Jumping and kicking in the false stick insect *Prosarthria teretrirostris*: kinematics and motor control

Malcolm Burrows[1],* and Harald Wolf[2]

[1]*Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK* and [2]*Abteilung Neurobiologie, Universität Ulm, Ulm D-89069, Germany*

*e-mail: mb135@hermes.cam.ac.uk

Summary

The false stick insect *Prosarthria teretrirostris* looks and behaves like a real stick insect but can jump and kick rapidly and powerfully like a locust, to which it is more closely related. It has an elongated body with slender hind legs that are some 2.5 times longer than the front and middle legs. A male with a body 67 mm long and weighing 0.28 g can jump 90 cm with a take-off angle of 40° and velocity of 2.5 m s^{-1}, requiring an energy expenditure of 850 μJ. The body is accelerated at 165 m s^{-2} for only 30 ms. The larger and heavier females (mean body length 104 mm and weighing 1.5 g) can jump on average a distance of 49 cm.

During jumping, the tibiae of the hind legs are extended in 30 ms with maximum rotational velocities of 11.5° per ms, but during kicking, when there is no body weight to support, extension is complete in 7 ms with rotational velocities as high as 48° per ms. The short time available to accelerate the body indicates that the movements are not powered by direct muscle contractions and that there must be storage of elastic energy in advance. The motor patterns responsible for generating the necessary forces in the hind legs for jumping and kicking are similar and consist of three phases; an initial flexion of the tibia is followed by a co-contraction of the small flexor and large extensor tibiae muscles lasting several hundred milliseconds while the tibia remains fully flexed. Finally, the flexor motor neurons stop spiking so that the tibia is able to extend rapidly. The small semi-lunar processes at the femoro-tibial joints are not distorted, so that they cannot act as energy stores. Some 7 % of the energy is stored transiently by bending the thin tibiae during the initial acceleration phase of a jump and releasing it just before take-off.

The jumping and kicking mechanisms of *Prosarthria teretrirostris* have features in common with those used by locusts but also have their own characteristics. The evolution of jumping in Orthoptera is discussed in this context.

Key words: locust, motor neuron, motor pattern, joint mechanics, false stick insect, *Prosarthria teretrirostris*.

Introduction

To increase their speed of locomotion or to escape from predators, many insects can jump rapidly and powerfully. Fleas (Bennet-Clark and Lucey, 1967; Rothschild et al., 1972), springtails (Brackenbury and Hunt, 1993), click beetles (Evans, 1972, 1973) and the larvae of some flies (Maitland, 1992) are all able jumpers, but the supreme specialists are the Orthoptera, most notably the locusts and grasshoppers (Bennet-Clark, 1975; Brown, 1967; Godden, 1975; Heitler, 1977; Heitler and Burrows, 1977a,b). The use of different mechanisms by these diverse insects suggests that the ability to jump has evolved many times. Despite these different mechanisms, one basic problem remains; small bodies and short legs mean that the distances over which the body can be accelerated before take-off are very short (Alexander, 1995). For a flea to produce the high take-off velocities of 1 m s^{-1} characteristic of its powerful jump, acceleration has to be as high as 1300 m s^{-2} and achieved in less than 1 ms. The contraction kinetics of even the fastest twitch muscles are much too slow to generate such rapid acceleration. By contrast, larger animals such as tigers (Grzimeks, 1979) with a body mass of 350 kg, or tarsiers, *Galago senegalensis* (Hall-Craggs, 1965), with a body mass of 250 g, can generate standing jumps, respectively, of 1.3 and 2.25 m. Their long legs allow acceleration over a longer distance and for a longer time and thus muscle contractions can be used to power the jump directly.

Jumping height, however, is almost the same for small and large animals if the same percentage of body mass is invested in the muscles used in jumping. The jump of the tarsier is achieved by an investment of some 10 % of body mass in muscles used in jumping (Alexander, 1995) rather than the 4–5 % invested by locusts (Bennet-Clark, 1976). In insects, the overall design of the small body has resulted in mechanisms that store elastic energy from muscle contraction in advance of

the movement, usually by the deformation of cuticular elements. To generate the high acceleration needed for jumping, this stored elastic energy is then released rapidly.

Locusts generate and store the 9–11 mJ of energy needed to accelerate their body in 30 ms and achieve a take-off velocity of $3.2\,\mathrm{m\,s^{-1}}$ for a jump that can displace them by as much as 1 m (Bennet-Clark, 1975; Brown, 1967). Locusts have evolved specific mechanisms that involve structural specialisations of the hind legs and specialisations of the neural machinery in the central nervous system that generates a detailed and appropriate sequence of muscle actions (Burrows, 1995; Burrows and Morris, 2001; Godden, 1975; Heitler and Burrows, 1977a). In preparation for a jump, the tibiae are first flexed and fully apposed to the femur, and the flexor and extensor muscles of the tibia then co-contract (Heitler, 1974; Heitler and Burrows, 1977a). The energy from the co-contraction of the muscles is stored by bending the spring-like semi-lunar processes at the femoro-tibial joint and in the extensor tendon and femoral cuticle (Bennet-Clark, 1975). The stored elastic energy is released when the flexor tibiae motor neurons are inhibited rapidly, allowing the tibia to extend.

To determine whether these structural and neural specialisations for jumping are a common evolutionary thread, we have analysed jumping and kicking in an unusual orthopteran from South America. *Prosarthria teretrirostris* walks slowly and shows freezing behaviour (thanatosis) like a stick insect (Schultz, 1981; Wolf et al., 2001), thereby readily disguising itself amongst the vegetation upon which it feeds. Like a locust, but unlike a stick insect, it jumps powerfully for considerable distances and shows strong and rapid kicking movements, which it uses to deter adversaries. We show that there are few specialisations of the femoro-tibial joints in the large hind legs that distinguish them from the front and middle legs, so that the joint mechanics and the way energy is stored are different from those in a locust. These insects, nevertheless, use the same motor patterns as locusts to generate the jumping and kicking movements. As a member of the proscopiid family, *P. teretrirostris* probably has relatively primitive jumping legs. Comparison of the features of a *P. teretrirostris* hind leg with those of more advanced and specialised jumping legs may illustrate a path the evolution of the specialised jumping legs of grasshoppers and locusts could have taken.

Materials and methods

Adult male and female false stick insects *Prosarthria teretrirosris* used were from a culture maintained in Ulm. They were kept at room temperature and fed a diet of bramble (*Rubus fruticosus*) leaves. The founder colony was introduced to Germany by Klaus Riede, who deposited a voucher specimen at the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany. Preliminary determination of the species *Prosarthria teretrirostris* (*sensu lato*) was according to (Brunner von Wattenwyl, 1890). It belongs to the order Orthoptera and suborder Caelifera, superfamily Eumastacoidea, family Proscopiidae and subfamily

Proscopiinae. Locusts such as *Schistocerca gregaria* belong to superfamily Acridoidea, family Acrididae and subfamily Cyrtacanthacridinae (Dirsh, 1961; Flook et al., 1999).

A high-speed camera and associated computer (Red Lake Imaging, San Diego, CA, USA) enabled images of jumping and kicking movements to be captured at a frame rate of $1000\,\mathrm{s^{-1}}$ and with a shutter speed of 1/2000 s. Selected images were stored on a computer for later analysis with Motionscope (Red Lake Imaging) or with Canvas (Deneba Systems Inc, FL, USA) software. Jumps were performed by unrestrained insects and kicks by both free and restrained insects in which the hind femora were fixed in Plasticine but the tibiae and tarsi were free to move. Eleven jumps by three adult males at right angles to the optical axis of the camera were captured. With this orientation, the legs project laterally from the body at angles that change as the coxae are rotated at the joints with the thorax. This may lead to error in measurements of the absolute femoro-tibial angle, but the analysis of this joint concentrated on its angular changes during a jump. Eight kicks by four insects were also analysed in detail.

Body size and the proportions of legs were compared with those of locusts *Schistocerca gregaria* and stick insects *Carausius morosus* and *Cuniculina impigra*. The anatomy of the femoro-tibial joint was examined in intact insects, in legs preserved in 50 % glycerol so that the joint was still moveable and in legs in which the cuticle was cleared by boiling in 5 % potassium hydroxide. Drawings of the hind legs and the femoro-tibial joint were made with the aid of a drawing tube attached to a Zeiss stereo microscope. The centre of gravity was determined by suspending insects from a nylon filament attached first to the tip of the abdomen and then to the metathorax just behind the coxae of the hind legs. The intersection of these two lines projected beyond the nylon filaments (read from superimposed photographs) marked the centre of gravity.

Lever ratios of the flexor and extensor tibiae muscles were measured in freshly autotomized hind legs of females glued by the anterior surface of the femur to a vertical cork board so that the tibia was free to move at the femoro-tibial joint. The tibia could then be rotated in the vertical plane of the cork board, the axis of rotation of the femoro-tibial joint running perpendicular to the board in the horizontal plane. The flexor and extensor tendons were exposed by opening the posterior surface of the femur, and one tendon was then clamped to a force transducer. The measurements were then repeated with the other tendon. The transducer was mounted on a small micromanipulator that allowed fine adjustment of the tension exerted on a tendon. This whole apparatus could be rotated in the vertical plane around the axis of the femoro-tibial joint. Weights of 1 or 1.5 g were attached to the tibia 10 mm from the femoro-tibial joint with a nylon filament. When the extensor tendon was attached to the transducer, the weight was suspended from the ventral side of the tibia to exert a flexion force; when the flexor tendon was attached, the weight was suspended from the dorsal surface to exert an extension force. By adjusting the force applied to the flexor or extensor tendon,

respectively, the tibia was maintained in a horizontal position. The femur and attached force transducer were rotated through the whole range of femoro-tibial joint angles, and the force applied to a tendon to keep the tibia horizontal was determined.

To record the activity of the muscles during jumping and kicking, pairs of stainless-steel wires 50 μm in diameter, insulated but for their tips, were inserted into the extensor and flexor tibiae muscles of one hind leg. The wires were waxed to the dorsal thorax and suspended from the roof of a Faraday cage in which the insect was free to move. Movements of the right hind leg were monitored by attaching to the proximal end of the tibia, a small piece of foil that reflected a light beam focused onto a position-sensitive diode (von Helversen and Elsner, 1977). Muscle activity and the movement recordings were digitised at 5 kHz (Cambridge Electronic Design, 1401) and written to CDs for later analysis with Cambridge Electronic Design Spike2 software.

Significance levels between measurement samples were assessed using the *U*-test after Wilcoxon, Mann and Whitney (significance level 5 %); data are given as mean values ± standard errors of the mean (S.E.M.).

Results

Prosarthria teretrirostris has long thin legs and a long thin body to which the elongated head is set at an angle, but it has no wings. It therefore looks more like a stick insect than a locust (Fig. 1). The two sexes are markedly dimorphic in body size. Adult females weighed 1.54±0.1 g (*N*=16) (Table 1) and were almost 5–6 times heavier than adult males and, with a mean body length of 104.4±1.4 mm (*N*=16), almost 40 % longer. In both males and females, the centre of gravity of the body was behind the coxae of the hind legs. In males it was at, or up to, 2 mm behind the border between the first and second abdominal segments (mean 1 mm, *N*=5). In females (*N*=7), the mean position was at the border between second and third abdominal segments with a range of 1.5 mm in front to 2.5 mm behind depending on the gravidity of the female. When the body flexed dorsally, the centre of gravity moved dorsally outside the body plane in the dorso-ventral axis.

The feature common to both jumping and kicking movements was the rapid extension of the tibiae of the hind legs. During jumping, both tibiae were extended at the same time, and the posture of the body was adjusted to give an appropriate take-off angle. It is important that the centre of gravity is just behind the hind-leg coxae, where the force exerted by the legs accelerates the body. This allowed the take-off angle to be adjusted appropriately

by changes in body posture but avoided destabilisation as the body was accelerated. Kicking typically involved the movement of just one hind leg, although on occasion both were used. The hind leg(s) was rotated at the joint with the body so that the kick was aimed at its target.

Jumping performance

The most powerful jumps were completed in 30±2.1 ms (*N*=11) measured from the time when the joints of the hind legs first began to move until the insect became airborne (Fig. 2). Different jumps by the same insect took different times to complete and propelled it different distances. The highest take-off velocity was 2.5 m s^{-1}, with the body being accelerated at up to 165 m s^{-2} for 30 ms or less, and the take-off angle, measured from the centre of gravity, ranged from 20 to 50 ° (mean 40.7 °, *N*=11). It requires 850 μJ of energy to lift the body with a mass of 0.28 g (Table 1) off the ground with this velocity.

Males jumped an average horizontal distance of 66±6.7 cm (*N*=5), reaching a height of 13–15 cm. The longest jump we observed was 90 cm. The larger and heavier females jumped shorter distances, averaging 49±8.4 cm (*N*=7). These values are close to those calculated assuming non-ballistic conditions with no air resistance or aerodynamic effects of the body. With a take-off velocity of 2.5 m s^{-1} and a take-off angle of 40 °, a male would be predicted to jump a distance of 63 cm and to a height of 13 cm.

In preparation for a jump, the tibiae of the hind legs were flexed to their maximum extent about the femur, but the curved tibiae could not be apposed to the femora along their length (Fig. 2A). The coxae were also rotated forward so that the
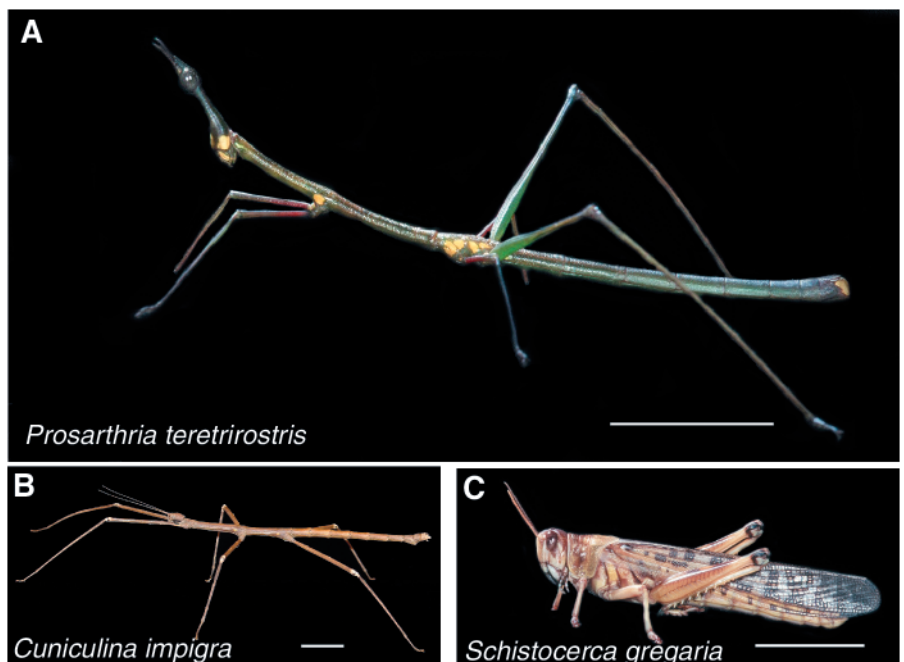

Fig. 1. The body shapes of (A) *Prosarthria teretrirostris*, (B) *Cuniculina impigra*, a stick insect, and (C) *Schistocerca gregaria*, a locust. Scale bars, 25 mm.
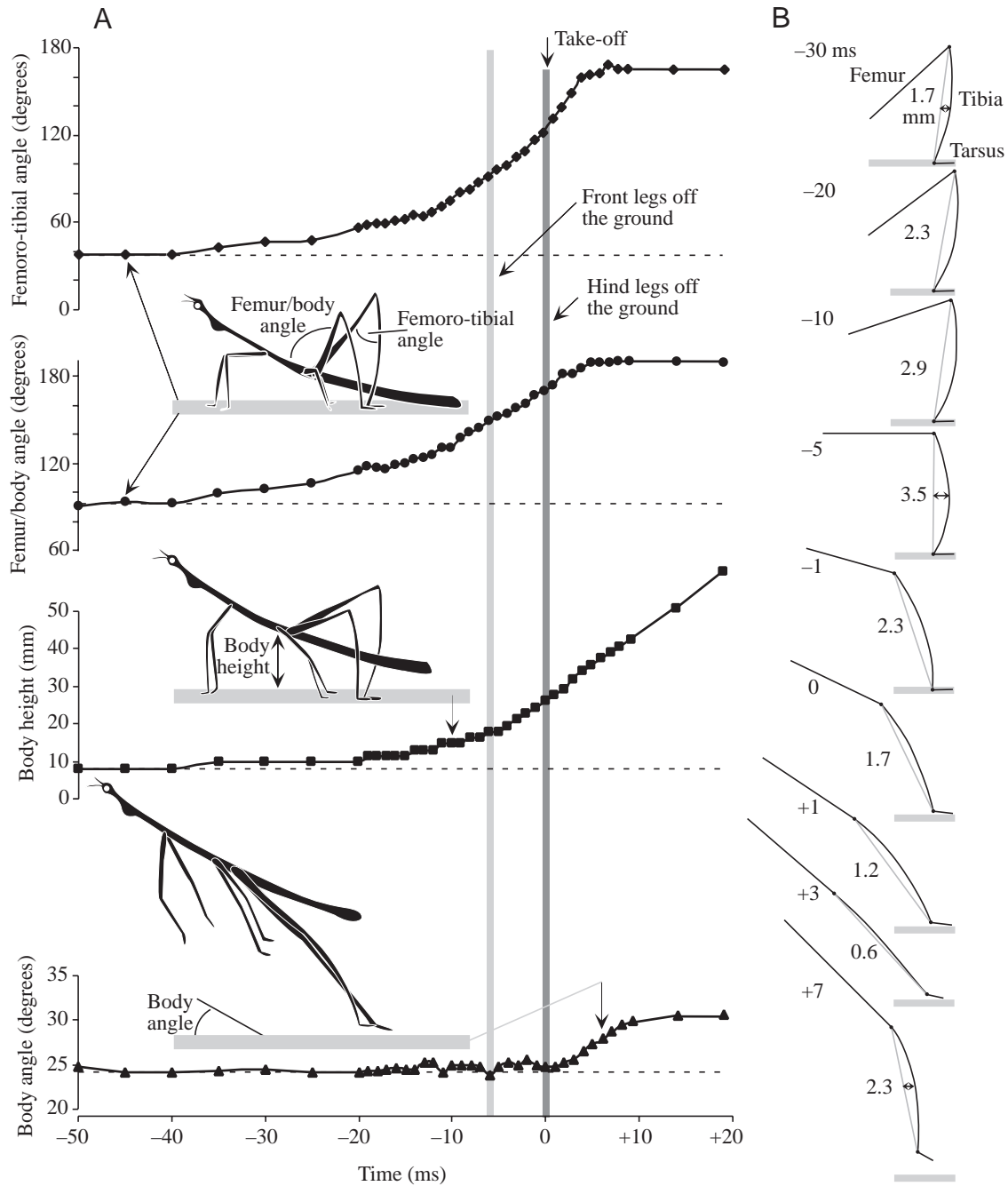
Fig. 2. Movements of the femoro-tibial joint and body during a jump by a freely moving adult male captured by high-speed images at 1000 frames s^{-1}. (A) Plot of hind-leg femoro-tibial angle and femur/body joint movements, changes in height of the body and angle of the body relative to the ground. Time zero was taken as the point when the hind legs left the ground and the insect became airborne. Tibial extension takes 40 ms. The inset diagrams are tracings from single frames, at the times indicated, to show body posture, leg movements and the way the various measurements were made. The vertical lines show when the front and hind legs are lifted from the ground. (B) Bending of the tibia of a hind leg during the jump plotted in A at the times (in ms) indicated. Horizontal lines indicate ground level. The degree of bending is measured as the distance from the centre of the tibia to a line (chord) joining the femoro-tibial and tibio-tarsal joints. The values (in mm) are given in the right-hand column. The drawings are tracings from single images in the jump.

femora were pointing upwards at an angle of 90° to the body. The tibiae of the hind legs then started to extend at the same time as their coxae were depressed, so that the net effect was to raise the body higher from the ground. The continuing depression of the coxae resulted in the further elevation of the body so that, eventually, the two femora of the hind legs were below the body. Similarly, the continuing extension of the two tibiae both elevated the body and moved it forwards. The same joints in the front and middle legs also underwent similar movements, resulting first in the tarsi of the front pair of legs

Table 1. *Body length, body mass and ratios of lengths of legs in* Prosarthria teretrirostris, Carausius morosus *and* Schistocerca gregaria

	Relative length			Body length (mm)	Body mass (g)
	Front leg	Middle leg	Hind leg		
Prosarthria teretrirostris ♀				104.4±1.4 (16)	1.54±0.1 (16)
Femur	1	1.0	2.6		
Tibia	1	0.9	2.4		
P. teretrirostris ♂				67.5±0.8 (10)	0.28±0.01 (8)
Femur	1	0.9	2.1		
Tibia	1	1.3	3.0		
Carausius morosus ♀				78±0.15 (10)	1.1±004 (10)
Femur	1	0.7	0.9		
Tibia	1	0.8	0.9		
Schistocerca gregaria ♀				65.6±1.0 (5)	2.0±0.04 (5)
Femur	1	1.2	3.2		
Tibia	1	1.3	3.2		

Values are means ± S.E.M. (*N*).

and then, approximately 5 ms before take-off, the tarsi of the middle legs leaving the ground. When the tibiae of the hind legs reached full extension, the insect became airborne. The tibia moved about the femur with a peak rotational velocity of 11.5 ° per ms.

Considerable bending of the hind-leg tibiae occurred during the acceleration phase of the jump. As the body was raised, the tibiae bent progressively so that they were maximally bowed when the femora were parallel with the ground. The bowing was quantified as the radius of curvature of the tibia, which decreased from its natural value of 41 to 25 mm in this example of a male jumping, and by the distance between the centre of the tibia and a line (chord) linking the femoro-tibial and tibio-tarsal joints. This doubled from its natural value of 1.7 mm to a maximum of 3.5 mm (Fig. 2B). As the tibiae were progressively extended, the bowing progressively diminished so that, at the point when the tarsi left the ground, the tibiae were almost straight (the radius of curvature was 96 mm and the distance as above was now only 0.6 mm). Once the insect was airborne and the hind legs were no longer bearing any load, the tibiae resumed their natural bowed shape. The force acting on each hind leg to bend a tibia in this way, estimated from the acceleration of the body mass during a jump, was approximately 23 mN.

The spring constants (Young's modulus) for a tibia at moderate static deformation were measured to estimate the larger transient deformations observed in normal jumping. Force was applied to a tibia of five males, and the amount of bending was measured. The speed of bending and recovery was critical because, when the force was applied more slowly than observed in the high-speed images, the tibiae showed gradual (semi-) plastic deformation well before the amount of bending observed during jumping was reached. The change, however, fully reversed within minutes of the force being released. Experiments with transient bending at rates and for periods of approximately 100 ms, similar to those observed during jumping, showed that elastic deformation was possible. The measured spring constants were approximately 20 mN mm^{-1} for axial compression (along the chord indicated in Fig. 2B, although bending perpendicular to this axis yielded similar results). With a typical amount of bending of 1.8 mm observed in jumping – which corresponds to an axial compression of approximately 1.2 mm – the elastic energy stored in one tibia was approximately 29 µJ. The elastic energy stored in the bent tibiae of both hind legs will, therefore, be approximately 7 % of the total kinetic energy requirement for a jump.

Kicking performance

Kicks by an individual hind leg occurred when the tarsus was lifted from the ground and aim was directed by rotation of the leg at the coxa. In restrained insects with no external load to work against, the extension movements of a tibia were very rapid (Fig. 3). The fastest full extension was achieved in 7 ms (mean 8 ms, *N*=7, range 7–11 ms), with maximum velocities of tibial rotation more than four times higher than during jumping at 48 ° per ms. The velocity and consequent inertial forces were sufficiently high that the tibia was over-extended at its extreme position and rebounded, often through several cycles of progressively slower and smaller flexion and extension movements. Close-up images of the femoro-tibial joint showed no bending of the semi-lunar processes either preceding or accompanying tibial extension. Similarly, no distortions in the cuticle of the femur or tibia around the femoro-tibial joint were observed.

Structure of the hind legs

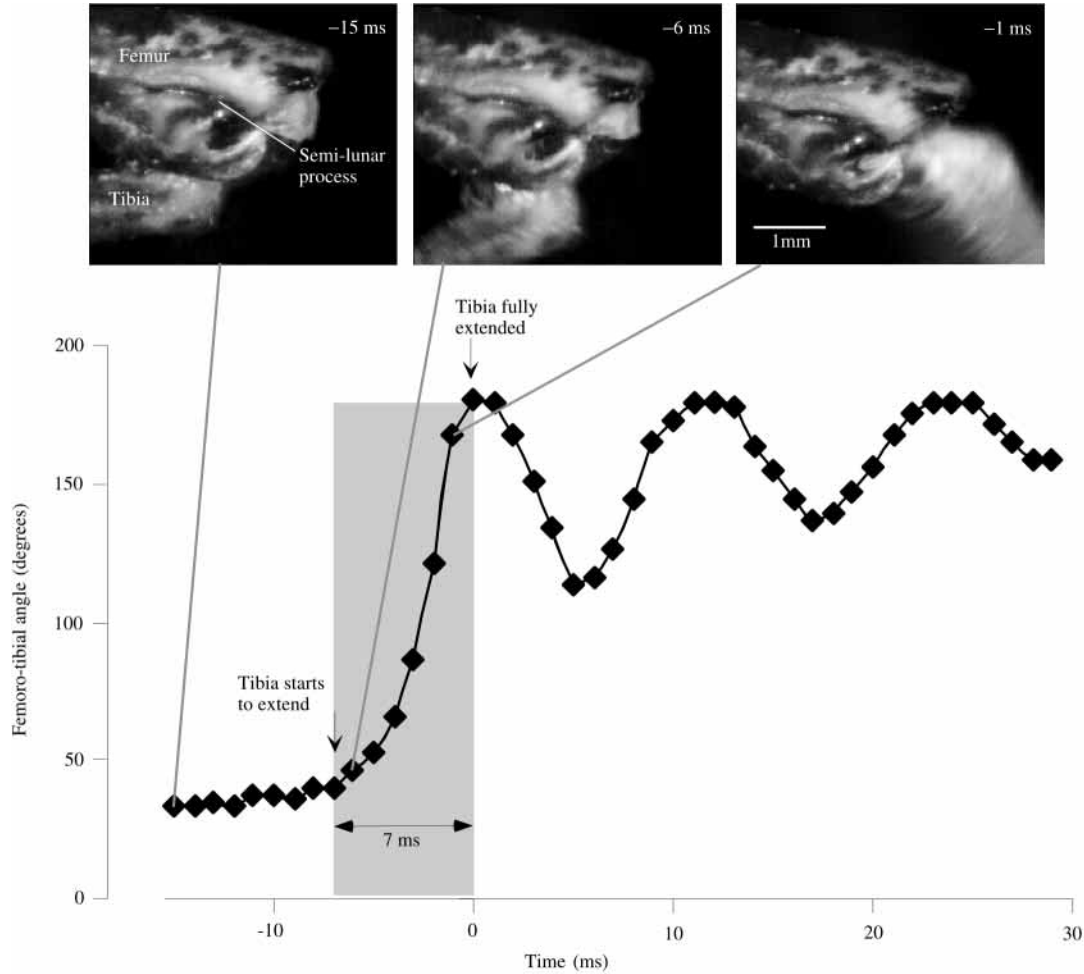The structure of the hind legs, and in particular their femoro-

Fig. 3. Movements of the femoro-tibial joint during a kick by a restrained adult female captured by high-speed images at 1000 frames s^{-1}. The angular changes of the tibia about the femur are plotted against time, with the point of maximum extension designated as zero. The tibia extends fully in 7 ms. Oscillations in movements occur when the tibia reaches its maximum excursion. Three single frames are shown from this kick at the times indicated. The femur as a whole moved slightly in the Plasticine during the rapid extension of the tibia, but no distortions are apparent in the semi-lunar process (see Fig. 4A) when the tibia is flexed in advance of the kick or when it is extending rapidly.

tibial joints, were analysed to understand how they could generate the powerful and rapid movements of both jumping and kicking. The general structure of the hind legs and joints was very similar to that of the front and middle legs. The mean length of a hind femur of an adult female *P. teretrirostris* was 32.8±0.5 mm (*N*=18), whereas in the smaller males it was shorter at 23.9±0.3 mm (*N*=11) (Table 1). The hind femora were, therefore, approximately 2.5 times the length of the femora in both the front and middle legs in both sexes. This is similar to the locust, in which the femora of the hind legs are 3.2 times longer than those of the front legs, but contrasts with the stick insects *Carausius morosus* or *Cuniculina impigra*, in which the femora of the front legs are slightly longer than those of either the middle or hind legs (Fig. 1; Table 1). Relative to body mass, however, the hind legs of *P. teretrirostris* are proportionately longer than those of a locust, in males by a factor of almost 8 and in females by a factor of 2.

The femur of a hind leg was oval in cross section and not hexagonal like that of a locust. At its proximal end, where it

contains the main bodies of the extensor and flexor tibiae muscles, the femur of females measured 2.2±0.09 mm (*N*=5) in the dorso-ventral axis (males 1.5±0.03 mm, *N*=7), but narrowed distally, where it contains only muscle tendons, tracheae and branches of nerve 5, to 1.0±0.06 mm (males 0.6±0.02). The most distal fibres of the main body of the extensor muscle of a female inserted some 13 mm short of the femoro-tibial joint, with only the few fibres of the accessory extensor muscle closer to the joint. The extensor tibiae muscle in females had a mass of 22.7±3.0 mg (*N*=6) and in males a mass of 7.7±0.17 mg (*N*=4). The flexor tibiae muscles were smaller, with a mass of 5.2±0.4 mg in females and 1.6±0.2 mg in males. The maximal cross-sectional area of the extensor tibiae muscle was approximately 3.3 mm^2 in females and 0.9 mm^2 in males.

The tibia was thin, with a diameter of 0.8±0.01 mm (*N*=5), in adult females (males, 0.5±0.02, *N*=7). In females, it was 34.8±0.6 mm long (*N*=18) and in males 26±0.3 mm (*N*=11) so that in both it was some 2 mm longer than the femur. The tibia
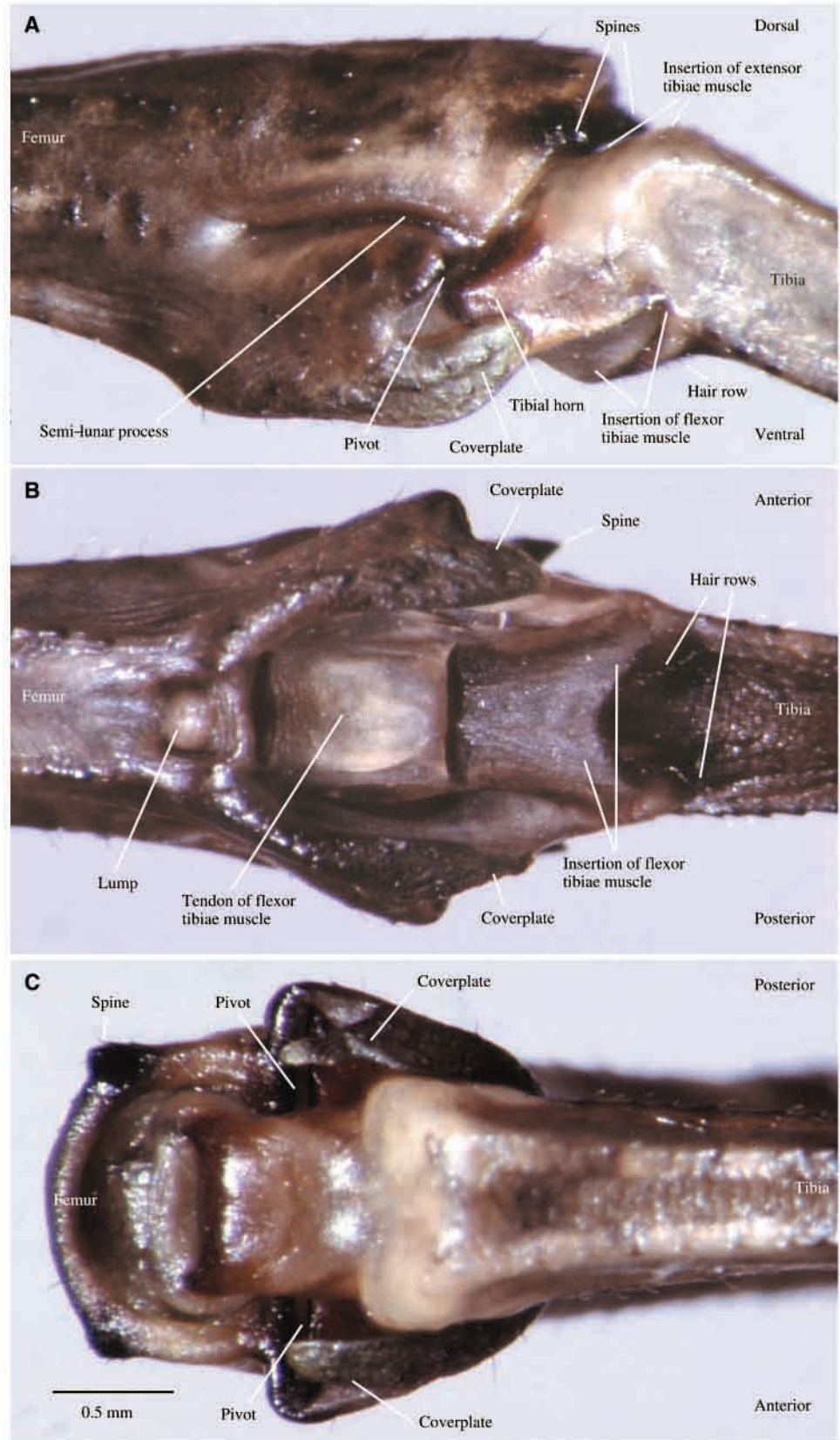
Fig. 4. The femoro-tibial joint of the left hind leg of an adult female *Prosarthria teretrirostris*. (A) View from the anterior surface. The anterior semi-lunar process is a thin curved structure forming a dark groove in the femur. The coverplate is sculpted so that the pivot of a tibial horn with the incurving part of the anterior semi-lunar process is visible. The extensor tibiae muscle inserts on the dorsal rim of the tibia and the flexor tibiae muscle around a ventral U-shaped rim of tibial cuticle. (B) Ventral view with the tibia extended. The ventral femur has infoldings that form an internal lump over which the tendon of the flexor tibiae muscle slides (see Fig. 5B). The membrane surrounding the tendon is folded to form a pocket. Hair rows on the proximal tibia can be seen. (C) Dorsal view of the tibia and its articulation with the femur with the joint flexed. The pivot between the femur and the tibia is seen as a pair of close appositions between the two semi-lunar processes of the femur and the horns of the tibia.

was bowed so, when the insect was standing, the convex surface was lateral. In females, the radius of curvature of the tibia was 52±0.2 mm (N=16) and in males 41±0.2 mm (N=14).

The tibia could move about the femur by some 140° from a minimum flexed angle of 30–35° to a maximum extended angle of approximately 170° although, at the end of a kick,
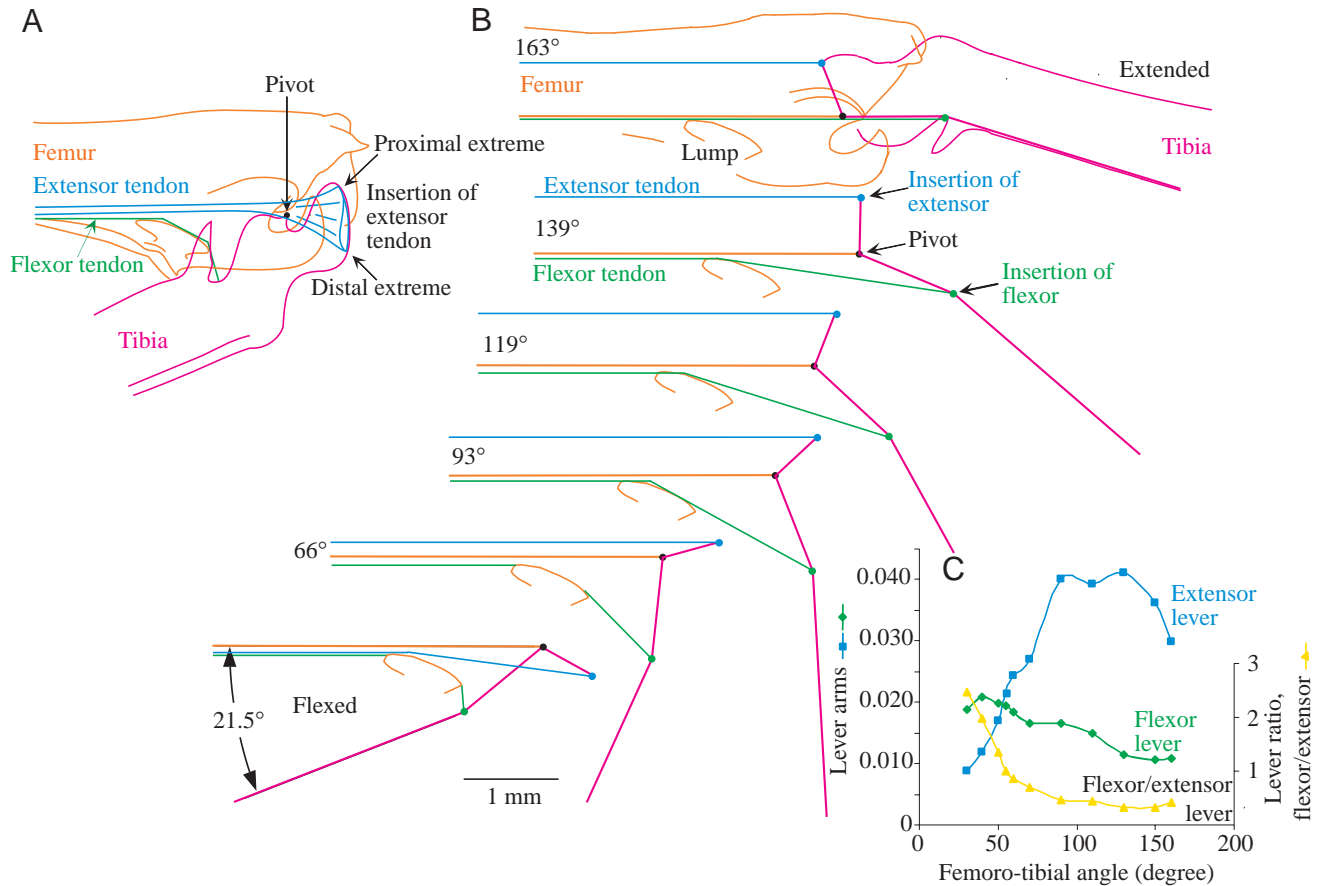
Fig. 5. Movements of the insertions of the flexor and extensor tibiae muscles relative to the pivot of the femoro-tibial joint as the tibia moves about the femur. (A) Drawing of the femoro-tibial joint of a left hind leg viewed anteriorly. The distributed insertion of the tendon of the extensor tibiae muscle is shown. The outline of the femur and tibia are colour-coded in orange and red, respectively, and the pivot of the joint is represented by a black dot. The tendon of the extensor tibiae muscle is blue and that of the flexor is green. (B) Six diagrams made from scale drawings of the femoro-tibial joint angles from 163° (extended) to 21.5° (flexed). The outline of the joint is drawn only for the most extended position of the tibia, but the lump over which the flexor tibiae tendon slides is drawn in each. At the most flexed angle, which was never observed during natural movements of the joint, the action of the extensor tendon is over centre. (C) Graphs of the extensor and flexor lever arms (expressed as fractions of tibial length) at different joint angles measured from the forces that have to be applied to the tendons to effect joint movements. The lever arms of the flexor and extensor are equal (lever ratio=1) at a joint angle of 55°.

over-extension by a further 10–20° often occurred. Externally, the femoro-tibial joint is characterised by thin, recessed semi-lunar processes, two black spines on the distal dorsal rim of femur and a sculptured anterior coverplate (Fig. 4). The semi-lunar processes, one on the anterior and one on the posterior face of the femur, are set in deep grooves and are only some 0.07 mm wide and 0.9 mm long (Fig. 4A). The articulation of the femur with the tibia is very similar to that of a locust hind leg (Burrows and Morris, 2001). The most distal ends of both semi-lunar processes turn inwards, and each has flat distal edges that form the femoral half of the hinge joint with the tibia (Fig. 4C). Ventral to the semi-lunar processes, the lateral and medial walls of the femur bulge outwards to form cavities into which the lateral and medial projections, or horns, of the tibia respectively locate (Fig. 4A). The anterior coverplate is sculptured so that the anterior of the two horns of the tibia is visible as it rotates in the bulge of the femur, but covers the ventral part of the tibia when it is fully flexed. The proximal

part of the tibia consists of two flat edges that hinge with the flat edges of the inward projections of the femoral semi-lunar processes (Fig. 4A,C) and are held together with tough membrane. On the proximal ventral tibia are two rows of hairs each containing 5–6 short and prominent hairs (Fig. 4A,B) that are deflected by contact with the ventral femur when the joint is fully flexed.

Femoro-tibial joint

In the proximal femur, the stiff tendon of the extensor tibiae muscle is approximately 1.1±0.04 mm wide in females (N=5) and 0.8±0.03 mm in the smaller males (N=5), and is oriented vertically (dorso-ventrally). It then twists through 90° so that in the narrow distal femur it is horizontal and 0.3 mm wide in females (0.2 mm in males). Closer to the femoro-tibial joint, the tendon becomes flexible and forms a broad insertion around the U-shaped inside rim of the dorsal tibia (Figs 4A, 5A). Similarly, the tendon of the flexor tibiae muscle is stiff where

A Kick

Flexor muscle

Extensor muscle

Tibial movement

Co-contraction

Flexion
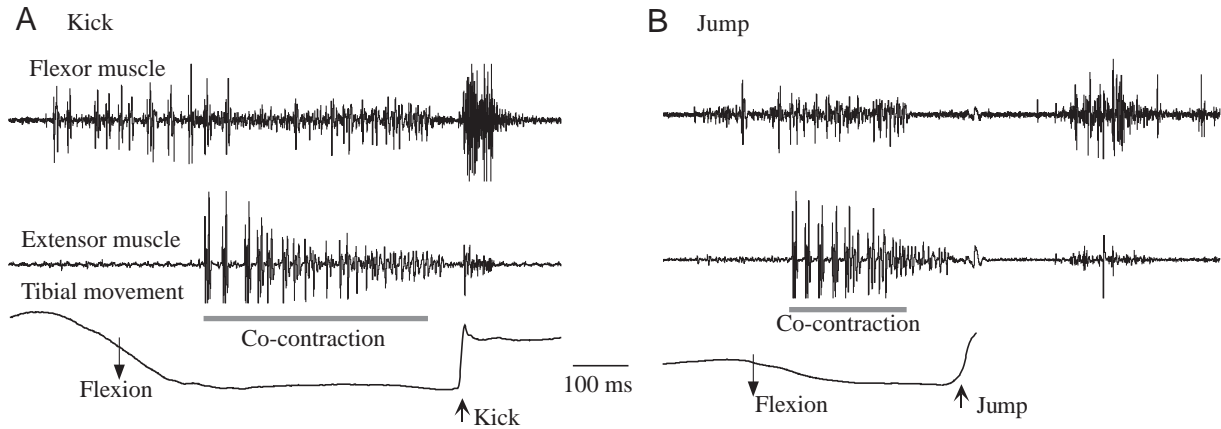
↑Kick

B Jump

Co-contraction

Flexion

↑Jump

100 ms

Fig. 6. Actions of the extensor and flexor tibiae muscles during kicking and jumping. (A) A kick by a restrained female. The flexor muscle is active first and moves the tibia to a flexed position. The flexor and extensor muscles then co-contract. The large spikes in the extensor have been distorted by the amplifier. The flexor muscle spikes stop just before the tibia extends rapidly, while those of the extensor continue for another 15–20 ms. (B) A jump by an unrestrained female. The pattern of muscle action is similar to that during kicking, with a period of co-contraction followed by cessation of flexor activity before the tibia extends and the insect takes off. The jump propels the insect beyond the limits of the tibial movement detector so that the movement trace is lost.

the muscle fibres insert and is 0.2 mm wide in females (0.15 mm in males). In the narrow part of the distal femur, it slides over a small oval lump formed by an invagination in the ventral cuticle that protrudes dorsally approximately 0.2 mm, or approximately 15 % of the thickness of the femur at this point (Figs 4B, 5A). Closer to the femoro-tibial joint, the tendon broadens into a tough flexible structure that divides into two parts, linked by tough membrane, to insert on the heavily sclerotised rim of the ventral tibia (Fig. 4B). As the tibia flexes, the ventral wall of the tibia protrudes into the ventral part of the femur and pushes between these two arms of the tendon.

Lever arms of hind-leg flexor and extensor tibiae muscles

To estimate the forces that muscles could exert the throughout the range of femoro-tibial joint positions of a hind leg, the lever arms of the flexor and extensor tibiae muscles were analysed in two ways.

First, lever arms were determined from scale drawings of hind legs (Fig. 5A,B) dissected to reveal the attachment sites of the muscle tendons. At extended joint angles, the extensor muscle has a much larger lever than the flexor muscle because it attaches to the tibia at a position that is dorsal and proximal relative to the pivot of the joint. The flexor tendon runs almost through the pivot because of its ventral and more distal attachment to the tibia. At flexed joint angles, by contrast, the flexor tendon has a larger lever arm than the extensor because its tendon runs over, and is deflected by, the cuticular invagination, or lump, in the distal ventral femur (Figs 4B, 5B). In this way, the flexor tendon pulls on the tibia at angles close to 90 ° when the tibia is flexed. At the most flexed joint angles into which the tibia can be forced, the flexor and extensor tendons run close to each other over the femoral lump so that the extensor tendon crosses the axis of rotation and, therefore, goes over centre.

Determining lever arms from morphological inspection does

not take into account that both flexor and extensor tendons attach as membranous and highly flexible structures to U-shaped sclerotised rims on the tibia (Figs 4A,B, 5A). The effective attachment site to which force is applied may therefore vary with femoro-tibial angle. For example, when the joint was extended, the extensor tendon seemed to pull mainly at the base of the U-shaped attachment; when it was flexed, the primary force appeared to be exerted on the two tips. This means that, when the joint was flexed, the effective point of attachment for the extensor moved into a more proximal (ventral) position on the tibia (compared with Fig. 5B) and that the extensor tendon did not cross the axis of rotation. Furthermore, in a morphological analysis, it remains unresolved whether the extreme joint positions are ever attained in natural movements. Indeed, our high-speed images of natural jumping and kicking movements showed that the tibia did not flex to angles of less than 35–40 °. For both these reasons, it is doubtful that, in normal usage, the extensor acts over centre.

The second method of analysis was to simulate the forces acting on the joint by replacing the flexor and extensor muscles with weights and force transducers. This allowed the lever arms of the two muscles to be determined directly by measuring the forces needed at the two tendons to balance the joint in different positions (Fig. 5C). The lever arms of the two muscles were equal at a joint angle of 55 °. If balanced and constant loads were applied to the two tendons at this angle, the tibia extended further when moved beyond 55 ° and flexed further below 55 °. The extensor muscle showed consistently larger lever arms in the force measurements compared with the morphometric measurements. This indicates that the morphological identification of the attachment site of the extensor tendon was not appropriate in functional terms. The effective attachment point appeared to be located more proximally on the tibia so that the extensor tendon did not cross the axis of rotation of the joint even in

the most flexed joint position. Similarly, the force measurements indicate that the morphometric data underestimate the flexor lever in extended leg positions and overestimate it in flexed positions. This again suggests a shift in the effective site at which force is applied to the distributed attachment on the U-shaped rim of the tibia.

Muscle activity during jumping and kicking

To understand how the muscles generate the necessary forces during jumping and kicking, myograms were recorded from one hind leg and related to the movements of the tibia of that leg. The motor patterns and muscle actions that underlie jumping and kicking had the following features in common (Fig. 6A,B).

First, the flexor tibiae motor neurons spiked so that the resulting contraction of the flexor tibiae muscle pulled the tibia into its most flexed position. Second, the extensor and flexor tibiae muscles then co-contracted. In some electrode placements, it seemed as if additional flexor motor neurons were active from those that initially flexed the leg. In the 29 kicks analysed, the duration of the co-contraction averaged 416 ms (range 220–1003 ms), and in the 19 jumps the average was 333 ms (range 147–585 ms). The prominent feature of recordings from the extensor tibiae muscle were the large potentials resulting from spikes in a single motor neuron presumed to be the fast extensor tibiae motor neuron. During kicks, there were an average of 24 of these spikes (range 12–56, $N=29$) and during jumps there were 19 (range 12–23, $N=19$) at a mean frequency of almost 60 Hz. The differences in the number of spikes during kicks appeared to correlate with the power and speed of tibial extension and during jumps with the distance that the body was propelled. The large muscle potentials showed a marked decrement in amplitude as the co-contraction progressed. This could be caused by a frequency-dependent change in neuromuscular transmission or by the powerful contraction moving the electrodes.

Third, activity in the flexor muscle stopped on average 20 ms before a tibial movement could be detected during a kick or a jump. Spikes in the extensor continued after those in the flexor ended, but also stopped before the rapid extension of the tibia began. At the end of a kick or a jump, the flexor muscle was active, often with a low level of co-activity in the extensor, so that the tibia was moved slowly to a more flexed position.

Discussion

Prosarthria teretrirostris can jump and kick rapidly and powerfully despite its elongated body and long spindly legs. The propulsion for the jump is provided by the rapid extension of the hind legs, which takes only 30 ms and yet propels the body forwards by as much as 90 cm. During kicking, when there is no body weight to support, extension of a hind leg takes only 7 ms. Both rapid movements are preceded by a prolonged co-contraction of the extensor and flexor tibiae muscles of the hind legs during which force is built up slowly and stored before being delivered suddenly to power the movements.

Comparison with locust jumping

The jumping performances of *P. teretrirostris* and locusts are similar but, because the locust has to propel a much heavier body, it needs to generate much higher forces. During jumping, locusts extend the tibiae of their hind legs fully in 20–30 ms (Brown, 1967) to achieve take-off velocities of 3.1 m s^{-1} (Bennet-Clark, 1975), while *P. teretrirostris* takes 30 ms to extend its hind legs and reaches take-off velocities of 2.5 m s^{-1}. These data fit with the energy requirements of the jump, which are almost 1 mJ in a male *P. teretrirostris* with a body mass of 280 mg, and almost 10 mJ in a male locust with a mass of 1.6 g. Similarly, there is much overlap in the kicking performances of the two species, but the fastest kick observed in a locust took only 3 ms with the tibia rotated at a maximum rate of 80° per ms (Burrows and Morris, 2001), whereas the fastest kick in *P. teretrirostris* took 7 ms during which the tibia achieved maximal rotational velocities of 48° per ms.

This similarity in jumping performance results from the investment by both species of a similar muscle mass relative to body mass for use in jumping; the muscles used by *P. teretrirostris* in jumping account for 4–6 % of the body mass and in the locust 4–5 % (Bennet-Clark, 1976). This will allow similar jumping performance in animals of similar size, regardless of whether the jump is directly powered by muscle contractions or muscle energy is stored as elastic energy (with similar efficiency). Even animals of different mass will produce jumps of comparable absolute size because the mechanical energy delivered by a muscle scales almost linearly with muscle mass (Bennet-Clark, 1976) and, thus, with body mass if similar proportions of body muscle are used for jumping.

A more detailed comparison of data from *P. teretrirostris* with that from the locust (Bennet-Clark, 1975) suggests that the properties of the muscles used in jumping are similar in the two species. The extensor tibiae muscle in male *P. teretrirostris* has a mass of approximately 8 mg, and the energy generated by a slow contraction of these muscles in the two hind legs in preparation for a jump should amount to some 1.2 mJ, by extrapolation from the 75 mJ g^{-1} measured in the locust extensor tibiae. This agrees with the maximum energy content of almost 1 mJ calculated from the jumping performance of *P. teretrirostris* and indicates an efficiency of approximately 70 % for the transformation of muscle energy into kinetic energy of the jump, including intermediate elastic energy storage. The maximal cross-sectional area of the extensor tibiae muscle was some 0.9 mm^2 in male *P. teretrirostris*, which should thus be able to generate forces of approximately 0.7 N per leg. In the locust, the whole muscle has a cross-sectional area of 16–17 mm^2 and can generate 15 N, or 0.8 N mm^{-2}. The maximum lever of the extensor tibiae muscle of *P. teretrirostris* (Fig. 5C) is 0.04 times tibia length, and this again agrees with the force requirements calculated from the maximum acceleration of 165 m s^{-2} measured during a jump, amounting to approximately 0.6 N per leg.

It is clear from the above comparison that *P. teretrirostris*, much like the locust, has to store elastic energy to generate the

brief (but high) acceleration necessary for the jump. The main reason that stored elastic energy is required is the short time available for acceleration before take-off. Tibial extension is complete within 30 ms, yet the extensor tibiae muscle of the locust needs a few hundred milliseconds to develop peak force and a minimum of 59 ms to reach peak twitch force (Cochrane et al., 1972). The mechanisms used by the locust and *P. teretrirostris* to transform muscle energy into the kinetic energy of a jump or a kick and thereby achieve the comparable performances show many similarities. There are, however, notable differences.

First, in proportion to body mass but not body length, the hind legs of *P. teretrirostris* are much longer than those of locusts; in the lighter males, they are proportionately eight times longer, and even for the heavier females they are twice as long. The longer legs allow (lower) acceleration over a longer distance and thus require the generation of proportionately less muscular force. They also require a less sturdy construction of the femoral cuticle. Heavier locusts, therefore, require additional specialisations for jumping; stronger muscles, sturdier cuticle and additional stores for muscle energy to achieve higher acceleration.

Second, in the locust, the tibia of a hind leg, but not of a middle or a front leg, can be flexed fully about the femur so that the two are closely apposed along their length in a groove on the ventral wall of the femur. In *P. teretrirostris*, the hind leg is similar to the other legs in that it cannot be fully apposed to the femur. The most flexed angle that the tibia was observed to achieve during natural jumping or kicking was 35°. This is in part due to the marked curvature of the tibia and in part because, if the joint were flexed further, the lever arm of the extensor tibiae muscle would go over centre. Instead, the lever arms of the flexor and extensor muscles are such that, at the most flexed angles, that of the extensor is close to zero while that of the flexor is maximal, and at 55° they are balanced. The lever arms then reverse so that, at angles of 90–130°, the extensor lever arm is maximal and that of the flexor is close to zero.

Third, in the locust, the structure of the femoro-tibial joint of a hind leg is dominated by the presence of large semi-lunar processes that are bent during a jump or a kick and are estimated to provide almost half the energy storage for these movements (Bennet-Clark, 1975). By contrast, the semi-lunar processes in *P. teretrirostris* are small, and high-speed images show that neither they nor the distal part of the femur are noticeably distorted during kicking, so that they cannot act as an energy store. Instead, we assume that most of the energy is stored in the tendon of the extensor tibiae muscle, in the muscle itself and in the femoral cuticle. The smaller mass of *P. teretrirostris* and the proportionately longer legs mean that less elastic energy storage is required to provide the acceleration for a jump.

Fourth, in the locust, the lump (Heitler, 1974) protrudes into the distal femur for 40 % of the diameter of the femur, but in *P. teretrirostris* it extends for only 15 %. In the locust, the flexor tendon forms a pouch that fits over the lump when the tibiae is fully flexed and locks it in this position as long as the flexor continues to contract. It is only when the flexor muscle relaxes and releases the pouch from the lump that the tibia can extend. In *P. teretrirostris*, the consequence of having only a small lump is that the angle of the flexor tendon is altered less at extreme flexed angles of the joint, and it is probably less effective in locking the flexor tendon. The ability of the small flexor to restrain the action of the larger extensor tibiae muscle during the co-contraction phase must, therefore, depend more on the respective lever ratios determined by the anatomy of the joint than on the locking mechanism provided by the femoral lump.

Despite these differences in the structure and operation of the femoro-tibial joint, the motor pattern that produces a jump or a kick is strikingly similar in the locust and *P. teretrirostris*. In both, it consists of three phases: first, an initial flexion brings the tibia close to its maximally flexed position; second, a co-contraction of flexor and extensor tibiae muscles, that can last several hundred milliseconds, allows the force generated by the extensor tibiae muscle to be built up slowly and stored; third, the spikes in the flexor motor neurons stop abruptly so that the flexor muscle relaxes, allowing the stored force to be delivered rapidly. By contrast, most crickets kick but do not jump, powered by brief contractions of the extensor tibiae muscle and not by long periods of co-contraction (Hustert and Gnatzy, 1995).

Evolution of jumping legs

Does the design of the hind legs of *P. teretrirostris* represent an ancestral design of orthopteran jumping legs, intermediate between a normal walking leg and the specialised jumping leg of locusts and grasshoppers? Alternatively, does this convergent evolution represent two solutions derived from a more primitive design that has emerged to generate similar behaviour?

The close resemblance between the structure of all *P. teretrirostris* legs is striking, particularly in the structure of the femoro-tibial joints, contrasting strongly with the evident specialisation of the hind legs in locusts.

Most notable are: first, semi-lunar processes that are small, with only the hinge area sclerotised; second, the structure of the hinge itself; and, third the structure of the attachment sites of the flexor and extensor tendons. The main specialisations of the hind leg for jumping include: first, a ventral lump in the femur that alters the lever ratio of the flexor muscle at flexed joint angles; second, increased femoral and tibial lengths; third, a larger muscle mass; and, fourth, a more sturdy structure.

Locusts and grasshoppers have carried hind-leg specializations for jumping much further, particularly with regard to heavy sclerotisation of the semi-lunar processes and their use in elastic energy storage, stronger cuticle and sclerotisation of several other parts of the leg, the hexagonal cross section of the femur, a more pronounced ventral lump in the femur and a pouch in the flexor tendon, which locks over that lump.

Even if the main features of *P. teretrirostris* jumping legs do

not represent ancestral traits (i.e. they are symplesiomorphic for the saltatoria), they may illustrate how the ability to jump evolved gradually in the saltatoria and without the need for *ad hoc* invention of qualitatively new characters. It is possible that the features that enabled jumping evolved gradually with only small proportional changes in different parts of the walking legs. For example, the basic features of angle-dependence of the lever arms at the femoro-tibial joint, which are important for co-contraction, and elastic energy storage are already present in a walking leg. Likewise, the specialised locust hind legs may have evolved from hind legs like those of *P. teretrirostris* through small and gradual changes. Even novel characteristics such as the pouch in the flexor tendon fit into this scheme. A small pouch, originating from the softer central part of the splaying flexor tendon, would confer the advantage of increased friction during co-contraction. Any further increase in pouch size would increase this advantage, allowing a gradual transition to the pouch with locking function seen in the locust.

The fossil record suggests that *P. teretrirostris* hind legs represent primitive jumping legs in the sense outlined above. More basic extinct groups of orthopterans such as the Oedischidae and Tcholmanvissidae all appear to have had hind legs that are similar to those of present-day proscopiids (Sharov, 1961). The Jurassic *Locustopsis germari* (Locustopsidae) was more locust-like, with well-developed and compact jumping legs, although some other species of that group (Sharov, 1961) also had proscopiid-like hind legs. Final assessment must await further completion of the fossil record, since there are no records of fossil proscopiids, or progress in the molecular approaches to resolve details of the relationships between the orthopteran groups (Flook et al., 1999).

References

Alexander, R. McN. (1995). Leg design and jumping technique for humans, other vertebrates and insects. *Phil. Trans. R. Soc. Lond. B* **347**, 235–248.

Bennet-Clark, H. C. (1975). The energetics of the jump of the locust *Schistocerca gregaria*. *J. Exp. Biol.* **63**, 53–83.

Bennet-Clark, H. C. (1976). Energy storage in jumping insects. In *Insect Integument* (ed. H. R. Hepburn), pp. 421–442. Amsterdam, Oxford, New York: Elsevier Scientific Publishing Company.

Bennet-Clark, H. C. and Lucey, E. C. A. (1967). The jump of the flea: a study of the energetics and a model of the mechanism. *J. Exp. Biol.* **47**, 59–76.

Brackenbury, J. and Hunt, H. (1993). Jumping in springtails: mechanism and dynamics. *J. Zool., Lond.* **229**, 217–236.

Brown, R. H. J. (1967). The mechanism of locust jumping. *Nature* **214**, 939.

Brunner von Wattenwyl, C. (1890). *Monographie der Proscopiiden. Vh. Zool. Bot. Ges. Wien* **40**, 87–123.

Burrows, M. (1995). Motor patterns during kicking movements in the locust. *J. Comp. Physiol. A* **176**, 289–305.

Burrows, M. and Morris, G. (2001). The kinematics and neural control of high-speed kicking movements in the locust. *J. Exp. Biol.* **204**, 3471–3481.

Cochrane, D. G., Elder, H. Y. and Usherwood, P. N. R. (1972). Physiology and ultrastructure of phasic and tonic skeletal muscle fibres in the locust, *Schistocerca gregaria*. *J. Cell Sci.* **10**, 419–441.

Dirsh, V. M. (1961). A preliminary revision of the families and subfamilies of Acridoidea (Orthoptera, Insecta). *Bull. Br. Mus* **10**, 349–419.

Evans, M. E. G. (1972). The jump of the click beetle (Coleoptera: Elateridae) – a preliminary study. *J. Zool., Lond.* **167**, 319–336.

Evans, M. E. G. (1973). The jump of the click beetle (Coleoptera, Elateridae) – energetics and mechanics. *J. Zool., Lond.* **169**, 181–194.

Flook, P. K., Klee, S. and Rowell, C. H. F. (1999). Combined molecular phylogenetic analysis of the Orthoptera (Arthropoda, Insecta) and implications for their higher systematics. *Syst. Biol.* **48**, 233–253.

Godden, D. H. (1975). The neural basis for locust jumping. *Comp. Biochem. Physiol.* **51A**, 351–360.

Grzimeks, B. (1979). *Grzimeks Tierleben*, vol. 12, *Saugetiere 3*. München, Germany: Deutscher Taschenbuch Verlag.

Hall-Craggs, E. C. B. (1965). An analysis of the jump of the Lesser Galago (*Galago senegalensis*). *J. Zool., Lond.* **147**, 20–29.

Heitler, W. J. (1974). The locust jump. Specialisations of the metathoracic femoral–tibial joint. *J. Comp. Physiol.* **89**, 93–104.

Heitler, W. J. (1977). The locust jump. III. Structural specializations of the metathoracic tibiae. *J. Exp. Biol.* **67**, 29–36.

Heitler, W. J. and Burrows, M. (1977a). The locust jump. I. The motor programme. *J. Exp. Biol.* **66**, 203–219.

Heitler, W. J. and Burrows, M. (1977b). The locust jump. II. Neural circuits of the motor programme. *J. Exp. Biol.* **66**, 221–241.

Hustert, R. and Gnatzy, W. (1995). The motor program for defensive kicking in crickets: performance and neural control. *J. Exp. Biol.* **198**, 1275–1283.

Maitland, D. P. (1992). Locomotion by jumping in the Mediterranean fruit-fly larva *Ceratitis capitata*. *Nature* **355**, 159–161.

Rothschild, M., Schlein, Y., Parker, K. and Sternberg, S. (1972). Jump of the oriental rat flea *Xenopsylla cheopis* (Roths). *Nature* **239**, 45–47.

Schultz, J. (1981). Adaptive changes in antipredator behaviour of a grasshopper during development. *Evolution* **35**, 175–179.

Sharov, A. G. (1961). Phylogeny of the Orthopteroidea. *Trans. Inst. Palaeontology (Akad. Nauk. SSR) Trudy Paleontologischeskogo Instituta (Israel Program of Scientific Translations, 1971)* **118**, 1–251.

von Helversen, O. and Elsner, N. (1977). The stridulatory movements of acridid grasshoppers recorded with an opto-electronic device. *J. Comp. Physiol. A* **122**, 53–64.

Wolf, H., Bassler, U., Speil, R. and Kittmann, R. (2001). The femur–tibia control system in a proscopiid (Caelifera, Orthoptera): a test for assumptions on the functional basis and evolution of twig mimesis in stick insects. *J. Exp. Biol.* **204**, 3815–3828.