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The effects of load bearing on muscle-tendon interaction during locomotion

Summery

Introduction; The purpose of this study was to investigate the separate and combined effects of speed and external loading on muscle-tendon interaction and length change during locomotion. We hypothesised that due to the increased demand on the ankle towards forward propulsion, GM MTU interaction may no longer be optimised for energy conservation and power amplification during loaded gait, therefore i) load carrying will affect the SEE loading and fascicular shortening patterns, and ii) increased walking speed will affect these patterns. **Method;** Participants comprising of 14 volunteers from the Norwegian School Of Sport Sciences were asked to walk at two different predetermined speeds on a treadmill, one slow (sp1)(1.3m/s+/-0.05) and one fast (sp2) (1.7m/s +/-0.08), with and without a weighted vest equal to half their total body weight. During walking on the treadmill, data recordings consisted of lower extremity joint kinematics and ultrasound imaging of the gastrocnemius medialis (GM) muscle fascicles. **Results;** Both speed (>0,001) and loading (0,0065) were found to have a significant interaction effect on the average length change of the MTU (0,0023). No significant difference was found between the loaded condition during slow walking (sp1), but a significant difference between the loaded conditions in fast walking (sp2) (0,05 at 95% conf.). No change was observed in GM muscle fascicle length change or shortening velocity. The SEE stretched therefore had a similar pattern to that of the whole MTU, showing a significant interaction effect (0,0007) with both speed (>0,0001) and load (0,005). A post hoc Sidak test revealed no significant difference between load or no load during slow walking (sp1), but a significant difference between the loaded conditions in fast walking (sp2)(0,05 at 95% conf.). **Conclusion;** There was no change in GM muscle fascicle or SEE behaviour when applying an external load in the form of a weighted vest, during walking at a presumed optimal speed (sp1) for metabolic efficiency. When increasing speed (sp2) the GM muscle fascicles behaviour remained the same as under the optimal conditions, however the whole GM MTU stretched less due to a more plantar flexed ankle and flexed knee. This was even more evident when applying an external load at the faster speed. However the GM fascicles remain operating at what is presumed to be optimal conditions for force production and metabolic efficiency. This results in a smaller stretch of the SEE, meaning less loading on the GM MTU thereby decreasing the total energy contribution from elastic strain.

1. Introduction

Backpacks are the most common mode of load carrying during leisure activities and in professional environments, including military activity (Grenier et al. 2012). Understanding the mechanisms contributing to effective load carrying may help improve comfort and reduce injury risk in backpack carriers. Energetically optimal walking speeds and loads have been identified during backpack walking (Bastien et al. 2005;Falola, Delpech, and Brisswalter 2000). However, the mechanisms supporting these findings remain largely unknown. Importantly, the behaviour of the muscle-tendon unit (MTU) during this activity, one of the most important parameters of walking efficiency, has never been studied in this context.

The MTU of the triceps surae complex, comprising of the two gastrocnemius muscle heads and the soleus muscle, has been extensively studied during walking and running due to its role in generating ankle plantar flexion moment (Spanjaard et al. 2008), thereby being a vital source of mechanical power for human locomotion. The main tasks of plantar–flexor muscles during walking is to provide body weight support, contribute to propulsion, and accelerate the limb into swing (Neptune et al. 2001). Using real-time ultrasonography, a scanning method that allows reliable and non-invasive measurements of intact human fascicular and tendon kinematics (Aggeloussis et al. 2010), several studies have been conducted on muscle dynamics during locomotion. Findings presented by Fukunaga et al. (2001) show that during walking the medial gastrocnemius (GM) muscle fascicles appear to show relative isometric behaviour during mid-stance followed by a shortening in late stance, whereas the series elastic elements (SEE) are stretched and subsequently recoil during push off. This is similar to several other studies, concluding that MTU behaviour is well described during walking, however there is no available information when body mass is increased with external loading. An increase in external loading must go hand in hand with an increased in the internal moment of the joint supporting this load. Therefore one might assume the dynamics of the MTU might function similarly to other situations where we see an increase in joint moment. Running, although very different from walking in a kinematics point of view, is a task during which lower limbs joint moments are increased. As walking speed increases, GM muscle fascicle velocity increases simultaneously, thereby impairing the muscles ability to produce force Farris and Sawicki (2012). However, muscle fascicles

of the gastrocnemius medial head (GM) shorten through mid- and late stance during running, resulting in a much larger stretch of the Achilles tendon and a greater contribution of the series elastic elements in the form of strain energy (Farris & Sawicki 2012). Unlike running, energy storage and release occurs at lower rates during loaded walking, arguably increasing SEE hysteresis. This implies that most additional elastic energy gained from load carrying would be lost during walking, affecting energy conservation. Yet the additional mass inherent to this condition will increase force and energy requirements upon the triceps surae muscles.

Hence, MTU interaction may no longer be optimised for energy conservation and power amplification during loaded gait. The hypothesis of this study are that i) load carrying will affect the SEE loading and fascicular shortening patterns, and that ii) walking speed will affect these patterns.

The purpose of this study is to compare the muscle-tendon interaction pattern between two separate gait speeds, with and without an additional external loading.

2. Theory
2.1 Tendon structure

Tendons transfer force generated by the contractile machinery to bones, producing moments about joints. Several factors affect the mechanical forces on tendons during movement. (1) Different tendons are subjected to different levels of mechanical loading. Peak force transmitted through the Achilles tendon, during running has been estimated at 9kN, which is the equivalent of 12,5 times body weight (Komi 1990). Whereas during passive mobilization of the wrist, the flexor tendon force was found to range between 1 and 6 N, and up to 9 N during similar mobilization of the fingers (Schuind et al. 1992). (2) Level of muscle contraction and the tendons relative size, influence mechanical forces on a tendon. A tendon with a larger absolute cross sectional area (CSA) will experience a smaller strain at the same muscular force then a tendon with a smaller CSA. (3) Different activities induce different levels of forces, even on the same tendon. Similarly, varying the rate and frequency of mechanical loading result in different levels of tendon forces. This is due to the structural composition of the tendon (Wang 2006)

2.1.1. Tendon structure

Collagen molecules, fibrils, fiber bundles, fascicles are the elements composing the multi-unit hierarchical structure of a tendon unit. The smallest tendon structural unit, the fibril consists largely of rod-like collagen molecules aligned end-to-end in a quarter-staggered array. Multiple collagen fibrils are bound together by *endotenon*, a thin layer of connective tissue assisting intratendinous gliding and also containing blood vessels, lymphatics and nerves, forming fibers (Kastelic et al. 1978; Ochiai et al. 1979. Fiber bundles form fascicles, and bundles of fascicles are enclosed by the *epitenon,* constituting the tendon unit. A third layer of connective tissue surrounding the tendon, paratenon, acts with the epitenon making up the peritendon reducing the friction with adjacent tissue. The above described structure, were a fibril is formed by the aggregation of several collagen molecules in a quaternary structure, can be observed under an electron microscope as repeating bands on the fibrils due to overlapping molecules. By arranging adjacent collagen molecules in a quarter-stagger, oppositely charged amino acids are aligned (Nordin & Frankel 2001). This creates a stable structure that will re-

quire large amounts of energy and force to separate affording the tendon tensile strength (Wang et al. 2006).

2.1.2. Outer structure and insertion into bone

The site at which tendon attaches to bone is referred to as an *enthesis*, also known as an insertion site, or osteotendinous junction. The enthesis can bare tensile, compressive and shear forces, and it is estimated that the tensile forces at this site may be four times that of the tendon midsubstance (McGonagle et al. 2003. Benjamin et al. (2006) distinguish two broad categories of attachment sites according to their structure. These have been termed fibrous and fibrocartalege according to the type of tissue present at the attachment sites. Also described by Woo et al. (1988) as indirect and direct attachments, respectively. At fibrous entheses, the tendon or ligament attaches either directly to the bone or indirectly to it via the periosteum. In both cases, dense fibrous connective tissue connects the tendon/ligament to the periosteum and there is no evidence of (fibro) cartilage differentiation. Fibrocartilaginous entheses are sites where chondrogenesis has occurred and thus four zones of tissue are commonly present: pure dense fibrous connective tissue, uncalcified fibrocartilage, calcified fibrocartilage and bone (Benjamin et al. 2006). The inclusion of a zone of pure dense fibrous connective tissue and a zone of bone at a fibrocartilaginous enthesis highlight the difficulty of defining with any degree of precision where such an enthesis begins and ends. The dense fibrous connective tissue is of course continuous with (and indistinguishable from) that of the rest of the tendon/ligament and equally the bone at an enthesis blends imperceptibly with that in the remainder of the skeleton.

In the junction between tendon and muscle, the tendons collagen fibrils are inserted into deep recesses formed by myofiroblasts. This site is known as the myotendinous junction, and allows for tensile forces generated by contractile proteins, actine and myosin, of muscle fibers to be transmitted to tendon collagen fibers (Michna et al. 1983; Tidbal 1991, 1984). The myotendinous junction reduces tension on tendons during muscle contraction, it is also known to be the weakest point of the muscle-tendon unit (Garret et al. 1990; Jarvinen et al. 1991).

2.1.3. Tendon Composition

Tendons consist of collagens, proteoglycans, glycoproteins, water and cells. Type I collagen being most abundant, 60% of dry mass and 95% of total collagen (Wang 2006)

2.1.4. Vascularisation

Kolliker stated in 1850 that tendons were relatively avascular. However it is now know that tendons have a vascular system, although somewhat limited. Tendons receive their blood supply directly from vessels in the perimysium, the periosteal insertion and the surronding tissue via vessels in the paratenon or mesotenon (Nordin & Frankel 2001). They enter along endotenon but do not penetrate bundles. At insertions, they surround junction but do not cross them. Tendons have been characterized as vascular if they are surrounded by paratenon and avascular if surrounded by a tendon sheath. This is because in tendons surrounded by paratenon, vessels enter from many points on the periphery and anastmose with a longitudinal system of capillaries. Tendons surrounded by a tendon sheath are different, in that the mesotenon are reduced to vincula, leading researchers to propose a dual pathway for tendon nutrition: a vascular pathway, and, for the avascular regions, a synovial (diffusion) pathway. The concept of diffusional nutrition is of primary clinical significance in that it implies that tendon healing and repair can occur in the absence of a blood supply (Nordin & Frankel 2001).

2.1.5. Histology

Besides collagens, tendons also contain proteoglycans in small quantities. Depending on the tendon site, proteoglycan content can vary due to mechanical loading conditions (e.g., tension vs. compression, Berenson et al., 1996; Riley et al., 1994b). There are many proteoglycans, including aggrecan, which holds water within the fibro cartilage and resists compression, and decorin, a small leucine-rich proteoglycan located on the surface of the middle portions of collagen fibrils and is thought to facilitate fibrillar slippage during mechanical deformation (Pins et al., 1997; Vogel and Heinegard, 1985; Graham et al., 2000).There are several glycoproteins present in the extracellular matrix of the tendon. These include tenascin-C, contributing to the mechanical stability of the extracellular matrix through its interaction with collagen fibrils, and fibronectin located on the surface of collagens, and its synthesis increases to facilitate wound healing (Jozsa

et al., 1989a; Williams et al., 1984; Elefteriou et al., 2001). Additionally, tendons contain elastin, which composes about 2% of the dry weight of the tendon (Jozsa et al., 1989b). The elastic fibers, which comprise elastin and microfibrillar proteins, may contribute to the recovery of the crimp configuration of the collagen fibers after stretching (Butler et al., 1978). Fibroblasts (tenoblasts and tenocytes) are the dominant cell type, however there is also endothelial cells, synovial cells and chondrocytes are present in tendons,. Tendon fibroblasts align in rows between collagen fiber bundles and are responsible for synthesising extracellular matrix proteins (e.g., collagens, fibronectin, and proteoglycans), producing an organised collagen matrix, and remodelling it during tendon healing.

2.1.6. Collagen

The great mechanical stability of collagen gives the tendons their characteristic strength and flexibility (Wang, Guo, and Li 2012)

The tropocollagen triple helix, a long thin portein is synthesized in the fibroblas as a large precursor (procollagen), which is then secreted and cleaved extracellulary to become collagen (Fitton-Jackson 1965 as cited in Nordin & Frankel 2001). Type I collagen constitutes about 60% of the tendons dry weight and about 95% of the total collagen content. The remaining collagen-content consists mainly of type III and V. Type III collagen is mainly found in the endotendon and epitendon, forming smaller less organized fibrils. Type V collagen is interlaced into the core of type I collagen fibrils and regulate fibril growth (Birk et al. 1990).

Cross-links are formed between collagen molecules and are essential to aggregation at the fibril level. The cross-link character of the collagen fibril gives strength to the tissues they compose, increasing the youngs-modulus of the tendon and reducing its strain at failure (Thompson & Czernuszka 1995) allowing the tissues to function under mechanical stress (Nordin & Frankel 2001). The collagen fibers composing tendons have an orderly, parallel arrangement, which equips the tendon to handle high unidirectional tensile loads to which they are subjected daily. The fibrils are "crimped" with an irregular periodicity, giving the material a low compressive stiffness (Ker 2002)

2.2. Mechanical properties (behaviour)

When analysing the biomechanical properties of tendons, it is common to subject the tendon to tensile deformation using a constant rate of elongation. The tendon is elongated until it ruptures, and the resulting stress-strain curve is plotted. The resulting plot has four regions characteristic to the tendinous tissue (Nordin & Frankel 2001). (1) First is the "toe region", here the tissue stretches easily, without much force, and the collagen fibres become straight and lose their wavy apperance as the loading progresses (Hiersch 1974; Woo et al. 1994 as cited in Nordin & Frankel 2001). (2) Second comes the "linear" region where progressively greater force is required to produce equivalent amounts of elongation. (3) Eventually the curve will level off reaching the yield point of the tissue, knowned as the "plastic) region. This is the beginning of failure, and will result in irreversible changes. (4) Further elongation of the tissue will result in the occurrence an unpredictable major failure of fibers bundles. The ultimate tensile strength of the tissue is registered before ultimate failure (rupture) and the load-bearing abilities of the tendon is substantially reduces (Nordin & Frankel 2001).

The modulus of elasticity for tendons is based on the relationship between stress and strain during the "linear" region of the curve. Stress is load over area, while strain is the percentage of length change to a given stress.

Another characteristic of tendons is demonstrated during loading and unloading of the tissue between two limits of elongation, the elastic fibers allow the material to return to its original shape and size after being deformed. Part of the energy spent on deforming the tissue is stored; what is left will represent the energy loss during the cycle and is called *hysteresis*. The area enclosed by the loop represents energy loss.

2.2.1. Viscoeleastic behavior (rate dependency)

The ultimate tensile strength of tendons is of limited interest from a functional standpoint, due to the stress magnitude tendon are subjected to under normal physiological condition being one third of this value. However it is of interest that tendons exhibit viscoelastic, or rate-dependent (time-dependent) behavior under loading, in other words, their mechanical properties change with different rates of loading. Measurement of mechanical hysteresis allows assessment of a) the possibility of tendon thermal damage, and b) the amount of metabolic energy that can be saved during locomotion (Maganaris

et al. 2000). There are two standard tests demonstrating the viscoelasticity of tendons, stress-relaxation and creep test. During the stress-relaxation test, strain is kept constant over an extended period (ie. the amount of elogngation is held constant). The stress decreases rapidly at first, and the more slowly, the increase in stress becomes gradually less pronounced when this test is performed cyclically. During a creep test, the stress is kept constant over an extended period. The strain increases relatively quickly at first, then more and more slowly, the increase in strain becomes gradually less pronounced when this test is performed cyclically.

2.2.2. Failure and injury mechanisms

As mentioned during the introduction of this chapter, different tendons are subjected to very different stresses from their muscles. This leads to varying susceptibility to fatigue damage. The fatigue quality of each tendon is matched to the stress it experiences, so that, in life, all tendons are similarly prone to damage. On-going damage must be routinely repaired to maintain homeostasis and prevent damage from becoming symptomatic. However it is recently discovered differences in fatigue quality among tendons, which had previously seemed fairly similar in their mechanical properties (Ker 2002). The material property of tendons that can be quantitatively assessed by measuring the time-to-rupture under a given loading regime (or by assessing the loading regime required to achieve a given time-to-rupture) is called fatigue resistance (Ker 2002). This ability is sharply dependent on temperature, much more so than Young's modulus or hysteresis loss (Wang and Ker, 1995 as cited in Ker 2002). For tendons in an oscillatory test with a given load range, the time-to-rupture is shortened by increasing the frequency (Wang et al., 1995 as cited in Ker 2002).

2.2.3. Function

The main function of tendons is to transfer the force generated by the contractile elements (muscle) to bone, thereby creating movement. There has however been a rising interesting in the tendinous tissues ability to storage and/ or return energy, functioning in practicality as a spring (Wang 2006).

By definition a spring element follows a very simple behaviour, when force is applied the spring will deform, thereby storing energy in the form of elastic strain ener-

gy, the spring will recoil when the force is released, also releasing the stored energy while adverting to its original resting shape. This behaviour applies to materials loaded in tension, like a rubber band, or in compression, like a rubber ball. The amount of stored energy will then depend on the materials stiffness and degree of deformation (Roberts & Azizi 2011). Although springs cannot produce mechanical energy alone, only return energy previously loaded by an external source, there are a variety of ways they may be applied in contexts with the muscle-tendon unit. Roberts & Azizi (2011) propose an energy-based framework for categorising the different functions of elastic mechanisms, where the functional role of tendon is categorised into three patterns according to the directional flow of energy. *Energy conservation*; energy from the body or a body segment is temporarily stored in tendons, and then returned to the body. *Power amplification*; the mechanical energy produced by a muscle contraction is stored in a tendon, and then released to increase mechanical energy of the body or a body segment. *Power attenuation*; Energy from the body or body segment is temporarily stored in the tendon, and then released to do work on muscle that is actively lengthened to absorb energy (Roberts & Azizi, 2011). These applications may be considered to use elastic mechanisms to enhance the muscle-tendon system to function beyond the limits of the stand-alone muscle motor.

2.2.4. Energy conservation

Early studies of spring mechanics in locomotion can be separated into mechanical and energetic studies based on how they have been conducted. One combines an anatomical, mechanical and mathematical approach, showing that a significant fraction of the work done in a step could result from spring like action of tendons, rather then muscular work alone (Alexander & Vernon, 1975). The second argues that the combined measurement of mechanical work during running and the energy input necessary to sustain this work, show efficiency values so high they can only be explained by an elastic mechanism contributing some of the work for free (Cavagna et al. 1964). Both study formats conclude that much of the cyclical work done during running could be attributed to energy stored and released by elastic structures with each step.

This would reason the question as to why we do not have longer tendons, which favours grater elastic recovery? The simple answer would be it might constrain the

muscles ability to control changes in length. Control, meaning here the neuromuscular systems ability to achieve accurate positioning of a limb segment over a wide range of motion, as well as maintaining or achieving a given position after perturbation. Thinner tendons experience both greater stress for a given force, because of their reduced cross sectional area, and grater strain, which favours increased elastic energy storage. Implying thinner tendons are favourable to be efficient in locomotion. Two constraints operate to limit the tendons thinness. Safety first, ratio of rupture-stress to functional-stress. Second, the amount of series elastic stretch should be maintained within the functional shortening range of the muscles fibers. The effectiveness for length control versus the capacity for elastic energy recovery has been seen to result in various muscle-tendon designs. Some are well suited for economical force development (short fascicles with a pinnate architecture) and elastic energy savings (long thin tendon). While other designs (long fascicles with little or no tendon) favor the ability of a muscle to produce mechanical power and control length and position (Biewner & Roberts 2000)

2.2.5. Power amplification

Muscle work applied to elastic elements over the course of relatively slow muscular contraction can be released rapidly to produce transient power outputs that exceed the capacity of the muscle. The energy released from the tendon is equal to (or slightly less, given some energy loss) the work done by the muscle, but it is released in a shorter amount of time to produce higher power outputs (power=work/time). It is important not to misunderstand the use of the term amplified, as the elastic mechanism in animals do not add energy to the system, but rather amplify power only in the sense that they release energy more rapidly than is stored.

Evidence for an amplifying mechanism exists when the peak power output of a jump exceeds the power-producing capacity of the muscles involved. Systems using elastic-based power amplification can also typically display an asymmetric power profile, with most of the power applied to the body late in the jump (Aerts 1997; Roberts & Marsh, 2003; Henry et al. 2005). This seems to be the case in several animals, both specialized and not in jumping.

The temporarily storage of muscular work in elastic structures during locomotion has several benefits. One being already mentioned, energy storage and release in

springs allow power outputs that exceed the power available from muscle motors. It also allow muscles to perform work during a period (of a stride cycle, for example) when the application of power to the body or limbs is constrained by kinematics or kinetics. Alternatively, elastic mechanisms may allow muscles to produce power at lengths and/or velocities that are more favorable for performance given muscle force–velocity or length–tension properties (e.g. Wainwright et al. 1978).

2.2.6. Power attenuation

The role of elastic mechanisms in energy absorption has received less attention than for power generation, but tendons may play an important role in activities that require the dissipation of mechanical energy. Studies on isolated muscle–tendon preparations (Griffiths 1991) and in vivo studies have demonstrated that rapid stretches applied to muscle–tendon units can be taken up by the stretch of tendons, sometimes so effectively that the muscle remains isometric (Reeves and Narici, 2003) or shortens during the 'eccentric' (muscle–tendon unit lengthening) event. Griffiths (1991) proposed that this action provides a mechanical buffer against damage to muscles, which are particularly susceptible to damage when muscle fibers are actively lengthened (Proske and Morgan, 2001; Lieber and Friden 2002). Of course, tendons cannot completely insulate muscles from active lengthening. The net absorption of energy can only be achieved by active lengthening of muscle fibers, as the energy temporarily stored in stretched elastic elements must be released. Just as muscle fibers must be the ultimate source of energy in power-producing events, muscle fibers must be the sink for energy when muscle–tendon units act to reduce the energy of the body or a body segment. Thus, the initial stretch of tendon in an activity like a jump landing is followed by a period in which the tendon releases its potential energy by recoiling to stretch active muscle fibers. This mechanism may be important in that it provides for attenuation of power input to muscle contractile elements (Roberts & Azizi, 2010). Just as power amplification by tendons allows for power outputs beyond a muscle's capacity, power attenuation via tendons may allow muscle–tendon systems to absorb energy at a rate beyond the muscle's maximum capacity for energy absorption. This elastic mechanism can result in reductions in the peak power input, lengthening velocity, and force experienced by lengthening muscles. Which are factors that have been associated with muscle damage (Proske and Morgan,

2001; Lieber and Friden, 2002), thus the shuttling of energy through tendons before muscles absorb it may provide a protective mechanism.

2.3 Mechanics and energetics of locomotion

Muscular forces generated during locomotion depend on an animal's speed, gait, and size and underlie the energy demand to power that locomotion. In human locomotion muscles work in synergy to satisfy the task demands including body support, forward propulsion and swing initiation (Biewener 2004). Changes in limb posture affect muscle forces by altering the mechanical advantage of the ground reaction force (R) and therefore the effective mechanical advantage (EMA = r/R, where r is the muscle mechanical advantage) for muscle force production (Biewener 2004). According to existing metabolic and mechanical power data, movement efficiency is greatest at intermediate walking speeds, where the exchange between kinetic and potential energy is greatest and thus the total mechanical work requirement of the muscles is minimised (Cavagna and Kaneko, 1977). Ultimately this efficiency is dependent on the efficiency with which all muscles do positive work and this is dependent upon the intrinsic force – velocity and force – length properties of skeletal muscle (Farris and Sawicki 2012a). Slower shortening velocities of muscle fibres, at optimal lengths are optimal for efficient muscular force production (Hill 1938). Walking at slower than optimal speeds may be mechanically less efficient (e.g. deviating more from natural frequency of the pendular movement so that additional muscular effort may be required) and less conducive to the storage and recovery of elastic energy in the muscle tendon unit (Neptune, Sasaki, and Kautz 2008). The efficiency of movement is reflected in measurements of energetic cost of transport (COT), which is essentially a measure of the cumulative metabolic rates of the muscles that power locomotion, and is defined as the energetic cost of moving a unit mass a unit distance. In human walking, COT exhibits a U-shaped curve when plotted against speed; it is lowest at intermediate speeds of ~4.5 km/h and increases at speeds faster or slower than this optimum demanding both more positive and negative mechanical work per stride (Cronin et al. 2013). In a study by Farris and Sawicki (2012a) they examined the effects of walking and running at a range of steady-state speeds, on lower limb joint mechanics and metabolic cost of transport in humans. Using inverse dynamics to calculate individual joint moment contributions to positive and negative powers

and summed joint average powers to get total limb power output. Within each gait, there was no difference in the proportion of power contributed by each joint (hip, knee, ankle) to total power across speeds. However, changing from walking to running resulted in a significant shift in power production from the hip to the ankle (which may explain the higher efficiency of running at speeds above 2.0 m/s and shed light on a potential mechanism behind the walk–run transition). It was inferred from these data that plantar–flexor muscle mechanics were adjusted to accommodate faster walking speeds and then again with the switch to running gait (Farris and Sawicki 2012a). During walking at 2.0m/s efficiency was following a decreasing trend, whereas running efficiency was maintained as speed increased beyond 2.0 m/s. This coincided with a significant increase in the percentage of total average positive power provided at the ankle and a decrease at the hip as gait switched to running. COT was greater for running at 2.0 m/s than walking at the same speed because of the greater absolute mechanical power demand. However, the shift in distribution of power generation to more distal muscles may improve efficiency and this could be why humans switch to running (Farris and Sawicki 2012a).

Distal leg muscles such as the triceps surae exhibit morphologies well suited to reducing muscle fibre velocities, because much of the muscle tendon unit length change during locomotion is taken up by stretch and recoil of their long compliant series elastic elements. More proximal muscles do not have these compliant series elastic elements and so must provide most of their length change from fibre length changes. This makes the contractile behaviour of proximal muscles less efficient. The potential influence of intrinsic muscle properties on muscle coordination was evident in a recent study showing that the ability of the ankle plantar flexors to produce force as walking speed increased was greatly impaired, despite an increase in muscle excitation, due to sub-optimal contractile conditions (i.e. increased muscle fiber lengths) (Neptune 2005). Since the plantar flexors have been shown to be important contributors to support, forward propulsion and swing initiation during normal walking, increased output from other muscle groups would appear necessary to compensate for the decreased plantar flexor output (Neptune, Sasaki, and Kautz 2008).

An inherent limitation of inverse-dynamics analyses is the inability to determine the contributions of individual muscles to joint mechanics. The major plantar flexors

(gastrocnemius and soleus) have highly pennate fascicles that insert on the calcaneous through the very compliant Achilles tendon and aponeurosis. This architecture decouples the actions of the muscle fibers from the mechanics of the whole MTU, and thus the separate contributions of fascicles and elastic tissues are hard to determine. Therefore, to truly understand how plantar–flexor muscle mechanics are adjusted with speed and gait, studies at the muscular level are necessary.

2.3.1 Increasing load

Bastien et al. (2005) studied the effect of speed and load on the energy expenditure of walking. The O2 consumption and CO2 production were measured in ten subjects while standing or walking at different speeds from 0.5 to 1.7 m/s with loads from 0 to 75% of their body mass (Mb). Results showed that the mass-specific gross metabolic power increases curvilinearly with speed and is directly proportional to the load at any speed. For all loading conditions, the gross metabolic energy cost (J/kg/m) presents a U-shaped curve with a minimum at around 1.3 m/s. At that optimal speed, a load up to 1/4 Mb seems appropriate for long-distance walks. In addition, the optimal speed for net cost minimisation was around 1.06 m/s and was independent of load.

2.4 Ultrasound in vivo

Kinematics, kinetics and electromyography have long been the traditional measurements for analysis of human movement, providing insight into movement performance and enabling inferences to how muscle and tendon function (Cronin & Litchwark 2011). The examination of joint kinematics and muscle action has lead to the introduction of several musculoskeletal models that estimate muscle-tendon unit (MTU) lengths based on joint posture (Hawkins & Hull 1990). Due to the elastic nature of tendons they will stretch when transferring force from muscle to bone, this as well as the difference in fiber geometry (pennation angle) relative to the muscle, makes MTU length a bad predictor of muscle fascicle length. To examen muscle and tendon separately and their interaction in vivo, ultrasound has become a commonly used non-invasive method.

This is useful for both static and dynamic measurements of muscle structure, and was pioneered in the late 1990s when (Ito et al. 1998; Narici et al. 1996) examined pennation angle changes as a function of both muscle contraction and joint movement

(Kawakami, Ichinose, and Fukunaga 1998). Ito et al. (1998) were one of the first in using this method to show that during isometric dorsiflexions contractions, MTU length remains approximately constant, while GM muscle fascicles shorten while tendinous tissue lengthens. Confirming that human MTU and fascicle length changes are not always concordant.

2.4.1 Muscle and tendon function during locomotion

Walking

The vast majority of locomotion studies using ultrasound have focussed on the triceps surae complex of young, healthy individuals, due to its unique interaction with elastic tendinous tissue and its relative ease of imaging. Both the fascicles and MG MTU shorten immediately after ground contact due to rapid plantar flexion of the ankle. Throughout the majority of the support phase of stance, MG fascicles tend to remain approximately isometric or exhibit moderate lengthening, before shortening again during push off. This behaviour has been seen across a variate of walking speeds (Fukunaga et al. 2001;Ishikawa 2005;Lichtwark, Bougoulias, and Wilson 2007;Lichtwark and Wilson 2006;Farris and Sawicki 2012).

Several functional differences have been observed between the muscles of the triceps sure complex. MG exhibits time- and speed-dependent decreases in operating length, and shortens faster during the pushoff phase at faster walking speeds (Fukunaga et al. 2001). Soleus however exhibited consistent contractile behaviour regardless of walking speed or duration, and shortens slower than MG during pushoff. Cronin et al. (2013) argued soleus appears to play a more important functional role than MG during walking. And that this may be especially true when walking for prolonged periods or at speeds above the most energetically efficient, where the force potential and thus the functional importance of MG appears to declin. This was demonstrated by Cronin et al. (2013), where when walking at faster then optimal speeds and for prolonged periods, the force potential of MG decreases due to exercise-induced changes in its force–length and force–velocity relationships. Showing shorter operating length for MG fascicles and a ~20% faster shortenings velocity during pushoff, neither of which occurred in soleus.

During the support phase of stance, the triceps surae MTUs lengthen significant-ly more than the muscle fascicles in all three muscles. This is possible through stretch of both the Achilles tendon and aponeurotic tissues (Lichtwark and Wilson 2006) due to its high compliance and rebound ability, elastic energy is stored when force is applied. This elastic energy can subsequently be utilised during the propulsion phase in late stance. During propulsion the muscle fascicles of all triceps surae muscles shorten, but this oc-curs at a rate much slower than that of the tendinous tissues and thus the MTU. Conse-quently, the muscle fascicles are able to shorten at speeds much less than their maxi-mum shortening speed, enabling them to efficiently generate propulsive power (Cronin and Lichtwark 2013). Studies investigating both MG fascicle length change and the di-rect measurement of achilles tendon (AT) length change, find a large difference between the strain of the AT and the calculated SEE length (Lichtwark and Wilson 2006). This demonstrates that other tissues must be stretching. Experimental studies have demon-strated that the aponeurosis strain is significant, although it appears to be stiffer than the AT (Magnusson et al., 2003). Others have also argued that series elastic tissue such as the aponeurosis may be selectively recruited based on muscle activation levels and that this may alter the stiffness of the entire elastic component (Hof, 1998), thereby influ-ence estimations of fascicle force, work and power output.

A near isometric behaviour of the MG muscle during mid-stance, does not allow for a substantial amount of mechanical work to be done by the contractile components. However it allows for the operating length of the muscle to be around the highest force region of the force-velocity curve, thereby supporting bodyweight without excess use of metabolic energy (Hill 1938). The stretch and subsequent recoil of the tendon from single support to toe off indicates that the GM tendon functions as a spring, yielding elastic energy. The energy released by the tendon during recoil may be partly dissipated to stretch the GM muscle during push off, and partly used to aid plantar flex-ion of the ankle joint and move the body forward.

Energy saving in walking is accomplished via a pendulum-like interchange be-tween potential and kinetic energies within the stance phase of each step cycle (Cav-agnaetal.1963, 1977;Cavagna&Margaria 1966 as cited in Fukunaga et al. 2001). The amount of energy conserved depends on the functional interaction between the muscle and SEE as described above. Consider that muscle length changes actively in stance. If

the muscle is forcibly lengthened instead of maintaining a near-constant length around optimal values as described, less fibres will be recruited (or lower discharge frequencies will be attained (Henneman et al. 1965)) to support body weight (Katz 1939). This will decrease energy expenditure. However, for a given MTU length, tendon elongation during single support will be smaller under muscle lengthening conditions compared with isometric conditions. A smaller tendon stretch will result in less elastic energy recovered by passive recoil of the tendon in push-off. To make up for this loss, additional metabolic energy will be consumed. Conversely, if the muscle shortens in stance instead of contracting isometrically, the tendon will stretch more. This will yield a more effective operation of the elastic stretch-recoil mechanism of energy saving. As opposed to isometric contractions, however, concentric contractions are associated with shortening heat losses (Hill 1938), and thus additional metabolic energy will be required to bear body weight. This trade-of between elastic strain energy provision and metabolic cost of muscle contraction suggests that eliciting isometric tension at optimal muscle lengths may be an optimal mechanism for maximising the overall energetic benefit in walking (Fukunaga et al. 2001).

Shortening velocity of MG fascicles increases with walking speed and this impairs the muscle's ability to produce force. Switching to a running gait reduced fascicle velocity at the time of peak force and correspondingly increased peak and average muscle force production and recycling of energy in the series elastic structures (Farris and Sawicki 2012)

Running

When walking speed increases, so does the MG muscle fascicle shortening velocity during push off. At around 2.0 m/s it becomes natural to switch to running, even though this corresponds to a greater metabolic effort, it decreases the speed at which fascicles operate with (Farris and Sawicki 2012b). During running the fascicles shortened throughout the stance phase to produce the greater amount of work required (Lichtwark, Bougoulias, and Wilson 2007), this corresponds to an increase in the strain of the series elastic elements (SEE), therefore also an increase in elastic energy during rebound. The compliance of the SEE allows the muscle fascicles to shorten at a much slower speed, more natural associated with their optimal speed for maximal power output and effi-

ciency, with high velocity shortening during take off in both walking and running achieved by recoil of the SEE. Energetically, it seems more expensive to have to shorten the muscle fascicles during running. However in a study by Lichtwark, Bougoulias, and Wilson (2007) it was apparent that the muscle fascicle never exceeded a shortening velocity of above 1.5 lengths per second during running. They demonstrated at the point of peak tendon stretch (peak force) the velocity of the muscle fascicles did not exceed 0.54 lengths per second at all levels of the muscle. Meaning the muscle contracts at a very slow speed considering that the maximum velocity of muscle contraction is about 10–13 lengths per second (Zajac, 1989). Giving the muscle the ability to act at a relatively optimal level to produce high forces with small amounts of work and high efficiency (Roberts and Scales, 2002). MTU shortening velocities where found to be of up to six-muscle fascicle lengths per second to be achieved during recoil of the tendon at take-off.

In the same study they found that the SEE is loaded at the end of the swing phase so that the tendon is strained during initial foot contact during running (Lichtwark, Bougoulias, and Wilson 2007). This corresponds with EMG data, suggesting that there is a co-activation of the tibialis anterior and the gastrocnemius at the end of the swing phase, likely to load the SEE in preparation for foot contact (Modica and Kram, 2005). This was also found in invasive measures of tendon force during running in humans (Komi, 1990) and turkeys (Roberts et al., 1997).

3. Method

3.1 *Participants and Experimental design*

Participants comprised of 14 subjects from the Norwegian School of Sport Sciences (weight-, leg length+/-SD) (72.7+/-12.9, 88.1+/-4.4). They were given written information outlining the study and participated on a voluntary basis, all data was anonymised. No participant had any severe health issues or history of Achilles tendon pain.

Participants were asked to walk at two different predetermined speeds on a treadmill, one slow (sp1)(1.3m/s+/-0.05) and one fast (sp2) (1.7+/-0.08), with and without a weighted vest (W, Wo) equal to half their total body weight. During walking on the treadmill, data recordings consisted of lower extremity joint kinematics and ultrasound imaging of the gastrocnemius medialis (GM) muscle fascicles. A total of six valid gate cycles were recorded during all four conditions.

3.2 Kinematics

Six spherical retro-reflective markers were attached to the skin of the right leg (greater trochanter, the lateral femoral condyle, lateral malleolus, most posterior point of the calcaneus and the second and fifth metatarsal head). The 3D positions of these were recorded using 6 Oqus 400 cameras (Qualisys Mediacal AB, 41119 Goteborg, Sweden). Sagittal plane knee and ankle angles were determined during stance phase, i.e from heel strike (HS) to toe off (TO) for all trials. Ankle angels below 90 degrees were defined as ankle dorsi-flexion, while knee flexion was defined as angles below 180 degrees.

3.2.1 Determination of events

Joint kinematic data captured with Qualisys Track Manager (QTM) 2.7 was converted to .c3d files and exported to Matlab R2013a (The MathWorks, Inc. Natick, MA 01760-2098, USA). There the events of interest in the stride cycle, HS and TO, were determined as the farthest anterior position of the heel marker, and the farthest posterior position of the second metatarsal marker in the sagittal plane. HS and TO were given as the frame numbers in the kinematic recording in which the events occurred. It was then necessary to down-sample the kinematics data to match the lower acquisition frequency of US recording.

Length changes of the SEE was reported relative to the average length of the SEE at toe-off for each condition. A time when zero force is applied through the tendon (Komi, 1990)

3.3 Muscle architecture, fascicle length and pennation angle

Ultrasound imaging of the medial gastrocnemius muscle (GM) fascicles were visualised in a two-dimensional picture of the sagital plane, using a PC based system (Echo Wave II software 3.0.3, TELEMED Ltd.). A flat ultrasound probe (LV7.5/90/96) with the cable exiting one end of the probe in line with the imaging face, and a view depth of 50mm operating in B-mode, was fixed to the GM muscle belly of the right leg. The scanning head of the probe was coated with transmission gel to obtain acoustic coupling, and oriented along the mid-sagittal axis of the muscle (Aquasonic 100, Parker laboratories, InC., Farfield, New Jersey 07004, USA). The usage of a lightweight custom-made fixation, fastened with elastic bandage and velcro straps (3M, CobanTM, StarppalC) enabled visualisation of both the deep and superficial aponeurosis throughout the stance phase, and provided a clear images of fascicle throughout the entire period of each stride. As described by Litchtwark, Bougoulias and Wilson (2005D), muscle fascicles perform the same actions along the length of the human GM muscle during locomotion. Hence, measurement at mid belly provided a good approximation of the average fascicle length changes across the length of the muscle.

Tracking of the muscle fascicles was done by a semiautomatic tracking script in MATLAB, manually defining fascicles and automatic tracking (Cronin et al. 2011; Gillett et al. 2011). Assuming that the fascicular trajectory is linear, fascicle length was defined as the

Figure 1; *Ultrasound image of a highlighted (yellow) GM muscle fascicle.*

distance between the insertions of the fascicle into the superficial and deep aponeurosis (fig 2). This measurement was consistently made in the middle of the image where the
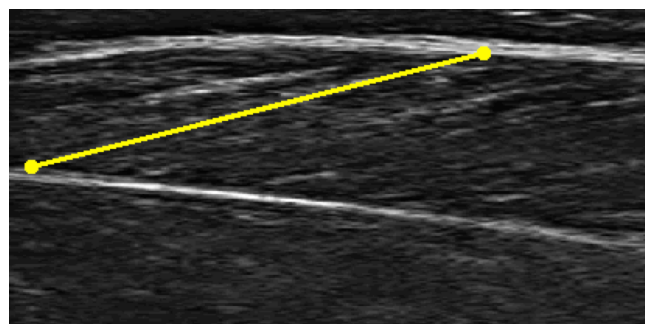
full length of the fascicle could be imaged. Pennation angle was defined as the angle between the deep aponeurosis fascia and the direction of the muscle fascicles.

A minimum of six successive stance phases were recorded for further analysis, based on the findings of Aggeloussis et al. (2010) were 2-6 successive measurements provided good reproducibility of fascicle length.

3.5 Synchronisation of data

A pulse from the ultrasound system, that was high (3-5 V) during recording and low (0 V) before and after, was used to trigger collection of kinematic data synchronously. The images were saved as a video file for further analysis.

3.6 Muscle-tendon unit and Series elastic elements

The length of the entire GM MTU (lMTU) was calculated with the regression equation provided by Hawkins and Hull (1990) using knee and ankle angles as independent variables and shank length for individual scaling. As proposed by Fukunaga et al. (2001), a MTU model was used to estimate the length of the SEE during walking;

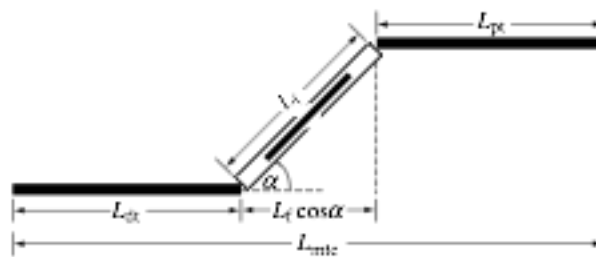$$\text{SEE } (L_{\text{SEE Ldt+Lpt}}) = L_{\text{mtc(MTU)}} - L_f \times \cos(\alpha)$$

Figure 2; *schematic drawing of GM MTU. See text for details.*

where l_{fl} is the fascicle length and [α] the pennation angle. The pennation angle is defined as the angle of insertion of the muscle fascicle into the deep aponeurosis and is also determined from the ultrasonographic images acquired during walking. This definition of the SEE includes all series elastic structures within the MTU (e.g. series-elas-

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tic structures within the muscle, proximal and distal tendon and aponeurosis (Albracht & Arampatzis 2012).

3.7 Statistical analysis

A recent study (Aggeloussis et al. 2010) demonstrated that fascicle length shows a good reproducibility for successive measurements, both within the same day and between 2 days throughout the walking cycle. Revealing that 2–6 trials were needed to determine fascicle length reliably. Therefore in this study, GM muscle fascicle length and pennation angle was recorded for a minimum of six strides for each participant and each condition. Three of these strides were then analysed according to compatibility between ultrasound and kinematic data (meaning, markers for heel strike were concordant with peak stretch on the UL graphs, as demonstrated in fig. 1), and a general consistent appearance of the ultrasound curves.

Figure 3; *window view of GM muscle fascicle length change across several strides. Red circles mark estimated heel strike*

Knee and ankle angles, fascicle length changes, pennation angles and total MTU length values from the three strides were interpolated to 100 points across each individual stance phase (from heel contact to toe-off) and an average for each participant and each condition was determined at each one percent of the stance. The data from each participant were then pooled to get a group average and standard error for each variable across one complete stance phase, as represented in graphs under results. GM muscle fascicle average shortening velocity was determined during the stance phase.

A Two-way repeated-measures ANOVA was used to assess the effects of speed and loading on muscle and SEE parameters. Where significant main effects were observed, *post hoc* Sidak corrections were used to identify the location of differences. For all tests, the minimum level of statistical significance was set at $P<0.05$.
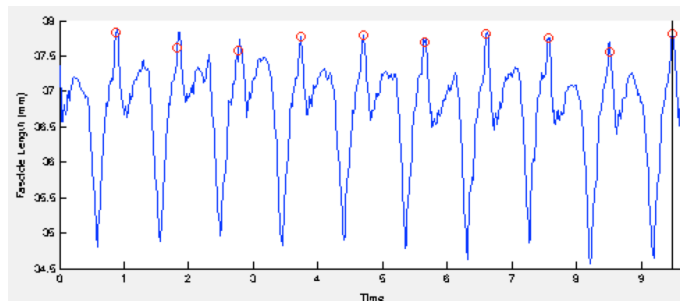
4. Results

4.1 *Kinematics and MTU*

A comparison between the average knee and ankle joint angles and the calculated MG MTU length change for each condition is shown in figure 1. Each trace shows the average of three stance phases per subject and condition, which was normalised to a hundred data points over the stance phase and group averaged (this is the same for all graphs unless otherwise stated). Both speed (>0,001) and loading (0,0065) were found to have a significant interaction effect on the average length change of the MTU (0,0023). A post hoc Sidak test revealed no significant difference between load or no load during slow walking (sp1), but a significant difference between the loaded conditions in fast walking (sp2) (0,05 at 95% conf.).
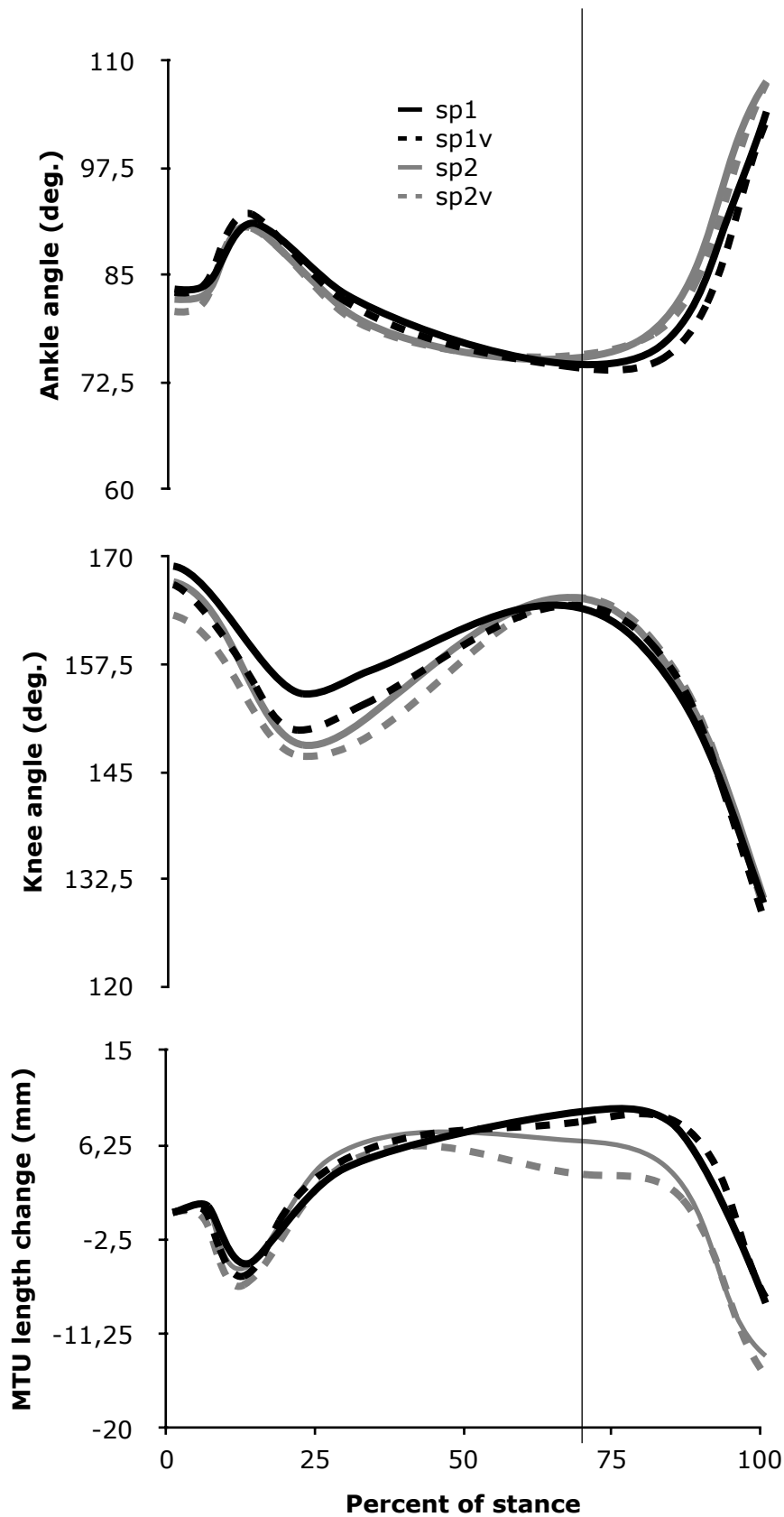
Figure 4. *Average ankle and knee angles and medial gastrocnemius MTU length shown as percentage of stance phase during all conditions.Vertical line at 70% of stance shows were average length changes were used for statistical analysis.*

4.2 *Muscle fascicle behaviour*

The average change in muscle fascicle length for each condition is showed in figure 2., both as absolute values and corrected for differences at heel strike. Speed and loading made no difference in how the muscle fascicle changed length during stance. Speed does seem to have influenced a shift in operational length of the fascicles, however not significant.
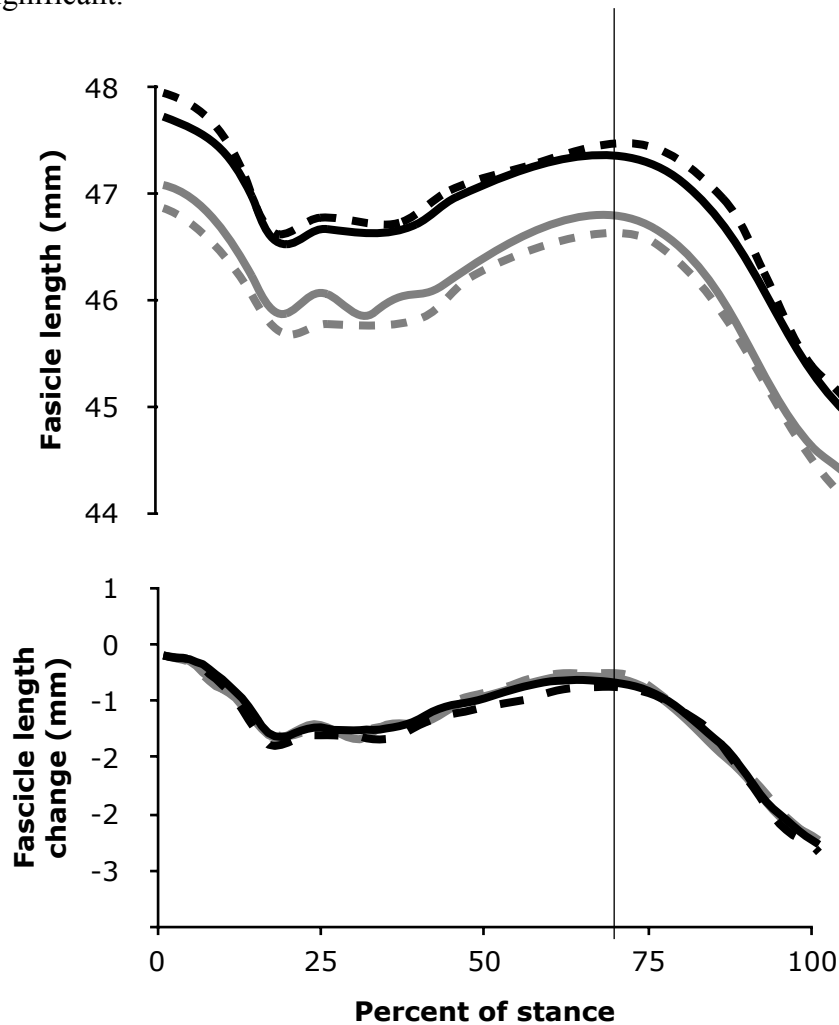
Figure 5; *Average medial gastrocnemius fascicle length change (top) and length change corrected for differences in length at heel strike (bottom), shown as percentage of stance phase during all conditions. Note that stride duration may differ between speeds, which is not evident in this figure due to normalisation. Vertical line at 70% of stance shows were average length changes were used for statistical analysis.*

4.3 *SEE length changes*

The estimated change in SEE length for all conditions is shown in figure 3. The SEE stretched in a similar pattern to that of the whole MTU, showing a significant interaction effect (0,0007) with both speed (>0,0001) and load (0,005). A post hoc Sidak test revealed no significant difference between load or no load during slow walking (sp1), but a significant difference between the loaded conditions in fast walking (sp2)(0,05 at 95% conf.).
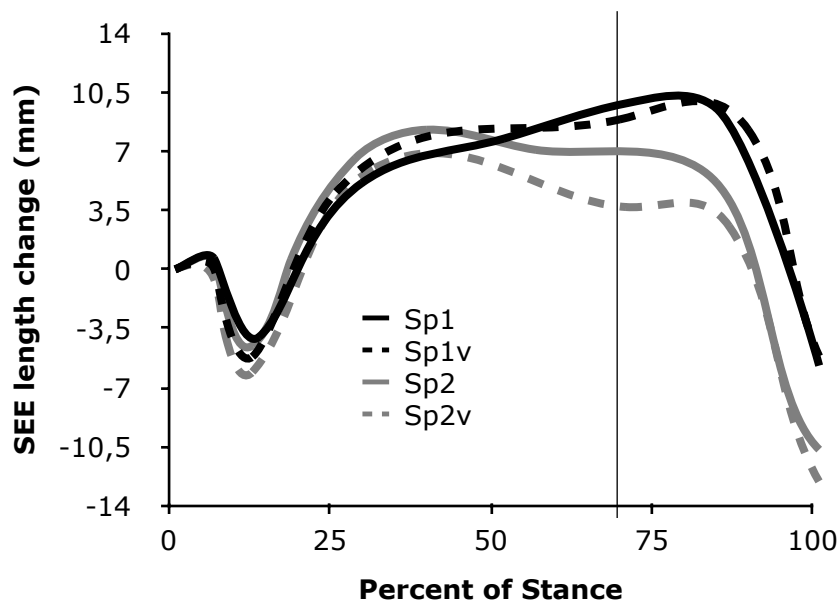
Figure 6; *Average of the estimated series elastic length changes during walking, shown as a percentage of stance phases during all conditions. Vertical line at 70% of stance shows were average length changes were used for statistical analysis.*

4.4 Muscle velocity

Average instantaneous muscle velocity is shown as a percentage of stance for all conditions in figure 4. No interaction was found between this variables and speed and loading.
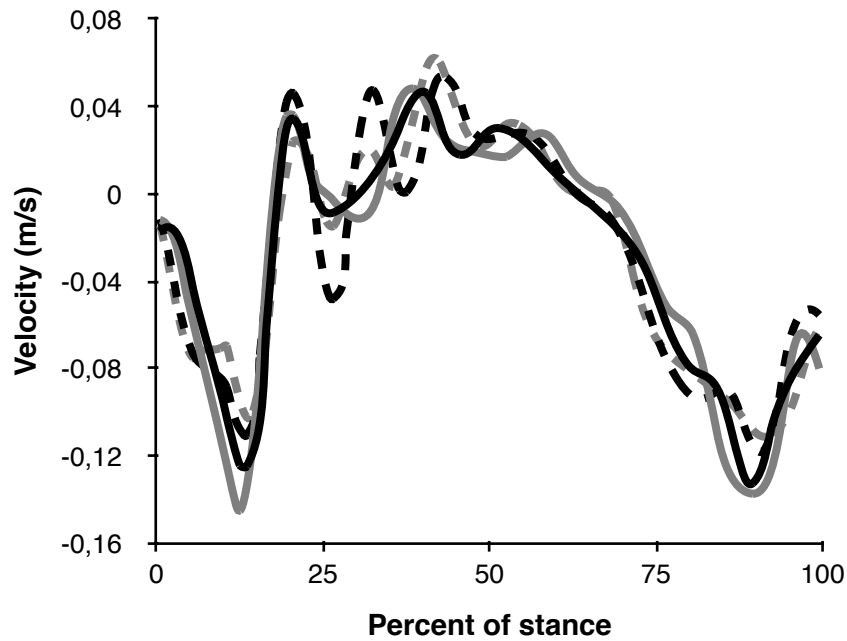

Figure 7; *Average instantaneous GM muscle fascicle velocity shown as a percentage of stance*

5. Discussion

The purpose of this study was to investigate the separate and combined effects of speed and external loading on muscle-tendon interaction and length change during locomotion. We hypothesised that due to the increased demand body weight support and power towards forward propulsion, GM MTU interaction may no longer be optimised for energy conservation and power amplification during loaded gait, therefore i) load carrying will affect the SEE loading and fascicular shortening patterns, and ii) increased walking speed will affect these patterns. We found that applying an external load when walking at a slow pace (sp1) had no effect on GM MTU and muscle fascicle length changes. Increasing walking speed to a fast pace (sp2) altered the joint angles to a degree that significantly altered the GM MTU length change during stance. The GM muscle fascicle length changes remained the same, implying the observed smaller stretch of the SEE. The combination of a fast walking pace and external loading further altered the MTU length changes, while fascicle length change again remained constant. Indicating a substantial decrease in SEE elastic strain energy, however continuously keeping the GM muscle fascicles operating at optimal force-velocity and force-length relationships .

The length change of the GM MTU is significantly smaller when increasing speed, and again when increasing load during the faster speed. This comes from a change in knee and ankle joint positioning throughout the stance phase. The knee joint seems to be more and more flexed during heel strike and early stance with increasing demand of support and forward propulsion. The ankle seems to be slightly more dorsi flexed during early stance, and then more plantar flexed during push off. The combination of a flexed knee and plantar flexed ankle joint substantially decreases the stretch on GM MTU du to the fact that it crosses both the knee and ankle joint. An increased knee flexion is also associated with increased work done by the supporting muscles (i.e. knee extensors), thereby increasing energy demand. A more plantar flexed ankle joint during push off is concurrent with observations made by Lewis et al. (2008), when increasing the push off by "verbal cuing". This was also associated with lower peak hip flexion moment, power and angular impulse as well as lower peak hip extension moment and angular impulse. Overall these changes would infer a shift in gate strategy, however ground reaction forces and hip joint kinematics are necessary to better understand the implications of this change.

As shown in previous studies (Fukunaga et al. 2001) the MG muscle fascicles follow a different displacement pattern compared with the MTU over the whole stance phase. The fascicles maintained a near constant length during mid stance, and shortened toward toe off. This pattern did not change with increased speed or external loading. Also, GM fascicles contracted at similar velocities during all conditions. This is a somewhat surprising finding, due to the fact that the fast paced speed was for many near the preferred walk to run transition speed of 2 m/s observed by Farris and Sawicki (2012), which is characterised by an increase in GM muscle fascicles contraction velocity. The Froude number of 0,2 used to calculate the fast velocity (sp2), is also a ratio between kinetic and potential energy were humans prefer to change gait from walk to run (Alexander 1989).

We assume that the observed GM muscle fascicle velocity during the slow walking is optimal being its relatively slow or partly isometric shortening behaviour, during easy walking conditions. Therefore the GM muscle fascicle behaviour observed when increasing speed and loading continuous under optimal conditions. A near-isometric behaviour of the muscle allows no substantial mechanical work to be done by the contractile component. It does allows the contractile component to operate around the highest force region of the force- velocity curve, thus supporting body weight economically (Hill 1938). This energy-saving effect would be maximised if the contractile component operated over the plateau region of its force-length curve. However, although not significant. The operating length of the fascicles seems to be shorter for the faster walking condition both with and without external loading (fig.5). This agrees well with the findings of Cronin et al. (2013), suggesting when walking at faster than optimal speeds, the force potential of MG decreases due to exercise-induced changes in its force–length relationships. To compensate for this decrease in force production soleus may particaped with a greater contribution.

When walking at slow speed both with and without an additional external load, the SEE stretches during most of the stance phase, then subsequently shortens during toe off. These findings are similar to several other studies, concluding the recoiling effect indicates the SEE act as a spring yielding elastic strain energy, thereby functioning as a mechanism for metabolic energy saving. Also allowing the muscle to operate under economically favourable conditions. The elasticity of the SEE allows for significantly

slower shortening velocities of the GM muscle fascicles, compared to that of the whole MTU during stance and push off. A muscle fiber operating at intermediate shortening velocities to develop maximum power output produces one-third the force of the same muscle fiber contracting isometrically (Roberts 2002). Also, if the tendon did not stretch the muscle would have to. Risking at worst, forcible detachment of the sarcomeres, and at best an unfavourable operating length to produce force.

Walking at a faster speed elicited a change in GM MTU lengthening, resulting in a smaller SEE length change estimated at 70 percent of stance, compared to slow walking. When adding an external load, this was evident even more so. The change in SEE stretch is thought to allow the GM fascicles to continue operating under optimal length-force and length speed conditions, this is in agreement with several in vivo human studies (Lichtwark, Bougoulias, and Wilson 2007) and previous animal studies, turkey ankle extensor data of Roberts et al. (1997). However a smaller stretch of the SEE would also result in a smaller contribution of elastic energy to forward propulsion, this may suggest an overall smaller contribution of the ankle plantar flexors, and again a shift in strategy of the involved muscles.

We know increasing speed and loading during walking increases metabolic energy consumption (Bastien et al. 2005;Falola, Delpech, and Brisswalter 2000), however the results of this study show that GM muscle fascicle condition remain optimal. What than may elicits the increased use of energy? An increased excitation of the GM muscle would result in increased usage metabolic energy and force output at the ankle, for forward propulsion. However due to the fact the SEE did not lengthen more, this is unlikely. It would also be necessary with additional data analysis of EMG activity and ground reaction force. Alternatively, the ankle did not experience an increased demand for forward propulsion when increasing speed and adding an external load, because of a greater contribution from muscles. This phenomenon is mentioned in the study by Albracht and Arampatzis (2013), where a redistribution of the muscular output within the lower extremities, because of a change in EMA, might explained the improved running economy they observed after a training intervention. In this case it might mean a redistribution of power production to muscle that are not as well suited for economical locomotion as the GM. Forward dynamics simulations of human walking suggest that changes in walking speed are modulated by increasing the work done by all lower limb

muscle groups (Neptune, Sasaki, and Kautz 2008). This is also the case with Farris and Sawicki (2012a) how found that increasing positive mechanical work output associated with faster locomotion would be met by proportional increases in power output at the ankle, knee and hip joints. Proximal muscles do not have the same compliant SEE as the triceps sure complex (Albracht and Arampatzis 2013), and so must provide most of their length change from fibre length changes. Also the human plantar-flexor muscles have relatively short fascicles (Wickiewicz et al. 1983) and are metabolically less costly than long-fibred muscles to generate the same force (Biewener and Roberts 2000). This makes the contractile behaviour of proximal muscles less efficient. Sawicki et al. (2009) predicted, based on morphological differences between proximal and distal muscles, that power output at the hip and knee joints during human walking would be provided at lower efficiency than power output at the ankle joint. Therefore, one possible explanation for the observed optimal conditions of the GM MTU while we presume a higher overall metabolic cost, is that work is redistributed between distal and proximal muscle groups with changing locomotor speed and loading. Alternatively, the relative contributions to total power at each joint might not change with speed and loading but rather, changes in overall efficiency might be reflective of underlying changes in contractile conditions within muscles across all joints throughout the lower limbs. Furthermore, Cronin et al. (2013b) argues it is more energetically sensible that a decreases in MG force would be compensated by increased recruitment of soleus, rather than increased recruitment of MG. The functional importance of MG likely declines with increasing walking speed, whereby MG operates at a progressively shorter length and shortens faster, and thus the contribution of MG force to total ankle torque decreases (Farris and Sawicki, 2012b).

In a study by Spanjaard et al. (2008), they concluded an increased external load on the body while negotiating stair accent resulted in an increased ankle joint moment, however they observed a longer double support and concluded the added mass was supported by the trailing leg. This again gives the impression of the bodies ability to manipulate its posture, and work ergonomically to support additional load.

6. Conclsuion

In conclusion this study shows no change in GM muscle fascicle or SEE behaviour when applying an external load in the form of a weighted vest, during walking at a presumed optimal speed for metabolic efficiency. When increasing speed the GM muscle fascicles behaviour remains the same as under the optimal conditions, however the whole GM MTU stretches less due to a more plantar flexed ankle and flexed knee. This is even more evident when applying an external load at the faster speed. However the GM fascicles remain operating at what is presumed to be optimal conditions for force production and metabolic efficiency. This results in a smaller stretch of the SEE, meaning less loading on the GM MTU thereby decreasing the total energy contribution from elastic strain. From that, one can speculate that the relative contribution of the gastrocnemius is decreased (or at least maintained) at the faster speed, with higher load. Other muscles (soleus, knee extensor) may increase their contribution to compensate for this, but further data would be required to confirm this.

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8. Figures