

Research article

Muscle Actuators, Not Springs, Drive Maximal Effort Human Locomotor Performance

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Abstract

The current investigation examined muscle-tendon unit kinematics and kinetics in human participants asked to perform a hopping task for maximal performance with variational preceding milieu. Twenty-four participants were allocated post-data collection into those participants with an average hop height of higher (HH) or lower (LH) than 0.1 m. Participants were placed on a customized sled at a 20° angle while standing on a force plate. Participants used their dominant ankle for all testing and their knee was immobilized and thus all movement involved only the ankle joint and corresponding propulsive unit (triceps surae muscle complex). Participants were asked to perform a maximal effort during a single dynamic countermovement hop (CMH) and drop hops from 10 cm (DH10) and 50 cm (DH50). Three-dimensional motion analysis was performed by utilizing an infrared camera VICON motion analysis system and a corresponding force plate. An ultrasound probe was placed on the triceps surae muscle complex for muscle fascicle imaging. HH hopped significantly higher in all hopping tasks in comparison to LH. In addition, the HH group concentric ankle work was significantly higher in comparison to LH during all of the hopping tasks. Active muscle work was significantly higher in HH in comparison to LH as well. Tendon work was not significantly different between HH and LH. Active muscle work was significantly correlated with hopping height ($r = 0.97$) across both groups and hopping tasks and contributed more than 50% of the total work. The data indicates that humans primarily use a motor-driven system and thus it is concluded that muscle actuators and not springs maximize performance in hopping locomotor tasks in humans.

Key words: Tendon, hopping, biomechanics, ankle, titin.

Introduction

The system dynamics within the context of propulsive units for different species varies to a great degree (Abbott et al., 2019; Biewener, 2016; Divi et al., 2020; Lidstone et al., 2018; Nishikawa et al., 2018; Robertson et al., 2018). While there are multi-faceted unit paradigms, typical components comprise structures for some amalgamation of active and passive work (Biewener, 1998; Lieber et al., 2017; Nishikawa et al., 2018). A molecular motor such as muscle, produces active work via energy transfer from the third bond between adenosine diphosphate and an additional phosphate group (Matusovsky et al., 2020). Passive structures stereotypically consist of elastic component structures such as collagen in tendon and individual construct components of muscle tissue, such as nebulin and titin (Handsfield et al., 2017; Mijailovich et al., 2019;

Wheatley, 2020). There are a variety of theories concerning how a muscle-tendon unit functions (Abbott et al., 2019; Divi et al., 2020; Lindstedt et al., 2002). This includes general conceptions of motor-driven and spring-driven theorems (Abbott et al., 2019; Divi et al., 2020; Olberding et al., 2019). Motor-driven theories propose muscle as an actuator driving the locomotor performance of the controller. The spring-driven theory diverges into a collective of various models of a spring and latch passive work initiated by an active work actuator. There are several variations of these models that have been hypothesized to be an evolution of task requirements (Deban et al., 2020). An incredibly quick movement pattern may necessitate a spring and latch model system, whereas in sustained high velocity movements a direct muscle driven system may be required (Patek, 2019; Usherwood and Gladman, 2020; Wilson et al., 2013). The size of the biological system might also play a role due to force to mass ratio limitations (Biewener, 2005; Sutton et al., 2019). A small mammal has mass constraints that may limit the possibility of sufficient muscle mass to fully utilize a motor-driven model (Ilton et al., 2018). Thus, they may utilize a spring-driven model to repetitively translate from potential to kinetic to stored elastic energy during locomotion for efficiency during sustenance procurement (McGowan and Collins, 2018). A very large mammal may use a motor-driven model for optimal locomotor intelligence due to unconstrained mass allotments and perhaps non-time dependent active movement patterns such as grazing or tree felling (Asner and Levick, 2012; Ren et al., 2010; Sutton et al., 2019). Humans are perhaps more complex in nature in that the variety of tasks they are evolutionarily required to complete vary on a spectrum from efficiency to maximal performance (Ferretti et al., 2011; Peyre-Tartaruga and Coertjens, 2018). Thus, humans may have a multiple compulsory technique arsenal to address these by using various combinations of motor-driven and spring-driven models. However, the specific physical tasks that would predispose the use of either of these models in humans is irresolute.

Spring-system models of biological propulsive function have been presented extensively in the literature (Lee et al., 2014; Olberding et al., 2019; Sobhani et al., 2017). These models fall into one of two groupings. The first being a spring-latch arrangement that allows for rapid movement patterns, observed particularly in crustaceans (Patek et al., 2013). In this described model a motor drives or ratchets a spring into a cocked or latched position and awaits release (Gronenberg et al., 1993). The second

grouping is the use of elastic tissue such as tendon as a momentary carrier of energy being transferred during locomotion from potential energy to kinetic energy to stored elastic energy (Biewener et al., 1998; McGowan et al., 2007; McGowan and Collins, 2018). Effective use of an elastic material as a mediator promotes efficiency of movement which is supported by conceptions of free energy minimization (Bruineberg et al., 2018). This model involves muscle acting in a quasi-isometric fashion during stretch-shortening cycle movement patterns such as hopping, running and jumping (Biewener et al., 1998). The muscle does not change length and thus essentially performs no work while the associated tendon acts as a passive contributor to work thus a minimized ATP usage model (Biewener et al., 2004). This is common to hopping animals such as the kangaroo and wallaby (Biewener et al., 1998; Biewener et al., 2004; Ettema, 1996).

There have been competing theories concerning the use of stored elastic energy in smaller versus larger mammals (Abbott et al., 2019; Bullimore and Burn, 2005). The concept that larger mammals use elastic energy more so than smaller animals is based on comparison of hopping animals not quadrupeds (Biewener and Blickhan, 1988; Biewener et al., 1998). Humans fall within a range of mammalian mass just above more moderate mid-sized mammals that includes some of the highest sustained speed mammals such as greyhounds, antelope and cheetah (Usherwood and Gladman, 2020). However, humans fall well below the mass associated with some of the largest mammals that use a purely motor-driven system for propulsive activities such as the rhinoceros, elephant and blue whale (Hazen et al., 2015; Ren et al., 2010). Humans also have unique bipedal capabilities required for a broad range of activities (Preuschoft, 2004). Humans engage in long distance activities requiring efficiency (food gathering, emigration) and high power activities for predatory behaviors, danger avoidance and conquest (Preuschoft, 2004). The muscle-tendon unit within humans could be argued as the most unique and multi-faceted among the animal kingdom due to its diversity of function (Zajac, 1989). Humans may use a motor-driven model or spring-driven model depending on skill requirements (Zajac, 1989). The focus of this current investigation was to elucidate what type of system humans would utilize in a task requiring brief maximal effort when presented with various preceding environmental conditions. An isolated ankle stretch-shortening cycle model common to many mammals, countermovement hopping, was utilized. Additional hops were performed that were preceded by various levels of impact force (drop hops at increasing heights) to further elucidate the effect of this factor on muscle-tendon unit function emulating various scenarios such as obstacle navigation or patterns prevalent in danger avoidance. It was hypothesized, based on the human form, function and mass that a motor-driven model would prevail when attempting maximal performance.

Methods

Participants

All participants were recreationally active (performing physical activity 3 times per week for 1 hour) but not

trained hoppers or jumpers and were free of any musculoskeletal injuries, particularly the ankle, within the past year. The initial participant pool ($n = 24$, age = 21.9 ± 2.4 yrs, height = 1.74 ± 0.09 m, body mass = 74.7 ± 17.0 kg) was allocated post-data collection into those participants with an average hop height lower than 0.1 m (LH, $n = 11$, age = 22.3 ± 2.7 yrs, height = 1.68 ± 0.09 m, body mass = 64.8 ± 13.7 kg, average hop height = 0.08 ± 0.01 m) or higher than 0.1 m (HH, $n = 13$, age = 21.5 ± 2.1 yrs, height = 1.79 ± 0.05 m, body mass = 83.1 ± 15.2 kg, average hop height = 0.13 ± 0.01 m). The Institutional Review Board at Appalachian State University granted ethics approval for all methods in this study which were performed accordingly by the investigator (reference number: 20-0047). Voluntary written consent was obtained from each participant before commencement of any testing.

Locomotor tasks

Participants were placed on a carriage attached to rails on a customized sled at a 20 degree angle while standing on a force plate as described previously (Rice et al., 2018) (Figure 1A). Participants used only their dominant ankle for all testing and their corresponding knee was completely immobilized. Thus, all movement was isolated to that single ankle joint and corresponding propulsive unit (triceps surae muscle complex). The non-dominant leg remained in a relaxed bent position secured to the carriage. First, the carriage was locked into place so that the ankle joint was at a 90 degree angle and the participants were asked to perform a maximal isometric plantarflexion test in which they attempted to maximally plantarflex their ankle while the force-time curve was recorded from the corresponding force plate. The participants performed three trials of this test with two minutes of rest between each trial. The carriage was then unlocked and the participants performed two practice trials of a dynamic countermovement hop (CMH) and drop hops from 10 cm (DH10) and 50 cm (DH50). After these practice hops, three trials of each hop type were performed in a randomized fashion in which data was collected. Instruction for the CMH was to begin on their toes in a plantarflexed position and then to go downwards (eccentric phase) and then upwards (concentric phase) attempting to leave the force plate and hop as high as possible. For the DH10 and DH50 trials participants were elevated to the respective height and then the carriage was released. The carriage slid down the rails and the participants were asked to land on the force plate with their extended leg while in a plantarflexed ankle position, then go downwards (eccentric phase) and then upwards (concentric phase) attempting to hop as high as possible. All trials were separated by two minutes of rest. The best performance trial (highest hop height) for each test was used for analysis and comparisons.

Data recording

Participants were fitted with 16 retro-reflective markers that were placed in specific anatomical locations for motion capture (Figure 1B). Three-dimensional motion analysis was performed by utilizing a 3D infrared 9-camera VICON motion analysis system (Oxford Metrics, Oxford, UK) and a force plate (AMTI, Watertown, USA). Motion

capture data was collected at 250 Hz and force plate data was collected at 1000 Hz. In addition, an ultrasound probe (Telemed, Vilnius, Lithuania) was placed on the lateral aspect of the triceps surae muscle complex of the participant with the superficial and deep aponeuroses in parallel as viewed on the ultrasound image. An image of both the gastrocnemius and soleus could be observed. The gastrocnemius was analyzed with no discernable difference in soleus activity. Data was collected at 15 Hz and time sequenced with all kinematic and kinetic data.

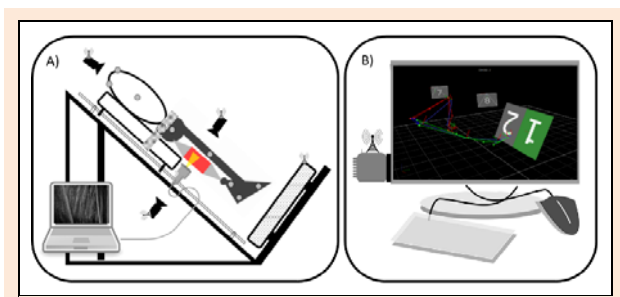


Figure 1. Data collection (A) included 3D motion capture, force plate and ultrasound for calculation of ankle joint and triceps surae muscle-tendon unit kinematics and kinetics (B).

Biomechanical analysis

A zero-lag fourth-order low-pass Butterworth filter was utilized to filter marker trajectories (11 Hz) and force plate data (14 Hz) for all locomotor tasks (McBride and Nimphius, 2020). Calculation of participant center of mass (COM) z-axis acceleration (axis along the length of the carriage motion along the rails of the sled) was performed by dividing the respective vertical force-time curve (minus the force associated with acceleration due to gravity) by the participant's body mass. Forward dynamics were then utilized to determine the velocity and displacement of the COM with displacement being used to determine hop height. Ensemble force-displacement curves for the COM were created by resampling all participant data to 100 Hz

and averaging them across the respective groupings. Ankle moment in the sagittal plane was calculated through inverse dynamics using the motion capture kinematic data and the corresponding force plate kinetic data. Area under the ankle moment versus ankle displacement curve was utilized for calculation of eccentric and concentric phase work (McBride and Nimphius, 2020). Ensemble ankle moment-displacement curves were created by resampling all participant data to 100 Hz and averaging them across the respective groupings. The intraclass correlation coefficient for calculation of hop height between trials was reliable at a criterion level of 0.7 (countermovement hop = .94; 20-cm drop hop = .79; 30-cm drop hop = .91; 40-cm drop hop = .85) based on a previous publication from our laboratory (Rice et al., 2018). The intraclass correlation coefficient for the calculation of force-time, power-time and displacement-time curves was 0.96 based on previous publication from laboratory as well (Cormic et al., 2007; Rice et al., 2018).

Muscle-tendon unit kinematics and kinetics

The following methods have been previously explained and utilized to examine muscle-tendon unit length change variables (Kurokawa et al., 2003). Muscle-tendon unit (MTU) length was estimated by anatomical measurements from the lateral epicondyle of the femur to the lateral malleolus of the ankle (Figure 2). MTU length changes were calculated using the angular displacement of ankle rotation from motion capture and the measured moment arm of the triceps surae muscle complex around the ankle as previously described (Lidstone et al., 2018; Lidstone et al., 2016). Video analysis of ultrasound imaging was performed using Kinovea open source video analysis software (Kinovea for Windows, Version 0.8.15, kinovea.org) (Figure 2). Pennation angle was calculated as the average of five angles measured at different positions on the ultrasound image (Lidstone et al., 2016).

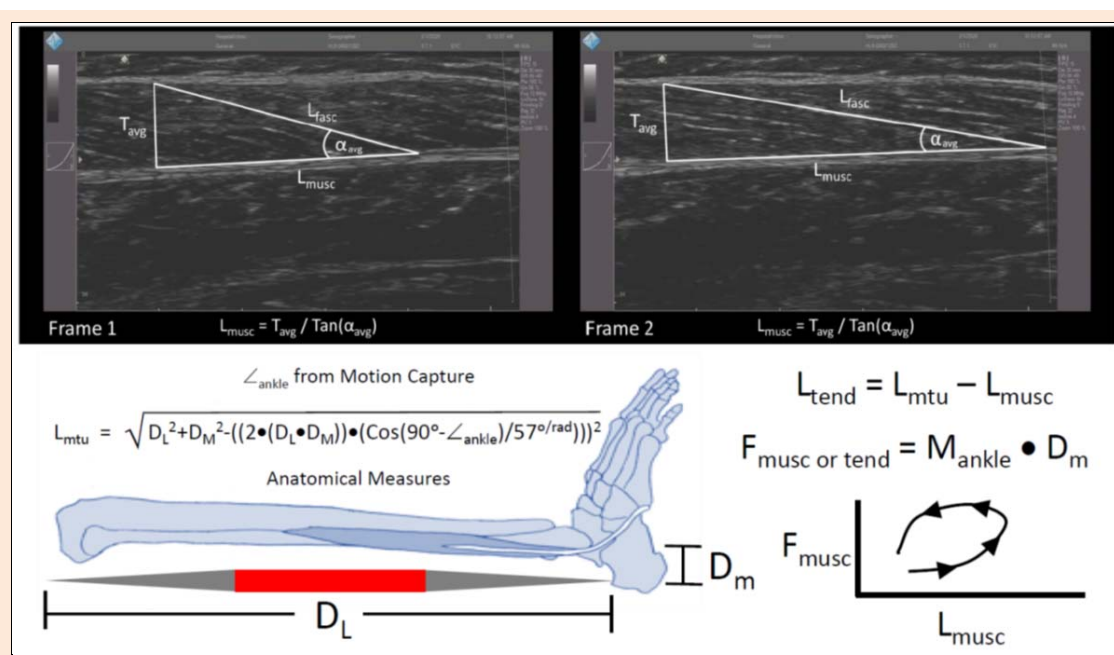


Figure 2. Calculation of muscle-tendon unit length change (L_{mtu}), tendon length change (L_{tend}) and muscle length change (L_{musc}) and muscle/tendon force ($F_{musc \text{ or } tend}$) through methods by Kurokawa et al. (2003).

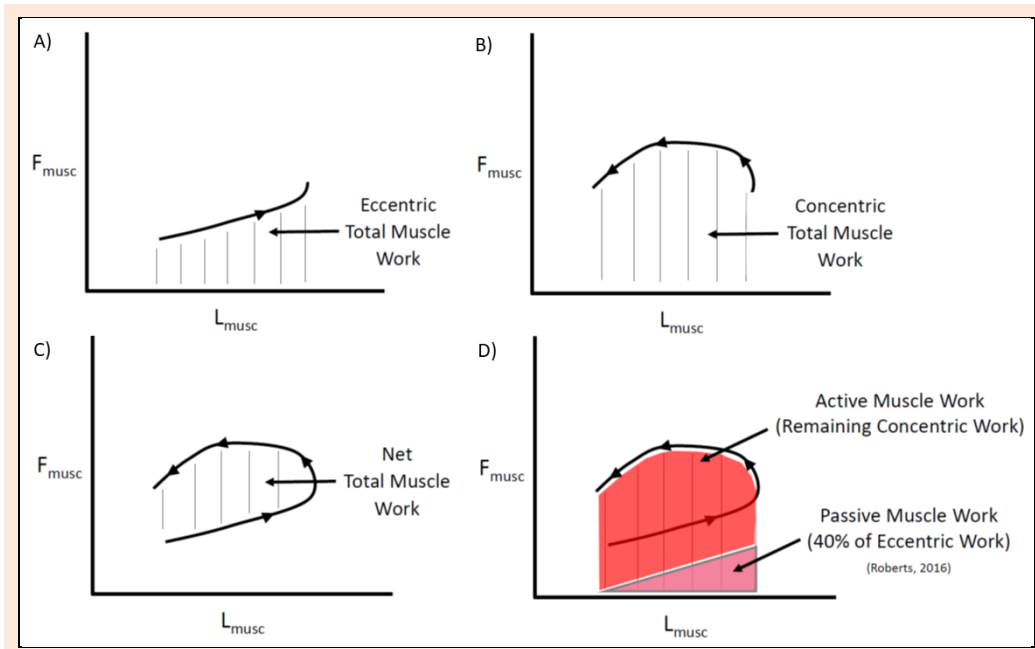


Figure 3. Calculation of eccentric total muscle work, concentric total muscle work, net total muscle work, active muscle work and passive muscle work via muscle length change (L_{muscle}) and corresponding muscle/tendon force (F_{muscle}).

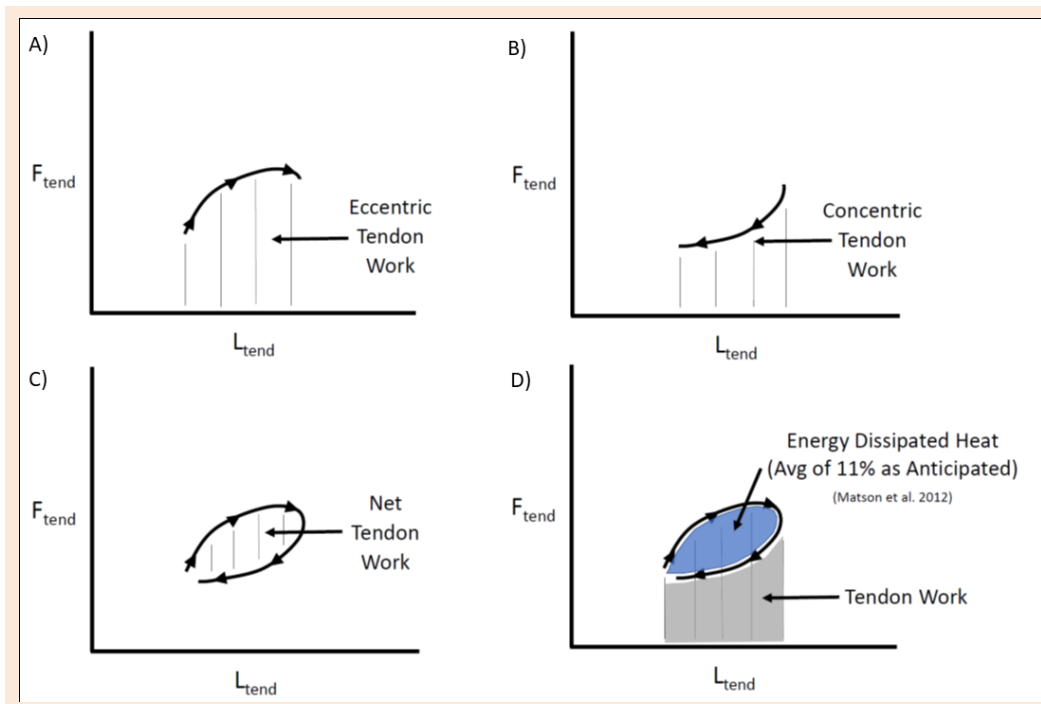


Figure 4. Calculation of eccentric tendon work, concentric tendon work, net tendon work, and energy dissipated (presumably by heat) via tendon length change (L_{tendon}) and corresponding muscle/tendon force (F_{tendon}).

The muscle thickness was defined as the average vertical distance between the deep and superficial aponeuroses. This was calculated as the average of the distance between the aponeuroses on both sides of the image. Muscle length was defined as the average thickness divided by the tangent of the average of the five pennation angles. This calculated muscle length indicates the component of the triceps surae length parallel to the tendon. Tendon length was calculated as the difference between the MTU and the muscle length (Lichtwark and Wilson, 2006).

The corresponding muscle/tendon force was calculated by using the measured ankle joint moment arm and the ankle joint moment. Muscle and tendon displacements were plotted against the respective muscle or tendon force and the area under these curves was utilized to calculate the following variables outline in Figures 3 & 4 (Figure 3A - eccentric total muscle work, Figure 3B - concentric total muscle work, Figure 3C - net total muscle work, Figure 3D - active muscle work, Figure 3D - passive muscle work, Figure 4A - eccentric tendon work, Figure 4B - concentric

tendon work, Figure 4C - net tendon work, Figure 4D - energy dissipated (presumably by heat) of the tendon). Ensemble muscle and tendon force-displacement curves were created by resampling all participant data to 100 Hz and averaging them across the respective groupings. Net tendon work was simply the addition of the negative and positive work from the respective phases of the locomotor task. Tendon energy recovery averaged approximately 89% (during DH10) which is consistent with the literature (Ker, 1981; Matson et al., 2012; Shadwick, 1990). Positive passive muscle work was calculated as 40% of the negative work performed during the eccentric phase. This value of 40% is based on the typically observed value concerning recovery of stored elastic energy in a lengthened muscle (Roberts, 2016). The remaining positive concentric phase work of the muscle was considered active muscle work as any additional work in the concentric phase would have to be accounted for by active muscle contraction via ATP driven myosin, actin and titin interaction (Sweeney and Hammers, 2018). An additional model of calculating passive muscle work is described in the results but was inconsequential as it did not significantly alter the findings.

Statistical analysis

Data was normally distributed, and a general linear model one-way analysis of variance was utilized for effect comparison between groups (LH, HH) for hop height and ankle, muscle and tendon work. Pearson product correlation coefficients (r) were calculated for select variables. All analyses were performed using SPSS (Version 24.0, Chicago, USA) and significance was chosen at $p \leq 0.05$.

Results

Center of mass and ground reaction force

Average hopping height across all hops as determined by center of mass (COM) displacement derived from ground reaction force (GRF) was significantly different between the low hoppers (LH) and high hopper (HH) (Figure 5). The hopping height for the best trial was significantly different between HH and LH for the countermovement hop (CMH) and drop hop from 10 cm (DH10) and 50 cm (DH50) (Figure 5A). When examining the force-time curves, the GRF was higher in HH compared to LH between 81-88% of relative time for CMH, between 49-58% for DH10 and between 19-30% and 58-83% for DH50 (Figure 5B-D – areas of significance highlighted in light blue). The HH group (11.8 ± 2.0 N/kg) also exerted a significantly higher relative peak force in comparison to LH (10.0 ± 2.4 N/kg) in a maximal isometric plantarflexion test. Thus, the HH group had significantly higher isometric force capabilities and exerted more GRF during all the dynamic hopping trials.

Ankle work, total muscle work (passive + active), passive muscle work, active muscle work and tendon work

There were no significant differences in eccentric phase ankle work between LH and HH for any of the locomotor tasks (CMH, DH10, DH50) (Figure 6A and Figure 7A-C). However, there was a significant difference in eccentric total muscle work and tendon work between LH and HH in CMH (Figure 6B,C and Figure 7D,G). Concentric ankle work and total muscle work was significantly higher in HH

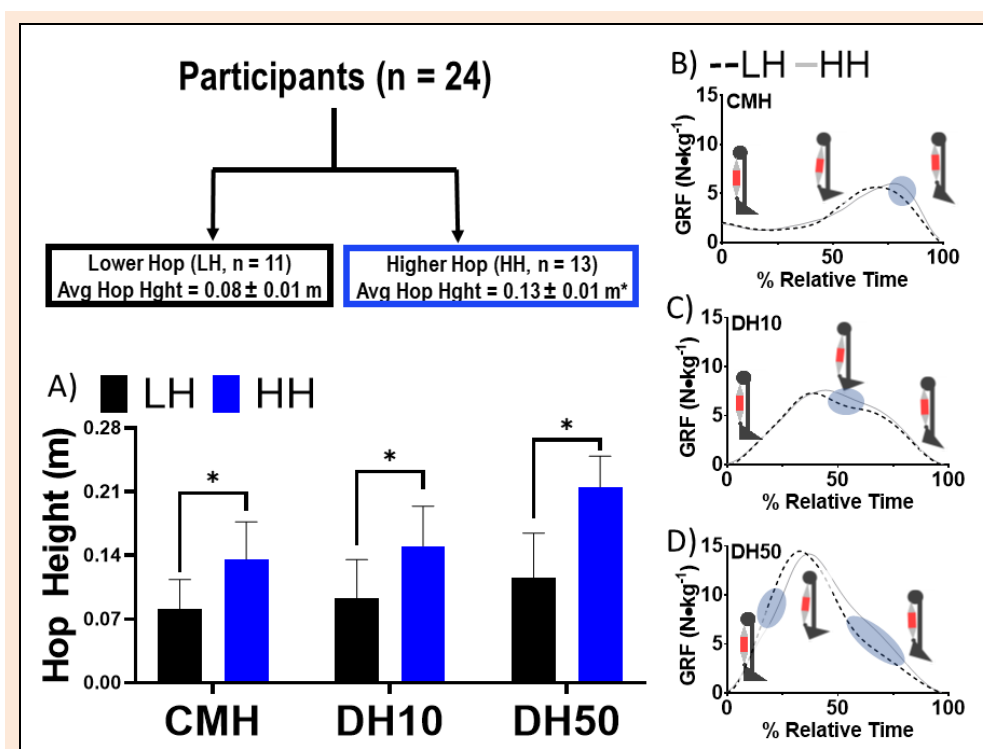


Figure 5. Experimental design involved dividing participants into lower hoppers (LH) or higher hoppers (HH). Participants performed 3 trials of a single countermovement hop (CMH), a single drop hop from 10 cm (DH10) and a single drop hop from 50 cm (DH50) in which the carriage was lifted and dropped from each respective height. The HH group hopped significantly higher (A) than LH group for the CMH, DH10 and DH50. The average ground reaction force (GRF) curves (B-D) in relative time are presented for LH and HH. In general, the HH group exhibited more statistically significant GRF during the concentric (upward) phase of the movement as indicated by the shaded light blue areas ($p \leq 0.05$). * indicates statistically significant difference between LH and HH ($p \leq 0.05$).

in comparison to LH for CMH, DH10 and DH50 (Figure 6D,E and Figure 7A-C and Figure 7D-F)). There was no significant differences between the groups for concentric phase tendon work for any of the locomotor tasks (Figure 6F and Figure 7G-I). Net ankle work was significantly different between HH and LH in CMH and DH10 (Figure 6G, Figure 7A-B). Net total muscle work was significantly higher in HH in CMH and DH50 (Figure 6H and Figure 7D,F). There were no significant differences in net tendon work between the groups (Figure 6I and Figure 7G-I).

There were significantly higher levels of concentric phase active muscle work in HH in comparison to LH in all locomotor tasks (Figure 8A-C and Figure 9A-D). There were significant differences in concentric phase passive muscle work between LH and HH during CMH and DH10 only (Figure 8A-C and Figure 9B-D). In LH, the percentage of active muscle work was significantly greater than passive muscle work in all locomotor tasks (Figure 8D and Figure 9B-D). In LH during DH10 the percentage of tendon work, passive muscle work and active muscle work were all significantly different from each other (Figure 8D and Figure 9B-D). In HH, the percentage of active muscle work was significantly greater than tendon work and passive muscle work in CMH (Figure 8E and Figure 9B-D). During DH10 in HH, the percentage of tendon work, passive muscle work and active muscle work were all significantly different from each other (Figure 8E and Figure 9B-D). In HH during DH50, the percentage of tendon work and active muscle work were both significantly higher than passive muscle work (Figure 8E and Figure 9B-D).

Relationships between hopping height and work

There was a significant Pearson product moment correla-

tion between average hopping height and active muscle work ($r = 0.97, p = 0.001$) and tendon work ($r = 0.87, p = 0.031$), but not passive muscle work ($r = 0.69, p = 0.126$), when observing LH and HH during the CMH, DH10 and DH50 (Figure 10A-C). Passive muscle work contributed 14.2%, tendon work contributed 34.9% and active muscle work contributed 51.1% to total concentric phase work and these were all significantly different from each other.

Discussion

The results of this study indicate that a muscle actuator governs maximal hopping performance in humans. This is supported by two observations: first, most of the total work performed was from active muscle work (51%) and second, the strong positive relationship between active muscle work and maximal hopping height ($r = 0.97$). However, the role of tendon work to hopping height cannot be discounted completely. There was a significant correlation between these two variables as well ($r = 0.87$), but tendon work only contributed 35% of the total work. In addition, concentric phase tendon work was not significantly different between the higher and lower hopping groups for any of the hopping tasks. Passive muscle work does not appear to play a major role in maximal hopping performance in humans. However, there was a significant difference in passive muscle work between higher hoppers and lower hoppers during the countermovement hop and drop hop from 10 cm that warrants further investigation. The model used in the current investigation to calculate passive muscle work utilized reported values of strain energy return from lengthened muscle of 40% (Roberts, 2016).

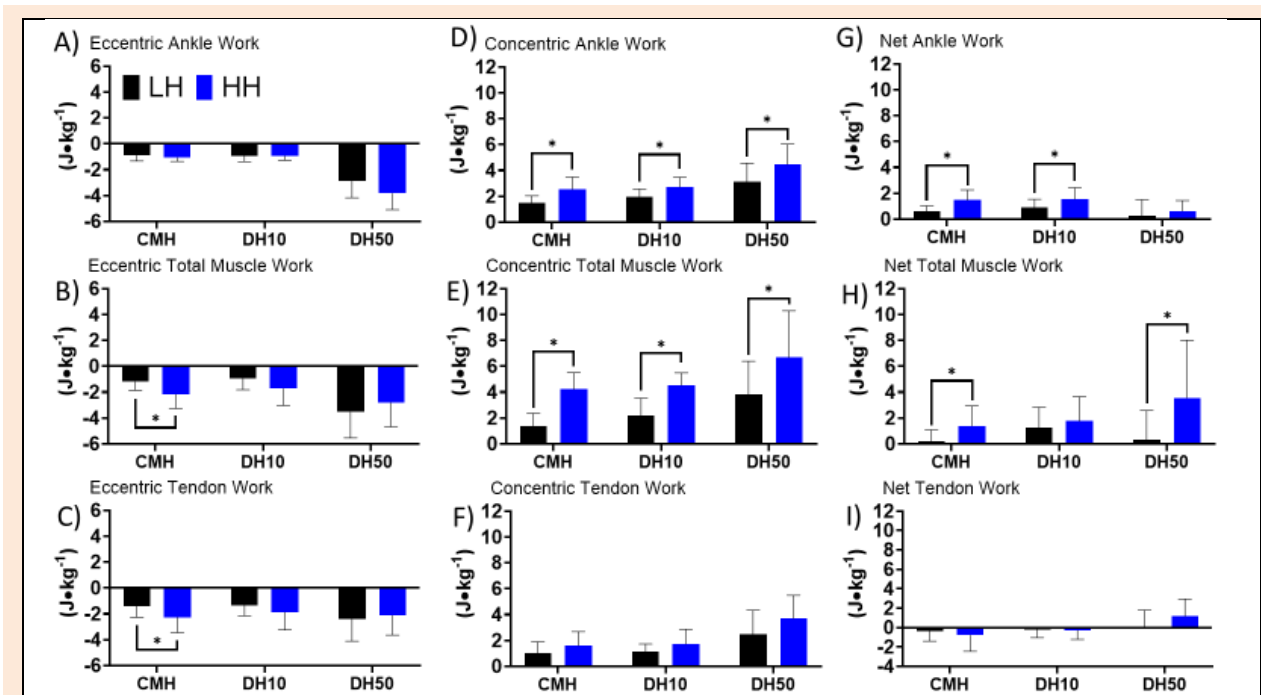


Figure 6. The relative eccentric (downward phase), concentric (upward phase) and net work during the countermovement hop (CMH) and drop hop from 10 cm (DH10) and 50 cm (DH50) are shown for the ankle (A-C), total muscle (passive + active) (D-F) and tendon (G-I) in the lower hoppers (LH) and higher hoppers (HH). * indicates statistically significant difference between LH and HH ($p \leq 0.05$).

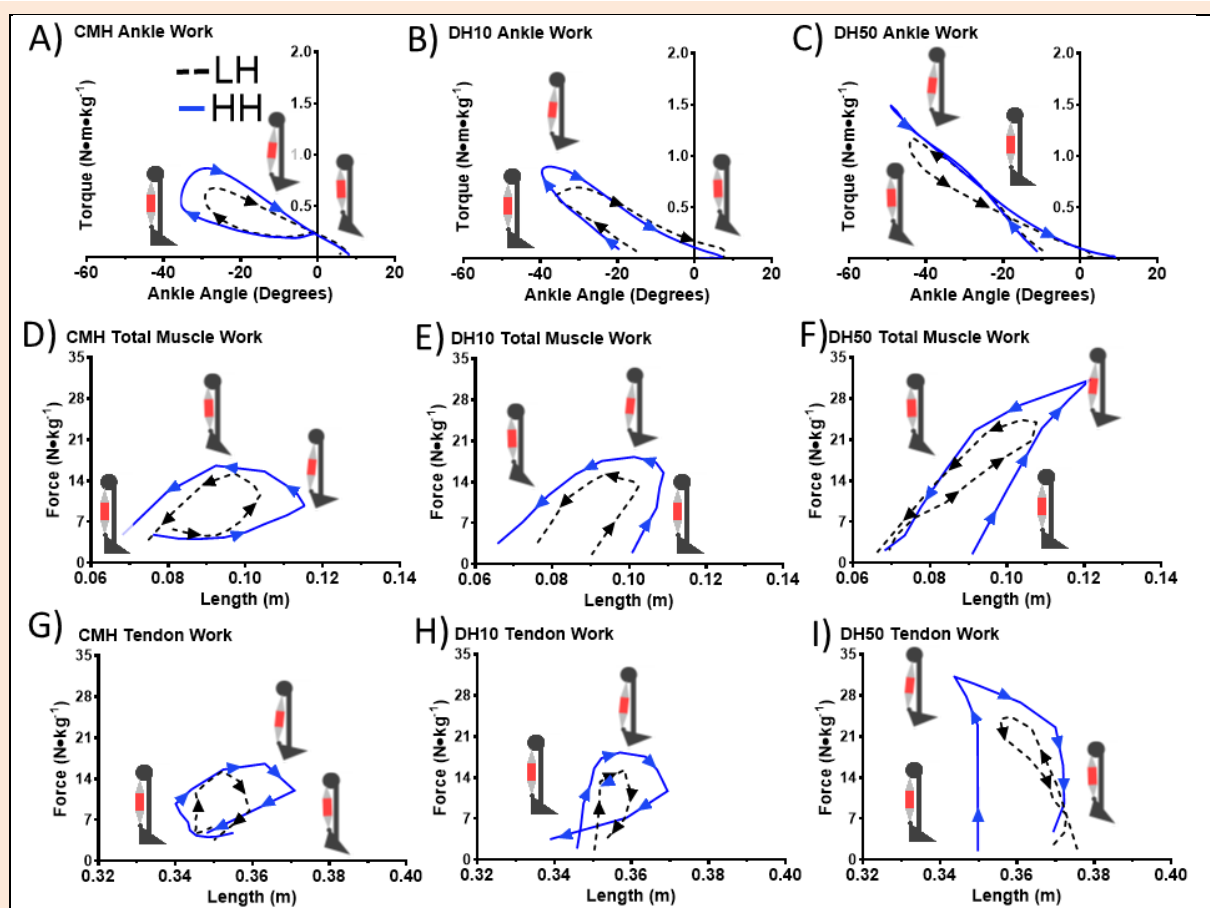


Figure 7. Work loops for the ankle (A-C), muscle (passive + active) (D-F) and tendon (G-I) during the counter movement hop (CMH) and drop hop from 10 cm (DH10) and 50 cm (DH50) in the lower hoppers (LH) and higher hoppers (HH).

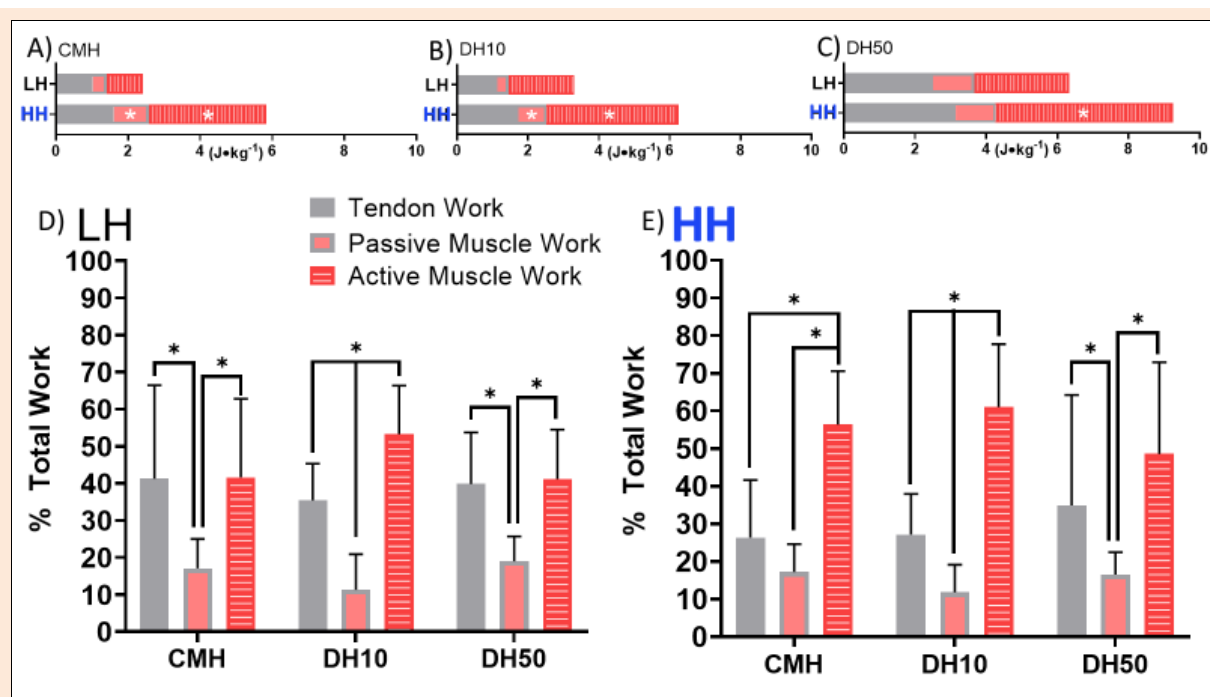


Figure 8. Absolute (A-C) and relative (D-E) tendon work, passive muscle work and active muscle work during concentric (upward) phase of the counter movement hop (CMH) and drop hop from 10 cm (DH10) and 50 cm (DH50) in the lower hoppers (LH) and higher hoppers (HH). * indicates statistically significant difference between tendon work, passive muscle work and active muscle work ($p \leq 0.05$).

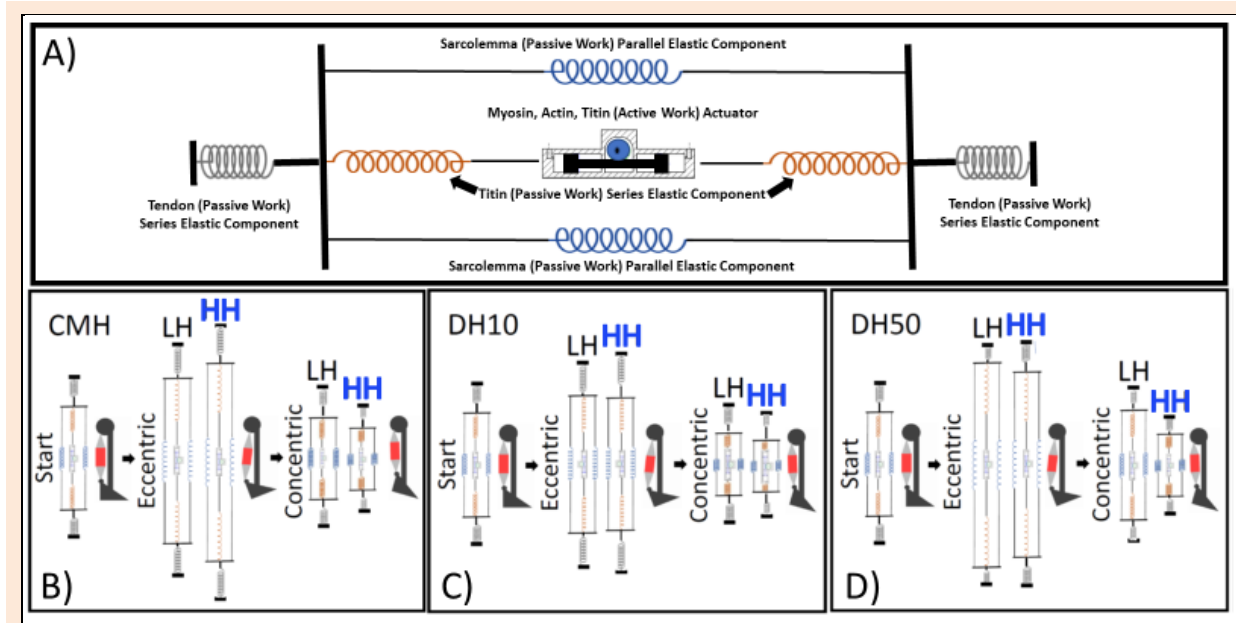


Figure 9. Pictorial (A) representation (to scale) of the corresponding changes in length of the muscle and tendon and the percentage contribution (to scale) of tendon work, passive muscle work and active muscle work during the (B) countermovement hop (CMH) and drop hop from (C) 10 cm (DH10) and (D) 50 cm (DH50) in the lower hoppers (LH) and higher hoppers (HH).

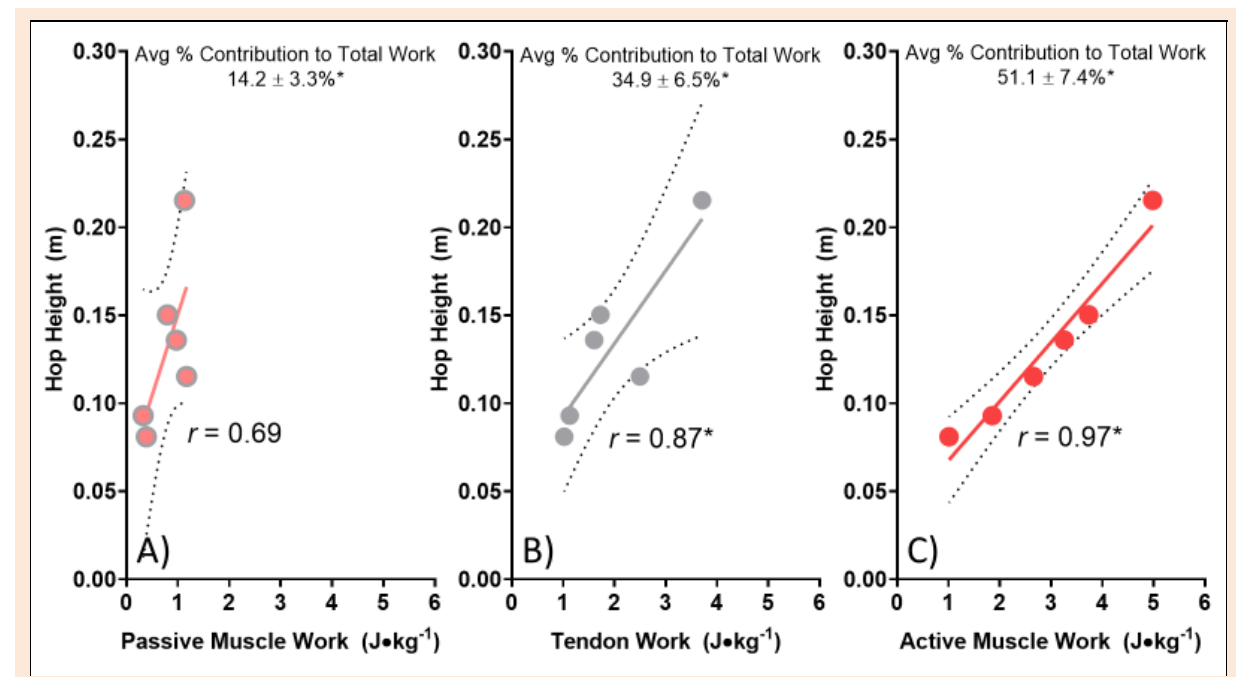


Figure 10. Pearson product correlation coefficients between average hop height and average tendon work (A), average passive muscle work (B) and average active muscle work (C) for the countermovement hop (CMH) and drop hop from 10 cm (DH10) and 50 cm (DH50) for both the lower hoppers (LH) and higher hoppers (HH) combined. * indicates statistical significance ($p \leq 0.05$).

Studies have also indicated that the stored elastic energy capabilities of muscle may be higher than this value or maybe variable based on the condition of the pre-stretch, particularly the rate of stretch (Herzog, 2019; Ward et al., 2020). The rate of stretch and preload on the muscle would increase as participants performed the CMH, DH10 and DH50 (Voigt et al., 1995). Thus, in the current investigation an additional model assuming a progressive increase in the strain energy from passive muscle work was examined as well. This model involved using a value of 40% strain energy return of muscle for the CMH, 60% for the

DH10 and 80% for the DH50. In this model, the correlation between passive muscle work and hopping height decreased to a statistically non-significant value of 0.67. The percentage of passive muscle work to total work increased to 21.1%. Thus, the second model examined in the current investigation did not significantly alter the results and conclusions. Given the described observations, the hypothesis that a motor-driven model would be utilized in a maximal locomotor task in humans was positively supported.

Two types of animal movement conditions have been outlined by Biewener (1998), who theorized both a

power model and an efficiency model. The power model involves a large amount of muscle work (Biewener, 1998). Therefore, the observed optimal performance no longer becomes a factor of tendon storage of elastic energy and efficiency, but of single maximal force contractility of the muscle (Wade et al., 2019). Humans may have the capability to use their muscle-tendon unit in both capacities. For food gathering or when searching for resources, a spring-model may be utilized in an activity such as walking for conservation of energy (Lichtwark and Wilson, 2006). However, when avoiding danger or sacrificing prey for sustenance perhaps a motor-driven model may be employed to maximize the chance of success (Wade et al., 2019). This means a possible dichotomy of tendon function. In the instance of efficiency, the tendon is storing energy, and in the second instance tendon is merely a transmitter of muscle contractile force to the origin-insertion points for generation of limb movements. The limb movement translates into GRF and the subsequent movement pattern. It is clear from the current investigation that when a human attempts to perform a rapid ballistic activity for maximal performance a motor-driven model prevails. Thus, the determining factor of skill optimization depends on active muscle contractility.

The fact that a motor-driven model would be used in maximal performance hopping in humans may not be surprising. Many investigations indicate that muscle contractile strength is significantly correlated to maximal sprinting speed and jump height in athletes (Nuzzo et al., 2008; Townsend et al., 2019; Wisloff et al., 2004). In addition, adding increasing load during jumping has been shown to result in greater active muscle work (Wade et al., 2019). The exact role of tendon and the percentage of total work during locomotion in mammals that can be attributed to tendon is unclear (Bullimore and Burn, 2005; Ker, 1981; Wade et al., 2018). Investigation of tammar wallabies indicate that the actual amount of muscle work performed during repeated hopping is minimal and the transfer of energy from potential to kinetic to stored is optimized via the tendon (Biewener et al., 1998). Gutmann and Bertram (2017) presented a model in which the muscle impulse (integration of force and time) is the determining factor for repeated stretch-shortening cycle performance and not muscle work. However, as previously mentioned, results must also always be placed in the context of the type of activity that the participant is asked to perform (Biewener and Blickhan, 1988; Wade et al., 2019). The role of tendon in low force repetitive tasks may be quite different from the role of tendon during a single maximal effort (Wade et al., 2020). During low force tasks in which the performer acts as though efficiency is the important factor, muscle perhaps is acting as a latch to secure optimal tendon lengthening for storage of elastic energy (Lidstone et al., 2018; Lidstone et al., 2016). It could be argued that observation of tendon from the current investigation indicate that while tendon is not the primary component of total work, its importance cannot be completely discounted.

Another component of the current investigation was passive muscle work which has been the focus of several studies (Biewener, 1998; Ettema, 1996; Herzog, 2019; Lindstedt et al., 2002; Monroy et al., 2007). Titin, for

example, has been shown to contribute to 2.6% more work in single muscle fibers as a result of a stretch-shortening cycle (Tomalka et al., 2020). However, the contribution of titin is multifaceted with respect to its relationship to passive work and active work due to the calcium mediated binding of titin to actin as well (Nishikawa, 2020; K. Nishikawa et al., 2020; Tomalka et al., 2020). The role of titin in a large mammalian locomotive capacity appears indeterminate at this time (Lindstedt et al., 2001). The small percentage of passive muscle work contribution to total work in a gross feature unit system questions the significance of a tunable molecular spring outside the realm of a bench top (Pertici et al., 2019). However, there is data to suggest that variations of titin isoforms do exist among species and that there are some adaptable mechanisms of titin to chronic mechanical stimuli such as exercise (Kyrolainen et al., 2005; Kyrolainen et al., 2003; McBride et al., 2003; McGuigan et al., 2003; Nishikawa, 2020). Therefore, passive muscle work cannot be completely ruled out, especially in light of the current investigation's findings.

Conclusion

In conclusion, humans clearly use a predominance of active muscle contractility to enhance a single maximal effort performance. Active muscle work made up the largest component of the total work and correlated the highest with the resulting performance. However, this data must be kept within the context of the locomotor task utilized in this investigation. A single hop may vary biomechanically from larger multi-joint movements such as running or jumping (Ferretti et al., 2011; Lidstone et al., 2018; Wade et al., 2018). These activities may use a motor-driven or spring-driven model or some combination of these two competing theories. Further investigation warrants examining such activities but technological limitations in estimating contribution of active versus passive work to optimal performance in a multi-joint bipedal task is daunting. The current investigation used an isolateral single joint movement in which the function of all the contributing components could be targeted and thus provides compelling data supporting that muscle actuators, not springs, drive maximal effort human locomotor performance.

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Key points

- Humans use a predominance of active muscle contractility to enhance single maximal effort performance as opposed to tendon stored elastic energy
- Single effort maximal performance in humans may entail a motor-driven system as opposed to a spring-driven system
- However, the role of passive work (elastic components) from both muscle and tendon cannot be completely discounted as their contribution to performance may have activity dependent significance

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