

Anatomy of the hind legs and actions of their muscles during jumping in leafhopper insects

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Summary

The rapid and simultaneous depression of the trochanters about the coxae of both hind legs of leafhoppers are the key joint movements powering a jump. The present study analyses the structure of these joints and the actions of the muscles that move them. The hind coxae are huge and are linked to each other at the midline by a protrusion from one coxa that inserts in a socket of the other and acts like a press-stud (popper) fastener. This asymmetry is not reflected in any left- or right-handed preference either within one species or between species. The movements of the joints in a jump are monitored by a number of possible proprioceptors that should be activated when a hind leg is fully levated in preparation for a jump: a hair row and two hair plates on the coxa, a hair plate on a trochanteral pivot with a coxa, and femoral spines at the femoro-tibial joint. The depressor and levator muscles that move the trochanter are of similar size and together occupy the greater part of the metathorax. Their lever arms are

similar when the leg is fully levated, but the lever arm of the depressor increases with initial depression of the coxo-trochanteral joint while that of the levator declines. A jump is preceded by activity in the trochanteral depressor and levator muscles, which results in a forward movement of the coxa and metathorax with the trochanter fully levated. This period of co-contraction could result in storage of energy in skeletal structures in the thorax. Just before the rapid depression of the trochanter in the jump movement the frequency of depressor spikes increases while that in the levator declines, releasing any force stored by the preceding muscle contractions. These bursts of depressor spikes occur at the same time in the left and right muscles but none of the individual motor spikes appeared to be synchronous on the two sides.

Key words: kinematics, muscle, motor pattern.

Introduction

Leafhopper insects (Hemiptera, Auchenorrhyncha, Cicadellidae) power their jump largely by the simultaneous extension of their two long hind legs (Burrows, 2007a). These movements of the hind legs accelerate the body in an average of 5–6 ms to a peak take-off velocity of 1.1–16 m s⁻¹, though in the best jumps the performance can be considerably better with the acceleration lasting less than 3 ms and the take-off velocity reaching 2.9 m s⁻¹. The jumping performance is, however, less than that of their close relatives the froghoppers (Hemiptera, Auchenorrhyncha, Cercopidae) (Burrows, 2003; Burrows, 2006a), despite their proportionately longer hind legs. The key movements in the jumping of insects in both families is the rapid depression of the trochanteral joints of the hind legs about the coxae. The difference in performance therefore raises the question of whether there are different structural arrangements of these joints in leafhoppers and different mechanisms of neural control of the muscles moving these joints.

In general, insects with short legs have to store energy in advance of a jump and then release it suddenly in a catapult action because the direct action of the muscles cannot generate enough energy in the short acceleration times available (Alexander, 1995). Fleas (Siphonaptera, Pulicidae) (Bennet-

Clark and Lucey, 1967; Rothschild and Schlein, 1975; Rothschild et al., 1972) and froghoppers (Hemiptera, Auchenorrhyncha, Cercopidae) (Burrows, 2003; Burrows, 2006a) are examples of insects with short legs that use a catapult mechanism. Insects with long legs, such as bush crickets (Orthoptera, Ensifera, Tettigoniidae) (Burrows and Morris, 2003), power their jumps by direct action of the muscles acting on the long levers. Some insects, such as locusts (Orthoptera, Caelifera, Acrididae) (Bennet-Clark, 1975), combine the storage of energy with the extra leverage provided by long legs.

An analysis of the jumping mechanisms used by leafhoppers with long hind legs should therefore reveal their particular specialisations that enable jumping compared with their shorter legged close relatives and with other insects. This paper shows that the structure of the coxa of a leafhopper hind leg is different from that of froghoppers and apparently has no mechanism that enables it to lock the femur in place when preparing to jump. The anatomical arrangement of the antagonistic muscles also indicates that their lever arms are similar when fully levated in preparation for jumping. Recordings from the muscles moving the trochanter indicate that there is only a short period of co-contraction and that the frequency of depressor spikes rises while that of the levator falls just before the trochanter is moved rapidly.

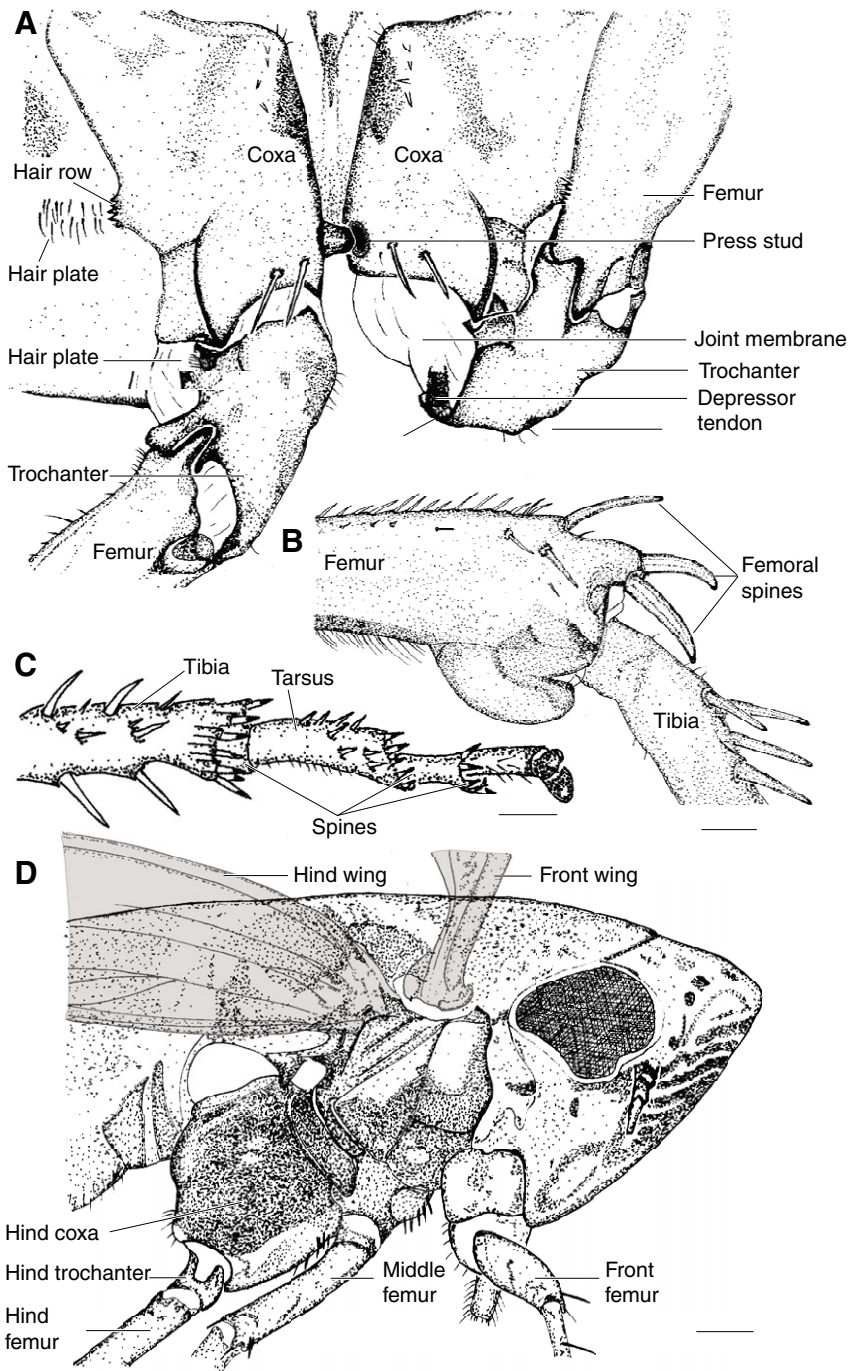


Fig. 1. Drawings of joints in the hind leg critical for jumping. (A) The proximal hind leg joints of *Aphrodes* as viewed ventrally. The left hind leg is shown fully levated, and the right hind leg almost fully depressed. (B) Femoro-tibial joint of a large unidentified Cicadellid from Venezuela. Prominent ridged spines project dorsally and laterally from the end of the femur. The ventral coverplate is notched but the surrounding area is not heavily sclerotised. The tibia has rows of prominent lateral spines. (C) Ventral view of the distal tibia and the tarsus to show the arrays of short spines at the tibio-tarsal joint and at the joints of the tarsus. (D) Side view of *Aphrodes* to show the greatly enlarged coxa of the right hind leg compared to that of the other two legs. The distal parts of the legs are omitted in A and C. Scale bars, 200 μm .

alcohol; fixed and stored in 70% alcohol; preserved in 50% glycerol; cleared by boiling in 5% potassium hydroxide. Drawings of the legs, joints and muscles were made with the aid of a drawing tube attached to a Leica MZ16 stereo microscope. Individual colour photographs were taken with a Nikon DXM1200 digital camera attached to the same microscope. Dried specimens were also mounted on specimen holders, sputter coated with gold and then examined in a Philips XL-30 Scanning Electron Microscope.

To record the electrical activity of muscles generating jumping, a leafhopper was restrained on its back in PlasticeneTM with the hind legs free to move. Rapid and co-ordinated movements of the two hind legs occurred spontaneously or could be induced by the same mechanical stimuli used to promote unrestrained jumping. As in froghoppers (Burrows, 2006a), the sequence of movements of the hind legs was the same as that observed in unrestrained jumping. Pairs of 30 μm steel wires, insulated but for their tips, were inserted through small holes in the sternal plates of the metathorax and into the trochanteral depressor and levator muscles of the hind legs. The positions of the electrodes were confirmed by dissection of the muscles at the end of the recording session. Movements of a hind leg were recorded at the same time as the electrical activity of the muscles, by capturing images at rates of

250 frames s^{-1} with a Photron Fastcam 512 or 1024 PCI camera [Photron (Europe) Ltd, Marlow, Bucks., UK] attached to a Wild M7A microscope viewing the insect ventrally. The captured images were stored on one computer. The electrical signals from the muscles were digitised at sampling rates of 25 kHz with a CED (Cambridge Electronic Design) interface running Spike 2 version 5 software and were then written directly to a second computer. The data files of images and muscle recordings were synchronised on the two computers to a resolution of 4 ms, by feeding a 0.5 ms long electrical pulse to a separate channel of the CED interface, and that simultaneously triggered a light flash of a miniature LED in the visual field of the camera. Eighty two

Materials and methods

Four species of leafhoppers were analysed: *Empoasca vitis* Goethe, *Cicadella viridis* (Linnaeus), *Graphocephala fennahi* Young, 1977, and *Aphrodes* of the *makarovi* Zachvatkin, 1948/*bicinctus* (Schrank) group. They all belong to the order Hemiptera, suborder Auchenorrhyncha, to the superfamily Cicadelloidea and to the family Cicadellidae. They were collected around Cambridge and Wells next-the-sea, England; Llandinam, Wales; Ljubljana, Slovenia; and Aachen, Germany.

The anatomy of the hind legs and metathorax was examined in intact insects and in leafhoppers preserved in the following ways: fixed in 5% buffered formaldehyde and stored in 70%

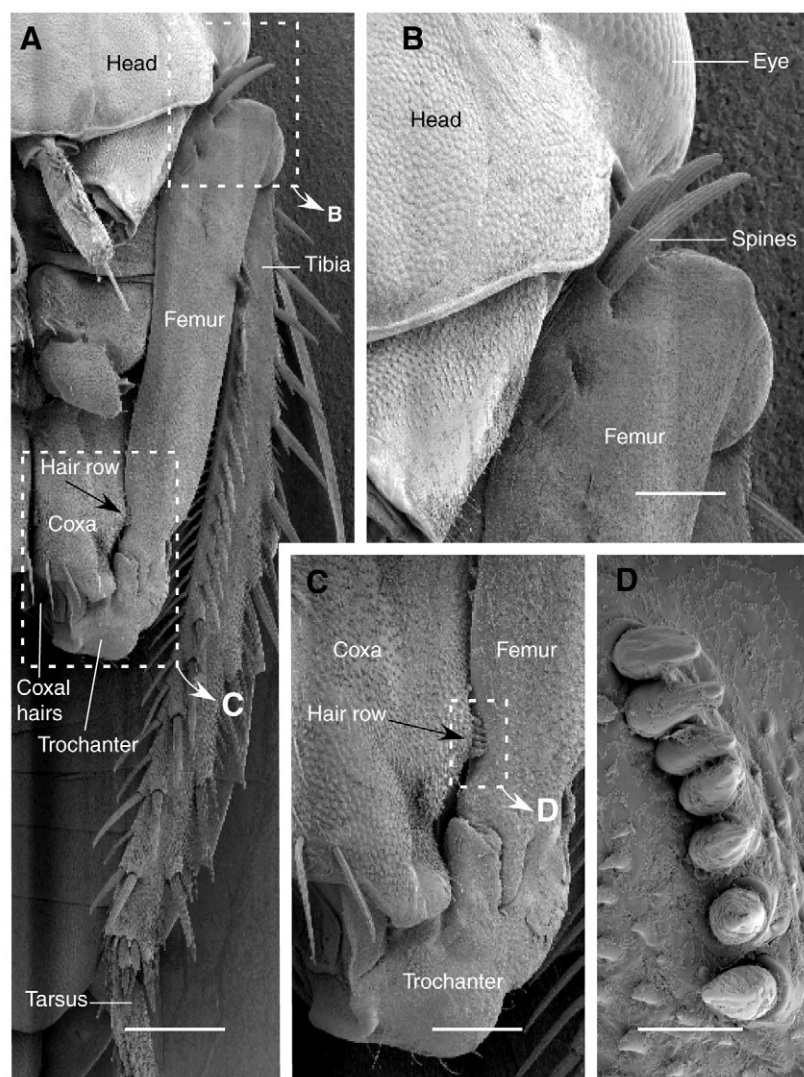


Fig. 2. Scanning electron micrographs of *Empoasca* to show the organisation of the joints of a hind leg and some of their associated proprioceptors. (A) The left half of the body, as viewed ventrally and with anterior at the top. The left hind leg is fully levated about the coxo-trochanteral joint and the distal part of the femur bearing a group of spines fits into a sculpted region of the head capsule. The proximal part of the femur is pressed against a hair row on the coxa. Parts of the left, middle leg distal to the trochanter, and parts of the left, front leg distal to the coxa have been removed to reveal the hind leg more clearly. Scale bar, 250 μm . (B) Further detail of the area in A outlined by the top broken box, to show the engagement of the femoral spines with the sculpted region of the head capsule when the left hind leg is fully levated. Scale bar, 100 μm . (C) Detail of the area in A outlined by the lower broken box to show the proximal femur pressing against the hair row on the coxa (black arrow) when the leg is fully levated. Scale bar, 100 μm . (D) Structure of the hairs (within the broken box in C) making up the hair row. Scale bar, 10 μm .

(Fig. 1A,D). The coxae therefore move only with the metathorax. This contrasts with the design of the hind legs in froghoppers where each coxa can rotate about the metathorax (Burrows, 2006b). A further feature of the hind coxae is their close apposition to each other at the midline. They are linked by particular structures (see below), which ensure that both coxae move as a single unit with the rest of the metathorax. This arrangement provides a stable base for the movements of the more distal segments of the hind legs. A hind coxa, unlike that in froghoppers (Burrows, 2006b), also has no ventral protrusion from its more lateral part that could engage with the femur when the hind leg is fully levated. Furthermore, the dorsal surface of the proximal femur has no structural specialisations that would allow engagement with the coxa.

The trochanter is heavily sclerotised on its medial rim where the tendon of the large trochanteral depressor muscle inserts and at the two points of its articulation with the femur. Its articulation with the coxa consists of a ventral and a dorsal pivot, with curved horns of the trochanter engaging with sockets in the coxa (Fig. 1A). The coxo-trochanteral joint can move through some 130° . In its fully levated position the femur rests in a hollowed part of the ventral coxa so that proximally it is pressed against a hair row on a ridge in the coxa (Fig. 2A,C). The femoro-tibial joint and its associated femoral spines fit into a sculpted region of the head just behind a compound eye (Fig. 2A,B). This recess allows the hind femur to move further medially so that in turn the trochantero-femoral joint can be fully levated. In its fully levated position, a hind leg therefore comes to lie in a position bounded dorsally by the thorax and ventrally by the front and middle legs.

The femur articulates with the trochanter at a ventral and a dorsal pivot by projections from the femur inserting into sockets on the trochanter. The movement is in a plane almost orthogonal to that of the coxo-trochanteral joint but is restricted to a small arc of some $15\text{--}20^\circ$. The femoro-tibial joint consists

jumps by five *Aphrodes* were analysed in which both muscle recordings and images of the movements were captured. Temperatures in all experiments ranged from $24\text{--}30^\circ\text{C}$.

Results

Structure of hind legs

The hind legs are twice the length of the front and middle legs due to greatly lengthened tibiae and longer femora (Burrows, 2007a). They have other structural differences that distinguish them from the front and middle legs.

The arrangement of the hind coxae is quite different to those of the front and middle legs. The coxae of the front legs are widely separated at the ventral midline with the sucking mouthparts projecting posteriorly between them, and can rotate laterally and medially about the prothorax. The coxae of the middle legs are closer to each other at the ventral midline, but still do not touch. They are again able to rotate about the mesothorax in a plane that results in a forwards and downwards movement and a backwards and upwards movement of the whole middle leg. By contrast, each hind coxa is huge and extends from the ventral midline to the lateral edge of the metathorax, and is largely immobile relative to the metathorax

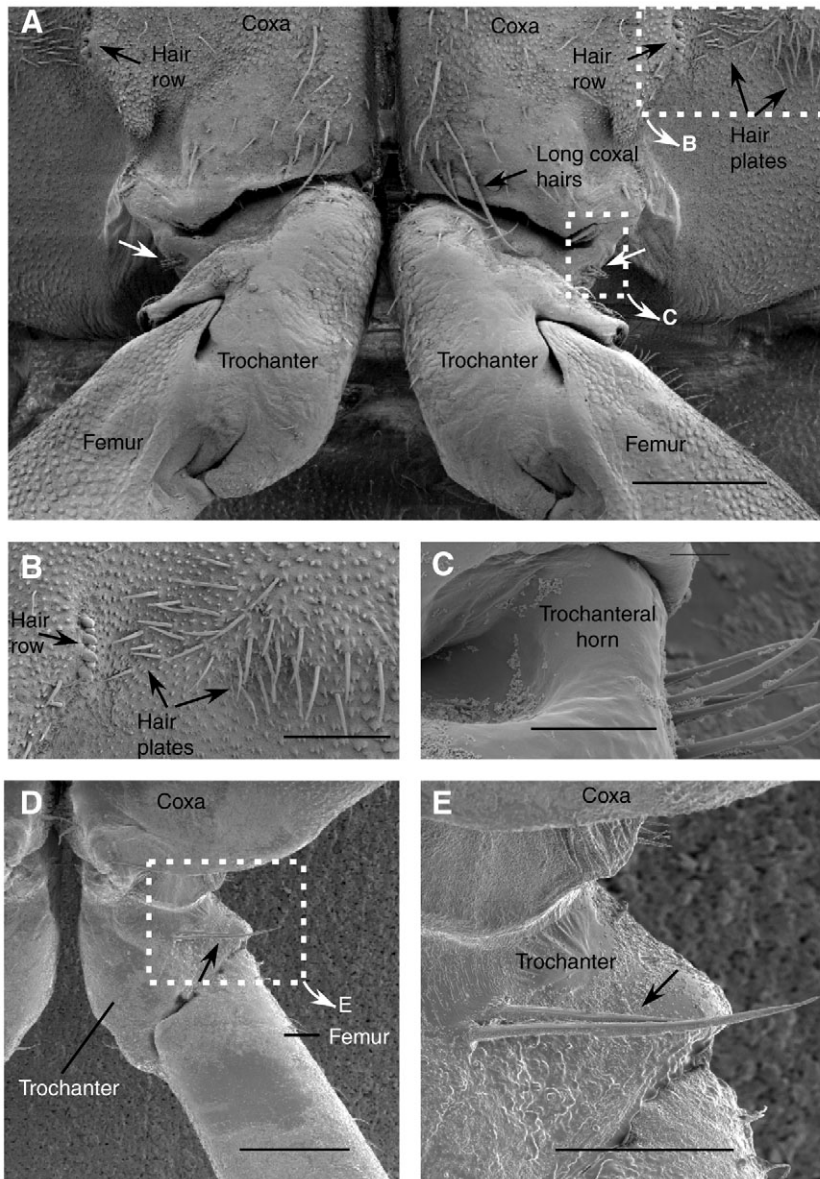


Fig. 3. Scanning electron micrographs of *Aphrodes* to show possible proprioceptors associated with the proximal joints of a hind leg. (A) Lateral to the hair rows on the coxa are two hair plates (black arrows) in the hollowed region of the coxa that will accommodate the femur when the leg is fully levated. A small group of long hairs (black arrow) project posteriorly from the posterior and medial region of the coxa. A hair plate (white arrows) is present on the lateral surface of a ventral horn of a trochanter as it articulates with a coxa. Scale bar, 200 μm . (B) Detail of the two coxal hair plates from the leg on the right (top broken box) in A. Scale bar, 100 μm . (C) The trochanteral hair plate, again from the leg on the right (lower broken box) in A. Scale bar, 20 μm . All photographs in A–C are of ventral views with anterior at the top. (D) Dorsal view of the trochanter to show two long hairs. Note also that the dorsal femur has no protrusion. Scale bar, 200 μm . (E) The boxed region in D at higher magnification. Scale bar, 100 μm .

joints. This arrangement means that during a jump three of the main joints of the leg move in the same plane.

Proprioceptors

There are many arrays of hairs associated with the proximal joints of a hind leg that would appear to be positioned to act as proprioceptors, rather than as exteroceptors, monitoring the movements of these joints during jumping (Figs 1–3).

A prominent hair row and two hair plates on the coxa are likely to be stimulated when a hind leg is fully levated in preparation for a jump. The leg movements associated with walking on a horizontal surface do not bring the femur into contact with these arrays of hairs. The hair row on the medial edge of the ventral hollow of the coxa consists of some seven stout hairs, only

10 μm long but 5 μm wide at their base (Fig. 2A,C,D). The femur abuts against this hair row only when a hind leg is fully levated. The two hair plates in the ventral hollow of the coxa each consist of some 15 hairs, with the medial hairs 30–45 μm long and the more lateral ones 60–70 μm long (Fig. 3A,B). These hairs will be stimulated by the dorsal surface of the femur as it locates into the coxal hollow during levation of the coxo-trochanteral joint, and then presses on them while it remains in the fully levated position.

The coxa and trochanter also have a number of prominent hairs that are longer than the more numerous surrounding hairs. The coxa has a group of 2–4 hairs (the number depends on the species) 125–150 μm long on its posterior ventral surface that point posteriorly (Fig. 1A, Fig. 2A, Fig. 3A). They are likely to be deflected by the trochanter as it moves in its most depressed position. The trochanter also has two prominent hairs 200 μm long on its dorsal surface that point laterally and slightly anteriorly (Fig. 3D,E). They may be deflected by the coxa as the trochanter is levated.

of a double pivot articulation with a lateral covering plate and has no distinct semi-lunar process or other heavily sclerotised structure that could store energy (Fig. 1B). The joint allows the tibia to be flexed and extended about the femur through an arc of 160–170° in the same plane as that of the coxo-trochanteral joint.

The elongated tibia has a series of longitudinal rows of spines of different lengths, the largest of which are directed laterally and outward. The tibia also has a semi-circular row of short, highly sclerotised spines at the ventral surface of its articulation with the tarsus (Fig. 1C). A similar arrangement of ventrally directed short spines also occurs at the two joints between segments of the tarsus. These spines, which are not present on the front and middle legs, should provide enhanced traction with the ground when the hind legs power a jump.

The tarsus consists of three segments with two terminal pads (arioli) (Fig. 1C) and can be levated and depressed about the tibia through an angle of 40–50°. This movement is again in the same plane as that of the femoro-tibial and coxo-trochanteral

The ventral horn of the trochanter that engages in a socket in the coxa, and thereby forms one of the two joint articulations, has a prominent hair plate on its lateral surface (Fig. 3A,C). The plate consists of a group of some six slender hairs, 25–30 μm long and 2.5 μm wide at their base but tapering to their tip. As the trochanter is fully levated the rotation of the horn in its coxal socket will progressively deflect the hairs.

Ribbed and articulated spines that are some 200 μm long and 35 μm in diameter at their base project distally from the femur close to the femoro-tibial joint (Fig. 1A, Fig. 2A,B).

Typically there are five spines, but both the number and their arrangement differs between species. In *Cicadella*, two pairs of spines point forwards toward the joint while a fifth is set more proximally and points ventrally. *Aphrodes* also has five spines, but one of the four pointing toward the joint is smaller. *Iassus* has three spines that all point toward the joint. In all species, these spines will be distorted when the hind leg is fully levated in preparation for a jump and the distal end of the femur engages with a recess in the lateral head capsule.

Press studs

The coxae of the two hind legs are closely apposed to each other at the midline. If prised apart they are then seen to be linked by a protrusion from the medial wall of one coxa that engaged in a socket of the medial wall of the other coxa (Fig. 4A,B). In prising the coxae apart this structure was the last to remain engaged before suddenly giving way under sustained applied force. Once forcibly separated in this way, the insect can re-engage the protrusion with the socket. The dome-shaped protrusion extends 60 μm from the wall of the coxa and has a diameter of 50 μm at mid height. The diameter and depth of the apposing socket match these values, allowing a tight engagement of the protrusion. The protrusion is soft and flexible but turgid, and could stretch when a disengagement was forced. In both form and action the structure resembles a press-stud fastener (snap or popper). Adjacent to both the protrusion and to the socket were two arrays of microtrichia, which also engaged with each other when the two coxae were naturally apposed to each other (Fig. 4B, Fig. 5A,B). Each microtrichia is 5–8 μm wide at its base and 8–10 μm high. One of the patches has a diameter of 70 μm and the other is more ovoid with its longest diameter about 130 μm .

Both the press stud and the microtrichia were found in adults of all the species analysed but were absent in the larvae of all ages examined. In larvae the medial walls of the coxae were smooth with no protrusion or a matching socket and no microtrichia (Fig. 5C). The larvae are nevertheless proficient jumpers despite the absence of these structures (Burrows, 2007a).

A structure involving a protrusion from the coxa of one hind leg engaging with a socket on the other hind leg is clearly bilaterally asymmetrical. In some leafhoppers the protrusion was from the left coxa (Fig. 4) and in others, of the same or different species, from the right coxa (Fig. 5). To determine whether there was bias in favour of the protrusion arising from one particular side, 101

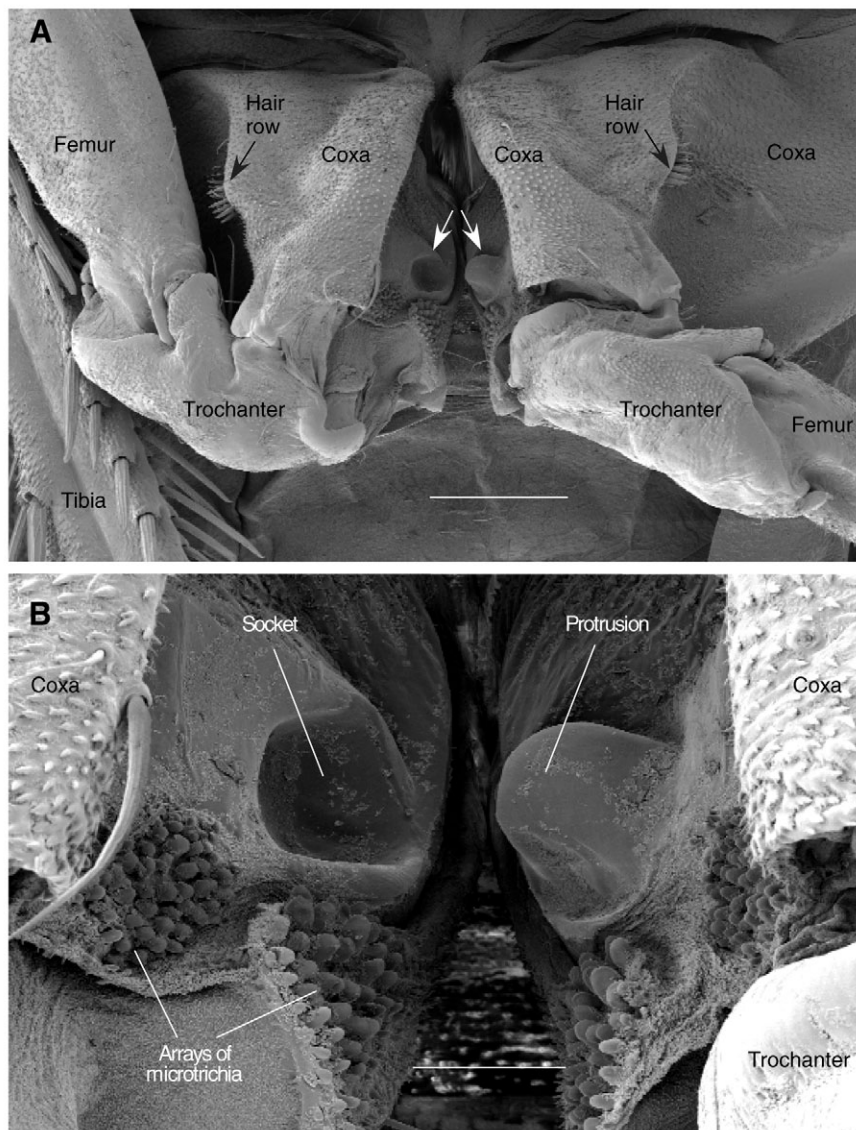


Fig. 4. Scanning electron micrographs of *Cicadella* to show the mechanical linkages between the medial surfaces of the hind coxa. The legs were pulled apart before fixation to show the structures involved; ventral views with anterior at the top. (A) Low power, of the two coxae, with the coxo-trochanteral joint on the left more levated than on the right. The white arrows indicate a medially directed protrusion from the coxa on the right and a corresponding socket in the coxa on the left with which it engages. Scale bar, 200 μm . (B) Higher magnification view from the same perspective to show the protrusion and socket, and two arrays of microtrichia on each coxa. These two arrays will also engage the corresponding arrays on the other leg, when the coxae are apposed to each other. Scale bar, 50 μm .

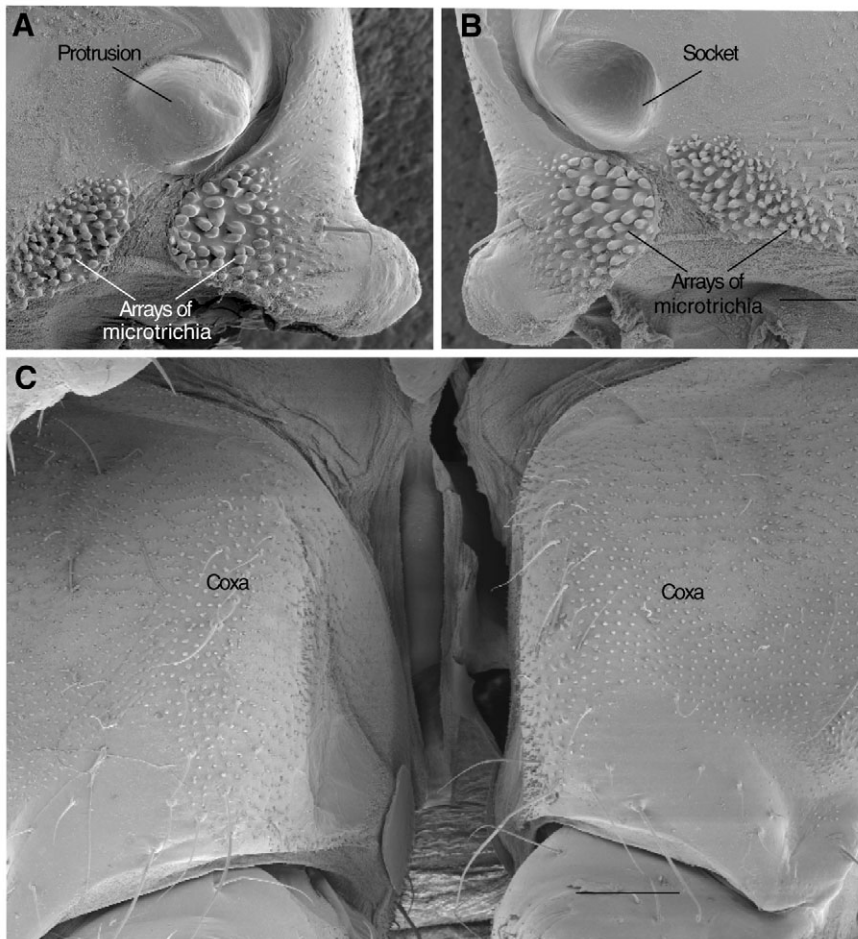


Fig. 5. Mechanical linkages between the hind coxae. (A,B) The two hind coxae of *Cicadella* were separated and then mounted so that their inner faces point toward the observer. The anterior midline is therefore between the two pictures and the posterior midline is at their lateral edges. If the two pictures are folded toward each other along the vertical white bar separating them, then the protrusion (in this insect on the left) and socket (on the right), and the two fields of microtrichia engage with each other. Scale bar, 50 μm . (C) No press stud is present in a nymphal stage of *Iassus lanio*. Scale bar, 200 μm . Ventral view with anterior at the top.

leafhoppers of several different species and of either sex were analysed. Pooling the data from all these insects showed that 45 protrusions were from the left coxa and 56 from the right. A χ^2 test gave a value of 1.198 and a P value of 0.27, indicating therefore that there was no statistical difference in the frequency of left or right protrusions. If data were separated into individual species, there was again no statistical difference in the frequency of left or right protrusions within a species [for example, *Empoasca* ($N=24$) left=12, right=12; *Iassus* ($N=32$) left=18, right=14, $\chi^2=0.5$, $P=0.48$].

Muscles involved in jumping

Movements of the trochanter are powered by large muscles that occupy most of the space within the coxa (Fig. 6). The large depressor muscle arises from the anterior and ventral wall of the metathorax and inserts on the sclerotised medial rim of the trochanter (Fig. 6A). The two parts of the levator are both more lateral and of similar mass to the depressor (Fig. 6A,B). The

more medial part arises from the anterior and ventral wall of the metathorax just lateral to the origin of the depressor and the lateral part from the lateral wall of the metathorax. They both insert on the lateral edge of the trochanter.

Lever arms

The lever arms of the trochanteral muscles, defined as the perpendicular distance from the line of force of their tendon to the coxo-trochanteral pivot, was measured over the full range of joint movements in live insects and in insects preserved in glycerol (Fig. 7A–D). When the hind leg was fully levated, the lever arms of the levator and depressor muscles were similar, so that neither muscle had a mechanical advantage over the other. The lever arm of the depressor rose gradually as the joint depressed to reach a maximum at a coxo-trochanteral angle of about 80° (Fig. 7D). By contrast the lever arm of the levator remained the same over this range of joint movements. As the joint depressed still further, the depressor lever arm remained the same while that of the levator declined. The difference between the lever arms of the two muscles was therefore greatest at full depression.

Actions of muscles during jumping

Recordings were made from the trochanteral depressor and levator muscles in an insect restrained ventral surface uppermost and with its hind legs free to move. In this position the insect would perform rapid and simultaneous movements of both its hind legs that had the same characteristics as those observed during jumping, except that they were even faster

as the legs did not propel the body from the ground. A similar arrangement has been used to record the muscular activity that may underlie jumping of froghoppers (Burrows, 2007b). The following descriptions of jumps recorded in this experimental arrangement all carry the above caveats.

The first movements in preparation for a jump were a levation of the trochantera of both hind legs. The jump may follow this initial levation or there may be a delay lasting several hundred milliseconds before simultaneous recordings from the levator and depressor of one trochanter showed that both muscles were activated at the same time (Fig. 8). The actions of both muscles resulted in a forward movement of the coxae, as indicated by the horizontal lines on the first two frames of Fig. 8. Just before the jump occurred there was an increase in the frequency of spikes in the depressor muscle, while the frequency of spikes in the levator muscle declined. The total duration of the electrical activity in the two muscles was 79.3 ± 14.8 ms ($N=23$ jumps, range 12–222 ms) as measured from the start of their joint

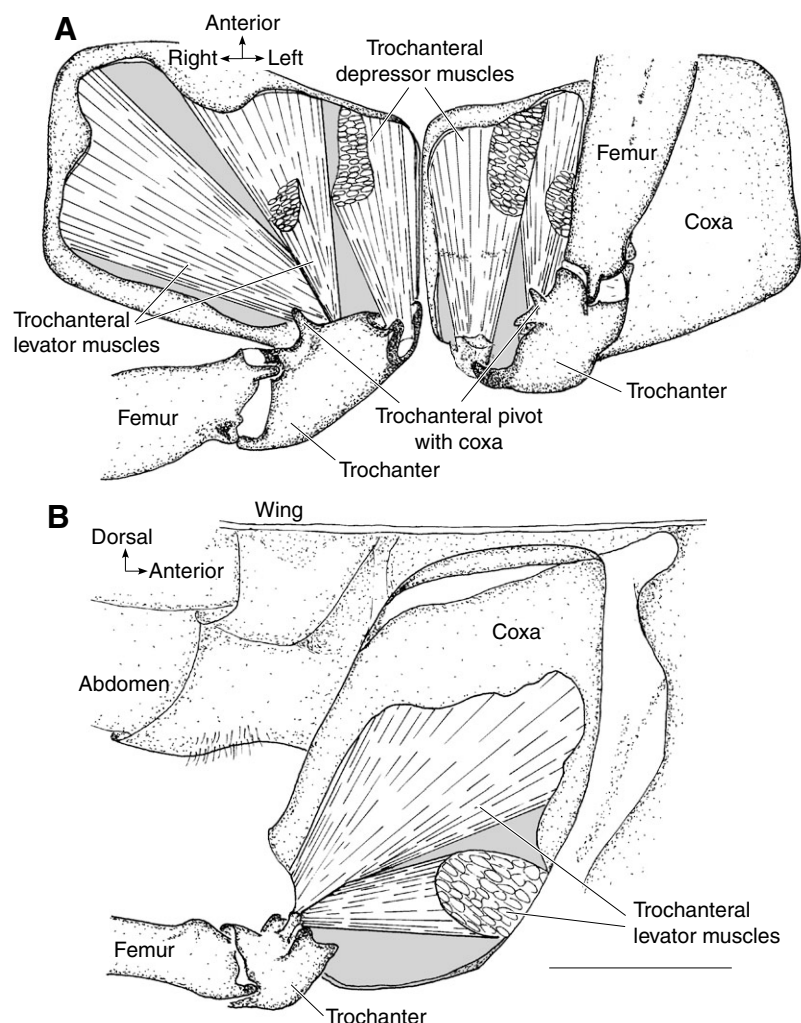


Fig. 6. Anatomy of the muscles moving the coxo-trochanteral joint of a hind leg of *Aphrodes*. (A) Ventral view with the left hind leg shown fully levated, and the right hind leg partly depressed. The trochanteral depressor muscle of each hind leg is medial and the different parts of the levator muscle are more lateral. (B) Side view of the right metathorax exposed to show the laterally placed trochanteral levator muscles of the right hind leg in a depressed position. Scale bar, 500 μm .

activity until the jump movement. The different durations of activity in a trochanteral depressor muscle was seen in different *Aphrodes* and during different jumps by the same one (Fig. 9).

Simultaneous recordings from the depressor muscles of the right and left hind legs showed that spikes occurred at the same time in each muscle before a jump movement of both hind legs (Fig. 10A). The activity in each muscle appeared to result from the activity of more than one motor neuron. The spikes of an individual motor neuron could not be readily distinguished so that the summation and interactions of these spikes in the myogram recordings precluded determination of spike frequencies. Viewing the spikes on an expanded time scale indicated that the spikes on the two sides were not closely coupled and simultaneous spike occurrences did not appear to be common to the muscles on each side (Fig. 10B).

On rare occasions one hind leg would kick rapidly but the other hind leg would not move from its fully levated position (Fig. 11). There was then a clear burst of spikes in the depressor muscle that leg was to kick, but in the depressor muscle

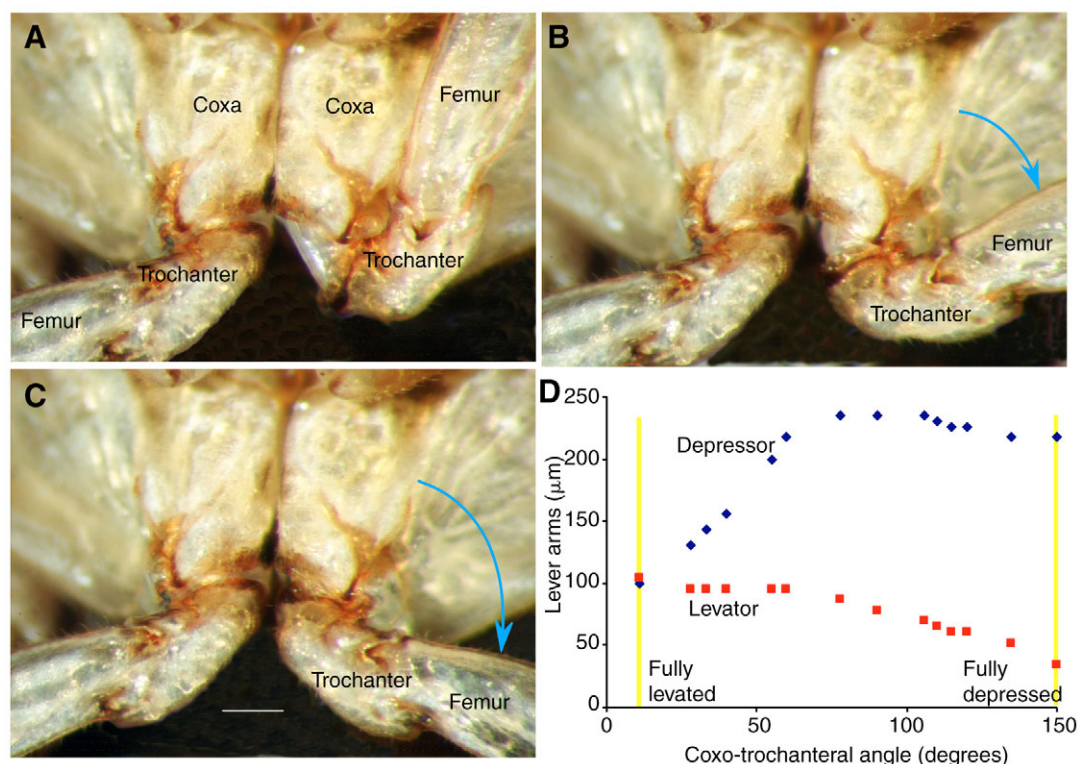


Fig. 7. Movements of the coxo-trochanteral joint of *Aphrodes*. (A–C) Ventral views of the joint if the left hind leg is forcibly moved (blue arrows) into different positions from fully levated (A) to almost fully depressed (C). The right hind leg remains in the same partially depressed position throughout. Scale bar, 200 μm . (D) The lever arms of the trochanteral depressor and levator muscles plotted over the full range of coxo-trochanteral movements.

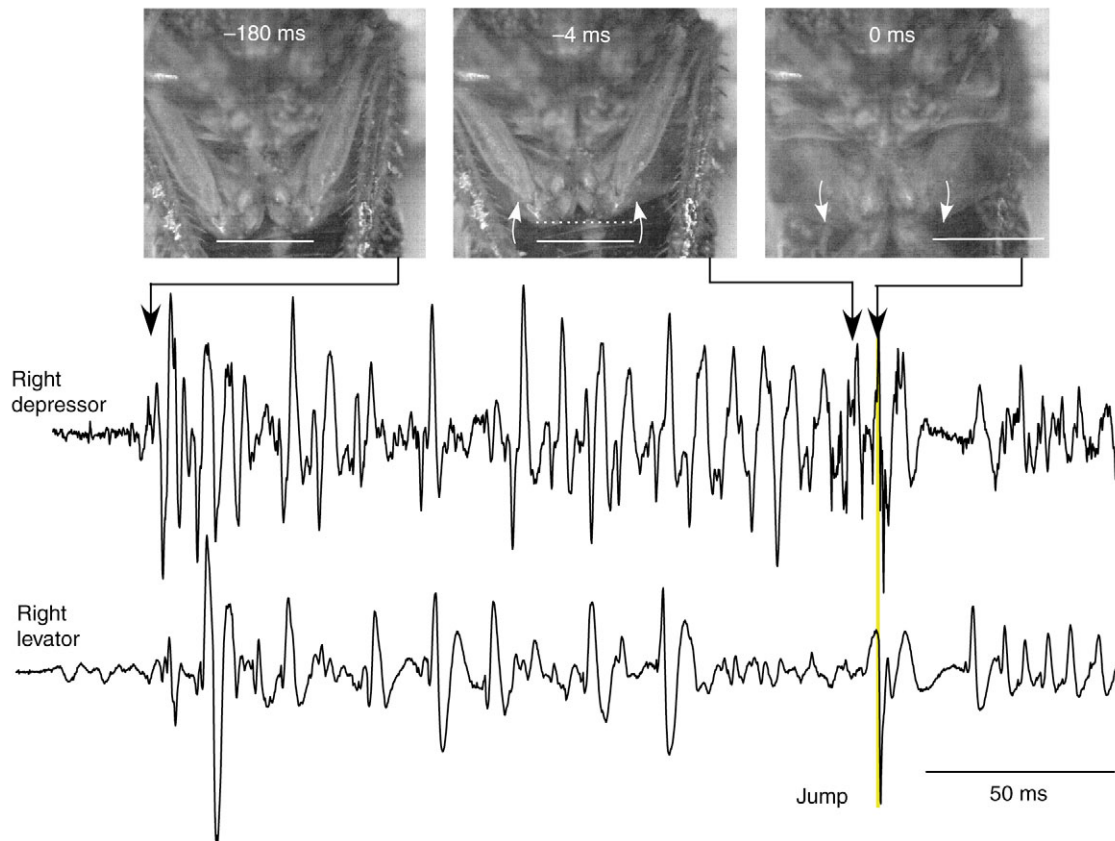


Fig. 8. Actions of hind leg trochanteral muscles of *Aphrodes* during jumping. Simultaneous recordings from trochanteral depressor (upper trace) and levator (lower trace) muscles of the right hind leg during a jump. Selected frames of the leg movements from high-speed images are shown above at the times indicated in this and Figs 10, 11 (scale bar on right frame, 1 mm). The activity in the two muscles began when both hind legs were already levated and resulted in an anterior movement of both (horizontal lines). The activity in the depressor increased before the jump movement while that in the levator declined.

of the other stationary leg, only sporadic spikes of similar frequency to those in the preceding period were recorded (Fig. 11A,B).

Discussion

Design for jumping

The present study shows that leafhoppers have modified the strategy to produce their very effective jumping compared with their close relatives the froghoppers. The strategy of froghoppers is to use short hind legs and a powerful catapult mechanism involving mechanical locking mechanisms to generate the necessary power for jumping. The leafhoppers studied here have long hind legs and a much shorter period of muscle activity before a jump, but must also be storing energy in advance of a jump. No mechanical locking mechanisms are apparently present. The strategies for jumping are both based on the same principle of powering simultaneous movements of the hind trochanters about the coxae. These movements occur in the same plane as each other beneath the body and are produced by muscles located in the thorax so that the legs can be light. The different strategies involved in achieving the same final behaviour are accompanied by distinctive differences in the skeletal structure of the hind legs and in the muscles that control the key movements of the coxo-trochanteral joints. The

requirements of these different strategies result in an impressive, but less effective, jumping performance by leafhoppers compared to froghoppers.

Mechanical specialisations

The most obvious specialisation of the hind legs of leafhoppers is their long length relative to their body and to the other pairs of legs. This increased length is due largely to an increase in the length of the tibiae with their longitudinal arrays of spines. Leafhoppers, like froghoppers, have arrays of small spines on the distal tibia and on the tarsal joints that should increase traction when jumping.

Each coxa can move only with the metathorax at its articulation with the mesothorax. In jumping this is manifest as an anterior movement of the two halves of the metathorax during the holding phase (see Fig. 8). The rigidity of the two coxae and their simultaneous movements are further enhanced by an unusual mechanism that links them both. This consists of a protrusion from the medial surface of one coxa that inserts in a matching socket on the other coxae, which has been described briefly before (Emeljanov, 1987; Gorb, 2001). The linkage is reinforced by two arrays of microtrichia on each coxa that engage with each other. Microtrichia are typically found in insects where two surfaces need to be held

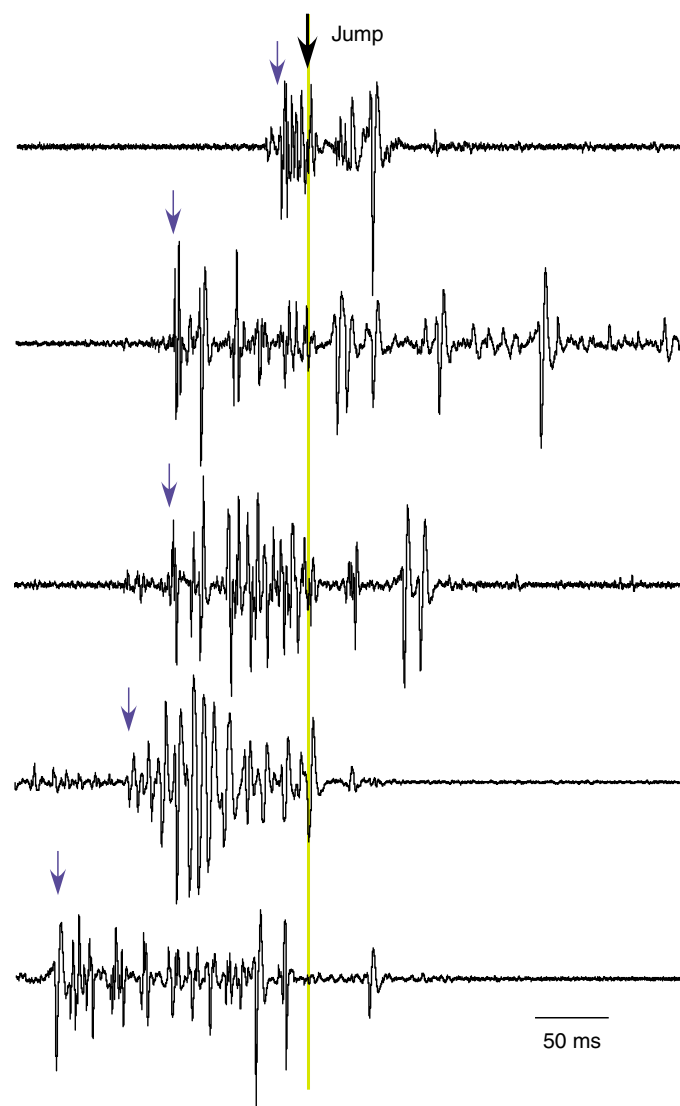


Fig. 9. Recordings from the trochanteral depressor muscle of the right hind leg during five jumps by the same *Aphrodes*. The timings of the jump movements were recorded with high-speed images. The duration of the muscle activity ranged from 20–160 ms.

together under certain circumstances but still capable of release under different circumstances (Gorb, 2001). The protrusion can arise from either coxa and there is no statistical preference for one side in the different species or within a particular species. The protrusion and the corresponding socket are, however, absent from larvae where the medial coxal walls are smooth and also lack the microtrichia. The larvae are nevertheless proficient jumpers (Burrows, 2007a), thus posing the question as to whether the linkage between the two coxae is an essential specialisation for jumping. Perhaps there are subtle differences between the jumping mechanisms or performance of larvae and adults that have yet to be revealed.

Leafhoppers lack a mechanical mechanism that could restrain movements of the hind legs during the holding phase of the jump. Froghoppers have a ventral protrusion from a coxa that

is covered in microtrichia and which engages with a protrusion from the dorsal surface of a femur, also covered in microtrichia, when a hind leg is fully levated in preparation for a jump (Burrows, 2006b). Disengagement of this lock precedes the release of the leg in rapid jumping movements. Leafhoppers do not have a ventral protrusion from a coxa or a dorsal protrusion from the proximal femur that could engage with each other to provide a lock. Instead the femur fits into a hollow on the ventral coxa when the hind leg is fully levated, but this would not restrain a depression movement.

Muscular specialisations

The levator and depressor muscles that operate the coxo-trochanteral joint are of similar size and mass. The levator muscle has a mechanical advantage over the depressor when the hind legs are fully depressed, but when the legs are fully levated their lever arms are the same. This contrasts with the arrangement of the equivalent muscles in froghoppers, where the huge depressor muscle occupies most of the metathorax but the much smaller levator muscles are restricted to the coxa (Burrows, 2007b). Moreover, the small levators have a mechanical advantage over the large depressor when the trochanters are fully levated.

Neural specialisations

Arrays of hairs appear to be positioned to act as proprioceptors, which could monitor the positions and movements of the hind legs that are adopted and used in jumping but not in walking. One of the most obvious movements in jumping but not walking is the full levation of the trochanter that engages the femur with the hollowed ventral region of the coxa, and the femoro-tibial joint with the sculpted region of the head. A hair row and two hair plates on the ventral coxa and the femoral spines at the femoro-tibial joint should all signal when this movement occurs and the final fully levated position achieved. A hair plate on the ventral horn of the trochanter that inserts into a socket in the trochanter and thereby forms one of the two articulations of this joint should also signal the more extreme levation movements. Long hairs on the coxa and trochanter should also be stimulated when the trochanter moves into in most levated and depressed positions. Froghoppers also have an array of proprioceptors that could monitor their specific jumping movements, but the arrangement is different reflecting the different organisation of the joints (Burrows, 2006b).

The motor pattern underlying the jump consisted of an initial co-activation of the trochanteral levator and depressor muscles that resulted in a full levation of the leg and a forward movement of the coxa and metathorax. Once in the fully levated position the two muscles have a similar mechanical advantage so that a co-contraction of the two muscles should not result in a movement of the trochanter. Instead their combined contractions move the coxa and metathorax forward with the potential to store energy in skeletal structures.

The duration of the muscle activity was very brief with the whole pattern lasting on average about 80 ms (range 12–222 ms). This contrasts with the several seconds of contraction by the depressor muscles preceding jumps by froghoppers and which are accompanied by little activity in the

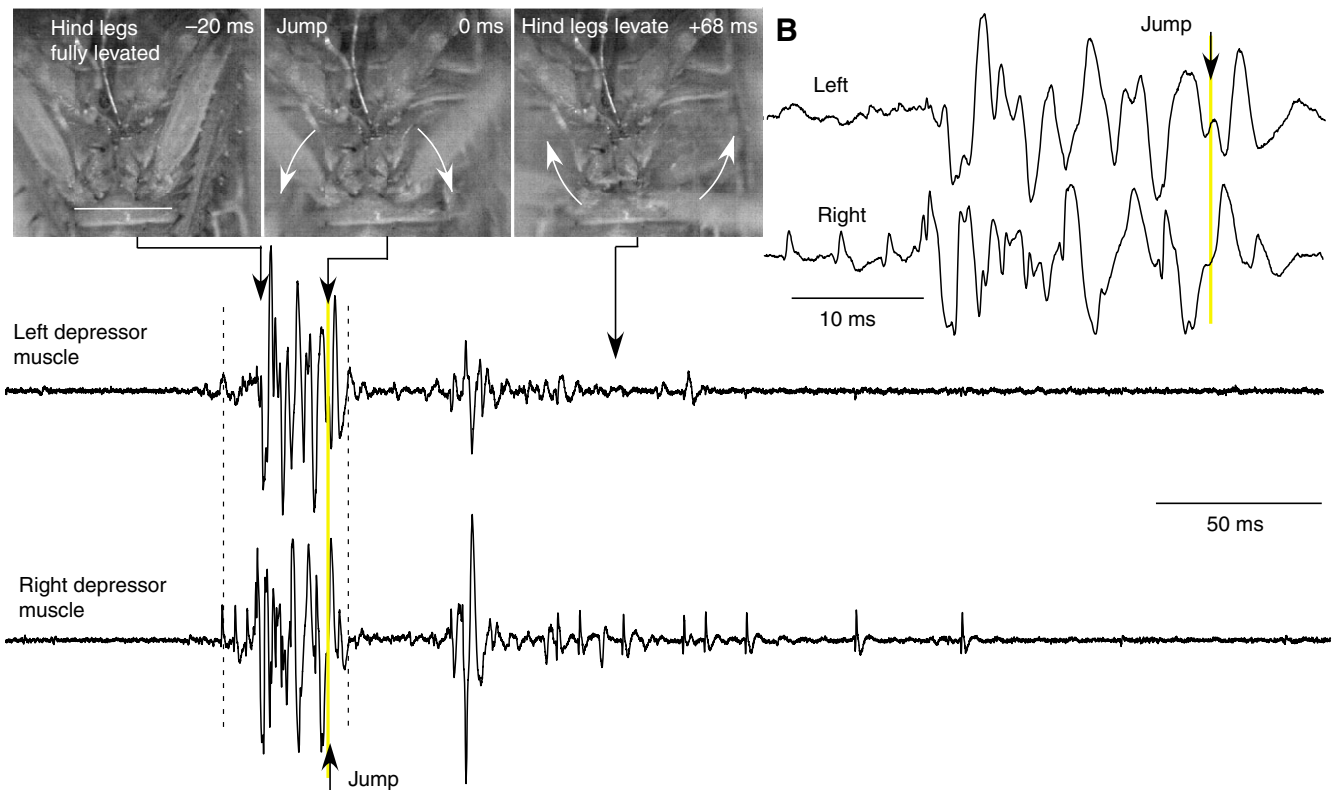


Fig. 10. Simultaneous recordings from the trochanteral depressor muscles of the left and the right hind legs of *Aphrodes*. (A) The rapid and simultaneous jump movements of both hind legs (arrows) were preceded by a high frequency burst of spikes in both depressor muscles. Scale bar on left frame, 1 mm. (B) Displaying this burst of spikes (between the broken lines in A) on a faster time scale showed that the spikes on the two sides were not tightly coupled.

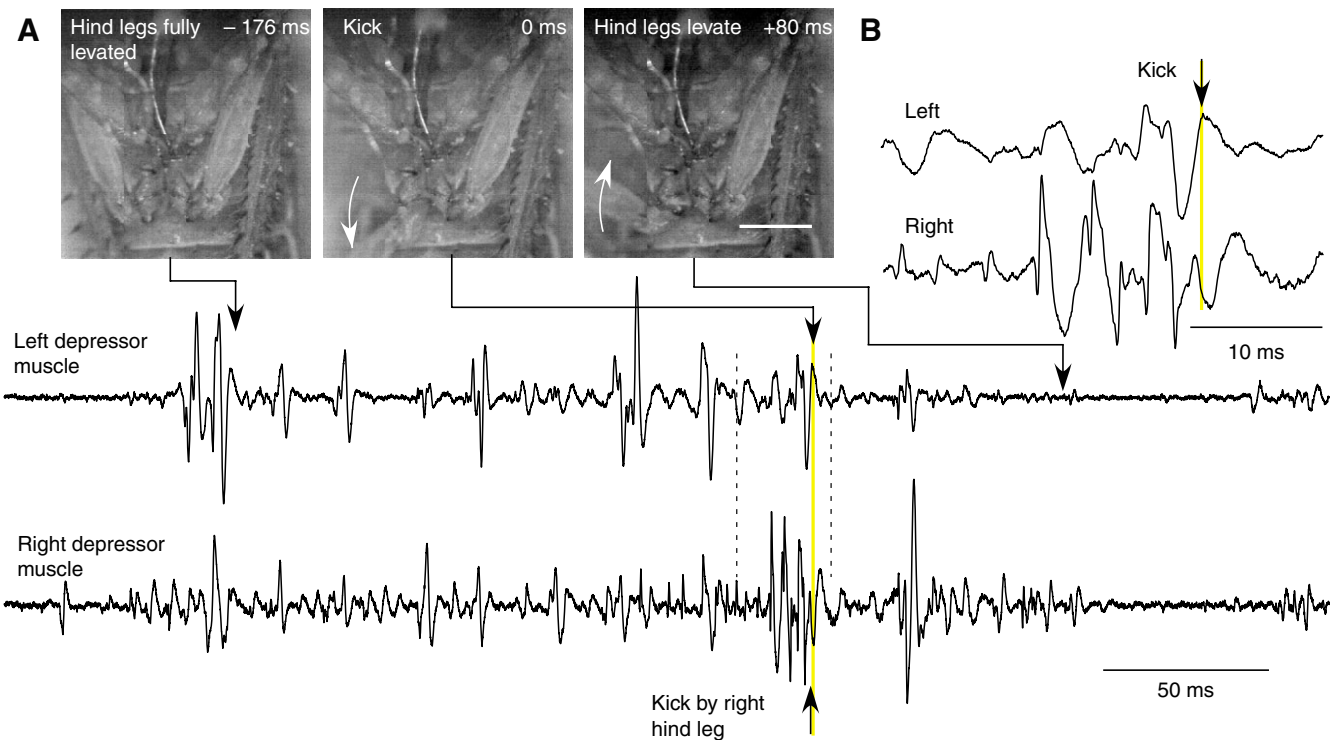


Fig. 11. Independent movements by the two hind legs. Simultaneous recordings were made from the trochanteral depressor muscles of the left and the right hind legs of the same *Aphrodes* as Fig. 10. (A) A rapid kick by the right hind leg alone was preceded by a burst of spikes only in the right depressor muscle. Scale bar, 1 mm. (B) The burst of spikes on a faster time scale.

levators (Burrows, 2007b). The low mechanical advantage of the depressor when the hind leg is fully levated and the presence of a mechanical lock prevent depression of the hind legs during this period. In leafhoppers, storage of energy could occur during the much briefer holding period. The final burst of spikes in the depressor when the levator activity has declined must generate sufficient force to depress the trochanter, at the same time rapidly releasing any force stored by the preceding muscle contractions.

The spikes in a trochanteral depressor muscle appeared to result from the activity of more than one motor neuron. The spikes of an individual motor neuron could not be readily distinguished so that the summation and interactions of these spikes in the myogram recordings precluded determination of spike frequencies. The motor spikes in the depressor muscles on the two sides do not appear to be tightly coupled, to the extent that the spikes cannot be matched in a one to one fashion. This again strongly contrasts with the activity of the left and right depressor muscles of froghoppers during jumping, in which the spikes in the two muscles were synchronous with only a few exceptional failures on one side (Burrows, 2007b).

The resulting jump of leafhoppers is much slower than that produced by froghoppers. The hind legs take on average 5–6 ms to be fully depressed and extended (Burrows, 2007a) compared to less than 1 ms in froghoppers (Burrows, 2003; Burrows, 2006a) and the take-off velocity of 2.9 m s^{-1} , although impressive, falls well short of the 4.7 m s^{-1} achieved by froghoppers. The energy expended by leafhoppers in their best jumps is, however, only about a third of that expended by froghoppers (Burrows, 2006a; Burrows, 2007a). A comparison of jumping between two different groups of insects with similar body designs – leafhoppers with froghoppers, and bush crickets with locusts – indicates a potential trade-off between movements that are energetically more expensive but which can deliver better performance. In locusts, the power-producing extensor tibiae muscle of a hind leg co-contracts with the antagonistic flexor tibiae muscle without moving the leg but stores energy in distortions of the cuticle (Burrows, 1995; Burrows and Morris, 2001; Heitler and Burrows, 1977). By contrast bush crickets, which like leafhoppers also have proportionately longer hind legs, power their jumps (Burrows and Morris, 2003), and crickets their kicks (Hustert and Gnatzy, 1995), by muscle contractions moving long levers. The energy that bush crickets expend in jumping is also less than that expended by locusts, but their performance is inferior.

Many members of the other families of Auchenorrhyncha are also prolific jumpers. This offers the opportunity to explore the way that different families have adapted specific elements from this panoply of jumping mechanisms to meet their own behavioural needs. For example, some cicadellids do not have long hind legs like those described here but are said to be proficient jumpers.

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