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Medial gastrocnemius muscle fascicles shorten throughout stance during sprint acceleration

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The compliant nature of distal limb muscle-tendon units is traditionally considered suboptimal in explosive movements when positive joint work is required. However, during accelerative running, ankle joint net mechanical work is positive. Therefore, this study aims to investigate how plantar flexor muscle-tendon behavior is modulated during fast accelerations. Eleven female sprinters performed maximum sprint accelerations from starting blocks, while gastrocnemius muscle fascicle lengths were estimated using ultrasonography. We combined motion analysis and ground reaction force measurements to assess lower limb joint kinematics and kinetics, and to estimate gastrocnemius muscle-tendon unit length during the first two acceleration steps. Outcome variables were resampled to the stance phase and averaged across three to five trials. Relevant scalars were extracted and analyzed using one-sample and two-sample t-tests, and vector trajectories were compared using statistical parametric mapping. We found that an uncoupling of muscle fascicle behavior from muscle-tendon unit behavior is effectively used to produce net positive mechanical work at the joint during maximum sprint acceleration. Muscle fascicles shortened throughout the first and second steps, while shortening occurred earlier during the first step, where negative joint work was lower compared with the second step. Elastic strain energy may be stored during dorsiflexion after touchdown since fascicles did not lengthen at the same time to dissipate energy. Thus, net positive work generation is accommodated by the reuse of elastic strain energy along with positive gastrocnemius fascicle work. Our results show a mechanism of how muscles with high in-series compliance can contribute to net positive joint work.

KEYWORDS
locomotion, muscle mechanics, running, sprint start, ultrasonography

1 | INTRODUCTION

During acceleration movements, humans and animals aim to increase the velocity of the body. Hence, joints and ultimately muscle-tendon units (MTUs) are required to produce net positive mechanical work to accelerate the body,[1] which requires active shortening of skeletal muscle. The ability to accelerate quickly can be critical for animals to capture prey or to avoid predation. For modern humans, fast acceleration is mainly important in sports, particularly in sprint running, where a high horizontal force impulse in a short time [2] is essential to build high horizontal velocity.[3] Thus, during acceleration, it

is critical to generate mechanical work quickly and to retain existing energy (ie, avoid energy dissipation).

During movements requiring either high power production or power conservation, such as vertical jumping or running, animal and human studies have shown a distinct interaction of muscle and elastic tissue to optimize function.[4] Series elastic compliance in the MTU allows decoupling of muscle fiber length changes from joint movement (ie, MTU length changes), enabling muscles to operate at lengths and shortening velocities that maximize power output.[4] During vertical jumping, power can be amplified to accelerate the body by slowly storing muscle work in tendinous tissue and releasing it rapidly,[5] and during running, compliance of the elastic tissue allows the MTU to recycle elastic energy.[6] Both mechanisms (power amplification and power conservation) have been shown in vivo in the human triceps surae muscle group, that is, gastrocnemius medialis and soleus.[7-9]

The gastrocnemius medialis muscle is known for its high pennation angle, short muscle fibers, and long viscoelastic Achilles tendon favoring a spring-like function (ie, elastic energy savings). Although MTU architecture varies between these muscles, their characteristics compared with other muscles are traditionally not considered optimal for generating positive net work, for which long fascicles and a stiff tendon would be expected.[10] Nevertheless, plantar flexor muscles can amplify power, for example, during jumping.[8] It is also known that plantar flexors are a major contributor to body propulsion during sprint running[11] and analyses of ankle joint kinetics have shown positive net work during running acceleration.[12,13] Interestingly, despite the large amount of positive joint work generated during the ground contact phase of accelerative sprinting, the phase immediately after touchdown is characterized by negative work at the ankle joint.[12] This negative work may result from the compliance of the plantar flexor muscles, although a stiff system would be expected to generate net positive work. Before the advent of in vivo methods of measuring muscle behavior, Jacobs and van Ingen Schenau[13] speculated that plantar flexor muscles work eccentrically after touchdown due to ankle dorsiflexion, which can now be investigated using ultrasonography.

Animal studies were the first to suggest that plantar flexor muscle fascicles cannot only function as effective struts (ie, generate force with minimal length change) but may also work as power-generating motors that effectively perform net positive mechanical work during acceleration.[14] In humans, Farris and Raiteri[15] have elegantly shown how plantar flexor muscles can contribute to net positive work in accelerative walking. They confirmed their hypothesis that biarticular muscles produce more positive work by shortening more during MTU stretch in accelerative walking compared with constant-speed walking. Simulations of sprint accelerations[16] showed a similar link between greater fascicle work and body acceleration. In this study, Lai and colleagues also showed that the work at the gastrocnemius medialis MTU increased

with progressing acceleration.[16] Collectively, these prior studies suggest that plantar flexor muscles can be effective contributors to positive work production during accelerative sprinting that may depend on the progress of the acceleration; however, the mechanisms have not been studied in vivo during sprint acceleration.

Therefore, this study aimed to estimate gastrocnemius medialis MTU and fascicle behavior during rapid acceleration to provide insight into net positive work generation of MTUs with high in-series compliance. Typically, sprint acceleration requires positive net work at the ankle joint, while the body has already gained kinetic energy from the forces applied during block clearance.[17] Hence, we measured human gastrocnemius medialis fascicle and MTU behavior during the first two steps of a sprint start in female sprinters. We hypothesized an uncoupling of gastrocnemius muscle fascicle and MTU length changes: While the MTU undergoes a stretch-shortening pattern, fascicles shorten throughout the stance phase to permit positive work production. As a secondary hypothesis, we predicted less fascicle shortening during MTU stretch of the second step compared with the first step because more kinetic energy can be reused, and the body accelerates less as its velocity increases.

2 | MATERIALS AND METHODS

2.1 | Subjects and experimental protocol

Eleven female sprinters (age: 22 ± 1.8 years; height: 172.6 ± 4.4 cm, body mass: 61.7 ± 5.5 kg) participated in the study. All subjects were experienced sprinters competing at the national level in Germany in sprint events or the heptathlon (100 m personal best times: 12.66 ± 0.49 s) and were free of neuromuscular and musculoskeletal impairments. The protocol was approved by the ethical committee of the German Sport University Cologne, and all subjects provided written informed consent to participate in the study.

After completing their pre-competition warm-up program, each subject performed ten starts (over 5 m with maximum effort and enough space to slow down) on a tartan indoor track. During all starts, subjects started from their preferred position and used their individual spiked shoes. The block position was adjusted to ensure that the first two ground contacts occurred on two force plates. All subjects were asked to accelerate as rapidly as possible from the starting blocks, while an ultrasound transducer was attached to their front or rear lower limb for five trials each (Figure 1), and their limb motion was captured. Both legs were measured in random order. We provided the standard starting command from speakers. Between trials, subjects were allowed enough rest to avoid fatigue and ensure they achieved maximum effort during each start.
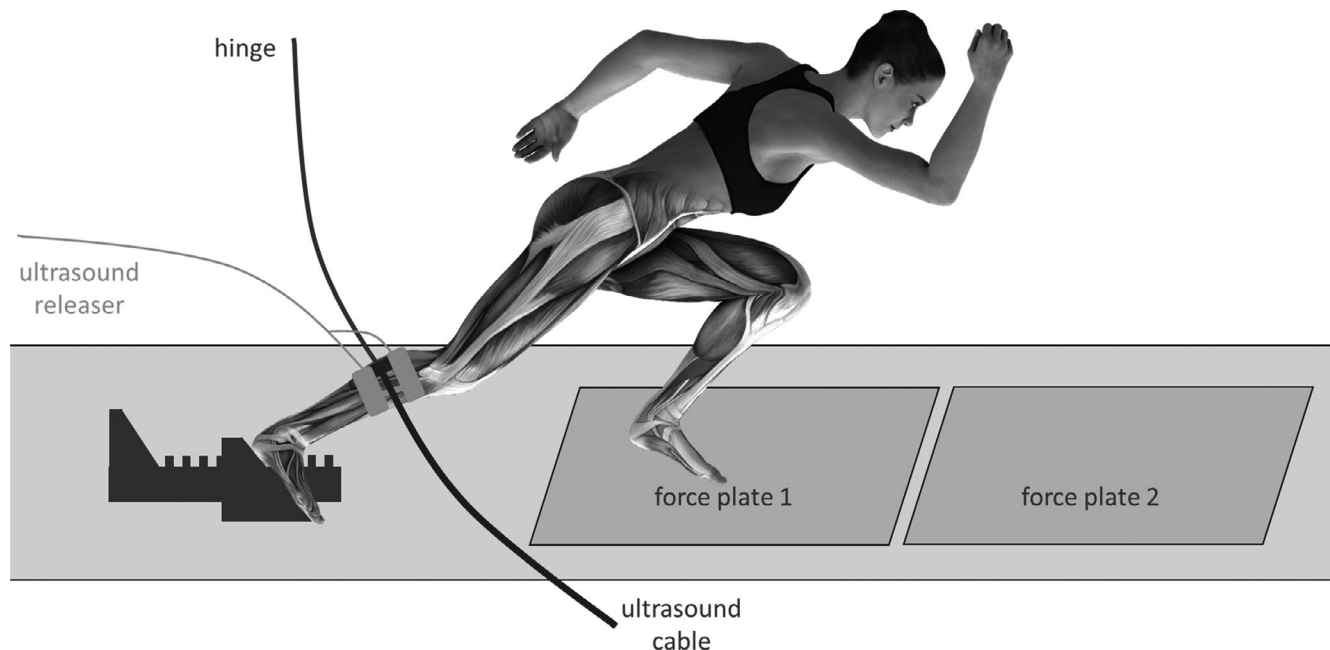
FIGURE 1 Experimental setup with the ultrasound transducer (here attached to the rear leg) to measure gastrocnemius medialis fascicle length during the first two steps of the sprint start. An ultrasound image sequence was recorded simultaneously with GRF and motion capture data (markers are not displayed here for clarity). The length of the "ultrasound releaser" was adjusted so that the transducer was removed after the second step (on force plate two) and caught by the hinge

2.2 | Joint and MTU mechanics

We acquired ground reaction forces of the first and second steps using two force plates embedded in-series in the ground (Kistler, 900 × 600 mm) and sampling at 1 kHz. GRF data were filtered using a low-pass fourth-order recursive digital Butterworth filter (cutoff frequency 100 Hz).

A seventeen-camera motion capture system (Vicon, Oxford) operating at 100 Hz was used to record the three-dimensional position of 45 retro-reflective markers attached to the subject's pelvis and lower limbs. Marker coordinates were filtered using a fourth-order recursive digital Butterworth filter (cutoff frequency: 20 Hz). Marker trajectory data of each body segment were optimized to meet rigid body assumptions better using the method proposed by Søderkvist and Wedin.[18]

3D inverse dynamic calculations were performed on a model consisting of nine segments (pelvis and respective left and right thigh, shank, rearfoot, and forefoot). That process was used to calculate joint angles of the ankle and knee as well as the ankle joint power in the sagittal plane as previously described in detail elsewhere.[19] In brief, regression equations from Seidel and colleagues[20] were used to calculate hip joint centers. The knee joint center was defined as the midpoint between the femoral condyle markers, and the ankle joint center was defined as the midpoint between the malleoli markers for both legs. Body segment parameters were taken from equations of De Leva.[21] In a standing reference measurement, the anatomical coordinate system of each segment

was defined. During the dynamic trials, at least three marker trajectories per segment were used to track segment motion. Joint angles were derived from the rotation matrices describing the rotation of adjacent segments while assuming that the distal segment was moving relative to the proximal. Standard inverse dynamics procedures were applied to calculate lower extremity joint moments.[22] Joint power was calculated as the product of the instantaneous joint moment and angular velocity, and joint work was calculated by integrating the negative and positive joint powers using trapezoidal integration with respect to time. To test whether there were any systematic differences in efforts between the trials measuring the first or second steps, we calculated the change in velocity during the first step of both conditions by dividing the horizontal net impulse by body mass. Finally, instantaneous gastrocnemius medialis MTU length was estimated using a regression equation based on cadaveric data. Input parameters to the equations were individual shank length (defined as distance between the lateral epicondyle and the lateral malleolus) and joint angle data.[23]

2.3 | Muscle fascicle length measurements

Gastrocnemius medialis fascicle length was recorded at 73 Hz using ultrasound imaging [24] (ProSound α-7) performed with a flat-shaped 60-mm-width transducer (13 MHz, UST-5713 T). The transducer was securely fastened over the gastrocnemius muscle at the intersection of the mediolateral

and proximodistal midline. A custom-made elastic bandage with press studs was used to fix the transducer. After the first or second step (depending on which leg was tested), a cord pulled the bandage off and removed the ultrasound to ensure a normal continuation of the acceleration phase (Figure 1). The length of the cord was adjusted before each trial. To avoid damage to the ultrasound transducer due to the release mechanism, the transducer was caught with a hinge before hitting the ground. The position of the ultrasound transducer was marked on the skin during the first trial to ensure similar positioning in all trials.

Fascicle length was measured in each image using semi-automated tracking software [25,26] and defined as the distance between the insertions of the fascicle into the superficial and deep aponeuroses (Figure 2). Fascicle orientation was defined parallel to the main orientation of visible fascicles. Linear extrapolation was used in cases where fascicle length exceeded the image. Manual corrections were made where the tracking algorithm did not track the fascicle length well. We used a rectangular pulse generated by a hand switch through the ECG input of the ultrasound device to time-synchronize the collected ultrasound image sequence with motion capture and force data collected in the Vicon Nexus (1.8.5) software. Fascicle length data were smoothed with a fourth-order recursive Butterworth low-pass filter with a 5 Hz cutoff frequency. Muscle fascicle velocities were calculated as the time derivative of the length using the central difference method.

2.4 | Data reduction and statistics

Data were divided into individual ground contact phases of the respective steps based on ground reaction force data (using a 10 N threshold) and resampled to 101 data points. Individual subject data for all variables were averaged across steps. Trials were excluded from the analysis when the ultrasound transducer was removed before toe-off so that on average 4.3 ($\pm$0.8) and 3.7 ($\pm$0.9) trials were analyzed for the first and second steps, respectively.

Total fascicle length change, mean absolute fascicle length, and mean fascicle velocity from touchdown to toe-off (ie, during ground contact) were calculated for both steps. Fascicle length changes and mean velocities were also calculated separately during MTU lengthening and subsequent MTU shortening to account for energy absorption (negative MTU power) and energy generation (positive MTU power) of the MTU. To assess whether fascicles shorten throughout the stance phase, a one-sample t-test ($\alpha = 0.05$), evaluating whether the sample means were statistically different from zero, was used. A paired t-test ($\alpha = 0.05$) was used to identify differences in fascicle length changes and mean shortening velocities between the first and second steps. Similarly, we analyzed differences between both steps in ground contact duration, change in horizontal center of mass velocity during first ground contact, MTU lengthening, shortening, and velocity, ankle dorsiflexion, and plantar flexion, as well as negative, positive, and net joint work. The statistical analysis was performed in GraphPad Prism (v 8.4.3). The data distributions were assessed using the Shapiro-Wilk normality test.

To compare the continuous time series of joint kinematics and fascicle and MTU length, we used statistical parametric mapping. [27,28] This method uses random field theory to analyze where signals differ by considering the dependency of data at different timepoints of the ground contact phase. We performed one-sample t-tests ($\alpha = 0.05$) to analyze fascicle length change with respect to touchdown in each step using the statistical parametric map (SPM) one-dimensional package in MATLAB (available at www.spm1d.org/). Statistically significant results were indicated when the parametric maps crossed the critical threshold estimated using random field theory. Effect sizes (Cohen's d) were calculated using MATLAB (MathWorks). Thresholds of 0.2, 0.5, and 0.8 were defined as small, moderate, and large effects. [29]
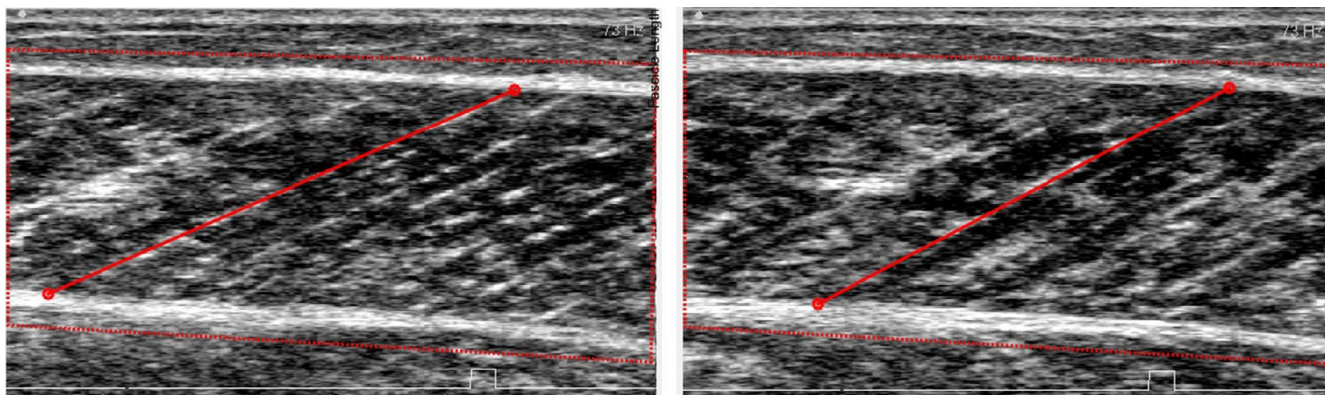

FIGURE 2 Example of an ultrasound image of the gastrocnemius medialis muscle (marked with the red dotted lines) at touchdown and take-off of the first step of a sprint start. Fascicle length (red line) was determined as the straight-line distance between intersecting points of the representative fascicle orientation with the superficial and deep aponeuroses

3 | RESULTS

3.1 | Kinematics and kinetics

The average ground contact duration in the sprint acceleration was 0.20 ($\pm$0.02) s for the first step and 0.17 ($\pm$0.02) s for the second step ($p < 0.01$, $d = 2.64$). Ankle and knee joint kinematics during both steps are presented in Figure 3. During both steps, the ankle joint underwent dorsiflexion during the first half of stance with no statistical difference between steps (17 ± 3 deg and 18 ± 3 deg during the first and second steps, respectively; $p = 0.07$, $d = 0.61$) and subsequently a plantar flexion movement with no statistical difference between steps (45 ± 6 deg and 44 ± 5 deg during the first and second steps, respectively; $p = 0.25$, $d = 0.37$). Comparing joint angles using SPM between both steps revealed no statistical differences for the ankle or knee joint at any time ($p > 0.05$). Ankle joint power was negative after touchdown (until 45 ± 9 and $42 \pm 5\%$ of the first and second stances, respectively) and positive during the rest of the stance phase, whereas net ankle joint work was positive during both steps (Figure 4). Absolute values for negative work at the ankle joint were smaller during the first step compared with the second step (-0.32 ± 0.14 vs. -0.36 ± 0.15 J kg^{-1}; $p = 0.04$, $d = 0.72$). Positive work at the ankle joint was not statistically different between steps (1.58 ± 0.17 vs. 1.61 ± 0.18 J kg^{-1}; $p = 0.56$, $d = -0.18$). Similarly, net work at the ankle joint did not differ statistically between steps (1.26 ± 0.13 vs. 1.25 ± 0.12 J kg^{-1}; $p = 0.77$, $d = 0.09$). Knee joint power was positive during most of the stance phase (Figure 4). Change in velocity during the first ground contact was not different between trials measuring the first or second step (1.09 ± 0.06 vs. 1.12 ± 0.07 m s^{-1}; $p = 0.28$, $d = -0.34$).

3.2 | Fascicle behavior during stance

Gastrocnemius medialis MTU underwent a stretch-shortening cycle during the first and second steps (Figure 5), while gastrocnemius muscle fascicles shortened during the stance phase in both steps (Figure 5). During both steps, fascicle

length changes and mean fascicle velocities were on average negative (Figure 6) and statistically different from zero for the whole stance and the phases of MTU lengthening and shortening (Table 1). Effect sizes (Cohen's d) were very large for fascicle length changes and velocities (Table 1).

3.3 | Comparison of fascicle behavior between steps one and two

Gastrocnemius medialis fascicle length changes and mean fascicle shortening velocities were not statistically different between steps with small to very small effect sizes (Table 1). MTU length changes did not differ between steps either, but MTU lengthening velocity was greater during step two compared with step one (Table 2). Comparisons of fascicle length change with respect to touchdown using SPM showed statistically significant shorter fascicles compared with fascicle length at touchdown, starting from 53% during the first step (for all timepoints after 53% of stance, $p < 0.01$) and from 86% during the second step (for all timepoints after 86% of stance, $p < 0.01$) (Supplementary Figure S1).

4 | DISCUSSION

This study aimed to examine gastrocnemius medialis muscle fascicle behavior during the first two steps of accelerative sprinting. As hypothesized, we found that gastrocnemius medialis muscle fascicles shortened throughout the first and second steps despite the characteristic phase of MTU stretch and negative ankle joint work after touchdown in sprint acceleration (Figure 4).

4.1 | Fascicle shortening during maximal acceleration

Gastrocnemius medialis fascicles shortened on average by 19% and 14% during the first and second steps, respectively. These findings support our first hypothesis that muscle
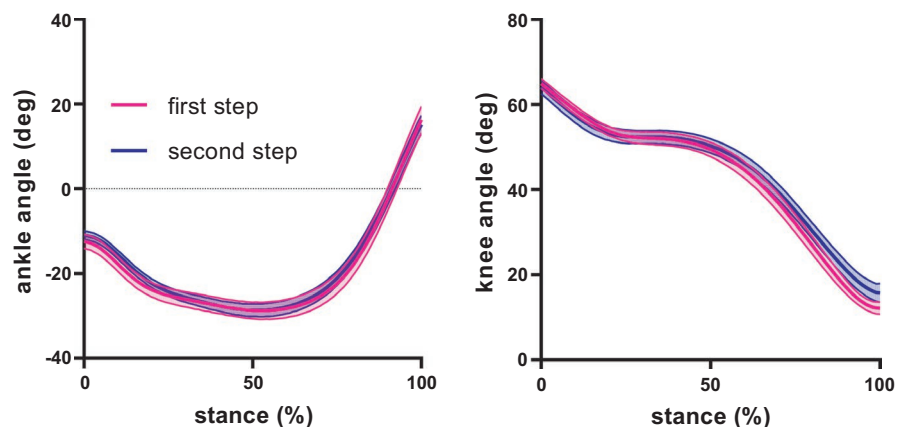

FIGURE 3 Instantaneous joint angle data ($\pm$SEM) for ankle and knee joints during the first and second stance phases of maximum sprint acceleration. Data are time-normalized to 101 points and displayed as group means ($n = 11$)
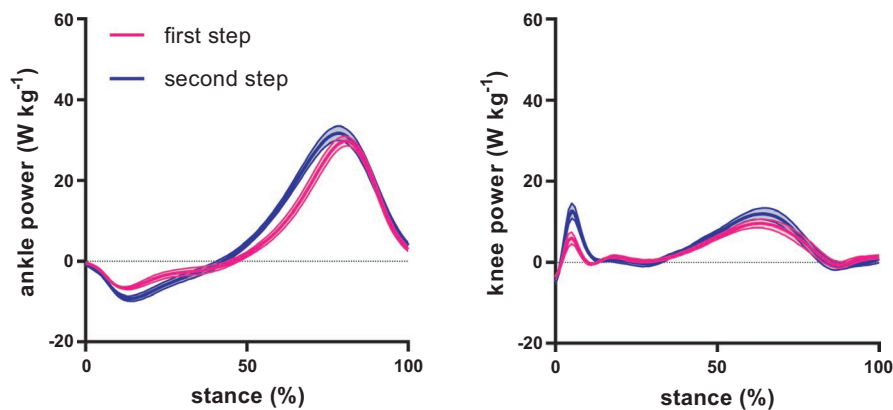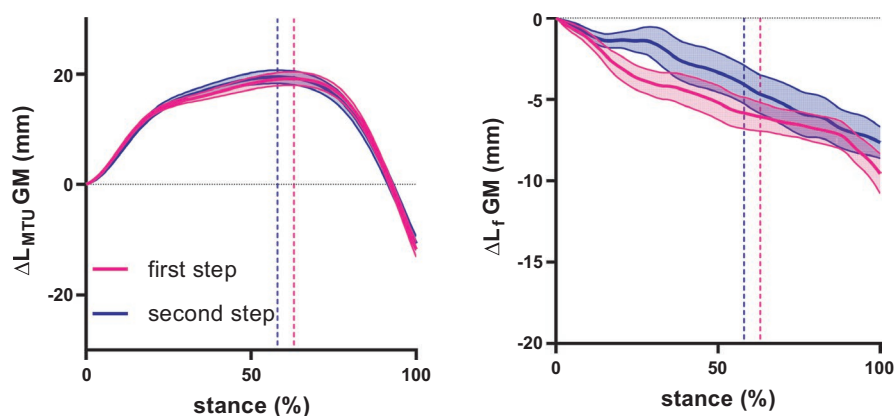
FIGURE 5 Length changes (ΔL) of the gastrocnemius muscle-tendon unit (MTU) and its fascicles (f) (±SEM)) during the first and second stance phases of maximum sprint acceleration. Lengths at touchdown were (mean±standard deviation) 51 ± 7 and 54 ± 8 mm for fascicles and 443 ± 23 and 442 ± 24 mm for MTU during the first and second steps, respectively. Vertical lines indicate the phase of MTU stretch and shortening. Data are time-normalized to 101 points and displayed as group means ($n = 11$).

fascicles produce positive work throughout the first and second steps of maximum acceleration sprinting. The absence of fascicle lengthening during the phase of MTU stretch after touchdown suggests elastic energy storage during this phase. Importantly, the biarticular gastrocnemius medialis muscle is also influenced by knee joint behavior; thus, energy may additionally be transferred between the joints. However, it may be important to note that the phase of positive work at the knee was short and this finding may be treated with caution. A previous analysis of knee joint kinetics found that knee joint kinetics excessively fluctuated during early stance in sprinting,[30] which could have affected our data. When comparing our results to previously reported gastrocnemius MTU and fascicle length changes during constant-speed running (eg, at different constant running speeds [31]), it is noticeable that the slow fascicle velocities at mid-ground contact are not present during rapid acceleration. Fascicle shortening, particularly during MTU lengthening, highlights the modulation of muscle-tendon interaction to do positive net work.

Fascicle shortening behavior in our study is consistent with a simulation study investigating the whole acceleration phase, which concluded that positive fascicle work was higher during acceleration than constant-speed sprinting.[16] Similarly, a previous *in vivo* study showed that plantar flexor MTUs can contribute to net positive work during accelerative walking.[15] The authors of this study show that fascicles do more mechanical work during accelerative walking compared to constant-speed walking. Along with these studies, our results corroborate the importance of considering lower leg muscle mechanics for locomotor tasks that require acceleration.

Mechanisms to generate positive net work in the lower limbs have previously been demonstrated in humans aiming to accelerate the body vertically from a resting position (ie, during squat jumps).[8,32] Here, elastic elements are stretched by the muscle to store energy that can be released later at a faster rate, showing similarities to the elastic mechanism in sprint acceleration in this study. Farris and colleagues[32] identified gravitational loading as a mechanism to stretch in-series elastic tissue by muscle contraction. Gravitational loading may also be used for elastic tissue lengthening during accelerative sprinting. In addition, the energy of the body that was gained during block clearance may likely contribute by

TABLE 1 Gastrocnemius muscle fascicle length changes during the whole stance phase, and during MTU lengthening and shortening phases for the first (step 1) and the second (step 2) stance phase of maximum effort accelerative sprinting (n = 11)

	Phase	Step 1			Step 2			Difference (step2-step1)			
		Mean ± SD	d	p-value	Mean ± SD	D	p-value	Mean ±SD	95% CI	d	p-value
Fascicle length changes (mm)	Stance	−9.6 ± 4.0	3.35	<0.001	−7.6 ± 3.2	3.40	<0.001	1.9 ± 6.2	−6.1–2.2	−0.31	0.327
	MTU lengthening	−5.9 ± 3.4	2.49	0.001	−4.1 ± 3.8	1.54	0.005	1.8 ± 5.1	−5.2–1.7	−0.35	0.278
	MTU shortening	−3.6 ± 3.3	1.57	0.004	−3.5 ± 2.2	2.20	<0.001	0.1 ± 3.0	−2.1–1.9	−0.04	0.885
Mean fascicle velocities (mm s^{-1})	Stance	−46 ± 19	3.45	<0.001	−45 ± 21	2.97	<0.001	1.7 ± 48.0	−24–21	−0.05	0.910
	MTU lengthening	−46 ± 26	2.54	<0.001	−44 ± 44	1.43	0.007	1.7 ± 40.5	−34–31	−0.03	0.939
	MTU shortening	−47 ± 46	1.42	0.008	−47 ± 27	2.46	<0.001	−1.0 ± 33.5	−26–28	0.02	0.861

Notes: Data for fascicle lengths were obtained during the stance phase; *p*-values show the results of one-sided *t*-test for each step and the comparison of step 1 and step 2 using paired *t*-tests (degree of freedom = 10).

Cohen's *d* (*d* ≥ 0.01 very small ES, *d* ≥ 0.20 small ES, *d* ≥ 0.50 medium ES, *d* ≥ 0.80 large ES, and *d* ≥ 1.20 very large ES).

Abbreviations: CI, confidence interval; *d*, effect size (ES); MTU, muscle-tendon unit; SD, standard deviation.

TABLE 2 Gastrocnemius muscle-tendon unit (MTU) length changes during MTU lengthening and shortening phases for the first (step 1) and the second (step 2) stance phase of maximum effort accelerative sprinting (n = 11)

	Phase	Step 1			Step 2			Difference (step2-step1)			
		Mean ± SD	d	p-value	Mean ± SD	d	p-value	Mean ± SD	95% CI	d	p-value
Changes (mm)	Lengthening	19.4 ± 3.9	7.00	<0.001	19.6 ± 4.0	6.89	<0.001	0.22 ± 1.79	−1.42–0.98	−0.12	0.695
	Shortening	−31.2 ± 6.0	−7.36	<0.001	−30.2 ± 4.3	−10.01	<0.001	0.92 ± 2.63	−2.69–0.85	−0.35	0.275
Mean velocities (mm s^{-1})	Lengthening	−156 ± 39	5.59	<0.001	201 ± 47	6.05	<0.001	45.22 ± 38.65	−71.18—19.25	−1.19	0.003
	Shortening	−395 ± 86	−6.50	<0.001	−400 ± 69	−8.22	<0.001	−5.49 ± 37.88	−19.95–30.94	0.15	0.641

Notes: Data for MTU lengths were obtained during the stance phase; *p*-values show the results of one-sided *t*-test for each step and the comparison of step 1 and step 2 using paired *t*-tests (degree of freedom = 10).

Cohen's *d* (*d* ≥ 0.01 very small ES, *d*≥ 0.20 small ES, *d* ≥ 0.50 medium ES, *d* ≥ 0.80 large ES, and *d* ≥ 1.20 very large ES).

Abbreviations: CI, confidence interval; MTU, muscle-tendon unit; SD, standard deviation; *d*, effect size (ES).
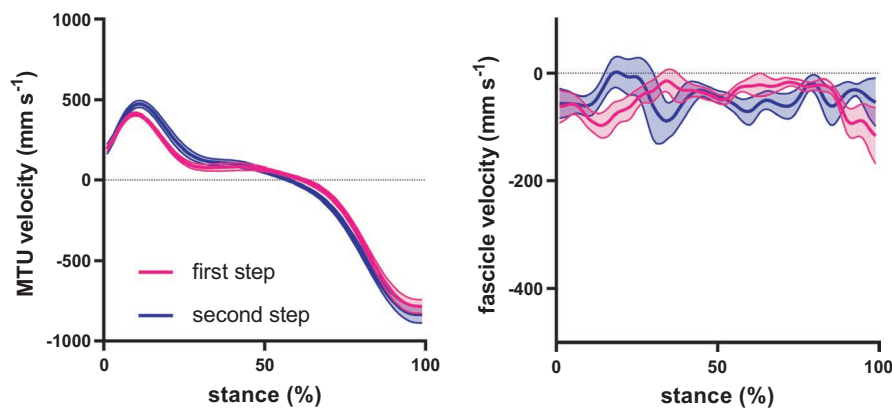
FIGURE 6 Gastrocnemius medialis muscle-tendon unit (MTU) and fascicle velocity (±SEM)) during the first and second stance phases of maximum sprint acceleration. Data are time-normalized to 101 points and displayed as group means (n = 11)

increasing forces and hence elastic tissue stretch. The notion of altered contractile properties of plantar flexor muscles during movements producing positive work is consistent with findings of a recent study investigating mechanisms to adjust joint kinetics during countermovement jumps.[33] In line with this study, the authors conclude that ankle joint kinetics are modulated by muscle contractile properties, while voluntary activation is modulated in proximal muscles.

Besides lower leg muscles, the different contributions of the knee and hip joints may influence power production during sprint acceleration. A direct comparison of joint power contribution during the acceleration phase and constant-speed sprinting is missing in the literature, but different studies indicate that negative knee joint work is low during acceleration [12,34] compared with constant-speed conditions.[35,36]

4.2 | Differences between first and second ground contacts

Our findings are at odds with our hypothesis of less fascicle shortening with increasing acceleration (second step compared to the first step) when using statistical analysis based on parameter extraction. Fascicle shortening during the whole stance or different parts of the stance phase based on MTU behavior was not statistically different between the first and second steps. However, statistical parametric mapping showed that fascicle length became significantly different from length at touchdown during late stance in both steps. Interestingly, the statistical difference in length started later during step two compared with step one. A decrease in gastrocnemius medialis positive fascicle work with progressing acceleration would be consistent with simulations of accelerative sprinting: Lai and colleagues[16] showed increased MTU stretch and reduced fascicle shortening throughout the entire acceleration phase by examining five ground contact phases from steps one to nineteen. Notably, although fascicle length changes and velocities did not differ between steps, MTU lengthening velocity was greater during step two with a large effect size.

The small differences between the two steps in our study could result from the low contrast between two consecutive steps during sprint acceleration. Yet, the decrease in ground contact duration from step one to step two indicates that greater force production of the MTU is required during step two, which in turn would induce a greater tendon stretch. We did not show that muscle fibers operated at different velocities that favor greater force production, but ~20% less mean fascicle shortening during the second step is in line with the simulation study by Lai and colleagues.[16] Contractile mechanics could also have been altered due to other factors such as differences in pennation angle, muscle activation, or fascicle operating length. Unfortunately, a comparison of operating length between steps in this study could have been confounded by potential differences in fascicle length between legs and ultrasound transducer placement and should be normalized in future studies. Alternatively, the low number of subjects could have prevented clear results for the step comparison. For this reason, we decided not to adjust the alpha level for multiple comparisons.

4.3 | Methodological considerations and limitations

We assumed in our interpretation of the data that concomitant MTU lengthening and fascicle shortening imply a stretch of elastic elements, although we have not directly measured the behavior of elastic tissue. Elastic tissue behavior is complicated due to, for example, region-dependent biaxial shape and strain changes of tendon and aponeurosis.[37-39] Thus, we think it is appropriate to make this inference instead of attempting to calculate elastic tissue strains.[40] It should also be noted that we assume that the gastrocnemius medialis muscle was active during the stance, although muscle activity was not measured directly. Besides muscle activation, factors such as co-contractions, muscle gearing, and history dependence are not considered in this study.

While our measurements provide information about the modulation of gastrocnemius medialis muscle-tendon

mechanics, questions about the behavior of other plantar flexor muscles and their interplay remain open. Although gross trends in fascicle behavior were similar between the biarticular gastrocnemii and monoarticular soleus, soleus exhibited distinct behavior during constant-speed running [41] and accelerative walking.[15] During sprint acceleration, soleus MTU lengthening is not facilitated by knee extension, which could induce relatively more fascicle shortening. Furthermore, it is important to note that using an ultrasound sampling frequency of 73 Hz during this explosive movement can limit the chance of discovering very small changes.

5 | PERSPECTIVE

The importance of elastic tissue for the storage and return of elastic energy and for optimizing muscle contractile conditions has long been recognized during constant-speed locomotion. Despite the distinct muscle-tendon architecture of the lower limb muscles, which traditionally is considered suboptimal to generate net positive joint work compared with more proximal muscles, it has also been established that these muscles contribute to vertical acceleration during jumping. Consistent with recent findings in humans during accelerative walking [15] and simulations of accelerative sprinting,[16] we show here that gastrocnemius medialis muscle fascicles contribute to acceleration during maximum effort sprinting by doing positive work, despite its short, highly pennated muscle fibers and the long compliant Achilles tendon. Our results indicate that elastic energy is stored during dorsiflexion to later amplify positive power output from the muscle-tendon unit. These findings contribute to increasing evidence of the importance of considering muscle-tendon mechanics to understand net positive work generation during tasks requiring net work generation.

CONFLICT OF INTEREST
The authors declare no conflict of interest, financial or otherwise.

AUTHOR CONTRIBUTIONS
A.W., S.W., and K.A. conceived and designed the research, performed experiments, analyzed data, and interpreted results of experiments. A.W. prepared figures and drafted the manuscript. A.W., S.W., and K.A. edited and revised the manuscript and approved the final version of it.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES
1. Van Caekenberghe I, Segers V, Willems P, Gosseye T, Aerts P, De Clercq D. Mechanics of overground accelerated running vs. running on an accelerated treadmill. *Gait Posture*. 2013;38(1):125-131.
2. Čoh M, Jošt B, Škof B, Tomažin K, Dolenec A. Kinematic and kinetic parameters of the sprint start and start acceleration model of top sprinters. *Gymnica*. 1998;28:33-42.
3. Bezodis NE, Willwacher S, Salo AIT. The biomechanics of the track and field sprint start: a narrative review. *Sports Med*. 2019;49:1345-1364.
4. Roberts TJ, Azizi E. Flexible mechanisms: the diverse roles of biological springs in vertebrate movement. *J Exp Biol*. 2011;214(3):353-361.
5. Astley HC, Roberts TJ. Evidence for a vertebrate catapult: elastic energy storage in the plantaris tendon during frog jumping. *Biol Lett*. 2012;8(3):386-389.
6. Roberts TJ, Marsh RL, Weyand PG, Taylor CR. Muscular force in running turkeys: the economy of minimizing work. *Science*. 1997;275(5303):1113-1115.
7. Lichtwark GA, Wilson AM. Interactions between the human gastrocnemius muscle and the Achilles tendon during incline, level and decline locomotion. *J Exp Biol*. 2006;209(21):4379-4388.
8. Kurokawa S, Fukunaga T, Fukashiro S. Behavior of fascicles and tendinous structures of human gastrocnemius during vertical jumping. *J Appl Physiol*. 2001;90(4):1349-1358.
9. Cronin NJ, Avela J, Finni T, Peltonen J. Differences in contractile behaviour between the soleus and medial gastrocnemius muscles during human walking. *J Exp Biol*. 2013;216(5):909-914.
10. Biewener AA. Muscle function in vivo: a comparison of muscles used for elastic energy savings versus muscles used to generate mechanical power. *Am Zool*. 1998;38(4):703-717.
11. Charalambous L, Irwin G, Bezodis IN, Kerwin D. Lower limb joint kinetics and ankle joint stiffness in the sprint start push-off. *J Sports Sci*. 2011;30(1):1-9.
12. Brazil A, Exell T, Wilson C, Willwacher S, Bezodis I, Irwin G. Lower limb joint kinetics in the starting blocks and first stance in athletic sprinting. *J Sports Sci*. 2017;35(16):1629-1635.
13. Jacobs R, van Ingen Schenau GJ. Intermuscular coordination in a sprint push-off. *J Biomech*. 1992;25(9):953-965.
14. Roberts TJ, Scales JA. Mechanical power output during running accelerations in wild turkeys. *J Exp Biol*. 2002;205(10):1485.
15. Farris DJ, Raiteri BJ. Elastic ankle muscle-tendon interactions are adjusted to produce acceleration during walking in humans. *J Exp Biol*. 2017;220:4252-4260.
16. Lai A, Schache AG, Brown NAT, Pandy MG. Human ankle plantar flexor muscle–tendon mechanics and energetics during maximum acceleration sprinting. *J R Soc Interface*. 2016;13(121):20160391.
17. Willwacher S, Herrmann V, Heinrich K, et al. Sprint start kinetics of amputee and non-amputee sprinters. *PLoS One*. 2016;11(11):1-18.
18. Söderkvist I, Wedin P-Å. Determining the movements of the skeleton using well-configured markers. *J Biomech*. 1993;26(12):1473-1477.
19. Willwacher S, Kurz M, Menne C, Schrödter E, Brüggemann G-P. Biomechanical response to altered footwear longitudinal bending

stiffness in the early acceleration phase of sprinting. *Footwear Sci*. 2016;8(2):99-108.

20. Seidel GK, Marchinda DM, Dijkers M, Soutas-Little RW. Hip joint center location from palpable bony landmarks—A cadaver study. *J Biomech*. 1995;28(8):995-998.

21. De Leva P. Adjustments to Zatsiorsky-Seluyanov's segment inertia parameters. *J Biomech*. 1996;29(9):1223-1230.

22. Hof AL. An explicit expression for the moment in multibody systems. *J Biomech*. 1992;25(10):1209-1211.

23. Hawkins D, Hull ML. A method for determining lower extremity muscle-tendon lengths during flexion/extension movements. *J Biomech*. 1990;23(5):487-494.

24. Van Hooren B, Teratsias P, Hodson-Tole EF. Ultrasound imaging to assess skeletal muscle architecture during movements: a systematic review of methods, reliability, and challenges. *J Appl Physiol*. 2020;128(4):978-999.

25. Farris DJ, Lichtwark GA. UltraTrack: software for semi-automated tracking of muscle fascicles in sequences of B-mode ultrasound images. *Comput Methods Programs Biomed*. 2016;128:111-118.

26. Cronin NJ, Carty CP, Barrett RS, Lichtwark G. Automatic tracking of medial gastrocnemius fascicle length during human locomotion. *J Appl Physiol*. 2011;111(5):1491-1496.

27. Pataky TC, Robinson MA, Vanrenterghem J. Vector field statistical analysis of kinematic and force trajectories. *J Biomech*. 2013;46(14):2394-2401.

28. Penny WD, Friston KJ, Ashburner JT, Kiebel SJ, Nichols TE. *Statistical Parametric Mapping: The Analysis of Functional Brain Images*. Elsevier; 2011.

29. Cohen J. *Statistical Power Analysis for the Behavioral Sciences*, 2nd edn. Á/L. Hillsdale, NJ, USA: Erbaum Press. 1988.

30. Bezodis NE, Salo AIT, Trewartha G. Excessive fluctuations in knee joint moments during early stance in sprinting are caused by digital filtering procedures. *Gait Posture*. 2013;38(4):653-657.

31. Lai A, Schache AG, Lin Y-C, Pandy MG. Tendon elastic strain energy in the human ankle plantar-flexors and its role with increased running speed. *J Exp Biol*. 2014;217(17):3159-3168.

32. Farris DJ, Lichtwark GA, Brown NAT, Cresswell AG. The role of human ankle plantar flexor muscle–tendon interaction and architecture in maximal vertical jumping examined in vivo. *J Exp Biol*. 2016;219(4):528.

33. Wade L, Lichtwark GA, Farris DJ. Joint and muscle-tendon coordination strategies during submaximal jumping. *J Appl Physiol*. 2020;128(3):596-603.

34. Bezodis NE, Salo AIT, Trewartha G. Lower limb joint kinetics during the first stance phase in athletics sprinting: three elite athlete case studies. *J Sports Sci*. 2014;32(8):738-746.

35. Schache AG, Blanch PD, Dorn TW, Brown NAT, Rosemond D, Pandy MG. Effect of running speed on lower limb joint kinetics. *Med Sci Sports Exerc*. 2011;43(7):1260-1271.

36. Bezodis IN, Kerwin DG, Salo AIT. Lower-limb mechanics during the support phase of maximum-velocity sprint running. *Med Sci Sports Exerc*. 2008;40(4):707-715.

37. Shin DD, Hodgson JA, Edgerton VR, Sinha S. In vivo intramuscular fascicle-aponeuroses dynamics of the human medial gastrocnemius during plantarflexion and dorsiflexion of the foot. *J Appl Physiol*. 2009;107(4):1276-1284.

38. Raiteri BJ, Cresswell AG, Lichtwark GA. Three-dimensional geometrical changes of the human tibialis anterior muscle and its central aponeurosis measured with three-dimensional ultrasound during isometric contractions. *PeerJ*. 2016;4:e2260.

39. Farris DJ, Trewartha G, McGuigan MP, Lichtwark GA. Differential strain patterns of the human Achilles tendon determined in vivo with freehand three-dimensional ultrasound imaging. *J Exp Biol*. 2013;216(4):594-600.

40. Herzog W. The problem with skeletal muscle series elasticity. *BMC Biomed Eng*. 2019;1(1):28.

41. Lai A, Lichtwark GA, Schache AG, Pandy MG. Differences in in vivo muscle fascicle and tendinous tissue behavior between the ankle plantarflexors during running. *Scand J Med Sci Sports*. 2018;28(7):1828-1836.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.