

The Effects of Muscle-Tendon Length Change During a Fatiguing Hopping Protocol on
Time to Exhaustion

by

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Abstract:

Background: Previous research studies conclude that exhaustive stretch-shortening cycle (SSC) exercise has induced in vivo length changes in muscular architecture. Literature has also proven that muscle architectural changes from fatiguing SSC activities results in a loss of ability to store elastic energy for exercise performance and may increase contractile component (CC) length. However, it is unclear if these neuromuscular adaptations are an altered response to the already occurring changes in muscular architecture during repetitive, exhaustive SSC exercise, and whether or not these changes are inducing alterations in total time to exhaustion (TTE). The purpose of this study was to use an exhaustive SSC task to understand the correlations between changes in length of the muscular architecture with the onset of fatigue, and to determine how these length changes relate to TTE. Plantarflexor (PF) and dorsiflexor (DF) CC length, muscle thickness, and pennation angle changes were examined. *Methods:* Eight college-aged males participated in an exhaustive single-joint hopping task to fatigue. At different time-points, motion capture data of the hopping kinetics and kinematics, and medial gastrocnemius (MG) muscle activity were collected, as well as in vivo ultrasound data of the MG. TTE was defined as the total time each subject was able to continuously hop. *Results:* CC lengths were found to significantly increase as subjects approached exhaustion. With significant correlations of $p \leq 0.01$ correlational relationships to percent changes in muscle thickness ($r=0.87$; $p=0.005$ and pennation angle ($r= 0.94$; $p=0.000$) were noticed when compared to TTE. *Conclusion:* Findings from the current study suggest that changes in CC muscle lengths, occurring during repetitive hopping to exhaustion, will increase as subjects approach fatigue. Furthermore the amounts of CC length change, as well as, changes in pennation angle and muscle thickness were strongly related to TTE.

Introduction:

Through the completion of an investigative, extensive, and methodical research protocol a greater knowledge of the SSC and the influence of muscle-tendon length change on exercise performance will be obtained. This study will more directly focus on muscle tendon length changes during repeated SSC exercise, instead of single maximal SSC exercise, and will examine how these changes might influence the overall TTE. Through the measure of TTE performance, a greater understanding of muscle-tendon length change alteration during fatigue will be obtained. In addition, the magnitude of this length change will help to explain better its relation to total hopping time withstood by the testing subject.

Stretch-Shortening Cycle:

There are various types of contractions and related functions. The term “contraction” refers to the state of muscle tissue when tension is generated across a number of actin and myosin filaments (Fukunaga et al., 2002). Concentric contraction refers to the phase when the muscle’s length is shortened during contraction. When concentric exercises are performed, positive mechanical work is produced. In an eccentric contraction the muscle is lengthened during contraction, thus consequently the mechanical work is negative. However, in an isometric contraction, mechanical work performed by the muscle is neither positive nor negative, as neither the muscle tendon nor joint angle experience any changes (Komi, 1984).

These types of contractions rarely occur alone in normal human muscle movements. Through locomotion, human skeletal muscles generate force and movement by employing a combination of pre-activation and succeeding eccentric and concentric actions (Komi and Gollhofer, 1997). This combination of eccentric and concentric contractions creates a natural type of muscle function known as the SSC. Occurring in most natural movements, the

purpose of the SSC is to enhance performance (greater force or power output) of the final concentric action phase when compared to the isolated concentric action (Norman and Komi, 1979).

During repetitive SSC exercise (such as walking, hopping, jumping, and running) movement would be characterized by prolonged eccentric and transition phases requiring minimal assistance from the passive elastic movements (Ishikawa et al., 2006). As a result, exercise performance has a greater dependence on contractile properties of the muscle during the concentric phase (Ishikawa et al., 2003). When evaluating the muscular and performance behavior of the ankle joint, the Achilles tendon is a large contributor to the force output and overall success of the movement occurring as an outcome of exercise. The significant contribution of this tendon can be attributed to its ability to store and release greater amounts of elastic energy through the use of elastic recoil (Fukunaga et al., 2002). A study by Fukashiro et al., 2005, employing movement at only the ankle joint revealed an increase in performance when there was a greater amount of elastic energy stored throughout the tendon, and a release of that energy during the concentric contraction of the muscle. As a result of this muscle force-velocity relationship, the quasi-isometric behavior of the MG muscle allows for a greater force production, while the tendon utilizes elastic recoil to contribute to concentric power (Fukashiro et al., 2005). The stretching of activated muscle modifies the condition of the muscle, and the consequential force output from the succeeding concentric contraction is then enhanced. Studies by Cavagna et al. (1965, 1968) observed basic mechanistic features resulting in increased performance potentiation following pre-stretching, and concluded that the function is completely elastic. It was found that when the active muscle was stretched, or when the passively stretched muscle was rapidly activated,

potential elastic energy was stored within the series elastic component and there was an observed increase in muscle tension (Cavagna et al., 1968).

Rapid recoil of stored elastic energy in the series elastic component allows for a decreased CC shortening velocity and is advantageous for the force production (Bobbert, 2011; Roberts and Azizi, 2011; Finni et al., 2003). These decreased CC conditions are positively correlated to the similar decrease seen in energy requirements for muscular contraction, eventually resulting in an overall high, positive-power output at the ankle joint (Beltman et al., 1987; Moritani et al., 1990). The mechanisms mentioned throughout the repetitive SSCs are essential for high mechanical work production, while also having minimized energy expenditure.

Pennation Angles and Muscle-Length Changes:

Pennate muscles are characterized by having fascicles that attach obliquely to the tendon, typically allowing for increased force production with a decreased range of motion (Mitsukawa et al., 2009). The velocity potential of a muscle during a contraction can be estimated based on the muscle fiber length. Muscles with longer fascicles have a greater velocity potential. In contrast, longer tendinous tissues and shorter fascicle lengths result in a greater potential to store elastic energy (Maganaris et al., 1998). In addition, pennation angles are greater in the muscles with longer tendon lengths and, thus, smaller fascicle lengths. These concepts were supported in a study by Fukunaga et al., (2002) comparing muscular architecture of the leg muscles: vastus lateralis (VL), gastrocnemius medialis (MG), and tibialis anterior (TA). Researchers found that the MG and VL both had longer tendinous tissues, with tendon lengths of 378mm and 319mm respectively, while the TA had a significantly smaller tendon length of 294mm. Additionally, it was found that the MG and

VL had greater pennation angles of 24° and 23° respectively, compared to the TA, with a pennation angle of 10°. Still, supporting the commonly accepted muscle-tendon circuit concepts, the MG was found to have a significantly smaller fascicle length of 52mm compared to the shorter tendinous TA, with a fascicle length of 87mm. The only variation of results in this study, contrary to the concepts above, was that the VL was also concluded to have a larger fascicle length of 88mm, despite also having a longer tendon length, though not as long in comparison to the MG (Fukunaga et al., 2002).

Fatigue Induced Changes and Total Time to Exhaustion:

Exercise-induced fatigue can be defined as the point where any reduction in maximal voluntary force and performance is noticed, through the comparison to previous and/or baseline performance measurements, following muscle activation (Lepers et al., 2002). It is an ongoing process during muscle activities, rather than a failure at a specific point in time (Shi et al., 2010). During fatiguing SSC activities, the muscle is damaged, and changes in muscle-tendon length result in a loss in the ability to store elastic energy. Muscles perform less work when the tendon is less elastic and the work is more energy consuming. A decreased storage of elastic energy results in a decline of overall performance (van Ingen Schenau et al., 1997). In addition, these architectural and mechanical changes from fatiguing SSC exercise may increase CC length, resulting in decreased force transfer and stiffness regulation to the tendon (Komi and Rusko 1974). However, the relationship between altered contractile function during repetitive SSC exercise protocols is neither well developed nor understood, and warrants further investigation.

Repetitive and prolonged protocols have been found to result in metabolic changes in the recruited muscle fibers. These changes alter parts of the excitation-contraction coupling

process resulting in a decrease in the ability to generate force (Lepers et al., 2002). Previous studies on fatigue during long-duration exercise protocols have focused on the effects from different substrate utilization (Coyle et al., 1986, Davis et al., 1992). One study examining the onset of fatigue during a relatively intense two-hour cycling protocol found that there was an alteration in metabolism of the skeletal muscles resulting from a progressive depletion in muscle glycogen and was thus able to conclude that fatigue also occurred progressively (Coyle et al., 1986; St. Clair et al., 2001). However, neither of these studies looked at the time course of impairment of the target muscle nor the relative contribution of contractile factors to fatigue during a prolonged and repeating SSC exercise. In addition, one cannot assume sole causation of fatigue from depletions in muscle glycogen storage (Fitts, 1994), and decrements in overall muscle performance outputs has not been strongly correlated with metabolic changes (Bangsbo et al., 1992).

A study by Lepers et al. (2002) evaluated nine, trained males during a five-hour cycling protocol performing at 55% of their maximal aerobic power. This study aimed to examine the time course of impairment during a repetitive and exhausting SSC protocol, and also evaluated contractile properties of the quadriceps muscle every hour. Results from this study showed that the time course was such that the contractile properties were considerably altered after the first hour of exercise, suggesting that an alteration of the excitation-contraction coupling process of the SSC occurred early in the cycling exercise. The alterations in SSC ability could also explain the observed decrease in the force-generating capacity of the quadriceps muscle within this study (Lepers et al., 2002).

Studies by Komi and Rusko (1974) and Wood et al. (1993) have revealed, following a series of eccentric exercises, the optimum length of active tension shifts towards the direction

of a longer muscle length. Following fatigue, there is a greater amount of muscular architecture compliance, which could influence the force transfer between the corresponding muscle fibers, tendons, and bones (Lieber et al., 1992; Morgan, 1990), and is thought to result in an increase in muscle length (Ishikawa et al., 2006). Thus, it can be concluded that the onset of fatigue and the eventual exhaustion point is likely influenced by the force-length relationship. It was advised by the researchers, however, that results from the later study should not be generalized to all SSC muscle function, as it was concluded in another project by the same researcher (Ishikawa et al. 2003) that the fascicle length changes were muscle specific during the SSC exercises. It would be important to know, then, if these neuromuscular adaptations are an altered response to changes already occurring in the muscle architecture during repetitive exhaustive SSC exercise, and if these changes are inducing changes in TTE. The relationships between changes of the muscle, tendon, and TTE during repetitive SSC protocols are not well understood and warrant additional investigation.

Exhaustive SSC and eccentric exercises induce immediate and also delayed secondary responses in mechanical and reflex performance (Komi and Nicol, 2000; Proske and Morgan, 2001). Following eccentric and SSC actions there is strength loss, though the mechanisms responsible for this effect are still not completely understood (Ishikawa et al., 2006). Several studies have looked at muscle length changes to determine the cause of resulting fatigue. A study by Aljure and Borrero (1968) and one by Fitch and McComas (1985) found that there was greater fatigue in the muscles that were fatigued at optimal lengths, and then evaluated at long lengths, compared to the muscles that were fatigued at short suboptimal lengths and evaluated at long lengths. From these results, both studies concluded that the primary reason for muscle fatigue was the metabolic events associated

with cross-bridge interactions. At optimal length the greatest generation of fatigue occurred as a consequence of contractile activity when cross-bridge interactions were maximal (Aljure and Borrero 1968; Fitch and McComas 1985; Lee et al., 2007).

However, Aljure and Borrero (1968) also concluded that fatigue was greatest in the muscles that were both fatigued and evaluated at the suboptimal lengths compared to the muscles fatigued and tested at the optimal lengths. This was not the only study that had contradictory findings on muscle fatigue, depending on which length the muscle was at during fatiguing exercise and which length was used for testing. Sacco et al., (1994), studied foot dorsiflexor muscles. Their data supported both metabolic factors and excitation-contraction coupling impairments as explanations for muscle fatigue. When observing muscle that was fatigued at the suboptimal lengths and then tested at the optimum lengths, diminished levels of fatigue were noted. This attenuation of fatigue from the foot and ankle was attributed to the successive work output from movements of the leg (Lee et al., 2007; Sacco et al., 1994).

Muscle fatigue causes many changes in muscular architecture. Ultrasound imaging has proven to be an effective tool for investigating skeletal muscle arrangements in-vivo. It has accurately depicted changes in muscle-tendon lengths, pennation angles, cross sectional area, etc. in both isometric and dynamic environments (Mitsukawa et al., 2009; Shi et al., 2010). Through the use of ultrasonography, fascial changes will be observed and continuous investigation of the muscle architecture changes during maximal single-joint hopping task will be performed. Previous research has revealed little information on direct correlation and causation between changes occurring within a target muscle during prolonged and repeating SSC exercise to the onset of fatigue. It is also unknown whether these changes seen in the

muscular architecture are in direct relation and induction to TTE. The relationships of change, during prolonged SSC exercise, at the muscle, tendon, and TTE are not well understood and warrant further investigation. This study will provide a greater understanding of muscle-tendon length change during fatigue, and the magnitude of this change will help to explain better its correlation to total hopping time withstood by a testing subject.

To establish and understand better the correlations between changes in muscular architecture and TTE, with fatigue and performance, the current study has two main purposes: (1) to examine if muscle-length change increases with fatigue and (2) to examine if muscle-length changes are related to TTE. It is hypothesized that (1) muscle length change will increase with fatigue, and (2) increased muscle length change will be correlated to a reduction in TTE.

Methods:

Subjects

Eight college-aged males (age: 25.1 ± 3.0 years; body mass: 79.4 ± 12.5 kg; height: 1.79 ± 0.06 m) with no musculoskeletal injury, neuromuscular disease, or functional limitations in their legs, took part in the study. Prior to any participation, Appalachian State University Institutional Review Board approval was obtained and each subject provided informed consent.

Hopping Protocol

Subjects were prepped for the hopping protocol. Using a Delsys Adhesive Sensor Interface (Delsys Inc., Natick, Massachusetts, USA), a wireless electrode was attached to the

skin of each subject's right leg over the mid-muscle belly of the MG. To obtain a longitudinal visual image of the MG, an ultrasound probe (HL9.0/60/128Z, Teleded Echo Blaster 128, Lithuania) was attached to the skin surface of the left leg using NexcareTM Athletic Wrap and athletic tape (Kubo et al., 2000; Kurokawa et al., 2001). Ultrasound data was collected at 76 frames per second and synchronized with kinematic and ground reaction forces. To achieve a single joint-hopping protocol, subjects were then fitted with secure knee braces on each leg. This method eliminated movement at the knee joint and isolated the ankle joint. Four retro-reflective markers (fifth metatarsophalangeal joint, lateral malleolus, lateral epicondyle of the knee, and greater trochanter) were placed on each leg, and a sacral marker was tracked in real-time using videography (Vicon Nexus, Centennial, CO, USA). Once positioned in the center of the force plate, and also central to the motion capture area, subjects were instructed to hop with legs fully extended and their arms folded across their chest. Throughout the duration of the protocol the hopping frequency and hopping height were individually determined by each subject. The subjects were told to continue hopping until they could no longer complete two successive hops or until they achieved volitional fatigue.

The hopping protocol was separated into four periods and marked with a one minute rest break between each period. The first period was three minutes of continuous hopping, while the duration of the two successive periods were each two minutes, and the fourth, and final hopping period, continued until exhaustion. The first minute (0-1 minutes) of the protocol was allotted for subjects to establish their self-selected hopping frequency. At four different time-points ultrasound and motion capture data were collected. Collection lasted for a total of 10 seconds, 10 seconds into each hopping period (1:10-T₁, 4:10-T₂, 7:10-T₃, and 10:10-T₄) (Figure 1). Data were analyzed for CC changes. TTE was defined as the total time subjects

were able to hop. The session was stopped if the subject could no longer sustain the energy and work output to complete two consecutive hops by leaving the ground, or if volitional fatigue was achieved.

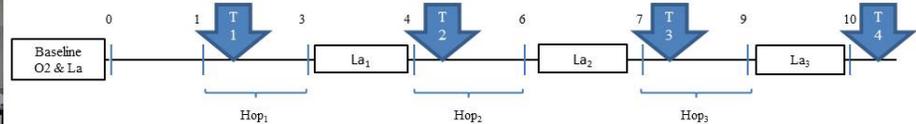


Figure 1: Hopping protocol. *Left:* Example of the knee joint stabilization, VO₂ mask, positioned sensors, and the force plate requirements for this protocol. *Right:* The layout of the time within each hopping period is shown. Data were collected at four separate time-points for a total 10 seconds, 10 seconds into each hopping period (T₁, T₂, T₃, and T₄). Five hops were analyzed at each time point to calculate average MG CC lengths. For each hopping period (Hop₁, Hop₂, Hop₃) total energy expenditure was also calculated as the sum of aerobic and anaerobic energy expenditure. Mechanical efficiency was calculated as the ratio of mechanical work and total energy expenditure for each hopping period.

Contractile Component-Tendon Lengths, Pennation Angle, and Thickness

Placed initially at the mid-muscle belly, with the superficial and deep aponeuroses in parallel view on the ultrasound image, the ultrasound probe was then rotated 90°. This rotation ensured that the image being captured was in line with the mid-longitudinal fascicle plane, so that the frames of interest could be viewed and digitized (Bénard et al., 2009). Using the Kinovea software program, frames of interest throughout the protocol were video analyzed to detect changes in muscular architecture. Pennation angle (α) was determined from the average of five measured pennation angles located at various positions on the ultrasound image (Figure 2). It should be noted that the measured pennation angles are not actually true pennation angles, but are instead the angle of the muscle fascicle relative to the horizontal axis of the image. Muscle thickness was determined by measuring the average vertical distance between the deep

and superficial aponeuroses on both sides of the ultrasound image (Figure 2). CC length of the muscle was defined as:

$$\text{MG}_{\text{CC Length}} = \text{thickness}_{(\text{AVG})} / \tan(\alpha)_{(\text{AVG})}$$

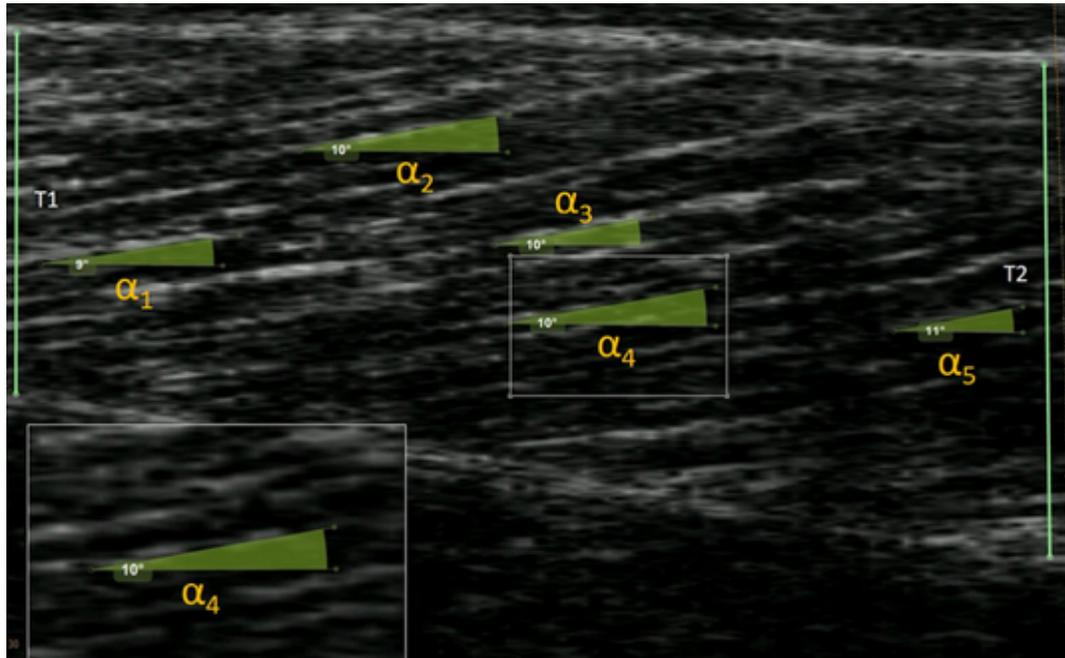


Figure 2: An ultrasound image of the MG muscle in the sagittal plane at the level of the muscle midbelly. It was analyzed by Kinovea software to estimate changes in the CC length. The tan average of five determined pennation angles (1-5) and the average distance from the deep to superficial aponeuroses measured on both sides of the image (T₁ and T₂) provided ways to analyze length changes at maximal DF and PF.

The calculated fascicle length is indicative to the component of the fascicle length parallel to the tendon. All lengths reported were analyzed at the end of the eccentric and concentric phases at which maximal PF and DF were observed (Lichtwark and Wilson, 2006). Five cycles from maximal PF to DF were selected to calculate muscle lengths and the corresponding CC lengths in each of the four hopping stages (T₁ T₂ T₃ T₄). Average muscle and CC lengths were then expressed as the average of five values for maximal PF and DF (Takeshita et al., 2006).

Results:

Contractile Component-Tendon Lengths, Pennation Angle, and Thickness

Muscle-Tendon Lengths

CC length was significantly shorter at T₁ than any other subsequent hopping time periods at both PF_{max} and DF_{max} ($p \leq 0.05$), with lengths of $7.0\text{cm} \pm 1.9\text{cm}$ and $8.5\text{cm} \pm 2.4\text{cm}$, respectively. The CC length change was found to have a significant increase from T₁ to all subsequent time periods ($p \leq 0.05$). In addition, overall CC length change significantly increased between T₂ and T₄ ($p \leq 0.05$) (Table 1).

Pennation Angle and Thickness

Muscle thickness was determined to be $1.5\text{cm} \pm 0.3\text{cm}$ for both PF_{max} and DF_{max} at T₁, while pennation angles of $12.6^\circ \pm 3.2^\circ$ and $11.1^\circ \pm 3.7^\circ$ were recorded at T₁ for PF_{max} and DF_{max} respectively. There was a significant decrease in both muscle thickness and pennation angles from T₁ to any of the other subsequent time periods during both PF_{max} and DF_{max} ($p \leq 0.05$) (Table 1). In addition there were no observable significant changes noted in pre-activity, eccentric, and concentric MG muscle activity during any of the time periods.

Time to Exhaustion

Correlations:

The TTE was 12.38 ± 3.95 minutes. There was a significant and strong relationship with T₄ MG CC length change ($r = -0.7$; $p = 0.05$) and hopping TTE. A significant, decreasing correlation to percent changes in muscle thickness ($r = 0.87$; $p = 0.005$) and pennation angle ($r = 0.94$; $p = 0.000$) were also noticed when compared to TTE (Table 2). With significant correlations of $p \leq 0.01$, a near perfect correlational relationship and a strong correlational

relationship to TTE was determined between MG pennation angle and MG thickness, respectively (Table 2). As there were greater decreases in percent pennation angles and greater CC length change, a faster onset of TTE was achieved.

Hopping Period Characteristics:

There were no observable differences seen in either self-selected hopping frequency (Hz) or knee angle ($^{\circ}$) at any of the time periods throughout the exercise protocol. Average knee angles ($^{\circ}$) were calculated for T₁, T₂, T₃, and T₄ and were 11.1 ± 4.6 , 8.9 ± 4.2 , 9.9 ± 4.5 , and 11.2 ± 7.1 , respectively. Hopping frequencies (Hz) were calculated for T₁, T₂, T₃, and T₄ and were 2.87 ± 0.31 , 2.91 ± 0.25 , 2.90 ± 0.22 , and 2.88 ± 0.19 , respectively.

Table 1: Muscular Architecture Changes from T₁ to T₄ (n=8)

	T ₁	T ₂	T ₃	T ₄
<i>PF_{max}</i>				
CC (cm)	$7.0 \pm 1.9^{b,c,d}$	8.4 ± 2.5^a	8.7 ± 3.4^a	8.6 ± 3.1^a
Thickness (cm)	$1.5 \pm 0.3^{b,c,d}$	1.4 ± 0.3^a	1.4 ± 0.3^a	1.4 ± 0.3^a
Pennation ($^{\circ}$)	$12.6 \pm 3.2^{b,c,d}$	10.4 ± 3.4^a	10.5 ± 4.1^a	10.4 ± 4.0^a
<i>DF_{max}</i>				
CC (cm)	$8.5 \pm 2.4^{b,c,d}$	$11.1 \pm 4.1^{a,d}$	$11.8 \pm 4.6^{a,d}$	$12.4 \pm 5.0^{a,b,c}$
Thickness (cm)	$1.5 \pm 0.3^{b,c,d}$	1.4 ± 0.3^a	1.4 ± 0.3^a	1.4 ± 0.3^a
Pennation ($^{\circ}$)	$11.1 \pm 3.7^{b,c,d}$	8.3 ± 3.2^a	8.0 ± 3.5^a	7.7 ± 3.4^a
<i>Length Change</i>				
CC (cm)	$1.5 \pm .89^{b,c,d}$	$2.7 \pm 1.8^{a,d}$	3.0 ± 1.6^a	$3.7 \pm 2.1^{a,b}$

^a Significantly different from T₁ ($p \leq 0.05$);

^b Significantly different from T₂ ($p \leq 0.05$);

^c Significantly different from T₃ ($p \leq 0.05$);

^d Significantly different from T₄ ($p \leq 0.05$)

Table 2: Time to Exhaustion Correlations (n=8)

	Time to Exhaustion	Strength of Relationship
T ₄ MG CC LC	-0.7^* ($p=0.05$)	High
% ↓ in MG Penn (from T ₁ to T ₄)	0.94^{**} ($p=0.000$)	Near Perfect
% ↓ in MG Thick (from T ₁ to T ₄)	0.87^{**} ($p=0.005$)	High

*Significant correlation ($p \leq 0.05$); **Significant correlation ($p \leq 0.01$)

Discussion:

The purpose of this study was to use a maximal, single-joint hopping task to examine if muscle-length changes with the onset of fatigue, and to determine how these length changes are related to TTE. Throughout the SSC exercise, CC length changes were analyzed through analysis of pennation angles using the Kinovea software program. The main findings of this study support the first hypothesis that muscle length change will increase as subjects approached fatigue. The second hypothesis, that increases in muscle length change will be related to a reduction in TTE was also supported by the findings of this study. CC length and CC length change, via elongation, both significantly increased throughout the hopping periods. Pennation angle, and muscle thickness significantly decreased from T_1 to T_4 . In addition, changes in CC length and pennation angle were strongly correlated to TTE.

When comparing muscular architecture pre-and post-fatiguing protocols, it has been seen that during a muscle contraction/shortening period, the pennation angle will decrease (Mitsukawa et al., 2009). As a consequence of their arrangement, muscle fibers with a shorter pennation angle will thus have an increased length (Maganaris et al., 1998). Another study examining changes in muscle and tendon arrangements following exhaustive rebound SSC exercise found significant soleus muscle length increases coupled with a decreased pennation angle (Ishikawa et al., 2006). Results from the current study are consistent with the previous literature and suggest that changes in CC length change and pennation angle may alter the muscles ability to generate force due to the force-length relationship. This relationship likely influences when the onset of fatigue occurs.

Muscle fatigue causes many changes in muscular architecture. The significant relationships between changes in both MG CC length and pennation angle during fatigue are

supported by prior studies (Mitsukawa et al, 2009; Ishikawa et al, 2006; Thomas et al, 2015). Mitsukawa et al. (2009) reported significant decreases in MG pennation angle and elongation of CC length during repeated maximal isometric PFs when compared to values prior to fatigue onset. Ishikawa et al. (2006) also stated that increased muscle-length change following fatiguing SSC exercise could persist for two days. In the current study, CC length change significantly increases across the four time periods and the findings were thus in agreement with the previous research. The increasing CC length change from T1 to all subsequent time periods suggests an increase in contribution from the CC to the total length change in the muscle.

Earlier *in vivo* research showed increased CC length and decreased pennation angles and thickness resulting from an exhaustive, repeating, SSC exercise and isometric contractions protocol (Mitsukawa et al., 2009; Ishikawa et al., 2006; Thomas et al., 2015). These studies have also provided evidence that structural muscle damage induced by these repetitive exercise routines results in a reduction of effective utilization of elastic energy via increased CC length (Ishikawa et al., 2006; Kuitunen et al., 2007). Based on these studies, and the increasing CC length change observed in this current study, it can be concluded that the performance-potentiating effect of storage and utilization of the elastic energy might be diminished as a result of the increased CC length concluding the eccentric/breaking phase.

From initial values at max PF and DF, decreases in muscle pennation angles and thickness were observed later in the exercise protocol. Calculated at max DF, the average percent change in the MG pennation angle and thickness between T₁ and T₄ was significantly negatively correlated to TTE. Such results probably indicate a reduced tolerance to eccentric loading and increased levels of fatigue in the MG muscle belly.

In the current study, subjects with a greater CC length change may have utilized the greater muscle tension in the lengthening contractions to transfer force to the tendon effectively. Since there were no observable CC length changes between T_2 and all other time points during the hopping sessions at PF, results indicate that the significant changes in CC length occurring later in exercise ensued from the lengthening action at the muscle. In an exhaustive exercise state it is possible for sarcomeres to become damaged if there is an increased reliance on passive lengthening work of the CC. This correlation between injury and fatigue could explain the significant relationship between increased CC length changes following the exhausting protocol. This same explanation could possibly apply to the significant relationship observed between CC length changes and TTE. Reliance on passive CC tension in the final session of the hopping protocol may decrease TTE by increasing the amount of sarcomere damage leading to neuromuscular inhibition (Garland, 1991).

With the relationship between CC length changes and pennation angles as they relate to TTE in mind, one could conclude from this study that the greater the percent length change, the shorter the subject's TTE. This is illustrated by the MG CC length change seen at T_4 . Greater changes in CC length likely resulted in shorter TTE as the subject was unable to regulate stiffness in the eccentric phase. There was too great a change in the muscle architecture relative to time.

This current study only had a sample size of eight subjects, which is recognized as a limitation. In addition, there was no protocol for the hopping frequency or hopping height. As a result, TTE may have differed between each subject based on self-selection of frequency and height. Subjects may have taken advantage of their ability to adjust exercise performance to maintain the hopping protocol and prolong TTE. For future protocols

investigating CC length changes and evaluating TTE, hopping height and frequency could be controlled. In addition, energy expenditure was not evaluated in this study. Succeeding studies may look to incorporate energy expenditure evaluations to determine how muscle architectural changes and the onset of fatigue might affect overall exercise performance.

Conclusion:

In conclusion, the hypothesis, following an exhaustive single-joint hopping protocol, that the changes in CC muscle length will increase as subjects approached fatigue could be supported by the findings. In addition, the results indicated that changes in pennation angle and muscle thickness are strongly related to TTE. Future studies should reexamine CC length changes and TTE following exhaustive SSC protocols when exercise performance parameters are established for hopping height and frequency. Correlations between these changes and energy expenditure following an exhaustive SSC protocol could also be examined. In addition, the above research was conducted on trained subjects. Future studies could look to determine the rate of muscular architecture changes and time to TTE following onset of fatigue to see what correlational differences, if any, exist between untrained and trained subjects.

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