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Medial gastrocnemius muscle-tendon interaction and architecture change during exhaustive hopping exercise ☆

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Background: Previous literature has shown in vivo changes in muscle-tendon interaction during exhaustive stretch-shortening cycle (SSC) exercise. It is unclear whether these changes in muscle-tendon length during exhaustive SSC exercise are associated with changes in mechanical efficiency (ME). The purpose of the study was to investigate whether changes in plataflexor contractile component (CC) length, tendon length, and changes in plantarflexor muscle activity could explain reduction in ME during exhaustive SSC exercise. *Methods:* Eight males participated in an exhaustive hopping task to fatigue. Mechanical work and energy expenditure were calculated at different time-points during the hopping task. Furthermore, hopping kinetics and kinematics, medial gastrocnemius (MG) muscle activity, and in vivo ultrasound of the MG were also collected at different time-points throughout the hopping task. *Results:* ME did not change during the hopping protocol despite shorter tendon and longer CC lengths as subjects approached exhaustion. Percent decreases in pennation angle and muscle thickness were most strongly correlated to time to exhaustion ($r = 0.94$, $p \leqslant 0.05$; $r = 0.87$, $p \leqslant 0.05$; respectively). Percent changes in CC length change and pennation angle were strongly correlated to percent decrease in maximal voluntary isometric plantarflexion (MVIP) force ($r = -0.71$, $p \leqslant 0.04$; $r = 0.70$, $p \leqslant 0.05$; respectively). Braking/push-off EMG ratio increased from initial pre-fatigue values to all other time points showing neuromuscular adaptations to altered muscle lengths. *Conclusion:* Findings from the current study suggest that changes in CC and tendon lengths occur during repetitive hopping to exhaustion, with the amount change strongly related to time to exhaustion. ME of hopping remained unchanged in the presence of altered CC and tendon lengths.

1. Introduction

Human dynamic movements usually result in combinations of active muscle stretching prior to shortening called stretch-shortening cycle (SSC) action (Cavagna et al., 1964). During SSC exercise (such as walking, hopping, jumping, and running) efficiency is higher compared to concentric only muscle action through neuromuscular mechanisms that minimize muscle length change during whole muscle-tendon unit (MTU) lengthening (Ishikawa and Komi, 2007). The result is strut-like behavior of the muscle during the braking phase that allows greater contribution of the tendinous tissues to whole MTU length change and storage of elastic potential energy (Fukunaga et al., 2002; Kawakami et al., 2002). Rapid recoil of stored elastic energy in the series elastic component allows decreased contractile component (CC) shortening velocity (Bobbert, 2001; Roberts and Azizi, 2011; Finni et al., 2003), which is advantageous for force production. These conditions decrease the energy requirements of muscular contraction (Beltman et al., 2004; Aura and Komi, 1987; Moritani et al., 1987), and increases series elastic component contribution to rapid MTU shortening (Kurokawa et al., 2001) resulting in high positive ankle joint power. These aforementioned mechanisms and associated CC-tendon interaction during repetitive SSCs are necessary for high mechanical work production and minimized energy expenditure. The result is increased mechanical efficiency (ME) during SSC exercise compared with concentric only contraction (Aura and Komi, 1986; McCaulley et al., 2007).

ME is defined as the ratio between mechanical work and energy expenditure and is used for examining the contribution of stored elastic potential energy to concentric force production during

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repeated SSC exercise (Aura and Komi, 1986). Previous studies have shown in vivo increased CC length and decreased pennation angle and thickness following exhaustive repetitive SSC exercise and isometric contractions (Mitsukawa et al., 2009; Ishikawa et al., 2006; Thomas et al., 2015). Increased CC length and shorter tendon lengths at the end of the eccentric/braking phase may decrease the performance potentiating effect of storage and utilization of elastic energy. It is currently unknown whether in vivo changes in CC and tendon lengths during repetitive SSC exercise decreases the ME of exercise.

Previous investigations have found decreases in ME with fatigue in isolated muscle preparations (Barclay, 1996; Woledge, 1998), however, it is currently unknown if ME changes in human subjects when performing repetitive SSCs. It is possible that ME does not change during exhaustive SSC exercise since previous work has shown humans select movement frequencies that maximize efficiency by taking advantage of the viscoelastic properties of the muscles around the ankle joint (Bach et al., 1983; Dean and Kuo, 2011; Merritt et al., 2012). Performing SSC exercise at resonant frequency has been shown to be significantly related to a reduced energy cost of running (Dalleau et al., 1998). Furthermore, changes in muscle activity influence the viscoelastic properties of the MTU (Agarwal and Gottlieb, 1977) and assist in maintenance of leg stiffness during exhaustive SSC (Kuitunen et al., 2007). Increased leg stiffness in running has also been shown to be significantly related to a reduced energy cost (Dalleau et al., 1998).

Previous research has also shown evidence that structural muscle damage induced by repetitive SSC exercise may reduce effective utilization of elastic energy from the MTU through decreased eccentric stiffness regulation and increased CC lengths (Ishikawa et al., 2006; Kuitunen et al., 2007). A neuromuscular activation strategy resulting in a high braking/push-off EMG ratio allows the CC to resist length change during the eccentric (lengthening) phase and to effectively transfer force to the tendon (Kuitunen et al., 2007). This strategy along with increased pre-activity may be important for regulating CC stiffness during the braking phase of repetitive SSC exercise (Horita et al., 1996).

A shift to increased CC lengths during SSC exercise may also increase fatigue more rapidly from metabolic factors associated with contractile activity (Fitch and McComan, 1985; Lee et al., 2007). Furthermore, SSC induced contractile damage and reduced stiffness regulation in the braking phase is associated with increased energy expenditure, increased lactate (LA) production and acidosis, and the reduction of muscle spindle sensitivity to stretch (Gollhofer et al., 1987; Horita et al., 1996, 1999; Nicol et al., 1996). ME during fatiguing SSC exercise may therefore decrease from increased CC length during the braking phase possibly indicating decreased stiffness regulation and force transfer to the tendon. The relationship between altered contractile function and ME during repetitive SSC exercise is not well understood and warrants further investigation.

The purpose of the study was to investigate whether changes in platarflexor CC length, tendon length, and changes in plantarflexor muscle activity could explain reduction in ME during exhaustive SSC exercise. We hypothesized that ME would decrease as subjects approached exhaustion due to increased CC lengths and shorter tendon lengths that may result in decreased force transfer to the tendon and storage of elastic energy.

2. Methods

2.1. 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 participated in the study. Appalachian State University Institutional Review Board approval was obtained and each subject provided informed consent.

2.2. Hopping protocol

Following 5 min of quiet sitting the subject's resting metabolic values were assessed for 2 min while the subject was seated to establish baseline oxygen consumption and aerobic energy expenditure (EE_a). A resting baseline lactate measurement was performed after baseline O_2 consumption (Lactate Plus, Nova Biomedical, Waltham, MA). The lactate analyzer was calibrated using two control solutions prior to each testing session.

Following baseline measurements subjects were prepped for the hopping session. On the right leg of each subject a wireless electrode was attached to the skin on the MG using a Delsys Adhesive Sensor Interface (Delsys Inc., Natick, Massachusetts, USA). Furthermore, 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 NexcareTM Athletic Wrap and athletic tape at 30% of the lower leg length to obtain a longitudinal image of the MG (Kurokawa et al., 2001). Ultrasound data was collected with a scanning frequency of 76 Hz and synchronized with kinematic data, ground reaction forces, and surface electromyography (EMG). Subjects were then fitted with knee braces on each leg to restrict knee flexion during hopping. Four retro-reflective markers (fifth metatarsophalangeal joint, lateral malleolus, lateral epicondyle of the knee, greater trochanter) on each leg and a sacral marker were tracked 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. Subjects were instructed to hop at a self-selected frequency until they were unable to leave the force plate on two consecutive hopping attempts (resulting in discontinuous hopping) or they reached volitional fatigue. The hop height was self-selected by the subjects and they were instructed to keep their legs fully extended with their arms folded across their torso during the hopping period. The knee braces worn by the subjects effectively limited excessive knee movement and isolated the ankle joint. Subjects were verbally encouraged by the testers to reach maximal exertion in the final hopping period.

The hopping bout was separated into four separate periods with 1-min rest between periods. The first hopping period was 3 min of continuous hopping with the following two periods 2 min each. The last hopping period was to exhaustion. One minute at the start of the protocol (minutes 0–1) was allowed for subjects to find their self-selected frequency. Total mechanical work (W_e) and total energy expenditure (EE) were calculated for two consecutive minutes at three different time points from minute 1 to 3 (Hop_1), 4 to 6 (Hop_2), and 7 to 9 (Hop_3). One minute was allotted for a blood sample immediately following each hopping bout to give a total of three blood samples (La_1, La_2, La_3). Ultrasound, EMG, and motion capture data were collected at four separate time-points for a total 10 s, 10 s into each hopping period (1:10-T_1, 4:10-T_2, 7:10-T_3, and 10:10-T_4) with five consecutive hops analyzed for EMG, CC, tendon, and MTU length. Total time to exhaustion (TTE) was defined as the total time subjects were hopping and excluded the 1 min La periods (see Figs. 1 and 2).

2.3. Energy expenditure, external work, and mechanical efficiency

2.3.1. Energy expenditure

During the hopping protocol, oxygen consumption was obtained using a Parvo Medics Metabolic cart (TrueOne 2400, Parvo Medics, Sandy, UT). The metabolic cart was placed next to the force plate and expired gases were analyzed continuously