JS-V) and parallel depth (JS-P) or no training (C) are shown.

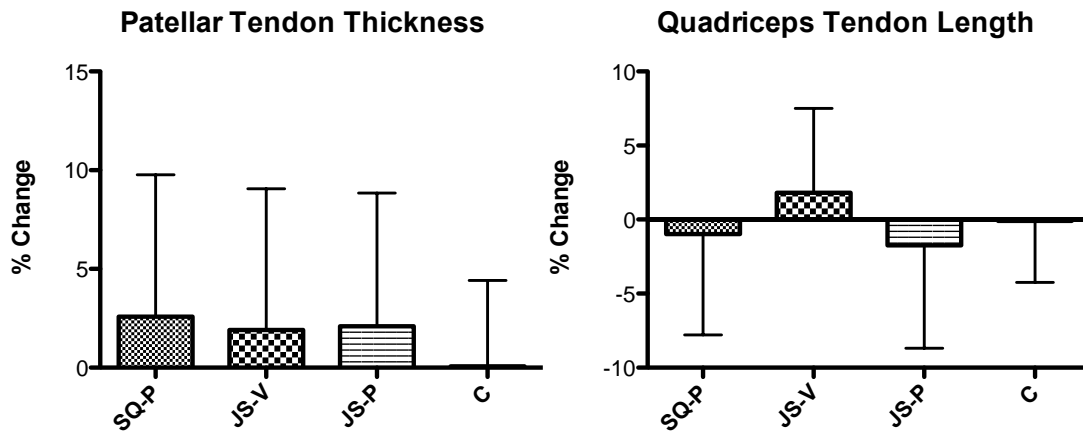


Figure 47: Changes in quadriceps tendon length and patellar tendon thickness in response to 8-weeks of parallel depth squat training (SQ-P), jump squat training performed with volitional depth (JS-V) and parallel depth (JS-P) or no training (C).

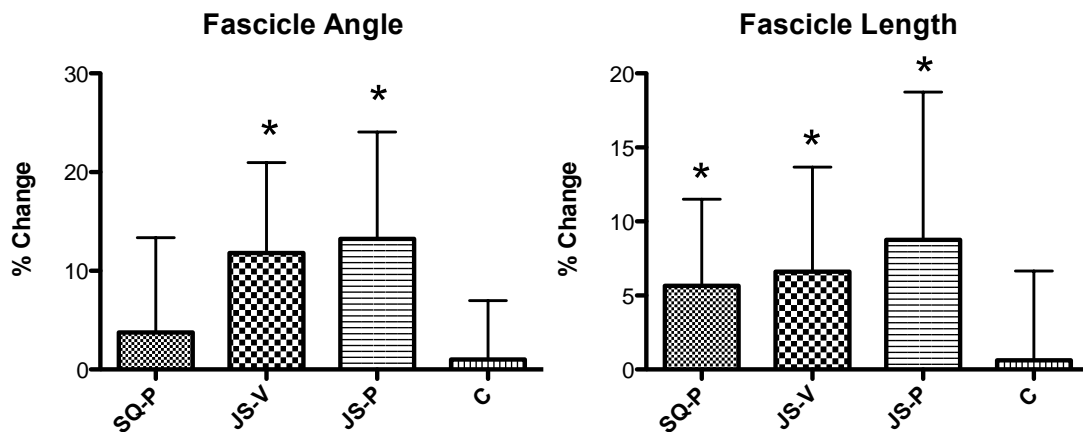


Figure 48: Changes in fascicle angle and length in response to 8-weeks of parallel depth squat training (SQ-P), jump squat training performed with volitional depth (JS-V) and parallel depth (JS-P) or no training (C). * indicates a significant increase in response to training.

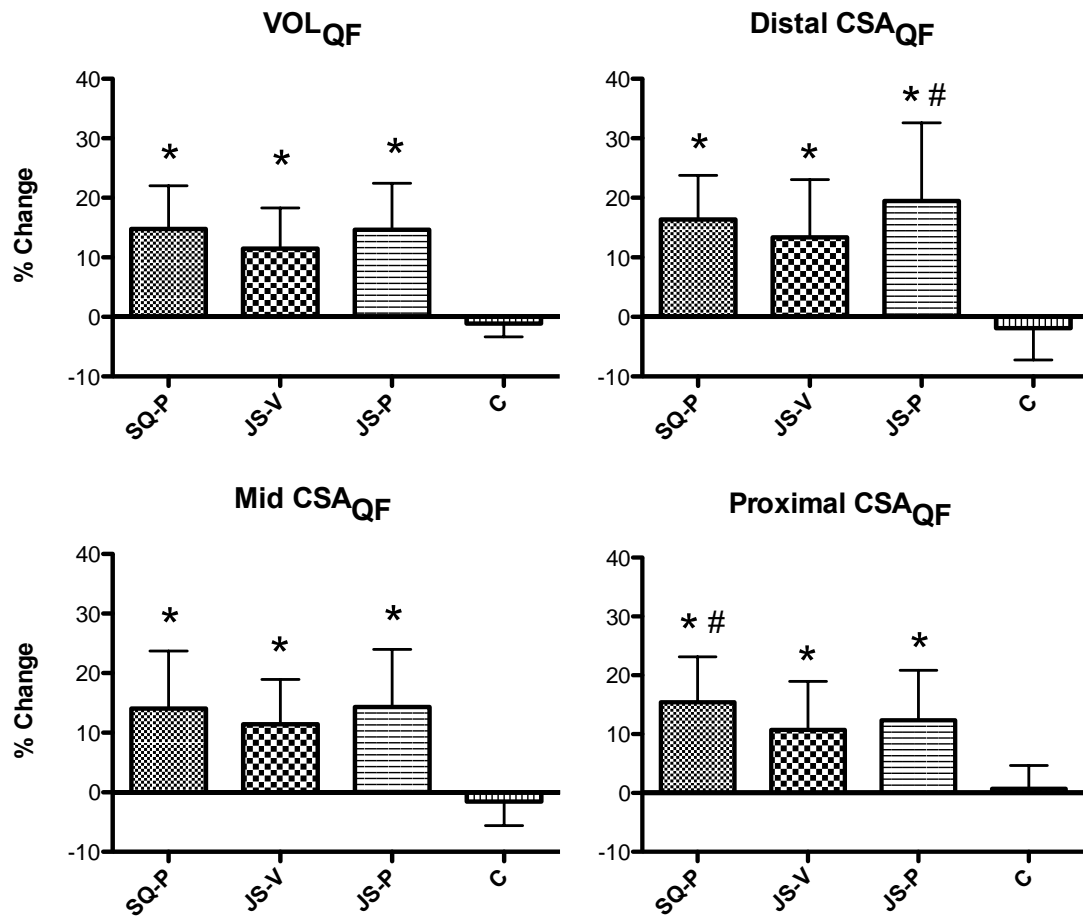


Figure 49: Training specific adaptations in quadriceps femoris muscle volume (VOL_{QF}) and cross-sectional area (CSA) at the distal-, mid-, proximal thigh in response to 8-weeks of parallel depth squat training (SQ-P), jump squat training performed with volitional depth (JS-V) and parallel depth (JS-P) or no training (C). * indicates a significant increase in response to training, # indicates a significantly greater increase than other groups.

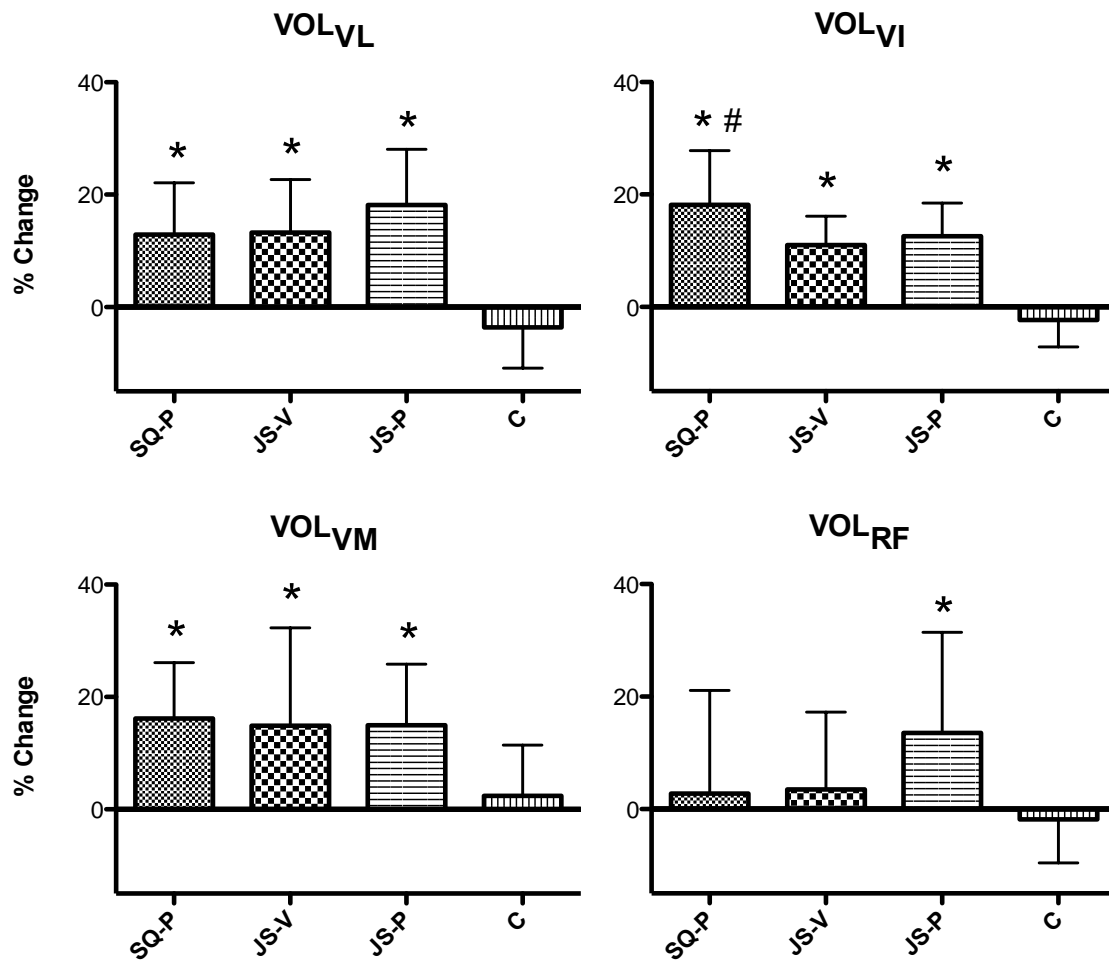


Figure 50: Training specific adaptations in vastus lateralis (VL), vastus intermedius (VI), vastus medialis (VM) and rectus femoris (RF) muscle volume (VOL) in response to 8-weeks of parallel depth squat training (SQ-P), jump squat training performed with volitional depth (JS-V) and parallel depth (JS-P) or no training (C). * indicates a significant increase in response to training, # indicates a significantly greater increase than other groups.

DISCUSSION

In the present study, physically active but non-strength trained men took part in different training programmes to determine variations in training specific adaptations when different speeds and loads were used in training. Both of the exercises used in this study (the heavy squat and the jump squat), are commonly used in resistance training programmes to elicit specific performance adaptations (7, 23, 62), but this has been the first study to evaluate differences in underlying structural and mechanical adaptations. The primary findings of the present study were that training-specific adaptations occurred in muscle structure and tendon stiffness of the knee extensors in response to training with different loads and speeds. Of particular interest is that only by training with high loads at relatively slow speeds (SQ-P) were subjects able to increase the stiffness of their tendons. In contrast, only when subjects performed fast-speed relatively light loaded ballistic movements (JS-V and JS-P) did subjects increase their A_f . Other differences were observed in muscle specific and regional-specific increases in muscle CSA and VOL. A secondary finding of the current study was that the range of motion performed during training resulted in differences in training specific adaptations in muscle CSA, but not muscle architecture or the tendon's mechanical properties.

In the present study we observed that only when training with sufficient loads at a relatively slower speed did k_t increase. Similar results have been reported in the plantar flexors in response to SHL and FLL training (105, 164). In the knee extensors, increased tendon stiffness has been reported in response to SHL training. However, to our knowledge this is the first study to show that no changes in stiffness occur in the QT when performing jump squat and loaded jump training. In the SQ-P, changes in stiffness occurred despite no measureable changes in T_{pt} or L_{qt} suggesting that changes in the intrinsic properties of the tendon occurred (112, 204, 225). However, there was a non-significant trend for increased tendon thickness in all training groups compared to C. Even if an increase in T_{pt} does occur in response to FLL training; it is possible

that changes in tendon thickness either do not occur at a fast enough rate to be measurable after eight weeks, or that using ultrasonography is not able to accurately measure the slight changes that occurred (49). Adaptations other than T_{pt} , which could have resulted in an increase in k_t , include changes in collagen fibre type, tendon cross-stitching and changes in the extra cellular matrix of the tendon (30, 243).

Muscle architecture (L_f and A_f) of the VL was another location of training specific adaptations. In the current study, A_f significantly increased in both the JS-V and JS-P groups, but did not significantly increase in the SQ-P or C groups. While previous research has observed an increase in A_f in response to SHL training [such as SQ-P: (1, 40, 215)], to our knowledge no studies have reported an increase in A_f in response to plyometric training. In fact, Blazeovich et al. (40) found no change in A_f after 5-weeks of sprint and jump training, despite concurrent SHL training groups showing a significant increase. However, it should be noted that in Blazeovich et al. (40) subjects were athletes who already engaged in regular resistance training. It is possible that differences between the current study and that published by Blazeovich et al. (40) could be attributed to either the sprint element of the training protocol or the training status of the subjects. An increase in A_f can be beneficial to increase the physiological cross-sectional area of a muscle and thus the potential of that muscle to forcefully exert and resist high eccentric loads (11, 35, 76). The results of the current study suggest that loaded jump squat training may be a more effective way to increase A_f in healthy untrained subjects. Similar to most previous studies, we observed an increase in L_f in response to SHL training (1, 12, 37, 38) and FLL training (40). However, the present study was the first to investigate the adaptations in VL- L_f in response to SHL and FLL training in healthy untrained subjects and the results showed all forms of training were effective in increasing L_f . Nevertheless, it should be noted that while no significant differences were present in the current study between the types of training, the mean change was slightly greater in the JS-P (8.76% increase, effect size = 1.48) than the SQ-P (5.65% increase, effect

size = 0.91). Thus, this may be an area of future investigation as an increase in L_f has been highly linked to increases in the ability to produce force during high contractile velocities, and the ability to produce force rapidly (38, 42, 76, 77).

The secondary purpose of the present study was to determine if training adaptations varied in accordance to the depth of countermovement used for training. This was done by comparing differences in training specific adaptations of JS-V and JS-P groups, from which similar changes (or lack of changes) in both muscle architecture and tendon stiffness and structure were found in both groups. These results also allow us to conclude that the observed differences in training specific adaptation between SHL (SQ-P) and FLL (JS) training were realised due to the speed and load used for training rather than the range of motion the action was performed through. To our knowledge such an approach had never been undertaken when comparing these or other similar movements. It has previously been suggested that adaptations in L_{qt} and L_f are related to the fascicle and/or tendon being stressed at long lengths (14), but by matching the depth to which the movements were performed we were able to control for the length of the muscle tendon unit (MTU). However length of the MTU does not accurately reflect the length of the muscle or tendon. In the previous chapters we explored such differences when we observed that at heavier loads and slower speeds the tendon goes through greater active strain during the eccentric phase of the movement. Thus it is likely that such MTU behaviour was the underlying mechanical stimuli necessary for tendon adaptation (Figure 38). Results from the previous chapters also suggest that the force expressed through the tendon may be greater during loaded SQ-P compared to unloaded JS-P. However, it should be noted that statistical comparisons were not made between these movements directly in the previous study. A note of caution should also be taken in that some training specific adaptations observed in the JS-V and JS-P groups may have also arisen from the landing phase of the jump (123) and that the stresses and strains on the muscle and tendon were not measured during landings in this study or in previous chapters.

In addition to the training specific adaptations previously mentioned, several key differences were present when comparing regional and muscle specific adaptations in quadriceps CSA and VOL. It is interesting to note that all training groups increased their estimated VOL_{QF} to a similar extent. This is in contrast to several previous training studies, which have found that SHL training increases hypertrophy to a greater extent than plyometric/FLL training (109, 169, 233). However, these differences are most likely attributed to the subject demographic of the current study (physically active, but untrained), as well as the high weekly volume of training and the added external load (30% 1RM) used by the JS-V and JS-P groups. All forms of training were able to elicit significant increases in CSA_{QF} in each of the three regions of interest as well as muscle VOL of the VM, VI and VL. However, proximal CSA_{QF} increased to a greater extent in the SQ-P group than any other group, and the distal CSA_{QF} increased to a greater extent in the JS-P group than any other group. It is difficult to accurately predict the underlying stimuli for such differences in training specific adaptation. Nonetheless, comparisons of the intrinsic forces (Figure 38) and muscle activity (Figure 37) between the movements show that during the SQ-P forces are high throughout the eccentric and concentric phases and that muscle activity decreases throughout the concentric phase. In contrast, forces and muscle activity are maintained through a greater proportion of the concentric phase and thus at shorter muscle lengths during JS-P. Therefore, we can speculate that the joint angle and phase of movement (eccentric or concentric) at which the muscle is active or at which forces are great may contribute to differences in regional-specific adaptations. It should also be noted that since differences in training specific adaptations were present, it is suggested that future studies, which compare changes in CSA resulting from these forms of training, should assess multiple locations instead of the common practice of only mid-thigh measurements.

Muscle specific adaptations were also present between training groups. In particular, while all training groups increased VOL of the VL, VI and VM, the SQ-

P group increased VOL_{VI} to a greater extent than any other training group and only the JS-P group increased VOL_{RF} . Once again these adaptations may have been caused by differences in intrinsic forces or muscle activity, but this is only speculation. However, further research is warranted investigating the nature of these adaptations as during slow velocity contractions the VI, which is deep and pulls on the QT towards the femur, would likely function to increase tendon excursion and allow variable gearing of the muscle to occur (21). Furthermore, the RF, which is the only biarticular muscle of the QF, is likely to function differently to the vasti muscles. Biarticular muscles function as joint stabilisers during slow velocity movements like the SQ-P, but at high velocities this behaviour may change (73, 103). But once again, it is beyond the scope of the current study to speculate about these differences.

In summary, differences in training specific adaptations were found in several key variables. Most importantly tendon stiffness only significantly increased in response to SHL training, while fascicle angle only increased in response to FLL training. As tendon stiffness only increased in the SHL group and high loads and slow speed were previously found to be associated with increased tendon strain it is likely that an initial tendon strain threshold is necessary for these adaptations to occur. In contrast, many training specific adaptations such as fascicle length, QF volume and cross-sectional area at the mid-thigh were not significantly different between groups. Thus, while both forms of training result in a plethora of positive adaptations, there are some key differences. Currently, it can be suggested that training programmes with similar populations should contain both SHL and FLL training modalities to ensure all aspects of the MTU receive sufficient stimuli for adaptation.

Chapter 8

Summary and Conclusions

In this thesis great emphasis has been placed on vastus lateralis (VL) muscle-tendon unit (MTU) structure, behaviour/movement and adaptation. Of particular interest was how external loading and movement speed influence these variables. In the first study (Chapter 3) we developed a new methodology by which electromyography (EMG) could be normalised during large range of motion (ROM) knee extensions. Such a methodology was observed to be important because of the vast changes in MTU structure across the ROM. This methodology was then used as part of a larger study, which investigated how external loading influenced the interaction of muscle and tendon (MTU behaviour) during stretch shortening cycle (SSC) isoinertial knee extensions, and how muscle activity and intrinsic forces influenced MTU behaviour (Chapter 4). We then investigated how external loading influenced MTU behaviour during parallel depth jump squats (JS-P), which is a more complex but also more commonly performed movement (Chapter 5). Then we investigated how speed of movement influences MTU behaviour during parallel depth squatting-type movements (Chapter 6). Lastly, we compared the training specific structural and mechanical adaptations to slow-speed, high-load (SHL) squat training to determine how this might differ to relatively fast-speed, light-load (FLL) jump squat training (Chapter 7).

All human movements are influenced by the interaction of muscle and tendon, which has been shown to increase the work capabilities of the muscle, joint power and velocity and movement economy (43, 94, 208, 227). However, this interaction is largely dependent on the mechanical properties of MTU, which is dictated by the activation of that muscle (18, 19, 163), and the tendon to which it's associated. Tendons are viscoelastic, and thus possess complex mechanical properties, which result in the tendon acting with both elastic and viscous characteristics. These complex properties result in MTU behaviour being influenced by the amount of force applied to the tendon (F_t) (159, 163), the rate at which that force is exerted (RFD_t) (29, 116) and the speed at which tendon lengthening occurs (116). It is also possible for the mechanical properties of

tendons to be altered due to specific adaptations resulting from different types of training (52, 164, 166).

Because MTU behaviour can be greatly influenced by muscle stiffness, and hence muscle activation, Study 3 aimed to determine if maximal volitional muscle activity, changes across a large ROM. In this study we found that the EMG of the quadriceps varied significantly over the ROM in conjunction with changes in muscle length and fascicle angle. With this information we developed a new methodology, using polynomial fitted EMG-joint angle curves obtained during an isokinetic knee extension, to normalise EMG signals obtained during SSC knee extensions. This method was observed to more accurately estimate muscle activation than the conventional method of normalising to a single peak value and hence was used to normalise EMG during the following study, which investigated the influence of external loading on SSC, isoinertial knee extension (Chapter 4).

Prior to this thesis no studies had directly investigated the influence of external loading on MTU behaviour. Because of their viscoelastic properties, tendons lengthen as increasing forces are exerted upon them. Tendon lengthening has been previously observed to increase as the tendon loading (F_t) increases when jumping to higher heights (132), drop jumping from higher heights (138) and running at increasing velocities (139). However, we know from isometric and isolated tendon studies that due to their viscous properties, tendons will resist lengthening as the F_t approaches maximal contraction threshold (159, 190), the RFD_t increases (29) or movement velocity increases (116). Thus, we set out to determine if increasing external load during an isoinertial leg extension would result in the tendon behaving as a predominately elastic structure, as was seen in the unloaded jumping and running studies, or if the external load would result in a predominance of the tendon's viscous properties. We observed the latter to occur. During the eccentric phase of the leg extension, tendon lengthening was diminished when a heavier load [90% of one repetition maximum (1RM)] was lifted compared to a lighter load (20% 1RM). This MTU behaviour demonstrated

the tendon acting as an essentially rigid structure with the heavy load, thus its viscous properties predominated the MTU behaviour. When comparing the results from this study to previous *in vivo* research we found that tendon forces during the isoinertial knee extension were significantly greater than those previously experienced in jumping and drop jumping (90, 133). Furthermore, we found with the 20% 1RM load that tendon lengthening during movement mirrored the RFD_t . Specifically, when force exerted on the tendon increased the tendon lengthened and when force was reduced it recoiled. However, this same relationship was not observed with the 90% 1RM load. Instead with the heavier load, the RFD_t increased at a much faster rate and the tendon functioned as an essentially rigid force transducer.

In the next study (Chapter 5) we took this same concept and applied it to a loaded JS-P. The JS-P is a complex SSC movement that is often performed with a variety of loads, thus the applicability of this research was greater than that of the loaded isoinertial SSC leg extensions at the cost of simplicity and control of the movement. To maintain similar movement patterns, subjects performed all jump squats to parallel depth (JS-P). We chose not to use the EMG normalisation protocols designed in Chapter 5, as we felt it inappropriate to use a knee extension for EMG normalisation of JS-P because of the influence of the hip angle on muscle length and potentially EMG (15, 103, 242) as well as the large number of muscles (9 in total) from which EMG was recorded. The results of this study showed that the tendon went through two distinct loading and unloading phases / SSCs. When we compared MTU behaviour as loading increased we found that during the eccentric phase the tendon went through significantly greater lengthening. Thus, in the JS-P the tendon acted as a predominately elastic structure, similar to what has been found in jump and drop jump studies (89, 132, 133), but different from what we had previously found in loaded leg extensions. However, further comparisons between these studies revealed that the F_t obtained during JS-P was similar to that obtained during jump and drop jump studies and much less than those obtained in the leg

extension study. The RFD_t was also significantly less than that of the previous study suggesting that sufficient force was not developed fast enough to elicit predominance of viscous properties of the tendon.

When comparing JS-P at different loads we found that as loading increased, F_t greatly increased, joint velocity decreased and RFD_t did not significantly change (despite a moderate mean increase). Since velocity decreased and RFD_t showed a tendency to increase, we would expect to see an increase in tendon stiffening with loading. However because of the large differences in F_t , we found the opposite to be the case. This is further supported by studies investigating jumping (89, 133, 136) and running (139, 170, 171) that found as speed increased in conjunction with F_t the tendon went through greater lengthening. Thus to determine how movement speed can influence MTU behaviour during a commonly used training movement we compared performing squat-type movements with a moderate load (60% 1RM) at different movement speeds: parallel depth slow-tempo squat (TS-P), parallel depth volitional speed squat (SQ-P) and JS-P. The results from this study reiterated that the tendon went through two distinct SSCs during the movement; one during the eccentric phase (initial tendon loading) and a second during the concentric phase. However, in this study we found that the influence of movement speed on MTU behaviour differed between the eccentric and concentric phases. During initial tendon loading in the eccentric phase of the movement, the tendon went through less lengthening at faster speeds, despite encountering greater F_t . In contrast, during the concentric phase the fast speed JS-P, which had a more sustained muscle activity and F_t than the squatting movements (TS-P and SQ-P), had greater tendon lengthening. Thus we found that during the eccentric phase the tendon behaved as a predominately viscous structure while during the concentric phase it behaved as a predominately elastic structure. This difference in behaviour occurred despite similar F_t in the eccentric and concentric phases. However, when we compare the RFD_t between the two phases of movement we found that RFD_t of the concentric phase was only a fraction of its eccentric value because F_t

was largely maintained throughout the movement. Thus, we can conclude that it is likely the RFD_t that dictates the tendon acting as either a predominately viscous or elastic structure during movement.

Because of the difference we found in MTU behaviour, intrinsic forces and muscle activity resulting from using different movement speeds and external loads, the last study was designed to determine the training specific adaptations which result from SHL squat training and FLL jump squat training. The SHL, SQ-P is commonly used to increase strength and muscle size (23, 192). In contrast, jump squat training performed with relatively light loads (0-30% 1RM) is commonly performed to elicit training gains in speed and power during unloaded movements such as sprinting or jumping (23, 62, 223). However, non-movement specific adaptations have often been found in response to both forms of training (7, 62, 164, 166, 231), suggesting that underlying training specific adaptations occur which influence performance across of spectrum of movements and loads. The primary finding of this study was that only SHL, SQ-P training was able to increase tendon stiffness. This increase in stiffness is most likely a result of the increased eccentric strain of the tendon that was observed in the previous study and will likely have a large effect on MTU behaviour and movement kinetics during a variety of movements. In contrast, only jump squat training was able to increase fascicle angle, which may have resulted from the mechanical need to handle the high eccentric loads observed during jump squats. Increased fascicle angle can increase musculotendinous stiffness during SSC movements (35, 76) and has been linked with the ability to handle high eccentric loads (76). Thus it appears that both SHL and FLL training stimulate adaptations in different aspects of the MTU because of the different stresses placed upon the muscle and tendon during training.

CONCLUSIONS

Based on this thesis the following conclusions can be made:

1. Quadriceps muscle activity varies across different knee angles due in part to large changes in muscle length and fascicle angle. In addition, the use of a single filtered peak EMG value to normalise EMG signals may result in an underestimation of the true physiological neural activation because of these differences.
2. Polynomial fitted curves can be used to determine the EMG-joint angle relationship and normalise EMG during kinetically similar movements.
3. During isoinertial SSC knee extensions as external loading increases, F_t and RFD_t increase while joint concentric velocity decreases. This results in a change in MTU behaviour highlighted by the tendon going through less lengthening. Thus, when extremely high forces are exerted quickly through the tendon, its dynamic stiffness increases and the tendon serves as a rigid force transducer. In contrast, the tendon serves as a compliant power amplifier with light loads.
4. During JS-P as external load increases, F_t and RFD_t increase while joint velocity decreases. However, the forces encountered are much less than those encountered during SSC knee extensions, resulting in the tendon acting as a predominately elastic structure; increasing in length as F_t increases.
5. During squatting-type movements, as the speed of movement increases the tendon stiffens during its initial lengthening in the eccentric phase. However during the concentric phase the opposite occurs. These disparities can be linked to the high RFD_t during the eccentric phase and the relatively low RFD_t during the concentric phase.
6. In healthy untrained subjects, both SHL squat training and FLL jump squat training are effective ways to increase strength, quadriceps cross-sectional area and volume as well as vastus lateralis fascicle length. However, only SHL squat training is an effective way to increase quadriceps tendon stiffness, while only FLL jump squat training is effective at increasing vastus lateralis fascicle angle.

7. The training specific vastus lateralis MTU adaptations that occur in response to jump squat training are in large part independent of the depth of the countermovement used. However, training at different depths may result in training specific regional and muscle specific hypertrophy.

PRACTICAL APPLICATIONS

1. When normalising EMG during large ROM knee extensions, the use of a polynomial fitted EMG-joint angle curve obtained during a slow isokinetic contraction is a valid method to account for changes in maximal EMG signals over the ROM.
2. MTU behaviour appears to be largely movement specific, as it varies based on the F_t and RFD_t encountered during a given movement. Thus it is inappropriate to make assumptions about MTU acting in a consistent manner between different exercises.
3. Tendons are viscoelastic, but during movement they can act as either a predominantly elastic or viscous structure depending on the MTU kinetics. When comparing movements, if differences in F_t are present then elastic properties may be evident and predominate MTU behaviour. However, if large differences in RFD_t are present then the viscous properties of the tendon will predominate. Thus to illicit maximal eccentric strain of the tendon, high F_t should be developed over a relatively long period of time.
4. In untrained, physically active men, increases in tendon stiffness appear to result from SHL squat training, but not FLL jump squat training. Thus, individuals who want to increase their tendon stiffness should use SHL training, as this type of training has adequate stimuli necessary for tendon adaptation.

5. In untrained, physically active men, increases in fascicle angle appear to result from FLL squat jump training, but not SHL squat training. Thus, individuals who want to increase their fascicle angle should use FLL training, as this type of training has adequate stimuli for this adaptation.
6. As training specific adaptations to SHL-squat and FLL-jump squat training differ in some key aspects it is recommended that individuals incorporate both forms of training in periodised fashion into any long-duration training programmes.

Chapter 9

Future Research Directions

The results obtained from the current thesis have addressed many important research questions, but have also prompted several additional questions relevant to the central purpose of this thesis.

EMG-ANGLE RELATIONSHIP: NEW APPLICATIONS AND TESTS

In the first study (Chapter 3), we developed a test to measure the EMG-angle relationship of the knee extensors during a slow velocity ($30^{\circ}\cdot\text{s}^{-1}$) isokinetic leg extension. This relationship provides information about how the maximal volitional muscle activity of a muscle changes across a large ROM. This method was then used for normalisation of EMG during SSC leg extensions; which was a kinetically similar movement (open-chain leg extension over a similar ROM). Such a method may also be able to replace tests such as multiple isometric leg extensions performed at different joint angles, which has been used to determine training induced shifts in the EMG-angle relationship. Adopting this practice would have many potential benefits in assessing such shifts, as the method would drastically reduce the number of contractions necessary to determine this relationship. However, prior to adopting such a practice the inter-day reliability of these measures must be determined, as it is likely that a small change in electrode placement could drastically change the EMG values obtained. However, this is also a limitation of the current practice so the benefits most likely will outweigh the costs.

The major drawback we encountered after developing this methodology is that joint angle specific EMG normalisation is most likely only applicable in kinetically similar movements. In fact, after much deliberation we decided not to use isokinetic leg extensions to normalise EMG values obtained during squatting and jump squatting movements. This decision was made primarily because hip angle changes simultaneously as knee angle changes during squatting and jumping movements. Thus, the muscle length of the biarticular rectus femoris would also change, making the joint angle normalisation an invalid process. This hypothesis is supported by previous research which found that knee angle influenced

gastrocnemius length and EMG regardless of ankle angle (15, 46, 234). Another limitation of the current study was that we examined a single joint movement (knee extension) and this would not allow us to normalise other muscle groups involved in squatting and jumping (i.e. hip flexors and plantar flexors). To account for these limitations two different approaches could be taken. The first would be to determine the muscle specific EMG-joint angle relationships for the plantar flexors, dorsiflexors, knee flexors and hip extensors using similar single joint isokinetic contractions. However, this technique would still not account for the influence of biarticular muscles. An alternative approach one could adopt would be the use of a kinetically similar movement, such as an isokinetic squat to normalise EMG based on the respective joint positions throughout the movement. However, both of these approaches would first need to be validated to ensure the movements are kinetically similar and that EMG-angle relationships do exist in the muscles in question.

EXAMINATION OF THE RELATIONSHIP BETWEEN TENDON LENGTHENING AND RFD_t

A key finding of the current thesis was that the tendon, which is viscoelastic in nature, can function as a predominately elastic or viscous structure. Furthermore, the predominating aspect of the tendon is largely determined by interplay of the rate of force development (RFD_t) and force (F_t) expressed through the tendon. Specifically, we found with high RFD_t a drastic stiffening of the tendon occurs, while with low RFD_t , even if high F_t is present the tendon will behave as an elastic structure. These relationships between tendon lengthening and F_t and RFD_t make it difficult to apply findings in MTU behaviour observed during specific movements to other movements, or to produce a descriptive MTU model in which RFD_t and/or F_t may differ from the observed movement. This complex interaction of F_t and RFD_t on tendon lengthening is an area in which a great deal of future research could be performed, as we only have a limited understanding of this interaction at present. Obtaining this knowledge can add a

great deal to our basic understanding of human movement and allow for MTU models to be designed that more accurately represent those in the human body.

THRESHOLD OF DYNAMIC TENDON STIFFENING

An observation made during pilot testing and data collection throughout this thesis, was that a load threshold existed at which dynamic stiffening of the tendon occurs, and that this threshold varies between subjects. For each individual the tendon will lengthen more and more as external load is added. However, past a certain load the tendon will start to stiffen and less tendon lengthening will occur. It is possible that the F_t or RFD_t at which dynamic stiffening occurs may be dependent on either the inherent stiffness of the tendon, the thickness and length of the tendon, or the strength of the subject. Thus, an area of future research could be to explore if such a threshold exists and if so, how the variables previously mentioned may influence this threshold.

ECCENTRIC AND CONCENTRIC CONTRACTIONS

In our analysis of the influence of speed and load on MTU behaviour during squatting and jumping we found two distinct tendon lengthening and shortening phases (SSCs) occurred. The first SSC occurred in the eccentric phase and the second in the concentric. In previous research that investigated how to increase tendon stiffness, eccentric contractions have been shown to be most effective and thus are often prescribed in rehabilitation settings. Thus it is likely that the specific MTU behaviour and intrinsic forces that occur during this phase will provide a greater stimulus for tendon adaptation. However, in the training study in the presented thesis, all movements were performed with both an eccentric and concentric phase so it is impossible to say with certainty that the MTU behaviour during the eccentric phase was the primary stimulus for adaptation. Thus, future research could be pursued to investigate if differences exist in MTU behaviour during eccentric only, concentric only and SSC movements. Then a

follow up training study could be performed to determine if similar training specific adaptations were obtained from these different movements.

CHANGES IN MTU STRUCTURE AND MECHANICAL PROPERTIES INFLUENCE MOVEMENT

In the final study of this thesis we found that training with SHL squats and not FFL jump squats, increased tendon stiffness. Previous studies have shown both forms of training as being effective in increasing jump performance (7, 62, 166, 179), however the differences in adaptation between squat and jump squat training may indicate that this increase in performance comes from separate pathways. A stiffer tendon shortens at a greater speed when stretched, but requires greater forces to stretch it. During a bodyweight movement, such as a vertical jump, one of the most effective ways to develop greater force is to increase the eccentric velocity and thus downward momentum. This means that if an individual increases their tendon stiffness, they will likely move at faster eccentric and concentric speeds during a vertical jump. It is likely that the observed increase in tendon stiffness results in a decreased amount of time needed to complete the jump. If this holds true, this could be a major benefit for sport performance, as performance outcomes are often determined by who is able to perform powerful movements quickly (i.e. rebounding in basketball). However, at the moment this is only speculation and more research is needed to investigate any associations between changes in tendon stiffness and changes in jump kinetics.

DO FINDINGS IN UNTRAINED SUBJECTS REFLECT THOSE IN TRAINED SUBJECTS?

In the final study of this thesis untrained, physically active subjects performed different types of training. Subjects were stratified into training groups according to their baseline strength values (body mass to one repetition maximum ratio), however, the subjects in this study were relatively weak compared to athletic

populations. One question that remains unanswered is if the observed adaptation in MTU structure and the mechanical properties of tendon in the current study would accurately reflect training adaptation in an athletic population. Previous studies have found limited adaptations in muscle hypertrophy and cross-sectional area in response to FLL training (109, 169, 233). Furthermore, the only study to previously measure changes in fascicle angle in response to FLL training used well-trained subjects and found a decrease in fascicle angle in response to training (40). However, in this study sprint training was performed in conjunction with jump training, which may have influenced the observed adaptations. It is also possible that jump training in strength trained subjects who already possess relatively stiff tendons may result in a decrease in tendon stiffness over time; however, at this moment more research is needed to explore these possibilities.

THE INFLUENCE OF PERIODIZATION ON MTU PROPERTIES

In the final study of this thesis we found that differences in training specific adaptations occur in response to SHL squat and FLL jump squat training. Because of this we speculated that both forms of training should be performed to provide stimuli for a wide range of MTU adaptations. However, while this would appear sound advice, it is not yet known if concurrent training with both forms of training would result in an interference effect, which would blunt any of the observed adaptations. This is one potential topic for future research. Additionally, most strength and conditioning professionals design resistance training programmes that shift training focus over time, in a process called periodization. Lastly, if an interference affect was present it would be of interest to see if it could be limited or eliminated by periodization.

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Appendix A

Scientific Publications

Earp JE, Newton RU, Cormie PU, Blazeovich AJ. Knee angle-specific EMG normalization: The use of polynomial based EMG-angle relationships. *J Electromyogr Kinesiol.* 2012 Oct (Epub ahead of print).

Scientific Conference Presentations

Earp JE, Blazeovich AJ, Cormie P, Newton RU. The influence of external loading on tendon behaviour in knee extensor stretch-shortening cycle exercise. American College of Sports Medicine, Annual Meeting. May 2012.

Earp JE, Blazeovich AJ, Cormie P, Newton RU. Differential quadriceps femoris muscle-tendon unit anatomical adaptations in response to squat versus jump squat training. National Strength & Conditioning Association, National Conference. July 2012.

Earp JE, Newton RU, Cormie PU, Blazeovich AJ. The influence of loading on muscle-tendon unit behaviour during stretch shortening cycle knee extensions. European College of Sports Science, Congress 2011.

Earp JE, Newton RU, Blazeovich AJ. Multiple force producing events occur during stretch shortening cycle knee extensions. Sports Medicine Australia. Australian Conference of Sports Medicine in Sport 2011.

Scientific Poster Presentations

Earp JE, Newton RU, Blazeovich AJ. Normalization of knee extensor sEMG to joint angle. *European College of Sports Science, Congress 2011.*