Erratum

Kinematics of jumping in leafhopper insects (Hemiptera, Auchenorrhyncha, Cicadellidae)

Malcolm Burrows

There was an error published in the on-line version of *J. Exp. Biol*. **210**, 3579-3589. The print version is correct.

The spacing of some of the data in Table 2 was incorrect. The correctly laid out Table is presented below.

Table 2. *Jumping performance of Cicadellids*

	N	Body mass (mg)	Body length (mm)	Time to take off (ms)	Take off velocity (m s⁻¹)	Take-off angle (degrees)	Body angle at take-off (degrees)	Acceleration (m s⁻²)	*g* force	Energy (μJ)	Power (mW)	Force (mN)
Empoasca												
Mean	7	0.86±0.07	3.5±0.03	4.7±0.10	1.1±0.11			253	26	0.6	0.1	0.2
Best				4	1.6			400	41	1.0	0.3	0.3
Aphrodes												
Mean	43	18.4±1.30	8.5±0.22	4.4±0.18	2.5±0.09	37.1±4.40	36.7±5.0	568	58	58	13	11
Best				2.75	2.9			1055	108	77	28	19
Cicadella												
Female												
Mean	10	19±1.10	9.2±0.33	6.4±0.21	1.2±0.13	34.3±5.90	26.7±5.20	188	19	14	2	4
Best				5	1.6			320	33	24	5	6
Male												
Mean	10	10.9±0.50	6.4±0.16	6.4±0.21	1.2±0.13	34.3±5.90	26.7±5.20	188	19	8	1	2
Best				5	1.6			315	33	14	3	3
Graphocephala												
Mean	16	13	9.0	5.6±0.25	1.6±0.07	29.5±3.60	15.7±2.40	285	29	17	3	4
Best				4.5	1.85			411	42	22	5	5
Iassus Nymphs												
Best		4	4.3	2.5	2	45	32	800	82	8	3.2	3.2

Values are means ± s.e.m.

We apologise for any inconvenience this error has caused.

Kinematics of jumping in leafhopper insects (Hemiptera, Auchenorrhyncha, Cicadellidae)

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Summary

The jumping movements and performance of leafhopper insects (Hemiptera, Auchenorrhyncha, Cicadellidae) were analysed from high-speed sequences of images captured at rates up to 5000 frames s^{-1}. The propulsion for a jump was delivered by rapid and synchronous movements of the hind legs that are twice the length of the other legs, almost as long as the body, and represent 3.8% of the body mass. The wings were not moved before take-off, but the jump frequently launched a flight. The front and middle legs set the attitude of the body in preparation for a jump but were usually raised from the ground before take-off. The movements of the hind legs occurred in three distinct phases. First, a levation phase of 15–30 ms, in which both hind legs were moved forward and medially so that they were positioned directly beneath the body with their tibio-tarsal joints pressed against each other. Second, a holding phase lasting 10–200 ms, in which the hind legs remained stationary in the fully levated position. Third, a rapid jump phase, in which both hind legs were simultaneously depressed about their coxo-trochanteral joints and extended at their femoro-tibial joints. This phase lasted 5–6 ms on average, with the fastest movements accomplished in 2.75 ms and involving rotations of the coxo-trochanteral joints of 44 000 deg. s^{-1}. In the best jumps by *Aphrodes*, a peak take-off velocity of 2.9 m s^{-1} was achieved by an acceleration of 1055 m s^{-2}, equivalent to 108 times gravity. This jumping performance required an energy output of 77 μJ, a power output of 28 mW and exerted a force of 19 mN, or 100 times its body mass.

Supplementary material available online at
http://jeb.biologists.org/cgi/content/full/210/20/3579/DC1

Key words: locomotion, kinematics, motor pattern, muscle.

Introduction

Many insects are able to jump as a means of increasing the forward speed of their locomotion, launching themselves into flight, or escaping from predators. In those insects that use their hind legs to propel their jumps, the froghoppers (Hemiptera, Auchenorrhyncha, Cercopidae) have so far proved to be the most effective jumpers, accelerating their bodies to a take-off velocity of 4.7 m s^{-1} in less than 1 ms in a jump that reaches heights of about 115 times their body length and exerting a force some 400 times their body mass (Burrows, 2003; Burrows, 2006a). They achieve these feats, although they have only short hind legs, by storing energy in advance of the jump and then releasing it suddenly in a catapult action. This jumping strategy (Alexander, 1995) contrasts with insects such as bush crickets that have long hind legs and use mostly direct muscle contractions acting on these long lever arms to generate their jumps (Burrows and Morris, 2003).

The Auchenorrhyncha, to which the froghoppers belong, contains many families and a huge diversity of insects, but jumping is a behavioural characteristic that most of them share. One of these families, the Cicadellidae or leafhoppers, differs from the others in that most of its members have long hind legs and one species is reported to reach take-off velocities of 1.3 m s^{-1} (Brackenbury, 1996). The family is one of the largest insect families, containing 22 000 known species distributed world wide (Dietrich, 2004), and totalling more than those of all birds, mammals, reptiles and amphibians combined. The body design is typically characterised by long hind legs, a wedge-shaped head, and a thorax and abdomen that are streamlined by being encased by the folded front wings. The long hind tibiae, with several prominent rows of spines, are used in jumping and walking, and as combs to distribute brochosomes over the integument. These are 0.3–1.4 μm spheres of a protein–lipid complex with an intricate surface structure (Rakitov, 2000), secreted by specialised regions of the Malpighian tubules, which may act as a protective and waterproof coating. The larval stages are free-living on plants and can jump, unlike the larvae of froghoppers, which either develop underground, or in masses of foam above ground.

This paper analyses the jumping performance of leafhoppers to determine what sorts of movements and mechanisms might be involved and how these are influenced by having long hind legs. It shows that in the best jumps by some species of leafhoppers, the body is accelerated at 1055 m s^{-2} in under 3 ms to a peak take-off velocity of 2.9 m s^{-1}. On average the acceleration period is 5–6 ms and the take-off velocity is

1.1–1.6 m s^{-1}. The performance, while matching that of fleas (Bennet-Clark and Lucey, 1967; Rothschild and Schlein, 1975; Rothschild et al., 1972), locusts (Bennet-Clark, 1975) and some flea beetles (Brackenbury and Wang, 1995), falls short of that of their close relatives the froghoppers, despite the extra leverage of the long hind legs and their similar body shape, size and mass.

Materials and methods

The jumping mechanisms of four species of leafhoppers were analysed in detail: *Empoasca vitis* Goethe, *Cicadella viridis* (Linnaeus), *Graphocephala fennahi* Young, 1977, and *Aphrodes* of the *makarovi* Zachvatkin, 1948/*bicinctus* (Schrank) group, with some features supplemented by observations on *Iassus lanio* (Linnaeus) and other unidentified species. They all belong to the order Hemiptera, suborder Auchenorrhyncha, super family Cicadelloidea and family Cicadellidae. They were collected around Cambridge and Wells next-the-Sea, England; Llandinam, Wales; Ljubljana Slovenia; and Aachen, Germany.

Sequential images of jumps were captured at rates of 1000–5000 frames s^{-1} with a Photron Fastcam 512 or 1024 PCI camera [Photron (Europe) Ltd, Marlow, Bucks., UK] that fed images directly to a computer. High-speed videos of jumps by *Graphocephala*, with images captured at 4000 frames s^{-1} and each with an exposure time of 0.125 ms, and *Cicadella* (5000 frames s^{-1} and 0.05 ms) are included as Movie 1 and Movie 2 in supplementary material. Spontaneous jumps and jumps encouraged by delicate mechanical stimulation with a fine paintbrush or a 100 μm silver wire, were performed in a chamber of optical quality glass 80 mm wide, 80 mm high and 25 mm deep with a floor of high density foam. All jumps by the small *Empoasca* were spontaneous and were performed in a circular chamber (diameter 15 mm, depth 8 mm) with a glass floor and roof. Selected image files were analysed with Motionscope camera software (Redlake Imaging, San Diego, CA, USA) or with Canvas X (ACD Systems of America, Miami, FL, USA). The time at which the hind legs lost contact with the ground and the insect therefore took off and became airborne was designated as time $t=0$ ms, so that different jumps could be aligned and compared. The time at which the hind legs first moved is also marked on the figures, therefore defining the time over which the body was accelerated. The acceleration was calculated as the average over this period. A detailed analysis was performed on 52 jumps by 12 *Empoasca*, 43 jumps by 9 *Aphrodes*, 33 jumps by 7 *Cicadella*, and 17 jumps by 4 *Graphocephala*.

Measurements are given as means ± standard error of the mean (s.e.m.). Temperatures in all experiments ranged from 24–30°C unless otherwise stated.

Results

Body shape

The four species of leafhoppers analysed in detail here, had a 22-fold range of masses and a 2.6-fold range of body lengths (Table 1). For example, the smallest species examined, *Empoasca*, had a mass of 0.9 mg and body length 3.5 mm, *Aphrodes* a mass of 18.4 mg and body length 8.5 mm, and female *Cicadella viridis* a mass of 19 mg and body length 9.2 mm. *Graphocephala* were lighter at 13 mg, body length 9 mm. The centre of mass was determined by balancing a dead insect on a pin, and lies above the coxae of the hind legs.

The hind legs are much longer than the front or middle legs so that the ratio of front to middle to hind leg lengths in *Empoasca* is 1:1.1:2.1, rising to 1:1.2:2.9 in the larger *Graphocephala* (Table 1, Fig. 1). These ratios increase through successive larval stages. In *Iassus*, for example, the small nymphs have a ratio of 1:1.2:1.6, which increases in later and larger nymphs to 1:1.2:2.0, finally reaching 1:1.2:2.3 in adults. The hind legs are 82–84% of overall body length in *Empoasca*, *Aphrodes* and female *Cicadella*, rising in male *Cicadella* to 93%. Their long length also means they have a greater mass that represents 3.8±0.09% (*N*=5) of the total body mass in *Cicadella*, even excluding the huge coxae
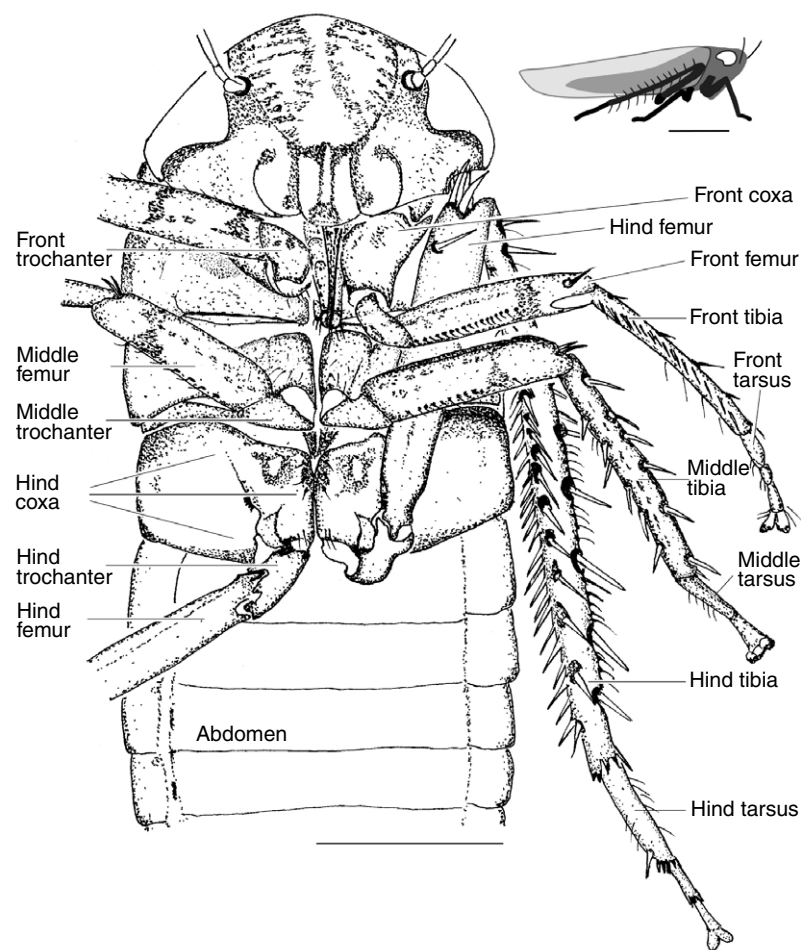

Fig. 1. Drawing of a ventral view of *Cicadella viridis*. The left hind leg is in its fully levated position and the right hind leg in an extended position with the coxo-trochanteral joint almost fully depressed. The distal parts of the right legs and the posterior part of the abdomen are omitted. The cartoon at top right shows the body shape of *Empoasca*. Scale bars, 1 mm.

Table 1. *Body form in Cicadellids*

Insect	N	Body mass (mg)	Body length (mm)	Hind leg Tibia (mm)	Hind leg Femur (mm)	Ratio of leg lengths			Hind leg length as % of body length
						Front	Middle	Hind	
Empoasca	7	0.86±0.72	3.5±0.03	1.5±0.05	0.7±0.05	1	1.1	2.1	82
Aphrodes	8	18.4±1.3	8.5±0.22	3.8±0.06	2.2±0.03	1	1.2	2.2	84
Cicadella									
Male	5	10.9±0.50	6.4±0.16	3.1±0.06	1.6±0.10	1	1.1	1.9	93
Female	6	19.0±1.10	9.2±0.33	3.8±0.05	2.0±0.10	1	1.1	1.9	82
Graphocephala	4	13	9.0	4.0	2.0	1	1.2	2.9	91
Iassus									
Nymphs <4 mm	5		2.5±0.27	1.1±0.05	0.7±0.06	1	1.2	1.6	75
Nymphs >4 mm	8	9.0±0.08	5.7±0.28	2.0±0.15	1.3±0.05	1	1.2	2.0	73
Adults	7	18.2±0.06	7.1±0.29	3.0±0.01	1.8±0.04	1	1.2	2.3	87

Values are means ± s.e.m.

(Burrows, 2007a), and thus almost twice that of froghoppers (Burrows, 2006a).

The increased length of the hind legs relative to the body is due to a greatly enlarged tibia and a longer femur. For example, in *Aphrodes*, a hind tibia was 3.8±0.06 mm long and 125% longer than a middle tibia and 202% longer than a front tibia, while a hind femur was 2.2±0.03 mm long and therefore 69% longer than both the front and middle femora. The hind legs are therefore much longer relative to the other legs and to the body compared with those in the Cercopidae and Aphrophoridae families of froghoppers (Burrows, 2006a; Burrows, 2006b).

Kinematics of the jump

Jumping is powered by the rapid and simultaneous movements of both hind legs moving in the same plane underneath the body. The movements occurred in a distinctive and repeatable pattern divisible into three phases (Fig. 2).

First: in the initial preparatory phase (levation phase) for a jump that lasted from 15–30 ms, the hind legs were first moved anteriorly and medially (Fig. 2A) from their position on the ground outside the lateral edges of the body and wings normally adopted when standing or walking. Both hind legs were slowly levated at the joint between the coxa and the trochanter, and flexed at the joint between the femur and tibia. The result was that both hind legs were swung forwards and medially so that their tibio-tarsal joints were now closely apposed to each other under the ventral midline of the abdomen. The femur was also closely pressed into a ventral hollow on the coxa, and in some species the femoro-tibial joint of each hind leg engaged with the sculpted ventral region on each side of the head (Fig. 1). In the fully levated position, both hind legs therefore came to be tucked between the thorax dorsally and the front and middle legs

Table 2. *Jumping performance of Cicadellids*

	N	Body mass (mg)	Body length (mm)	Time to take off (ms)	Take off velocity (m s^{-1})	Take-off angle (degrees)	Body angle at take-off (degrees)	Acceleration (m s^{-2})	*g* force	Energy (µJ)	Power (mW)	Force (mN)
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Iassus Nymphs												
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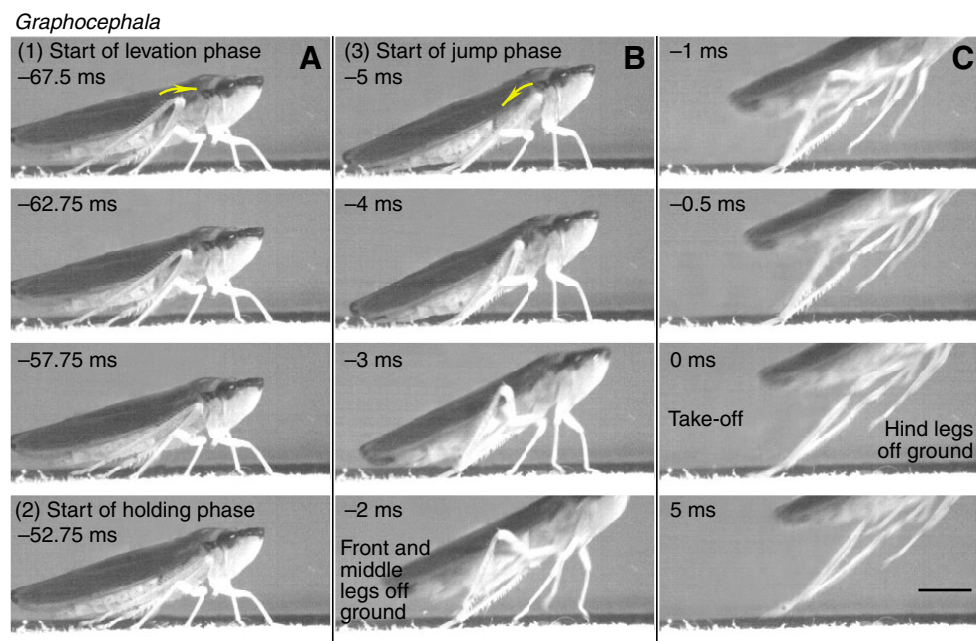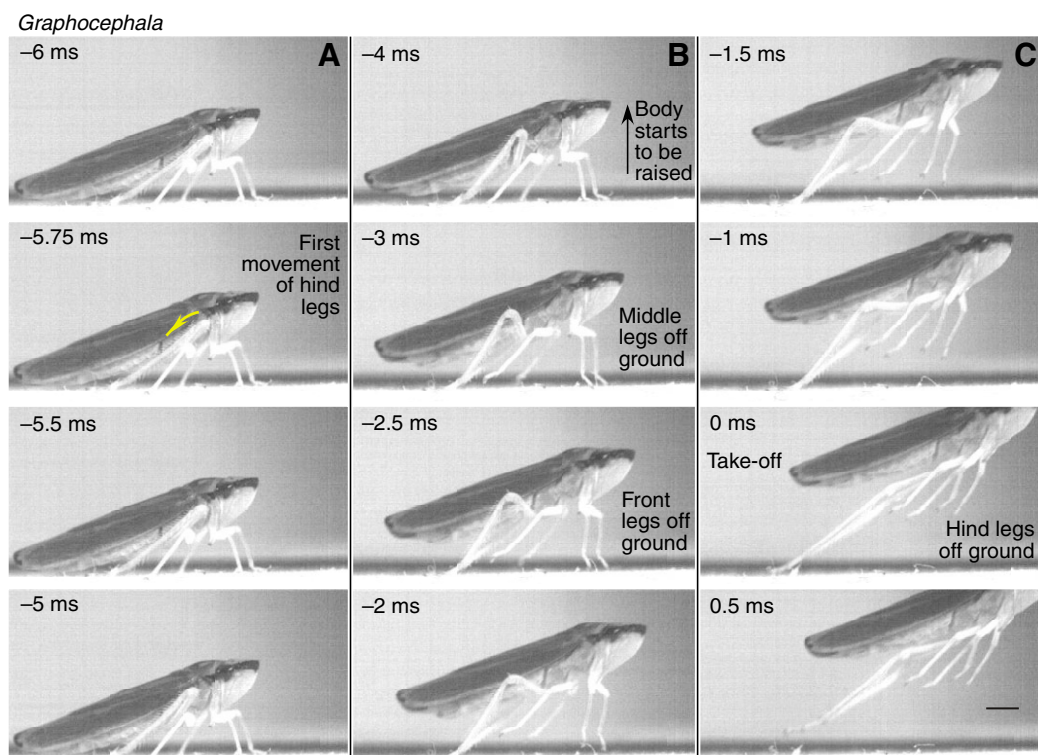Fig. 2. Images of a jump by *Graphocephala* viewed from the side, captured at 4000 frames s⁻¹ and each with an exposure time of 0.125 ms. Selected images are arranged vertically in three columns with the timing of a frame indicated relative to the frame designated as *t*=0 ms when the insect became airborne. (A) The levation phase. The hind legs were sequentially levated forwards and medially into their fully levated position. The time between the lowest frame of column A and the top frame of column B represents the holding phase, lasting 47.75 ms, during which the hind legs remained stationary in their fully levated position. (B,C) The jump phase. 5 ms before take-off, the hind legs began to depress and the downward thrust of the hind legs gradually raised the body. The front and middle legs lost contact with the ground at –2.0 ms. Scale bar, 2 mm.

Fig. 3. Sequential mages of a jump by *Graphocephala* viewed from the side, captured at 4000 frames s⁻¹ and each with an exposure time of 0.125 ms. (A) The first movement of a hind leg occurred 5.75 ms before take-off. (B) The continuing backwards movement of the femur and extension of the tibia raised the body from the ground so that first the middle legs and then the front legs lost contact with the ground. (C) Take-off was achieved when the hind legs were close to full extension. Scale bar, 2 mm.

ventrally (Fig. 1).

Second: a holding phase lasting from 10–200 ms, in which the hind legs remained stationary in the fully levated position (Fig. 2A,B). During this phase, the body angle was adjusted by movements of the front and middle pairs of legs but the hind legs remained stationary.

Third: a rapid jump phase, in which both hind legs were simultaneously depressed about their coxo-trochanteral joints and extended at their femoro-tibial joints (Fig. 2B,C). These movements of the hind legs provided the major propulsive force for the jump as the front and middle legs had left the ground before the depression of the hind legs was completed. Across all the species examined the average time from the first movement of a hind leg until take-off was 5.0±0.1 ms (*N*=138). This time therefore represents the period during which the body was accelerated to its take-off velocity. The shortest acceleration period was 2.75 ms in the best jumps by *Aphrodes* (average 4.4±0.18 ms, *N*=43) and the longest was 8 ms (average 6.4±0.21 ms, *N*=20) in *Cicadella* (Table 2).

Movements of the hind legs in jumping

The detailed movements of the hind legs powering a jump were determined by analysing sequential images taken from a side, a frontal and a ventral view (Figs 3–5).

The first movement of the hind legs in the jump phase was a depression of the trochanter about the coxa and was most obviously manifested as a backward and lateral movement of the femur (Fig. 3A, Fig. 4A). The continuing depression of the trochanter moved the femoro-tibial joint further backwards and was accompanied by a progressive extension of the tibia about the femur. These movements raised the body and resulted in the middle and front legs losing contact with the ground before the hind legs had completed their trochanteral depression and tibial extension movements and while their tarsi remained firmly placed on the ground (Fig. 3B, Fig. 4B). The hind legs continued to straighten, caused by the progressive depression of the trochantera and extension of the tibiae, and accelerated the body forwards and upwards (Fig 3C, Fig. 4C). When the hind legs were almost fully depressed extended take-off was achieved.

Viewing a jump ventrally, showed clearly the angular changes of the coxo-trochanteral and femoro-tibial joints and the simultaneous actions of both hind legs (Fig. 5). When the legs were first drawn into their fully levated positions, the tibio-tarsal joints of each hind leg touched each other beneath the ventral midline of the abdomen (Fig. 5A). From this starting position the first movement of a hind leg in the jump phase was a depression of the trochanter about the coxa and an extension of the tibia about the femur. Capturing images at 4000 frames s^{-1}, giving a time resolution of 0.25 ms, revealed that trochanteral movements of both hind legs occurred at the same time. No recordings revealed any differences in the relative timing of the movements by the two hind legs at this time resolution. While the tarsi remained at the same position on the ground, the progressive depression of the two hind trochantera about their respective coxae resulted in a backwards movement of the two femora and, together with the extension of a tibia about a femur, resulted in the acceleration of the body forwards (Fig. 5A,B). Take-off was achieved when the

trochantera were fully depressed and the tibiae almost fully extended (Fig. 5C). The two tarsi remained apposed throughout the progressive depression and extension movements and only drifted apart when they lost contact with the ground after take-off. Once airborne, the extended hind legs were trailed beneath and behind the body.

Plotting the movements of the legs and the body, as viewed from the side, against time (Fig. 6A) or as their positions on the *x* and *y* coordinates (Fig. 6B) emphasised the following features of the jump. First, the initial movement in the jump phase was a trochanteral depression by the hind legs. Second, the front and middle pairs of legs both lost contact with the ground at least 2 ms before take-off, so that the final power for the jump was delivered only by the hind legs. The time at which the front and middle legs lost contact with the ground varied from jump to jump and was correlated with the attitude assumed by the body.
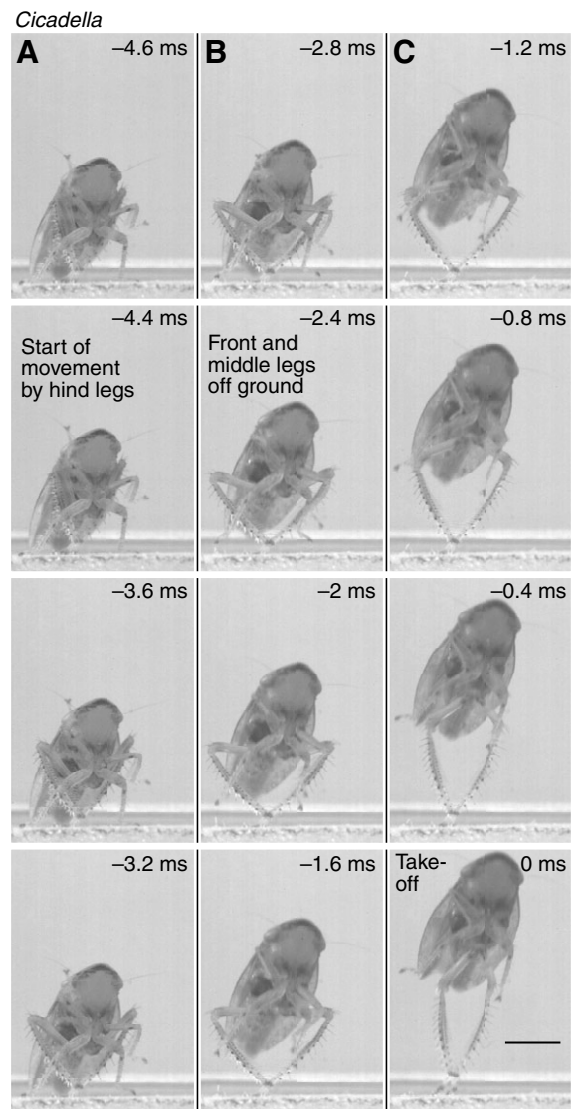

Fig. 4. Images, arranged in three columns, of a jump by *Cicadella* towards the camera, captured at 5000 frames s^{-1} and each with an exposure time of 0.05 ms. The hind legs started to move at –4.4 ms and take-off occurred in the last frame at time 0 ms. Scale bar, 2 mm.

Fig. 5. Images of *Cicadella* viewed from underneath as it jumped from the front wall of the chamber. (A–C) Sequence of images of the movements leading to take-off were captured at 5000 frames s⁻¹ with an exposure time of 0.05 ms, and are arranged in three columns. Scale bar, 2 mm.


Cicadella

In the example shown in Fig. 6, the middle legs were the first to lose contact at –3.75 ms followed by the front legs at –2.5 ms (Fig. 6A). Third, the trajectories illustrate the rotation of the femur that resulted from the depression of the trochanter (Fig. 6B). The path of the femoro-tibial joint was initially backwards relative to the body as the trochanter progressively depressed. It then moved forwards relative to the ground as the trochanteral depression and tibial extension movements accelerated the body forwards, before assuming the same trajectory as the other parts of the body after take-off. The wings did not open before the insect became airborne and thus did not contribute any force to the take-off.

Plotting the angular changes of the coxo-trochanteral, and the femoro-tibial joints from images captured from a ventral view, showed that the coxo-trochanteral joint was rotated at 44 000 deg. s⁻¹ and the femoro-tibial joint at 47 000 deg. s⁻¹ during the jump phase of the movement (Fig. 7). These plots further indicated that the movements of both joints started at the same time as each other in both *Cicadella* (Fig. 5) and *Aphrodes* (Fig. 7). In the other species the joint rotations were slower: in *Cicadella* the average values were 19 000 deg. s⁻¹ for the coxo-trochanteral joint and 20 000 deg. s⁻¹ for the femoro-tibial joint; in *Empoasca* they were 26 000 and 28 000 deg. s⁻¹, respectively; and in *Graphocephala* 21 000 and 23 000 deg. s⁻¹, respectively.

Trajectories

The angle of the body relative to the ground (Fig. 8A) varied

Fig. 6. Graphs of leg and body movements during the jump by *Graphocephala* shown in Fig. 3. (A) Six points on the legs and body (indicated in the cartoon) are plotted against time for 7 ms preceding and 3 ms following take-off. Zero on each axis represents the position of the body before any jumping movements began. The first movement of a hind leg started 5.75 ms before take-off (left black arrow and yellow bar). The middle legs lost contact with the ground 3.75 ms before take-off and the front legs 2.5 ms before take-off. (B) Sequential movements of the same points as the insect jumped through the field of view of the stationary camera. The vertical co-ordinate of a point is plotted against its horizontal co-ordinate, with each point separated by 0.25 ms in time. The horizontal arrowheads and the linking lines indicate the positions at take-off and allow the corresponding positions of these points to be read frame by frame at different times during the jump.
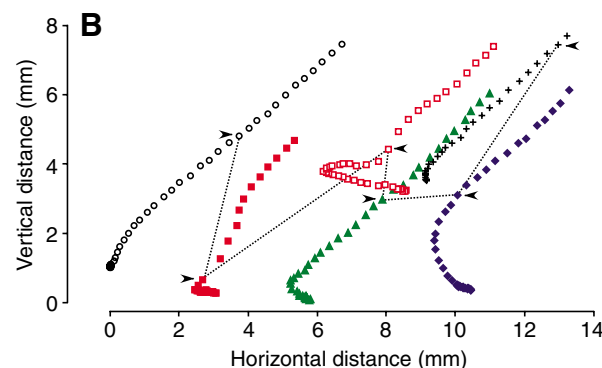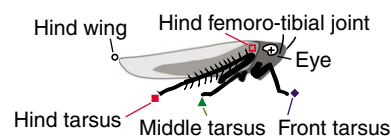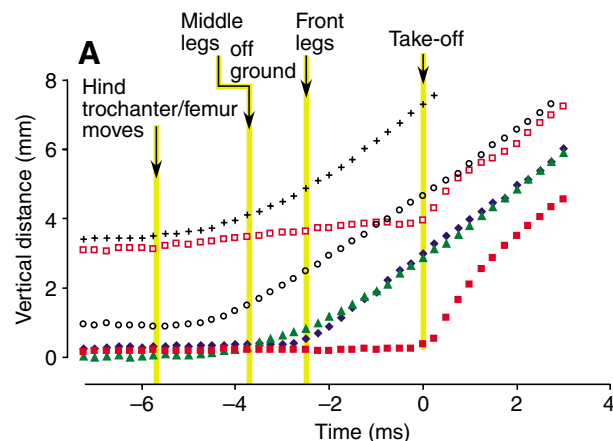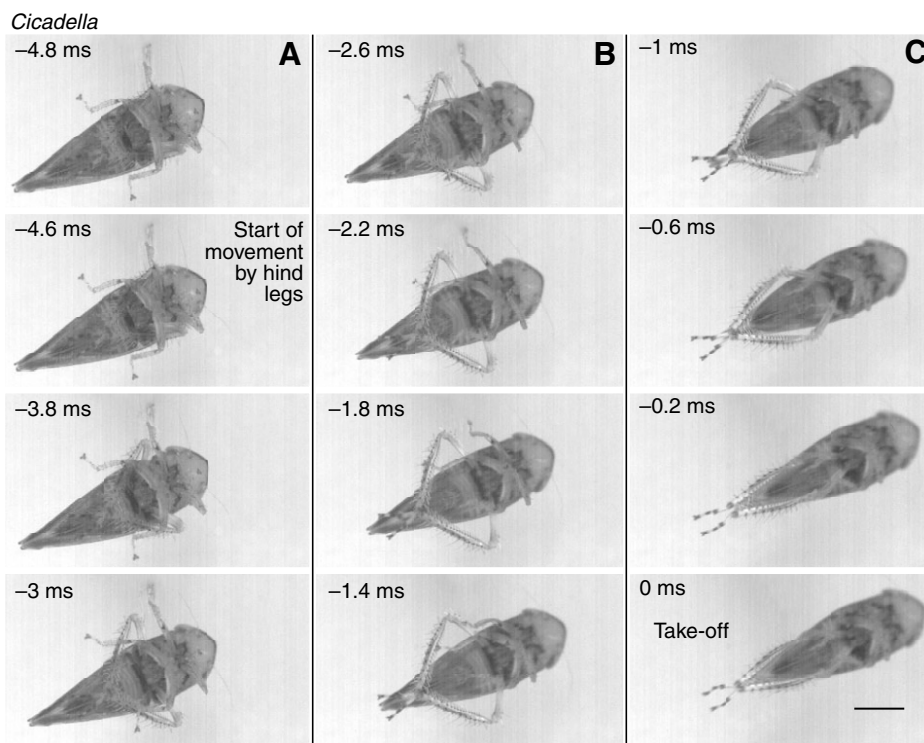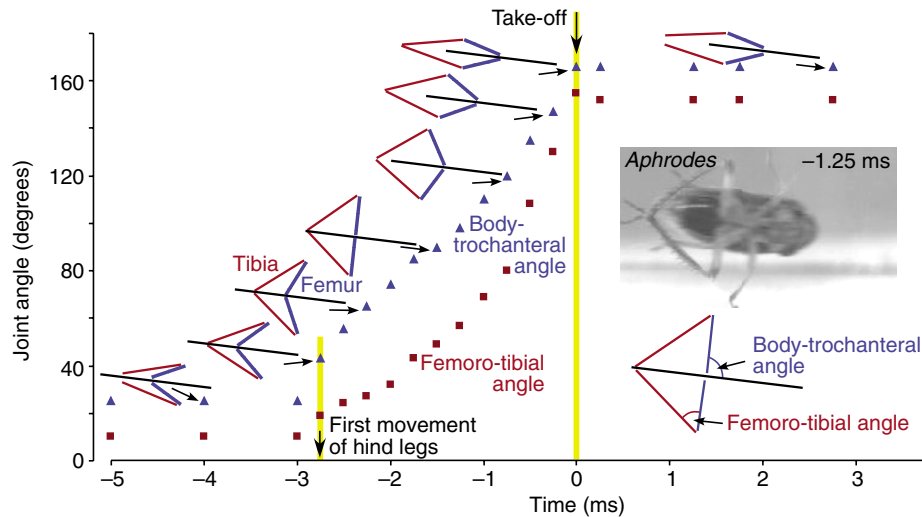
Fig. 7. Graphs of the angular changes of two joints of a hind leg during a jump by *Aphrodes*. The trochanter was progressively depressed about the coxa and the tibia extended about the femur. The first depression movement of the trochanter (left yellow bar) began at –2.75 ms before take-off (right yellow bar). The body–trochanteral angle (blue lines and triangles) was measured as the angle of the femur against the longitudinal axis of the body and therefore includes any changes in the angle between the trochanter and femur (see inset photograph and drawing). These are likely to be small relative to the changes at the coxo-trochanteral joint. The femoro-tibial angle is represented by red lines and squares and the body by black lines.
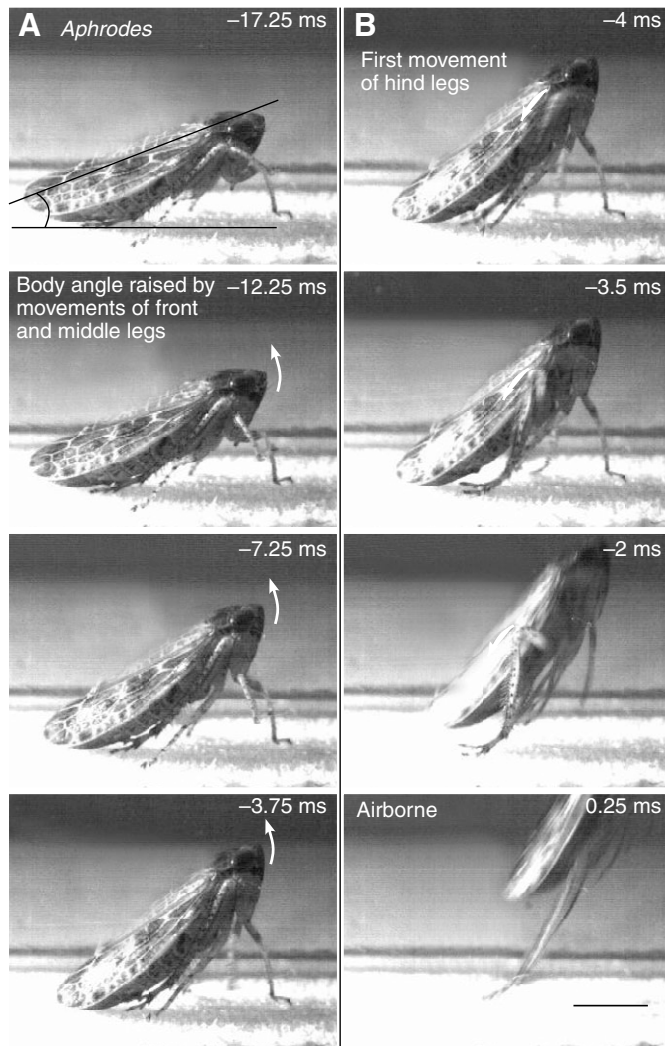

at take-off from 15.7±2.4° (*N*=10) in *Graphocephala* to 36.7±5.0° (*N*=10) in *Aphrodes*. The range of take-off angles was similarly large, 10–64°, but averages for individual species showed much smaller differences, ranging only from 29.5±3.6° (*N*=10) in *Graphocephala* to 36.7±4.4° (*N*=10) in *Aphrodes* (Table 2). Both the body angle and the take-off angle were set initially by the movements of the front and middle legs. For example, at the start of a jump by *Aphrodes*, the body was at an angle of 23° relative to the ground (Fig. 8A). Movements of the front and middle legs, but not of the hind legs, raised this angle to 42° (Fig. 8B). This set the angle at which the depression and extension of the hind legs exerted their thrust on the ground and their rapid movements resulted in a final body angle at take-off of 58° and a take-off angle of 50° (Fig. 8B).

This jump gave a clear indication of the separation of actions between the different pairs of legs; the body attitude was set initially by the front and middle legs and take-off was propelled by the hind legs. In other jumps, the front and middle legs may have contributed to the thrust for take-off, but they always lost contact with the ground a few milliseconds before the hind legs and thus did not contribute to the later stages of propulsion.

Fig. 8. The attitude of the body (see angle measured in top frame of A) is set by movements of the front and middle pairs of legs. Selected frames from a jump of *Aphrodes* viewed from the side, captured at 4000 frames s^{-1} and with an exposure of 0.25 ms. (A) During the holding phase, the front and middle legs were depressed and extended so that the angle of the body was raised from 23° to 42°. (B) The hind legs were then depressed further raising the body angle to 58° at take-off and launching the jump at a take-off angle of 50°. Scale bar, 2 mm.

Fig. 9. Jumps and wing movements by *Empoasca*. Images were captured at 1000 frames s^{-1} and an exposure of 0.5 ms, with the insect viewed ventrally. (A) A jump in which the wings were initially opened but then only flapped once the jump was complete and the insect was airborne. The images are arranged in four columns. Scale bar, 2 mm. (B) A second jump by the same *Empoasca* in which the angular changes of the coxo-trochanteral and femoro-tibial joints are plotted together with the forward movement of the body and the wing movements. The drawings are tracings from the original images to show the movements of the hind legs.
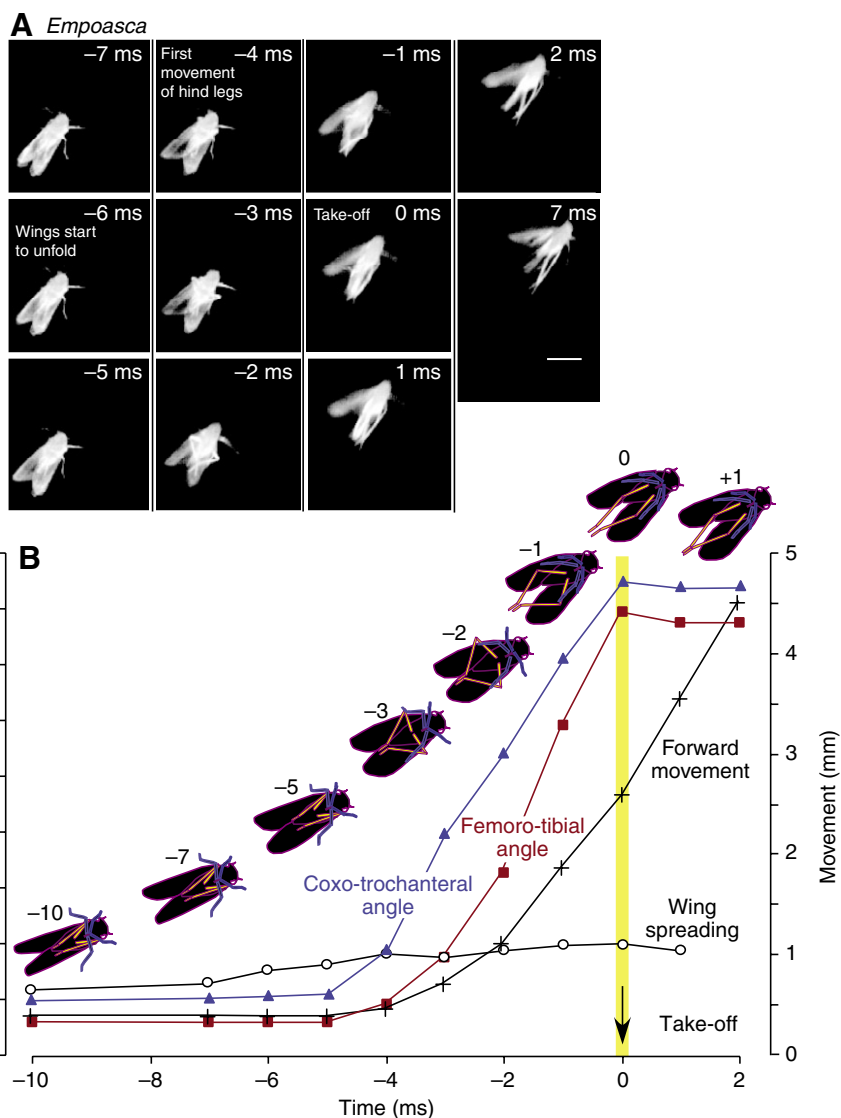
Contribution of the wings to jumping

The wings of three species (*Graphocephala*, *Aphrodes* and *Cicadella*) normally remain folded during a jump and did not open either before take-off or in the first few milliseconds when airborne. Flight was, however, frequently observed to start later in the trajectory of a jump. In these species the jump itself was therefore not assisted by movements of the wings but was nevertheless a common means of launching into flight.

By contrast, in *Empoasca*, wing movements commonly accompanied or even preceded the leg movements of a jump (Fig. 9). In the examples shown, the wings started to spread laterally 6 ms (Fig. 9A) or 7 ms (Fig. 9B) before take-off and 2 ms before the first movement of a hind leg was detected. The wings then progressively unfolded and were elevated as the trochantera of the hind legs were depressed about the coxae (Fig. 9B). At take-off, the wings were still being elevated and the first depression movement began only after take-off. The wing movements therefore allow a smooth transition from the jump to the assumption of flapping flight.

Jumping in larvae

The free-living larvae lack functional wings but nevertheless still jump. The jumps by nymphs of *Iassus*, for example, showed many of the features of jumps by the adults of the species already described (Fig. 10A–C). The acceleration for the jump was applied in 2–2.5 ms by the rapid movements of the hind legs and involved depression of the trochantera about the coxae and extension of the tibiae about the femora. A notable difference was the placement of the hind tarsi lateral to body and not touching each other beneath it as in adults (see Figs 4, 5). This was seen most clearly in jumps away from (Fig. 10B) or toward (Fig. 10C) the camera. From this lateral position, the two hind tarsi became apposed to each other only after take-off

and not during the application of thrust that powered the take-off.

Jumping performance

Jumping performance was calculated from the data obtained from the high-speed images (Table 2). *Aphrodes* achieved the highest take-off velocity calculated as the average of the distance moved in the 1 ms preceding and following take-off by a point in the middle of the body. In 10 jumps by different individuals the average value was 2.5±0.09 m s^{-1}, with the best jumps reaching 2.9 m s^{-1}. The average take-off velocities in the other species were lower, ranging from 1.1 m s^{-1} in *Empoasca* to 1.6 m s^{-1} in the heavier *Graphocephala*, though nymphs of *Iassus* achieved 2 m s^{-1}. The time from the first visible movement of the hind legs first until the insect became airborne defined the period over which the body was accelerated. The average period for all the species analysed ranged from 4.4 ms in *Aphrodes* to 6.4 ms in female *Cicadella*, with the shortest period of 2.75 ms recorded in *Aphrodes*. In the best jumps the acceleration over this period therefore ranged from 320 m s^{-2} in female *Cicadella* to 1055 m s^{-2} in *Aphrodes*. In their best jumps

these insects would thus experience a force greater than 100 *g*. The energy (0.5 mass×velocity^2) required by *Aphrodes* in its best jumps was 77 μJ, but in the much lighter *Empoasca* this fell to 1 μJ, and in the nymphs of *Iassus* to 0.01 μJ. The power output in a jump depends on the time during which the energy is expended. In the 2.75 ms that *Aphrodes* took to accelerate its body in its best jumps, the power output was thus 28 mW, but only 0.3 mW in the 4 ms that it took *Empoasca* to accelerate its body. Similarly, the force (mass×acceleration) exerted during the best jumps by *Aphrodes* was 19 mN, but was only 0.3 mN in the lighter *Empoasca*.

Fig. 10. Jumping by *Iassus* nymphs that do not have moveable wings. Images were captured at 2000 frames s^{-1} and with an exposure of 0.1 ms. (A) A jump viewed from the side. (B) A jump away from the camera. (C) A jump toward the camera. Scale bar, 2 mm.

After take-off the body was rarely observed to spin, indicating that little energy was lost by conversion to rotational kinetic energy of the body. There is still rotational kinetic energy in the legs, but calculations indicate that this is only 0.5–2.% of the total energy expended. By contrast, many jumps were assisted by flapping movements of the wings once the insect was airborne. The height or distance achieved after a jump is thus the product of the forces exerted during a jump itself and those generated by the wing movements during flight. *Empoasca* with a mass of 0.86 mg and a body length of length of 3.5 mm (Table 1) reached an average height of 47±6.3 mm (*N*=58 jumps) and a horizontal distance of 53±5.5 mm. Jumping performance declined with repeated attempts to encourage an individual to jump so that these averages underestimated jumping performance. Individual best performances were almost three times better, reaching heights of 180 mm or 51 × body length, and distances of 170 mm.

Assuming that a jump was not assisted by the wings and that the body did not experience any slowing due to wind resistance, then the height and distance achieved are given by Eqn 1 and Eqn 2:

$$s = U\cos\theta\,(2U\sin\theta\,/\,\boldsymbol{g})\,, \qquad (1)$$

$$h = (U\sin\theta)^2\,/\,2\boldsymbol{g}\,, \qquad (2)$$

where *s*=distance jumped, *h*=maximum height reached, *U*=instantaneous velocity at take-off, θ=take-off angle, *g*=acceleration due to gravity (9.81 m s^{-2}). In the best jumps, *Aphrodes* should therefore reach a height of 156 mm (or 18 times its body length) and a distance of 825 mm, *Iassus* nymphs 102 mm and 407 mm, *Cicadella* 41 mm and 243 mm, and *Graphocephala* 42 mm and 300 mm, respectively. Assuming that *Empoasca* takes off at an angle of 35°, it will reach a height of 42 mm and reach a distance of 245 mm. For *Empoasca*, these equations are a good predictor of the real height achieved in a jump but not of the distance, suggesting that the latter is more strongly influenced by flapping the wings. The wind resistance experienced by these differently sized insects, which is not considered in these equations, is likely to curtail the real distances achieved (Bennet-Clark and Alder, 1979; Vogel, 2005).

Walking

The size and the key role of the hind legs in powering jumping has an impact on other behaviour of leafhoppers, most notably walking (Fig. 11). All legs participate in walking on a horizontal surface, unlike those in froghoppers (Burrows, 2006a), and are coordinated in an alternating tripod gait. Each time that a hind leg executes a stance phase, however, the body is displaced laterally in addition to forwards. The alternate action of the two hind legs thus results in a sideways oscillation of the body so that the overall path of the insect involves rhythmical deviations to the left and to the right instead of being in a straight line. The hind legs are thus responsible
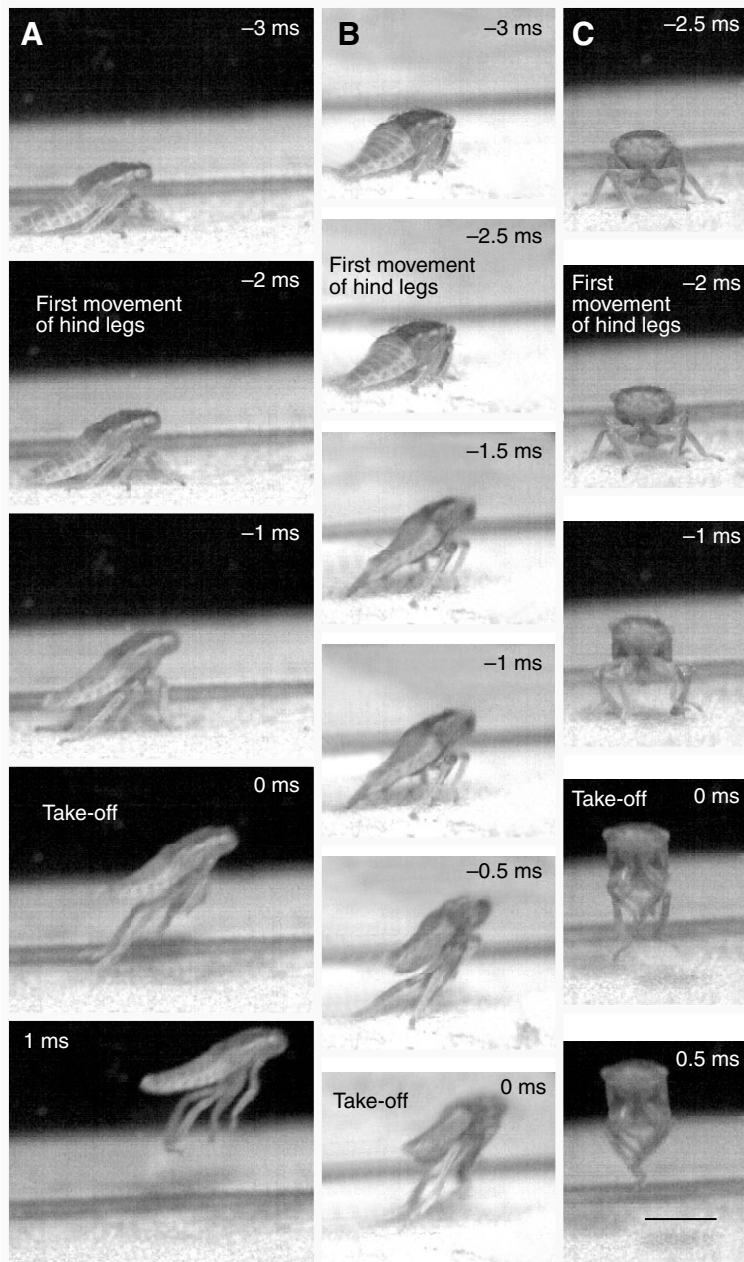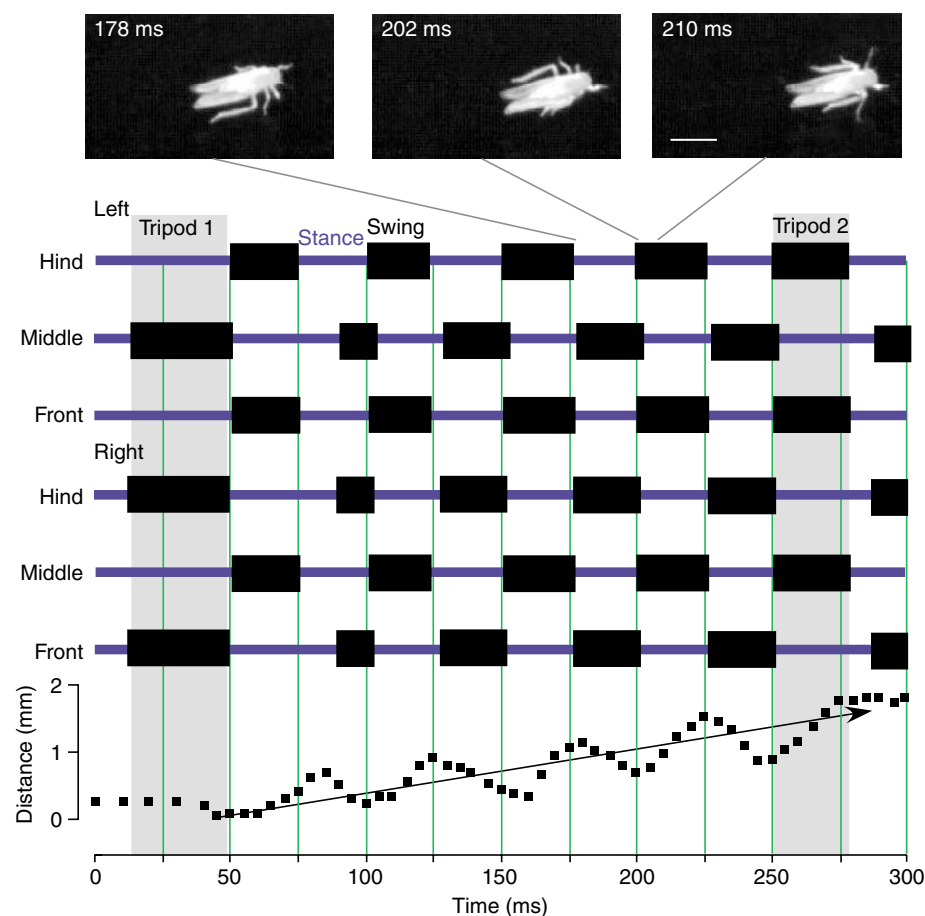
Fig. 11. Co-ordination of the legs during horizontal walking by a *Empoasca*. The legs were moved in a tripod gait with the hind legs contributing to each step. The contribution of the long hind legs imparted a sideways movement to the body so that it oscillated about the mean forward path. Images were captured at 1000 frames s^{-1}; pictures at the top show three images from one step cycle at the times indicated. Scale bar, 2 mm.

The high-speed images of leafhoppers jumping do not give any indication of whether the tibial movements are under active muscular control, or the passive result of the forces exerted by the depression of the trochantera. By contrast, in a locust the muscles generating the power for jumping are those that move the tibiae and which are located in the femora.

The design of the hind legs of leafhoppers therefore differs significantly from that of their close relatives the froghoppers in that their longer length should provide greater leverage with their acceleration, only marginally curtailed by their greater mass. The length of the hind legs also has an impact on other locomotion. When flying, the hind legs are held depressed and extended to trail behind the body and are moved in ways that suggest they are used as rudders to adjust steering. When walking horizontally, the extension of one hind leg in a stance phase pushes the body laterally, only for the movement to be reversed when the opposite high leg is extended, thereby imparting a waddling gait.

for the characteristic waddling gait of these insects when walking.

Discussion
Design for jumping

The body of leafhoppers, with their wedge shaped heads and stiff front wings, which when folded cover the thorax and the abdomen beyond its posterior extreme as a continuous smooth structure, seems ideally suited to reduce drag when jumping. The long hind legs would also seem designed to provide increased leverage for jumping. They are between 82–93% of the body length and are thus proportionately much longer than the hind legs of froghoppers (52–66% of body length) (Burrows, 2006a), almost reaching the proportionate length of locust hind legs (102–107%) but falling well short of those of bush crickets (180%) (Burrows and Morris, 2003). They are also proportionately longer than the front and middle legs by a factor of 1.9–2.9, the same as in fleas, greater than in froghoppers (factor of 1.4–1.6) but less than in grasshoppers (3.2). Their increased length is also reflected in their mass, which at 3.8% of body mass, is almost twice that of froghoppers, but much less than the whole hind legs of locusts which represent 14% of body mass (Bennet-Clark, 1975). The light weight of the hind legs of froghoppers (Burrows, 2007b), leafhoppers and presumably fleas, suggests that the force exerted by the extensor tibiae muscles is not great, and that the key movements in jumping are the depression of the trochantera about the coxae powered by muscles in the thorax.

Jumping performance

The high-speed images taken from different perspectives show that the main thrust for jumping is provided by the rapid depression of the trochantera of both hind legs at the same time. The front and middle legs adjust the take-off angle by raising or lowering the front end of the body before a jump, but as the hind legs unfurl and lift the body they typically lose contact with the ground some 2–4 ms before take-off. The movements of the hind legs in jumping occur in a distinctive pattern of three phases. First, the hind legs are moved in 15–30 ms from a standing placement lateral to the body to one directly underneath the body at the midline where the two tarsi touch each other. This involves a levation of the trochanter and the accompanying forward movements of the rest of hind leg so that the femoro-tibial joint may engage with a sculpted region of the head capsule and the femur sits in a ventral depression of the coxa. The whole hind leg is thus bounded dorsally by the body and ventrally by the front and middle legs on the same side. In the second, holding phase the hind legs remain stationary in their fully levated positions for

10–200 ms. The durations of the first two phases suggest that there is little time for contractions of the muscles to distort skeletal elements and thus store energy. In the third and final jump phase, the hind legs are rapidly depressed at the coxo-trochanteral joints and extended at the femoro-tibial joints in movements that lead to take-off. The movements in this phase last 5–6 ms on average across the different species analysed, but in the best jumps can be accomplished in 2.75 ms. This period therefore represents the time over which the body is accelerated in a jump and is up to seven times slower than the time taken by froghoppers in their best jumps (Burrows, 2006a). As a consequence, the acceleration of 1055 m s^{-2} and the peak take-off velocity of 2.9 m s^{-1} that they experience in their best jumps are less than in froghoppers (5400 m s^{-2} and 4.7 m s^{-1}, respectively).

Wing movements do not appear to assist the leg movements in jumping by leafhoppers, and indeed the free-living larvae that lack functional wings are proficient jumpers. In the adults of three species examined, the wings always remained folded during preparations for a jump and during take-off. Only in *Empoasca* did the wings unfold and elevate before take-off so that they are unlikely to contribute greatly to the forces at take-off. The jump is too rapid for a single cycle of wing movements to be completed before take-off. It is clear, however, that many jumps represent a launch into flight. The flapping movements of the wings take over from the propulsion provided by the legs once airborne, and thus contribute to the height and particularly to the distance achieved. For this reason few reliable measurements of the heights and distances achieved by jumping alone were obtained. Instead, estimates of the heights and distances that might be achieved simply by jumping and ignoring the likely considerable impediment caused by drag (Bennet-Clark and Alder, 1979; Vogel, 2005), were made from measurements of the take-off angle and velocity. These estimates suggest that in its best jumps, *Aphrodes* should reach a height of 156 mm (or 18 times its body length) and a distance of 825 mm.

The jumping performance of leafhoppers is impressive when compared to other insects. The take-off velocity is higher than in fleas and the force of 100 times body mass that is exerted is comparable (Bennet-Clark and Lucey, 1967; Rothschild and Schlein, 1975; Rothschild et al., 1972). The much heavier locusts take 20–30 ms to accelerate their body (Brown, 1967) to a comparable take-off velocity (Bennet-Clark, 1975). This analysis of the movements involved in jumping and the resulting jump performance poses a key problem. Leafhoppers and froghoppers have a similar body shape and mass, but despite having longer hind legs, leafhoppers fail to outperform froghoppers when jumping. Do leafhoppers have different mechanical features of the joints in the hind legs, different arrangements of muscles, and different neuronal strategies for activating these muscles in jumping? Alternatively do both use catapult mechanisms in which the length of the hind legs is not critical. These issues will be analysed in the accompanying paper (Burrows, 2007a).

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