

Joint work and power associated with acceleration and deceleration in tammar wallabies (*Macropus eugenii*)

C. P. McGowan^{1,*}, R. V. Baudinette² and A. A. Biewener¹

¹Concord Field Station, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA and ²Department of Environmental Biology, University of Adelaide, Adelaide, SA 5003, Australia

*Author for correspondence (e-mail: cmcgowan@oeb.harvard.edu)

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Summary

Measurements of joint work and power were determined using inverse dynamics analysis based on ground reaction force and high-speed video recordings of tammar wallabies as they decelerated and accelerated while hopping over a force platform on level ground. Measurements were obtained over a range of accelerations ranging from -6 m s^{-2} to 8 m s^{-2} . The goal of our study was to determine which joints are used to modulate mechanical power when tammar wallabies change speed. From these measurements, we also sought to determine which hind limb muscle groups are the most important for producing changes in mechanical work. Because our previous *in vivo* analyses of wallaby distal muscle function indicated that these muscle–tendon units favor elastic energy savings and perform little work during steady level and incline hopping, we hypothesized that proximal muscle groups operating at the hip and knee joint are most important for the modulation of mechanical work and power. Of the four hind limb joints examined, the ankle joint had the greatest influence on the total limb work, accounting for 89% of the variation observed with changing speed. The hip and metatarsophalangeal (MP) joints also contributed to modulating whole limb work,

but to a lesser degree than the ankle, accounting for 28% (energy production) and -24% (energy absorption) of the change in whole limb work *versus* acceleration, respectively. In contrast, the work produced at the knee joint was independent of acceleration. Based on the results of our previous *in vivo* studies and given that the magnitude of power produced at the ankle exceeds that which these muscles alone could produce, we conclude that the majority of power produced at the ankle joint is likely transferred from the hip and knee joints *via* proximal bi-articular muscles, operating in tandem with bi-articular ankle extensors, to power changes in hopping speed of tammar wallabies. Additionally, over the observed range of performance, peak joint moments at the ankle (and resulting tendon strains) did not increase significantly with acceleration, indicating that having thin tendons favoring elastic energy storage does not necessarily limit a tammar wallaby's ability to accelerate or decelerate.

Key words: locomotion, hopping, joint power, inverse dynamics, tammar wallaby, *Macropus eugenii*.

Introduction

Terrestrial animals that move with a bouncing gait, such as running, trotting or hopping, take advantage of energy stored elastically in the limbs to reduce the metabolic cost of locomotion at steady speeds (Alexander, 1988; Cavagna et al., 1977; Taylor, 1994). Wallabies are among a large group of cursorial animals that have evolved muscle–tendon units with short fibers and long tendons that appear particularly well adapted for this purpose (Alexander and Vernon, 1975; Alexander et al., 1982; Dimery et al., 1986; Ker et al., 1986). Because the architecture of muscle–tendon units has a strong influence on muscle function, having muscle groups that are specialized for one function may therefore limit their ability to perform others. Specifically, muscle–tendon units that function well for storing elastic energy may be ill suited for producing

mechanical work (Biewener, 1998; Biewener and Roberts, 2000). Recent *in vivo* muscle studies (Biewener et al., 2004; Daley and Biewener, 2003; Roberts et al., 1997) have explored the role and potential constraints on function of distal muscle–tendon units during locomotion on level *versus* incline surfaces, but only a few studies have explored how an animal's limb as a whole functions to modulate power for non-steady activities (Aerts, 1998; Dutto et al., 2004; Jacobs et al., 1996; Prilutsky and Zatsiorsky, 1994; Roberts and Scales, 2004).

The goal of this study was to determine, through inverse dynamics analysis, which hind limb joints in tammar wallabies are active in modulating the changes in energy associated with changing speed. While this approach is unable to provide the direct evaluation of muscle function achieved

through *in vivo* studies, analysis of joint power and work provides a broader overview of how energy is modulated by the limb as a whole and thus provides further insight into how muscles and muscle groups are recruited to meet the demands of the environment.

During steady-state locomotion, an animal's muscles perform no net mechanical work on the center of mass. Although individual muscles may do both net positive (energy production) and negative work (energy absorption) during steady speed movement, many muscles probably act as struts, generating force under fairly isometric conditions. The tendons of these muscles provide elastic energy savings by being stretched to absorb energy in the braking phase of stance and recoiling to return their strain energy in the propulsive phase (Biewener and Roberts, 2000; Dickinson et al., 2000; Ker et al., 1986; Roberts et al., 1997). When animals accelerate or decelerate, however, they must produce or absorb net mechanical energy. Much of this is likely to occur in the muscles of the limbs.

On a mass- or volume-specific basis, vertebrate skeletal muscles have generally similar capacities to produce mechanical work. However, muscle-tendon unit architecture can greatly influence the role they play in locomotion (Biewener, 1998; Biewener and Roberts, 2000; Roberts et al., 1997; Roberts, 2002).

Muscles composed of short, pinnate fibers (and thus a relatively large cross sectional area) coupled in series with long, thin tendons form muscle-tendon units that are effective for storing elastic strain energy. This is in contrast to muscles with long, generally parallel fibers that may be better suited for changing length and doing mechanical work. However, longer fibered muscles probably cost more energy per unit mass when they contract because a larger volume of muscle must be recruited to generate a given amount of force (Roberts et al., 1998; Biewener, 1998; Biewener and Roberts, 2000). Hence, a trade-off may exist between a muscle's ability to store elastic energy and its ability to generate power.

In wallabies, as in most cursorial animals, the majority of musculature is located proximally in the limb. Consequently, many of the muscles acting at the hip and knee are large and of a design that favors power production, while those that act at distal joints appear better suited for elastic energy savings. This suggests a possible regional specialization in the functional role of muscle groups acting at different joints within the wallaby's limb.

An important question is the extent to which the contractile behavior of an individual muscle may change versus how muscle groups with differing architecture may be recruited to modulate changes in mechanical function during locomotion. Recent *in vivo* studies have begun to explore this question, focusing on more distal limb muscles that favor elastic energy savings. Work by Roberts et al. (1997) compared turkeys (*Meleagris gallopavo*) running on level and inclined surfaces, showing that the turkey's lateral gastrocnemius muscle-tendon unit shifts from low work and elastic savings on the level to net work production and elastic savings during incline running.

However, in a similar study of tammar wallabies, Biewener et al. (2004) found that the lateral gastrocnemius and plantaris muscles did not change their function. Both muscle-tendon units stored elastic energy during level and inclined hopping but contributed no net work to raising the animal's center of mass on a 10° incline. This suggests that the role of the ankle extensors in tammar wallabies may be more limited by their design than in turkeys, and that proximal limb muscles are recruited to provide the required work needed during incline hopping or acceleration. As a result, a 'division of labor' may exist among hind limb muscle groups in wallabies, such that work for acceleration would occur mainly at the knee and hip joints.

However, several hind limb muscles span multiple joints and studies exploring the role of bi-articular muscles in locomotion have shown that significant energy may be transferred between proximal and distal joints (Bobbert et al., 1986; Jacobs et al., 1996; Prilutsky and Zatsiorsky, 1994; Prilutsky et al., 1996). In activities such as sprinting, jumping and landing, in which substantial net mechanical work must be done on the center of mass (CoM) of the body, energy passes from distal to proximal joints during the braking phase of stance and from proximal to distal joints in the propulsive phase (Jacobs et al., 1996; Prilutsky and Zatsiorsky, 1994). This pattern is quite pronounced in jumping galagos (Aerts, 1998), in which 68% of total external work is delivered at the ankle and as much as 65% of this energy is transferred from the knee. Because of their similar musculoskeletal arrangement, it seems probable that significant energy transfer may also occur in wallabies. Thus, while proximal muscles are most likely to produce or absorb energy, we expect that external measurements will show that the work for accelerating or decelerating is delivered at the ankle joint, transferred from the hip and knee via the relatively isometric contraction of ankle extensors.

Assuming that the ground reaction force passes through or near the animal's CoM, which is located anterior to its hip, we also expect large extensor moments to be generated at the hip and ankle joints during stance. Therefore, these joints may play a role in producing the work needed to accelerate or decelerate the animal. This pattern has recently been observed in jumping horses (Dutto et al., 2004).

Our goal in this study, therefore, was to explore how proximal *versus* distal limb joints modulate the work necessary for tammar wallabies to change speed during level hopping, using inverse dynamics analysis. From this analysis, we sought to identify the roles of proximal versus distal muscle groups of tammar wallabies in relation to their fiber-tendon architecture and whether a division of labor exists within their hind limb. Based on the results of our prior *in vivo* studies of their distal ankle muscle-tendon units (Biewener et al., 1998; Biewener et al., 2004), we expect that much of the work necessary for acceleration and deceleration will be produced by proximal hind limb muscles, but will be delivered largely at the ankle joint through energy transfer *via* bi-articular muscles.

Table 1. Morphometric data from a cadaver

Segment	Mass (kg)	Length (m)	CG (%)	MoI (kg m ²)
Thigh	0.441	0.129	39.5	2.80×10 ⁻³
Shank	0.198	0.191	19.5	2.79×10 ⁻⁴
Foot	0.034	0.107	40.4	4.62×10 ⁻⁵
Toes	0.017	0.072	39.5	4.21×10 ⁻⁵

Body mass = 7.40 kg.

CG, segment centers of gravity (as a percentage of the segment length from the proximal end); MoI, segmental moment of inertia.

Materials and methods

Animals

Six adult tammar wallabies, *Macropus eugenii* L. (three male and two female, ranging from 5.77 to 7.15 kg body mass) were trained to hop in a 22 m outdoor runway. The animals were selected from a breeding colony maintained by Adelaide University at the Waite Institute campus in Adelaide, South Australia. The colony was housed in a system of large outdoor paddocks and animals used for experimentation were kept in a paddock separate from the main colony. The outdoor runway was constructed within the confines of one of the larger paddocks.

Runway and experimental protocol

A 22 m×0.75 m runway was constructed from light-gauge field fencing strung from fence posts placed in the ground over a level stretch of the grassy outdoor paddock. The runway was closed at both ends to completely contain the animals. A 0.60 m×0.40 m force-plate was set flush with the ground at approximately the midpoint of the runway. The force plate was positioned on a 5 cm thick concrete slab buried in the ground and a wooden frame the same depth as the force-plate was used to keep the surrounding soil from contacting the plate. The wallabies were placed in the runway area and encouraged to hop from end to end. Accelerations were elicited by startling the animal from behind as it approached the plate at a steady speed. Decelerations occurred often with little outside prompting from the investigators. Approximately 15–20 trials were collected from each animal but only a small subset could be analyzed for this study. For trials to be included, the wallaby

had to make at least one hop preceding the hop on the plate, both feet had to strike the plate simultaneously, and all joint markers had to be visible for video analysis. In addition, only those trials in which the animal's acceleration was primarily in the horizontal direction were analyzed, excluding trials in which the animals jumped more vertically from the plate. Twenty-nine trials, ranging from four to seven trials from each animal, fit these criteria for analysis. There was no significant effect of individual on the variables measured as determined by an analysis of variance (ANOVA).

In all five animals, segment lengths and muscle moment arms were palpated and measured with digital calipers. These measurements were later confirmed by dissection of four of the animals that were killed after being used in a subsequent experiment. In the dissected animals, masses and moment arms were recorded for all muscles in the limb. An additional cadaver was used to determine segment masses and moments of inertia for the thigh, shank, foot and toes (following the method of Blickhan and Full, 1992) for use in the inverse dynamics calculations (Table 1) (see below). These values were corrected to individual values for each of the animals used in this study assuming geometric scaling (Table 2).

Ground reaction forces

Ground reaction forces (GRF) were recorded using a multi-component piezoelectric force-plate (Kistler type 9286AA; Kistler Instruments Corp., Amherst, NY, USA) with an integrated charge amplifier (crosstalk between channels <1.0%). Forces were recorded in the vertical, horizontal and lateral directions. Lateral forces were always quite small and for the purposes of this study were ignored. Force-plate recordings were sampled at 1000 Hz and transferred to computer and stored by means of a BioWare™ type 2812A1-3 A/D system (DAS1602/16 A/D board) operated using BioWare v.3.0 software (Kistler Instruments Corp.).

Kinematics

Trials were filmed in the lateral view with a digital high-speed video camera (Redlake Motionscope PCI-500, San Diego, CA, USA) recording at 125 Hz. Video and force-plate data were synchronized *via* a trigger that simultaneously stopped video recording and sent a voltage pulse to a separate

Table 2. Morphometric data from the five animals used in this study

	Animal					Mean
	1	2	3	4	5	
Body mass (kg)	6.78	6.74	5.77	6.76	7.15	6.64±0.52
Segment lengths (m)						
Thigh	0.122	0.124	0.113	0.120	0.119	0.120±0.004
Shank	0.189	0.187	0.178	0.191	0.191	0.187±0.005
Foot	0.075	0.074	0.076	0.066	0.068	0.072±0.004
Toes	0.050	0.063	0.053	0.059	0.057	0.056±0.005

These values were used to calculate the center of gravity (CG) and mass moment of inertia (MoI) for each segment based on the values from Table 1 and assuming geometric scaling. Values are means ± s.d.

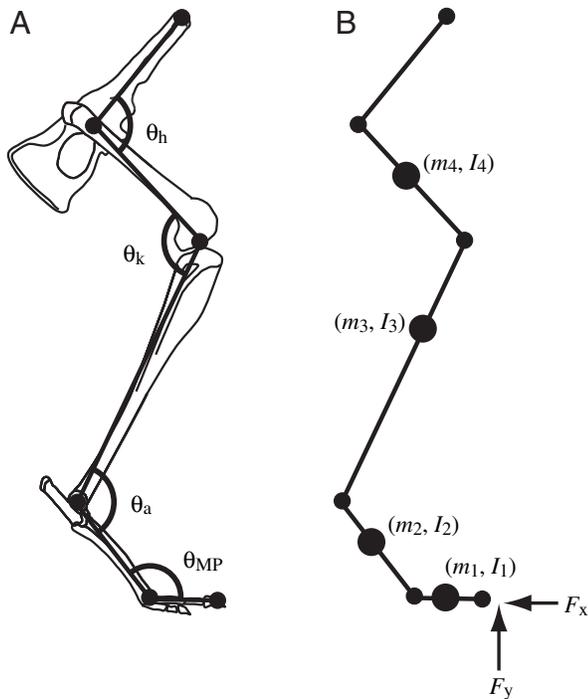


Fig. 1. A schematic diagram of the linked segment model used to calculate joint moments, power and work. (A) The internal angles that were measured. Angles (θ) were measured at hip (h), knee (k), ankle (a) and metatarsophalageal joint (MP). (B) Elements of the linked segment model used in the inverse dynamics calculations, where m is the mass of each segment, I is the mass moment of inertia of each segment and F_x and F_y are the horizontal and vertical ground reaction forces (GRF), respectively. The center of pressure of the GRF on the foot was determined by the force plate.

channel being recorded in conjunction with the force-plate outputs. The camera was positioned approximately 7 m from the runway to reduce the effects of parallax. The hind limbs of the animals were shaved using small animal clippers and the joint centers of rotation were palpated and marked with white paint. Points marked included the hip, knee, ankle, metatarsophalageal (MP) joint and the tip of the longest phalange as well as a trunk point identified by the anterior tip of the ilium (Fig. 1). Joint markers, as well as the location of the force-plate and in-field scale bars were digitized using a customized MATLAB (v.6.5, The MathWorks, Natick, MA, USA) routine. Because of the skin movement over the knee during locomotion, the coordinates of the knee joint were calculated by generating the equations for circles centered at the coordinates of hip and ankle, with the length of the femur and tibia being their radii, respectively. The knee joint location was determined by the intersection point of these two circles that most closely matched the digitized knee point. The other intersection point was always clearly incorrect. The trigger pulse, in conjunction with the digitized coordinates of the scale bar and force-plate were used to scale and align the kinematic data with GRF data.

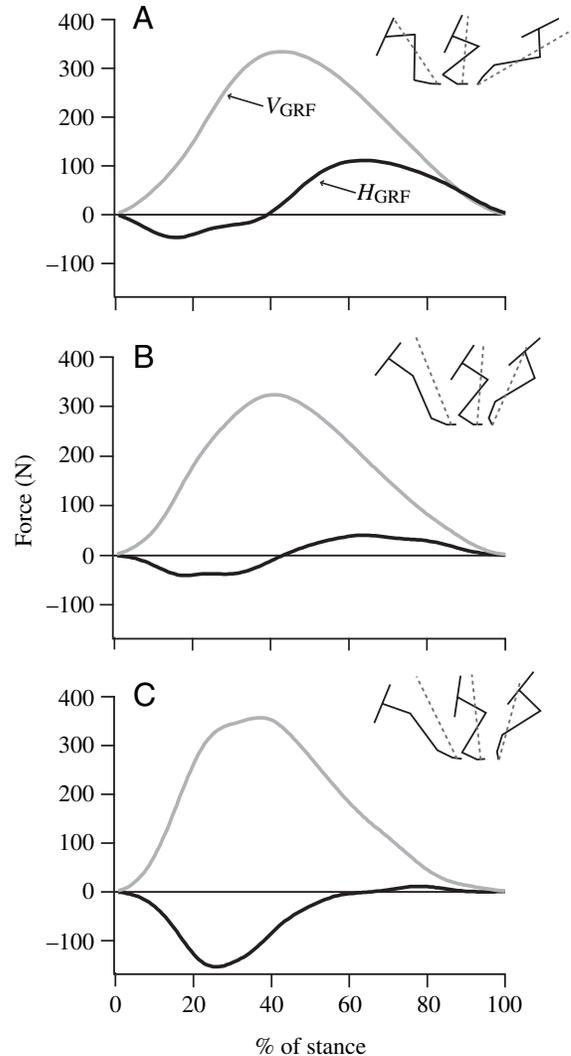


Fig. 2. Representative GRF recordings from (A) a large acceleration trial, (B) a steady speed trial and (C) a large deceleration trial, normalized to percentage of stance time. The insets show the average limb position at the time of first contact, midstance and last contact relative to the orientation of the GRF vector (red broken line). Note the broken red line does not represent the magnitude of the GRF.

Calculation of joint moments, power and work

Inverse dynamics analysis was used to calculate the total net moment at each joint. The analysis consisted of combining GRF, kinematics and morphometric data to create a linked segment model consisting of a toe, foot, shank and thigh (Fig. 1). The following equations were solved for each segment, beginning with the most distal, where the GRF was applied:

$$\sum F_{x,y} = ma_{x,y} \quad (1)$$

$$\sum M_j = I_j \alpha_j, \quad (2)$$

where $F_{x,y}$ are the external forces in the horizontal and vertical directions (including forces due to gravity), m is the mass of

the segment, $a_{x,y}$ are the linear accelerations of the center of gravity (CG) in both directions, M_j is the moment generated by $F_{x,y}$ about the CG, I_j is the moment of inertia about the CG, and α_j is the angular acceleration. It was assumed that, at each instant, the value derived for M was equal to the net moment being exerted by the muscles acting at that given joint (Aerts, 1998; Winter, 1990). In this experiment, positive values for M represent an extensor moment (balanced by extensor musculature), and negative values a flexor moment (balanced by flexor musculature). The center of pressure (CoP) of the GRF acting on the toe was supplied by the force-plate. Errors in the alignment of kinematic data with CoP can have a considerable effect on the calculation of joint moment (up to 25% at the extremes in the case of a tammar wallaby). Therefore, each trial was checked graphically to ensure that the CoP lined up under the large fourth toe, which is the only portion of the foot in contact with the ground throughout stance. The CoP occurred at the proximal portion of the toe at initial contact and moved distally until it was centered under the toe tip just before the foot left the ground. In this way, the alignment of kinematics and CoP was as accurate as possible.

Instantaneous power at each joint was calculated by multiplying the joint moment by the angular velocity at that joint. Total limb power was derived by summing the instantaneous powers from each joint. The net work delivered by each joint during stance was determined by integrating the power curve for that joint over the stance time. Total limb work was the sum of work performed at all of the joints. These values were compared with the net center of mass work, calculated from GRF and the kinematics of the initial conditions (Cavagna, 1975).

Results

Ground reaction forces

Trials ranged from a maximum deceleration of -6 m s^{-2} to a maximum acceleration of nearly 8 m s^{-2} during a single stance phase, resulting in changes in the animal's hopping speed of approximately -0.70 and 0.80 m s^{-1} , respectively. Wallabies hopped at an average forward velocity of $4.15 \pm 1.15 \text{ m s}^{-1}$ (\pm S.D.) prior to contacting the force plate in these trials. No significant relationship was found between average velocity and acceleration ($r^2=0.12$, $P=0.068$).

Tammar wallabies controlled their acceleration by modulating the propulsive ($+H_{\text{GRF}}$) and breaking ($-H_{\text{GRF}}$) components of the horizontal ground reaction force, with little change in vertical force (V_{GRF}). Representative data from a large acceleration trial, a steady hopping trial, and a large deceleration trial (Fig. 2) show the extremes of the ground reaction force patterns that we observed. An initial breaking force was followed by a propulsive force in all but the largest acceleration and deceleration trials that we recorded (not shown in Fig. 2). Mean GRFs averaged over stance and normalized to the animal's body weight (**BW**) versus acceleration are shown in Fig. 3. When accelerating, mean $+H_{\text{GRF}}$ increased linearly with increased acceleration

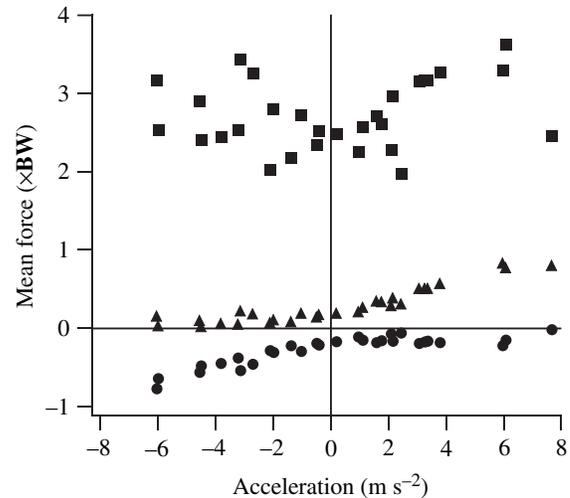


Fig. 3. The mean vertical (V_{GRF} , squares), propulsive ($+H_{\text{GRF}}$, triangles) and breaking ($-H_{\text{GRF}}$, circles) forces in \times BW versus acceleration. During accelerations, both V_{GRF} and $+H_{\text{GRF}}$ increased with acceleration; however, the trend for V_{GRF} was not significant ($r^2=0.93$, $P<0.0001$; $r^2=0.23$, $P=0.072$, respectively). During decelerations, only $-H_{\text{GRF}}$ was significantly correlated with acceleration ($r^2=0.89$, $P<0.0001$).

magnitude ($r^2=0.93$, $P<0.0001$) while $-H_{\text{GRF}}$ remained constant, averaging $-0.14 \pm 0.06 \text{ BW}$ (\pm S.D.). The mean V_{GRF} during accelerations also showed a small but non-significant increase with increased acceleration ($r^2=0.23$, $P=0.072$). Conversely, when decelerating, mean $-H_{\text{GRF}}$ increased linearly with increased acceleration magnitude ($r^2=0.89$, $P<0.0001$) whereas $+H_{\text{GRF}}$ changed very little, averaging $0.11 \pm 0.64 \text{ BW}$. During decelerations, the mean V_{GRF} was independent of acceleration ($r^2=0.08$, $P=0.320$).

Kinematics

Limb protraction and retraction angles were measured as the angle of a line joining the hip and toe, relative to vertical at first and last contact with the ground, respectively, with excursion angle being defined as the sum of these two angles. During accelerations, the retraction angle increased significantly (Fig. 4B; $r^2=0.63$, $P=0.0001$). The protraction angle also showed a trend towards increasing with increased acceleration, however with the current sample size this was not significant (Fig. 4A; $r^2=0.23$, $P=0.068$). During decelerations, both protraction and retraction angles increased significantly with increased deceleration magnitude (Fig. 4A,B; $r^2=0.53$, $P=0.008$; $r^2=0.66$, $P=0.0001$, respectively). Limb excursion angle also increased significantly with both acceleration and deceleration magnitude such that minimum limb excursions occurred during steady speed trials (Fig. 4C; $r^2=0.63$, $P=0.0002$; $r^2=0.74$, $P=0.0003$, respectively).

Because recorded acceleration trials represent a continuum of the animals' acceleration performance during hopping, we selected four trials from each condition to characterize differing kinematic patterns for acceleration and deceleration

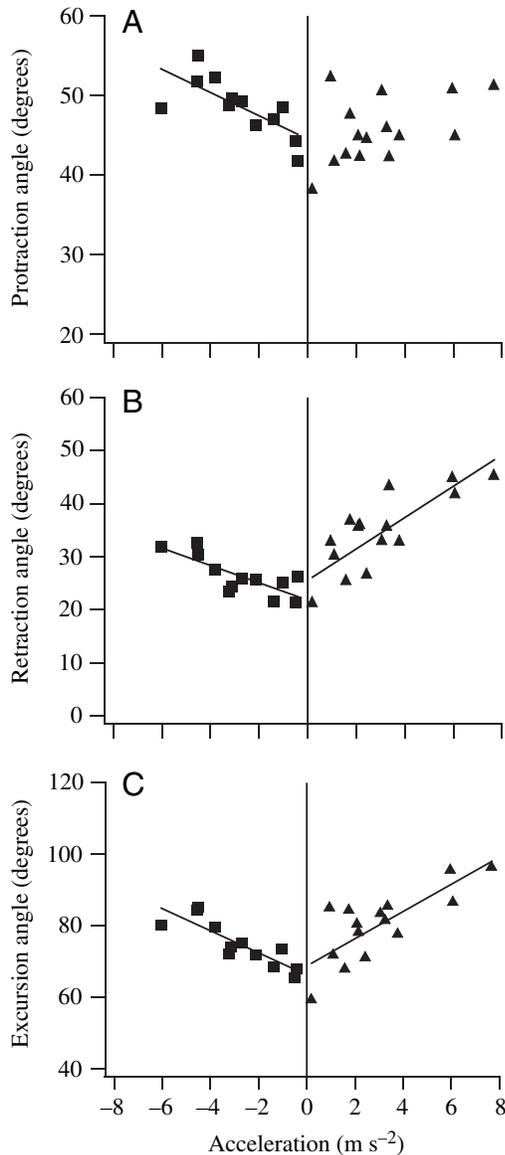


Fig. 4. Graphs of (A) limb protraction angle, (B) limb retraction angle and (C) limb excursion angle *versus* acceleration. During acceleration trials (triangles), limb protraction angle did not change significantly with acceleration, while retraction angle increased with increasing accelerations. In deceleration trails (squares), both limb protraction and retraction angles increased with increasing deceleration magnitude. Limb excursion angle increased linearly with both acceleration and deceleration magnitude. See text for further details.

versus steady speed (Fig. 5). The trials selected represented the extremes of acceleration and deceleration conditions. Mean accelerations for each of the resulting groups were $-5.27 \pm 0.86 \text{ m s}^{-2}$, $-0.07 \pm 0.45 \text{ m s}^{-2}$ and $5.88 \pm 0.80 \text{ m s}^{-2}$ for deceleration, steady speed and acceleration conditions, respectively. Comparisons among these three sets of trials reveal that the largest differences, with respect to steady speed trials, during decelerations occurred at the knee and MP joints (Fig. 5B,D). The knee showed earlier and increased flexion in the first half of stance followed by decreased extension in the

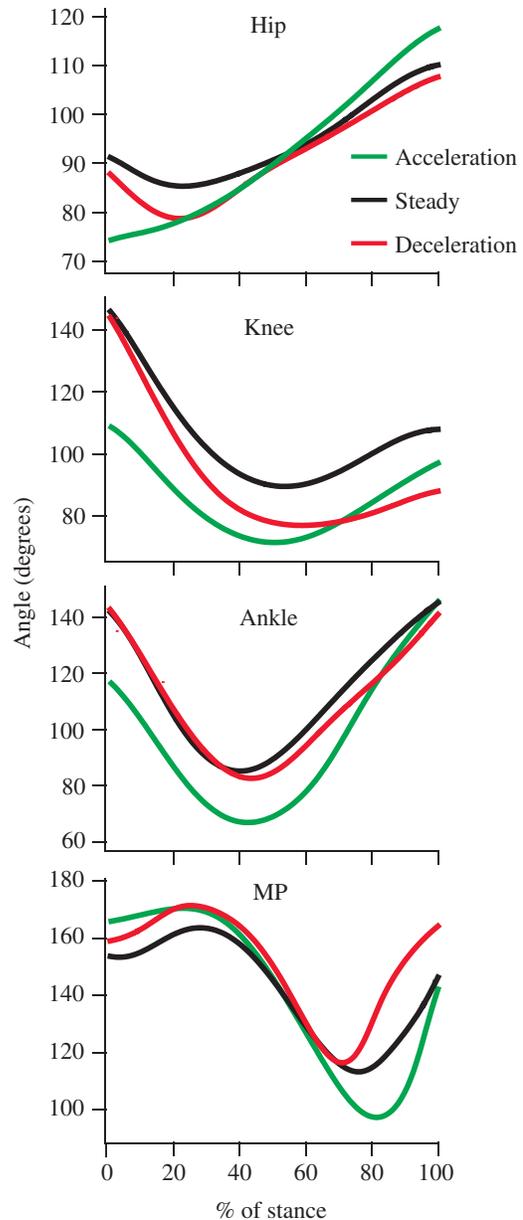


Fig. 5. Graphs of the average change in joint angle during stance for the hip, knee, ankle and metatarsophalangeal joint (MP) during accelerations (green), steady speed (black) and decelerations (red). Solid lines are the average of four trials for each condition. The mean accelerations of these groups were: $5.88 \pm 0.80 \text{ m s}^{-2}$, $-0.07 \pm 0.45 \text{ m s}^{-2}$ and $-5.27 \pm 0.86 \text{ m s}^{-2}$ for accelerations, steady speed and decelerations, respectively. Standard errors for each joint angle curve have been omitted for the sake of clarity.

latter half. The MP joint underwent a greater initial extension, followed by flexion and then greater extension in the last third of stance. This resulted in the limb being more flexed at mid-stance and at toe off (Fig. 2C, inset).

Differences in kinematic patterns during acceleration trials relative to steady speed were observed at all four joints. The hip, knee and ankle joints were all more flexed at the onset of stance. The hip then extended throughout the stance phase

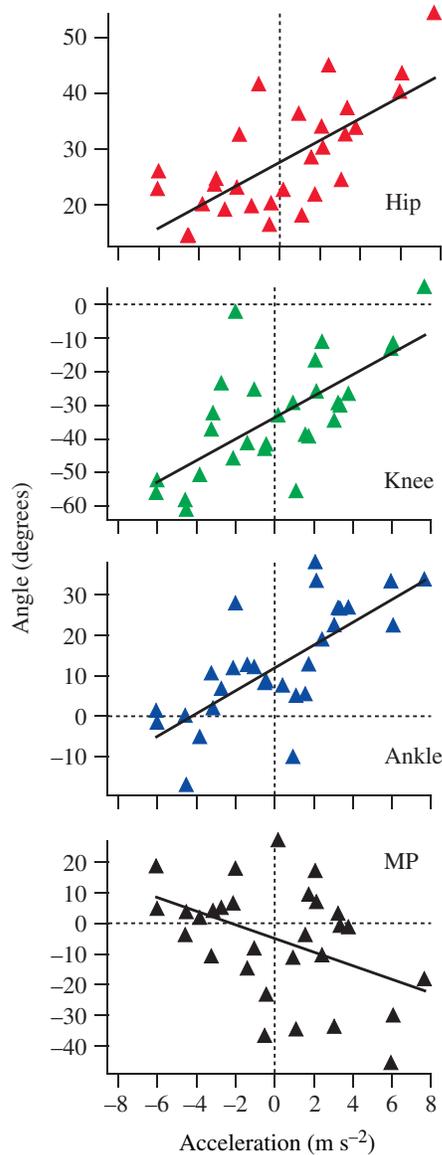


Fig. 6. A graph showing the net angle change during stance at each joint as a function of acceleration. Positive values represent net joint extension while negative values represent net joint flexion. The results of linear regressions showed significant correlations at all joints (hip: $r^2=0.50$, $P<0.0001$; knee: $r^2=0.47$, $P<0.0001$; ankle: $r^2=0.51$, $P<0.0001$; MP: $r^2=0.19$, $P=0.017$).

with no initial flexion (Fig. 5A). Correspondingly, the knee flexed less early in stance and extended more later in stance compared to steady speed trials (Fig. 5B). Being more flexed at the start of stance, the ankle reached peak flexion at mid-stance but then re-extended to a similar angle seen at the end of stance in both steady and deceleration trials (Fig. 5C). The MP joint flexed to a greater extent later in stance compared with both steady speed and deceleration trials, and then re-extended rapidly at the end of stance (Fig. 5D). The overall result was that the limb was more flexed at the start of stance and underwent a greater amount of net extension throughout stance (Fig. 2A, inset) when the animals accelerated.

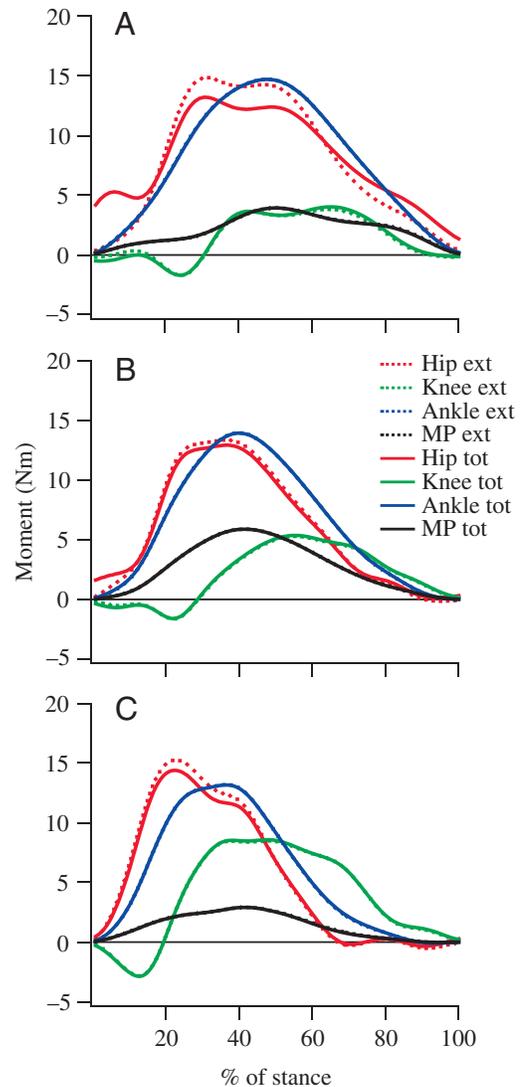


Fig. 7. Graphs of total joint moments (tot), including inertial and gravitational components (solid lines) and external joint moments (ext, dotted lines) from a representative trial for each condition: (A) acceleration, 5.97 m s^{-2} , (B) steady speed, -0.41 m s^{-2} and (C) deceleration, -5.99 m s^{-2} . During accelerations, moments reach a peak later in stance and are maintained for a longer duration of the stance period, as compared to steady speed trials. Conversely, during decelerations the moments reach a peak early in stance and fall to near zero for the later part of stance. Peak moments for all joints remains relatively constant across trails. Note that the difference between total joint moments and external joint moments is small and can only be seen at the hip.

Consistent with these patterns, net joint excursion angles recorded for all the trials showed a significant relationship with acceleration, with the hip, knee and ankle joints undergoing greater net extension and the MP increased net flexion with increased acceleration (Fig. 6).

Joint moments

External and internal (inertial plus gravitational) moments

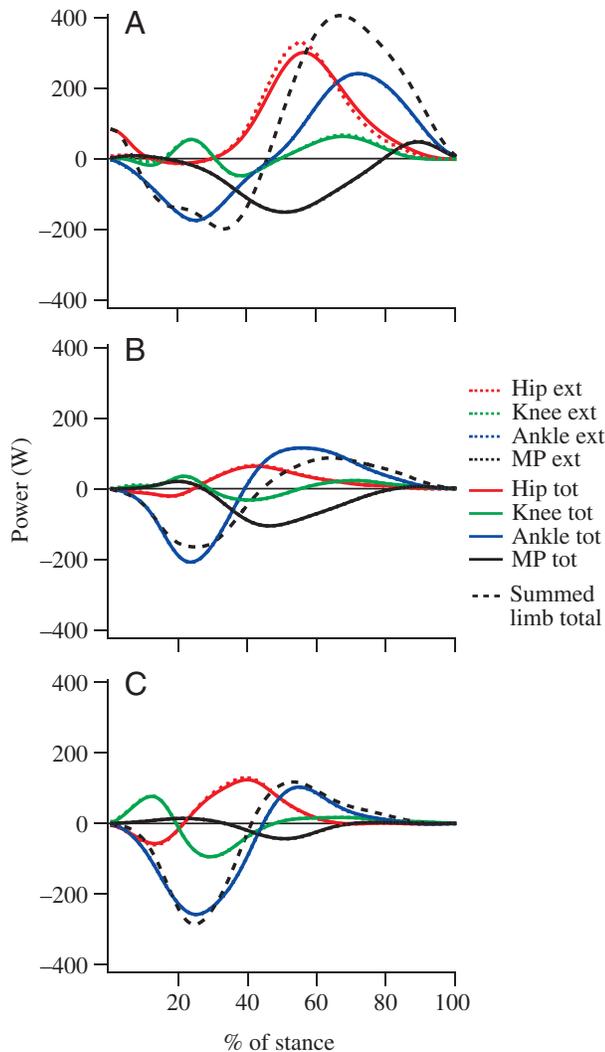


Fig. 8. Total joint power (tot, solid colored lines), external joint power (ext, dotted colored lines) and summed limb power (broken black lines) for the representative trials shown in Fig. 6. The majority of the power for changing speed is produced at the hip (red) and ankle (blue). Peak powers at the knee (green) increase during accelerations and decelerations, but the net work remains relatively constant. The MP (black) produces more negative power with increased accelerations.

were summed to give the total net moment at each joint. Internal moments were very small relative to external moments at all joints except the hip (Fig. 7). However, even at the hip joint internal moments never exceeded 15% of the peak external moment. Whereas the internal moment acts to increase the joint moment at the hip early in stance during acceleration and steady speed trials, it reduces the magnitude of the total moment during the middle third of stance when it is highest. This was the case for all trials. In general, total joint moments were similar in magnitude and differed between conditions mostly with respect to timing. For all conditions, the largest peak moments were recorded at the hip and ankle joints. During deceleration, total joint moments peaked earlier and fell to nearly zero for the last 20% of stance at all joints but the

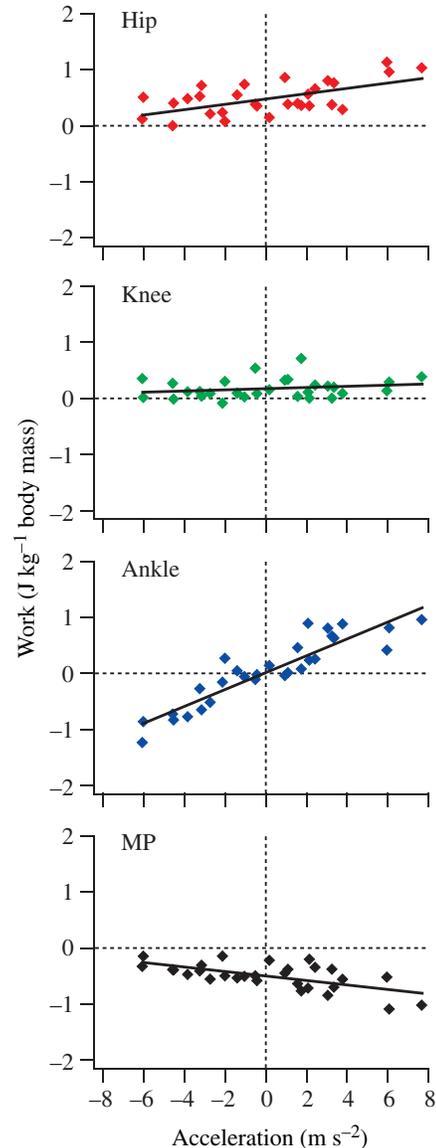


Fig. 9. Net work produced at each joint per kg body mass *versus* acceleration. The slope of regression lines was steepest at the ankle, indicating that the modulation of limb work during accelerations and decelerations occurred primarily at this joint. Work at the hip and MP also had a significant relationships with acceleration but with shallower slopes than at the ankle. The amount of work done at the knee was low and independent of acceleration. Linear regressions are: hip, $y=0.095x+0.954$, $r^2=0.035$, $P<0.001$; knee, $y=0.021x+0.347$, $r^2=0.05$, $P=0.256$; ankle, $y=0.302x+0.024$, $r^2=0.83$, $P<0.0001$; MP, $y=-0.08x-0.997$, $r^2=0.39$, $P<0.001$.

knee. Conversely, during acceleration joint moments generally peaked later in stance.

In all trials, the hip moment peaked before those of the other three joints, occurring between 20–30% of stance. When decelerating, the hip moment fell to near zero for the last 30% of stance. In contrast, during accelerations the hip moment declined less rapidly and was maintained until foot off. The joint moment pattern at the knee generally reversed

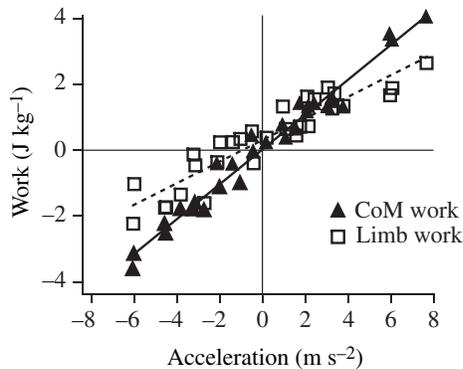


Fig. 10. Center of mass (CoM) work (filled triangles) and summed limb work (open squares) plotted against acceleration. The slope of the regression line for the summed limb work (broken line) was significantly lower than that for the center of mass work (solid line). Thus, at the maximum accelerations and decelerations, the work done by the limbs did not account for all of the work done on the center of mass. This suggests that the trunk and tail may also be recruited to power changes in speed (see Discussion). Linear regressions are: CoM work, $y=0.530x+0.022$, $r^2=0.97$, $P<0.0001$; limb work, $y=0.338x+0.328$, $r^2=0.87$, $P<0.0001$.

from an initial negative (flexor) moment during the first 20–30% of stance to a positive (extensor) moment for the remainder of stance, as the GRF vector moved posterior to the joint center of rotation. This switch tended to occur earlier in stance during breaking, with the ensuing peak positive moment also occurring earlier and being greater in magnitude. At the ankle joint, the total moment reached a peak at 40% of stance during breaking and steady speed trials, but occurred later during accelerations. Similar to the hip, the joint moment at the ankle declined more rapidly during the latter half of stance during breaking and remained higher during acceleration trials compared with when the animals hopped at a steady speed. The joint moment at the MP was positive in all trials and, like the ankle moment, peaked at 40–50% of stance.

Joint power and net work

Following representative patterns of joint moments (Fig. 7), Fig. 8 shows examples of joint power *versus* stance duration for the extremes of each condition. Consistent with the joint moment patterns observed, external and total power (including that caused by segment inertia and weight) differed only at the hip and was only detectable during the largest accelerations. Over all trials, internal work accounted for less than 1% of the total net work done at each joint. At all joints, except the knee, there was a significant relationship between net joint work and acceleration (Fig. 9).

In general, the hip joint absorbed a small amount of energy as the hip flexed in the first 20% of stance. This was followed by the production of positive power as the hip extended, resulting in positive net work in all trials. The amount of positive power and net positive work performed at the hip

increased with increasing acceleration (Fig. 9A). Increased work at the hip was the product of both higher peak power and a longer duration of positive power production (Fig. 8C).

Joint power at the knee generally began with a brief positive peak early in stance, as the knee flexed during a flexor moment. This was followed by a negative peak as the knee continued to flex while the moment shifted to an extensor moment, and finally a second positive peak as the knee re-extended at the end of stance during an extensor moment. The timing of the polarity shifts in knee joint power was variable, and the magnitudes of the peaks tended to be low relative to the other limb joints in any given trial. The resulting net work performed by the knee was nearly always positive and was independent of acceleration (Fig. 9).

The ankle joint showed a very consistent pattern of negative power for the first 40–45% of stance followed by positive power during the remainder of stance. This resulted from the generally symmetrical flexion-extension pattern of the ankle joint, as it was subjected to an extensor moment throughout stance (Fig. 7). The magnitude and duration of the peaks in negative and positive power were strongly associated with each condition (Figs 8 and 9C). During steady speed hopping, negative joint work during the first half of stance was similar to the magnitude of positive work performed during the second half of stance, yielding little or no net joint work. During breaking, shifts in the magnitude and duration of the negative and positive power peaks at the ankle resulted in more negative and less positive work, so that the ankle absorbed energy (net negative work). During accelerations, the magnitude, but not the duration, of positive joint power generated during the latter half of stance changed most. Peak negative power and negative work performed by the ankle remained similar to that observed for steady speed trials. The large increase in the magnitude of positive power resulted in a substantial increase in the amount of net positive work performed at the ankle as acceleration increased (Fig. 9C).

Power at the MP joint was near zero or slightly positive early in stance, but reached a negative peak at midstance and returned to near zero by 80% of stance. In some of the larger accelerations, a second small positive peak at the end stance occurred (Fig. 8A). Surprisingly, the peak magnitude and duration of negative power production increased with increasing acceleration due to greater joint flexion during an extensor moment, resulting in a significant increase in negative work at the MP joint (Fig. 9D).

The net work done on the center of mass (CoM) determined from integration of the ground reaction forces was also strongly correlated with acceleration ($r^2=0.97$, $P<0.0001$; Fig. 10). However, when compared with the total work done by the limb (summed joint work), CoM work exhibited a significantly steeper slope. Therefore, with increasing acceleration or deceleration, the work done by the limb was less than the overall work done on the animals' CoM. This suggests that a significant amount of power was produced *via* movements of the trunk and/or tail.

Discussion

Our goal in this study was to examine how tammar wallabies, which achieve substantial elastic energy savings in distal leg tendons during steady state locomotion, modulate mechanical power when accelerating and decelerating. In doing so, we also sought to determine how individual limb joints absorb or produce energy when wallabies change speed relative to overall changes in their center of mass (CoM) power output. Although an analysis of joint work and power represents an indirect measure of muscle–tendon function, it provides insight into which muscle groups may be most important to the modulation of whole limb and body work and power.

Results from recent *in vivo* studies in tammar wallabies suggested that a division of labor exists between the muscle groups of the hind limb, with power being modulated at the proximal joints by the large muscles acting at the hip and the knee. Biewener et al. (2004) showed that when hopping on level *versus* inclined surfaces, the ankle extensors retained spring-like function and contributed negligible net work to move the animal's center of mass. However, previous work in jumping and sprinting studies (Aerts, 1998; Dutto et al., 2004; Jacobs, 1996) showed that, while proximal muscles may produce most of the power for the jump, the power is delivered at the ankle via multi-joint muscles. The results of our study clearly show this same pattern. Of the four hind limb joints examined, the ankle displayed the strongest correlation of joint work relative to the animal's acceleration (Fig. 9), accounting for 89% of the change in whole limb work *versus* acceleration (Fig. 10). The hip and metatarsophalangeal (MP) joints also showed significant correlations between joint work and acceleration but contributed much less to changes in whole limb work and power compared with the ankle. Whereas the hip accounted for 28% of the change in whole limb work by contributing mainly to acceleration, the MP joint unexpectedly absorbed an increasing amount of energy with increased acceleration (negative slope). This energy absorption resulted from increased flexion of the MP joint, which is probably related to the wallabies increasing the retraction angle of their limb during accelerations, and represented –24% of the change in energy for the limb as a whole over the range of acceleration and deceleration observed. In contrast, the knee joint did not contribute to changes in limb power output.

Mechanical power and work

A goal of our work was to determine whether having muscle–tendon units specialized for elastic energy savings limits a wallaby's ability to produce power for accelerations. The potential trade-off that exists between muscles of differing architecture suggests that the spring-like properties of the wallaby hind limb may constrain their ability to generate power (Biewener, 1998; Biewener and Roberts, 2000). However, we found that this was not the case. The largest accelerations recorded in this study required that the animals generate $\sim 4.0 \text{ J kg}^{-1}$ body mass. Of this, the legs provided $\sim 2.6 \text{ J kg}^{-1}$, indicating that the additional work must be done by movements

of the trunk and tail (see below). This differs from turkeys, in which the legs provide all of the work for acceleration (Roberts and Scales, 2004). On average, the extensor muscles of the hind limb make up 12% of body mass, which indicates that for the maximum accelerations observed in this study the hind limbs produced $\sim 79 \text{ W kg}^{-1}$ leg muscle. This is consistent with values that have been reported for direct *in vivo* measurements of muscle power in diverse high power activities, such as bird flight and scallop jetting (Biewener et al., 1998; Marsh et al., 1992) and is well within the range estimated for skeletal muscle (Weis-Fogh and Alexander, 1977); suggesting no limitation to overall limb power production as a result of specialized spring-like muscle tendon units. Roberts and Scales (2002) reached a similar conclusion for accelerating turkeys, for which they reported center of mass power in terms of stroke power, or mean power during stance normalized to total limb muscle mass. Values reported for turkeys reached a maximum stroke power of 150 W kg^{-1} . The same calculation for the tammar wallabies studied here yields a maximum stroke power of $\sim 210 \text{ W kg}^{-1}$ extensor limb muscle. Roberts and Scales (2002) included flexor and adductor muscles in their measurement of muscle mass, but it seems unlikely that these muscles contribute similarly to major extensor muscle groups (on a per mass basis) to accelerate the animal, and thus were not included in our measurement of limb muscle mass. For the purpose of comparison, including the masses of these muscles yields a value of $\sim 145 \text{ W kg}^{-1}$ total hind limb muscle mass in the tammar wallabies, quite similar to that found for turkeys.

The amount of energy absorbed during the maximum decelerations observed in this study was $\sim 3.6 \text{ J kg}^{-1}$ body mass. As for our observed maximum accelerations, the hind limbs again accounted for only 61% of the energy change of the CoM (the remainder probably again resulting from energy absorption within the trunk of the animal). This equates to approximately -67 W kg^{-1} limb muscle averaged over a full locomotor cycle, or a stroke power of -177 W kg^{-1} extensor muscle over the period of stance. We are not aware of any direct *in vivo* measurements of the power absorption of vertebrate muscle, but isolated muscle experiments (Abbott et al., 1951; Hill, 1960) and studies of human running performance (Margaria et al., 1963) demonstrate that it is easier for muscles to absorb than to produce energy. In a demonstration before the Royal Society of an experiment first conducted by Abbot et al. (1952), A. V. Hill showed that, on two mechanically linked, opposing bicycles, a woman doing negative work could easily pedal to resist the efforts of a larger healthy male doing positive work. This likely relates to a muscle's ability to generate higher forces while being actively stretched, so that less muscle must be recruited (consuming ATP) to produce the same tension. Hence, it also seems unlikely that the negative powers observed during the maximum decelerations recorded here represent an upper limit to the wallabies' hind limb muscle ability.

It is generally assumed that the legs do the majority of the work of terrestrial locomotion. As bipeds, we therefore expected that nearly all of the power needed for changing

speed would be provided by the wallabies' hind limbs. Surprisingly, this was not the case. The amount of work done on the animal's CoM increased more rapidly with acceleration than did the work being done by the hind limbs (Fig. 10). For the largest accelerations and decelerations, the limbs accounted for only 60–65% of the work done on the CoM. During large accelerations, we observed that the wallaby's trunk and tail underwent considerable extension, substantially raising the animal's center of mass. Given that the average force experienced during stance in a large accelerating hop is approximately 245 N, a displacement of 1 cm would provide 2.45 J or 0.36 J kg⁻¹ body mass of CoM work. Therefore, only a small displacement of the center of mass (approximately 4 cm in this case) would be required to account for the difference in work provided solely by the limbs during accelerations and decelerations. While this calculation is only approximate, it demonstrates how movements of the body and tail could readily account for 35% or more of work done on the center of mass in more extreme cases of acceleration and deceleration. Accurate movements of the center of mass are difficult to track, and with our data we are unable to test the extent to which such movements of the trunk and tail contribute to CoM acceleration. Nevertheless, it seems that this is an important component by which wallabies change speed while hopping over level terrain and may also be important to their ability to generate power when jumping and absorbing energy when landing.

Do thin tendons limit acceleration?

The ability to generate power may not be the only constraint on having muscle–tendon units that favor elastic energy storage. In order to store a significant amount of strain energy, the tendons must be thin enough to undergo relatively high strains during steady speed locomotion. In general, many mammalian tendons are relatively thick and operate with an average safety factor of about eight or higher (Ker et al., 1988). However, the ankle extensor tendons of tammar wallabies hopping at sub-maximal steady state speeds have safety factors between three and four (Biewener et al., 1995). Because of this, it is possible that increased forces required to accelerate the animal could potentially damage or rupture their tendons. Indeed, recent studies of fatigue rupture in wallaby tendons (Ker et al., 2000; Wang et al., 1995) indicate that significant fatigue damage may occur on a regular basis, requiring ongoing tendon repair.

In the context of acceleration and deceleration, wallabies appear to minimize this problem by maintaining relatively uniform peak joint moments at the ankle (Fig. 7), resulting in a relatively constant safety factor for their leg tendons. We estimated the average peak ankle extensor tendon stresses here to be 24.16±5.48 MPa, based on peak joint moment (mean 15.89±3.60 Nm), muscle moment arm (25.30±1.70 mm) and tendon cross sectional area (0.26±0.02 cm²). Given a failure strength of 100 MPa for tendon (Ker et al., 1988), the wallabies in this experiment operated with an average safety factor of 4.32±0.88, which did not vary with acceleration ($r^2=0.02$,

$P=0.508$). The wallabies maintained uniform peak joint moments while changing speed by maintaining the alignment between their limbs and the resultant GRF vector. When accelerating, wallabies significantly increased the retraction angle of their limbs (Fig. 4B) with little increase in limb protraction angle (Fig. 4A). As a result, the limb was held in line with the anteriorly directed GRF vector through most of stance (Fig. 2A, inset). When decelerating, limb protraction and retraction angles both increased significantly (Fig. 4A,B). The former aligns the limb with the GRF vector when the forces are highest, while the latter may reduce the ankle joint moment in the last 20–30% of stance by aligning the joint more closely with the GRF vector (Fig. 2C, inset). Consequently, although wallabies operate with relatively low tendon safety factors that favor elastic energy savings, they are able to maintain fairly constant peak tendon stresses by shifting their hind limb orientation to match changes in the direction of the ground reaction force when accelerating to change speed.

Do wallaby ankle extensors perform substantial work?

Prior *in vivo* studies of tammar wallabies hopping on an incline showed that the ankle extensors do not contribute to the work of raising the animals' center of mass (Biewener et al., 2004), suggesting that the role of these muscle–tendon units in locomotion is restricted to spring-like behavior. However, during accelerations and decelerations, much of the work produced by the limb was delivered at the ankle. This raises the question of whether the work produced at the ankle is done by the ankle extensors or is transferred from more proximal joints via bi-articular muscles. While we cannot measure muscle work directly in this study, our results suggest that the ankle extensor muscles contribute some fraction of the work that appears at the ankle joint during acceleration and deceleration. Muscle–tendon length of the ankle extensors can be estimated from their moment arms at the knee and ankle and the angle changes at these joints. Net joint angle excursion increased significantly with acceleration and was of comparable magnitude at both the ankle and the knee (Fig. 6). Given the larger moment arm of the ankle extensors at the ankle (mean: 23.80±1.03 mm) *versus* the knee (mean: 9.50±2.13 mm), this indicates a significant increase in calculated muscle–tendon unit length with increased acceleration ($r^2=0.55$, $P<0.0001$). For the maximum accelerations recorded, we estimate that the muscle–tendon units underwent an overall net shortening of ~8% during stance. A similar magnitude of net lengthening was observed in maximum decelerations. Because net changes in muscle–tendon unit length can only be caused by net shortening or lengthening of the muscles, this indicates that some work was done while the muscles were generating tension. Although indirect and prone to error, this analysis suggests that the ankle extensors contribute to changes in limb work when wallabies change speed during acceleration and deceleration, in contrast to there being no evidence of this during inclined hopping (Biewener et al., 2004).

Even so, it seems probable that a large fraction of the work

and power delivered at the ankle joint is produced by more proximal muscles of the limb. Previous studies of jumping, landing and sprinting have shown that a substantial amount of power is transferred between joints via bi-articular muscles during these activities, with most of the power appearing at the ankle joint (Aerts, 1998; Jacobs et al., 1996; Prilutsky and Zatsiorsky, 1994). Consistent with these studies, we also observed that most of the power produced by the limb is delivered at the ankle joint when wallabies change speed. If this power were produced by the wallaby's ankle extensors alone, it would suggest a value as high as 325 W kg⁻¹ muscle, which seems unlikely (Weis-Fogh and Alexander, 1977; Peplowski and Marsh, 1997). Instead, much of the power at the ankle is likely to be transferred from hip and the knee extensors *via* the ankle extensors, which could do so by contracting with little net length change. The knee extensors, which constitute a larger percentage (29%) of the total hind limb muscle mass than the ankle extensors (20%), appear well suited for contributing this power. Effective power transfer also requires that the knee and ankle joints extend simultaneously, consistent with the pattern that we observed (Fig. 5). Based on these considerations, we conclude that power transfer between proximal muscles and distal joints likely plays an important role in power generation and absorption when wallabies change speed, similar to the patterns described for jumping galagos, humans and horses (Aerts, 1998; Jacobs et al., 1996; Dutto, 2004). Interestingly, however, these results differ from those recently found in accelerating turkeys (Roberts and Scales, 2004), in which power transfer is considered to be minimal. Such differences may be due to differences in the timing of limb extension patterns as well as relative proportions of knee and ankle extensor muscles. In turkeys, the mass of the ankle extensors is more than three times that of the knee extensors (Roberts and Scales, 2004).

Conclusions

Over the range of performance that we observed, our results show that the energy change required for accelerating and decelerating is predominately modulated at the ankle joint and to a lesser degree at the hip and metatarsophalangeal joint. Based on earlier work showing a limited contribution of ankle extensors in useful mechanical work during incline hopping (Biewener et al., 2004), combined with analyses of joint dynamics reported here, we interpret the power that emerges at the ankle joint as being largely produced by more proximal muscles acting at the hip and knee. This power is transferred via the bi-articular ankle extensor muscles, which themselves need not change length appreciably. Our preliminary analysis suggests that the ankle extensors do contribute some additional work to change the wallaby's speed, but it is difficult to quantify how work is partitioned between the ankle extensors and more proximal limb extensors. Further *in vivo* studies and more extensive muscle modeling will be required to evaluate the role of power transfer as we envision it here. While the changes in speed we were able to record probably do not

represent maximal performance, our estimates of mass-specific power for the wallabies' hind limb muscles are well within the range for mammalian skeletal muscle and are consistent with values reported for other high power output activities. Although we estimate tendon strains in the ankle extensors to be relatively high, an increased risk of tendon failure does not appear to pose a limit to a tammar wallaby's acceleration performance because peak ankle moments (and resulting tendon strains) do not increase significantly with acceleration. Therefore, we conclude that having muscle-tendon units specialized for elastic energy storage need not limit a tammar wallaby's ability to accelerate or decelerate.

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