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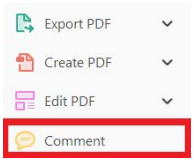

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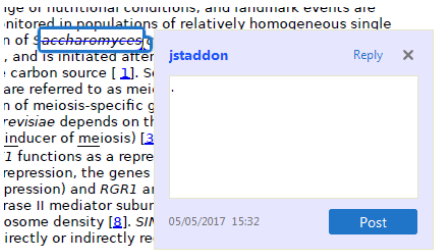

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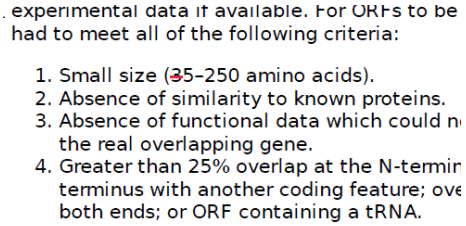

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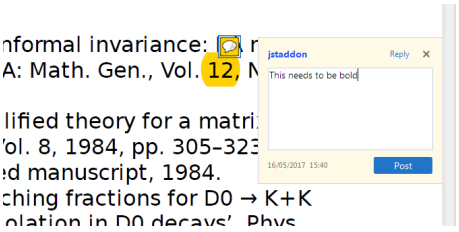

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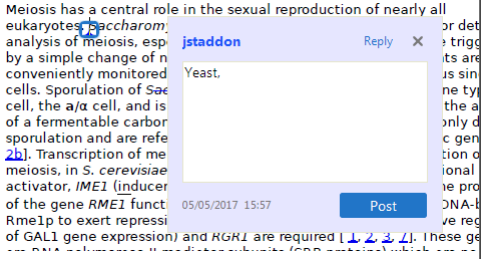

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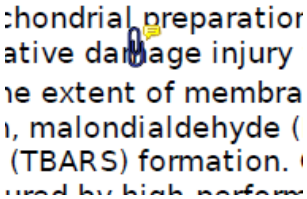

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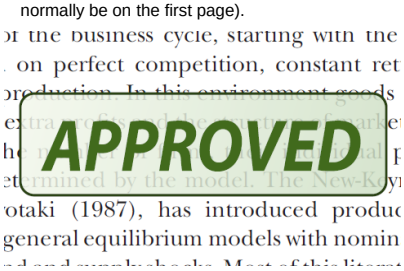

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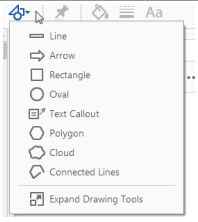

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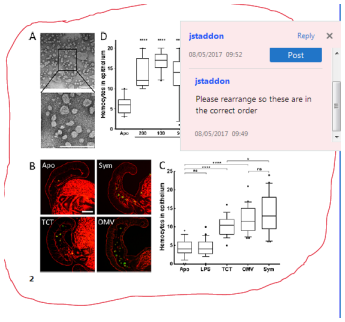

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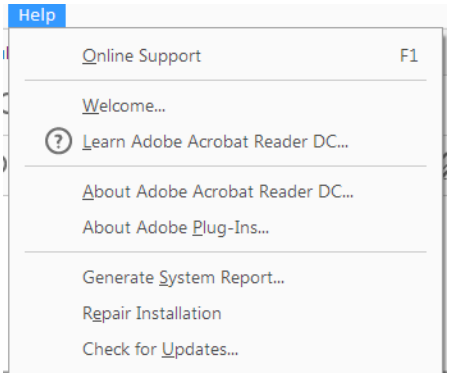

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ORIGINAL ARTICLE

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Interactions between fascicles and tendinous tissues in gastrocnemius medialis and vastus lateralis during drop landing

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Abstract

Animal tendons have been shown to act as shock absorbers to protect muscle fascicles from exercise-induced damage during landing tasks. Meanwhile, the contribution of tendinous tissues to damping activities such as landing has been less explored in humans. The aim of this study was to analyze in vivo fascicle-tendon interactions during drop landing to better understand their role in energy dissipation. Ultrafast ultrasound images of the *gastrocnemius medialis* (GM) and *vastus lateralis* (VL), lower limb electromyographic activity, 2-D kinematics, and ground reaction forces were collected from twelve participants during single- and double-leg drop landings from various heights. For both muscles, length changes were higher in tendinous tissues than in fascicles, demonstrating their key role in protecting fascicles from rapid active lengthening. Increasing landing height increased lengthening and peak lengthening velocity of VL fascicle and GM architectural gear ratio, whereas GM fascicle displayed similar length and velocity patterns. Single-leg landing lengthens the tendinous tissues of GM and, to a greater degree, VL muscles, without affecting the fascicles. These findings demonstrate the adjustment in fascicle-tendon interactions to withstand mechanical demand through the tendon buffer action and fascicle rotation. The higher VL fascicle contribution to negative work as the drop height increases would suggest muscle-specific damping responses during drop landing. This can originate from the distal-to-proximal sequence of joint kinetics, from differences in muscle and tendon functions (one- and two-joint muscles), architectural and morphological properties (eg, tendon stiffness), as well as from the muscle activity of the GM and VL muscles.

KEYWORDS

buffer mechanism, eccentric, fascicle lengthening, muscle mechanics, ultrafast ultrasound

1 | INTRODUCTION

The ability of muscle-tendon units to dissipate energy is fundamental in preventing muscle and bone injuries[1] in various daily-life and sport tasks that involve braking actions and eccentric muscle actions.[2] Griffiths' work on isolated cat muscles [3] first suggested that tendons act as a mechanical buffer during rapid stretching of the muscle-tendon unit. This buffer mechanism was recently elucidated by a series of animal studies that elegantly analyzed fascicle-tendon interactions involved in damping processes.[4-6] These works appended further evidence that tendons act as a shock absorber to avoid excessive fascicle lengthening and velocity to protect muscle fibers from subsequent damage.

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In humans, in vivo fascicle-tendon interactions of lower limb have been extensively studied using B-mode ultrasound [7] during stretch-shortening cycles[8,9] and concentric tasks.[10] These studies highlighted the role of tendons in enhancement of muscle fascicle's performance through a catapult mechanism.[11] In a study involving monoarticular eccentric exercises, Hicks et al[12] showed that the tendon partly accounts for the amplitude of muscle-tendon unit lengthening, suggesting its potential role in mechanical load modulation. Along this line, Guilhem et al [13] demonstrated that the amount of lengthening and braking work withstood by muscle fascicles influences the amount of exercise-induced muscle damage. These findings strongly suggest that the assessment of fascicle behavior during eccentric contractions is of primary interest to better understand the mechanisms involved in the shock absorption. Most of previous studies explored fascicle-tendon interactions in eccentric conditions during monoarticular tasks [12-14] or low-intensity exercises.[15,16] A recent study examined the fascicle-tendon interactions of the human triceps surae during a pure energy dissipation task of step landing.[17] These authors elegantly demonstrated that both *gastrocnemius medialis* and *soleus* muscles displayed quite similar fascicle lengthening during step landing irrespective of the loading condition (ie, body weight vs body weight with added mass) thanks to a buffering action of tendinous tissues. The greater stretch of tendinous tissues observed in the added mass condition underlines the key role of these structures to modulate energy dissipation.

Although the aforementioned study provides new insight into the role of fascicle and tendinous tissues when energy is dissipated,[17] only the muscles that cross the ankle joint were considered. However, with regard to the distal-to-proximal sequence of joint kinetics during landing tasks ,[18] the analysis of both ankle and knee extensor muscles might be required for a better understanding of the whole energy dissipation process throughout the lower limb. In addition, the load applied in this previous study remained relatively low (ie, ~2 times body weight) compared to more intensive tasks such as jump or drop landing (ie, more than 10 times body weight,[19]) that occurs in many sports. Indeed, regarding the high occurrence of injuries resulting from jump landings ,[20] these tasks have been especially studied from both biomechanical [19,21] and neurophysiological [22,23] points of view. In addition, it has been reported that the risk of sustaining a lower limb injury increased during a single-leg landing.[21] However, to date, the role of tendons in an intensive and multiarticular eccentric task, such as drop landing, remains poorly understood.

The main purpose of the present study was to analyzein vivo muscle fascicle and tendinous tissues interactions of the gastrocnemius medialis (GM) and vastus lateralis (VL) muscles during drop landing. We examined the influence of various heights (ie, 25, 50, and 75 cm) on these interactions. In order to appraise the impact of the load on the behavior of the muscle-tendon unit, we also analyzed a single-leg landing type that should be representative of the maximal load that could be applied during landing. Based on previous studies on the ankle extensors during landing [5,6,17] and considering the differences between GM and VL function during locomotion ,[7-9,24] we hypothesized that: (a) Elastic structures strongly contribute to the muscle-tendon unit lengthening of GM and VL to reduce both fascicle lengthening amplitude and velocity thanks to a decoupling mechanism between the fascicles and the tendinous tissues; (b) increasing landing height would not impact fascicle lengthening of the GM muscle due to a greater tendinous tissues contribution to the elongation of the whole muscle-tendon unit, while the VL fascicle would undergo higher lengthening and velocity; and (c) single-leg landing would decrease the knee joint flexion reducing the muscle-tendon unit elongation of the VL and increasing the one of the GM. This would result to an increase in the tendinous tissues lengthening of both muscles.

2 | MATERIALS AND METHODS

2.1 | Participants

Fifteen recreationally active men (age: 25.5 ± 3.8 years; height: 177.6 ± 5.8 cm; body mass: 72.2 ± 7.7 kg) volunteered to participate in the study. None of them had suffered a previous lower limb injury. All participants were fully informed about the nature and aim of the study before they gave their written informed consent to participate. The study was approved by the local ethics committee (Ouest IV) and conducted in accordance with the Declaration of Helsinki.

2.2 | Experimental design

2.2.1 | Familiarization session

Participants attended a familiarization session one day before the measurement session. They were instructed to drop from a box with both legs extended and to keep both hands on their hips throughout the movement. The motion of arms and feet was restricted to the sagittal plane of motion to ensure the two-dimensional nature of the task.[19] At the beginning of each trial, subjects were standing on the box on both legs. To impose a standardized drop height, participants were asked to start the movement with both legs over the box, to move their body forward with the right leg straight into the void while keeping a horizontal trajectory of the hip. The free fall then started, and a quick hip extension was performed to bring back the left leg. For the single-leg landing, participants did the same process without bringing back their left leg and landed on the right. To avoid extreme landing strategies (ie, too low or broad range of motion), we instructed to "land as naturally as possible

by avoiding too low or high body deceleration at impact." Participants were also familiarized to maximal voluntary isometric contraction (MVC) before the test sessions. During familiarization and test sessions, each participant wore the same pair of shoes (Essential Star 2.0, Adidas, Herzogenaurach, Germany). The lengths of shank, thigh, and GM muscle were measured using a measuring tape.[25,26]

2.2.2 | Test session

After a standardized warm-up and the assessment of isometric MVC peak torque, participants performed the same drop landing protocol twice to determine the behavior of both GM and VL muscle using one ultrasound scanner. Participants performed the vertical drop landing from a box onto the force platform. They executed double-leg drop landing from 25, 50, and 75 cm and a single-leg drop landing from 50 cm, with three trials for each condition. All participants were well familiarized to these tasks and the technical aspects of single- and double-leg drop landings thanks to a visual feedback during the familiarization session. Single-leg landings were performed on the right leg which was also the leg chosen for all measures in every condition (single- and double-leg drop landings). The order of ultrasound-tracked muscle, landing height, and landing type were randomized. The experimenter visually checked the following criteria: (a) no jump-off or step-down at the start to ensure similar drop height; (b) the feet were placed entirely on the force platform throughout the landing phase; and (c) the participant self-controlled his reception without loss of balance. Trials that did not meet one of these prerequisites were discarded and repeated.

2.3 | Instrumentation and data collection

2.3.1 | Force platform and motion analysis

Ground reaction force (GRF) data were recorded during landings by means of a force platform (60 × 40 cm, Kistler, Winterthur, Switzerland). The force signals were digitized at a sampling rate of 1000 Hz (DT 9804, Data Translation, Marlboro, MA). A motion-capture system (Vicon Motion Systems Ltd., Oxford, UK), with six infrared cameras, recorded the three-dimensional coordinates of eight reflective markers (12 mm diameter) located on the right part of the body at the following locations [27]: on the 5th metatarsal, lateral calcaneus, lateral malleolus, tibia head, lateral femoral epicondyle, great trochanter, iliac crest, and on the bony prominence on top of the shoulder. The sampling frequency was set to 250 Hz.

2.3.2 | Ultrasound

The fascicles of GM and VL were visualized using an ultrasound scanner (Aixplorer, Supersonic Imagine, Aix en Provence, France) and a linear transducer (5-12 MHz, 55 mm). The scanner was set at research mode to record raw radio-frequency signals during ultrafast acquisitions (1000 frames per second). For the GM, the transducer was placed on the skin surface over the muscle belly at different distances between the medial condyle and the musculo-tendinous junction depending on the subject's GM morphology. For the VL, the transducer was placed at the midpoint of the muscle to avoid fascicle curvature existing close to insertions.[28] For the VL muscle, as fascicles are often too long for the transducer size ,[24] optimization of the transducer orientation was achieved when most of the muscle fascicles could be traced between the aponeurosis to limit poor estimates in extrapolation of the visible part of the fascicle. We securely attached the transducers with custom-made equipment and carefully ensured that they were not displaced throughout the experimental protocol.

2.3.3 | Surface electromyography

Surface electromyography (EMG) was recorded with a wireless device (ZeroWire, Aurion, Italy) from *tibialis anterior* (TA), *gastrocnemius medialis* (GM), *soleus* (SOL), *vastus lateralis* (VL), *rectus femoris* (RF), *biceps femoris* (BF), and *gluteus maximus* (GMax) using bipolar silver/silver chloride surface electrodes (Blue Sensor Q-00-S, Baltorpbakken, Denmark). The electrodes were placed longitudinally with respect to the fibers' orientations. The skin was shaved and cleaned with alcohol, and electrodes were placed over the skin with an inter-electrode distance of 20 mm (center-to-center) according to the SENIAM (Surface Electromyography for the Non-Invasive Assessment of Muscles) recommendations. Raw EMG signals were pre-amplified (input impedance; 20 MM, common mode rejection ratio: 90 db; signal-to-noise ratio: >50 dB; gain: 1000), digitized at 2000 Hz, and then transmitted wirelessly to a remote unit.

2.3.4 | Synchronization

Ultrasound and EMG measurements were synchronized with force platform signals thanks to external triggers sent by both devices to the digital converter used to record force platform signals (DT 9804, Data Translation, Marlboro, MA). Before the drop landing task, a reflective marker was launched on the force platform. The impact was detected on the vertical ground reaction force to synchronize kinematic measurements and force platform signals. The temporal delay between GRF and kinematics data was very consistent between trials (ranged from 0.5 ± 1.4 ms to 3.5 ± 1.4 ms) and between sessions (2.2 ± 2.0 ms).

2.4 | Data processing

All data were analyzed using custom-written MATLAB scripts (The MathWorks, Natick, MA). The onset and offset

of each landing trial were detected as the initial contact on the force platform and the peak knee flexion angle, respectively. For each trial, the processing was focused on this landing phase (landing duration ranged from 96 ms at 25 cm to 272 ms at 75 cm) and the pre-activation phase starting 150 ms before the initial contact until initial contact. Due to the variability in landing duration, data were resampled and interpolated (ie, spline interpolation) such that they all have an equal number of points (ie, 101 points; time normalization) for both phases to allow between-participants and between-conditions comparisons. The trials that were the closest among the three GM and VL trials were selected for analysis. For that purpose, trials were compared in terms of joint angles, GRF, and center-of-mass displacement.

2.4.1 | Kinematics and kinetics

Raw force platform signals were low-pass filtered using a Butterworth second-order and zero-phase-lag filter at a cutoff frequency of125 Hz (Figure 1A). Peak vertical GRF was normalized to body weight. Vertical ground reaction forces were used to calculate center-of-mass acceleration, velocity, and displacement using the second law of Newton. To compute the center-of-mass velocity, we firstly determined the initial vertical velocity from the vertical coordinates of the hip marker over the last two video frames prior to foot-ground contact.[5] Center-of-mass displacement was obtained by integration of the center-of-mass velocity. The negative center-of-mass work was also calculated by taking the dot product of the vertical GRF and vertical center-of-mass displacement. We also computed the rate of force development (RFD) by dividing the peak vertical GRF by the GRF peak time. The reflective marker positions were low-pass filtered using a Butterworth second-order and zero-phase-lag filter at a cutoff frequency of 15 Hz.[27] Given the 3-D coordinates data from the reflective markers, we first calculated the absolute 2-D angles of lower limb segments to obtain relative ankle, knee, and hip angles in the sagittal plane (Figure 1B). By convention, the ankle angle was set to 0° when the foot is perpendicular to the shank. Knee and hip angles were set to 0° when fully extended.[27] A negative value of ankle angle corresponded to plantar flexion, while positive knee and hip angles were linked to flexion.

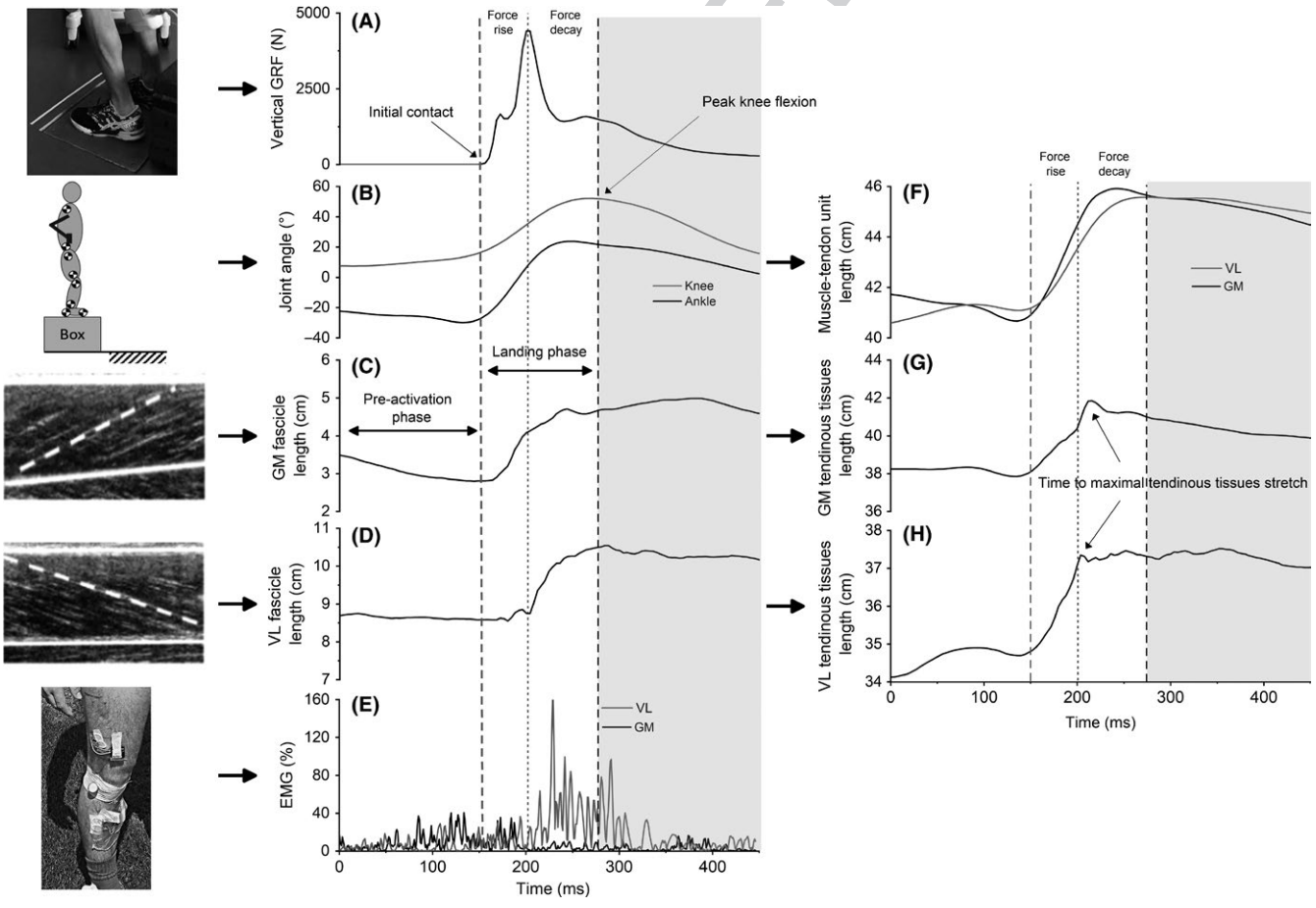

FIGURE 1 Individual examples of instrumentation and measurements from a double-leg drop landing from 50 cm. A, vertical ground reaction forces (GRF); B, ankle and knee joint angles; C, *gastrocnemius medialis* (GM) fascicle length; D, *vastus lateralis* (VL) fascicle length; E, GM and VL muscle activity. Joint angle and fascicle length data allowed the computation of muscle-tendon unit length (F) and tendinous tissue length (G and H)

2.4.2 | EMG analyses

Raw EMG signals of lower limb muscles were band-pass filtered (10-500 Hz, second-order zero-phase-lag Butterworth filter) and consistently analyzed with a 50 ms moving root mean square (RMS) window to produce a RMS envelope that was then normalized to the maximal corresponding muscle activity recorded during isometric MVC. The EMG RMS was averaged for pre-activation and landing phases in order to compare the same muscle between heights and landing types.

2.4.3 | Ultrasound analyses

Raw radio-frequency signals were converted to B-mode images through a classical beam-forming procedure. The displacement of fascicles and aponeuroses was automatically tracked on B-mode images using the method proposed by Cronin et al.[29,30] When the fascicle was not fully visible, its length was extrapolated as the length of the straight line between the superficial and deep aponeurosis using a trigonometry method.[9,24] The pennation angle was calculated as the angle formed between the fascicle and the deep aponeurosis. Muscle fascicle length and pennation angle were low-pass filtered using a Butterworth second-order and zero-lag filter at a cutoff frequency of 60 Hz. The fascicle lengths of GM and VL were derived to obtain fascicle velocities. Peak fascicle lengthening was calculated during the landing phase for each muscle and all drop landing conditions. According to the equations derived by Grieve et al [25] and Visser et al ,[26] we estimated the instantaneous length of the whole GM and VL muscle-tendon units using ankle and knee angles (Figure 1F). The length of tendinous tissues was estimated as the difference between muscle-tendon unit length and the horizontal projection of fascicle length (ie, fascicle length multiplied by the cosine of pennation angle) [8,10] (Figure 1G,H). Tendinous tissues length changes were computed during both pre- and landing phases, while tendinous tissues peak lengthening velocity was computed during the landing phase (Figure 1F-H). The effect of fascicle rotation has been characterized as the muscle's gear ratio [31,32] (AGR) calculated by the ratio between the horizontal fascicle length variation to the fascicle length variation during the landing phase (Δ horizontal fascicle length/Δ fascicle length [31,32]). This ratio was used to determine how the fascicle lengthening could be minimized by the fascicle rotation. Methodological differences existed to calculate the AGR between the original in vitro method of Brainerd & Azizi [32] and the in vivo adaptation in the current study. The horizontal projection of fascicle length [9,13] was considered rather than muscle length.

The moment of maximal stretch of the tendinous tissues was defined as the moment at which the tendinous tissues do not contribute any further to the muscle-tendon unit lengthening and expressed in ms (Figure 1G). In order to specify the muscle fascicle behavior, the landing phase was divided into two sub-phases based on GRF time course (Figure 1). First, we defined "force rise" as the phase between the ground contact (ie, 0% of landing phase) and the time of peak vertical GRF. "Force decay" corresponded to the phase between the peak vertical GRF and the end of the landing phase.[17] It must be noted that the phases we used are based on the vertical GRF [17] and differ from the method initially proposed by Konow & Roberts [4,5] based on the muscle-tendon unit force of turkeys. Fascicle lengthening amplitudes and AGR of the GM and VL muscles were calculated for these two phases.

2.5 | Statistical analyses

Statistical analyses were completed using Statistica (StatSoft, Tulsa, OK). Since the data consistently passed the normality test (Shapiro-Wilk's test), all data were expressed as mean ±standard deviation (SD). Statistical significance was set at $P < 0.05$.

First, reliability assessments (within-subject coefficient of variation [CV], intraclass correlation coefficient [ICC], and standard error of measurement [SEM]) were performed for relative peak vertical GRF, negative center-of-mass work, center-of-mass velocity, landing duration, and joint range of motion (ROM). Second, for double-leg drop landing conditions, one-way ANOVAs for repeated measures were used to assess the effects of landing height (25, 50, and 75 cm). These analyses were applied for the following: (a) kinetics variables (ie, relative peak vertical force; negative center-of-mass work); (b) kinematics variables (ie, center-of-mass velocity; landing duration; ROM for ankle, knee, and hip; RFD; and time to peak vertical force); (c) length changes and peak lengthening velocity for the muscle-tendon unit, fascicles, and tendinous tissues for both GM and VL; and (d) architectural gear ratio, the moment of maximal tendinous tissues stretch. All these parameters were tested only for the landing phase, except for the length changes in the muscle-tendon unit, fascicles, and tendinous tissues that were analyzed for pre-activation phase, landing phases, force rise, and force decay phases. Third, paired t tests were performed to determine the effect of landing type (single- vs double-leg for the 50 cm landing height) on the same parameters. Fourth, seven repeated measures two-way ANOVAs (2 phases ×3 heights) were performed to compare the activity of the seven muscles between phases (pre-activation, landing) and across the three landing heights (25, 50, and 75 cm). Fifth, seven repeated measures two-way ANOVAs (2 phases ×2 landing types) were performed to compare the activity of the seven muscles between phases (pre-activation and landing) and landing type (single- vs double-leg landing at 50 cm). When

TABLE 1 Kinematics and kinetics parameters obtained during drop landing task in the four tested conditions

	Double-leg 25 cm				Double-leg 50 cm				Double-leg 75 cm				Single-leg 50 cm			
Parameters	**Mean ± SD**	**CV (%)**	**ICC**	**TE**	**Mean ± SD**	**CV (%)**	**ICC**	**TE**	**Mean ± SD**	**CV (%)**	**ICC**	**TE**	**Mean ± SD**	**CV (%)**	**ICC**	**TE**
Peak vertical force (body weight)[a,b]	4.8 ± 1.1	7.9	0.89	0.5	6.5 ± 1.9	7	0.94	0.7	7.7 ± 2.3	7.8	0.93	0.7	5.7 ± 0.9	5.7	0.85	0.4
Landing duration (ms)[a,b]	143 ± 20	14.3	0.48	29	157 ± 36	5.4	0.94	11	183 ± 48	6.8	0.93	17	198 ± 29	10	0.66	22
Negative center-of-mass work (J)[a,b]	362 ± 97	7.8	0.91	36	589 ± 82	10.6	0.42	69	739 ± 114	8.6	0.68	150	447 ± 79	4.6	0.93	27
Center-of-mass velocity (m/s)[a,b]	2.1 ± 0.2	5.3	0.72	0.1	2.7 ± 0.3	6	0.63	0.2	3.1 ± 0.3	5.6	0.67	0.7	2.4 ± 0.3	3.5	0.94	0.1
Ankle range of motion (°)[a,b]	48 ± 9	7.4	0.74	5	57 ± 7	5.4	0.81	4	62 ± 7	4.3	0.84	4	60 ± 6	3	0.92	3
Knee range of motion (°)[a,b]	50 ± 8	5.6	0.87	4	64 ± 8	6.3	0.76	4	71 ± 9	6.5	0.71	6	57 ± 8	6.8	0.78	5
Hip range of motion (°)[a]	24 ± 6	14.8	0.66	4	35 ± 7	11.7	0.68	5	46 ± 14	15.1	0.74	9	34 ± 7	12.6	0.6	5
Time to peak vertical force (ms)[a,b]	58 ± 14	8.9	0.86	6.2	56 ± 11	6.5	0.89	5.4	52 ± 8	3.2	0.96	11.9	51 ± 8	2.2	0.98	1.7
Rate of force development (N/s)[a]	62.5 ± 27	14.5	0.89	11.8	87 ± 40.5	11.3	0.94	14.8	109.1 ± 50.1	9.3	0.96	17.8	80.7 ± 25.1	7.1	0.95	7.5

Positive ankle joint angle corresponds to ankle plantar flexion. Positive knee and hip joint angle correspond to knee and hip flexion. Values are presented as mean ± SD. Statistical significance was set at $P < 0.05$.

[a]Significant main effect of landing height.

[b]Significant effect of landing technique (single- vs double-leg landing).

TABLE 2 Gastrocnemius medialis and vastus lateralis behavior during the landing phase of drop landing task in the four tested conditions

Parameters	Double-leg 25 cm	Double-leg 50 cm	Double-leg 75 cm	Single-leg 50 cm
Gastrocnemius medialis				
Muscle-tendon unit behavior				
Length changes (pre-activation phase, cm)[b]	−1.1 ± 0.66	−1.37 ± 0.87	−1.17 ± 0.63	−1.82 ± 0.62
Lengthening amplitude (landing phase, cm)[a,b]	2.61 ± 0.91	3.08 ± 0.6	3.38 ± 0.62	3.48 ± 0.62
Peak lengthening velocity (landing phase, cm/s)[a,b]	44 ± 16	52.7 ± 12.1	59.7 ± 11.7	60.1 ± 11.1
Fascicle behavior				
Length changes (pre-activation phase, cm)[b]	−0.92 ± 0.52	−1.02 ± 0.66	−0.92 ± 0.41	−1.35 ± 0.51
Lengthening amplitude (landing phase, cm)	1.71 ± 0.81	1.71 ± 0.88	1.62 ± 0.81	1.64 ± 0.61
Lengthening amplitude (force rise, cm)[a]	0.93 ± 0.56	0.62 ± 0.37	0.6 ± 0.39	0.72 ± 0.48
Lengthening amplitude (force decay, cm)	0.78 ± 0.38	1.09 ± 0.78	1.02 ± 0.77	0.92 ± 0.58
Peak lengthening velocity (landing phase, cm/s)	42 ± 16.5	44.5 ± 18.4	43.1 ± 18.9	50.7 ± 15
Architectural gear ratio (landing phase, %)[a]	1.09 ± 0.02	1.1 ± 0.04	1.14 ± 0.06	1.13 ± 0.06
Architectural gear ratio (force rise, %)[b]	1.08 ± 0.08	1.09 ± 0.09	1.11 ± 0.07	1.14 ± 0.07
Architectural gear ratio (force decay, %)	1.12 ± 0.05	1.12 ± 0.09	1.16 ± 0.15	1.14 ± 0.05
Tendinous tissues behavior				
Length changes (pre-activation phase, cm)	−0.12 ± 0.11	−0.21 ± 0.26	−0.21 ± 0.21	−0.16 ± 0.16
Lengthening amplitude (landing phase, cm)[a]	2.08 ± 0.75	2.68 ± 0.62	2.93 ± 0.73	2.91 ± 0.82
Peak lengthening velocity (landing phase, cm/s)[a]	46.5 ± 28.7	63.1 ± 19.6	71.9 ± 19.5	65.2 ± 19.4
Time to maximal tendinous tissues lengthening (ms)	68 ± 12	66 ± 9	69 ± 13	66 ± 20
Vastus lateralis				
Muscle-tendon unit behavior				
Length changes (pre-activation phase, cm)[a,b]	0.62 ± 0.44	1.08 ± 0.49	0.95 ± 0.39	0.56 ± 0.37
Lengthening amplitude (landing phase, cm)[a,b]	4.38 ± 0.66	5.28 ± 0.67	5.43 ± 0.79	4.7 ± 0.69

(Continues)

TABLE 2 (Continued)

Parameters	Double-leg 25 cm	Double-leg 50 cm	Double-leg 75 cm	Single-leg 50 cm
Peak lengthening velocity (landing phase, cm/s)[a]	42.8 ± 6.8	50.1 ± 7.5	52.9 ± 7.8	47.3 ± 5.1
Fascicle behavior				
Length changes (pre-activation phase, cm)	0.27 ± 0.29	0.27 ± 0.4	0.17 ± 0.23	0.16 ± 0.23
Lengthening amplitude (landing phase, cm)[a]	1.45 ± 0.73	1.78 ± 0.69	2.04 ± 0.82	1.37 ± 0.4
Lengthening amplitude (force rise, cm)[b,c]	0.5 ± 0.45	0.58 ± 0.55	0.45 ± 0.31	0.2 ± 0.11
Lengthening amplitude (force decay, cm)[a,c]	0.92 ± 0.3	1.15 ± 0.31	1.56 ± 0.75	1.15 0.28
Peak lengthening velocity (landing phase, cm/s)[a]	23.2 ± 8.3	27.8 ± 6.4	37.7 ± 19.3	25.6 ± 11.4
Architectural gear ratio (landing phase, %)	1.03 ± 0.05	1.03 ± 0.04	1.03 ± 0.03	1.05 ± 0.05
Architectural gear ratio (force rise, %)	1.01 ± 0.04	1.01 ± 0.04	1 ± 0.06	1.01 ± 0.15
Architectural gear ratio (force decay, %)[c]	1.03 ± 0.03	1.04 ± 0.03	1.05 ± 0.03	1.07 ± 0.07
Tendinous tissues behavior				
Length changes (pre-activation phase, cm)[a,b]	0.33 ± 0.33	0.78 ± 0.29	0.76 ± 0.29	0.38 ± 0.22
Lengthening amplitude (landing phase, cm)[b]	2.48 ± 0.72	2.65 ± 0.75	2.8 ± 0.74	3.03 ± 0.82
Peak lengthening velocity (landing phase, cm/s)[a]	38.8 ± 11.7	43.8 ± 13.9	50.9 ± 8.9	49.6 ± 10.6
Time to maximal tendinous tissues lengthening (ms)[a]	118 ± 27	119 ± 29	94 ± 31	127 ± 25

A negative value of length changes corresponds to shortening. Values are presented as mean ± SD. Statistical significance was set at $P < 0.05$.

[a]Significant main effect of landing height

[b]Significant effect of landing type (single- vs double-leg landing)

[c]Significant effect of phase (force rise vs force decay)

the sphericity assumption was violated (Mauchly's test), a Geisser-Greenhouse correction was used. Bonferroni post hoc analyses ($\alpha = 0.05$) were conducted when appropriate.

3 | RESULTS

Due to the low quality of ultrasound data for three different trials (over 120 trials, representing 3.3%), two participants were discarded from the analysis. In addition, the kinematic data of another participant were erroneous. Therefore, results were obtained for 12 participants.

3.1 | Landing kinetics and kinematics

All the kinematics and kinetics parameters reported in Table 1 were significantly altered by both landing height (all P values <0.01) and landing type (all P values <0.009), except for hip ROM and RFD, which were affected by landing height ($P < 0.001$) but not by landing type (P values: 0.65 and 0.26). CV, ICC, and SEM are provided in Table 1. CVs for peak vertical force, center-of-mass velocity, negative center-of-mass work, time to peak vertical force, and knee and ankle ROM ranged between 3.0% and 10.6%. Landing duration, hip ROM, and RFD presented higher CVs with almost all

conditions higher than 10% with the maximal CV value of 15.2%. Overall, these results (ie, CV values of 20 conditions over 28 were under 10%) combined with those of ICC and SEM values demonstrated a satisfying reliability in the mechanics of landing.

3.2 | Gastrocnemius medialis behavior

Architectural measurements of *gastrocnemius medialis* are presented in Table 2 and patterns of muscle-tendon unit, muscle fascicle, and tendinous tissue length in Figure 2A-C. During the pre-activation phase, the muscle-tendon unit (Figure 2A, -1.10 ± 0.66 to -1.82 ± 0.62 cm) and muscle fascicles (Figure 2B, -0.92 ± 0.52 to -1.35 ± 0.51 cm) shortened, while tendinous tissue lengths remained almost constant (Figure 2C, -0.12 ± 0.11 to -0.21 ± 0.26 cm). In addition, there was no significant effect of the landing height for the muscle-tendon unit ($P = 0.19$), fascicles ($P = 0.27$), and tendinous tissue length changes ($P = 0.61$). The shortening was significantly larger for the single-leg condition compared to the double-leg for both muscle-tendon unit (+25%, $P = 0.004$) and fascicles (+24%, $P = 0.049$), while it was not significantly different for the tendinous tissues ($P = 0.45$).

During the landing phase, the muscle-tendon unit, fascicles, and tendinous tissues lengthened (Figure 2A-C, landing phase). Lengthening and peak lengthening velocity of

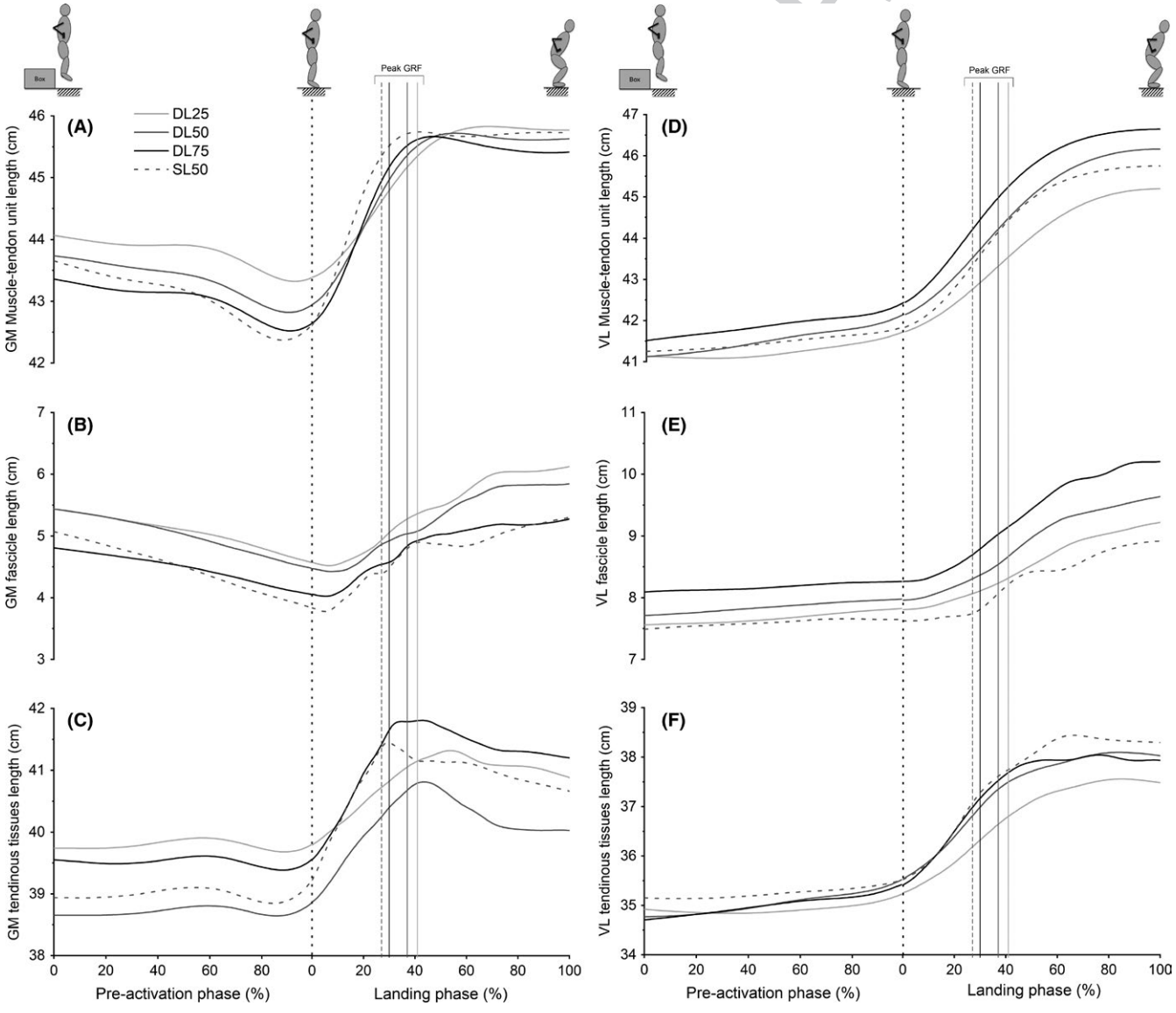

FIGURE 2 Averaged patterns of *gastrocnemius medialis* (GM) muscle-tendon unit (A), muscle fascicle (B), and tendinous tissue (C) length changes and averaged patterns of *vastus lateralis* (VL) muscle-tendon unit (D), muscle fascicle (E), and tendinous tissue (F) length changes throughout pre-activation and landing phases (in % of phase duration). Standard deviations are omitted for clarity. The vertical black dotted line between the two phases indicates the instant of foot-ground contact. The time of peak vertical ground reaction forces is represented in the landing phase by vertical lines with corresponding colors to each of the four conditions

the muscle-tendon unit increased with the landing height (lengthening: +23%, $P < 0.001$, and peak velocity: +24%, $P < 0.001$ for the 25 cm vs the 75 cm landing) and was higher in single-leg compared to the double-leg condition (lengthening: +11.5%, $P = 0.006$, and peak velocity: +12%, $P = 0.003$). Lengthening and peak lengthening velocity of tendinous tissues were also affected by increasing landing height (lengthening: +29%, $P < 0.001$, and peak velocity: +38%, $P = 0.007$ for 25 cm vs 75 cm landing), but not by the landing type (lengthening: $P = 0.31$ and peak velocity: $P = 0.32$, respectively). However, lengthening and peak lengthening velocity of fascicles were not significantly influenced either by landing height (lengthening: $P = 0.36$ and peak velocity: $P = 0.94$, respectively) or by landing type (lengthening: $P = 0.78$, and peak velocity: $P = 0.36$, respectively). When looking at the force rise phase, the GM fascicle lengthening decreased as the dropping height increased (25 vs 50 and 75, $P = 0.014$) without any effect of landing type ($P = 0.44$). We found no effect in the force decay phase for both landing height and type ($P = 0.72$ and 0.57). Therefore, the effect of landing height was accounted for only by the tendinous tissues without effects for the fascicles (all $P \leq 0.007$). Architectural gear ratio ranged between 1.09 ± 0.02 and 1.14 ± 0.06 during the whole landing phase and was increased with landing height ($P = 0.004$ for 25 cm vs 75 cm landing), but no significant effect was found for landing type ($P = 0.07$). In addition, there was an effect of landing type on fascicle rotation during force rise (+4% during single-leg landing, $P = 0.007$). We found no effect of landing height during force rise ($P = 0.49$) and landing height and type during force decay ($P = 0.65$ and 0.76). Finally, tendinous tissue maximal lengthening occurred almost at the same time between the four conditions (66-69 ms) without a significant effect of landing height ($P = 0.63$) or landing type ($P = 0.93$).

3.3 | Vastus lateralis behavior

Architectural measurements of vastus lateralis are presented in Table 2 and patterns of instantaneous muscle-tendon unit, muscle fascicle, and tendinous tissue length in Figure 2D-F. During the pre-activation phase, the muscle-tendon unit (Figure 2D, 0.56 ± 0.37 to 1.08 ± 0.49 cm) and tendinous tissues (Figure 2F, 0.38 ± 0.22 to 0.78 ± 0.29 cm) were slowly stretched, while muscle fascicles exhibited a quasi-isometric behavior (Figure 2E, 0.16 ± 0.23 to 0.27 ± 0.29 cm). In addition, lengthening of the muscle-tendon unit and tendinous tissues was significantly influenced by both landing height (muscle-tendon unit: +35%, $P = 0.02$, and tendinous tissues: +57%, $P < 0.001$ for 25 vs 75 cm) and type (muscle-tendon unit: +48%, $P = 0.004$ for the double-leg vs single-leg, and tendinous tissues: +51%, $P = 0.004$ for the double-leg vs single-leg). On the contrary, no significant effects of landing height ($P = 0.31$) and landing type ($P = 0.32$) were found for fascicle lengthening.

During the landing phase, the muscle-tendon unit, fascicle, and tendinous tissues lengthened (Figure 2D-F, landing phase). Lengthening (+16%, $P < 0.001$ for 25 cm compared to 75 cm landing) and peak lengthening velocity (+19%, $P < 0.001$ for 25 cm vs 75 cm landing) of the muscle-tendon unit were significantly increased with landing height. A landing type effect was not significant for lengthening ($P = 0.44$) or peak lengthening velocity ($P = 0.10$) of the muscle-tendon unit. For tendinous tissues, lengthening was not changed by landing height condition ($P = 0.23$), while peak lengthening velocity ($P = 0.002$) increased when height increased. Differences in landing types were significant for lengthening of tendinous tissues (+12.5% for the single-leg vs the double-leg landing type, $P = 0.036$) and not significant for peak lengthening velocity ($P = 0.10$). VL fascicle lengthening amplitude was affected by landing height (+29%, $P = 0.025$ for 25 cm vs 75 cm landing) but not by landing types ($P = 0.06$). Along the same line, the peak lengthening velocity of fascicles increased with landing height (+38%, from 25 to 75 cm landing; $P = 0.02$), while we observed no effect of landing type ($P = 0.56$). Fascicle lengthening was lower before than after the peak vertical GRF (phase effect, $P < 0.001$). During the force rise, the VL fascicle lengthening was significantly different between landing types (−34% of lengthening for single-leg landing, $P = 0.02$) with no effect of landing height ($P = 0.30$) suggesting a large contribution of the elastic structures during this phase. The fascicle lengthening during the force decay was greater as the drop height increased ($P = 0.006$) with no significant effect of landing type ($P = 0.97$). No significant effects of landing height ($P = 0.78$) or landing type ($P = 0.08$) on AGR values (1.03 ± 0.03 and 1.05 ± 0.05) were reported. Fascicle rotation was greater during force decay compared to force rise (phase effect: $P = 0.003$) suggesting that this mechanism helps the VL to dissipate the greater fascicle lengthening during the force decay. Finally, the time to maximal lengthening of tendinous tissues (ranging between 94 ms and 140 ms) displayed a landing height effect (−24 ms, $P < 0.01$ for 25 vs 75 cm landing), while there was no effect found for landing type ($P = 0.34$).

3.4 | EMG activity

The time course of EMG patterns for the seven lower limb muscles is displayed in Figure 3, and the mean EMG activity (expressed in percentage of the maximal RMS value) during each phase is provided in Table 3. Larger values were almost always obtained in the single-leg condition. In this condition, the highest values were reached by VL ($72.7\% \pm 37.4\%$ in the landing phase), GMax ($53.5\% \pm 35.8\%$ in the landing phase), and GM ($51.9\% \pm 14.5\%$ in the pre-activation phase).

A significant main effect of phase was found for all the muscles (all P values <0.042). All the muscles displayed a higher muscle activity during the landing phase compared to the pre-activation phase (all P values <0.043), except for the gastrocnemius medialis, which was significantly more activated in the pre-activation phase ($P < 0.001$). Indeed, GM muscle activity peaked in the pre-activation phase before decreasing slowly (Figure 3). Activities of BF, TA, and GMax remained relatively low until initial foot-ground contact. VL, RF, and SOL muscle activities increased slowly from ~75 ms before the impact and continued to increase during the landing phase.

A significant increase in muscle activity as the landing height increased was found for all muscles (25 vs 75 cm

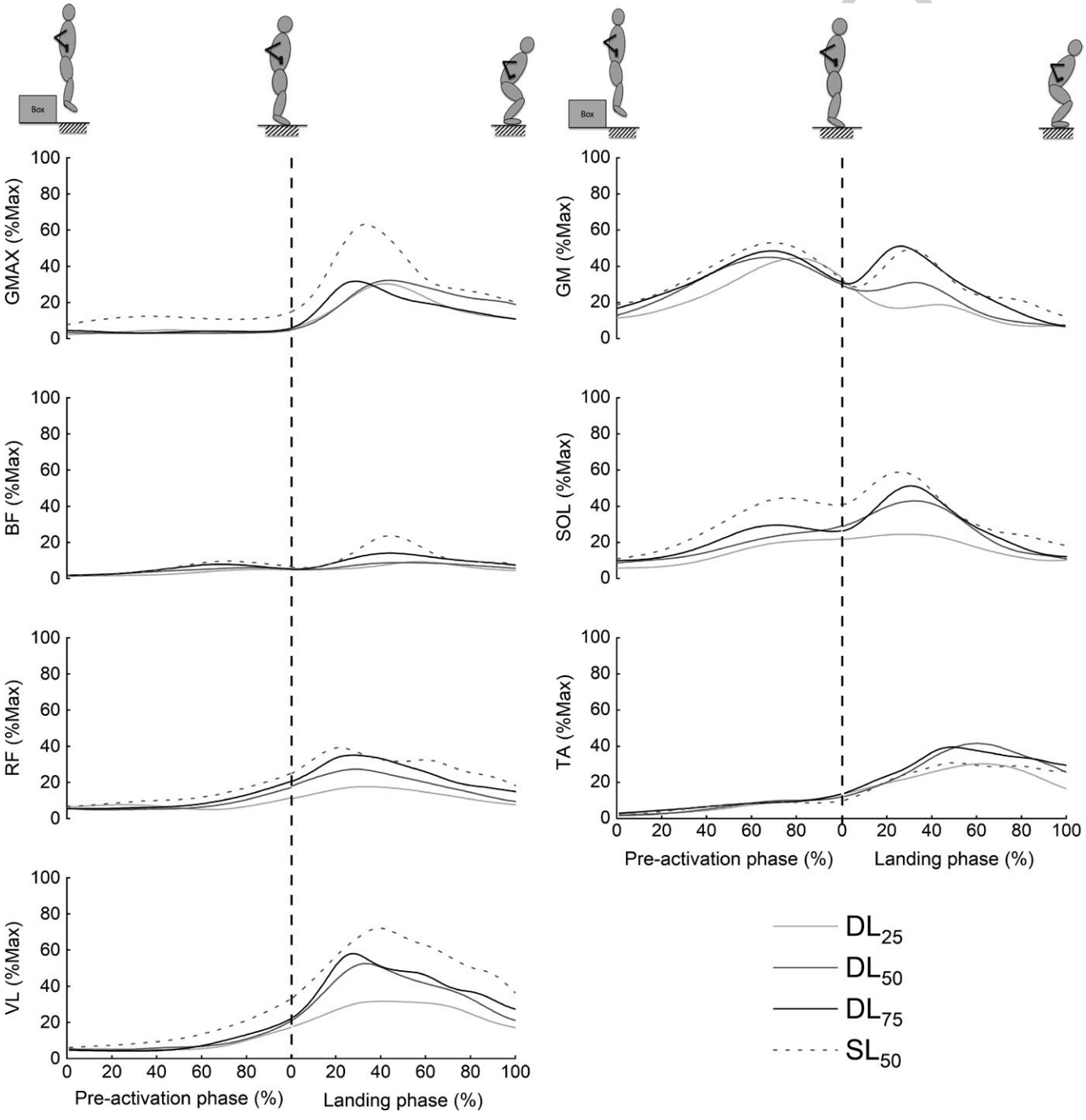

FIGURE 3 Averaged time course of normalized EMG activity patterns (%Max) from seven lower limb muscles during the different landing conditions. Standard deviations are omitted for clarity. The vertical dashed line indicates the instant of ground contact. The raw EMG data were full-wave rectified and smoothed using a second-order, low-pass, Butterworth filter with a cutoff frequency of 10 Hz to obtain a linear envelope. TA: *Tibialis anterior;* GM: *Gastrocnemius medialis;* SOL: *Soleus;* VL: *Vastus lateralis;* RF: *Rectus femoris;* BF: *Biceps femoris;* GMax: *Gluteus maximus*

landing; from +3.8% for the BF to +13.2% for SOL), except for GMax ($P = 0.20$). A significant main landing type effect was found for all muscles (all P values <0.05) with higher activity during the single-leg drop landing for all muscles (from +4.5% for the BF to +17.6% for the GMax), except for the TA, which displayed higher activity during a double-leg landing ($P = 0.04$, +4.6% of MVC).

4 | DISCUSSION

The present study confirms the key role of tendinous tissues to buffer the work done by muscle fascicle during a pure energy-dissipating task. Gastrocnemius medialis and vastus lateralis differently contributed to the dissipation of mechanical energy upon various landing conditions (height or type). The elastic structures of both muscles initially lengthened to account for the muscle-tendon unit elongation, while muscle fascicles actively lengthened after the foot-ground contact. In addition, the peak of fascicle lengthening was notably delayed according to the lengthening of tendinous tissues. This decoupling mechanism between the muscle-tendon unit, muscle fascicle, and tendinous tissues is consistent with previous animal[5,6] and human studies.[17] In accordance with our first hypothesis, GM tendinous tissues lengthened more when the loading increased allowing for a constant fascicle lengthening amplitude and peak velocity during landing. One could notice that GM muscle fascicle lengthening was reduced as the mechanical demand increased during the force rise phase (ie, first 50-60 ms after landing). This observation is strengthened by a greater fascicle rotation and muscle activity before landing. Conversely, VL fascicle lengthening amplitude increased concomitantly to the increase in VL muscle-tendon unit, while the tendinous tissues only increased their lengthening velocity. As the height increased, VL fascicle maintained the same range of lengthening during the force rise phase resulting to a higher storage of elastic energy by tendinous tissues during this period. For both muscles, single-leg landing resulted in tendinous tissues lengthening that preserves fascicles from high eccentric contractions.

The drop landing task used in the present study imposed mechanical loads that were in accordance with the literature (ie, exposing the body to forces ranging from 3.3 to 12.0 times body weight). Several previous studies reported increases in center-of-mass velocity and GRF as the drop landing height increased[19,21] and during a double-leg compared to single-leg drop landing type.[21] The higher mechanical demand resulting from a higher drop landing altered lower extremity kinematics as reflected by larger ankle and knee joint ROM.[19,21,33] Ankle ROM was higher during single-leg compared to double-leg drop landing due to higher plantar flexion in the preactivation phase, while the opposite was found for the knee ROM.[19,21] Consequently, the adopted strategy during single-leg landing seemed to alleviate the knee extensors and overload plantar flexors.[33]

TABLE 3 Averaged EMG from RMS during the pre-activation and landing phases of seven lower limb muscles

Muscle activity (% RMS_{max})	Double-leg 25 cm		Double-leg 50 cm		Double-leg 75 cm		Single-leg 50 cm	
	Pre	Land	Pre	Land	Pre	Land	Pre	Land
Tibialis anterior (TA)[a,b,d]	8.6 ± 8.6	31.3 ± 29.2	10.6 ± 14.4	40.2 ± 28.4	9.5 ± 7.4	40.8 ± 27.1	8.8 ± 5.3	32.7 ± 24.6
Gastrocnemius medialis (GM)[a,b,d]	39.5 ± 16.8	19.2 ± 18.8	47 ± 20.2	25.1 ± 20.2	47.2 ± 18.1	37.4 ± 41.4	51.9 ± 14.5	38.3 ± 36.8
Soleus (SOL)[a,b,d]	17.9 ± 9.6	23.5 ± 17.3	26.3 ± 18.7	36.5 ± 24	27.5 ± 11.3	40.2 ± 28.3	39 ± 17.8	48.7 ± 25.4
Vastus lateralis (VL)[a,b,c,d,e]	10.1 ± 6.2	34.4 ± 18.7	13.2 ± 12.7	49.3 ± 27.5	11.6 ± 6.3	54.1 ± 32.2	18.9 ± 8.7	72.7 ± 37.4
Rectus femoris (RF)[a,b,c,d,e]	9.6 ± 5	18.6 ± 10.6	11.6 ± 7.5	27.5 ± 13	12.7 ± 7.4	34.7 ± 21.6	17 ± 11.5	41.2 ± 17.6
Biceps femoris (BF)[a,b,d,e]	3.9 ± 3.2	8.4 ± 8	6.6 ± 6.5	9.3 ± 7.3	6.6 ± 6.3	13.3 ± 16.9	7.5 ± 5.8	17.5 ± 14.7
Gluteus maximus (GMax)[b,d,e]	5.3 ± 4	21.4 ± 28.3	8 ± 13.3	26.1 ± 39.4	5.6 ± 3.7	23.1 ± 26.2	16 ± 10.8	53.5 ± 35.8

TA: *Tibialis anterior;* GM: *Gastrocnemius medialis;* SOL: *Soleus;* VL: *Vastus lateralis;* RF: *Rectus femoris;* BF: *Biceps femoris;* GMax: *Gluteus maximus*. EMG data were normalized to the maximum isometric RMS and then averaged for each phase. Values are presented as mean ± SD. Statistical significance was set at $P < 0.05$.

[a]Main effect of landing height

[b]Significant effect of phase (pre-activation vs landing phase)

[c]Significant interaction height × phase effect

[d]Significant effect of landing type (single- vs double-leg landing)

[e]Significant interaction landing type × phase effect

The behavior of GM fascicle during drop landing presented a clear turning point (Figure 2B) from shortening to lengthening following the impact with a small delay of shortening between the foot-ground contact and the onset of fascicle lengthening (ranged from 3 to 12 ms). Our patterns of fascicle lengthening were similar to those reported during the landing phase of a step-down.[17] In the current study, although stretching of the GM muscle-tendon unit was greater as landing height increased, muscle fascicle length and peak lengthening velocity remained unchanged. This finding suggests that the increasing mechanical demand resulting from landing was buffered by tendinous tissues due to a greater stretch of elastic tissues (from 2.08 at 25 cm to 2.93 cm at 75 cm) compared to fascicles in GM muscle. This is in accordance with the recent work of Werkhausen et al [17] for lower intensities. They showed that the increase in muscle-tendon elongation due to the increased mass results in greater tendinous tissues lengthening without any additional participation of the fascicles. The step landing task analyzed in this previous study [17] induced relatively low ground reaction forces up to ~2 times body weight vs 12 times body weight in the present study. This suggests that, thanks to the buffering action of the tendon, there is a similar GM response in a continuum of lengthening demand from low to high loading constraint. While speculative, it is very likely that this limits the amount of exercise-induced muscle damage and potential risk of injury at high intensity. Furthermore, the maximal lengthening of GM tendinous tissues occurred 66-69 ms following ground contact, without significant differences between the four landing conditions (Figure 2F). Regardless of the drop height, the tendinous tissues reached their maximum length (ie, end of the stretch) at the same time (few milliseconds after the peak vertical GRF). This may be related to the buffering action of tendinous tissues enabled by the decoupling between the muscle-tendon unit, muscle fascicles, and tendinous tissues. The first milliseconds of muscle-tendon unit lengthening was mainly withstood by the tendinous tissues before the fascicles actively lengthened.[5,6,17] The lengthening of the GM tendinous tissues increased with the increase in height, while the global fascicle lengthening was unchanged. Moreover, the fascicle lengthening was even reduced for the higher height in the force rise phase. This can be seen as a protective mechanism for the GM muscle fascicles. These results are in agreement with Konow & Roberts [5] who found that tendinous tissues of turkeys reached their maximum length at the same time (~60 ms) during landing from various drop heights. However, contrary to animal studies ,[5] the stretch of fascicles started few milliseconds after the ground contact (on average after: 7 ms of GM shortening and 12 ms of VL isometric behavior) and muscle-tendon unit elongation was taken by both GM fascicle and tendinous tissues for most of the ankle and knee joints' excursion. Hence, in human GM, the stretch of tendinous tissues helps to reduce the lengthening velocity and amplitude of fascicles during landing with a smaller delay before the onset of fascicle lengthening as previously shown on turkeys.[5] The GM muscle-tendon unit lengthening amplitude and peak velocity were higher during a single-leg landing than during a double-leg landing. However, if the fascicles withstood the same level of lengthening at a similar rate, the tendinous tissues did not undergo additional lengthening. This may be due to the concomitant higher muscle activity and shortening amplitude of the GM during the pre-activation which stiffen the muscle to prepare the landing and allow a higher gearing potential thanks to a higher pennation during the force rise.

VL muscle fascicles contracted almost isometrically, while VL muscle-tendon unit and tendinous tissues slightly lengthened during the pre-activation phase. After the foot-ground contact, while VL fascicle started to lengthen after ~12 ms, muscle-tendon unit and tendinous tissues lengthened continuously until the maximum knee flexion similarly to that reported during a single support low-intensity braking task.[34] During a stair descent from 16 cm, larger VL fascicle lengthening amplitudes were reported (up to 3.2 cm) compared to a drop landing task (from 1.45 cm at 25 cm to 2.04 cm at 75 cm). These results confirm that modulation of fascicle length changes is highly dependent on the nature and intensity of the task.[9] The VL fascicle lengthening and peak lengthening velocity increased with landing height, while tendinous tissues stretched over a similar amplitude. However, VL tendinous tissues reached their maximal lengthening earlier as the drop height increased. This induced an increase in tendinous tissues peak lengthening velocity, while the lengthening amplitude was unchanged. Hence, VL fascicle lengthened earlier, over larger amplitude and upon higher velocity. This drop height effect occurred during the force decay with a similar lengthening amplitude of VL fascicle (~0.50 cm) during the first 50-60 ms of landing (ie, force rise). This demonstrates the crucial contribution of the VL fascicle in energy dissipation throughout landing. The VL muscle-tendon unit lengthening was higher during the single-leg in comparison with the double-leg condition. The fascicles lengthened similarly in both landing types, while the tendinous tissues stretched more when using one versus two legs. This behavior results in a lower VL fascicle lengthening during the force rise phase.

While the time course of fascicle length changes was similar for the two muscles (progressive increase during the whole landing phase,Figure 2B,E), our results clearly showed different muscle-tendon unit behaviors between GM and VL that could be mainly explained by five factors. First, GM is bi-articular while VL is mono-articular. GM contributes both to extend the ankle and to flex the knee, while VL only extends the knee joint. During the landing phase, the GRF tends to flex the ankle joint which is offset by the motion of the knee joint. Our results show that the bi-articular GM muscle mitigates length changes and

velocity associated with increases in landing height. We also observed that the increases in drop height increased the amplitude and peak velocity in the mono-articular VL. Second, the maximal stretching of the muscle-tendon unit and tendinous tissues occurred later for VL compared to GM. This can result from the joint sequence involved in landing [18,35] given that the ankle is the first joint impacted by ground contact. There is evidence that the shock-absorbing phase of a jump (ie, landing) would require a distal-to-proximal sequence of joint kinetics, with the proximal muscles helping the distal muscles to dissipate mechanical energy.[18,33,35] In our study, the peak joint angular velocity of the ankle, knee, and hip joint (ranging from the highest to the lowest) combined with the observed EMG patterns (Figure 3) support this previous finding of a distal-to-proximal sequence during drop landing. Third, the intrinsic tissue properties of Achilles and patellar tendons, such as stiffness, may also affect the elongation capacity of the tendinous tissues.[36,37] In humans, the Achilles tendon is categorized as a high-stress tendon that can sustain maximum stress about twofold greater than that of the patellar tendon.[36,37] Moreover, it has recently been shown in vivo that Achilles tendon stiffness is independent of loading rate [38] inversely to the patellar tendon.[12] The difference in viscosity between both tendons may explain why the GM tendinous tissues largely prevent the short GM muscle fascicles from rapid lengthening, while VL muscle fascicles stretched with increasing velocity when the landing height and velocity increased. FoFourth, the difference in muscle activity in the pre-activation phase could contribute to differentiate the fascicles behavior of VL and GM. In our study, increases in drop height increased the mean EMG amplitude of the GM over the pre-activation phase, attesting of "preparatory" muscle activity before ground contact. This may stiffen the muscle [23] and adjust active muscle force before ground contact to meet the demand resulting from the increased mechanical load.[23] This process may in turn reduce both fascicle lengthening amplitude and velocity during landing. Conversely, the low EMG activity of the VL in the pre-activation phase is reflective of a distal-to-proximal activation sequence that provides more time for the quadriceps to activate its larger muscle mass. Together with its longer fascicles, the high force-generating capacity of the VL then favors its contribution to braking work in the late phase of landing. Fifth, another important finding of the present study is related to the larger muscle fascicle rotation as the landing height increases for the GM (AGR from 1.09 to 1.14). This suggests that fascicle rotation substantially reduced the stretch sustained by GM fascicles throughout landing (between 9% and 14%) ,[31] while it remained constant for the VL (AGR from 1.03 to 1.05). This result may presumably be attributable to a larger lengthening potential allowed by longer fascicles.

Joint ROM data showed that the strategy adopted during single-leg landing seemed to unload the knee extensors and overload plantar flexors.[33] This is in agreement with the decrease in VL fascicle lengthening for the single-leg landing compared to double-leg and the higher activity of proximal muscles during single-leg landing compared to double-leg (mean 1.5-times higher in single-leg vs double-leg). In addition, higher EMG activity in knee joint muscles enables adequate dampening of excessive loading. It is also interesting to note that, thanks to the buffering action of tendinous tissues, this overload did not induce any overstretching of GM fascicles. Thus, the adopted strategy during single-leg landing seems efficient for limiting fascicle stretching of both muscles but overused both tendinous tissues which might lead to tendinopathy.[20]

Substantial methodological considerations should be kept in mind when interpreting the present data. Similar to all previous 2D ultrasound studies,[7] we assumed the linearity and homogeneity of fascicles' line of action, whereas previous reports showed a fascicle curvature close to aponeuroses' insertions resulting in slight length underestimation.[28] In addition, when the fascicle was not fully visible, mainly in VL, we used trigonometry computations to estimate fascicle length. The error for estimating fascicle with the extrapolation method has been reported to be 2%-7% [9,24] and could potentially be larger when considering the high speed of drop and ground contact intensity (>3 m/s at 75 cm). A recent study suggests that using two synchronized in-series transducers could overcome this limit and avoid absolute fascicle lengths misestimation compared to extrapolated method.[39] As previously reported with the single transducer method, the fascicle data set may not perfectly reflect fascicle behavior; however, it could be assumed that this method does not alter the effects of landing height and type (ie, "similar differences in muscle contraction dynamics within participants."[39]). In our study, we estimate tendinous tissues length changes from fascicle length estimation and lower limb joint angles. This approach is imperfect and has recently been questioned due to potential incorrect interpretations regarding tendon behavior.[40] While we acknowledge that tendinous tissues length changes must be seen in light of this limit, the changes in fascicle length remain valid. Since our main results are directly inferred from these length changes, the potential bias in estimating tendinous tissues length would not influence the main conclusions of our study. Considering the difficulty of the drop landing task, we only included the best trial per condition for the data analysis. In order to compare GL and VL behavior, this trial was chosen considering the reliability in the landing mechanics and the quality of ultrasound data. This choice prevented us to assess the reliability of our fascicle length measurement. Finally, due to our single ultrasound scanner, we were not able to track both muscles at the same time, and the procedure involved repeating the protocol twice. However, we found good reliability in the mechanics of landing measured at the global level, which is in line with

a previous work on landing from a hang bar (ie, height standardization) that revealed ICC coefficients ranging from 0.79 to 0.93.[41]

5 | CONCLUSION AND PERSPECTIVES

The present study demonstrated that, during drop landing, tendinous tissues of both*gastrocnemius medialis* and *vastus lateralis* act as shock absorbers by rapidly stretching and storing elastic energy, which is then released to the fascicles and dissipated through active muscle lengthening. A previous study showed that mechanical loading up to ~2 times body weight did not influence GM fascicle stretch or lengthening velocity.[17] The present study demonstrated that GM behavior remains similar for landings with GRF up to ~12 times body weight indicating that the elastic structures absorb mechanical energy to protect GM fascicles from potential damage and injury. In addition, novel evidence was provided that VL fascicle behavior differs by increasing its contribution to the muscle-tendon unit elongation as the landing height increased. This study showed that simultaneous analyses of fascicle-tendon interactions and muscle activity involved in multi-joint braking actions, especially at high intensity, allow to improve our understanding of the energy dissipation process in humans.

Among different perspectives, further studies could focus on the effect of surface mechanical properties on the fascicle-tendon damping responses during landing. As human lands, energy is absorbed and released by the surface depending on its intrinsic mechanical properties and at the end dissipated by muscle fascicles. Specifically, energy storage is a function of both surface stiffness and deformation. Hence, the transfer of mechanical energy between the body and the surface can have a considerable influence on athletic performance. Such investigations would be paramount to determine whether these interfaces influence the risk of injury in sports tasks like tendinopathies.[20]

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CONFLICT OF INTEREST

No conflict of interest, financial or otherwise, is declared by the authors.

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