THE MECHANICS OF THE MEDIAL GASTROCNEMIUS MUSCLE IN THE FREELY HOPPING WALLABY (*THYLOGALE BILLARDIERII*)

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Summary

Muscle force, electromyogram and length were monitored in the medial head of the gastrocnemius (MG) muscle in freely hopping wallabies (*Thylogale billardierii* Desmarest).

During take-off hops from rest, MG muscle developed force with an isometric contraction. For constant-speed hops, force was produced in MG muscle during rapid stretch. The muscle resisted this stretch with a constant impedance that was independent of hopping speed. The rate of stretch of the muscle during high-speed hopping was as high as $1\,\mathrm{m\,s^{-1}}$ (5–6 muscle lengths per second) at the onset of stretch and slowed to no stretch at the peak of force. Since the mechanical impedance was constant while the stretch velocity changed, there was no significant viscosity present in the muscle.

The tendon stretched by 3·2 % at $7\,\mathrm{km\,h^{-1}}$ hopping and by 4·4 % at $18\,\mathrm{km\,h^{-1}}$ hopping. Elastic energy storage in the tendons increased with hopping speed but the percentage of total work done by elastic recoil of the whole muscle did not increase at higher hopping speeds.

The significance of the muscle stretch is in producing high forces rapidly and, in addition, there is considerable energy storage in the tendons.

Introduction

Dawson & Taylor (1973) reported that red kangaroos (*Macropus rufus*) hopping on a treadmill did not increase their oxygen consumption as their hopping speed increased from 9 to $22\,\mathrm{km\,h^{-1}}$. To explain this phenomenon, Dawson & Taylor suggested that as speed of travel increases so also does energy storage in the tendons and ligaments of the rear limbs and tail. Release of these increased amounts of stored energy through elastic recoil was postulated to reduce the energy requirements of locomotion as speed increased. The Achilles tendons, particularly large in the macropodid marsupials, were considered a major

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contributor. Such an increasing percentage of energy recycling would seem not to be generally true, since oxygen consumption increases with increasing speed of travel in a variety of quadrupedal eutherian mammals (Taylor et al. 1970, 1982), although the lion appears to be an exception (Chassin et al. 1976).

For two reasons Dawson & Taylor's popular hypothesis can be questioned. First, gait character in cats is known to alter when they are travelling on a treadmill (Miller & Van der Burg, 1973; Stuart et al. 1973; Wetzel et al. 1975), as it does in humans (Nelson et al. 1972) and small (<3 kg) hopping animals (Thompson et al. 1980). Second, it is important to note that most of Dawson & Taylor's red kangaroo data are from a single animal. Indeed, in untrained small hopping animals an observation similar to Dawson & Taylor's was made before the animals became accustomed to the treadmill (Thompson et al. 1980). I have therefore used another marsupial with comparable muscle structure and comparable gait character to test directly the hypothesis put forward by Dawson & Taylor. To do so I have made direct estimates of whether progressively increasing energy storage occurs in the hindlimb tendons as hopping speed increases in the wallaby Thylogale billardierii.

To study the mechanics of the medial head of gastrocnemius (MG) muscle and to assess its energy storage capacity over the maximum range of hopping speeds, muscle force, length and electromyogram (EMG) were measured continuously and directly in unrestrained wallabies hopping freely over a 24 m stretch of flat ground. This was done using radiotelemetry techniques and high-speed cinematography over open ground to avoid the problems with locomotion on treadmills. Using these techniques, the evidence points to a decreasing or constant percentage of energy returned by elastic recoil rather than an increasing percentage as required by Dawson & Taylor's hypothesis.

Materials and methods

Ten wallabies (*Thylogale billardierii*) were employed in this study. Two wallabies of 4·5 kg (wallaby no. 5) and 7·0 kg (wallaby no. 6) were successfully implanted with force gauges and EMG electrodes in the MG muscle of the right hind leg. A further four animals, with no surgical implants, were used as controls to check that the gait of the implanted wallabies was not affected by the implants.

The technology for these experiments was developed using an additional four animals. These were also used to verify that the gait was not significantly different from that of the control animals. Two of these animals were also included in the measurements of muscle fibre and tendon dimensions in order to establish the range of values that exist between animals.

Preparation of animals

The wallabies were anaesthetized with a mixture of ketamine hydrochloride ($4 \, \text{mg} \, \text{kg}^{-1}$) and xylazine ($2 \, \text{mg} \, \text{kg}^{-1}$) given intramuscularly. The gastrocnemius tendon was split into medial and lateral sections over a small length and a 'buckle' transducer slipped over the MG tendon to measure force. The design of the

transducer was a larger version of that used by Walmsley *et al.* (1978). A semiconductor strain gauge (BLH type SPB1–20–35) was fixed to the long arm of the stainless-steel buckle, using water-resistant Araldite epoxy type K138, and then coated with Epoxylite 6001. The buckle transducer was calibrated by placing it on a string and suspending various weights. It gave a linear response to over 100 N. EMG was recorded with a pair of twisted, Teflon-insulated, stainless-steel wires that were bared for 2 mm and drawn through the MG muscle.

Telemetry

Stranded stainless-steel wires from the buckle transducer and from the EMG electrodes were passed subcutaneously to a dual-in-line package electronic socket (Utilux SO series) that was bolted to the skull and insulated and reinforced with dental acrylic (Paladur).

During recording sessions, an FM radio telemetry unit (Griffiths, 1984) was fitted to the wallabies in a shoulder harness and was connected to the head socket on the animal by a lightweight cable. The telemetry unit with batteries and shoulder harness weighed less than 100 g and would transmit over a distance of 20–30 m.

The buckle transducer signal was amplified differentially and low-pass filtered with a cut-off frequency of 550 Hz. The EMG was amplified differentially and band-pass filtered with cut-off frequencies at 30 and 550 Hz. It was then time-multiplexed, along with a ground reference voltage and the force signal, and sent to the radio transmitter.

The radio signal was received by an omnidirectional aerial and the multiplexed signal recovered by tapping the output of the intermediate-frequency amplifier of a commercial FM tuner. The signal was then demultiplexed and the force and EMG were stored on a portable FM tape recorder.

A high-speed ciné camera (Milliken model DBM-5) was used to film the wallabies. To synchronize the film frames with the EMG and force, a pulse from the camera shutter was used to trigger a counter. This, in turn, provided a coded count of the frames taken. This code was recorded on the third channel of the tape recorder. The first and last frames taken were also marked on the edge of the film by a neon lamp within the camera. The wallabies were filmed at 200 or 400 pictures s^{-1}.

Experimental procedure

Before recording from the wallabies, five dots were placed on the shaved right leg as a means of computing joint angles and MG muscle length. Black dots were made using an oil-based felt pen and were surrounded by a white ring of typing correction fluid. The dots were placed on the anterior superior iliac spine, on the top of the femur on the most lateral aspect of the greater trochanter, on the lateral malleolus of the fibula, on the end of the metatarsal and on the large toe-nail. A dot was not placed on the knee because the skin was too loose and could slide from the lateral to the medial surface of the leg during hopping. At the conclusion of the

recording experiments, the wallabies were killed and the lengths of both femur and tibia were measured. The knee position could then be calculated trigonometrically along with all joint angles (Griffiths, 1984). The distances from the MG origin to the centre of rotation of the knee joint, and from insertion to ankle joint, were also measured. With joint angles calculated from the marked dots, the MG muscle length was then also calculated trigonometrically (Griffiths, 1984). The velocity of muscle stretch was obtained by differentiating the equation to a fifth-order polynomial regression of the muscle length data.

Recordings were made from wallabies in a large outside enclosure with the animals being released from one corner to hop along the fence to the far corner (about 24 m). The animals were filmed by panning with the high-speed camera over a distance of 8 m in the middle of the fence, while recordings of force and EMG were made continuously. The chain-link fence provided distance markers and any small parallax errors were corrected by reference to a system of lines drawn on the ground perpendicular to the fence. The film provided a measure of joint angle, MG length, hopping speed and style. Instantaneous hopping speed of the wallabies was measured from the film as stride length divided by the duration of the step cycle (i.e. time from one foot lift to the next foot lift). 234 constant-speed hops were analysed in the six wallabies for comparison of gait.

The four phases of the step cycle (F, E1, E2, E3) are as defined by Philippson (1905). In the wallaby the F phase starts when the large toe-nail leaves the ground and the hip, knee and ankle flex, bringing the leg up close to the body. The E1 phase starts midway between when the knee and then the ankle start to extend in preparation for placing the foot on the ground. The E2 phase begins at first contact of the foot (usually the large toe-nail) with the ground. During E2, the knee and ankle yield under the force of landing and the hip extends. Midway between when the ankle and then the knee start to re-extend is the beginning of the E3 phase. During E3 the knee and ankle extend along with the hip, thrusting the wallaby forward in a ballistic manner until a new step cycle commences when the foot leaves the ground.

Isometric contractions

Wallabies nos 4 and 5 were anaesthetized and the MG muscle exposed in order to measure the rate of rise of force in 'isometric' contractions, as opposed to during the stretch that occurred during normal hopping. The hindlimb was rigidly clamped in a steel frame and the tendon attached to a steel frame *via* a T-shaped bar (Morgan *et al.* 1978). Supramaximal voltage and frequency were used to stimulate the MG nerve and the rate of rise of the force was measured during the onset of an isometric contraction at the optimal length.

Sarcomere measurements

To estimate the average stretch occurring per half sarcomere (the amount that could return energy by elastic recoil) during the E2 phase of the stretch cycle it was necessary to know the number of sarcomeres in series in the muscle fibres. At

the end of the experiments, the MG muscle was fixed in 10 % formalin in 0·9 % saline. Single muscle fibres were teased out and the total length of tendon in series with the muscle fibres was also measured. The average sarcomere length in the muscle fibres was measured using He–Ne laser techniques (Iwazumi & Pollack, 1979) and the number of sarcomeres in series was calculated by dividing the muscle fibre length by the average sarcomere length.

Results

Of the six wallabies used in these experiments, three required long periods of training. Two of these animals received implanted devices, whereas the third acted as a control animal, housed and trained in the same manner, but without implanted transducers. A further three wallabies were filmed that were wild, untrained and housed outside in the large enclosure. All six animals had the same step cycle pattern (Griffiths, 1984) and no changes could be found that reflected a change in gait in the animals with the implants. The three wild animals could hop at speeds of up to $28 \, \text{km h}^{-1}$, whereas the normal maximum speed for the wallabies housed indoors was $18–25 \, \text{km h}^{-1}$. The difference in speeds would appear to be one of physical fitness only.

Two gaits were normally used by the thylogale wallabies. At slow speeds, and when starting slowly from rest, the *slow progression* gait was used (i.e. at least two feet or paws were in contact with the ground throughout the step cycle) and produced low MG forces (Fig. 1A). The tail was not used for support in this gait, as it is in red kangaroos (Morton & Burton, 1973). At higher speeds the wallabies used a hopping gait.

When the wallabies started hopping from rest for a fast take-off, the first step cycle did not involve the forelimbs and will be referred to as a *bipedal take-off* hop. This step resembled that of normal hopping, and force production in the MG was more rapid and reached higher levels (Fig. 1B) than during slow progression.

Fig. 1C illustrates the MG muscle forces for a sequence of hops from bipedal take-off, through constant-speed hopping and finishing with a slow progression step. A small amount of passive tension often appeared during the swing phase owing to the stretch of parallel elastic components. These are the smaller force peaks that appear in Fig. 1C.

Constant-speed hopping

In constant-speed hopping, the MG muscle developed an EMG during the E1 phase about 30–40 ms prior to foot contact. The muscle was shortening at this time and there was no force produced. The EMG reached maximal levels just prior to foot contact. On landing, the toe-nail of the large fourth digit made contact first and dug into the ground, preventing slippage. A few milliseconds later the pad under the phalanges made contact, resulting in a very rapid and strong stretch of the ankle extensor muscles (Fig. 2A, C). This resulted in a rapid rise in force (Fig. 2B) that reached a maximum at the end of the stretch. Both the knee and the
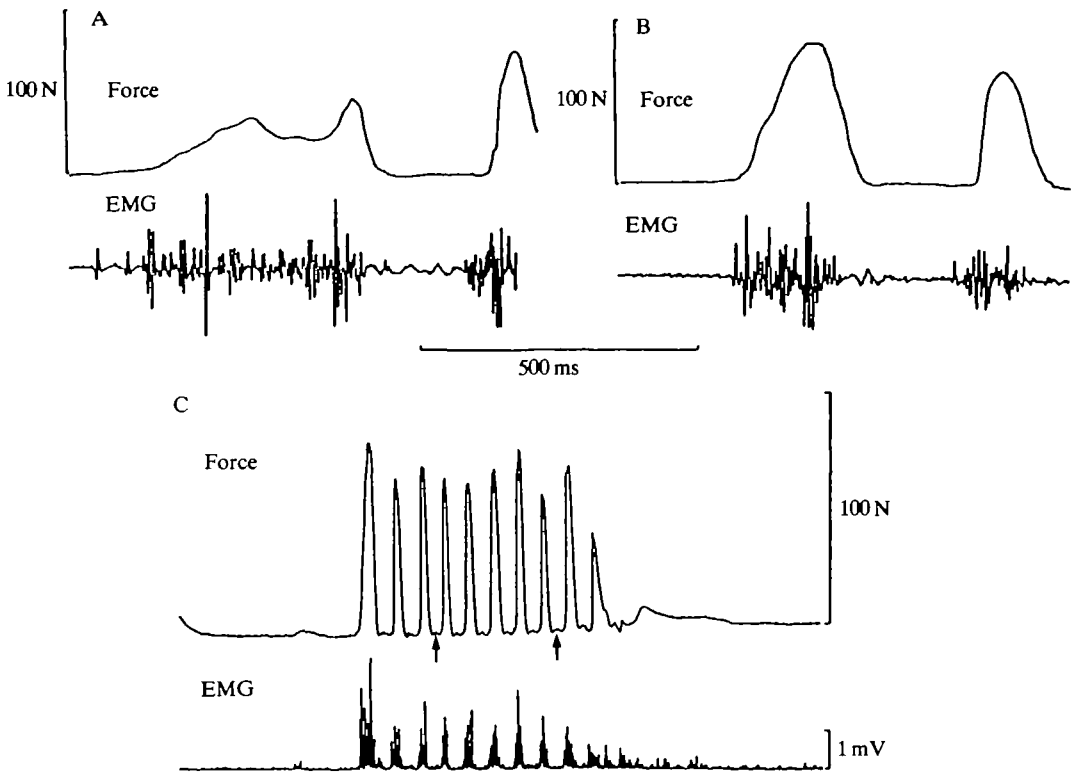
Fig. 1. Wallabies began hopping with either a slow progression (A) step cycle using all four limbs and producing small MG forces, or a bipedal take-off (B) step cycle that was very similar to constant-speed hopping except that the force increased more slowly. The second force peaks in A and B are constant-speed hops. (C) Force and EMG in MG muscle for a sequence of hops from a bipedal take-off through eight normal hops and finishing with a slow progression step. Stretch of the muscle during the swing phase produced small passive forces (arrows).

ankle yielded during the E2 phase, with the ankle yielding more at higher hopping speeds.

The foot provided a lever with a mechanical advantage of 0·77 during the E2 phase when the muscle was being stretched. The foot pad acted as the fulcrum. The applied force was provided by the mass of the wallaby accelerating under gravity, and was applied down the tibia to the talus. The load came from the stretch of the ankle extensor muscles. This low mechanical advantage protected the ankle extensor muscles from high forces when they were being stretched. During the E3 phase, the lever type changed (from class III to class II). The foot pad still acted as the fulcrum, the ankle extensor muscles now providing the applied force and the load being the tibia resting on the talus. Under these circumstances the mechanical advantage was 1·3 which enhanced the influence of these muscles in accelerating the animal in a ballistic manner.
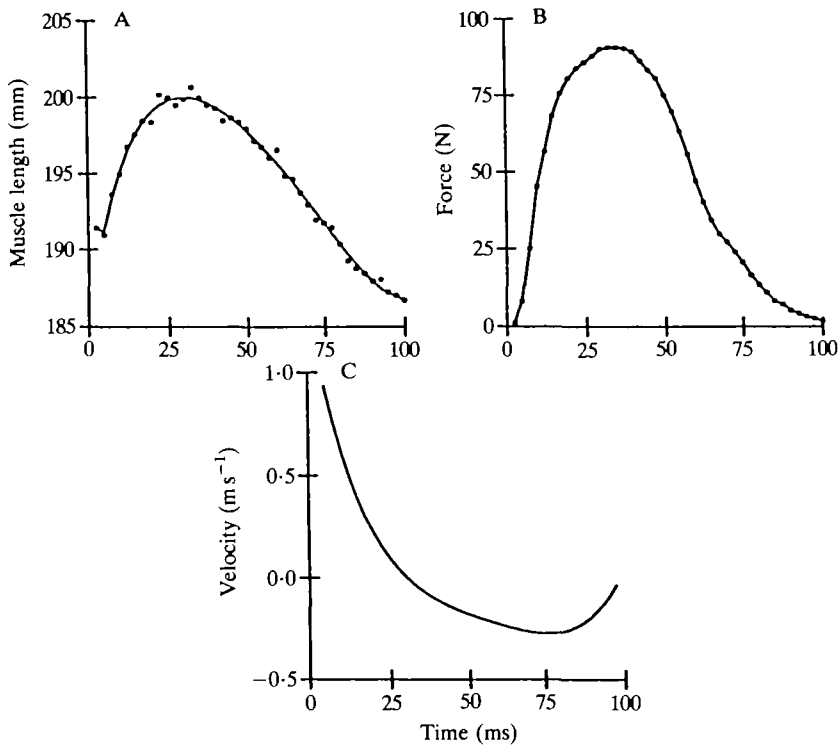
Fig. 2. MG muscle length (A), force (B) and velocity of movement (C) during a hop at a constant speed of 15 km h^{-1} (wallaby no.6). A positive velocity represents stretch of the muscle and a negative velocity represents shortening. A fifth-order polynomial regression was fitted to the length data to get the best fit. The equation for the velocity curve (C) was then produced by differentiating the equation to the polynomial regression of the length data.

Over the full range of hopping speeds, the wallabies landed with the MG muscle at about the same length. For wallaby no.6 (Figs 2, 3) this length was about 190 mm. At higher speeds of travel, the MG was stretched by larger amounts (Fig. 3A) and produced larger forces (Figs 3B, 4). The velocity of this stretch was very high at the start of the E2 phase (Fig. 3C), but declined as the muscle produced more force with which to resist the imposed stretch. This can be seen more clearly in Fig. 5. During the E2 phase the relationship between muscle force and length was linear (Fig. 6), showing that the MG muscle resisted the stretch with a constant mechanical impedance. For wallabies nos 5 ($N = 23$) and 6 ($N = 33$) this constant impedance was independent of the speed of travel (Fig. 7).

Since muscle force increased with speed (Fig. 4) and the mechanical impedance was constant, the amount of stretch of the muscle also increased as determined by the value of the mechanical impedance. This increased stretch at higher speeds was accompanied by a decrease in the E2 phase duration, resulting in a faster velocity of stretch of the muscle. As a result of the rapid stretch of the active
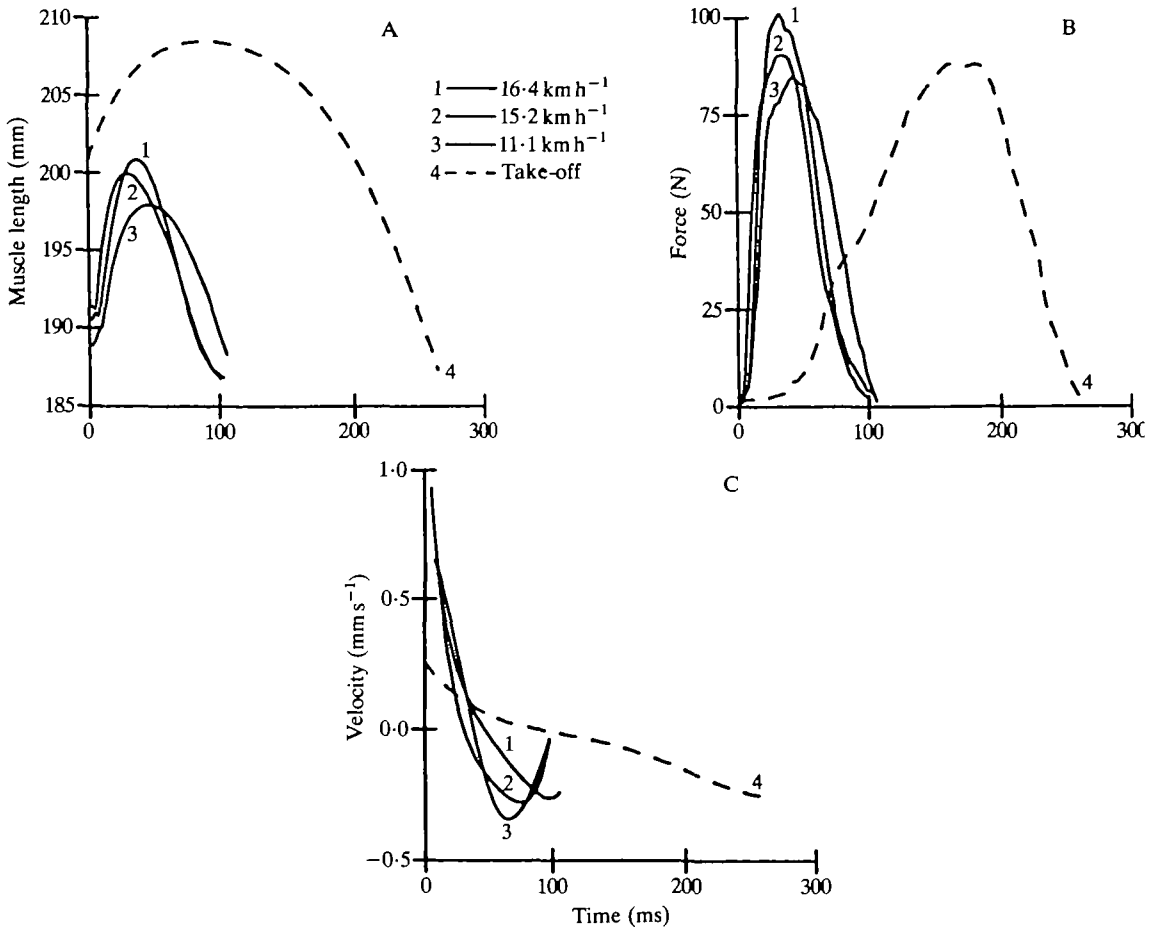
Fig. 3. A comparison of MG length (A), force (B) and velocity (C) during three constant-speed hops at speeds of 11, 15 and 16 km h^{-1} (solid lines), and a bipedal take-off hop (dashed line) from wallaby no.6. The length of stretch and the force both increased at higher speeds of travel in constant-speed hopping. The bipedal take-off hop produced force much more slowly than constant-speed hops and the muscle was not stretched during the rise in force as it was in constant-speed hopping.

muscle, the force increased at a rate 10 times faster than that measured later during the initiation of supramaximal isometric contractions (performed on the same wallaby under anaesthesia at the end of the experiment). During the E3 phase, the electrical activity ceased while force was continuing to decline.

The areas under the force vs length curves (Fig. 6) during stretch are a measure of the work performed on the muscle during the E2 phase. During the subsequent shortening in the E3 phase, a similar amount of work is performed by the muscle, but only a portion of this will come from recoil of elastic structures. The work done on the muscle during stretch and by the muscle during shortening increased with hopping speed in both animals up to 18 km h^{-1}. Above this speed, wallaby no.
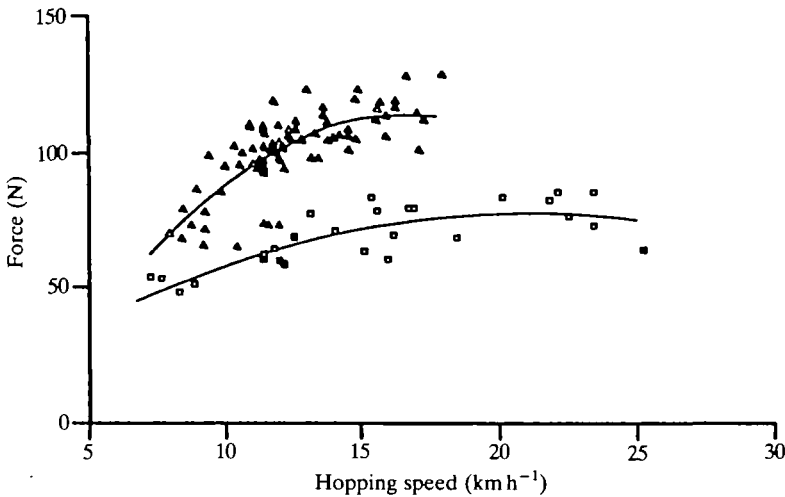
Fig. 4. Muscle force for constant-speed hopping over the full range of speeds at which wallabies nos 5 and 6 could travel. Quadratic regression lines are fitted to the data. Wallaby no.5; $N = 30$. Wallaby no.6; $N = 88$

increased its hopping speed by a more rapid increase in hop frequency rather than by an increase in stride length, and muscle force and work per hop remained constant.

Bipedal take-off

Five bipedal take-off hops were recorded from wallaby no.6. These hops all had the same essential properties; one example is shown in Figs 1, 3, 5 and 6. The resting MG muscle length in this wallaby was 197–199 mm when standing quietly. The muscle was stretched to 206 mm before generating force in a bipedal take-off (Fig. 6D) and the force was developed during an essentially isometric contraction (Figs 5, 6D). This resulted in a much slower rate of rise of force than in constant-speed hopping, where the MG muscle was rapidly stretched. In the bipedal take-off hops the time to peak force was 90–160 ms, or 2·7–4·0 times the time taken during constant-speed hops of similar speed. For bipedal take-off hops about twice as much work is done by the muscle during shortening than for a constant-speed hop of similar speed (Fig. 6).

Muscle fibre and tendon properties

To estimate the movement of the muscle fibres during the E2 phase, the tendon stretch was subtracted from the overall muscle stretch (Fig. 8). The muscle stretch was that measured in Fig. 6 with the muscle having constant mechanical impedance. The curve for tendon is an extrapolation for the whole tendon from measurements on a section of isolated free tendon (Proske, 1980) performed on a ♭ylogale of the same size and kept in the same reserve. This assumes that the unit compliance of the tendon that runs along the muscle belly is the same as that for
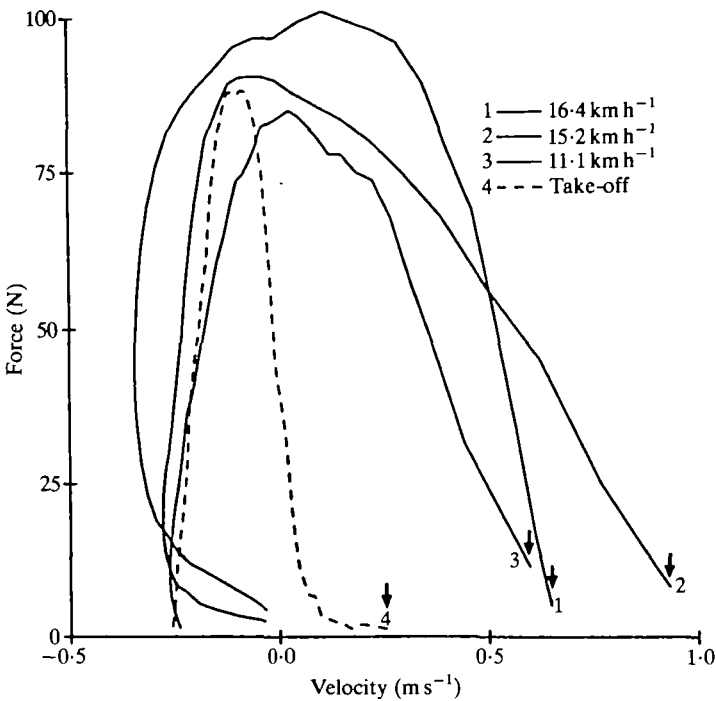
Fig. 5. Relationship between force and velocity of movement in the four hops shown in Fig. 3. When the wallaby lands on the ground during constant-speed hopping (1–3, arrows) the initial stretch of the MG muscle is very fast and slows down as the muscle force builds up to resist the stretch. Force production in the bipedal take-off hop (4) occurs during an essentially isometric contraction. During the E3 phase, shortening velocities of over $200 \, \text{mm s}^{-1}$ occurred at a force of 75 N (0·6 of maximal isometric force) when hopping at high speed ($16 \cdot 4 \, \text{km h}^{-1}$).

the free tendon. By subtracting this expected tendon yield from the total movement, a measure was calculated that included muscle fibre movement and any change in length due to a change in pennation angle of the muscle fibres, but with no means of separating the two components. When stretch was first applied to the muscle during E2, it appeared that the muscle fibres that were shortening in E1 prior to footfall continued to shorten due to the higher tendon compliance at low forces.

Table 1 summarizes the measurements of the number of sarcomeres in series and tendon length. Using the curve for tendon compliance in Fig. 8 and forces from Fig. 4 the tendon would be stretched by 3·2 % (5·4 mm) at $7 \, \text{km h}^{-1}$ and by 4·4 % (7·5 mm) at $18 \, \text{km h}^{-1}$.

Discussion

Mechanics of the MG muscle

When in the hopping gait, the MG muscle is stretched on landing but the muscle
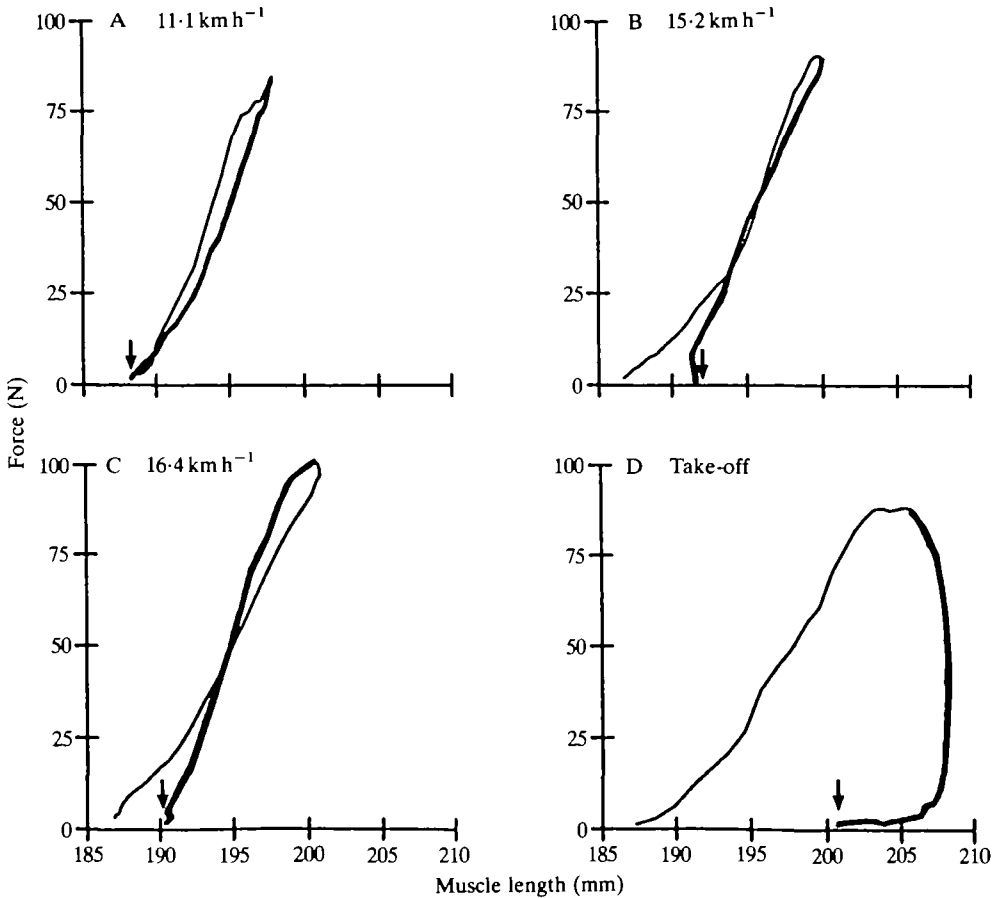
Fig. 6. Force *vs* length plots for MG muscle for the four hops of Fig. 3. The thick lines show force rising during the E2 phase, from zero at footfall (arrows) to peak levels at the end of stretch. The thin lines are the force declining during the propulsive E3 phase. During constant-speed hopping the muscle resisted stretch with a constant mechanical impedance. The areas under the graphs are a measure of the work done on the muscle during stretch or by the muscle during shortening.

Table 1. *Muscle fibre and tendon measurements*

Wallaby	Mass (kg)	Average sarcomere no.	Tendon length (mm)
1	5·7	9 728 (16)	140·1 (10)
2	7·2	8 908 (6)	156·5 (6)
5	4·5	7 799 (13)	171·1 (13)
6	7·0	10 952 (28)	170·1 (28)

The number of samples from each muscle is given in parentheses.

fibres initially shorten, with the tendon being stretched by applied forces at each end since it has a much higher compliance at low tensions (Viidik, 1972, 1973; Proske, 1980; Rack & Westbury, 1984). As force increases, the muscle fibres are stretched as well by the now stiffer tendons. The external stretch of the MG muscle takes up all of the tendon yield, effectively reducing the major part of the series elastic compliance (SEC) and allowing the muscle fibres to reach a high level of force in a much shorter period. This effect has been described previously by Hill (1951). Shortening of the muscle fibres during stretch of the whole muscle has also been recorded in cats (Griffiths & Hoffer, 1987).

Stretch of a contracting muscle will usually produce an enhancement of force (Abbott & Aubert, 1952; Joyce *et al.* 1969; Cavagna & Citterio, 1974) by as much as 70 % of the maximal isometric force. Since no hops at constant speed produced a force in the MG muscle more than 5 % above the maximal tetanic force, even at the fastest hopping speeds that the wallabies could achieve, it seems that maximal excitation of the muscle did not occur in the hopping gait. This is a similar result to that of Walmsley *et al.* (1978), who found that force in cat MG during slow galloping was less than 25 % of the maximal isometric force. However, the fastest speeds reached in these cats was less than one-third of maximal.
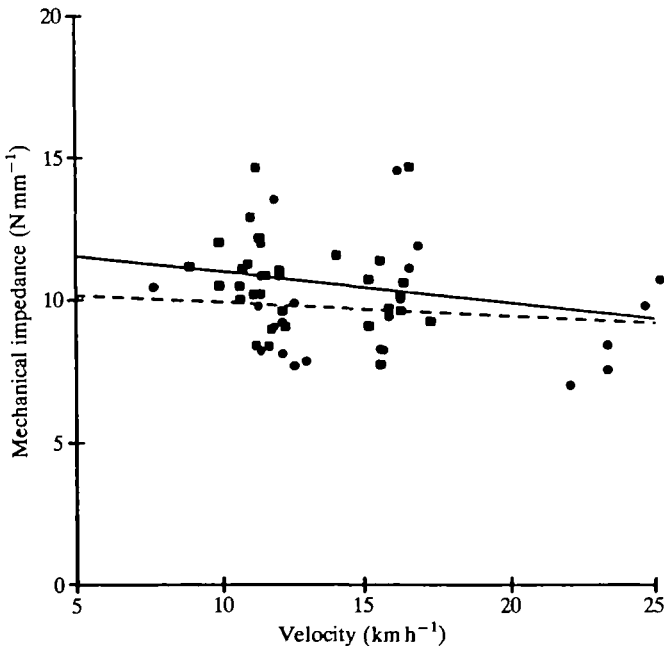

Fig. 7. The mechanical impedance of the MG muscle during the E2 phase of constant-speed hopping was constant and independent of the speed of travel in the two wallabies shown. The impedance was $10{\cdot}7 \pm 1{\cdot}6\,\mathrm{N\,mm^{-1}}$ $(N = 33)$ in wallaby no.6 and $9{\cdot}6 \pm 1{\cdot}9\,\mathrm{N\,mm^{-1}}$ $(N = 23)$ in wallaby no.5 (mean $\pm$ s.d.). The mechanical impedance of the MG muscle during the E2 phase stretch was constant, with correlation coefficients in the range $0{\cdot}97{-}1{\cdot}0$ in 56 of the 59 hops analysed.
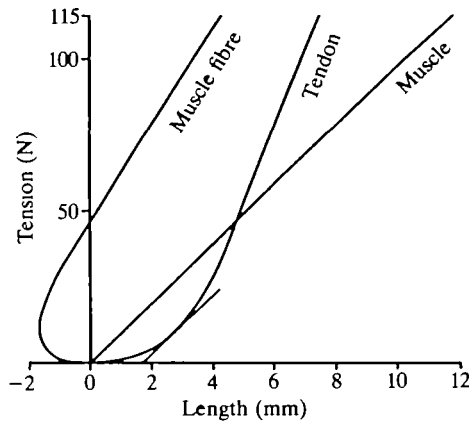
Fig. 8. For a constant-speed hop at $17\,km\,h^{-1}$ (wallaby no.6) the MG muscle produced a force of 115 N and had a mechanical impedance of $10.7\,N\,mm^{-1}$ (muscle line). The curve for tendon is an extrapolation of a curve produced on a section of free tendon. By subtracting the movement in the tendon from that in the whole muscle, muscle fibre length changes and any length change due to a change in pennation angle can be calculated (muscle fibre line). The muscle fibres continue to shorten until the force reaches 13 N.

Constant mechanical impedance of an ankle extensor muscle during stretch has been suggested by Houk (1979) and Houk & Rymer (1981) to be maintained by skeletomotor reflexes. In the MG muscle of the wallaby, a constant mechanical impedance was measured and is composed of two major elements. The first of these is an elastic stiffness present in the tendons, and it is in series with the second element, a relatively inelastic stiffness provided by the muscle fibres when they are stretched by a length greater than the short-range stiffness (Joyce *et al.* 1969; Rack & Westbury, 1974). The velocity of muscle stretch during the E2 phase changed from maximum values approaching $1.0\,m\,s^{-1}$ at the onset of stretch to $0\,m\,s^{-1}$ at peak length, but the mechanical impedance of the muscle was constant throughout the stretch (Fig. 6). At high hopping speeds MG was stretched at faster rates, but the mechanical impedance was again unaltered (Fig. 7). These results show no external sign of viscosity in the muscle. If the muscle had significant viscous properties, the force should have risen more steeply during the early stages of the stretch when the velocity was higher than at the end of the stretch. By contrast, Rack (1966) found cat soleus muscle did have viscous properties, but under conditions of slow sinusoidal stretches. The disparity may result from the large differences in the experimental conditions since, in the freely hopping wallabies, the stretch rate was much higher than Rack used and the muscle stimulation during normal locomotion was not constant.

Bipedal take-off hops

In the bipedal take-off hops, the force rose during an essentially isometric contraction and the tendons yielded as determined by their compliance. The

muscle fibres shortened and took up this yield. Hill (1938) suggested that this should occur and it has also been specifically measured by Griffiths (1987) in isometric contractions in cat MG muscle. If hopping consisted of a series of leaps of the bipedal take-off type, the speed of travel would be greatly reduced owing to the much greater time necessary to stretch the SEC and to produce the required forces. In constant-speed hopping a rapid external stretch is applied to the muscle that reduces the effective SEC (Hill, 1951).

The bipedal take-off hops not only took more time to achieve, but were also energetically more expensive. Constant-speed hops use about half the work of a bipedal take-off hop in MG during the E3 phase, because less muscle shortening occurs (Fig. 6). During landing, the momentum of the wallaby results in tendon stretch. This is in strong contrast to the bipedal take-off, where tendon stretch is a result of active muscle fibre shortening.

Sites of energy storage

With the knowledge gained about the mechanics of the muscle, the energy storage in MG can be calculated. Energy can be stored in the SEC of muscle which is divided between the muscle fibres and the tendons in proportions that vary enormously among skeletal muscles, and depend on tendon length and compliance and the number of sarcomeres in series in the muscle fibres. Tendons show elastic and viscous properties (Viidik, 1973) as well as creep behaviour (Goldstein *et al.* 1987; Hooley & Cohen, 1979). The most significant factor is the non-linear elastic property (Viidik, 1972), which allows the tendon to store energy. In addition, energy can be stored in the muscle fibres, but only over a very short length range. An elastic recoil is possible in the crossbridges if the stretch and release occur before crossbridge recycling. For cat muscle, Rack & Westbury (1974) suggested that the range of movement of the crossbridges was 25–35 nm. If this were the same in the thylogale wallaby muscle, it would suggest a maximum range of 0·77 mm over which the muscle fibres could be elastic. [For 10952 sarcomeres in MG (Table 1; wallaby no.6) with 35 nm movement for each half sarcomere = 35 nm × 10952 × 2 = 0·77 mm.]

In Fig. 8 the movements of each component of muscle are shown for the yield phase of a single constant-speed hop at $17 \, \mathrm{km \, h^{-1}}$ in wallaby no.6. The tendon will be essentially elastic with about 10 % loss due to hysteresis and, therefore, will store most of the work done in stretching it. This work will be returned during the propulsive E3 phase. For this hop, 0·72 J of work (the area under the length–tension curve) was done on the whole muscle, with 0·26 J being stored in the tendon. When the muscle fibres are also stretched, the crossbridges break and re-form, with the average crossbridge being only half extended by the end of the stretch. The energy that could be stored by stretching these crossbridges would thus be $0·5 \times 0·77 \, \mathrm{mm} \times 115 \, \mathrm{N} \times 0·5 = 0·02 \, \mathrm{J}$. This gives 0·28 J stored in elastic structures from 0·72 J of work done on the MG muscle during stretch. This equals 41 % for the MG muscle of wallaby no.6 hopping at $17 \, \mathrm{km \, h^{-1}}$ and compares with

Alexander & Vernon's (1975) figure of 39 % for the combined elastic recoil from all the leg muscles in a 10·5 kg Bennett's wallaby hopping at 8·6 km h^{-1}.

At higher hopping speeds the tendon stretches further (Fig. 8) and will store more energy. However, since the tendon stiffness is more than double that of the whole muscle, 25 N mm^{-1} compared with 10·7 N mm^{-1}, the muscle fibres are stretched by a greater amount than the tendons. Stretch of muscle fibres beyond the elastic limit of the crossbridges (0·77 mm for wallaby no.6) results in work absorption rather than energy storage (Rack & Westbury, 1974) and very little of the muscle fibre stretch is returned as elastic recoil. The important consequence of this result is that, although more energy is stored in the tendons at higher hopping speeds, the percentage of the energy put in during stretch and subsequently recovered by elastic recoil does not increase. This contrasts with the results derived by Alexander & Vernon (1975) for the red kangaroo hindlimbs. Using very different techniques they considered that the percentage of energy stored would increase with speed of travel.

For energy storage in the tendons to explain reduced oxygen consumption at higher speeds of hopping (Dawson & Taylor, 1973), a greater percentage of the work done on the muscles during stretch would have to be returned by elastic recoil at higher speeds. This does not appear to be the case in the thylogale MG muscle.

Energy storage and oxygen consumption

Thompson *et al.* (1980) demonstrated that small (<3 kg) hopping animals need specific training to be able to hop on a treadmill and show oxygen consumption rates that depend on this level of training. Untrained animals showed a sigmoidal relationship between oxygen consumption and speed of travel, while fully trained animals showed a linear relationship, like the quadrupedal mammals. The red kangaroos of Dawson & Taylor (1973) were considered well enough trained not to show this methodological artefact. The oxygen consumption of the red kangaroos was not independent of speed over the full range of speeds, since Dawson (1977) suggests that the curve for the red kangaroo data was sigmoidal when higher hopping speeds than those that could be obtained on the treadmill were considered. This highlights a major difference between the trained, small hopping animals showing a linear increase in oxygen consumption as hopping speed increases, and the data from the larger red kangaroo showing a sigmoidal increase in oxygen consumption at higher hopping speeds.

Kangaroo rats are a major example of the small (<3 kg) hopping animals described by Thompson *et al.* (1980). Biewener *et al.* (1981) recorded length–tension curves for the MG muscle in the kangaroo rat (*Dipodomys spectabilis*), hopping at constant speed, that clearly resemble the less efficient bipedal take-off hops in the thylogale wallabies (Fig. 6D). This is a significant difference in the gait of the small hopping animals compared with the thylogale and the red kangaroos. The thylogales in the present study were between the size of the small hopping animals used by Thompson *et al.* (1980) and the red kangaroo used by Dawson &

Taylor (1973). Oxygen consumption curves for this species hopping on a treadmill (Warren, 1979) are limited but suggest a lower level of consumption at higher speeds than would be expected for running quadrupeds, although not as low as the result for red kangaroos (Dawson & Taylor, 1973).

To investigate the energy storage capacity of the ankle extensor muscles that contribute to the Achilles tendon, force and length changes have to be measured during normal locomotion and over a range of speeds. Alexander & Vernon (1975) attempted to do this in red kangaroos and Bennett's wallaby *Protemnodon rufogrisea*, estimating individual muscle forces from force platform measurements and length from high-speed cinematography. Owing to vibration of the force platform, however, force records could not be taken during the early stance phase, making it very difficult to calculate the work done on the muscle during stretch.

The use of a treadmill may also have influenced the results obtained by Alexander & Vernon. In particular, it may have influenced the step cycle timing, as has been seen previously in the cat (Miller & Van der Burg, 1973; Stuart *et al.* 1973; Wetzel *et al.* 1975), human (Nelson *et al.* 1972) and small (<3 kg) hopping animals (Thompson *et al.* 1980). The Bennett's wallaby used by Alexander & Vernon did not extend its knee in the second half of the stance phase, whereas the thylogales in the present study did show knee extension. This could be a species difference or a property of the Bennett's wallaby accommodating its step cycle pattern to the treadmill.

It has been popular to consider kangaroo locomotion as a major example of elastic storage of energy. However, Ker *et al.* (1986) consider that the kangaroos are much less specialized for elastic storage in running than are the donkey and the deer. Morgan *et al.* (1978) compared thylogale MG muscle with cat soleus in anaesthetized preparations and suggested that in the wallaby MG muscle 5–8 times more elastic movement could occur in the tendon than in the muscle fibres at maximal isometric tensions. When the comparison is made in the same muscle, however, between the thylogale MG and the cat MG, the cat MG tendon has nearly 12 times the maximal elastic range of the muscle fibres, possibly giving it a greater specialization for elastic storage and recoil than the wallaby.

The thylogale MG muscle is inefficient in the bipedal take-off hops because it has actively to stretch the long compliant tendon. The slow progression gait (equivalent to the pentapedal gait in the red kangaroos) also requires the ankle extensor muscles actively to stretch the tendon during force generation and is similarly inefficient. When moving to the hopping gait, there is a marked increase in efficiency because the tendons are stretched externally, thus saving muscular effort. In addition, the energy provided to stretch the tendon is returned during elastic recoil.

The compliant tendon can therefore help to explain the higher than predicted oxygen consumptions in the slow progression (or pentapedal) gait. At hopping speeds of 18–22 km h^{-1} Dawson & Taylor (1973) recorded oxygen consumption levels slightly lower than those predicted for most quadrupeds. Above these speeds Dawson (1977) considered that oxygen consumption would increase. Red

kangaroos are reported to hop at speeds as high as $65\,\mathrm{km\,h^{-1}}$ and there is no evidence to support the generally held idea that, at high speeds, hopping is an inexpensive way to travel.

The significance of muscle stretch in constant-speed hops is in allowing a rapid rise in muscle force with which the muscle can resist the downward momentum and get on with the propulsion for the next step cycle. This allows for a faster step frequency than would be possible if the hops were all of the bipedal take-off type. Stretch is also significant in providing energy savings due to the stretch and recoil of the elastic tendons. A proportion of the work done in stretching the muscle during the E2 phase is stored in elastic structures. While the absolute energy saving increases with the speed of hopping, the proportion of the work done on the muscle, which is then saved in these elastic structures, does not increase.

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