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Gastrocnemius Fascicle And Achilles Tendon Length At The End Of The Eccentric Phase In A Single And Multiple Countermovement Hop

By: Daniel E. Lidstone, **Herman van Werkhoven**, **Alan R. Needle**, Paige E. Rice, and **Jeffrey M. McBride**

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Gastrocnemius fascicle and achilles tendon length at the end of the eccentric phase in a single and multiple countermovement hop

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ABSTRACT

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1. Introduction

Many investigations have examined fascicle and tendon lengths during the eccentric phase of a stretch-shortening cycle (SSC) (Brennan et al., 2017, Hirayama et al., 2017, Kummel et al., 2017). The purpose of these studies have been to elucidate the contributing role of the fascicle or tendon to enhanced performance in hopping, jumping and walking. This would be of particular interest to not only athletes, but the general population, as it would assist in the achievement of speci- fied goals during competition or in daily life. Specific goals, for ex- ample, could be the ability to jump higher, run faster or to be more efficient (conserve energy) during walking. Both computational models and experimental protocols using human subjects have reported that a countermovement, which involves the SSC, results in higher jump heights (Earp et al., 2011, Kubo et al., 1999, Kubo et al., 2007, Nagano et al., 2004). The countermovement may augment jump height due to

increased storage of elastic energy in tendinous structures during the eccentric phase and release of that energy in the subsequent concentric phase of the movement. Some data indicates that elastic recoil of the tendon occurs at a high velocity and may contribute to increased jump height (Fukashiro et al., 2005). Using hopping and isolating the movement pattern of the ankle allows for a more direct comparison of the influence of muscle-tendon lengths of the gastrocnemius as this muscle is the prime mover around the ankle for hopping. Utilizing a more complex model of ankle, knee and hip movement (such as in jumping) adds difficulties in terms of multi-articular muscles and overall number of muscle involved. It is acknowledged that a hopping model may not simulate a "real life" scenario as much, however, it provides a better model for isolating mechanisms that enhance SSC performance. A hopping protocol has previously been shown to dif- ferentiate SSC efficiency between elite and recreational endurance runners (McBride et al., 2015). Hopping has also been utilized to

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examine muscle-tendon interaction in elite Kenyan runners (Sano et al., 2013). In addition, a hopping model was used to explain changes in SSC with muscle fatigue (Lidstone et al., 2016). Hopping has been used to examine Achilles tendon function after rupture as well (Oda et al., 2017). Thus, hopping is a very practical model that has been used many times to examine SSC performance.

Ultrasound has been used previously to examine *in vivo* fascicle lengths during SSC movements (Fukashiro et al., 2006, Kubo et al., 2001, Takeshita et al., 2006). Principal findings from studies exploring muscle-tendon lengths have observed fascicles during the eccentric phase of a countermovement jump to remain in a quasi-isometric state (Finni et al., 2003, Fukashiro et al., 2005, Kubo et al., 2000). According to the force-length relationship, near isometric fascicle length during rapid muscle-tendon stretch may allow for a higher level of force pro- duction, increased force transmission to tendinous structures and thus, increased concentric phase power output through elastic recoil of ten- dons, ultimately resulting in higher jump height (Fukunaga et al., 2002). It has specifically been shown that during cyclical activities in sequence, tendinous tissues may contribute more to the total work performed than the fascicle component (Fukashiro et al., 2006, Lichtwark and Wilson, 2005, Nagano et al., 2003, Takeshita et al., 2006). While a single countermovement has been notably recognized to increase performance and efficiency, the effect of several counter- movements in sequence prior to center of mass (COM) displacement has not been examined to the same extent. In fact, van Werkhoven and Piazza (van Werkhoven and Piazza, 2013) found that three counter- movements, instead of a single countermovement strategy, resulted in a higher hop height during a maximal hopping task. In their experiment, a knee-brace was used to isolate the ankle joint and simplify their human model. Using a computational modelling approach, van Wer- khoven and Piazza (van Werkhoven and Piazza, 2013) theorized that a multiple countermovement strategy may result in greater storage and utilization of stored elastic energy in the tendon, ultimately increasing hopping height.

In a study by Fukashiro et al. (2005), the fascicle and tendinous behavior of the gastrocnemius during a vertical ankle jump and a drop jump were measured *in vivo*. Their findings suggested considerable contribution of the tendon to jump performance. During the push-off phase of the ankle jump, the tendon contributed 47% of the work performed by the muscle tendon unit (MTU) and 75% in the drop jump. During the drop jump, the Achilles tendon returned 76% of the elastic energy stored. Of interest is the quasi-isometric nature of fascicle length during the drop jump, which could increase strain on the tendon. This could possibly contribute to enhanced SSC performance via stored elastic energy and a resultant increase in work performed during the concentric phase. Lichtwark and Wilson (2005), measured MTU length during a one-legged hopping task and reported similar results to Fukashiro et al. (2005). They determined that the Achilles tendon contributed 80% of the total MTU length during hopping. Furthermore, the Achilles tendon was stretched in proportion to the force applied during the downward phase. Subsequently, the Achilles tendon re- turned 74% of force in the upward movement, contributing a total average of 16% of mechanical energy to the hopping task.

Evidence has shown that higher braking phase kinetics might elicit greater work performed. Total mechanical work done during counter-movement and drop jumps has shown to be significantly greater than that of a static jump, also corresponding with higher jump heights (McCaulley et al., 2007). Further examination of the relationship be-tween mechanical efficiency (total mechanical work/ total energy ex-penditure) and eccentric work during these jumps revealed a strong correlation to exist, demonstrating the involvement of the elastic component in overall SSC performance (McCaulley et al., 2007). This has been shown using a hopping model to exhaustion as well (Lidstone et al., 2016). Such increases of work performed are achieved either via

increased utilization of chemical energy (ATP) by the contractile component or greater strain energy stored and utilized within tendi-nous tissues (McBride and Snyder, 2012). Given the widely accepted concept that the countermovement is more metabolically efficient, in-creased work during SSC performance likely results from greater sto-rage and utilization of elastic strain energy in the tendinous tissues. Although work has been well-documented in the literature, work per-formed during multiple countermovements in sequence versus a single countermovement strategy has not yet been investigated.

Increased jump height when utilizing a countermovement has been proposed to be influenced by higher levels of eccentric phase muscle activity (McCaulley et al., 2007). A recent study by Hirayama and colleagues found that altered neuromuscular and biomechanical func-tion enhance SSC performance after 12 weeks of ankle-specific plyo-metric training (Hirayama et al., 2017). Specifically, triceps surae muscle activity and averaged ground reaction forces were reported to increase during the eccentric phase. During muscle contraction, the acto-myosin forces required to maintain fascicle length translate into better synchronization of muscle-tendon interaction. These training adaptations have implications on SSC performance in that not only muscle forces are augmented, but contact time is decreased as well, which causes lesser dissipation of heat stored within the tendinous tissues. McBride et al. found a strong, positive relationship to occur between eccentric phase muscle activity and peak concentric force during jumping (McBride et al., 2008). These findings support the no-tion that higher motor unit recruitment might occur during the coun-termovement and thus, muscle activity during the eccentric phase might play a role in fascicle length maintenance, tendon lengthening and ultimately, COM displacement.

As mentioned previously, van Werkhoven and Piazza (2013)) found that three countermovements, instead of a single countermovement strategy, resulted in a higher hop height during a maximal hopping task. However, this has not been shown experimentally in humans. Furthermore, it is not known whether multiple countermovements would also affect the muscle activity during successive eccentric phases, potentially resulting in a shorter fascicle length and longer tendon length. No known investigations have examined specifically fascicle and tendon length at the end of the eccentric phase when comparing a multiple countermovement versus a single countermovement strategy prior to hopping to a maximal height during a hopping task. As stated, this could have significant implications for optimizing athletic perfor-mance as well as activities of daily living. A hopping model has effec-tively been utilized to examine performance in trained and recreational runners, world elite distance runners and under conditions of muscle fatigue and prior injury (Lidstone et al., 2016, McBride et al., 2015, Oda et al., 2017, Sano et al., 2013). Therefore, the novel purpose of this investigation was to determine if, in fact, a multiple countermovement strategy in hopping would result in shorter fascicle length and longer tendon length. We hypothesized that during the multiple counter-movement strategy, sequential countermovements would result in: (1) a shorter muscle-tendon unit, (2) a longer tendon length, (3) a shorter fascicle length and, (4) a smaller fascicle length to tendon length ratio. We further hypothesized that during the final countermovement per-formed during the multiple countermovement strategy: (1) the tendon length would be longer, (2) the fascicle length would be shorter and, (3) the fascicle length to tendon length ratio would be smaller, in com-parison to the single countermovement strategy. We further postulated that muscle activity of the gastrocnemius would increase with each subsequent countermovement in the multiple countermovement strategy and the final countermovement would have greater muscle activity in comparison to the single countermovement strategy. Finally, we hypothesized that greater eccentric work, concentric work and hopping height would be observed in the multiple countermovement strategy in comparison to the single countermovement strategy.
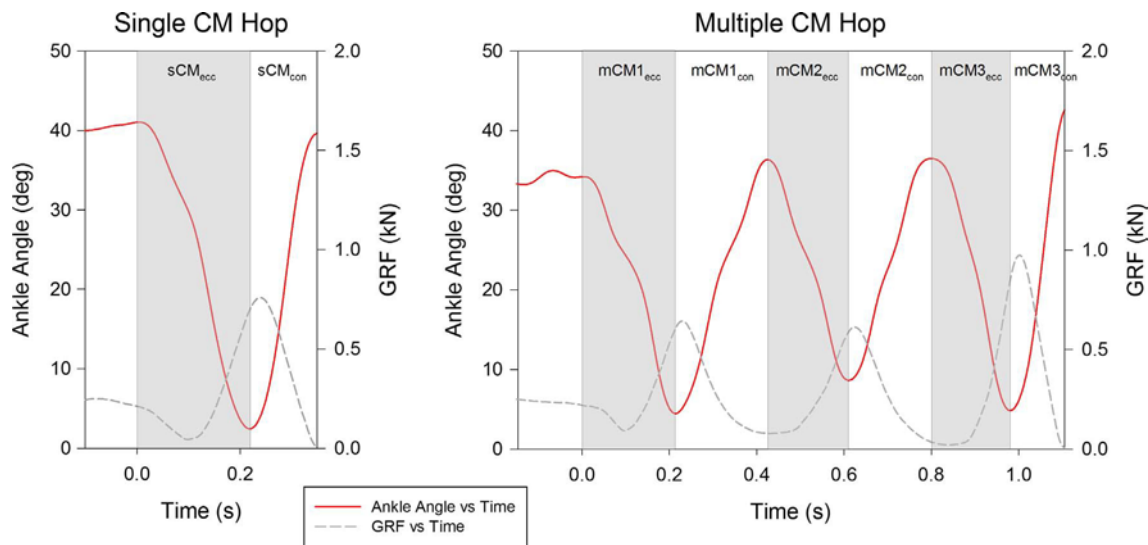
Fig. 1. Ankle joint angles and GRF during (i) single countermovement hop (sCM) and (ii) multiple countermovement hops (mCM) for one subject.

2. Methods

2.1. Participants

Seventeen male subjects between the ages of 18 and 25 participated in the current study (age = 23.8 ± 4.0 years, height = 1.76 ± 0.10 m, body mass = 79.7 ± 16.3 kg). All subjects were healthy with no musculoskeletal injury, neuromuscular disease, or history of lower limb surgery. Subjects did not engage in any type of regular exercise program. The Institutional Review Board at Appalachian State University approved this study. Prior to testing, each subject signed an informed consent and filled out a medical health history questionnaire.

2.2. Study design

Subjects visited the laboratory on one occasion for approximately one hour. After obtaining age, height and weight, subjects were asked to complete a series of maximal double leg hops. Hops were performed with either a single countermovement (sCM) or multiple (total of 3) countermovements (mCM1, mCM2, mCM3) prior to push-off in which they attempted to hop to a maximal height (Fig. 1). In the sCM, the subject started in a raised heel, plantar-flexed position and went downward, dorsi-flexing the ankle joint, one time and then hopped off the ground in efforts to achieve a maximal hopping height. Meaning that only one countermovement was utilized before attempting to leave the ground and hop to a maximal height. For the mCM, the number indicates the 1st (mCM1), 2nd (mCM2) and 3rd (mCM3) counter-movement performed in sequence before leaving the ground. Specifi-cally, the subject started in a raised heel, plantar-flexed position then went downwards, dorsi-flexing the ankle joint (mCM1), this was re-peated in rapid succession a second time (mCM2), then a third time (mCM3) followed immediately by the subject hopping off the ground in efforts to achieve a maximal height. Thus, in contrast to the single countermovement strategy multiple countermovements (three) were utilized before leaving the ground. Therefore, the aim of the multiple countermovement trials was for the subjects to perform three coun-termovements while staying in contact with the ground and then leave the force plate after the final (third) countermovement.

Subjects wore a knee brace on each leg to eliminate movement at the knee joint. Arm swing contribution to the movement was eliminated by having the subjects fold their arms across the body in a fixed position during hop trials. Subjects were allowed to complete 9 hop trials using a sCM and 9 hop trials using mCM with the order of all trials randomized. The trial with the highest hopping height was used for analysis for sCM

and mCM. Each hop was separated by a 2-minute rest period. Hops were performed with one leg on a force plate to collect ground reaction forces (GRF). In addition, four retro-reflective markers (fifth meta-tarsophalangeal joint, lateral malleolus, lateral epicondyle of the knee, greater trochanter) were placed on each leg to track real-time using videography (Vicon Nexus, Centennial, CO, USA) consisting of seven MX03 + NIR cameras at a frequency of 100 Hz using infrared detection of optical markers. An ultrasound probe (HL9.0/60/128Z, Telemed Echo Blaster 128, Lithuania) was secured to the surface of the skin on the left leg with Nexcare™ Athletic Wrap and athletic tape at 30% of the lower leg length to obtain a longitudinal image of the medial gas-trocnemius (Kubo et al., 2001, Kurokawa et al., 2001). Only the best hop (maximal hopping height) for each subject and each condition (mCM and sCM) was used for further analysis.

2.3. Measurement of fascicle, tendon and MTU length

The ultrasound probe was initially placed at the mid-muscle belly with the superficial and deep aponeuroses in parallel as viewed on the ultrasound image. The probe was then rotated 90° to ensure images were captured in line with the mid-longitudinal fascicle plane (Benard et al., 2009). Five fascicle angles (α) relative to the horizontal axis of the ultrasound image were measured at different locations (Fig. 2) as previously published by Lidstone et al. (2016). The vertical displace-ments (thickness) between the superficial and deep aponeuroses were measured on each side of the ultrasound image (T1 & T2) (Fig. 2). This was completed utilizing Kinovea open source video analysis software (Kinovea for Windows, Version 0.8.15, Kinovea.org). The fascicle lengths were calculated and not measured due to the fact that full fascicle length was not visible in the ultrasound image for many of the subjects.

The average of the five fascicle angles (α_{avg}) and the average of T1 and T2 (thickness$_{avg}$) were used for calculation of fascicle length as:

Fascicle Length = thickness$_{avg}$/Sin(α_{avg})

Tendon length was then calculated as:

Tendon Length = MTU-(thickness$_{avg}$/Tan (α_{avg}))

where MTU is the muscle-tendon unit length calculated using the equations of Grieve and colleagues (Grieve et al., 1978). This equation uses ankle joint angle, knee joint angle, and lower leg length to estimate MTU length. Instantaneous changes in ankle joint and knee joint angles were calculated using 3D videography. In order to observe the shift of fascicle elongation versus tendon elongation, the fascicle length (FL) to
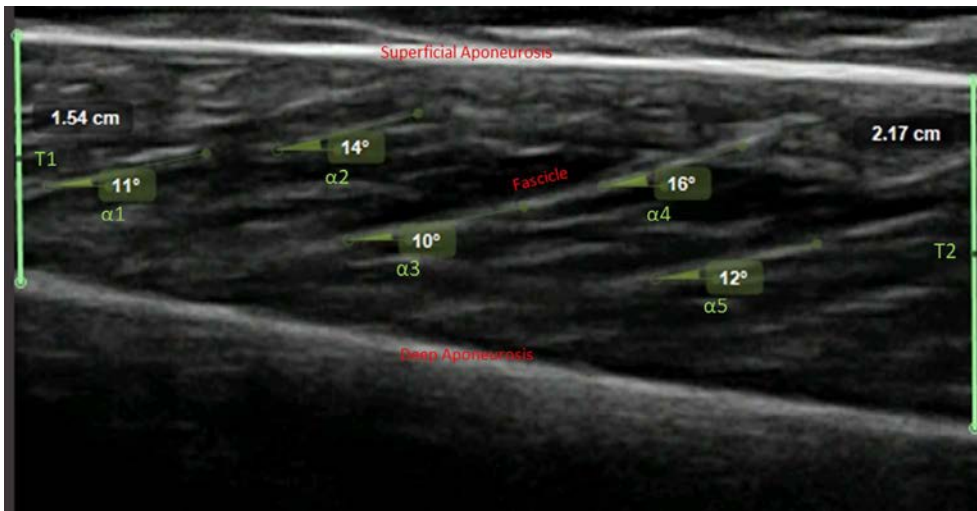
Fig. 2. Ultrasound image of the medial gastrocnemius muscle in the sagittal plane at the level of the mid-belly for analysis of fascicle length. Five fascicle angles (α) relative to the horizontal axis of the ultrasound image were measured at different locations. The vertical displacements (thickness) between the superficial and deep aponeuroses were measured on each side of the ultrasound image (T1 & T2).

tendon length (TL) ratio was calculated as:

FL−TL Ratio = FL/TL

All lengths reported were analyzed at the end of the eccentric phases at which maximal dorsi-flexion occurred. The eccentric phases started from the peak plantar-flexed position and ended at the peak dorsi-flexed position. The subsequent concentric phase started from peak dorsi-flexed position to the next peak plantar-flexed position, except for the final concentric phase before take-off, which ended when the subject's feet left the ground. This maximally dorsi-flexed position occurred three times during the mCM trial (mCM1, mCM2, mCM3) and once during sCM trial prior to maximal COM displacement (Fig. 1).

2.4. Maximal hopping height and work calculations

Force-time curves were collected and analyzed with a custom-designed program (National Instruments, LabVIEW, Version 8.2, Austin, Texas, USA) during hopping. A 1000 Hz sampling rate was utilized and analog signals were converted to digital signals (NI PCI-6014, National Instruments, Austin, TX) with a BNC-2010 interface box. Displacement-time curves were generated from sacral marker displacement with a custom-designed Matlab program (MathWorks, Natick, MA) (van Werkhoven and Piazza, 2013). All data were then down-sampled to 100 Hz for force- and displacement-time curve synchronization. Velo-city-time curves were then generated via LabVIEW by finding the change in displacement for each time point and dividing it by time. For calculation of total work performed, potential and kinetic energy-time curves were generated from the aforementioned force-, velocity- and displacement-time curves. Total energy was derived from the sum of the kinetic energies (E_k = ½mv^2) and potential energies (E_P = mgh) at each time-point, where m is the mass of the subject and g is acceleration due to gravitational force (9.81 m/s²). Negative work (W_{ecc}) was cal-culated from the start to the end of the eccentric (downward dis- placement) phase and is represented by the incremental summation of the energy-time curves (W_{ecc} = mgh + ½mv^2). Positive work (W_{con}) was calculated from the start to the end of the concentric (upward displacement) phase and is represented by the incremental summation of the energy-time curves (W_{con} = mgh + ½mv^2). W_{con} for the final concentric phase of sCM and mCM3 was determined until toe-off oc- curred. W_{ecc} and W_{con} was analyzed during sCM and mCM1, mCM2 and mCM3. Maximal hopping height was determined from sacral retro-re- flective marker displacement (van Werkhoven and Piazza, 2013). Standing marker height was subtracted out to account for height var- iation in subjects.

2.5. Muscle electrical activity

EMG was recorded from the medial gastrocnemius and lateral gas-trocnemius during the jumping protocols (Delsys Trigno Wireless System, Natlick, Massachusetts, USA). EMG electrodes with a dimen-sion of 27 × 37 × 15 mm with four 5 mm × 1 mm contact points (spaced at 10 mm) in a bipolar configuration were utilized with a gain of 909 and set bandwidth frequency of 20–450 Hz. The common mode rejection ratio was > 80 dB and data was collected at 1000 samples/ sec. Electrodes were attached to the skin over the distal two thirds of the muscle belly. The skin was abraded and cleansed with isopropyl alcohol after excess hair was shaved prior to placement. Electrodes were attached to the skin using Delsys Adhesive Sensor Interfaces (Delsys Inc., Natlick, Massachusetts, USA). Interference EMG signals were band-pass filtered (10–400 Hz) using a zero-phase 4th order Butterworth filter before being full-wave rectified and low-pass filtered (5 Hz) to create a complete linear envelope (Moritz et al., 2004, Sano et al., 2013). Data were then partitioned for the eccentric phase and concentric phase respectively for sCM and mCM1, mCM2 and mCM3. Time-averages were derived from the complete linear envelopes of EMG activity during the concentric and eccentric phases respectively.

2.6. Statistical analysis

All statistical analyses were determined utilizing SPSS software (IBM SPSS Statistics for Windows, Version19.0. Armonk, NY: IBM Corp.). Difference in hop heights was analyzed using a repeated-mea-sures analyses of variance (ANOVA) between sCM and mCM conditions (2 levels). MTU, tendon, and fascicle length, fascicle/tendon length ratio, muscle activity, and work comparisons between sCM and mCM1, mCM2 and mCM3 were analyzed using a repeated-measures ANOVA (4 levels). Bonferroni comparisons were utilized in the case of significant main or interaction effects. All assumptions for parametric statistics were met; and an *a priori* level of significance was set at P ≤ .05.

3. Results

Muscle-tendon unit (MTU) length, tendon length, fascicle length and the fascicle to tendon length ratio (FL-TL Ratio) at the end of the eccentric phase during the single countermovement (sCM) and multiple countermovement (mCM) trials are presented (Fig. 3). These values correspond to the end of the eccentric phase of the first (mCM1), second (mCM2) and third (mCM3) countermovement during mCM trials. Re-peated-measures ANOVA comparisons revealed a significant difference between fascicle length at mCM1, mCM2 and mCM3, with the fascicle length at mCM3 being the shortest (p ≤ .05). Fascicle length during
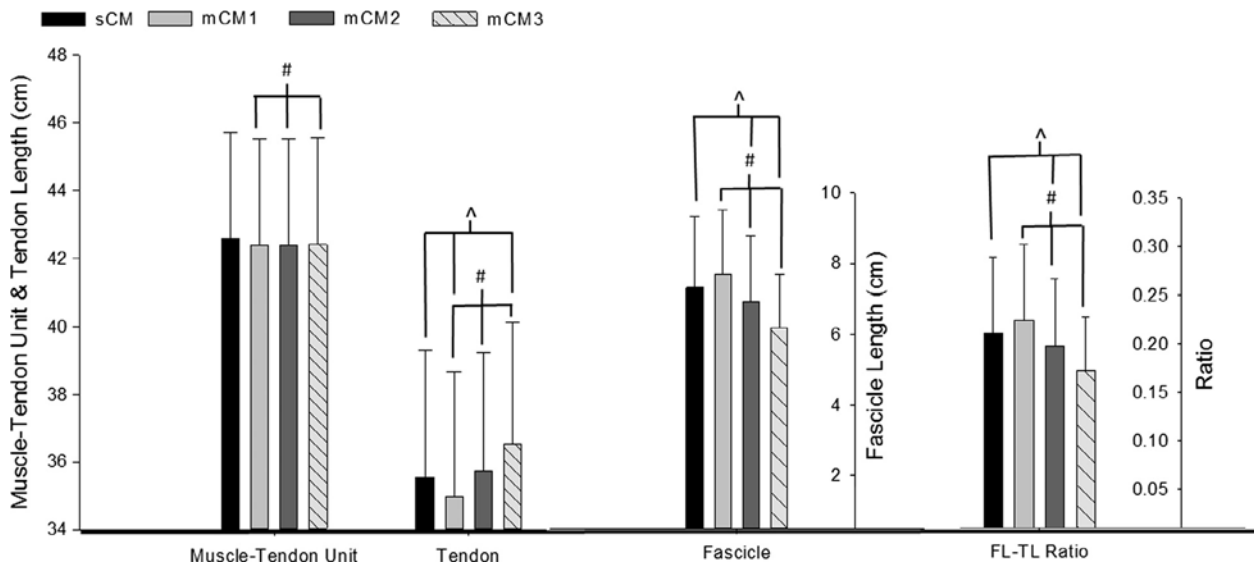
Fig. 3. Muscle-tendon unit length, tendon length, fascicle length and the fascicle length to tendon length ratio (FL-TL ratio) at the end of the eccentric phase during sCM and mCM conditions. # = significant difference between mCM1, mCM2 and mCM3, ^ = significant difference between sCM and/or mCM1 and/or mCM2 and/or mCM3 (p ≤ .05).

mCM2 and mCM3 were significantly shorter in comparison to sCM. Significant differences were observed between tendon length at mCM1, mCM2 and mCM3, with the tendon length at mCM3 being the longest. Tendon length during mCM3 was significantly longer in comparison to

sCM. Tendon length in mCM1 was significantly shorter in comparison to sCM. Statistical analyses revealed the FL-TL ratio significantly decreased from mCM1 to mCM2 and mCM3. The FL-TL ratio at mCM2 and

mCM3 was also significantly lower than that of sCM.

Time-averaged EMG data showed significant differences when comparing the eccentric phase of successive bounces of the mCM for both medial gastrocnemius and lateral gastrocnemius (Fig. 4). Muscle activity during the eccentric phase for mCM3 was higher than mCM1 and mCM2. Muscle activity during the eccentric phase for mCM3 was also significantly higher than sCM. During the concentric phases of movement, mCM3 muscle activity was higher than both mCM2 and mCM1. However, concentric phase muscle activity was not higher in mCM3 in comparison to sCM. The concentric phase muscle activities were the same across both medial and lateral gastrocnemii.

Maximal hopping height and eccentric and concentric work are presented in Table 1. Hopping height was significantly greater in mCM3

Table 1

Hop Height means ± SD during sCM and mCM hopping strategies. Eccentric and Concentric Work means ± SD during all hopping phases.

Hop type	Hop Height (cm)	Eccentric Work (J)	Concentric Work (J)
sCM	13.1 ± 2.5	38.5 ± 15.9[*+]	80.9 ± 27.6[*+]
mCM1	–	25.0 ± 7.5	27.9 ± 9.8
mCM2	–	30.6 ± 12.1	32.9 ± 13.7
mCM3	14.6 ± 3.1[#]	46.6 ± 19.4[#*+]	87.6 ± 26.5[#*+]

Note. sCM, single countermovement; mCM, multiple countermovement.
[#] Significantly greater (P ≤ .05) than sCM.
[*] Significantly greater (P ≤ .05) than mCM1.
[+] Significantly greater (P ≤ .05) than mCM2.

in comparison to sCM. Eccentric and concentric work were significantly lower during mCM1 and mCM2 than the sCM hopping strategy. Results also showed that eccentric and concentric work were significantly greater during mCM3 in comparison to sCM. Additionally, it was observed that mCM3 eccentric and concentric work performed were significantly greater than both mCM1 and mCM2.
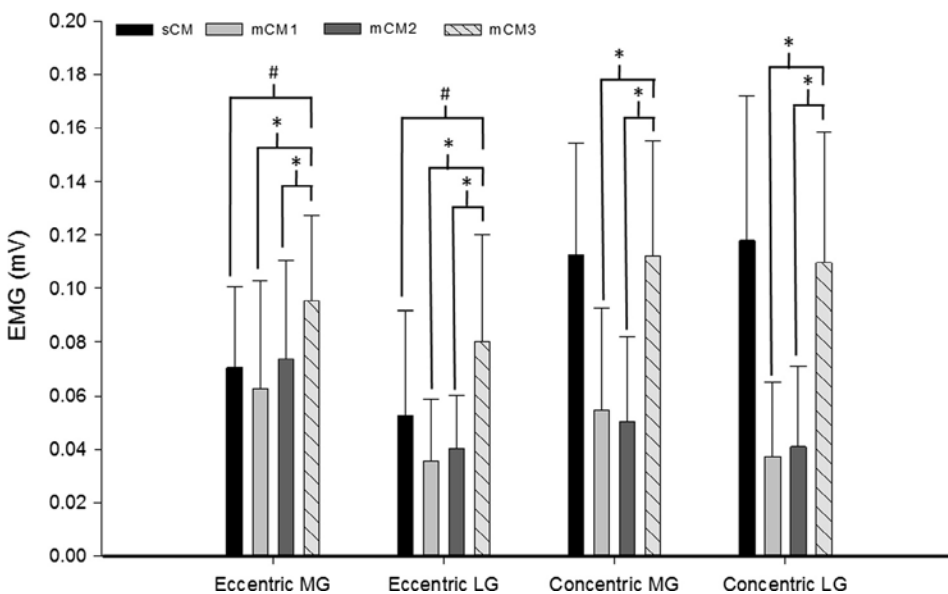

Fig. 4. Muscle activity for the medial gastrocnemius (MG) and lateral gastrocnemius during the eccentric and concentric phases of sCM and mCM conditions. * = significant difference between mCM3 and/or mCM2 and mCM1, # = significant difference between mCM3 and sCM (p ≤ .05).

4. Discussion

The primary finding in this investigation was that a multiple countermovement hopping strategy resulted in a pattern in which the fascicle length was shorter and the tendon length was longer at the end of the eccentric phase in comparison to a single countermovement strategy. The use of a countermovement, or bouncing pattern, of the ankle before take-off in hopping was first presented by van Werkhoven and Piazza (2013). This investigation reported that a computer model simulating hopping chose a multiple bounce strategy to maximize hopping height. In addition, data was collected from eight subjects in which four of the subjects hopped higher using a multiple bounce technique with a bouncing frequency of approximately 2.5 Hz. The authors speculated that these subjects were using mechanical resonance to store elastic energy in the Achilles tendon. It was further speculated that this allowed for a higher state of potential energy prior to take-off. In the current study, it was also observed that a multiple countermovement hopping strategy resulted in greater eccentric phase medial and lateral gastrocnemius muscle activity than a single countermovement. This increased muscle activity could have been a voluntary or involuntary response to bouncing prior to take-off similar to that observed in drop jumps from successively higher heights (Leukel et al., 2008, Ruan and Li, 2010). In addition, greater hopping height coin- cided with higher eccentric and concentric work during the multiple countermovement hopping strategy when compared to a single coun- termovement strategy. A computer model on hopping indicated that a non-bouncing simulation resulted in less tendon energy storage than a bouncing strategy (9.8 J versus 38.9 J respectively) (van Werkhoven and Piazza, 2013). It is the authors' contention that the increased hopping height and work during the mCM could possibly be attributed to the enhanced storage and release of elastic energy in the tendon, although not conclusive from the data. This has implications for un- derstanding enhancement of SSC performance such as in jumping, running and walking. Previous studies have effectively used a hopping model to delineate performance between recreational and elite runners and with fatigue and prior injury (Lidstone et al., 2016, McBride et al., 2015, Oda et al., 2017, Sano et al., 2013). Thus, the authors feel the model of hopping in this investigation appropriately supplements the previous investigations in terms of the concepts for effective SSC per- formance using cyclical patterns (multiple bouncing or counter- movements).

The concept of variation in fascicle and tendon length based on differing SSC conditions has been reported previously (Ishikawa et al., 2005a). Ishikawa et al. showed that fascicle length became progres- sively shorter during the eccentric phase when increasing drop height in a sledge apparatus (Ishikawa et al., 2005b). This was reflected in the results of the current investigation as well when using multiple coun- termovements. Finni et al. had similar findings when comparing a drop jump to a countermovement and static jump (Finni et al., 2001). A si- multaneous observed shift to a shorter fascicle length and longer tendon length at the end of the eccentric phase during multiple counter- movements re-emphasizes the natural occurrence of potentially en- hanced tendon elastic recoil and performance. A study by Fukashiro et al. suggested considerable contribution of tendon to jump perfor- mance with the tendon being responsible for between 47 and 75% of the work performed by the MTU (Fukashiro et al., 2005). Our data clearly supports this as a viable hypothesis for variation in fascicle length control for enhancing hopping height and eccentric and con- centric work. The significant contribution of tendon length is high- lighted by the commonly observed anatomical ratio of fascicle to tendon length in animals, particularly in which the tendon is often 5–6 times longer than the fascicle (Walmsley and Proske, 1981). Examina- tion of hopping animals, such as the wallaby, highlights the importance of the number and frequency of SSC actions, in which calculated stored energy in the tendon increases with hopping speed (Biewener et al., 1998). In the context of the current investigation, a single

countermovement seems less likely to result in a shorter fascicle length and longer tendon length (Hobara et al., 2010, Molkov et al., 2015).

Some scientists contend that the fascicle operates in an isometric state during conditions of locomotion, especially during the eccentric phase. Quasi-isometric fascicle length has further been associated with greater eccentric phase muscle activity (Hirayama et al., 2017). In the current investigation, shorter fascicle lengths with each subsequent countermovement were concomitant with increasing eccentric phase muscle activity in support of this previous data. This might be attrib- uted to enhanced eccentric contractile force stimulated by mechanisms such as the stretch-reflex and cross-bridge potentiation (Hobara et al., 2010). A pre-contracted muscle prior to stretch has been shown to in- crease force output per cross-bridge in vitro (Colombini et al., 2010). It is possible that decreasing fascicle length with each subsequent coun- termovement resulted in a fascicle length that optimized cross-bridging for maximal force production of the muscle. This concept has been presented by Mayfield et al. as force summation (Mayfield et al., 2015) in which activation of a muscle twice in quick succession results in increased force amplitude, duration and rate. This study indicated that force summation was a function of length with shorter muscle lengths optimizing force output (Mayfield et al., 2015). The authors from this previous publication further proposed that muscles experience force augmentation during accustomed stretch-shorten tasks like hopping (Mayfield et al., 2015). The aforementioned SSC variables could also influence other physiological factors such as intracellular calcium ki- netics and binding affinity, ultimately influencing contractile force as well (Balnave and Allen, 1995). These are mechanisms specific to SSC function as force production of pre-stretched MTU's rises above those observed within the confines of a single isometric contraction (Finni et al., 2000).

Another intriguing finding from the current investigation was the increased eccentric and concentric work performed during the mCM3 when compared to the sCM strategy. As formerly stated, external work results from a cascade of steps internally, that involve bioelectrical and biochemical processes, which dictate muscle contraction and eventually whole body movement. Contrary to muscle, tendon is a much less vascular tissue, which not only preserves energy but also returns energy during elastic recoil (Maganaris et al., 2017). Recent discussion sur- rounding morphological versus inherent capacity to store elastic strain energy within the tendon has led to more consideration of trainable characteristics in athletes (Wiesinger et al., 2017). The nature of most acute and chronic adaptations to training are improved mechanical efficiency and possibly a more refined ability to recover energy in the SSC during shortening (McCaulley et al., 2007). As mentioned, me- chanical efficiency and eccentric phase work correspondingly increase with one another (McBride and Snyder, 2012). Therefore, individuals utilizing multiple countermovements, whether in an athletic or ev- eryday life circumstance, might be optimizing the body's natural ten- dency to conserve energy by use of elastic strain energy (Brennan et al., 2017).

In conclusion, this study indicates that a multiple countermovement or bouncing strategy in hopping results in shorter fascicle length, longer tendon length, increased eccentric muscle activity, increased eccentric work and higher hopping heights. This supports the previously reported data from a computer simulation of hopping which found that multiple countermovements or bouncing optimizes performance (van Werkhoven and Piazza, 2013). The mechanisms indicated by van Werkhoven et al. include increased tendon stored elastic energy and mechanical resonance during the subsequent bounces (van Werkhoven and Piazza, 2013). This data is unique in indicating the benefits of a bouncing or multiple countermovement technique in hopping as other studies indicate that in vertical jumping with the hips and knees a single countermovement is optimal (Bobbert and Casius, 2005). Although this single-joint model of the ankle in hopping is not a typical movement pattern in everyday life, it allows for isolation of muscle-tendon prop- erties independent of the influences of more complex motor control

factors in multi-joint movement patterns. A hopping model has been used in several investigations to show differences in mechanical efficiency in runners and with fatigue and prior injury (Lidstone et al., 2016, McBride et al., 2015, Oda et al., 2017). Thus, the data from this study using a hopping model provides unique insight into possible muscle-tendon interactions that might occur with more typical move- ment patterns such as walking, running and jumping. However, lim- itations to this investigation might be the use of only the ankle joint and the utilization of videography for calculation of muscle-tendon length. In addition, the interpretation of the results may be limited to the subject population used in the current investigation.

Conflict of interest

The authors have no conflict of interests to report.

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