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IN VIVO MUSCLE FORCE AND ELASTIC ENERGY STORAGE DURING STEADY-SPEED HOPPING OF TAMMAR WALLABIES (*MACROPUS EUGENII*)

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Summary

In order to evaluate the role of elastic energy recovery in the hopping of macropodids, *in vivo* measurements of muscle–tendon forces using buckle force transducers attached to the tendons of the gastrocnemius (G), plantaris (PL) and flexor digitorum longus (FDL) of tammar wallabies were made as the animals hopped on a treadmill at speeds ranging from 2.1 to 6.3 m s^{-1}. These muscles and tendons constitute the main structures that are most important in energy storage and recovery. Electromyographic recordings from the lateral gastrocnemius and plantaris muscles, together with high-speed films (200 frames s^{-1}) and video (60 fields s^{-1}), were also used to correlate muscle activation and kinematic patterns of limb movement with force development. On the basis of *in situ* calibrations of the buckle transducers, we found that muscle forces and elastic energy storage increased with increased hopping speed in all three muscle–tendon units. Elastic energy recovery reached a maximum of 25 % of metabolic energy expenditure at 6.3 m s^{-1} and is probably greater than this at higher speeds. Force sharing among the three muscles was consistently maintained over this range of speeds in terms of recruitment. Although forces and stresses were generally comparable within the gastrocnemius and plantaris muscles, maximal tendon stresses were considerably greater in the gastrocnemius, because of its smaller cross-sectional area (peak muscle stress: 227 *versus* 262 kPa; peak tendon stress: 36 *versus* 32 MPa, G *versus* PL). As a result, energy storage was greatest in the gastrocnemius tendon despite its much shorter length, which limits its volume and, hence, energy storage capacity, compared with PL and FDL tendons. Forces and stresses (17 MPa maximum) developed within the FDL tendon were consistently much lower than those for the other two tendons. Peak stresses in these three tendons indicated safety factors of 3.0 for G, 3.3 for PL and 6.0 for FDL. The lower stresses developed within the tendons of the plantaris and, especially, the flexor digitorum longus may indicate the need to maintain sufficient stiffness for phalangeal control of foot placement, at the expense of reduced strain energy recovery.

Key words: muscle–tendon force, stress, elastic energy, hopping, tammar wallaby, *Macropus eugenii*.

Introduction

Many terrestrial mammalian species are believed to lower their energy expenditure by means of elastic energy recovery when running, trotting or hopping (Cavagna *et al.* 1977). In these gaits, the kinetic and potential energy that is lost when the animal lands is stored and subsequently recovered from the recoil of spring-like elements in its limbs and trunk, reducing the amount of work that the muscles must perform to re-accelerate the animal's body during each stride. Although some energy can be saved by elastic recoil of cross-bridges within active muscles, most of the energy is believed to be recovered by elastic recoil of tendons and ligaments, particularly within the limbs (Morgan *et al.* 1978; Alexander, 1988). It is also likely that additional energy is saved by the increased force that muscles can exert by being actively stretched, allowing fewer fibers to be recruited to generate a given force. Finally, there is some evidence that the energetic cost of muscles performing negative work when being stretched is considerably less than when they shorten to perform positive work (Margaria, 1968). Species that are believed to show specializations for elastic energy savings often possess long, slender tendons and ligaments, which favor greater strain energy recovery in addition to increasing locomotor efficiency by a reduction of distal limb mass. Among these are the larger macropodid marsupials (wallabies and kangaroos), ungulates (Alexander *et al.* 1982; Dimery *et al.* 1986) and humans (Ker *et al.* 1987).

The importance of elastic energy savings has been indirectly shown most dramatically in the energetics of hopping in red kangaroos (Dawson and Taylor, 1973) and tammar wallabies (Baudinette *et al.* 1992). In both macropodid species, oxygen consumption levels off with increased hopping speed, in contrast to the linear increase that is commonly observed for

most terrestrial species (Taylor *et al.* 1982). Although most of the data reported for red kangaroos are based on a single individual hopping at speeds well below the species' maximal range, Baudinette *et al.* (1992) have shown for tammar wallabies that, even when the effect of work against wind drag is taken into account, the increase in energy cost is still well below what would be expected for a typical quadrupedal mammal of similar size. Hence, there is good energetic evidence for the role of energy savings by means of elastic strain recovery within the tendons and ligaments of the limbs, trunk and tail of these two hopping species.

Past studies attempting to quantify the amount of elastic energy recovery in the locomotion of different mammalian species, and to verify its role in determining locomotor energetics, have relied on indirect calculation of muscle–tendon force based on combined kinematic and force platform recordings (Alexander and Vernon, 1975; Biewener *et al.* 1981), estimates of tendon and ligament stretch from kinematics alone (Alexander *et al.* 1982; Dimery *et al.* 1986) or mechanical analysis of the animal's tendons (Ker *et al.* 1986; Morgan *et al.* 1978). Consequently, these studies are limited in their ability to assess the actual forces generated by individual muscle–tendon units during the animal's locomotion. In only one study (Griffiths, 1989) have the forces generated by a muscle and its tendon been measured directly to evaluate the potential role of elastic energy savings. However, because Griffiths measured the forces generated by the medial gastrocnemius alone, his assessment of elastic energy storage in the hopping of the wallaby *Thylogale billardierii* relied on generalizations drawn from data for the medial gastrocnemius. In other studies of ankle extensor function of the cat hindlimb (Herzog, 1987; Herzog *et al.* 1993), forces have been measured simultaneously in different muscle agonists, but these measurements were carried out for walking and did not address elastic energy storage in relation to locomotor energetics.

Collectively, these studies suggest that elastic strain recovery of a muscle's tendon may reduce the amount of work that would otherwise have to be performed by the muscles by as much as 30–50 %. Although most workers interpret increased loading of tendons and strain energy recovery at higher speeds as a mechanism to explain the lower cost of locomotion in large macropodids, Griffiths (1989) argued that increases in energy storage within the tendon are offset by decreased storage within the muscle as it is stretched beyond the elastic limit of its cross-bridges (often referred to as the muscle's 'short-range stiffness') and, therefore, cannot explain the leveling off of oxygen consumption observed in these species at higher speeds.

The purpose of this study was to obtain direct *in vivo* force recordings for the principal hindlimb muscle–tendon complexes of tammar wallabies: medial and lateral gastrocnemius (G), plantaris (PL) and flexor digitorum longus (FDL). Each of these muscles transmits its force *via* a long tendon that has the potential to provide significant elastic energy recovery following the yield phase of support. By making combined force recordings for these three muscles over a range of steady hopping speeds, we sought to evaluate the relative contributions of these muscle–tendon units to strain energy recovery and how total energy recovery compares with the animal's metabolic energy expenditure over the same range of hopping speeds.

Materials and methods

Animals

Four tammar wallabies (three male and one female, ranging from 3.62 to 5.82 kg body mass) were trained to hop on a motor-driven treadmill (2.0 m×0.5 m bed) at speeds of up to 6.3 m s^{-1}. The animals were obtained from a breeding colony maintained at Flinders University, Australia, in outdoor pens located adjacent to the research laboratory. The animals were housed in these pens during their training but were housed inside following surgery. Prior to implantation of the force transducers, oxygen consumption data were recorded from each animal at multiple speeds, using the open-flow system described previously (Baudinette *et al.* 1992). These recordings were made to verify that the animals' oxygen consumption matched that obtained previously for tammar wallabies, which showed a leveling off in oxygen consumption over a range of speed from 2.5 to 9.0 m s^{-1}.

Buckle transducers and surgical procedures

E-shaped stainless-steel buckle transducers (Fig. 1A) of two internal widths (4.0 and 5.0 mm) were constructed to accommodate size differences in the three tendons. The force buckles were progressively polished with emery paper, finishing with 600 grit. A single-element metal foil strain gauge (type FLA-1, Tokyo Sokki Kenkyujo, Japan) was bonded to the central arm of the transducer using an oven-cured epoxy resin (AE-15, Micromeasurements Group), and 36-gauge etched Teflon-insulated lead wires were soldered to the gauge tabs. The tendon passes over and under the arms of the buckle, and tendon force is measured by calibrating the voltage output produced by the strain gauge mounted on the central arm, which is subjected to compression when the tendon is pulled. The strain gauge, solder joints and lead wires were then covered in epoxy resin. To minimize abrasive wear of the tendon against the transducer arms, the entire transducer was coated with a xylene-cured polyurethane (M-coat A, Micromeasurements Group). Each transducer was calibrated before and after use, using a nylon cord, to verify that no change in sensitivity occurred during the experimental period.

Force buckles were implanted on the plantaris and gastrocnemius tendons (Fig. 1B) using sterile surgical techniques under general anesthesia (isofluorane), following acceptable veterinary guidelines. A 3 cm incision was made laterally to expose the underlying Achilles tendon. The peritendinous fascia was cut longitudinally, allowing separation of the plantaris and gastrocnemius (medial and lateral) tendons. The buckles were spaced along the tendons so that the central arm of each was free from contact with the adjacent transducer.

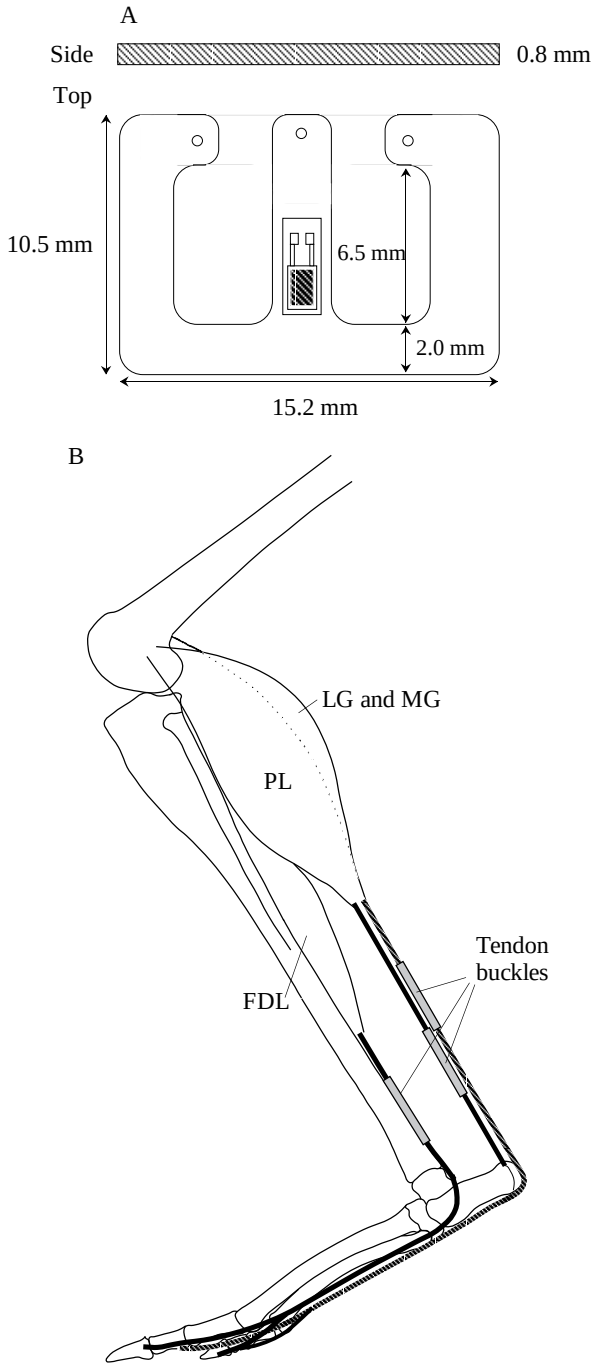

Fig. 1. (A) Schematic drawing of the force buckle design used to record tendon forces. (B) Diagram of the hindlimb of a wallaby, showing the muscles and tendons (bold solid and hatched lines) considered important to elastic energy recovery during hopping and the location of the buckle force transducers. The plantaris muscle (PL) arises from the posterior supracondyloid fossa of the femur, passing between the heads of the lateral (LG) and medial (MG) gastrocnemius muscle, which originate from the femoral epicondyles. The soleus (not shown) forms a small slip that attaches to the deep surface of the lateral gastrocnemius. The plantaris tendon (hatched) is distinct from the gastrocnemius tendon (solid), which forms the common tendon of insertion for the LG, MG and soleus muscles to the calcaneus. The plantaris tendon twists around to pass over the gastrocnemius tendon at the calcaneus, passing along the plantar surface of the foot to insert on the second phalanx of digits IV and V. The flexor digitorum longus (FDL) arises from the posterior aspect of the tibia and fibula. Its tendon (solid) passes along the posterior surface of the tibia, under the medial malleolus and, lying deep to the plantaris tendon, inserts on the distal phalanges of digits IV and V.

Small ties (4-0 gauge silk) were made through the end holes on the buckle's arms to the tendon to prevent the buckles from shifting position on the tendons. In two of the wallabies (nos 1 and 2), force recordings were made from only the plantaris and gastrocnemius tendons. In the other two wallabies (nos 3 and 4), recordings were also made from the tendon of the flexor digitorum longus. This tendon passes along the posterior aspect of the tibia (Fig. 1B) and could be reached from the same incision used to attach the plantaris and gastrocnemius buckles. When mounted on the digital flexor tendon, this buckle was free from contact with the other two buckles.

In addition to making recordings of tendon force, electromyographic (EMG) recordings of the plantaris and lateral gastrocnemius muscles were also made by means of fine-wire bipolar electrodes. The electrodes were constructed using insulated silver wire (0.1 mm o.d., California Fine Wire, USA) that was twisted along its length, with the wires bared for 0.5 mm at their ends and spaced 2.0 mm apart. The electrodes were implanted into the muscles by making separate incisions in the skin overlying each muscle belly, bending the wire ends back to form hooks, and inserting the tips into the muscle belly using a 23 gauge hypodermic needle (Basmajian and De Luca, 1985; Loeb and Gans, 1986). The electrodes were sutured to fascia close to their exit point from the muscle, leaving a small loop to ensure that they could move with the muscle as it contracted to reduce movement artifact in the EMG signal.

All lead wires were then passed subcutaneously to a small plastic connector (Amphenol, series 222) located just anterior to the animal's hip. The lead wires were soldered to pins inserted into the connector and sealed with RTV silicone rubber adhesive (Dow Corning). The connector was secured to the animal's skin using 0 gauge silk suture and all wounds were sutured close. The animals were administered an analgesic (10 mg Flunixin, Schering-Plough) and an antibiotic (50 000 i.u. procaine penicillin, Glaxovet) following surgery.

Experimental and calibration procedures

Following a 24 h period of recovery, force recordings were made from the ankle and digital extensor muscles while the animals hopped at speeds varying from 2.1 to 6.3 m s^{-1}. The force buckle signals were conditioned by a bridge amplifier (Vishay Instruments, model 2230). The EMG signals were amplified (1000×) and bandpass-filtered at 30–2000 Hz (Grass P511 amplifier). Both sets of signals were sampled at 1000 Hz *via* a Metrabyte Dash-16F A/D converter, using custom-developed Asyst software (Keithley Instruments), and stored for subsequent analysis. Treadmill force and EMG recordings were made over a 2 day period. Measurements of muscle–tendon

force were typically based on an analysis of data sampled for at least 32 hops for each animal at each hopping speed.

In addition, high-speed 16 mm films (Milliken model DBM-5 operated at 200 frames s^{-1}) and video recordings (Sony CCD model SSC-M350 operated at 60 fields s^{-1}) were made of a selected subset (film 2.1–5.0 m s^{-1} and videotape 3.0–4.5 m s^{-1}) of runs. The 16 mm films were digitized using a Summagraphics-Plus digitizing tablet to enter joint coordinate data into a microcomputer. The video-tape recordings were digitized using timebase-corrected fields (IDEN model IVT-7), played out from a Panasonic SVHS AG-1960 deck, that were captured *via* an Imaging Technologies PC-Vision Plus frame-grabbing board using MTV software (DataCrunch). Kinematic analysis of joint angle changes were then related to the timing of muscle force development by means of a timing pulse recorded from the camera shutter or synchronized to a light pulse in the video camera's field of view.

After the experimental recordings were completed, the animals were killed (900 mg pentobarbitone sodium injected intravenously) and their tendons and muscles dissected free for morphological measurements and calibration of the force buckles on the tendons. Each tendon was first cut free from the muscle belly, keeping the force buckles and lead wires to the connector intact. In general, the tendons were found to be in excellent condition following the experimental recordings, with little sign of wear or fibrous tissue response. The ends of the tendons were secured with a series of ties, using 2-0 gauge silk, to prevent them from splaying out when being clamped, and wrapped in saline-moistened gauze prior to their calibration. The ends of the tendon were then clamped and frozen in custom-designed serrated jaw clamps using liquid nitrogen. Small plastic sleeves positioned about the tendon at each clamp kept the central portion of the tendon and buckle transducer from freezing. With one clamp rigidly anchored to the countertop, each tendon was subjected to a series of pulls using a hand-held grip. The grip was free to rotate, ensuring that only axial tension was applied to the tendon. Forces were monitored by a force transducer (proving ring design, mounted with strain gauges in a full bridge configuration) positioned in series between the clamp jaw and grip handle. Forces were applied approximately once every 2 s (one-sixth of the rate of the animal's hopping frequency), making certain that they exceeded those measured during treadmill hopping. The outputs of the force transducer and the tendon buckle were sampled at 100 Hz and stored on computer (Fig. 2A shows calibration recordings). To obtain a dynamic calibration, the rise and fall in force were regressed against the voltage output of the buckle force transducer (Fig. 2B). In most cases, a slight hysteresis in the rise and fall of force was noted, in which case an average of the two slopes was used to establish the calibration for the buckle. Correlation coefficients greater than 0.97 were obtained for all regression calibrations, with 95 % confidence intervals being less than 3 % of the regression slope.

Morphological measurements

To obtain measurements of tendon and muscle cross-sectional area for computing tendon and muscle stress (force per unit cross-sectional area), the tendons of the contralateral limb were dissected free, their lengths measured and they were weighed to the nearest 0.1 mg. The distal portions of the plantaris and digital flexor tendons were cut free at the level of the proximal interphalangeal joint. The short portions of the plantaris and digital flexor tendons that pass over the calcaneus and around the ankle joint (Fig. 1B), respectively, were excised before weighing. Previous work (Ker *et al.* 1986) has shown that these portions have a lower elastic modulus than the intervening lengths of the tendons. Measurement of tendon area was made assuming a density of 1120 kg m^{-3} for tendon (Ker, 1981). Tendon volume was then calculated assuming a uniform tendon area from muscle origin to tendon insertion (base of second phalanges for plantaris and base of distal phalanges for digital flexor). The muscle's fiber length was subtracted from the combined muscle–tendon length to obtain the tendon's net 'total length'.

Before making measurements from the muscles, EMG electrode implantation sites were verified for proper location in the muscle's belly. The freshly isolated muscles were then weighed and, using a no. 10 scalpel, sectioned in a plane parallel to the muscle fibers. Measurements of muscle fiber length and pennation angle were then made at regular intervals (six per muscle) along the muscle's length using digital calipers and a protractor to calculate the muscle's fiber cross-sectional area. Fiber cross-sectional area was calculated using the mean values obtained for these measurements (Table 1), adopting the approach of Alexander (1983) and assuming a density of 1060 kg m^{-3} for skeletal muscle. Because of slight errors in the plane of section and possible distortion in the resting length of the fresh muscle during the sectioning and measurement procedure, some uncertainty of resting fiber length exists using this method.

Calculation of strain energy storage

To determine strain energy storage within a tendon, it is necessary to specify the tendon's elastic modulus, which defines the tendon's strain when it is subjected to a given level of stress. While elastic moduli for various mammalian tendons and the tendons of wallabies have been reported to range from 1.2 to 1.7 GPa (Ker *et al.* 1986; Bennett *et al.* 1986; Pollock and Shadwick, 1994), these values were obtained as tangent moduli near the elastic limit of the tendons, just before failure. Because the stresses that we found to act in the tendons of tammar wallabies are well below their failure limit, we used a lower elastic modulus (1.0 GPa) to calculate strain energy storage (U_{tot} in J) using the following equation:

$$U_{tot} = 0.5(\sigma^2/E)V_t \times 0.93,$$

where σ is tendon stress in MPa, E is the elastic modulus, V_t is tendon volume in m^3 and the constant 0.93 assumes a 7 % loss in energy recovery due to hysteresis that is commonly observed in dynamic loading and unloading tests of tendon (Bennett *et al.* 1986; Shadwick, 1990). The value of 1.0 GPa was determined as the mean tangent modulus for the stress–strain

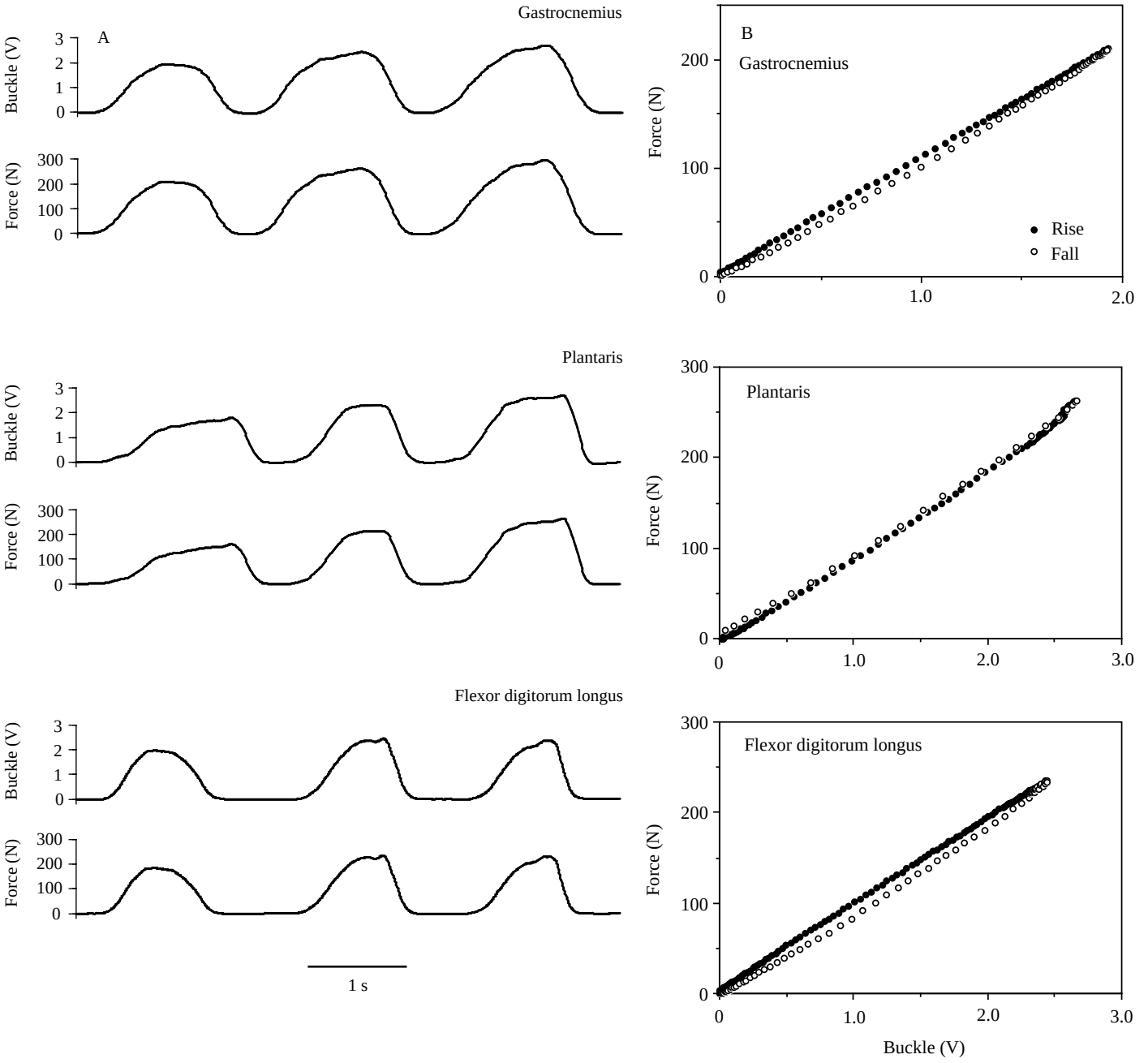

Fig. 2. (A) Calibration recordings of buckle output and tensile force applied to the tendons. (B) Buckle output plotted against applied force. In most instances, a small hysteresis was observed between the rise and the fall in force (e.g. gastrocnemius and flexor digitorum longus). Buckle force calibrations were determined by averaging the regression slopes obtained for the rise (filled symbols) and the fall (open symbols) in force. In all cases, the difference in regression slopes was less than 4%, with correlation coefficients exceeding 0.97.

curves of tendon reported in the above papers over the lower third of their elastic range (0–35 MPa or 0–0.035 strain).

Results

Muscle and tendon morphology

Morphological data for the muscles and tendons of the animals included in this study are reported in Table 1. The medial (MG) and lateral gastrocnemius (LG), soleus and digital flexor muscles are all unipennate, and the plantaris is multipennate. Whereas the mass and fiber area of MG and LG muscles combined are greater than those of the plantaris muscle, the cross-sectional area of the gastrocnemius tendon is consistently the smallest of the three tendons. The soleus muscle forms a small slip that inserts into the aponeurosis of the lateral gastrocnemius belly and was included with the MG and LG to calculate gastrocnemius muscle stress. Although the area of the flexor digitorum longus muscle is much smaller than that of the gastrocnemius or plantaris, its tendon is generally the largest in cross-sectional area. Elastic energy

Table 1. *Morphological data used to determine muscle stresses, tendon stresses and tendon elastic energy storage*

	Animal				
	1	2	3	4	Mean ± S.D.
Body mass (kg)	3.62	5.42	5.82	4.34	4.80±1.00
Muscle					
Medial gastrocnemius					
m (g)	12.40	17.38	18.39	13.01	15.30±3.03
L (mm)	14.3	16.4	18.8	17.4	16.7±1.9
α (degrees)	41	35	38	29	36±5
A (cm^2)	6.19	8.19	7.27	6.17	6.96±0.97
Lateral gastrocnemius					
m (g)	9.21	12.80	14.81	9.65	11.62±2.66
L (mm)	16.4	20.2	17.9	16.0	17.6±1.9
α (degrees)	27	30	32	24	28±4
A (cm^2)	4.71	5.18	6.62	5.20	5.43±0.83
Total gastrocnemius					
m (g)	21.61	30.18	33.20	22.66	26.91±5.67
A (cm^2)	10.90	13.17	13.89	11.37	12.38±1.47
Soleus					
m (g)	2.03	2.55	2.73	1.90	2.30±0.40
L (mm)	21.8	21.6	18.20	19.10	20.18±1.80
α (degrees)	18	11	15	17	15±3
A (cm^2)	0.88	1.09	1.32	0.90	1.05±0.20
Plantaris					
m (g)	18.96	24.93	30.70	20.25	23.71±5.32
L (mm)	15.5	19.5	16.3	14.1	16.4±2.3
α (degrees)	42	34	37	28	35±6
A (cm^2)	8.56	10.00	14.19	11.96	11.18±2.44
Flexor digitorum longus					
m (g)	8.06	14.26	16.56	10.34	12.31±3.82
L (mm)	14.2	15.9	14.9	12.6	14.4±1.4
α (degrees)	27	28	31	24	28±3
A (cm^2)	4.78	7.47	8.99	7.07	7.08±1.74
Tendon					
Gastrocnemius					
L (mm)	147	173	167	172	165±12
A (mm^2)	7.01	9.99	8.44	6.75	8.05±1.49
Plantaris					
L (mm)	282	310	295	313	300±14
A (mm^2)	8.50	10.15	10.72	7.55	9.23±1.46
Flexor digitorum longus					
L (mm)	239	269	277	283	267±20
A (mm^2)	9.18	10.81	10.74	8.72	9.86±1.07

m, muscle mass; *L*, muscle length; α, pennation angle; *A*, muscle area.

storage depends on both the level of strain within the tendon and its volume. The much longer plantaris and digital flexor tendons, therefore, favor greater strain energy storage, but this is offset by their having a greater cross-sectional area compared with the gastrocnemius tendon, which will reduce strains developed within the tendon for a given applied force.

In vivo *force and EMG recordings*

Representative force and EMG recordings obtained for wallaby no. 4 hopping at 4.5 m s^{-1} are shown in Fig. 3. Force recordings for each muscle were extremely consistent for a series of hops when the animals moved at a steady speed on the treadmill, with the coefficient of variation in force being between 8 and 11 % of mean peak force for the range of speeds recorded. Forces developed by gastrocnemius regularly reached a maximum 18±4 ms (mean ± S.D., *N*=105) prior to the peak forces developed by plantaris and flexor digitorum, which were generally simultaneous. The relative timing of muscle

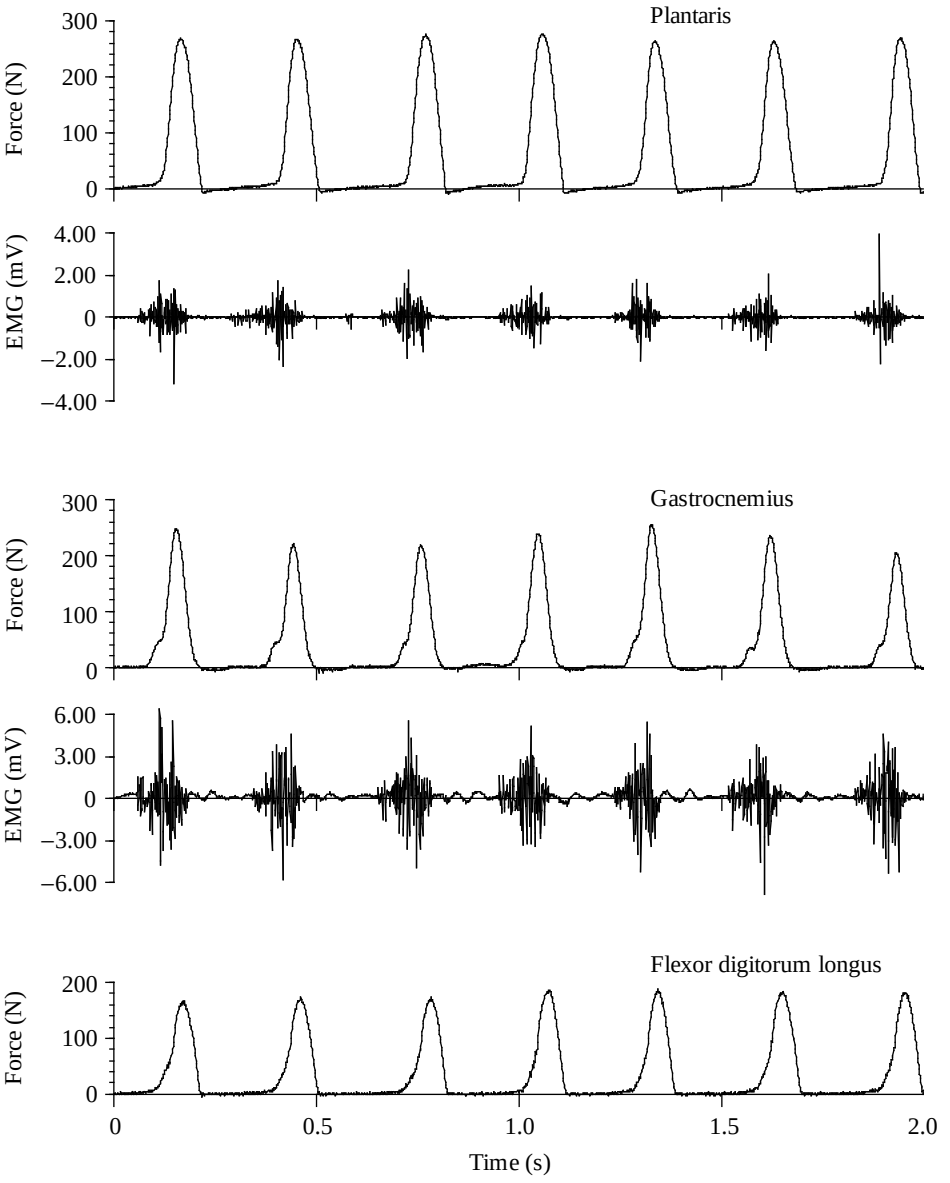

Fig. 3. Representative recordings of force output in the tendons of plantaris, gastrocnemius and flexor digitorum longus (FDL) of a wallaby (no. 4) hopping at 4.5 m s^{-1}. EMG recordings are also shown for the plantaris and lateral gastrocnemius (no EMG recordings were made of the FDL).

force development is clearly seen when the forces of each agonist muscle pair are plotted against one another (Fig. 4). The gastrocnemius begins to develop force prior to the plantaris, early in limb support, with the plantaris generating greater force later in support. The plantaris, in turn, develops force prior to the flexor digitorum longus (Fig. 4B), but once peak force is reached, the timing of force decay is similar in both muscles. The relative timing of force generation by these three muscle agonists matches patterns of joint kinematics (Fig. 5), in which ankle extension precedes plantarflexion of the metatarsophalangeal joint during the terminal phase of limb support. These patterns of joint motion and force development are consistent with the dual role of the plantaris to extend the ankle and to flex the digits: the former being shared with the gastrocnemius and the latter being shared with the FDL. Forces in the gastrocnemius and plantaris muscles peaked 14±6 and 12±6 ms (N=78), respectively, after EMG activity had ceased. The lag, or electromechanical delay, from the onset of EMG activity to the onset of force was 43±8 ms for the gastrocnemius and 41±6 ms for the plantaris (N=78). No consistent change in EMG timing relative to the onset and development of peak force as a function of hopping speed was observed. This is, in large part, due to the fact that stride frequency (Fig. 6) and the duration of force development changed little over the recorded range of hopping speeds.

Stride length, stride frequency, muscle force and energy storage versus *speed*

As the wallabies increased their speed of hopping from 2.1 to 6.3 m s^{-1}, most of their increase in speed was achieved by an increase in stride length (P<0.001); though significant (P<0.01), stride frequency increased only slightly over this speed range (Fig. 6). Associated with the increase in stride length, the peak forces developed within the three muscles increased with increased hopping speed (P<0.005 in all cases), as did strain energy storage within the tendons (Fig. 7).

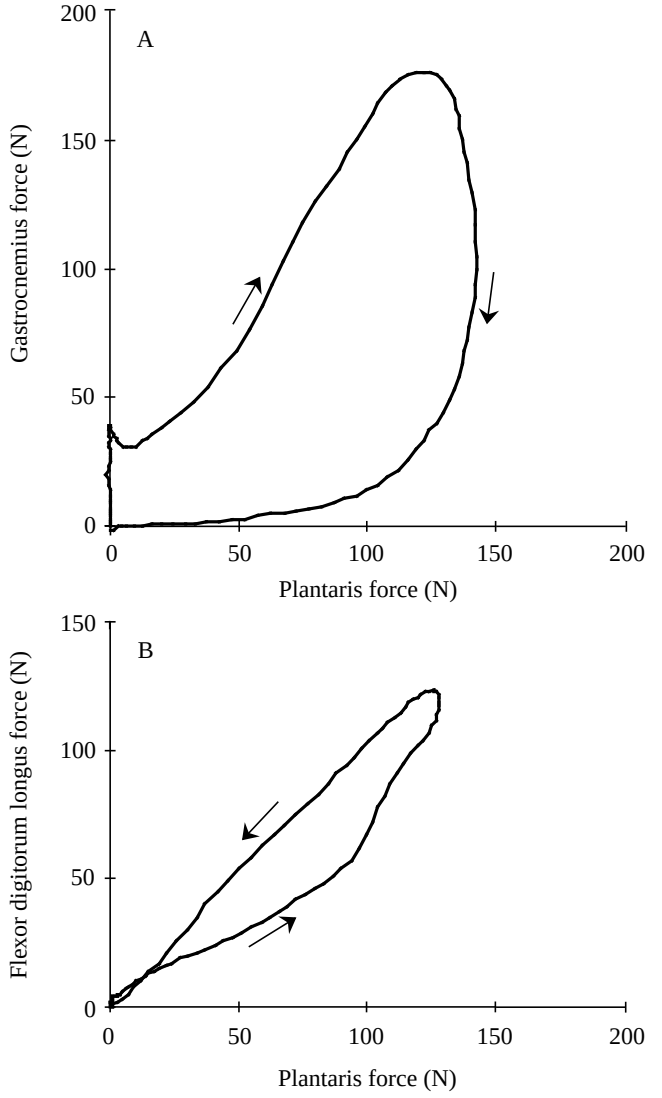

Fig. 4. Graphs of force output of (A) gastrocnemius *versus* plantaris and (B) flexor digitorum longus *versus* plantaris of wallaby no. 3 for one stride hopping at 4.5 m s^{-1}. Arrows indicate the relative timing of force development and decay for each pair of muscles.

Relative increases in force among the three muscle agonists to power faster hopping were generally consistent over the range of hopping speeds recorded within a given animal; however, minor differences in relative force production by the three muscles were observed among animals. This is best observed by comparing the stresses developed within the three muscles over a range of hopping speed (Fig. 8A), which allows a comparison of the different animals that is unaffected by differences in body size. Generally, higher stresses acted within the plantaris muscle at any given speed, with the lowest stresses developed by flexor digitorum longus. Stresses greater than 215 kPa (taken to be maximum isometric stress for skeletal muscle; Close, 1972, p.145; Cavagna and Citterio, 1974; Biewener *et al.* 1988; Biewener and Dial, 1992; but see Discussion) were commonly recorded at hopping speeds of 4.5 m s^{-1} or greater; with maximal stresses of 262 and 227 kPa being exerted by the plantaris and gastrocnemius of wallaby no. 3 hopping at 5.5 m s^{-1}. Peak stresses in the flexor digitorum longus only exceeded 215 kPa at the fastest speed recorded (5.5 m s^{-1}) for wallaby no. 4. Stresses in the FDL were well below this level in animal no. 3.

Whereas the highest muscle stresses were developed by the plantaris, the highest tendon stresses typically acted in the gastrocnemius tendon because of its smaller cross-sectional area (Fig. 8B). Stresses in the gastrocnemius tendon increased from 15 MPa to 36 MPa over the range of speeds from 2.1 to 6.3 m s^{-1}. Stresses in the plantaris tendon were slightly lower, increasing from 12 to 32 MPa. Stresses in the digital flexor tendon were significantly smaller at all hopping speeds, ranging from 8 to 17 MPa. Given a failure stress of 100 MPa for tendon (Ker, 1981; Bennett *et al.* 1986; Shadwick, 1990), these stresses indicate safety factors of 3.0, 3.3 and 6.0 for the gastrocnemius, plantaris and digital flexor tendons, respectively, at hopping speeds of up to 6.3 m s^{-1}.

Differences in muscle stress relative to tendon stress among the three muscle–tendon units resulted primarily from differences in the ratio of muscle fiber area to tendon area. Because of its smaller fiber area (Table 1), forces transmitted by the digital flexor muscle to its tendon were more limited than for the other two muscle–tendon units. As the digital flexor muscle also had the thickest tendon, much lower stresses were developed within its tendon, compared with the tendons of the gastrocnemius and plantaris. These differences in tendon stress, in turn, greatly affected the relative contribution of strain energy storage and recovery that each tendon provided to the animal.

Elastic power (W) provided by the recoil of the tendons of the three muscles is the product of the energy stored and recovered within each tendon during a hop multiplied by the animal's stride frequency. Normalization of elastic power to body mass (mass-specific power: W kg^{-1}) provides a better comparison between differently sized animals. Although the gastrocnemius tendon is considerably shorter (55 %) than the tendons of the plantaris and flexor digitorum longus, which limits its capacity for energy storage, the gastrocnemius contributed the greatest elastic power to the animal over the entire speed range recorded (Fig. 9A) because of the high strains developed within its tendon. In contrast, the elastic power contribution of FDL was only a small fraction of that provided by the G and PL, because of the low stresses developed within its tendon. Increases in force with increased hopping speed resulted in a significant increase in recovered strain energy within the gastrocnemius and plantaris tendons. When compared with the metabolic power expended by the animals hopping over this range of speed (Baudinette *et al.* 1992), elastic energy recovery represented an increasing percentage of energy expenditure as speed increased, reaching 25 % of metabolic power at the highest speeds recorded (Fig. 9B).

Discussion

Elastic energy storage

Our recordings of *in vivo* muscle–tendon forces show that a

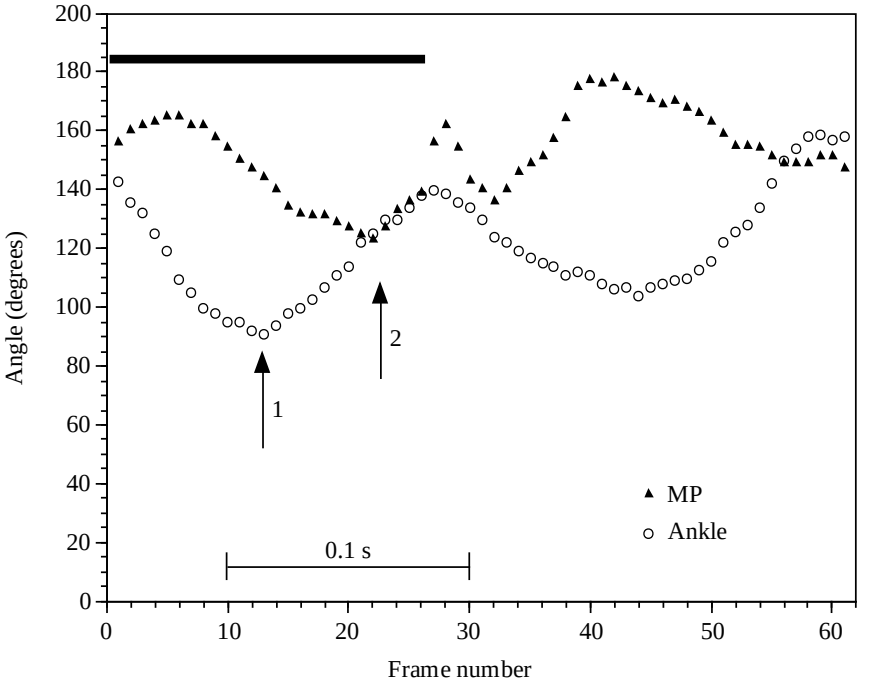

Fig. 5. Graph of angular changes of the ankle and metatarsophalangeal (MP) joints as a function of time for one complete stride of an animal (no. 2) hopping at 4.5 m s^{-1}. The arrows indicate the timing of maximal ankle flexion (1) and maximal MP flexion (2) during limb support (denoted by the black bar above).

significant fraction of metabolic power is usefully stored and recovered in the three principal hindlimb tendons (gastrocnemius, plantaris and flexor digitorum longus) of tammar wallabies when hopping at steady speeds. In contrast to our expectation, the majority of energy is stored in the much shorter gastrocnemius tendon (52 %, compared with 38 % by the plantaris tendon) because of the higher stresses developed in it over the speeds that we recorded. However, the tendon of the flexor digitorum longus contributes only a small fraction (less than 10 %) of the total elastic power delivered by these hindlimb tendons. Our findings are consistent with metabolic studies (Baudinette *et al.* 1992; Dawson and Taylor, 1973) of macropodids, which have indirectly implicated the importance of elastic energy recovery as a mechanism for reducing metabolic energy expenditure in these large hopping species. They are also consistent with mechanical work measurements made in a variety of terrestrial mammals (Cavagna *et al.* 1977) and estimates of elastic energy recovery made from force platform and film analysis of hops made by a red kangaroo and a Bennett's wallaby (Alexander and Vernon, 1975), which also found that elastic energy savings were greatest in the gastrocnemius tendons of these two species. Our results differ, however, from those of Ker *et al.* (1986), who estimated the reverse for a Bennett's wallaby (plantaris 53 % and gastrocnemius 38 % contribution to energy storage) on the basis of measurements of tendon compliance and estimates of force distribution from muscle cross-sectional areas.

In their study, Alexander and Vernon (1975) calculated stresses of 54 and 30 MPa, respectively, in the gastrocnemius and plantaris tendons for the hop of a wallaby moving at 2.4 m s^{-1}; correspondingly, peak stresses of 100 and 50 MPa were calculated for the gastrocnemius and plantaris tendons of a red kangaroo moving at 6.2 m s^{-1}. Because Alexander and

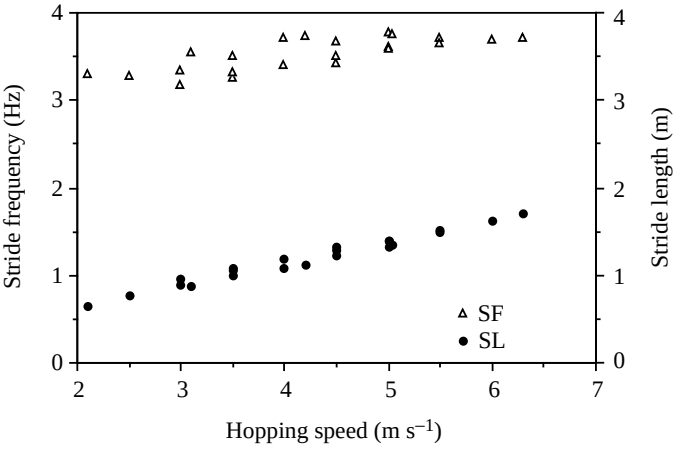

Fig. 6. Stride frequency (SF, open triangles) and stride length (SL, filled circles) plotted *versus* hopping speed, based on data obtained for all four animals. Both gait parameters increase significantly with increased hopping speed (least-squares regression slope ± 95 % confidence intervals; SF, 0.129±0.049, r^2=0.60, P<0.01; and SL, 0.242±0.015, r^2=0.98, P<0.001); however, the increase in stride length is twofold greater than the increase in stride frequency over the range of speeds recorded.

Vernon used a value for the density of tendon (1420 kg m^{-3}) that is probably too high, their values probably overestimate tendon stresses by 27 %. Recalculating their original stress values using the value for tendon density (1060 kg m^{-3}) reported by Ker (1981), which we use in the present study, we obtain stresses of 43 and 24 MPa in the gastrocnemius and plantaris tendons of the wallaby at 2.4 m s^{-1} and stresses of 79 and 39 MPa in the gastrocnemius and plantaris tendons of the red kangaroo at 6.2 m s^{-1}. Nevertheless, in comparison with our direct measurements of muscle–tendon force transmission, the

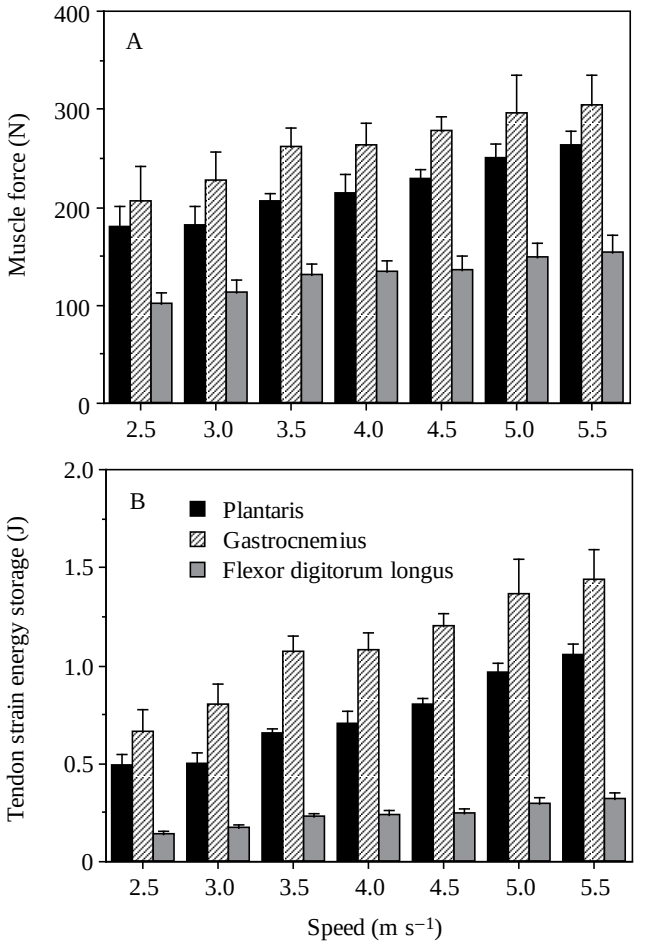

Fig. 7. Histograms of (A) muscle force and (B) strain energy storage in the tendons of wallaby no. 3 as a function of hopping speed. Forces generated by the three muscles increase with increased hopping speed, in association with increased stride length (Fig. 6). Forces generated by the gastrocnemius are consistently the highest. As a result, the largest fraction of strain energy is stored in the gastrocnemius tendon because of its smaller cross-sectional area, which offsets its shorter length (see Table 1). Much smaller forces and tendon strains were recorded in the flexor digitorum longus. Values are means ± S.D., $N \geqslant 57$.

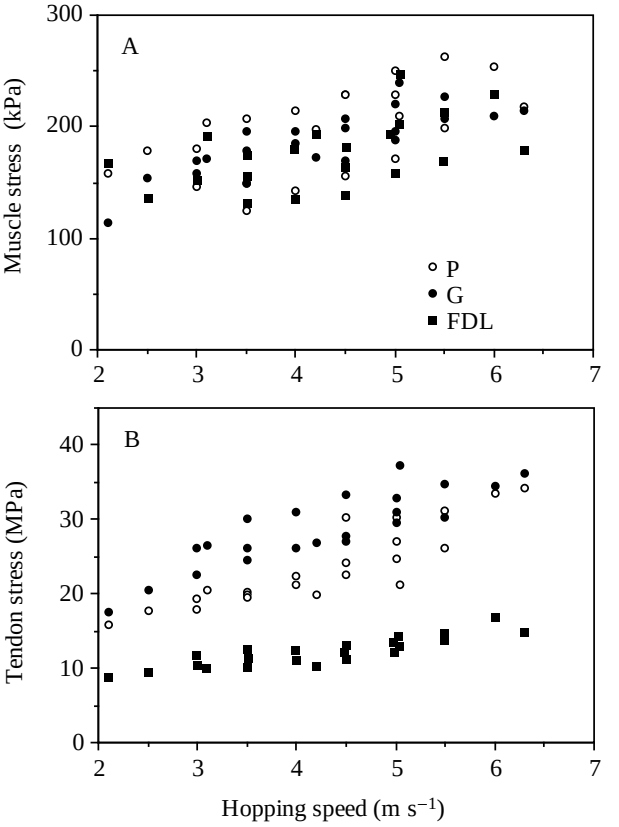

Fig. 8. (A) Muscle stresses and (B) tendon stresses plotted *versus* hopping speed. Data for gastrocnemius (G) and plantaris (PL) are for all four wallabies, data for the flexor digitorum longus (FDL) are for wallabies 3 and 4.

recalculated stresses of Alexander and Vernon seem high, particularly given the slow hopping speed of the Bennett's wallaby. Indeed, 79 MPa is close to the failure strength of tendon (100 MPa: Bennett *et al.* 1986; Ker *et al.* 1986; Shadwick, 1990), and it is certain that red kangaroos move at speeds considerably faster than 6.2 m s^{-1} (Dawson and Taylor, 1973). For the stresses calculated in the Bennett's wallaby, Alexander and Vernon (1975) determined that 5.6 J (recalculated from their original value of 9 J given lower values of peak stress) of energy was saved by the plantaris and gastrocnemius tendons of both hindlimbs (at 2.4 m s^{-1}). On the basis of our present measurements, we calculate that the total elastic energy saved by these tendons (including the FDL tendon) in tammar wallabies is 2.1 J at 2.5 m s^{-1} and 6.4 J at 6.0 m s^{-1}. These values would, of course, be greater in a larger animal. Alexander and Vernon (1975) calculated that the gastrocnemius and plantaris muscles performed 23 J of work during the same hop, indicating that elastic energy recovery provided a 24 % (corrected from an original value of 39 %) saving of muscle work. As we have not estimated muscle work in this study, we cannot calculate the fraction of muscle work saved by elastic recovery in the tendons of tammar wallabies. However, our measurement of the elastic power provided by these tendons shows that the percentage of metabolic power recovered by tendon strain energy increases from 5 to 25 % over the range of hopping speeds that we recorded. Presumably, the percentage savings would be greater at higher hopping speeds.

One way of interpreting the importance of elastic energy recovery to the animal is to calculate what its energy expenditure might otherwise be if there were no savings by elastic storage. This would require that the muscles perform all of the work required to hop. Assuming that muscles achieve a maximal efficiency of 25 % when performing positive work (Margaria, 1968; McMahon, 1984; Cavagna *et al.* 1977), savings of 25 % metabolic power by elastic storage would require that the muscles consume four times this energy to do the same amount of net positive work. Hence, the animal's total energy expenditure (at 6.0 m s^{-1}) would be doubled, compared with that observed. Given that some negative work must also be performed (costing metabolic energy), the

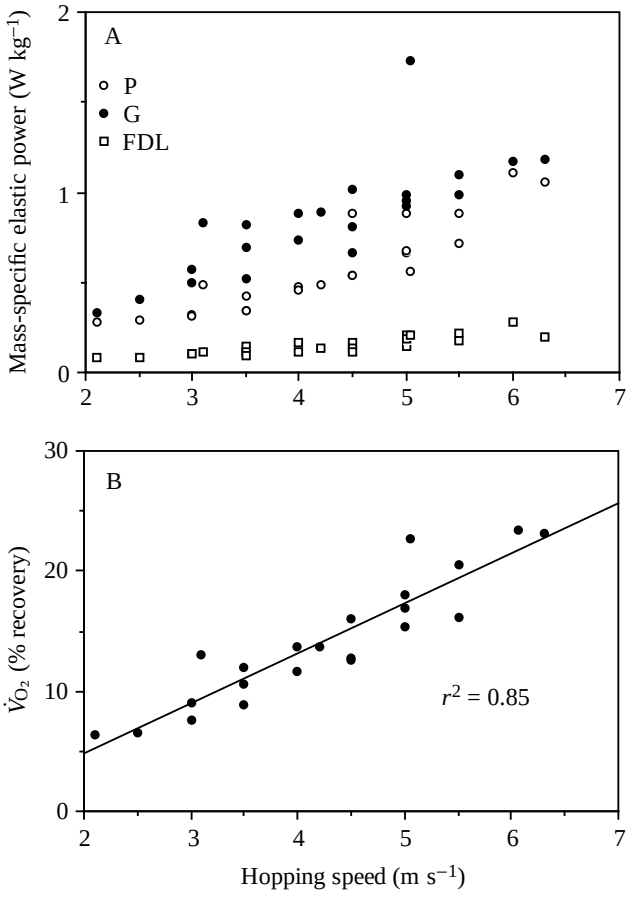

Fig. 9. (A) Mass-specific elastic power recovered from the tendons of gastrocnemius (G), plantaris (P), flexor digitorum longus (FDL) and (B) percentage recovery of metabolic power ($\dot{V}_{O_2}$) by tendon elastic power plotted *versus* hopping speed (least-squares regression: percentage recovery = $-3.63 + 4.19v$; r^2=0.85, P<0.001, where v is speed in m s^{-1}). Oxygen consumption was converted to watts (J s^{-1}), assuming that 1.0 ml of O_2=20.1 J, before calculating percentage recovery *via* elastic power.

increase in cost might be even higher than this if there were no energy saving by elastic energy storage. These savings in metabolic cost agree with the estimated 50 % or greater savings of a red kangaroo hopping at 8.0 m s^{-1} due to elastic energy storage (Cavagna *et al.* 1977).

The forces that we measured for the gastrocnemius (lateral and medial heads combined) are also comparable with those recorded by Griffiths (1989) for the medial gastrocnemius (after accounting for differences in size of the two species and division of force between the medial and lateral heads of gastrocnemius). In his analysis, Griffiths (1989) found that the stretch of the muscle fibers was 2.5-fold greater than the stretch of the tendon when measured *in situ*, indicating that muscle stiffness was about 40 % of tendon stiffness. Because of this, Griffiths concluded that increases in tendon strain and energy storage at faster speeds could not provide net savings to the animal because the muscle fibers would be stretched by the tendon beyond their short-range stiffness, causing the muscle to dissipate any additional energy that might otherwise be recovered by increased tendon stretch and recoil. As we do not estimate muscle fiber length changes and muscle stiffness here, we cannot document whether this is the case for the gastrocnemius, plantaris and digital flexor muscles of tammar wallabies. Our observation of a large increase in percentage recovery with increased hopping speed, however, supports the view that increased elastic energy saving *via* tendon strain energy is a viable mechanism by which these animals may increase speed with little increase in metabolic energy expenditure. This finding is in conflict with the finding of Griffiths (1989), whose interpretation depended on kinematic estimates of muscle fiber length change and force–extension data obtained from the tendon of another animal. It seems possible either that Griffiths may have underestimated muscle fiber stiffness in the thylogale medial gastrocnemius or that muscle fiber stiffness does not remain constant but increases with increasing levels of fiber recruitment and force generation at higher speeds; this would enable tendon stretch to contribute useful strain energy savings upon recoil, rather than being dissipated by increased stretch of the muscle. Improved measurements of muscle fiber length change under *in vivo* conditions are required before this issue can be better resolved.

Tendon stiffness and safety factor

An interesting finding obtained from our simultaneous measurements of the forces transmitted by the gastrocnemius, plantaris and digital flexor muscles is that the greatest forces are transmitted *via* the thinnest tendon (G) and that the smallest forces are transmitted by the thickest tendon (FDL). Because of their greater length, energy saving is favored in the tendons of the plantaris (PL) and FDL and would be significantly augmented if these tendons were thinner, subjecting them to higher stresses. As the maximum stresses that we measured are well within the failure strength (σ_f) of the animal's tendons (being 36, 33 and 16 % of σ_f for the G, PL and FDL tendons respectively), maintenance of an adequate safety factor would not appear to provide a good explanation for why the tendons of PL and FDL are so thick. Although the speed range examined (up to 6.3 m s^{-1}) is submaximal for this species, it is unlikely that, even at the animal's fastest hopping speeds, stresses in these tendons would be excessively high. Extrapolation of stresses to 10 m s^{-1}, based on regression lines for the data presented in Fig. 8, predicts stresses of 50, 48 and 20 MPa, respectively, in the G, PL and FDL tendons, providing safety factors of 2 for the G and PL tendons and 5 for the FDL tendon.

Another factor that is likely to influence tendon design is stiffness. Because the stresses experienced by a tendon are limited by the forces that the muscle can generate, tendon safety factors (in relation to failure strength) may theoretically be quite low (Alexander, 1981; Biewener and Bertram, 1990). Certainly, selection for increased elastic energy savings would favor a reduction in safety factor. However, by comparing muscle fiber area with tendon area, Ker *et al.* (1988) have estimated that many mammalian tendons probably operate with unusually high safety factors, having a mean of about 8. Because of their thickness,

therefore, most tendons are unlikely to be at risk of failure. Ker *et al.* (1988) and Rack and Ross (1984) suggest that the unusually high safety factors of most tendons reflect the need to maintain sufficient stiffness within the tendon, providing muscles with adequate control of overall length change and joint displacement in relation to the force–length properties of their fibers; thinner tendons require increased shortening of muscle fibers, to accommodate the tendon's stretch, in order to produce a given amount of shortening at a joint. The very low stresses that we observed in the flexor digitorum longus tendon of the tammar wallaby, in comparison with the gastrocnemius and plantaris tendons, suggest that control of digital flexion is a key function of this muscle, compromising its ability to contribute to increased elastic energy savings.

Muscle stress

The muscle stresses that we calculated from our recordings of tendon force, together with joint angle changes, indicate that all three muscles are initially stretched prior to shortening. Consistent with a stretch-enhancement of force generation by these muscles was our finding that, when the animals hopped at speeds of $4.5\,m\,s^{-1}$ or greater, peak stresses in the gastrocnemius and plantaris muscles regularly exceeded what we accept to be the maximum isometric stress (215 kPa) of mammalian skeletal muscle, reaching 227 kPa in gastrocnemius and 262 kPa in plantaris at speeds of $5.5–6.3\,m\,s^{-1}$. However, given that muscle stresses may be as much as 75 % greater than isometric stress during a stretch (Cavagna and Citterio, 1974; Flitney and Hirst, 1978; Harry *et al.* 1990), the levels of stress that we observe indicate that the muscles are only submaximally activated at these speeds. Griffiths (1989) reported a similar finding for the medial gastrocnemius, in which he found that maximal stresses at the fastest hopping speeds ($7\,m\,s^{-1}$) that he recorded were only 5 % greater than *in situ* measurements of isometric muscle stress. Extrapolation of the muscle stresses presented in Fig. 8, based on least-squares regression, indicates that stresses 1.75 times the isometric value (350 kPa) would be achieved at hopping speeds in the region of $12\,m\,s^{-1}$, which is probably close to the maximum speed of this species (Baudinette *et al.* 1992; R. V. Baudinette, unpublished observations). Alexander and co-workers have argued (Alexander, 1985, 1988; Alexander and Vernon, 1975; Ker *et al.* 1988) that the isometric stress-generating potential of skeletal muscle may be closer to 300 kPa, based on the results of Wells (1965), who reported an average value of 278 kPa for rat soleus and tibialis anterior muscles. If this is the case for wallaby muscles, the level of recruitment within these muscles would be less at any given speed, enabling the animals to achieve even higher speeds than we estimate above.

Although the stresses acting in the muscles and tendons of tammar wallabies are well below the maximum that these tissues are capable of transmitting, they are considerably higher than those that have been measured in the gastrocnemius and plantaris of the much smaller (0.11 kg) kangaroo rat *Dipodomys spectabilis* (Biewener and Blickhan, 1988), in which peak stresses of 80 kPa (muscle) and 8 MPa (tendon) were observed during hopping at speeds of up to $3.1\,m\,s^{-1}$. The low stresses observed in this small bipedal species were correlated with little elastic energy recovery during hopping but a considerable capacity for increased force generation to power more demanding activities, such as jumping. The diminished capacity for elastic energy storage observed in kangaroo rats compared with larger bipedal hoppers (wallabies and kangaroos), however, may not hold for different-sized quadrupedal species, which appear to show similar capacities for elastic energy recovery relative to mechanical power at equivalent speeds (C. T. Farley, unpublished observations).

In order to understand better the functional nature of how muscles power spring-like behavior in hopping and running, as well as their mechanical role in other activities, future work must begin to correlate measurements of force generation, as we present here, with improved measurements of length and velocity changes of the muscle fibers. Only by linking the force–velocity and force–length properties of a muscle fiber with its fiber characteristics and force-generating requirements during *in vivo* function can the design and neural control of muscle function be properly understood.

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