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RESEARCH ARTICLE

The influence of added mass on muscle activation and contractile mechanics during submaximal and maximal countermovement jumping in humans

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ABSTRACT

Muscle contractile mechanics induced by the changing demands of human movement have the potential to influence our movement strategies. This study examined fascicle length changes of the triceps surae during jumping with added mass or increasing jump height to determine whether the chosen movement strategies were associated with relevant changes in muscle contractile properties. Sixteen participants jumped at sub-maximal and maximal intensities while total net work was matched via two distinct paradigms: (1) adding mass to the participant or (2) increasing jump height. Electromyography (EMG) and ultrasound analyses were performed to examine muscle activation, fascicle length and fascicle velocity changes of the triceps surae during jumping. Integrated EMG was significantly higher in the added mass paradigm with no difference in mean or maximal EMG, indicating that the muscle was activated for a significantly longer period of time but not activated to a greater intensity. Fascicle shortening velocity was slower with added mass compared than with increasing jump height; therefore, intrinsic force–velocity properties probably enabled increased force production. Improved fascicle contractile mechanics paired with a longer activation period probably produced a consistently larger fascicle force, enabling a greater impulse about the ankle joint. This may explain why previous research found that participants used an ankle-centred strategy for work production in the added mass paradigm and not in the jump height paradigm. The varied architecture of muscles within the lower limb may influence which muscles we choose to employ for work production under different task constraints.

KEY WORDS: Fascicle, Ultrasound, EMG, Muscle co-ordination, Biomechanics

INTRODUCTION

Understanding how humans coordinate movement during everyday tasks necessitates the study of how we adapt movement to overcome various task constraints. Using jumping as a highly controlled multi-joint movement, previous studies have examined leg joint-level control strategies as jump height was increased, finding that ankle musculature is relied on during submaximal jumps and hip musculature is relied on during maximal jumps (Vanrenterghem et al., 2004; Wade et al., 2018). Carrying added mass is a common constraint that is placed on the body during everyday life; however, there has been little research into muscular coordination under this constraint during careful experimental manipulations, such as during jumping tasks. We have previously (Wade et al., 2018) designed a jumping experiment where two paradigms were used to match the total net work output during jumping, by either adding mass to the participant or increasing the required jump height. We found a distinct difference in strategy for generating the same total net work between increasing added mass or increasing jump height paradigms. When total net work was increased by adding mass, participants maintained their reliance on ankle musculature, increasing the net work about this joint above that produced with increasing jump height. Therefore, we believe that the additional net work produced by the ankle when mass is added is linked to the increased force production by ankle plantar flexors required to overcome the greater inertia and weight.

Increasing total net work as a product of greater force is difficult in normal jumping as increasing muscle force and torque about all joints simultaneously will probably result in early take-off and a lower jump height (Bobbert and Van Soest, 2001). Added mass increases the inertial resistance that muscles must overcome, facilitating a longer time in contact with the ground, and may produce a greater impulse. This is neatly summarised by rearranging the impulse–momentum relationship in the following equation:

$$V = \frac{Ft}{m}, \tag{1}$$

where V is the velocity at take-off, F is the average net vertical force acting on the body, t is the time over which force is applied and m is the mass of the body. In addition, because gravity is the only force acting on the body in the air, velocity at take-off will be proportional to the distance travelled in the air. When jumping to progressively increasing jump heights, with no added mass, a deeper countermovement depth permitting a longer period of force production is the only mechanism available to increase take-off velocity and impulse (Domire and Challis, 2007). In contrast, when mass is added to the body but jump height is held constant, the inertial resistance the body must overcome is increased, requiring a greater force to be generated. When combined with increased countermovement depth, this could enable a greater impulse compared with normal jumping with no added mass, but the same total net work. As total net work is increased in either paradigm, there will also be an increase in impulse, with the jump height paradigm requiring a greater take-off velocity while the added mass condition must overcome a greater load without a change in take-off velocity. In our previous study, net work about the hip increased similarly in the two paradigms to meet increasing net work demands. In contrast, net work at the ankle was increased to a

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greater extent in the added mass paradigm, which we believe is due to the influence of the compliant Achilles tendon on muscle contractile mechanics (Wade et al., 2018). To investigate this, and therefore understand the factors influencing control strategies, the underlying muscle mechanics must be examined.

Muscle work may be increased by increasing muscle force, increasing muscle contractile length change (fibre or fascicle length change) or a combination of the two. Our previous study demonstrated that when mass was added there was an increase in peak Achilles tendon force and peak ankle moment compared with when achieving the same work output by increasing jump height (Wade et al., 2018). We postulated that the additional net work produced at the ankle in the added mass paradigm was probably due to increased force production by plantar flexor muscles. While increased muscular force will probably be the primary mechanism for increased work, it is possible that increased force will also result in greater length change of muscle contractile components because the series elastic element (SEE) stretches (Griffiths, 1991; Roberts, 2002). Increased muscle force production may be achieved through recruitment of additional motor neurons (Henneman et al., 1974; Farina et al., 2004) as well as a change in muscle contractile mechanics to operate at optimal lengths (Burkholder and Lieber, 2001; Gordon et al., 1966; Lutz and Rome, 1996) or slower velocities (Fenn and Marsh, 1935; Hill, 1938; Huxley, 1985; Lichtwark et al., 2007). To fully capture changes to active muscle force production with and without added mass, it is necessary to study the interaction between muscle activation, length change and force production.

Experiments in frog species have provided much insight into muscular mechanisms that can produce power for jumping. Much of this work highlights the importance of a catapult-like action from the SEE of ankle extensor muscles (Astley and Roberts, 2014; Astley and Roberts, 2011). Previous *in vivo* human jumping experiments have demonstrated that plantar flexor fascicle velocity decreases to almost zero prior to take-off, allowing for high fascicle forces and significant energy storage and return from the elastic Achilles tendon (Fukashiro et al., 2005; Kurokawa et al., 2001, 2003). However, recent studies have suggested that peak power occurs prior to tendon recoil and compliant tendons optimise the shortening speed of the muscle to allow for greater force production, in addition to storing and returning energy for plantar flexion (Moo et al., 2017). Simulation studies comparing muscle force production between stiff and compliant tendons indicate that compliant tendons allow a greater force to be produced for a significantly longer period of time, increasing the net work and the impulse produced (Robertson et al., 2018). Furthermore, increasing the inertial load on a muscle–tendon unit may enhance net work production as a result of slower shortening velocities of contractile elements (Sawicki et al., 2015; Galantis and Woledge, 2003; Hartree and Hill, 1928). Our previous paper demonstrated that an increased time to perform the same jumping movement occurs with added mass, which is probably only possible if fascicles are shortening at a slower velocity (Wade et al., 2018). Electromyography and ultrasound imaging techniques make it possible to analyse whether muscle activation or fascicle length and velocity are altered with added mass during jumping in humans. This would reveal the contractile mechanism that is behind the additional work output observed for ankle plantar flexors during jumping with added mass, and why we rely on these muscles more in an added mass paradigm.

This study aimed to link the additional net work output previously observed for human plantar flexors when jumping with added mass to the underlying muscle mechanics *in vivo*. We hypothesised that when compared with normal jumping, jumping with added mass would enable the plantar flexors to contract at slower concentric velocities, facilitating greater force production and net work about the ankle joint.

MATERIALS AND METHODS

Protocol

Sixteen male participants (*N*=16, height 179.7±4.6 cm, mass 74.2±5.8 kg, age 23.7±3.3 years) gave written informed consent to participate in this study. Ethical approval was granted from the institutional ethics review committee at The University of Queensland (approval number: HMS15/1106). Data collected for this study were recorded at the same time as our previous study and therefore protocol and participants for the two studies were the same (Wade et al., 2018). Participants performed vertical countermovement jumps without arm swing at preferred countermovement depths over a range of experimental conditions, designed to manipulate the total mechanical work required for each jump. Work was manipulated either by adding mass to the participant or by varying jump height, or both. Target jump heights were determined based on the maximal jump height achieved with each of the three added masses within this study and with no additional mass (Fig. 1). Jump heights 1, 2, 3 and maximal were determined by the maximal jump height achieved with 60%, 40%, 20% and 0% additional body mass, respectively. Participants were first randomly assigned one of the four mass conditions (including no added mass). Once the maximal jump height at that mass had been determined, the participant completed jumps with all remaining lower masses to the same height in a random order. Thus, for jump height 1, participants first jumped maximally with 60% added mass and then matched this jump height with 0%, 20% and 40% added mass in a random order. This jumping protocol matched the total net work output of two paradigms at three incremental stages, starting from a shared condition (low work output). Direct comparisons could therefore be made between each condition in the added mass paradigm (no change in jump height) and the corresponding matched net work condition in the jump height

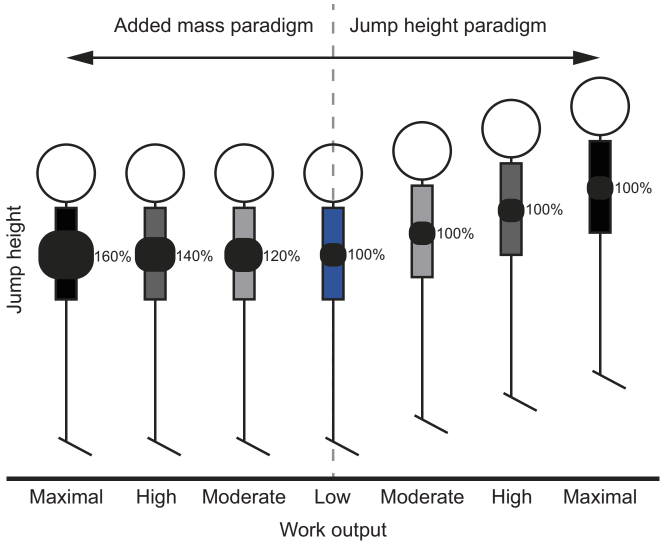

Fig. 1. Jumping conditions split into the added mass paradigm and jump height paradigm. Colours indicate matching net work output (moderate, high and maximal). The blue condition indicates low net work output and was shared by the two paradigms.

paradigm (normal jumping) (Fig. 1). In this study, the jump height paradigm served as a control paradigm in that this is the way the body normally increases total net work output when jumping.

Added mass was achieved by placing up to two weight vests on the participant that could each be loaded with up to 30 individual 1 kg blocks, for a combined maximum of 60 kg of added mass. Visual feedback for each jump height was provided via a light box containing a row of LEDs located behind a double-slit opening (Van Zandwijk et al., 2000) and was used in conjunction with verbal feedback of the exact jump height, calculated live from ground reaction force data. Prior to data collection, participants were familiarised with the jumping protocol, which included performing sub-maximal practice jumps with an empty weight vest and the light box until they were satisfied with their jump height consistency.

During experimentation, participants assumed a quiet standing posture with hands locked onto the side of the weight vest for 2 s before every jumping trial. Participants performed at least three jumps at each condition; however, sub-maximal jumps were only deemed successful if they were calculated to be within 1 cm of the target height. After each sub-maximal jump, the researcher informed the participant of their exact jump height and if they were within the targeted margin. All trials were recorded but only successful trials were used in data analysis. Submaximal conditions were deemed completed when three successful jumps were recorded or the participant had performed 10 jumps at that condition. Sub-maximal conditions were allocated at least 30 s rest between each jump. Maximal jumping conditions did not require a target height and therefore were only performed three times with 90 s rest. Participants were still informed of their jump height after each maximal jump as a motivational tool.

Kinetics and kinematics

An eight-camera, three-dimensional (3D) optoelectronic camera system (Oqus, Qualisys, AB, Sweden) was used to collect motion-capture data. Reflective markers were placed on the body for static and dynamic measures. Markers were placed on both legs at the distal phalanx of the first toe, metatarsal phalangeal joints 1 and 5, calcaneus, medial and lateral malleolus of the ankle, medial and lateral joint centre of rotation of the knee, left and right anterior superior iliac spine and posterior superior iliac spine, coccyx, vertebrae C7, suprasternal notch of the manubrium and on the acromion process of the left and right shoulders. Clusters of four markers on rigid plates were placed on the lateral side of the shank and thigh of each leg midway between the joints using Velcro straps. During all trials, marker position data was sampled at 200 Hz.

Ground reaction force data were recorded from two force plates located within an instrumented treadmill (Instrumented Tandem Treadmill, AMTI, MA, USA) with one foot placed on each force plate. Jump height and countermovement depths were calculated live using a custom-written LabVIEW script (National Instruments Corporation, Austin, TX, USA) from ground reaction force data sampled at 1000 Hz, using calculations described by Vanrenterghem et al. (2001). LabVIEW and Qualisys Track Manager (QTM) software (Qualisys, Gothenburg, Sweden) recorded the ground reaction force data via AMTI force plate amplifiers (AMTI Gen 5, AMTI, MA, USA). Data recorded in QTM was sampled at 2000 Hz for subsequent offline analysis.

Using QTM, markers were labelled for each trial and kinetic and kinematic data were exported to OpenSim. A generic OpenSim model, previously described by Hamner et al. (2010), was modified to remove the upper arms, forearms and hands with their masses added to the head and trunk segment and the cervical joint locked. Model segment lengths were scaled to the dimensions of the participant's segments using static calibration trials. In static trials, the participants assumed the quiet standing position prior to each jump while marker positions were recorded. A scale factor was generated based on the difference between the model and participant segment lengths, keeping the distribution of segment masses the same as for the generic model. Using OpenSim, an inverse kinematics analysis was completed using a weighted least-squares fit of the model markers to the experimental markers (Delp et al., 2007). Inverse kinematic joint angles were then combined with ground reaction force data in an inverse dynamics solution to calculate joint moments. The timing of maximal moment about the ankle joint was then identified using a custom-written Matlab script (MathWorks, Natick, MA, USA). Inverse kinematics and inverse dynamics data were filtered using a second-order two-way Butterworth low-pass filter (25 Hz). A common filter cut-off frequency of 25 Hz was used to account for the rapid changes in force during jumping, and to reduce inconsistencies between kinetic and kinematic data (Van Den Bogert and De Koning, 1996; Kristianslund et al., 2012).

Electromyography (EMG)

EMG data were collected from the soleus and lateral gastrocnemius using a wireless EMG system (MYON m320, MYON, Schwarzenberg, Switzerland). Bipolar EMG electrodes were placed over the belly of each muscle according to the SENIAM guidelines (Hermens et al., 1999). Raw EMG data were recorded in QTM at 2000 Hz. EMG signals were bandpass filtered (30–350 Hz), rectified and averaged using a rolling root-mean-squared (RMS) calculation over windows of 100 consecutive frames (50 ms). EMG data were normalised against the maximum values recorded in the low work output condition, as this condition was shared by the two paradigms.

Muscle mechanics

Muscle fascicles were imaged using a 96-element flathead ultrasound transducer (LZ 7.5/60/96Z, Telemed, Vilnius, Lithuania) placed over the lateral gastrocnemius (LG) and soleus (SOL) muscle bellies, enabling imaging of both muscles (as per Farris and Raiteri, 2017). Using ultrasound gel applied to the transducer surface, a suitable image location was found and then the probe was fixed to the participant using a self-adhesive bandage. Ultrasound data were recorded at 80 Hz and fascicle lengths were tracked using UltraTrack software (Farris and Lichtwark, 2016). Manual corrections were made when the tracking software was unable to correctly track fascicle length changes because of fast movement of the fascicles or large increases in pennation angle. The researcher tracking the fascicles was blind to the conditions so as not to introduce bias.

Data reduction and statistical analysis

Because of participant-specific low image quality, ultrasound data for three participants were excluded, resulting in N=13 for both LG and SOL muscle mechanics. EMG data of the LG for one participant were faulty and were therefore excluded, resulting in N=15 for this muscle. All variables previously outlined were statistically analysed over the period from maximum fascicle length until peak ankle moment. This represents the period from the start of muscle shortening until peak muscular force, beyond which force declines and force output is probably dominated by recoil of the tendon (Moo et al., 2017). Thus, we investigated how changes in muscle mechanics enable this peak force to be generated. All

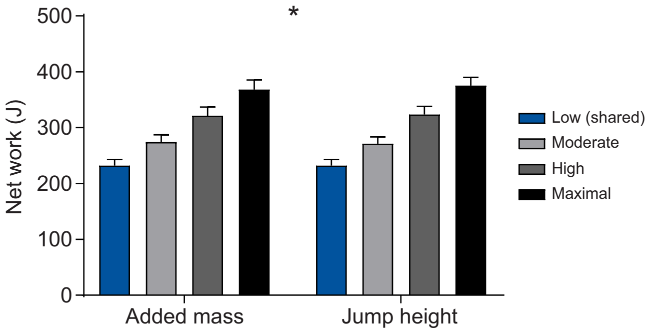

Fig. 2. Group mean (±s.e.m.) total net work output for each condition within each paradigm. Colours indicate matched total net work between paradigms. *Significant effect of increasing net work.

dispersion measures reported in the text and figures are means± s.e.m. except for participant descriptive statistics. Statistical analysis was performed in GraphPad Prism 7 software (GraphPad Software Inc., San Diego, CA, USA) using two-way repeated-measures ANOVA. Main effects of net work output, paradigm and their interaction were reported. A Benjamini and Hochberg (1995) false discovery rate (5%) approach was applied to account for multiple hypothesis testing. This correction resulted in the threshold for significant *P*-values decreasing from 0.05 to 0.021. Raw *P*-values are reported but only *P*-values below the adjusted threshold were considered significant. Statistical significance of net work indicated that the outcome variable changed as net work was increased. A significant effect of paradigm indicated that the outcome variable was of a different magnitude in the added mass paradigm compared with that in the jump height paradigm. A significant interaction effect indicated that differences between paradigms changed as mass was added.

RESULTS

Total work output

This study successfully matched incremental increases in total net work output produced by either adding mass or increasing jump height (Fig. 2). There was no statistical effect on total net work of paradigm (*P*=0.72) or interaction (*P*=0.491). Therefore, direct comparisons can be made between paradigms.

EMG

Mean EMG time series data of LG and SOL muscles (Fig. 3) demonstrated the temporal shift that was present when jumping under the added mass paradigm. Differences in time to perform the movement between paradigms increased as total matched net work increased, until maximal jumping in the added mass paradigm was 178±77 ms longer than maximal jumping in the jump height paradigm. There was a significant main effect of net work output on maximal EMG (Fig. 3) amplitude in both muscles (*P*<0.001), but no statistically significant main effect of paradigm for either LG (*P*=0.71) or SOL (*P*=0.972), paired with no interaction effect (LG, *P*=0.0942; SOL, *P*=0.3176). Therefore, maximal muscle activation

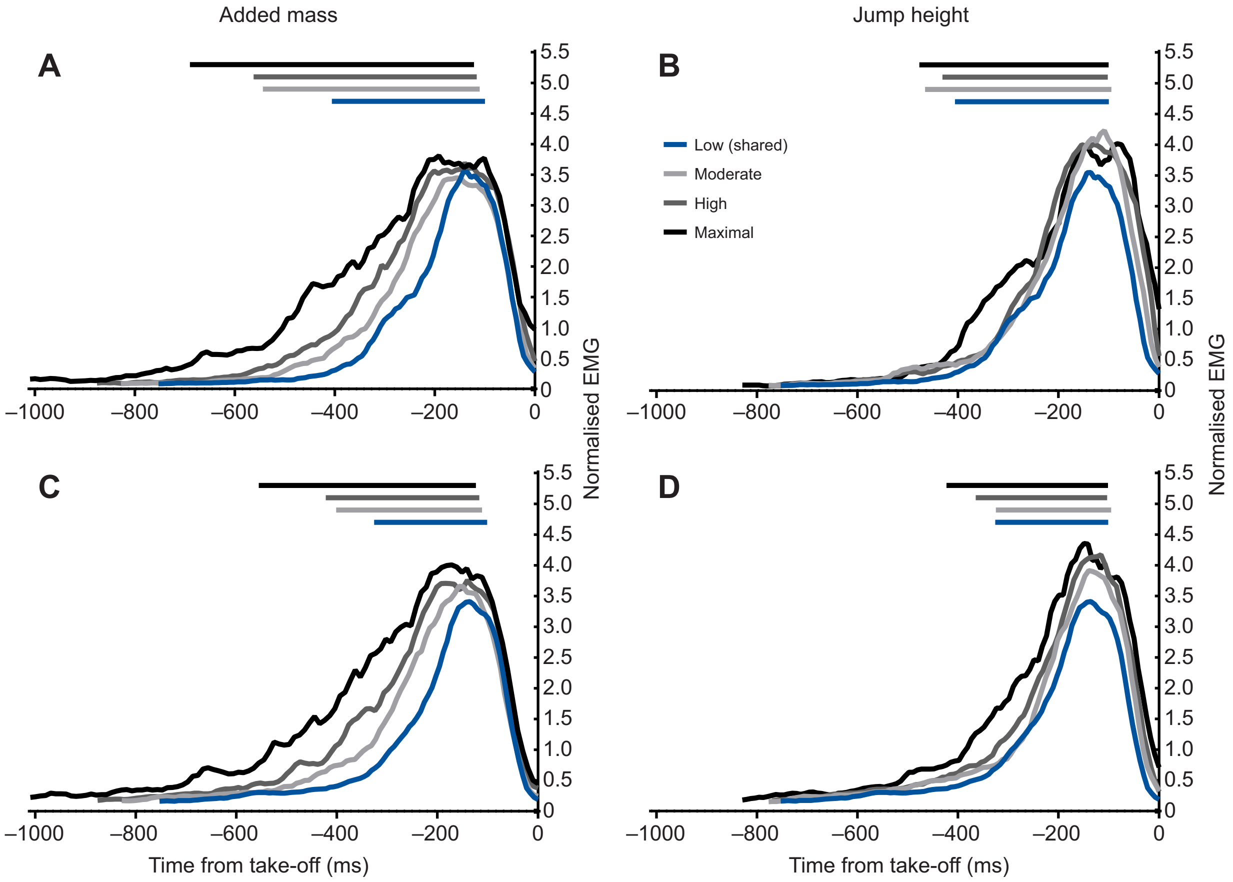

Fig. 3. Group mean processed EMG time series data for each paradigm. Data are from the lateral gastrocnemius (LG; A,B) and soleus (SOL; C,D) muscles under the added mass (A,C) and jump height (B,D) paradigms. Time zero is the point of take-off. Bars above EMG data indicate the period from maximum fascicle length for the LG and SOL, respectively, until the peak ankle moment. EMG was normalised to mean EMG of the low work condition.

increased as net work was increased but there was no difference in maximal muscle activation between the two paradigms (Fig. 3).

Mean integrated EMG (Fig. 4) displayed significant main effects of net work output, paradigm and their interaction for both muscles ($P<0.001$). Therefore, as net work in both paradigms increased, so did activation time; however, added mass on average reported longer activation times than normal jumping and this difference increased as mass was added. Mean EMG amplitude of both the LG and SOL reported no significant effect of net work (LG, $P=0.363$; SOL, $P=0.495$), paradigm (LG, $P=0.465$; SOL, $P=0.043$) or their interaction (LG, $P=0.1657$; SOL, $P=0.615$) and therefore average EMG amplitude was not significantly different between paradigms. These results suggest that mean muscle activation in both muscles was not significantly different between paradigms, while integrated EMG indicates that the period of activation was significantly longer in the added mass paradigm.

Muscle mechanics

Mean fascicle length change in the LG (Fig. 5A) was not significantly affected by increasing net work ($P=0.581$) or paradigm ($P=0.959$) and reported no interaction effect ($P=0.983$). Mean fascicle length change in the SOL (Fig. 5B) was not affected by increasing net work ($P=0.086$) or paradigm ($P=0.04$); however, there was an interaction effect as mass was added ($P=0.004$). Therefore, greater fascicle length change was only evident in the SOL and only with increasing work as mass was added (Fig. 5B). Mean fascicle shortening velocity in the LG (Fig. 5C) was significantly affected by net work ($P=0.005$), demonstrating slower velocities as net work was increased; however, this was not evident in the SOL ($P=0.075$, Fig. 5D). Mean fascicle velocity in both muscles (Fig. 5C,D) was significantly affected by paradigm (LG, $P=0.017$; SOL, $P=0.006$), demonstrating slower shortening velocities on average with added mass, and in the LG (Fig. 5C) this difference increased as mass was added (LG, $P=0.004$; SOL, $P=0.074$). Table S1 shows fascicle length time series data, muscle–tendon unit length times series data, EMG time series data and time stamps for every condition, normalised to 101 points, for each participant.

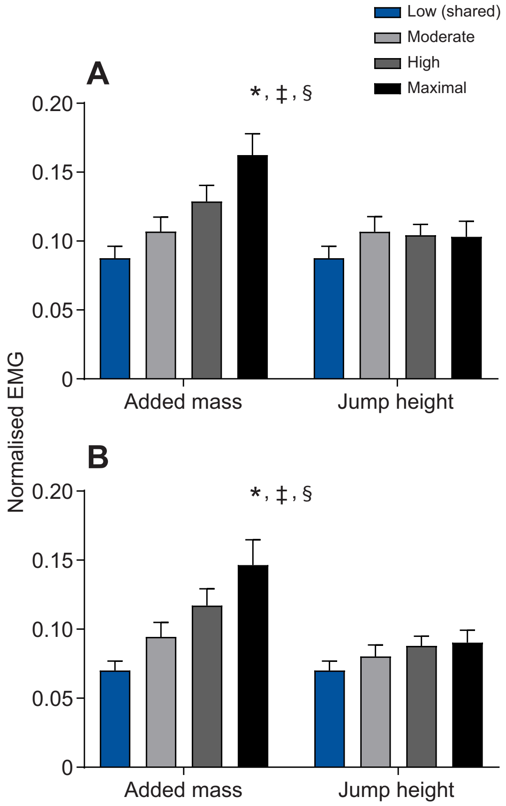

Fig. 4. Group mean (±s.e.m.) integrated EMG data from maximal fascicle length until peak ankle moment. Data are from the LG (A) and SOL (B). *Significant effect of net work; ‡significant effect of paradigm; §significant interaction effect.

DISCUSSION

This study aimed to link the increased net work output observed for human plantar flexors when jumping with added mass to the underlying muscle mechanics *in vivo*. We predicted that added mass would facilitate greater force and net work production by the plantar flexor muscles as a product of slower fascicle shortening velocity, which was supported by our observations. Additional net work produced about the ankle with added mass could have been achieved through either a greater muscle force output or greater fascicle shortening, or a combination of the two. No difference was found in fascicle shortening of the LG between paradigms (Fig. 5A) and therefore any additional positive work produced by the LG must be due to increased force production alone. While there was no difference in SOL fascicle length change as total net work increased or between paradigms, there was an interaction effect, suggesting that increasing work output with added mass was associated with greater fascicle shortening compared with normal jumping (Fig. 5B). Additional work about the ankle in the added mass paradigm reported previously (Wade et al., 2018) was therefore due, in part, to greater SOL contractile element shortening.

The LG and SOL demonstrated slower average shortening velocities with added mass (Fig. 5C,D), indicating a greater capacity for force generation, according to the muscle force–velocity relationship (Fenn and Marsh, 1935; Huxley, 1985). Additionally, this discrepancy between paradigms increased in the LG with increasing work levels, suggesting better muscle contractile conditions for force production as mass was added (Fig. 5C,D). As mentioned previously, jumping must be carefully controlled so that maximal force is produced while maintaining contact with the ground for as long as possible. In order to accelerate the centre of mass and increase momentum, there is a need to generate impulse (Hill, 1950; Marsh, 1994). Impulse may be increased by producing a greater force, increasing the duration of force production, or both. In sub-maximal movements, impulse may be generated by multiple coordination patterns, while at maximal efforts there will only be a single coordination pattern possible. Integrated EMG was significantly increased under the added mass paradigm compared with the jump height paradigm (Fig. 4). This was a function of increased time to perform the movement and was not due to increased motor-unit recruitment, as maximal and mean EMG (Fig. 3) were not significantly different between paradigms. Therefore, a slower fascicle shortening velocity combined with a longer muscle activation time in the added mass paradigm enables a greater force production to be maintained over an extended period, increasing impulse and generating greater net work about the ankle joint. Because of the increased time to perform the movement with added mass, a reduced contractile velocity would probably be expected to some degree across all lower limb joint muscles. However, with added mass, a compliant tendon enables muscle to produce a greater force for more of the contractile period compared with stiffer tendons (Robertson et al., 2018). Therefore, it appears that the maintenance of an ankle-centred strategy with added mass,

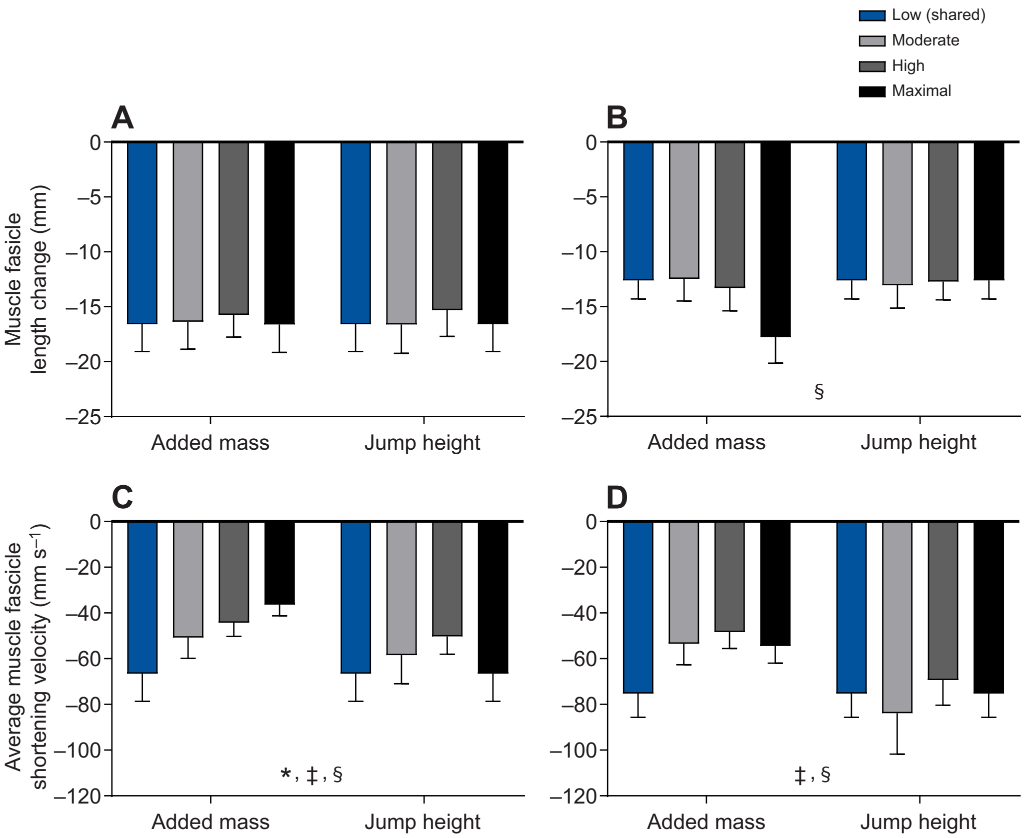

Fig. 5. Group mean (±s.e.m.) fascicle length change and shortening velocity. (A,C) Lateral gastrocnemius and (B,D) soleus data for fascicle length change (A,B) and shortening velocity (C,D). Data were averaged from maximal fascicle length until peak ankle moment. Negative values indicate increased shortening length and speed. *Significant effect of net work; ‡significant effect of paradigm; §significant interaction effect.

found in our previous study (Wade et al., 2018), was probably due to the highly compliant Achilles tendon further improving the operating position on the force–velocity curve, which may not be possible or may occur to a lesser degree in the hip and the knee. The current results are in line with previous theoretical research by Galantis and Woledge (2003) indicating that a compliant tendon facilitates decreased fascicle shortening velocity and increased time to perform the movement, as a result of increased inertial resistance due to added mass. Furthermore, an increase in muscle force due to slower shortening velocities will result in additional energy stored and released from the Achilles tendon based on the elastic force–strain relationship (Lichtwark and Wilson, 2005). This is supported by our previous study where we found an increase in peak Achilles tendon force in the added mass paradigm while it did not change significantly in the jump height paradigm (Wade et al., 2018). The increased time to perform the movement due to added mass is key to enabling humans to maintain reliance on power generated at the ankle during jumping, as we observed previously (Wade et al. (2018). All three joints are going to have an improved operating position on the force–velocity relationship, due to a slower movement, and therefore we see greater positive work done at all three joints. However, it is the compliant Achilles tendon, which further increases this ability to perform work and increase force with a greater mass, that enables us to maintain such a high ankle-centred strategy compared with normal jumping

Increasing time to perform jumping has been examined using jumping simulations with altered countermovement depth, revealing that a deeper countermovement facilitates longer movement time (Domire and Challis, 2007). Therefore, a deeper countermovement depth may result in a greater impulse and jump height, although this has not been replicated in experimental studies (Domire and Challis, 2007; Mandic et al., 2015). In the current study, increasing time to perform the movement was key to enabling additional net work about the ankle joint; however, without the additional inertial resistance facilitating the reduced velocity of plantar flexor fascicles, it is unlikely that an increase in force could have been attained. In order to estimate the potential effect of velocity changes on force output as a result of decreased shortening velocity, we compared mean fascicle velocities (Fig. 5C,D) with the force–velocity relationship presented in Lichtwark and Wilson (2007). Using a resting length (L_0) of 55 mm (taken from Lichtwark and Wilson, 2007), we identified that during the maximal added mass condition, the LG velocity was 0.66 L_0 s^{-1} and thus the maximum possible force producible would be approximately 88% of maximum isometric force. In the maximal jump height condition, the LG shortening velocity was 1.21 L_0 s^{-1} and thus a maximally active LG could only have produced approximately 63% of maximal isometric force. Using a L_0 of 44 mm (Ward et al., 2009), we identified that during the maximal added mass condition the SOL velocity was 1.24 L_0 s^{-1} and thus the maximum possible force producible would be approximately 64% of maximum isometric force. In the maximal jump height condition, the SOL shortening velocity was 1.71 L_0 s^{-1} and thus the maximum possible force that could be produced would be approximately 52% of maximum isometric force. This suggests that added mass facilitates a significant increase in the force-producing capabilities of the LG and SOL fascicles as a result of decreased contractile velocity. Furthermore, in our previous study we identified a continued reliance on ankle musculature as mass was added, compared with increased reliance on hip and knee musculature as jump height was increased (Wade et al., 2018). It appears that apart from high energy storage and return, the compliant Achilles tendon also facilitates improved muscle contractile mechanics with increased load. This potentially allows for a consistently higher force to be produced over more of the contractile phase, facilitating a greater impulse and net work about the ankle joint compared with normal jumping matched for the same total net work. During jumping with additional mass, this mechanism enables human jumpers to maintain an ankle-centred strategy for producing work instead of switching to a hip- or knee-centred strategy as was found previously (Wade et al., 2018).

Explosive movements such as jumping have been characterised as those performed faster than is possible to execute complex feedback (Van Soest and Bobbert, 1993). Previous research has demonstrated that muscle contractile properties also act to correct perturbations immediately, with the force–velocity relationship resisting dynamic perturbations and the force–length relationship resisting static perturbations (Van Soest and Bobbert, 1993; Gerritsen et al., 1998). The added mass task constraint must be overcome during dynamic tasks and therefore our current research supports the previous literature, also finding intrinsic fascicle force–velocity properties minimise the need for adjustments to neural drive between paradigms (Gerritsen et al., 1998; Bobbert et al., 2008). The coordination strategy employed to increase work with added mass produces the required impulse by increasing both force production and the time to perform the movement compared with the normal jumping paradigm. This occurs with only an increase in muscle activation time as muscle force production naturally shifts leftward on its concentric force–velocity curve (i.e. slower shortening velocity and greater active force). During sub-maximal jumping with added mass, an alternative strategy to achieve the same impulse could be to increase muscle activation, producing an even greater force over a shorter period of time. However, this would probably result in increased energy expenditure (Praagman et al., 2003; Carrier et al., 2011), which may be one of the main reasons that sub-maximal jumping with added mass is not performed in this manner (Vanrenterghem et al., 2004). Crucially, this enables sub-maximal and maximal jumping movements with added mass to employ very similar coordination patterns to normal preferred movements, adapting the muscle activation period to account for the movement being performed at a slower speed and allowing muscle contractile mechanics to be responsible for increasing force. This may allow various movements with added mass to be performed using very similar coordination patterns and may reduce the complexity of motor control. A joint- and muscle-level analysis is required for a range of movements such as walking and running to examine whether the coordination strategies found in this paper are transferable to other movements. We believe the maintained ankle-centred strategy found in our previous paper (Wade et al., 2018) was primarily the result of the highly elastic Achilles tendon facilitating more favourable contractile velocities for the plantar flexors. Therefore, the influence of added mass on movement strategies is consistent with the idea that humans will favour producing work via muscles with improved muscle contractile conditions.

Conclusion

To comprehend the control of human movement we must understand the contribution of different muscles and how coordination among these muscles is adapted to achieve task demands. We have shown that the interaction of added mass and muscle contractile mechanics plays an important role in how force and work are generated. Added mass during jumping provides an increased resistance against which the body is able to increase force production and mechanical work without resulting in an early take-off. Our previous work showed that the additional work done against the mass relies more on ankle plantar flexion work than does jumping without the mass (Wade et al., 2018). The current findings indicate that muscle activation was not required to change in order to increase the ankle plantar flexor contribution with added mass. Instead, a naturally occurring leftward shift of the fascicle shortening speed on the intrinsic force–velocity relationship in the LG and SOL muscles served to increase force production. This resulted in a slower movement, which was accommodated by a longer muscle activation, ultimately enabling a greater impulse and net work about the ankle joint compared with normal jumping. Future analysis of alternative locomotor tasks performed with added mass are required to examine whether shifts in fascicle operating speeds in the force–velocity relationship will facilitate adaptation to the additional task constraints, reducing the need for higher level control.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: L.W., G.A.L., D.J.F.; Methodology: L.W., G.A.L., D.J.F.; Software: L.W., G.A.L., D.J.F.; Validation: L.W.; Formal analysis: L.W.; Investigation: L.W.; Data curation: L.W.; Writing - original draft: L.W.; Writing - review & editing: L.W., G.A.L., D.J.F.; Visualization: L.W.; Supervision: G.A.L., D.J.F.

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Supplementary information

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References

Astley, H. C. and Roberts, T. J. (2011). Evidence for a vertebrate catapult: elastic energy storage in the plantaris tendon during frog jumping. *Biol. Lett.* **8**, 386-389.

Astley, H. C. and Roberts, T. J. (2014). The mechanics of elastic loading and recoil in anuran jumping. *J. Exp. Biol.* **217**, 4372-4378.

Benjamini, Y. and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Series B* **57**, 289-300.

Bobbert, M. F. and Van Soest, A. J. (2001). Why do people jump the way they do? *Exerc. Sport Sci. Rev.* **29**, 95-102.

Bobbert, M. F., Casius, L. J. R., Sijpkens, I. W. T. and Jaspers, R. T. (2008). Humans adjust control to initial squat depth in vertical squat jumping. *J. Appl. Physiol.* **105**, 1428-1440.

Burkholder, T. J. and Lieber, R. L. (2001). Sarcomere length operating range of vertebrate muscles during movement. *J. Exp. Biol.* **204**, 1529-1536.

Carrier, D. R., Anders, C. and Schilling, N. (2011). The musculoskeletal system of humans is not tuned to maximize the economy of locomotion. *Proc. Natl Acad. Sci. USA* **108**, 18631-18636.

Delp, S. L., Anderson, F. C., Arnold, A. S., Loan, P., Habib, A., John, C. T., Guendelman, E. and Thelen, D. G. (2007). Opensim: open-source software to create and analyze dynamic simulations of movement. *IEEE Trans. Biomed. Eng.* **54**, 1940-1950.

Domire, Z. J. and Challis, J. H. (2007). The influence of squat depth on maximal vertical jump performance. *J. Sports Sci.* **25**, 193-200.

Farina, D., Merletti, R. and Enoka, R. M. (2004). The extraction of neural strategies from the surface emg. *J. Appl. Physiol.* **96**, 1486-1495.

Farris, D. J. and Lichtwark, G. A. (2016). Ultratrack: software for semi-automated tracking of muscle fascicles in sequences of b-mode ultrasound images. *Comput. Methods Programs Biomed.* **128**, 111-118.

Farris, D. J. and Raiteri, B. J. (2017). Elastic ankle muscle–tendon interactions are adjusted to produce acceleration during walking in humans. *J. Exp. Biol.* **220**, 4252-4260.

Fenn, W. O. and Marsh, B. S. (1935). Muscular force at different speeds of shortening. *J. Physiol.* **85**, 277-297.

Fukashiro, S., Kurokawa, S., Hay, D. C. and Nagano, A. (2005). Comparison of muscle-tendon interaction of human m. Gastrocnemius between ankle- and drop-jumping. *Int. J. Sport Health Sci.* **3**, 253-263.

Galantis, A. and Woledge, R. C. (2003). The theoretical limits to the power output of a muscle–tendon complex with inertial and gravitational loads. *Proc. R. Soc. Lond. Series B Biol. Sci.* **270**, 1493-1498.

Gerritsen, K. G. M., Van Den Bogert, A. J., Hulliger, M. and Zernicke, R. F. (1998). Intrinsic muscle properties facilitate locomotor control—a computer simulation study. *Motor Control* **2**, 206-220.

Gordon, A. M., Huxley, A. F. and Julian, F. J. (1966). The variation in isometric tension with sarcomere length in vertebrate muscle fibres. *J. Physiol.* **184**, 170-192.

Griffiths, R. I. (1991). Shortening of muscle fibres during stretch of the active cat medial gastrocnemius muscle: the role of tendon compliance. *J. Physiol.* **436**, 219-236.

Hamner, S. R., Seth, A. and Delp, S. L. (2010). Muscle contributions to propulsion and support during running. *J. Biomech.* **43**, 2709-2716.

Hartree, W. and Hill, A. V. (1928). The factors determining the maximum work and the mechanical efficiency of muscle. *Proc. R. Soc. Lond. Series B* **103**, 234-251.

Henneman, E., Clamann, H. P., Gillies, J. D. and Skinner, R. D. (1974). Rank order of motoneurons within a pool: Law of combination. *J. Neurophysiol.* **37**, 1338-1349.

Hermens, H. J., Freriks, B., Merletti, R., Stegeman, D., Blok, J., Rau, G., Disselhorst-Klug, C. and Hägg, G. (1999). European recommendations for surface electromyography. *Roessingh Research and Development* **8**, 13-54.

Hill, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. B* **126**, 136-195.

Hill, A. V. (1950). The dimensions of animals and their muscular dynamics. *Sci. Prog.* **38**, 209-230.

Huxley, H. E. (1985). The crossbridge mechanism of muscular contraction and its implications. *J. Exp. Biol.* **115**, 17-30.

Kristianslund, E., Krosshaug, T. and Van Den Bogert, A. J. (2012). Effect of low pass filtering on joint moments from inverse dynamics: Implications for injury prevention. *J. Biomech.* **45**, 666-671.

Kurokawa, S., Fukunaga, T. and Fukashiro, S. (2001). Behavior of fascicles and tendinous structures of human gastrocnemius during vertical jumping. *J. Appl. Physiol.* **90**, 1349-1358.

Kurokawa, S., Fukunaga, T., Nagano, A. and Fukashiro, S. (2003). Interaction between fascicles and tendinous structures during counter movement jumping investigated in vivo. *J. Appl. Physiol.* **95**, 2306-2314.

Lichtwark, G. A. and Wilson, A. M. (2005). In vivo mechanical properties of the human achilles tendon during one-legged hopping. *J. Exp. Biol.* **208**, 4715-4725.

Lichtwark, G. A. and Wilson, A. M. (2007). Is Achilles tendon compliance optimised for maximum muscle efficiency during locomotion? *J. Biomech.* **40**, 1768-1775.

Lichtwark, G. A., Bougoulias, K. and Wilson, A. M. (2007). Muscle fascicle and series elastic element length changes along the length of the human gastrocnemius during walking and running. *J. Biomech.* **40**, 157-164.

Lutz, G. J. and Rome, L. C. (1996). Muscle function during jumping in frogs. I. Sarcomere length change, emg pattern, and jumping performance. *Am. J. Physiol. Cell Physiol.* **271**, C563-C570.

Mandic, R., Jakovljevic, S. and Jaric, S. (2015). Effects of countermovement depth on kinematic and kinetic patterns of maximum vertical jumps. *J. Electromyogr. Kinesiol.* **25**, 265-272.

Marsh, R. (1994). Jumping ability of anuran amphibians. *Adv. Vet. Sci. Comp. Med.* **38**, 51.

Moo, E. K., Peterson, D. R., Leonard, T. R., Kaya, M. and Herzog, W. (2017). In vivo muscle force and muscle power during near-maximal frog jumps. *PLoS ONE* **12**, e0173415.

Praagman, M., Veeger, H. E. J., Chadwick, E. K. J., Colier, W. N. J. M. and Van Der Helm, F. C. T. (2003). Muscle oxygen consumption, determined by nirs, in relation to external force and emg. *J. Biomech.* **36**, 905-912.

Roberts, T. J. (2002). The integrated function of muscles and tendons during locomotion. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* **133**, 1087-1099.

Robertson, J. W., Struthers, C. N. and Syme, D. A. (2018). Enhancement of muscle and locomotor performance by a series compliance: a mechanistic simulation study. *PLoS ONE* **13**, e0191828.

Sawicki, G. S., Sheppard, P. and Roberts, T. J. (2015). Power amplification in an isolated muscle–tendon unit is load dependent. *J. Exp. Biol.* **218**, 3700-3709.

Van Den Bogert, A. and De Koning, J. (1996). On optimal filtering for inverse dynamics analysis. Proceedings of the IXth Biennial Conference of the Canadian Society for Biomechanics, Vancouver, pp. 214-215.

Vanrenterghem, J., De Clercq, D. and Van Cleven, P. (2001). Necessary precautions in measuring correct vertical jumping height by means of force plate measurements. *Ergonomics* **44**, 814-818.

Vanrenterghem, J., Lees, A., Lenoir, M., Aerts, P. and De Clercq, D. (2004). Performing the vertical jump: Movement adaptations for submaximal jumping. *Hum. Mov. Sci.* **22**, 713-727.

Van Soest, A. and Bobbert, M. (1993). The contribution of muscle properties in the control of explosive movements. *Biol. Cybern.* **69**, 195-204.

Van Zandwijk, J. P., Bobbert, M. F., Munneke, M. and Pas, P. (2000). Control of maximal and submaximal vertical jumps. *Med. Sci. Sports Exerc.* **32**, 477-485.

Wade, L., Lichtwark, G. and Farris, D. J. (2018). Movement strategies for countermovement jumping are potentially influenced by elastic energy stored and released from tendons. *Sci. Rep.* **8**, 2300.

Ward, S., Eng, C., Smallwood, L. and Lieber, R. (2009). Are current measurements of lower extremity muscle architecture accurate? *Clin. Orthop. Relat. Res.* **467**, 1074-1082.