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The series elastic shock absorber: tendon elasticity modulates energy dissipation by muscle during burst deceleration

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During downhill running, manoeuvring, negotiation of obstacles and landings from a jump, mechanical energy is dissipated via active lengthening of limb muscles. Tendon compliance provides a 'shock-absorber' mechanism that rapidly absorbs mechanical energy and releases it more slowly as the recoil of the tendon does work to stretch muscle fascicles. By lowering the rate of muscular energy dissipation, tendon compliance likely reduces the risk of muscle injury that can result from rapid and forceful muscle lengthening. Here, we examine how muscle–tendon mechanics are modulated in response to changes in demand for energy dissipation. We measured lateral gastrocnemius (LG) muscle activity, force and fascicle length, as well as leg joint kinematics and ground-reaction force, as turkeys performed drop-landings from three heights (0.5–1.5 m centre-of-mass elevation). Negative work by the LG muscle–tendon unit during landing increased with drop height, mainly owing to greater muscle recruitment and force as drop height increased. Although muscle strain did not increase with landing height, ankle flexion increased owing to increased tendon strain at higher muscle forces. Measurements of the length–tension relationship of the muscle indicated that the muscle reached peak force at shorter and likely safer operating lengths as drop height increased. Our results indicate that tendon compliance is important to the modulation of energy dissipation by active muscle with changes in demand and may provide a mechanism for rapid adjustment of function during deceleration tasks of unpredictable intensity.

1. Introduction

During locomotion, muscles often act to dissipate mechanical energy, and this process is essential to active force production in normal gait, in maintaining stability, and for the ability to decelerate and stop [1,2]. To dissipate energy, muscles lengthen while generating force [3]. This task is common in terrestrial locomotion; in fact, many limb extensor muscles lengthen to act as brakes just as often as they shorten to act as the motors powering movement [4,5]. Active muscle lengthening is metabolically inexpensive [6] but it involves risks of stretch-induced muscle injury [7,8].

The spring-like properties of tendon can act to buffer energy absorption by muscle [9–11]. In rapid energy-dissipating events, such as when landing from a jump, energy can be stored rapidly in tendons as they stretch, and then released more slowly when force decays and tendon recoil does work to lengthen muscles. This mechanism can delay and reduce the rate of muscle lengthening and may protect against muscle damage [9,10].

The present study had two goals. First, we sought to determine how muscle and tendon function were modulated with varying demand for energy dissipation. We measured the mechanical function of the turkey lateral gastrocnemius (LG) as animals landed from three heights (0.5, 1.0 and 1.5 m). Muscular energy dissipation (negative work) can be increased via higher muscle force production, muscle strain or both. We hypothesized that both would contribute and that as landing height increased, energy dissipation by the LG would increase owing to (i) an increase in muscle force resulting from greater muscle recruitment; and (ii) an increase in

muscle strain associated with greater leg flexion during landing. Studying the function of the LG across a range of demands for energy dissipation also allowed us to determine whether the tendency of tendon function to absorb all of the energy in the first period of a dissipative event was common to a range of tasks, or occurred only during the most demanding events.

The second goal of our study was to determine the operating length of the LG during energy-dissipating events. Muscle is susceptible to injury at long sarcomere lengths, on the descending limb of its length–tension (LT) curve [7,8]. Therefore, we predicted that the LG would operate at short lengths, on the ascending limb and plateau of its LT curve, during landing from all heights. To test this hypothesis, we measured LT relationships in the LG of each animal to establish the lengths at which muscle fascicles operated during force production.

2. Material and methods

(a) Animals, training and instrumentation

Eight adult eastern wild turkeys, *Meleagris gallopavo* (electronic supplementary material, table S1), purchased from a licenced breeder, were maintained on a commercial poultry diet and water ad libitum in the Brown University animal care facility. All animal use was approved by the Brown University Institutional Animal Care and Use Committee. At experiment time, the body mass of the animals used was 4.7 ± 2.1 kg (mean $\pm$ s.d.), with two being significantly larger than the other six (Kolmogorow–Smirnov two-tail test; $p < 0.001$).

All birds were trained using gradual increases in drop-height to land safely and in a controlled fashion, absorbing energy via coordinated leg joint flexion. Release into a drop was always preceded by a verbal cue from the experimenter. We used a ceiling-mounted pulley and rope system tied to a custom-made webbing harness that was strapped around the proximal (humeral) wing segments (electronic supplementary material, figure S1). This system allowed us to release the birds from 0.5, 1.0 and 1.5 m elevation of the standing centre of mass (36.9 ± 2.4 cm), with the added benefit of almost entirely removing the effects of flapping on descent velocity.

The right LG muscle was instrumented in all subjects during sterile procedures as in previous studies [9,12]. Muscle force was measured via two strain gauges bonded with superglue onto the deep and superficial aspects of the bony tendon, in direct opposition. Muscle fascicle segment length was measured using a pair of sonomicrometry crystals implanted along a proximal fascicle in this pennate muscle. Muscle activity was measured via electromyography from the same muscle region via fine-wire in-dwelling electrodes. Carprofen was administered as analgesic and all subjects recovered from surgery for 24–36 h prior to experiments.

During experiments, the harness system ensured that the feet touched down near the centre of a three-axis force-plate. The instrumented limb was marked to identify joint locations and video recorded in lateral view of a Photron 1280 PCI high-speed camera. Motion capture of limb joint kinematics was carried out as in previous studies [9,12]. Strain gauge measurements were balanced and amplified $1000\times$ (Vishay 2210). EMG signals were amplified $1000\times$ and acquired with a 3 Hz to 10 kHz band-pass filter (WPI DAM50). A function generator generated a square-wave pulse that powered an LED in view of the video camera and was also recorded via A/D to facilitate synchronization of kinematics data with muscle mechanics and force-plate data. All signals were A/D converted at 4 kHz (NI-6259 DAQ) onto a PC running IGORPRO v. 6.0 (Wavemetrics). We analysed trials where high-speed videos showed both limbs making near-simultaneous contact (± 8 ms) and the animal maintained balance throughout limb joint flexion.

(b) *In situ* measurements

Following *in vivo* measurements, an *in situ* muscle preparation was used to calibrate strain gauges to force and to measure muscle LT properties. Details of the *in situ* preparation have been presented previously [12,13]. Animals were deeply anaesthetized and the femur and tarsometatarsus were secured in a custom jig. The LG tendon was dissected from its insertion and attached via a lightweight clamp and aircraft cable to a servomotor (Model 310-BLR, Aurora Scientific). A custom bipolar cuff was attached to the tibial branch of the sciatic nerve, and the muscle was stimulated with a Grass S48 stimulator. Force measured by the servomotor during tetanic contractions was used to calibrate strain gauge measurements [12]. Fixed-end contractions were used to calculate a stiffness constant for the tendon, by taking the shortening of the muscle fibres (measured by sonomicrometry) as a measure of tendon lengthening, and regressing this upon muscle force to calculate stiffness.

A tetanic LT curve was constructed from the fascicle segment length measured by sonomicrometry and the force measured by the servomotor [13]. Tetanic contractions were elicited over a range of fascicle lengths, and the fascicle length (L/L_0) and peak tetanic force (P/P_0) were taken from the force-plateau. The LT curve was constructed from six to ten contractions, with a 5-min resting period between contractions to reduce the chances of muscle fatigue. For three birds, we were unable to obtain tetanic LT curves. These birds were not used for analysis of operating length. For the purposes of calculating strains for animals without a measured LT curve, L_0 was estimated from the relationship between L_0 and length at toe-down (L_{td}) for the birds for which LT curves were measured ($L_0 = 0.55 \cdot L_{td} + 13.31$; $r^2 = 0.85$).

(c) Analyses

High-speed video recordings of joint positions were used to calculate total length of the muscle tendon unit (MTU). External marker points were digitized in the high-speed videos using a custom MATLAB script [14]. Knee position was calculated as the intercept of two circles, one with hip position as the centre and femur length as radius, and the other with the ankle position as centre and tibiotarsus length as radius. Changes in joint angles were calculated frame-by-frame from marker coordinates using a custom MATLAB script. Length of the MTU was then determined from moment arm values and kinematics [9].

As the sonomicrometer crystals were implanted a few millimetres from the ends of a fascicle, they did not directly measure whole fascicle length. We corrected for this discrepancy by placing the muscle at the reference length (L_0) and taking a calliper measurement of fascicle length while segment length was measured via sonomicrometry. We then multiplied all sonomicrometer measurements by the ratio of whole fascicle length to measured segment length for an estimate of the whole fascicle length, for both *in vivo* and *in situ* measurements.

Tendon length-change was calculated from the value of tendon stiffness measured *in situ* and the muscle force measured *in vivo*. Measured muscle force was divided by tendon stiffness to obtain tendon length-change. No attempt was made to account for tendon hysteresis, which is expected to be small [15]. Strains of the muscle fascicle are reported relative to muscle L_0 (26.9 ± 3.1 mm), and tendon strains are reported relative to the sum of free tendon and superficial aponeurosis resting lengths (100 ± 15 mm; electronic supplementary material, table S1).

Prior to velocity calculations, MTU, muscle and tendon length measurements were inspected for high-frequency noise, and if necessary smoothed using a quintic spline interpolation in IGORPRO (s.d. 0.01–0.1). Muscle and tendon velocities were calculated by differentiating muscle and tendon length.

Instantaneous powers were calculated as the product of velocity and force, using muscle fascicle velocity to calculate

Table 1. Peak GRF, MTU force and normalized muscle recruitment (iEMG) for the LG during drop-landings. Mean $\pm$ s.d. data.

	0.5 m	1.0 m	1.5 m	ANOVA
GRF (BW)	2.8 ± 0.50	5.1 ± 0.93	8.1 ± 2.47	$F_{2,86} = 40.46$ $p < 0.0001$
MTU force (P/P_0)	0.26 ± 0.11	0.54 ± 0.21	0.71 ± 0.28	$F_{2,114} = 9.45$ $p < 0.0001$
iEMG[a]	0.25 ± 0.16	0.49 ± 0.2	0.70 ± 2.2	$F_{2,99} = 5.55$ $p < 0.01$

[a]Normalized using the mean amplitude of the strongest EMG burst recorded from a given electrode during the experiment.

fascicle power, MTU velocity to calculate MTU power and tendon velocity for tendon power. Muscle, MTU and tendon powers were divided by muscle mass (30 ± 7.8 g) to obtain muscle mass-specific power values. Work values were calculated by integrating mass-specific power over the period of interest.

Force-plate measurements of ground-reaction forces (GRF) were used to measure total mechanical energy change of the body centre of mass. Standard equations for force-plate ergometry were used [16]. The duration of landing was measured from the first detectable force-plate impulse until total GRF equalled body weight. Force-plate ergometry was used to determine total energy absorption during landing [16,17]. Initial vertical velocity for integration was determined from video of the back marker over the last five video frames prior to toe-down. Work was calculated from the time of toe-down until total GRF equalled body weight. Total GRF was calculated using the sum of vertical and horizontal forces (table 1).

To evaluate the relative contribution of the LG to total energy dissipation during landing, we compared LG muscle mass-specific negative work (J kg^{-1} muscle) to the work measured from force-plate ergometry. For these calculations, we determined the mass of the musculature from $N = 3$ turkey hindlimbs to average $8.4 \pm 0.6\%$ body mass. Extensor muscles comprised $73 \pm 2.3\%$ of total leg muscle mass, and the LG comprised $6.1 \pm 0.4\%$ of all extensor muscle mass. Thus, we predicted that, in order to perform its muscle mass-specific share of energy dissipation, the LG of one limb should dissipate 6% of the external work of landing, as measured from the force-plate.

For statistical comparisons, we used mixed-model ANOVA designs in SYSTAT v. 12.0. Generally, we evaluated the effect of landing height on strain, velocity, power and work of tendon, muscle and the whole MTU. We also evaluated the effect of tendon compliance on the energy-absorbing function of the MTU as well as its muscle fascicles. To compare muscle and tendon behaviour during different periods of the landing event, we used an ANOVA design that included length, velocity, power and work for the muscle, tendon and whole MTU as dependent variables, and subject as well as tissue (i.e. MTU, tendon or muscle) as fixed effects. As random effects, we factored height, tissue nested within height (tissue[height]) and the interaction term (subject[tissue(height)]). To determine whether velocity or power differed between tissues and landing periods within a given height, we used hypothesis tests with the interaction term from the ANOVA as the denominator when calculating the mean square error [18]. Bonferroni-corrected post hoc tests were used to avoid type 1 error due to multiple comparisons.

3. Results

All subjects performed stereotyped landings from all three heights: After toe-down, the ankle and knee joints flexed to absorb energy, ultimately bringing the animal to a crouched stand-still (figure 1). Because we were interested in the role of tendon compliance in the process of energy dissipation, we divided the landing event into two periods for analysis: F_{rise}, the period leading to the time of peak muscle force and corresponding to the time during which elastic strain energy was stored in tendon, and F_{decay}, the period after peak force when elastic energy was released. The first period F_{rise} involved rapid rise in muscle force, lasting 0.06 ± 0.03 s, which was always significantly shorter than the F_{decay} period, which lasted 0.15 ± 0.07 s (ANOVA, effect of period; $F_{2,80} = 17.84$; $p < 0.0001$). The duration of each period did not change significantly across heights ($F_{2,116} = 1.03$; $p = 0.36$).

Increases in landing height were associated with increases in GRF, peak muscle force and muscle recruitment intensity (figure 1 and table 1). Increasing height involved significantly more flexion during F_{rise} at both the ankle ($F_{2,86} = 38.37$; $p < 0.0001$) and the knee ($F_{2,88} = 14.98$; $p < 0.0001$; figures 1 and 2a,b). Muscle strain differed significantly between landing periods ($F_{1,237} = 269.89$; $p < 0.0001$). During F_{rise}, the muscle operated nearly isometrically (0.06 ± 0.04 L/L_0; figures 1 and 2c) for all landing heights ($F_{2,114} = 6.11$; hypothesis tests, effect of height, $p > 0.05$). Almost all muscle fascicle lengthening occurred during F_{decay} ($F_{1,178} = 43.23$; $p < 0.0001$; figure 2c). Net muscle lengthening strain remained constant across heights (-0.21 ± 0.09 L/L_0) ($F_{2,115} = 0.56$; $p = 0.57$). Tendon stretch during F_{rise} increased significantly with height ($F_{1,116} = 88.80$; $p < 0.0001$; figure 2d).

We determined *in vivo* muscle fascicle operating lengths by measuring muscle LT relationships *in situ* with the same length transducers used for the *in vivo* measurements. This allowed us to superimpose instantaneous muscle fascicle operating length and force onto the whole-muscle LT relationship (figure 3a). The operating length of muscle fascicles at peak force decreased significantly with height (0.5 m, 1.01 ± 0.14 L/L_0; 1.0 m, 0.91 ± 0.11 L/L_0; 1.5 m, 0.88 ± 0.10 L/L_0; ANOVA, effect of height; 0.5–1.0 m, $F_{1,14} = 10.24$, $p < 0.05$; 0.5–1.5 m, $p < 0.01$). Isometric tetanic contractions at L_0 yielded peak force outputs of 421 ± 160 N, corresponding to peak stresses of 36.9 ± 1.2 N cm^{-2}.

To determine whether temporary energy storage by tendon reduced muscle fascicle lengthening rate and attenuated muscle fascicle power across heights, we compared mean MTU and muscle fascicle velocity and power between F_{rise} and F_{decay}. The average rate of MTU stretch during F_{rise} was three- to fourfold greater than the average rate of muscle fascicle lengthening during F_{decay} for landings from all heights (mixed-model ANOVA; hypothesis test on effect of height $\times$ [tissue]; $F_{1,20} = 30.86$; $p < 0.0001$; figure 4a,c). Power attenuation was evident during 1.0 m and 1.5 m
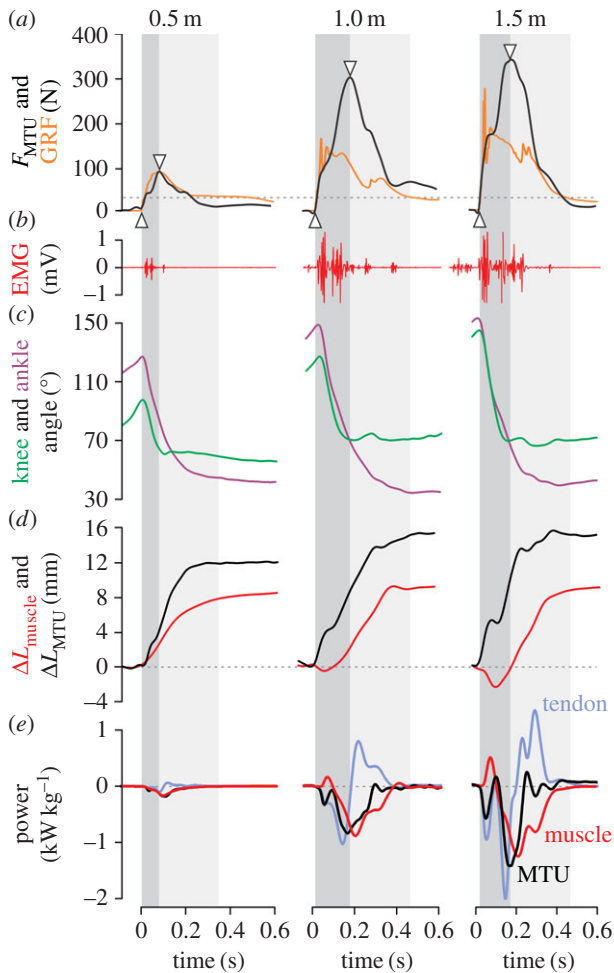
Figure 1. *In vivo* measurements taken during sample landings from 0.5, 1.0 and 1.5 m. (*a*) Landing starts with a sharp onset in ground force (△) and stops when ground force equals body mass (horizontal dashed line). Most analyses were divided into a period of rapid MTU force rise (F_{rise}, dark column) and a period of force decay (F_{decay}, light column) which defined the periods of elastic energy storage and recovery, before and after peak MTU force (▽). (*b*) Muscle recruitment intensity increased with height. (*c*) Joint flexion (numerical decrease) mainly happened during F_{rise} and increased with height, especially for the ankle. (*d*) Net MTU lengthening increased with height. Muscle lengthening was delayed relative to MTU lengthening, and mostly occurred during F_{decay} (tendon length-change is elastic and thus reflected by the MTU force trace in (*a*)). (*e*) The MTU (black) mainly absorbed energy (negative power values) during F_{rise}, and tendon (blue line) stored more energy with increasing drop height. During F_{decay}, energy was dissipated as tendon recoil did positive work to lengthen the muscle (red).

Figure 2. Time course of joint motion, muscle fibre and tendon strain. Flexion at (*a*) the ankle and (*b*) the knee mainly occurred during F_{rise} (dark column) and increased with landing height. (*c*) Muscle fascicles remained near-isometric during F_{rise} and lengthened during F_{decay} (light columns). Negative values in (*c,d*) indicate lengthening. Data are medians (circles) with quartile whiskers.
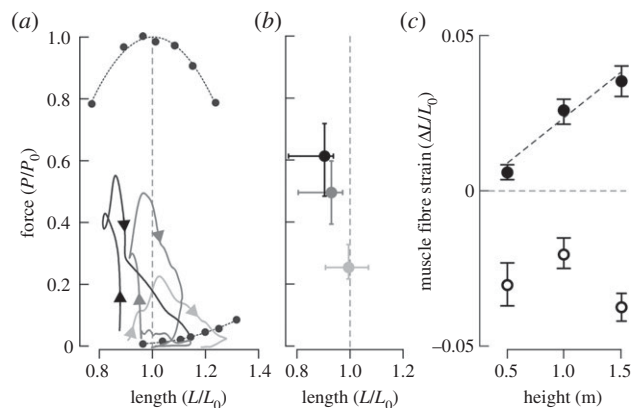
Figure 3. Muscle operating length during landings. (*a*) Representative active and passive LT curve, measured *in situ* for an LG preparation (black circles), and muscle force–fascicle length loops for representative landings for the same individual from the three heights (light grey, 0.5 m; medium grey, 1.0 m; black, 1.5 m). (*b*) Summary data from $N = 5$ muscle preparations shows that the LG operating length at the time of peak force is shorter at greater drop heights (ANOVA, $p < 0.05$). (*c*) Fascicle shortening during F_{rise} (filled circles) increased with landing height, a factor that contributed to the shorter operating length at peak force. No relationship existed between drop height and net muscle lengthening during the second part of F_{rise} (open circles). Data in (*b*) are medians (circles) with quartile whiskers, and data in (*c*) are means (circles) with s.d. whiskers.

landings (hypothesis test, effect of height[tissue]; $F_{1,20} = 30.80$; $p < 0.0001$), with a two- and three-fold difference observed between average power absorption by the MTU during F_{rise} (1.0 m, -370 ± 72 W kg^{-1}; 1.5 m, -644 ± 302 W kg^{-1}; figure 4*d*) and energy dissipation by the muscle fascicles during F_{decay} (1.0 m, -154 ± 136 W kg^{-1}; 1.5 m, -221 ± 192 W kg^{-1}; figure 4*f*).

Approximately the same amounts of energy were absorbed by the MTU during F_{rise} and F_{decay} for the 0.5 m landings (figure 5*a*) (effect of period; $F_{1,54} = 0.066$; $p = 0.8$). During 1.0 and 1.5 m landings, F_{rise} involved significantly more energy absorption by the MTU than F_{decay} ($F_{1,62} = 7.71$; $p < 0.01$; $F_{1,56} = 12.9$; $p < 0.001$). By contrast, the majority of energy dissipation by muscle fascicles occurred during F_{decay} in landings
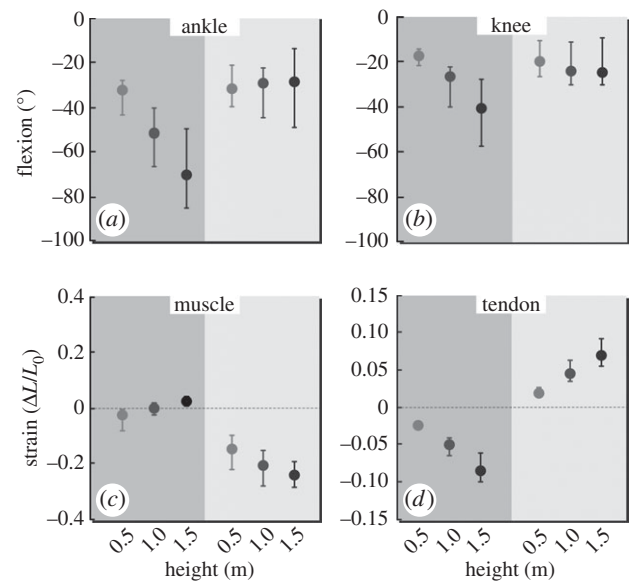
from 1.0 and 1.5 m. In landings from the lowest height, there was no statistical difference between negative work by the muscle fascicles during the two periods (effect of period; $F_{1,59} = 0.03$; $p = 0.86$). Measurements of total negative work by the MTU and the muscle during landing (figure 5*b*) were statistically different (mixed-model ANOVA; effect of tissue; $F_{1,172} = 22.4$; $p < 0.001$).

Force-plate measurements of energy absorbed agreed with the total potential energy loss calculated from body mass and fall height for 0.5 and 1.0 m landings (two-sample *t*-test, $p > 0.05$; figure 6*a*). During 1.5 m landings, force-plate
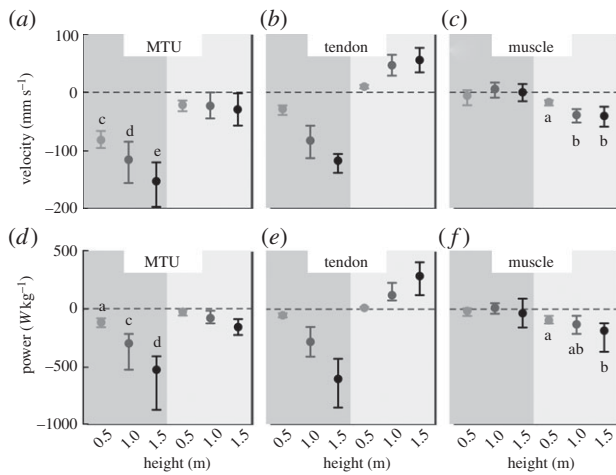
Figure 4. Velocity reduction and power attenuation across drop heights. Measurements across subjects for the periods of F_{rise} (dark column) and F_{decay} (light column) of average velocity for MTU (a), tendon (b) and muscle (c), as well as average muscle mass-specific power for MTU (d), tendon (e) and muscle (f). Negative velocity is lengthening and negative power is energy absorption. Statistically significant differences between MTU during F_{rise} and muscle during F_{decay} are indicated using lower case letters. Data are medians (circles) with quartile whiskers.
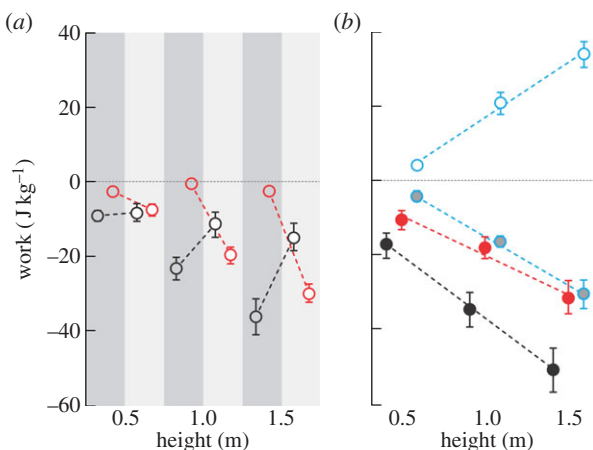

Figure 5. Mechanical work across drop heights. (a) Muscle mass-specific work during F_{rise} (dark grey bars) and F_{decay} (light grey bars), with negative values indicating energy absorption by the MTU (black) and energy dissipation by the muscle (red). The MTU absorbed energy during both periods, but the muscle did almost all of its energy dissipation during F_{decay}. (b) Energy storage by tendon (blue) during F_{rise} (grey fill) and tendon energy release during F_{decay} (white fill), compared with negative work by the MTU (black) and the muscle (red) over the entire landing. Points are staggered within height category for ease of viewing. Data are means (circles) with 1 s.e.m. whiskers.

ergometry measured less negative work than expected ($p <$ 0.05), possibly owing to friction in the pulley system, or inaccuracies in force-plate ergometry owing to rapid movement of the limb joints towards the centre of mass, and because the centre of mass height never reached zero.

To estimate the mass-specific negative work of all the hindlimb musculature, we divided the total energy dissipated by the total hindlimb muscle mass expected to be involved in resisting limb compression [12]. The total mass-specific negative work done by the hindlimb musculature was significantly greater than negative work observed for
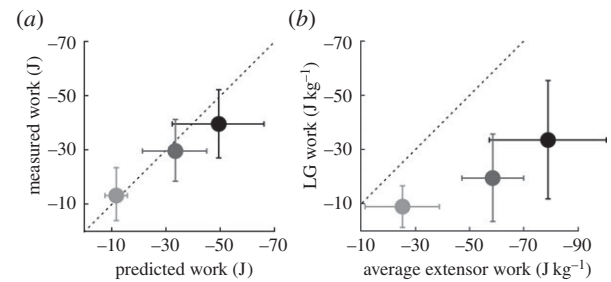

Figure 6. Energy dissipation performance by the LG. (a) For 0.5 m (light grey circle) and 1 m (dark grey circle) landings, negative work predicted from initial potential energy for a given drop height matched the negative work calculated from force-plate ergometry (t-test, $p > 0.05$). For 1.5 m landings (black circle), there was less negative work performed than predicted ($p < 0.05$), possibly owing to rope and pulley friction. (b) The LG dissipated less energy than predicted based on calculated average of muscle mass-specific work for all leg extensors. Data are means (symbols) with 1 s.d. whiskers.

the LG (figure 6b). These calculations indicate that the contribution of the LG to the total work required to decelerate the body was lower than expected if the task of energy dissipation was equally shared among the hindlimb muscles.

4. Discussion

We elicited landings from different heights to probe how the mechanical function of a single muscle was modulated with varying demand for energy dissipation. Energy dissipation by the LG increased as a function of drop height. Increases in energy input to the muscle resulted from progressively higher peak force, associated with an increase in muscle recruitment with drop height. There was no significant change in muscle strain with drop height, indicating that work was modulated primarily by changes in force. In landings from all drop heights, tendon elastic action significantly influenced the time course of energy dissipation by the muscle fascicles. Energy was initially absorbed rapidly by tendon during joint flexion, then released more slowly to do work on muscle fascicles. Tendon compliance also appeared to play an essential role in the modulation of energy absorption. Increases in joint flexion with drop height were accommodated by changes in strain of the tendon, and not the muscle fibres. These findings confirm previous observations of the importance of tendon elasticity in the process of rapid energy absorption by limb muscles [9] and demonstrate that series elastic compliance likely provides a critical mechanism for adjusting the response to varying and often unpredictable demand for energy absorption during terrestrial locomotion.

(a) The role of tendon in modulating energy dissipation

Across all drop heights, we recorded patterns of muscle length-change, force and power output that were consistent with the idea that tendon compliance provides an important safety mechanism during energy dissipation [9–11]. Tendon elastic action was characterized by an initial period of very rapid and powerful lengthening (figure 4) corresponding to rapid joint flexion, followed by a period of slower tendon recoil to release energy. Tendon stretch accommodated joint flexion, while tendon recoil drove lengthening of the active muscle. As a result of

tendon elastic stretch and recoil, length changes of active muscle fascicles were decoupled from joint movement. This decoupling led to a significant reduction in velocity of muscle fascicle lengthening for all heights, and a reduction in power input to the muscle fascicles for all but the lowest drop height (figure 4). This result supports the idea that temporary energy storage by tendon reduces peak muscle forces, rates of muscle fibre lengthening and the peak power input to muscle fibres [9,11]. The effect of this elastic mechanism under conditions where the demand for energy dissipation varies indicates that the buffering mechanism of tendons is broadly important, not just for maximal deceleration events.

The present results also suggest that tendon compliance plays an essential role in the modulation of energy dissipation with demand. During the first period of landing (F_{rise}), all increases in energy absorption with increases in drop height were owing to an increase in tendon stretch. The increase in tendon stretch with landing height was apparent in the increase in ankle flexion, thus tendon elasticity was responsible for the primary kinematic pattern of the landing. The increase in tendon stretch with drop height was owing to greater muscle recruitment (as indicated by EMG) and force (table 1). While muscle force during the first part of landing changed significantly across height, muscle fibre lengthening did not. Changes in ankle flexion, and in energy absorption, were owing to changes in the stretch of the tendon.

How are the mechanical events of energy absorption by the muscle and tendon controlled? The pattern of muscle length, force and electrical activity during landing provides some information about the possible role of sensory feedback and reflex mechanisms. It is possible that a reflex response plays a role in modulating muscle activity after the initial period of landing. A second burst of EMG activity typically occurred around halfway through the force rise period, approximately 30 ms after toe-down (figure 1). The effects of this burst, and of the brief period of inactivity preceding it, were apparent as inflexions in the muscle force profile. The stretch reflex latency, which is the earliest response to proprioceptive information from velocity-sensitive muscle spindles [19], has been determined to be 5–8 ms in a slightly smaller galliform, the guinea fowl [20]. Given this potentially very rapid response, the approximately 30 ms delay from toe-down until the second burst of activity observed in the turkey LG may be sufficient time to allow for a monosynaptic reflex response to the mechanical events following toe-down [19]. The pattern and timing of muscle length-change, however, suggest that the most common trigger of a monosynaptic reflex response, the rapid stretch of muscle spindles, may not contribute to the modulation of muscle activity in the turkey LG during most landings. In most cases, muscle fascicle lengthening did not occur until later in the landing period, usually approximately coincident with the second burst of EMG activity. Thus, there does not seem to be sufficient time, even assuming a very fast reflex response, for the observed muscle fibre lengthening to trigger a reflex response responsible for the prominent second burst of activity. Early responses would presumably be mediated by other sensory mechanisms.

Whether a reflex response is important or not, our data suggest that much of the energy absorption and joint flexion occur within a very brief (approx. 10 to approx. 20 ms) period immediately following toe-down. The rapidity of this event, as well as the prominent burst in EMG activity coincident with toe-down, suggest that essential components of muscle function during landing depend on planned, feed-forward muscle activation. One aspect of the mechanical behaviour of the muscle that is quite consistent across landing heights is the strain in muscle fibres during the initial landing period, which either undergo a small amount of shortening or remain isometric (figures 2c and 3c). How is the level of recruitment adjusted across landing heights to maintain a pattern of low muscle strain but high tendon strain during the early part of landing? It has been suggested that the combined effects of muscle force–velocity properties and tendon elasticity can make it difficult to lengthen muscle fibres during the period of muscle activation [10,11]. Any tendency to lengthen muscle fibres, for instance if landing turns out to be more forceful than anticipated, would lead to significant increase in muscle force owing to force–velocity effects [21,22]. Higher forces would tend to stretch the tendon more, thus limiting muscle strain. While the modulation in initial EMG activity with landing height indicates a planned change in muscle activation with anticipated demand for force, we propose that the dynamic interaction between muscle and tendon properties is also essential in providing some of the modulation in system behaviour with demand. The tendency of tendon to limit muscle stretch during a rapid rise in force may represent a mechanism of muscle protection that is resilient to perturbations of unpredictable intensity, and therefore highly effective for unsteady terrestrial locomotion.

(b) Muscle force–length behaviour and muscle injury risks

We found that, rather than increasing muscle strain, increases in joint flexion with drop height were accommodated by more tendon stretch. Although we did not test for muscle damage in our experiment, peak muscle stress values measured *in situ* immediately following *in vivo* measurements were quite high, and comparable to values previously measured in un-stretched preparations of the same muscle [13], suggesting that the drop-landing activities did not result in significant muscle damage.

The operating length of muscle has also been implicated as a determinant of injury risk [8]. Muscle is more prone to injury when operating on the descending limb of its LT relationship where the overlap of myofilaments in the sarcomeres decreases [8]. It has been suggested that the operating lengths of skeletal muscle should be confined to the ascending limb or plateau region of the LT curve, to reduce risks of muscle damage [7,8]. We constructed LT curves *in situ* from the same sonomicrometry crystal placements used to measure muscle length *in vivo* and could therefore map *in vivo* muscle operating lengths directly onto the LT relationship, to determine the operating length of the turkey gastrocnemius as it actively lengthened to absorb energy during landings (figure 3). We found that the muscle produced force actively over a range of lengths that included the ascending limb, plateau and descending limb of the LT curve (figure 3). However, the muscle operated on the descending limb only when forces were relatively low and when force was declining, during muscle relaxation (figure 3a). The operating length when peak force was developed varied with landing height. Peak force was developed when the muscle was on the ascending limb for 1.0 and 1.5 m landing heights, and on the plateau for the lowest landing height, 0.5 m. Early muscle shortening against tendon stretch may have contributed to allowing the muscle to develop high forces on the ascending

limb, as it reduced its operating length early in the landing during force development (figure 3c) consistent with recent findings from the toad anconeus [23]. Thus, one of the protective functions of tendon elasticity may be that it allows the muscle to operate at shorter, safer operating lengths when high forces are developed by the muscle fascicles.

Several challenges associated with interpreting whole-muscle LT measurements in the context of *in vivo* operating lengths must be acknowledged. First, our *in situ* LT curve measurement includes some error because the force measured at the tendon is not equivalent to the force in the fascicle, owing to the effect of fascicle pennation. Pennation angle changes with muscle length, thus this effect will be variable and has the potential to shift our measured value for L_0. Correction for this effect requires fibre pennation angle measurements. In experiments where this measurement is available (T. J. Roberts and N. Konow, unpublished data), correction for the effects of pennation angle yields only a small left shift of L_0 to fascicle lengths 6% shorter than shown in figure 3. Such a shift would not change the relative positions of the *in vivo* operating lengths and would not affect our conclusions about the relative operating lengths during landings.

Second, our LT curves are measured in maximally stimulated muscle, while the muscle is submaximally activated *in vivo*. It has been shown that the length at which peak force is developed is right-shifted to longer lengths in submaximally activated muscle, either owing to a length dependence of activation or to an influence on force transmission [24,25]. Such effects would influence the potential for force production at a given length. However, our primary aim was to identify the operating length of the muscle, because it is well established that muscles are more susceptible to damage at longer lengths, where sarcomere overlap is reduced [7,8]. The LT curve from maximally stimulated muscle is a faithful representation of filament overlap [26], thus it provides an accurate indicator of the relative operating length, and possible risk for damage, of the turkey gastrocnemius *in vivo*, even in submaximally activated muscle.

(c) Energy dissipation and peak muscle performance

We calculated two different measures of muscle work during landings. Negative work done by the MTU was calculated from force measured at the tendon and displacement of the MTU as calculated from kinematics and the measured joint moment arms. Negative work done by the muscle fascicles was calculated from force measured at the tendon and displacement of the fascicles, as measured by sonomicrometry. While we did expect instantaneous power to differ between MTU and fascicles at any given time, owing to tendon elastic action (figure 4), the work measured across the entire landing period, from toe-down to the end, should be equivalent as the tendon is expected to dissipate only a small fraction (approx. 5%) of the energy absorbed [15,27]. However, we found a significant difference in net energy absorbed by the MTU and the muscle fascicles, with about 1.6× as much work absorbed by the MTU (figure 5b). There are several possible explanations for this discrepancy. Estimates of MTU work relied on kinematic measurements from external skin markers in a planar view, and such estimates are subject to errors of estimating joint positions and motions [28]. Our measurements of fascicle work and power also include inaccuracies resulting from the nature of force and displacement

in pennate muscles. The displacement of the tendon owing to fibre shortening will exceed the length change measured at the fascicles, owing to the effects of fibre pennation angle and rotation of fibres during shortening [29]. Measured MTU excursions were greater than fascicle excursions over the entire event, suggesting that the effects of fibre rotation were significant (figure 1). We did not attempt to correct for the effects of fibre angle and rotation, or 'gearing', because this effect is variable and unknown for the pattern of muscle contraction in this study. Gearing values during lengthening contractions can be quite high [30]. The effects of gearing would tend to give us an underestimate of muscle work from the product of tendon force and fascicle displacement. The large discrepancy between MTU work measured from kinematics and MTU work measured from sonomicrometry and tendon strain gauges suggests that the effect of fibre gearing may be substantial during landings.

Our estimates of total muscle mass-specific energy absorption provide some insight into the possible limits of energy absorption by skeletal muscle. The present measurements involve demanding dissipative events, and we found that the total energy absorbed by the turkey gastrocnemius ranged from $-10.6 \, \text{J kg}^{-1}$ on average during landings from 0.5 m, to $-32.5 \, \text{J kg}^{-1}$ on average during landings from 1.5 m (figure 5). By comparison, the turkey LG absorbs approximately $-4.6 \, \text{J kg}^{-1}$ per step during downhill running on a 12° decline [12]. The mechanical energy *production* (positive work) per step for the turkey LG during running on a 12° incline is approximately 7 J kg^{-1} [12], and during acceleration the work done in a step by the hindlimb musculature reaches as high as 26 J kg^{-1} [17]. These comparisons suggest that the $-32.5 \, \text{J kg}^{-1}$ of work measured in the LG during landing is a substantial amount of energy absorption, and if the actual net energy dissipation is closer to our MTU work measurements, the average energy absorption by the LG during 1.5 m landings may be as high as $-51 \, \text{J kg}^{-1}$. Force-plate-based measurements of the total energy dissipated during turkey landings indicate that energy absorption by other muscles may be even greater. For the highest landings (1.5 m), the total energy absorbed per kilogram of hindlimb muscle significantly exceeded that measured for the LG (figure 6b), reaching an average of $-77.9 \, \text{J kg}^{-1}$ muscle mass. This calculation suggests that other muscles may absorb more energy than the LG, on a muscle mass-specific basis. Alternatively, non-muscular routes of energy dissipation may be important. In human walking, the damped vibrations of soft tissues dissipate energy [31], and this mechanism may occur in turkey landings as well. Thus, 77.9 J kg^{-1} of energy dissipated by the hindlimb extensor musculature might be an overestimate.

5. Conclusion

Limb muscles face risks of stretch-induced injury when undergoing active lengthening to dissipate energy and act as brakes to decelerate locomotor movements. Results from turkey drop-landings show that tendon spring-like mechanics permit modulation of muscular energy dissipation mechanics to meet variable demands for energy dissipation. Tendon compliance lets the muscle contract at shorter and potentially safer operating lengths during force development, and further reduces the risk of muscle injury by buffering against excessively rapid and powerful muscle lengthening.

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