



Research

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The kangaroo's tail propels and powers pentapedal locomotion

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When moving slowly, kangaroos plant their tail on the ground in sequence with their front and hind legs. To determine the tail's role in this 'pentapedal' gait, we measured the forces the tail exerts on the ground and calculated the mechanical power it generates. We found that the tail is responsible for as much propulsive force as the front and hind legs combined. It also generates almost exclusively positive mechanical power, performing as much mass-specific mechanical work as does a human leg during walking at the same speed. Kangaroos use their muscular tail to support, propel and power their pentapedal gait just like a leg.

1. Introduction

Kangaroos are well known for hopping on their muscular hind legs with their long tail outstretched behind. But these grazing animals spend much more time moving slowly than hopping quickly [1], and when they do so, kangaroos use their tail quite differently. They plant it on the ground in sequence with their front and hind legs in a distinctive gait referred to as 'pentapedal' locomotion [2,3], with the fifth point of contact being the tail (figure 1; see also the electronic supplementary material, Video).

This unique use of a tail has long been of scientific interest [3,5,6], with much speculation as to whether the tail functions as an additional leg during pentapedal locomotion [7–9]. Kangaroo tails appear to be biomechanically and physiologically capable structures—the tail muscles are much larger than the muscles of the front limbs and they are dense with mitochondria suggesting a large aerobic capacity [10]. The kangaroo's tail anatomy, however, is quite distinct from the front and hind limbs—it comprises more than 20 caudal vertebrae rather than a few long bones [11]. The highly articulated anatomy of tails is not normally associated with leg-like behaviour but instead with prehensile or balancing functions [12–14]. Indeed, the ancestors to modern-day kangaroos were arboreal [15,16] and thus likely used their tails to grasp and balance. Is it possible for an appendage other than the front and hind limbs to truly function as a leg? Here, we use biomechanically meaningful measurements to quantitatively test whether kangaroos indeed use their tail as an additional leg to propel and power their pentapedal gait.

2. Material and methods

(a) Experimental set-up

We trained five red kangaroos (*Macropus rufus*) to 'walk' pentapedally over a force-measuring platform while we videotaped their movements (figure 1). Four adult females (28.8 ± 1.6 kg) and one juvenile male (15.3 kg) traversed a walkway across a flush-mounted force plate (Kistler 9281A) that recorded vertical and fore–aft forces

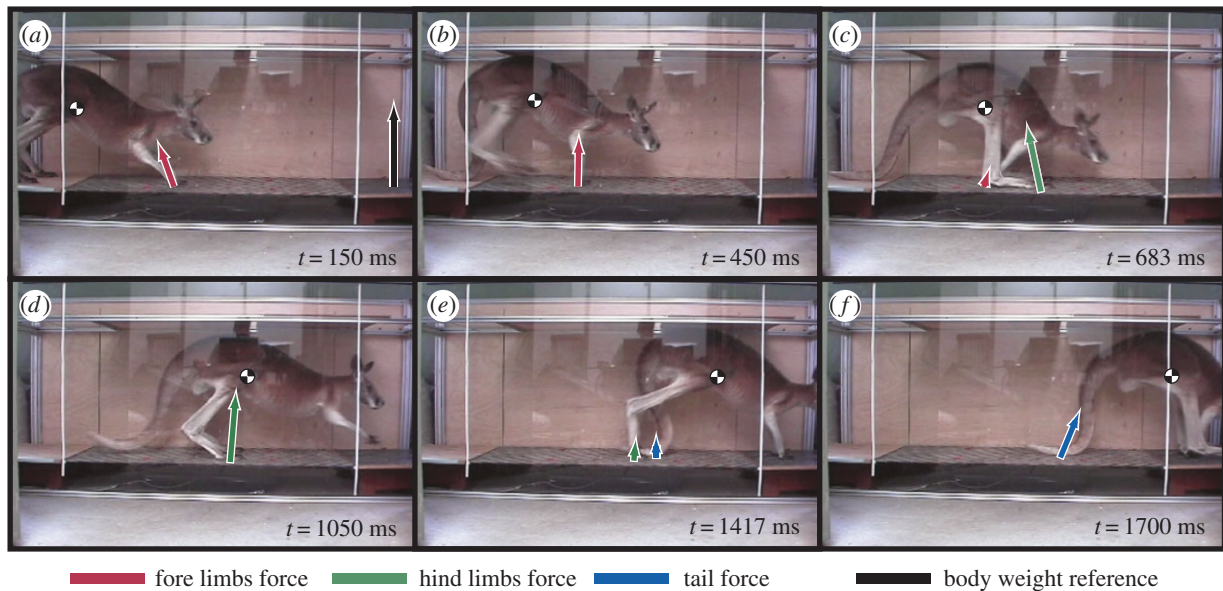


Figure 1. Pentapedal locomotion in the red kangaroo. Kangaroos moved pentapedally across a force platform (checkered flooring). (a–d) A complete stride starting with contact of the front limbs ($t = 0$). Following the onset of front limb stance (a), the tail contacts the ground and the hind limbs begin swinging forward (b). After the hind limbs contact the ground again (c), the front limbs and then the tail swing forward (d). We measured the ground reaction forces (GRFs) generated by the pairs of limbs and tail over multiple strides (a–f). Tail forces were isolated after the other limbs no longer made contact with the force plate (f). The red, green, blue and black arrows represent force vectors associated with the front limbs, hind limbs, tail and reference body weight, respectively, for the represented trial. The checkered circles approximate centre of mass (COM) locations based on Alexander *et al.* [4] and are for illustrative purposes only.

at 1000 Hz. A ceiling was positioned over the walkway, designed to not interfere with the kangaroo's pentapedal gait while preventing them from hopping across the walkway. A video camera (JVC GRDV 9800) recorded sagittal plane motion at 60 Hz.

(b) Video analysis

From the video recordings, we determined the timing of ground contacts by the front limbs, hind limbs and tail. In pentapedal locomotion, the front and hind limb pairs each move in unison. Consequently, we report the combined results for these front and hind limb pairs. We calculated speed for each trial as the distance between consecutive front limb ground contacts divided by the elapsed time. We restricted our analysis to a single range of speeds used consistently by all the animals ($0.63\text{--}0.88\text{ m s}^{-1}$). We also eliminated trials with irregular limb contact timings and those involving substantial acceleration ($|\text{net fore-aft acceleration}| > 0.4\text{ m s}^{-2}$) (see also the electronic supplementary material).

(c) Estimation of limb forces

We analysed trials in which the limbs contacted the force platform in a manner that allowed us to separate the ground reaction forces (GRF) generated by the front limbs, hind limbs and tail. These included trials wherein the tail or a pair of limbs began and ended a contact phase completely on the force platform without the other limbs exerting force on the platform. We also included trials in which there were other limbs in contact with the platform for a short period at the beginning or ending of a contact phase. We estimated the forces during that period by interpolating between the time at the onset of multiple limb contact and the time at the beginning or ending of the contact phase, when the force was assumed to be zero (see also the electronic supplementary material). For each animal, we computed the consensus force signals exerted by the tail or pair of limbs over a stride by averaging the respective GRF across trials and synchronizing them to the average ground contact timings from video (see also the electronic supplementary material). We then estimated total force of a consensus stride for each animal by

summing the average tail forces, front limb forces and hind limb forces. In total, 22 trials were used for the final analysis with an average speed of $0.77 \pm 0.07\text{ m s}^{-1}$ (mean \pm s.d.).

(d) Estimation of power generated by limbs

We used established methods to estimate the power generated, and work performed, by the individual limbs for each animal ([17]; see also the electronic supplementary material). Briefly, we first found the time-varying velocity of the centre of mass (COM) by calculating the accelerations of the COM from the total force for the consensus stride for each animal and then integrating with respect to time, using the average measured fore–aft velocity and a zero average vertical velocity as boundary conditions. We then calculated the instantaneous external mechanical power generated by the front limbs, hind limbs and tail from the dot product of their GRF and the velocity of the COM, and then normalized by animal mass. The average positive and negative power performed per stride is the time-integral of the positive and negative portions of external mechanical power normalized by stride period. We calculated the average positive and negative forces generated per stride similarly.

3. Results

We discovered that kangaroos use their tail as a very capable leg when moving pentapedally. The tail exerts very little braking force but generates a large propulsive force—as much as the front and hind limbs combined ($p = 0.08$, paired t -test) (figure 2a). The lone role previously attributed to the tail during pentapedal gait was body-weight support [3,5]. Indeed, we find the tail exerts appreciable vertical force on the ground, although it only contributes $13.6 \pm 1.0\%$ (mean \pm s.d.) of the average vertical force required to support the body over a stride (figure 2b). However, the support role of the tail is more pronounced when the hind legs are off the ground, contributing an average

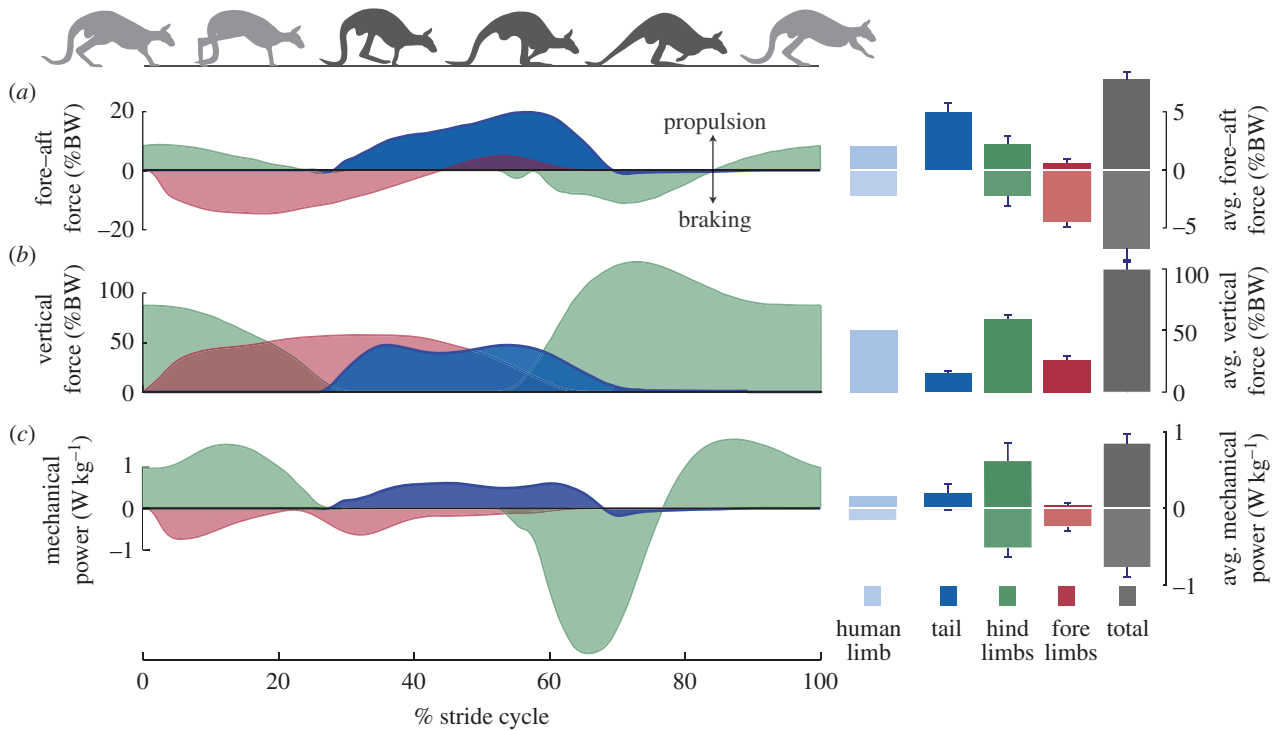


Figure 2. Force and power generation by the limbs during pentapedal locomotion. The illustrative drawings at the top are placed directly above their corresponding time points during a complete stride cycle with the darker animals indicating the period of tail ground contact. (a) Instantaneous (left) and average (right) fore–aft GRFs demonstrate that the tail (dark blue) provides most of the propulsive force. (b) Vertical GRF illustrates that the tail plays a lesser role in helping to support body weight. (c) Instantaneous and average individual limb mechanical power demonstrate that the tail performs substantial mechanical work, especially when compared with that performed by the human leg during bipedal walking at the same speed (light blue). Instantaneous signals are the average of all kangaroos measured. Average metrics were calculated from the time-integral of the positive and negative portions of the corresponding instantaneous signals for each kangaroo, normalized by stride period and body mass and then averaged across animals. All error bars represent standard deviations. Human data are from Donelan *et al.* [17].

vertical force of $36.2 \pm 2.6\%$ of body weight during this time period.

Perhaps most striking was the contribution of the tail to powering pentapedal locomotion. The tail generated almost exclusively positive mechanical power, thereby performing positive mechanical work to lift and accelerate the body (figure 2c). While the hind limbs were responsible for most of the positive mechanical work ($72.9 \pm 15.7\%$), the tail's role was substantial ($22.1 \pm 15.2\%$). Per kilogram of body mass, kangaroos performed as much positive work with their tail ($0.17 \pm 0.10 \text{ W kg}^{-1}$) as humans do with one of their legs when walking at the same speed [17].

4. Discussion

Kangaroo tails appear to function biomechanically just like a leg during pentapedal locomotion. That is, they periodically push on the ground to provide meaningful body-weight support, propulsion and power. This biomechanical definition gauges leg-like behaviour by functional role independent of the primary use of a limb, its position within the body or its evolutionary history. But why does a kangaroo need a fifth leg when other quadrupeds walk well with only four?

A typical quadrupedal walking gait would seem difficult for a kangaroo, given the geometric constraints imposed by limbs of unequal lengths. During quadrupedal walking, at least one front and one hind leg are always in contact with the ground [18]. Step length, forward progression and thus speed, are limited by range of motion of the shorter leg. Kangaroos are freed from this constraint by pairing their front

legs, pairing their hind legs and then swinging the front legs independently from the hind legs. This gait adaptation appears to be related to front–hind limb asymmetry and not to kangaroos *per se*, as other mammals with comparatively long hind limbs also move with paired limbs [8] and the smaller tree kangaroo (*Dendrolagus*) with more symmetric limb lengths uses a quadrupedal-like gait when moving along branches [3].

However, walking with paired limbs has disadvantages if an animal's mass is distributed towards the hind limbs, as in kangaroos. Without a tail to widen the fore–aft base of support, the kangaroo would face a severe propensity to fall backwards when the hind legs are lifted and only the front legs remain on the ground (e.g. figure 1b). The total mechanical work and thus metabolic cost of walking gaits can be substantially reduced by sequentially performing trailing leg positive work and leading leg negative work when redirecting the COM velocity during support transitions [19–21]. However, the relatively slight front legs appear less capable, in terms of both work capacity and geometrical arrangement, of performing this pre-emptive positive work during the transition to the hind leg support phase (e.g. figure 2c). Without a tail to perform positive work during this transition, the kangaroo would be less able to take advantage of this energy saving mechanism and would presumably be forced to choose between other more costly gaits.

So why do kangaroos have such differently sized front and hind limbs? A reasonable biomechanical hypothesis is that bipedal hopping performance is improved by having larger hind limbs for power production and smaller front limbs for weight reduction. Having the use of a tail as a leg

may have freed the kangaroo's front limbs to play a reduced role during slow-speed grazing [2,10].

Kangaroo tails have evolved considerably from the prehensile role they played in arboreal ancestors to modern-day terrestrial kangaroos [15]. While the most obvious current role for the kangaroo's tail may well be to provide counterbalance to the body during hopping [4], a complementary role has evolved for walking. Kangaroos do not waste the bio-mechanical resource of the tail when moving slowly. Instead, they use this muscular appendage as an additional leg to support, propel and power their motion.

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Data accessibility. Individual kangaroo kinetics data have been uploaded as the electronic supplementary material.

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