

## Jumping in a winged stick insect

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### Summary

The Thailand winged stick insect (*Sipyloidea* sp.) flees rapidly from a disturbance by jumping forwards when stimulated on the abdomen and backwards when stimulated on the head. The mechanisms underlying these fast movements were analysed by measuring movements of the body and legs from images captured at 250 Hz.

A forward jump of both adults and nymphs involves movements of the abdomen and the middle and hind pairs of legs. The abdomen is raised and swung forwards by flexion at the joint with the metathorax and at the joint between the meso- and metathorax. At the same time, the tibiae of the hind and middle legs are extended and their femora depressed. The femoro-tibial joints of the legs are not fully flexed before a jump, and no structures in these joints appear to store muscular energy. The whole jumping sequence takes approximately 100 ms and results in take-off angles of 10–35° at velocities of 0.6–0.8 ms<sup>-1</sup> and with an acceleration of 10 ms<sup>-2</sup>. The abdominal angular velocity was 2000° s<sup>-1</sup> and the tip of the abdomen moved at linear velocities of some 1 ms<sup>-1</sup>, while the maximum rate of tibial extension was 4000° s<sup>-1</sup>.

Rapid backward movements result either in the collapse of the body onto the ground, with a displacement away from the stimulus of approximately half a body length, or in the propulsion of the insect off its perch. Neither movement involves curling of the abdomen.

From a horizontal posture, the forward jumps result in a displacement of a few body lengths. More lift can be generated in adults by elevating the hind wings as the abdomen is swung forwards and depressing them as the legs lose contact with the ground. In this way, jumps can lead directly to flapping flight. Take-off into flight can, however, be achieved without the abdominal movements seen during jumping.

From a vertical posture, a forward jump propels the insect upwards and backwards before it falls to the ground horizontally displaced from its perch. Backward movements result in the insect falling with little horizontal displacement from its perch.

Key words: kinematics, joint mechanics, locomotion, *Sipyloidea*, Thailand winged stick insect, *Sipyloidea* sp.

### Introduction

Insect jumping as a means of escape or rapid movement involves several different mechanisms. The most prodigious jumpers are orthopterans such as locusts, which use large, specialised hind legs to generate and then store the 9–11 mJ of energy needed to propel the body off the ground in 30 ms at a take-off velocity of 3.2 ms<sup>-1</sup> and to displace the body by as much as 1 m (Bennet-Clark, 1975; Brown, 1967). Fleas store the energy developed by large depressor muscles in the hind legs (Bennet-Clark and Lucey, 1967; Rothschild et al., 1972), springtails rapidly extend an abdominal appendage (Brackenbury and Hunt, 1993) and click beetles jack-knife their body at the junction between the pro- and mesothorax (Evans, 1972, 1973). The ant *Gigantiops destructor* jumps by rapidly extending both the middle and hind pairs of legs while simultaneously moving the gaster (part of the abdomen) forwards and holding it there during a jump (Baroni et al., 1994; Tautz et al., 1994). This moves the centre of mass, thereby ensuring that the body does not spin during a jump,

and may also provide kinetic energy to propel the body forward (Tautz et al., 1994).

Stick insects usually have an elongated body shape that closely resembles the branches of plants on which they climb, perch and feed. They respond to a threat by freezing their body position – catalepsy (Bassler, 1983; Bassler and Foth, 1982; Bassler et al., 1982; Driesang and Büschges, 1993; Godden, 1974) – enabling them to remain motionless for long periods and, therefore, to become difficult for predators to detect amongst vegetation. Nevertheless, some stick insects have active defensive displays and active escape responses. In some, the hind wings and the modified front wings are raised to increase the apparent size of the insect and to reveal previously hidden patches of colour (Bedford, 1978). These movements may be accompanied by buzzing (Rehn, 1957) or swishing (Bedford and Chinnick, 1966) sounds generated by rubbing the front and hind wings together or by rubbing the two antennae together (Henry,

1922). In other species, the hind legs are spread apart, often to reveal patches of colour, and then struck together. If a male *Onctophasma martini* is grabbed, it will curve its abdomen dorsally and forwards while the femoro-tibial joints of the hind legs are flexed (Robinson, 1968b). Males of *Eurycantha calcarata* and *E. horrida* raise their abdomen in a similar way but then evert the copulatory organ to release an odour (Bedford, 1976). They will also swing the hind legs together to trap and impale an offending object on their femoral spines. *Anisomorpha buprestoides* squirts a deterrent spray at its predators from glands in the thorax that open just behind the head (Eisner, 1965). These startle responses may grade into active escape responses. *Orxines macklotti* (*Pseudodiactina macklotti*) curls its abdomen forwards and jumps from its vertical perch before dropping to the ground (Robinson, 1968a), and the males of *Onctophasma martini* push off from their perch while the females simply drop (Robinson, 1968b). *Metriotes doicles* and *Bacteria ploiaris* also jump (Robinson, 1969). The net result is a backward movement because the common posture is vertical with the head pointing upwards.

All the descriptions of these escape movements of stick insects have been brief and preliminary. We have, therefore, used high-speed imaging to analyse the detailed movements involved in escape responses of the Thailand winged stick insect *Sipyloidea* sp. This stick insect has an elongated body shape with long thin legs and an ability to show catalepsy, but has an unusual mechanism of jumping. We show that it jumps forwards from a horizontal stance by flicking its abdomen forwards and then backwards while extending the middle and hind pairs of legs. From a vertical posture, a jump using the same movements launches it into a backward and downward movement. In the winged adults, jumping may propel the animal into flapping flight.

### Materials and methods

Stick insects were obtained from Small Life Supplies (Bottlesford, Nottinghamshire NG13 0EL, UK) and then bred in our laboratory and fed bramble (*Rubus fruticosus*) leaves. The species has not yet been described but belongs to the genus *Sipyloidea* (Order: Phasmida; Family: Heteronemiidae; Subfamily: Necroschiinae) and is currently called *Sipyloidea* sp. 'Thailand 8', the Thailand winged stick insect (J. Marshall, personal communication).

To measure the distribution of mass within different parts of the body, adult males and females were weighed, frozen and then reweighed to check that there had been no change in mass during the freezing process. Body parts were removed sequentially and the carcass reweighed at each stage. Body length and the lengths of the different segments of the three pairs of legs were also measured and compared with data for other stick insects and selected orthopterans (Burrows and Morris, 2001). The resting posture was observed in large cages containing branches of bramble. Behavioural responses to an initial tactile stimulus to the abdomen and a second stimulus

applied 5 s after the response to the first had stopped were analysed in the same surroundings. Tactile stimuli were applied to the head in a separate series of experiments.

Jumps were induced by a light touch with a fine paint brush or by gently tapping a 20 mm×70 mm Styrofoam platform raised on a pillar some 200 mm from the bench. The unrestrained insect stood on the horizontal or, when rotated by 90°, the vertical surface of this platform. Images were captured directly to a computer with a Redlake Motionscope (Red lake Imaging, San Diego, CA, USA) at a rate of 250 Hz and with an exposure time of 1/1000 s. Selected images were analysed with the Motionscope camera software (Red lake Imaging) to obtain the coordinates of the various parts of the body and legs. These data were then imported into Excel (Microsoft), where angles were calculated. Seventy-seven forward jumps from a horizontal starting posture by 20 stick insects, 40 jumps from a vertical posture by 10 insects and 21 rapid backward movements by 14 insects from a horizontal posture in which the take-off trajectory was at right angles to the optical axis of the camera were captured and analysed. 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 leads to error in measurements of the absolute femoro-tibial angle, but the analyses of this joint are focused on its angular changes during a jump. We also estimate that the measurements of take-off velocity from the frame rate we used (250 Hz) could lead to an error of  $\pm 0.05 \text{ m s}^{-1}$  and that this will carry forward into other calculations.

## Results

### Body structure

*Sipyloidea* has a thin and elongated body with a head that is the same diameter as the body and long antennae of similar length to the body (Fig. 1A). Females were more than five times heavier than males; females weighed  $924 \pm 37.8 \text{ mg}$  ( $N=18$ ), males  $164 \pm 4.6 \text{ mg}$  (means  $\pm$  S.E.M.,  $N=10$ ) (Fig. 1B). Similarly, body length (head to tip of abdomen) was greater in females than in males: females measured  $92 \pm 0.9 \text{ mm}$  ( $N=13$ ), males  $65 \pm 0.5 \text{ mm}$  (means  $\pm$  S.E.M.,  $N=10$ ) (Fig. 1C). In females, the mass of the abdomen comprised 44 % of the total body mass and was approximately five times the mass of all its legs; in males, the mass of the abdomen comprised 35 % of body mass and was almost twice the mass of all the legs (Fig. 1D,E). The thorax can be flexed dorsally at the joint between the meso- and metathoracic segments, and the abdomen can be curled dorsally by movements at the joint with the metathorax and at each abdominal segment.

Only the adults have wings. The hind wings are long (50 mm in females, 35 mm in males), whereas the front wings are short (8 mm in females, 5 mm in males). Males could gain height in flapping flight, but the flights of the heavier females were infrequent and usually resulted in a loss of height.

The three pairs of legs are all long and thin. The front and hind pairs of legs are similar in length and the middle legs slightly shorter so that the ratio of femoral lengths is

(front:middle:hind) is 1:0.7:1. In males, the total length of either a front or a hind leg was 68% of the body length, and in females it was 50%. The front legs frequently did not support the weight of the body and were instead often extended anteriorly off the ground (Fig. 1A). The femur of a hind leg was approximately 8% larger dorso-ventrally than the mesothoracic femur, but no differences were apparent in the structure of the femoro-tibial joint compared with the other legs. There are no prominent semi-lunar processes, but there are curved grooves on both the medial and lateral surfaces of the cuticle. The extensor and flexor tibiae muscles of both meso- and metathoracic legs insert on similar sites on the dorsal and ventral surface of the tibia respectively.

*Resting posture*

To determine the orientation of the body normally adopted by the stick insects, observations were made of two cages each containing 30–40 insects. The undisturbed positions adopted by large nymphs or adults fell into four broad categories (Fig. 2A): (i) vertical, head-up, perched on a twig or the side of the cage with the body's long axis perpendicular to the floor and the head pointing upwards; (ii) vertical, head-down, as for vertical, head-up, but with the head pointing downwards; (iii) horizontal, upright, standing on the floor or a twig with the body's long axis parallel to the floor; and (iv) horizontal, upside-down, upside-down on the ceiling of the cage with the body's long axis parallel to the floor.

A chosen posture could be

maintained for long periods, often with no apparent movement. Most male and female adults and nymphs tended to assume the first posture. Adult males were found upside-down on the ceiling more frequently than females or nymphs. We selected two specific starting postures to analyse jumping movements because it was from these that jumps were most frequently initiated: (i) horizontal and upright and (ii) vertical and head-up.

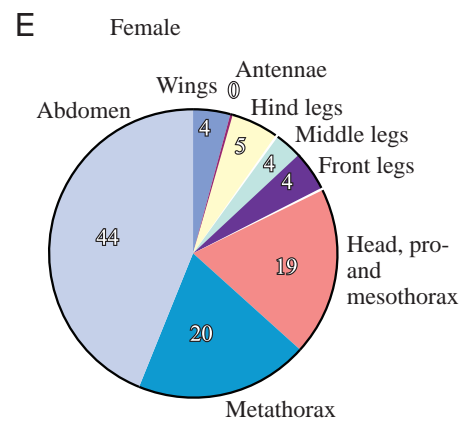
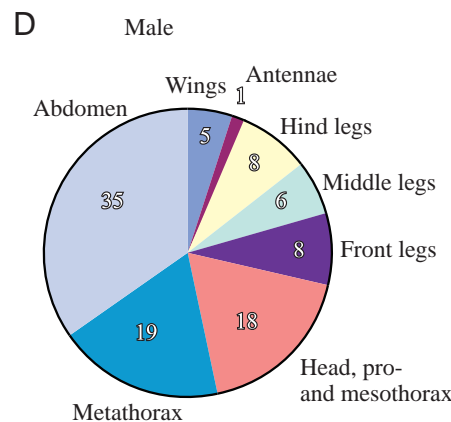
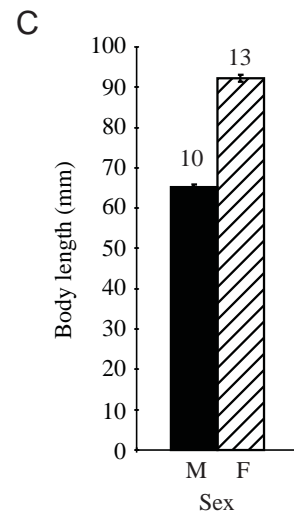
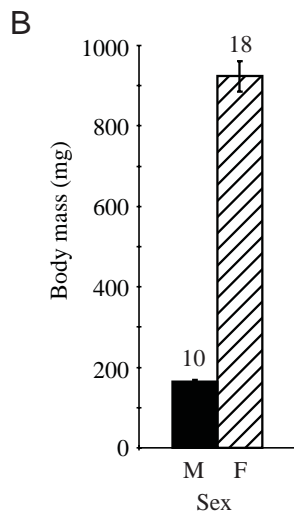
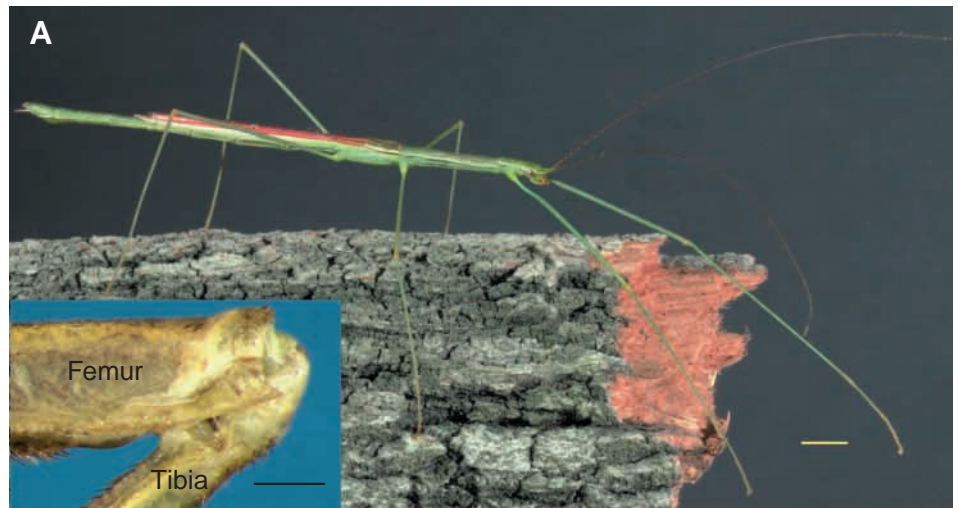


Fig. 1. Morphometry and mass of the body. (A) Photographs of an adult male *Sipyloidea* to show the elongated body and long thin legs. Scale bar, 5 mm. The inset shows a close-up of the femoro-tibial joint of a hind leg, which lacks any clear specialisations for jumping. Scale bar, 0.5 mm. (B,C) Bar charts showing the dimorphic body mass (B) and body length (C) of adult males (M) and females (F). Values are means  $\pm$  S.E.M. Values of N are given on the graphs. (D,E) Pie charts of the distribution of mass in different parts of the body (as a percentage of total body mass) in three males (D) and six females (E).

*Avoidance and escape movements*

Tactile stimulation caused the stick insects to respond in different ways (Fig. 2B–D), with some responses more common than others, and there was evidence of differences between adult males, adult females and nymphs. The responses to stimulation of the abdomen were categorised as follows: (i) freeze/no response, no overt movement and resting posture maintained; (ii) withdraw, rapid retraction of the legs and forward curling of abdomen, often holding it in this flexed position; (iii) walk, walking for two or more steps away from the point of stimulation; (iv) jump, rapid flicking of the abdomen accompanied by extension of the middle and hind legs, resulting in a jump; and (v) fly, adults opened their wings and took off with or without a preceding jump.

The most frequent response of adult females to both the first and second stimulus was rapid withdrawal and curling of the abdomen. Their next most common response to the first stimulus was to freeze and, to the second, to walk away (Fig. 2C). Males and nymphs froze, withdrew or walked away from the first stimulus but more frequently walked away from the second stimulus. Jumping was more common in response to the second stimulus for all three groups. Only adult males took off into flapping flight when stimulated. On the assumption that the order of activity was represented by the sequence freeze<withdraw<walk<jump<fly, responses of all insects to the second stimulus tended to be more active than those to the first (Fig. 2D).

Tactile stimuli to the head led to two types of rapid backward movement. First, from a horizontal position, the body moved backwards, collapsing progressively so that the abdomen came to rest on the

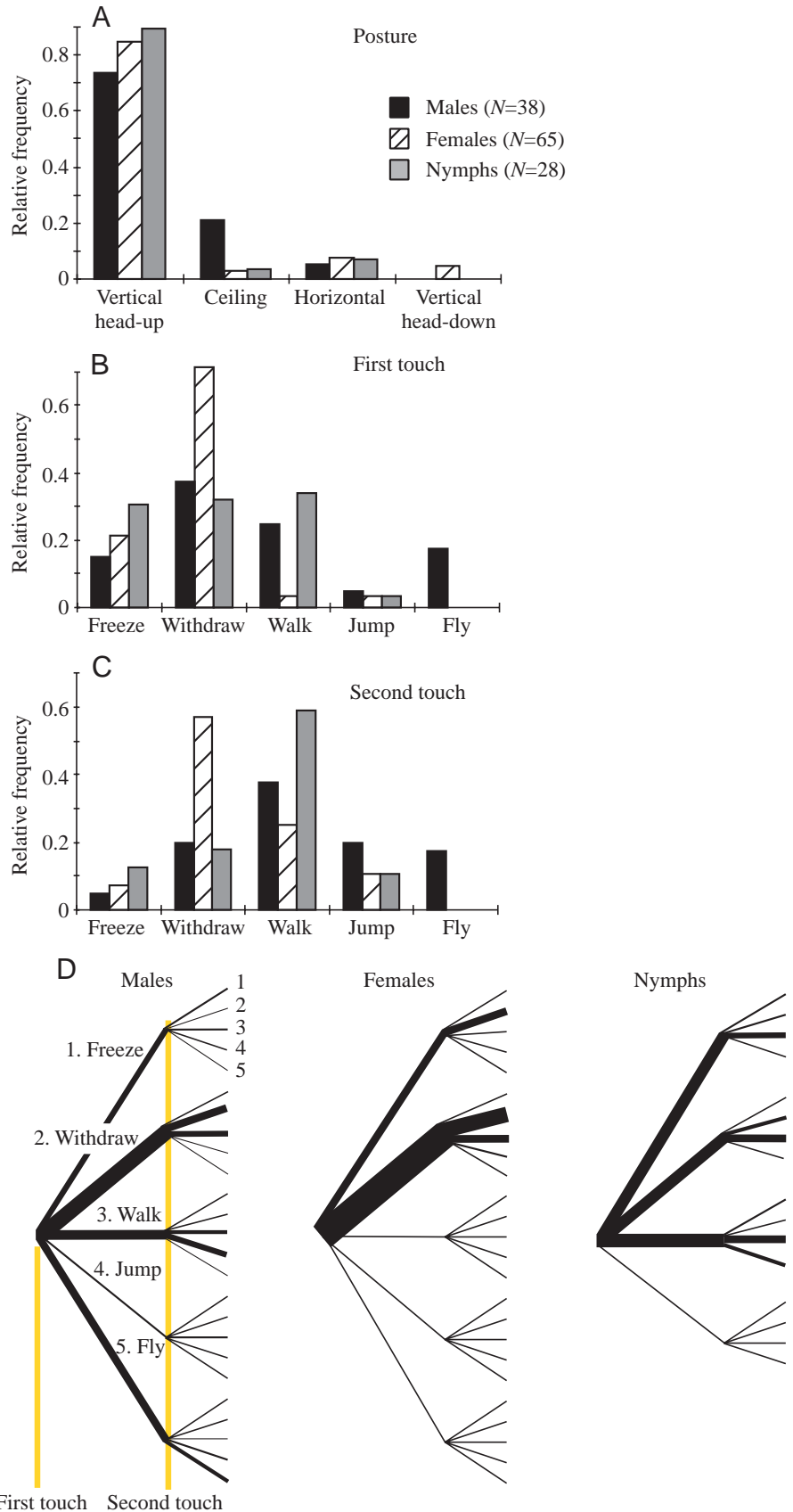


Fig. 2. Resting posture and responses to tactile stimulation of the abdomen. (A) Histograms of the different postures adopted by nymphs, by adult males and by adult females. (B) The responses of the same three groups of insects to an initial touch to the abdomen. (C) The responses to the same stimulus delivered 5 s after the preceding response had stopped. (D) Choice trees of the responses to touch; data as in B and C. The five choices made by adults are shown but, because nymphs cannot fly, they can make only four choices. The thickness of a line represents the frequency with which that choice was made. Forty adult males, 28 adult females and 56 nymphs were used.

ground with the head displaced from its original position by approximately half a body length. Second, the body height could be maintained so that the backward thrust of the legs launched the insect into a backwards jump.

To understand the movements underlying rapid jumping, high-speed images of the behaviour were captured and analysed.

### Jumping

Both nymphs and adults jumped. Two movements appeared to contribute to a forward jump; first, a forward and then a backward flick of the abdomen caused by flexion at the joint between the meso- and metathoracic segments and at the joint between the metathorax and the abdomen; second, extension of the femoro-tibial joints and depression of the femora of the middle and hind legs. In some jumps by adults, the wings were also unfurled and then flapped as the insect launched into flight.

Before initiating a jump, the thorax and abdomen were held straight and horizontal with the weight of the body apparently supported largely by the middle and hind legs. The start of the jump was marked by the beginning of a forward curling of the abdomen and by initial movements of the femoro-tibial joints of the hind and middle legs. The abdomen was flicked forwards in 60–80 ms through angles of 80–90° by flexion at the joints between the meso- and metathorax and between the metathorax and abdomen. The femoro-tibial joints of the hind and middle legs were not fully flexed in preparation for jumping, and their starting angle was variable. Frequently, the front legs had no contact with the ground throughout a jump and were extended in front of the body (Fig. 3).

In the jump of a nymph illustrated in Fig. 3, the initial movement was a flexion of the joint between the meso- and metathoracic segment, followed some 15 ms later by a flexion at the joint between the metathorax and the abdomen (Fig. 3A–C). The forward abdominal movement lasted 60 ms, during which the joint between the meso- and metathorax moved through 40° and that between the metathorax and abdomen moved through 35°, each joint reaching maximum angular velocities of 600° s<sup>-1</sup>. This resulted in the tip of the abdomen moving 32 mm dorsally relative to the joint with the metathorax and 57 mm relative to the ground at a linear velocity of 0.6 m s<sup>-1</sup> and a maximum angular velocity of 2000° s<sup>-1</sup>. The abdomen reached its maximal forward excursion some 10 ms before the hind legs had extended fully and as the middle legs lost contact with the ground. It then reversed its motion as the body started to move forwards for the last 20 ms preceding take-off.

As the abdomen started to move forwards, the hind legs flexed at their femoro-tibial joints so that the body was lowered and moved backwards. This flexion of the hind legs could be due either to an active contraction of the leg muscles or to a passive reaction to the forces generated by the abdominal movement. The body does not, however, collapse onto the substratum, implying that some opposing force is generated by the legs. The tibia of the hind legs started to extend and the femora of the middle legs were depressed some 20 ms before the abdomen reversed direction. The body was lifted by as

much as 10 mm or 77% higher than the resting posture, as measured at the mesothoracic coxae 10 ms after the reversal of the abdominal movement. Complete extension of the femoro-tibial joint of a hind leg in the jump took 30 ms, with maximum angular velocities of 4000° s<sup>-1</sup>. The middle legs lost contact with the ground first, followed 10 and 30 ms later by the hind legs. The insect became airborne 80 ms after the initial abdominal movement with a take-off velocity of 0.8 m s<sup>-1</sup>. The mean acceleration during the jump was some 10 m s<sup>-2</sup>.

The translational kinetic energy ( $E_k$ ) of the jump was 86 μJ, as given by the formula  $E_k = mV^2/2$ , where  $m$  is the body mass in kg and  $V$  is the take-off velocity in m s<sup>-1</sup>. Rotational kinetic energy was negligible since the insect did not spin once airborne. The total energy required for the jump is the sum of  $E_k$  at take-off and the potential energy  $E_p$  due to height gain at take-off.  $E_p = m^1gh$ , where  $m^1$  is the mass of body in kg (not including the legs since these are still in contact with the ground),  $g$  is the acceleration due to gravity and  $h$  is the height gained until take-off. For this nymph,  $E_p \approx 10 \mu\text{J}$  (assuming that 80% of the body mass resides outside the legs), so that the total energy required was approximately 96 μJ. The mean power output was estimated to be almost 1 mW by taking the energy expenditure over the duration of the jump. The trajectory of the body at take-off was almost parallel with the ground, so that the displacement was away from the platform and then downwards.

### Jumping performance in different animals

The mean time during which the body of either males or nymphs was accelerated in jumping was 102 ± 5 ms (mean ± S.E.M.,  $N=18$ ), measured from the first visible movement to when the insect was airborne. The maximal excursion of the abdomen also varied in different jumps, ranging from 65° (see Fig. 3) to 110° (see Fig. 5). Similarly, the femoro-tibial joints of the hind legs could begin at a flexed angled or could be almost fully extended at an angle of 130° (see Fig. 5). In different jumps by the same or different insects, the movements of the different legs were not always closely synchronised. For example, one tibia of a pair of legs could extend before the other, and the hind legs could leave the ground before the middle legs. Some insects could jump from a prone, cataleptic posture in which they lay on the ground with the antennae, front and middle legs extended forwards and parallel with the long axis of the body and the hind legs extended backwards. From this position, the abdomen was flicked forwards and the femora of the middle legs were depressed, resulting in the body being raised and accelerated forwards. The hind legs were already fully extended and did not appear to contribute to the movement.

The mean take-off velocity in all nymphs and adult males analysed was 0.6 ± 0.03 m s<sup>-1</sup> ( $N=18$ ), estimated as the mean velocity for the last 24 ms (six frames) before leaving ground. The angle of the anterior thorax relative to the horizontal just before take-off was 5 ± 0.9° ( $N=16$ ), and the take-off angle was low, ranging from 10 to 35° (means ± S.E.M.,  $N=18$ ). The forward and horizontal displacements of the body during a

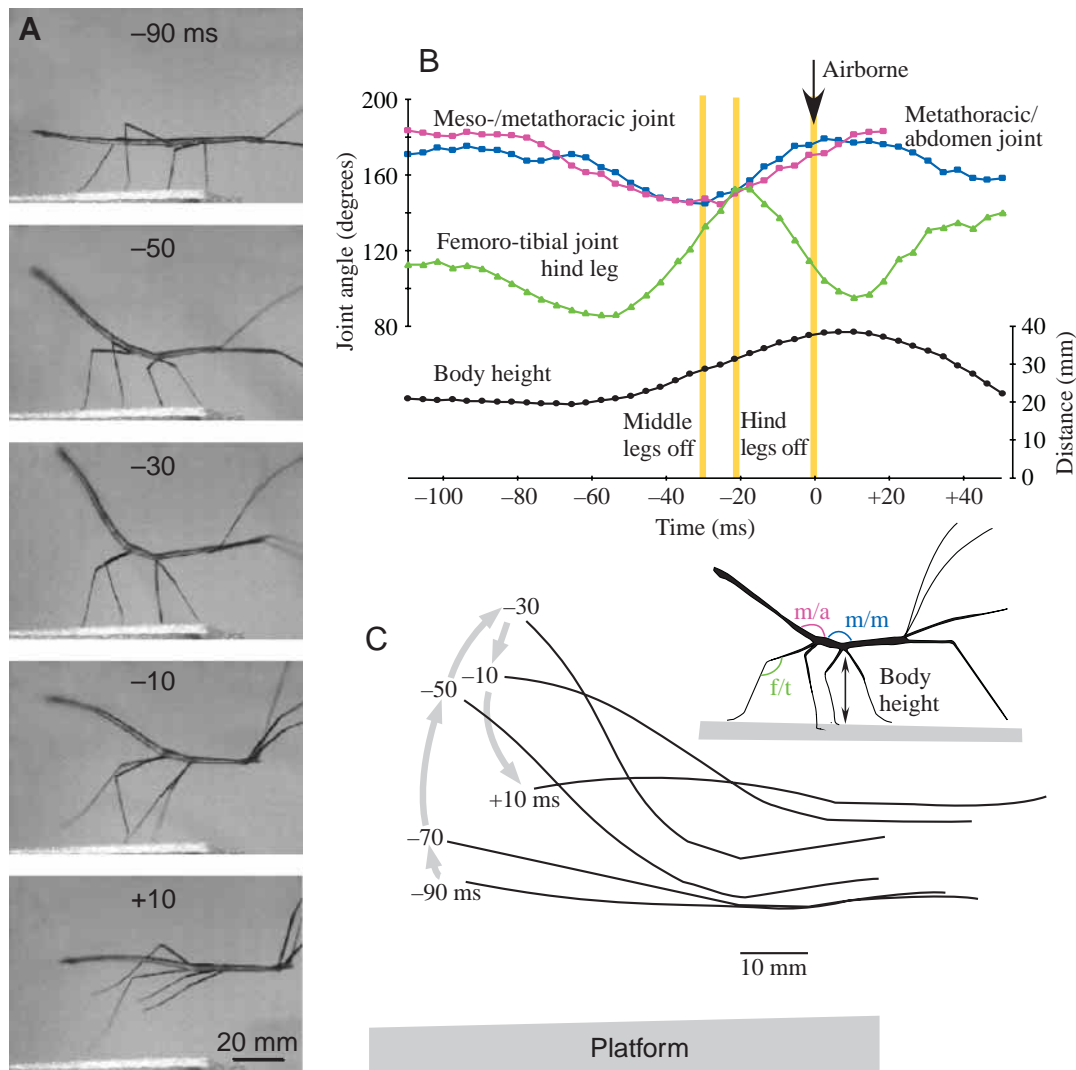


Fig. 3. A jump by a nymph from a horizontal stance. (A) Selected images from a jump captured at 250 Hz. The timing of the images refers to the graphs in B and the outlines in C. Take-off occurred at 0 ms. (B) Graph of the changes in angle of the joints between the meso- and metathorax (m/m in the inset diagram of the insect), between the metathorax and abdomen (m/a) and between the femur and tibia (f/t) of a hind leg. The change in height of the mesothoracic coxa above the ground is also plotted (Body height). Each point is measured from contiguous images separated in time by 4 ms. The vertical yellow bars indicate when the legs lost contact with the ground and when take-off occurred at 0 ms. The same colour coding is used in subsequent figures. (C) Tracings of the movements of the head, thorax and abdomen during the jump. The jump trajectory was forwards and downwards with a take-off velocity of  $0.8 \text{ m s}^{-1}$ .

jump were usually no more than a few body lengths. Few jumps that were not assisted by wing movements led to a gain in height, but rather resulted in a dive from the platform away from the stimulus and, thereby resulting in a rapid displacement of a few body lengths away from a potentially threatening stimulus.

#### *Jumping and abdominal movements*

The movements of the abdomen and their relationship to the posture and movement of the body were readily seen when individual points on the body were plotted and superimposed on one image of an insect captured during a jump (Fig. 4A). As the tip of the abdomen moved upwards and forwards, the whole body moved backwards. This was apparent as an initial

backward movement of the joint between the metathorax and abdomen and the joint between the meso- and metathorax and by the position of the head. The legs sometimes flexed so that the initial movement of the whole body was also slightly downwards in addition to backwards. As the abdomen reached its most anterior position and slowed, the whole body began to move forwards, and the velocity of this forward movement continued to increase as the abdomen reversed its movement and moved backwards.

Changes in the position of the centre of mass during a jump were calculated and superimposed on plots of the movements of the abdomen tip and the meso/metathoracic articulation (Fig. 4B). The calculation assumed that 80% of the body mass was in parts of the body other than the legs (Fig. 1D,E) and

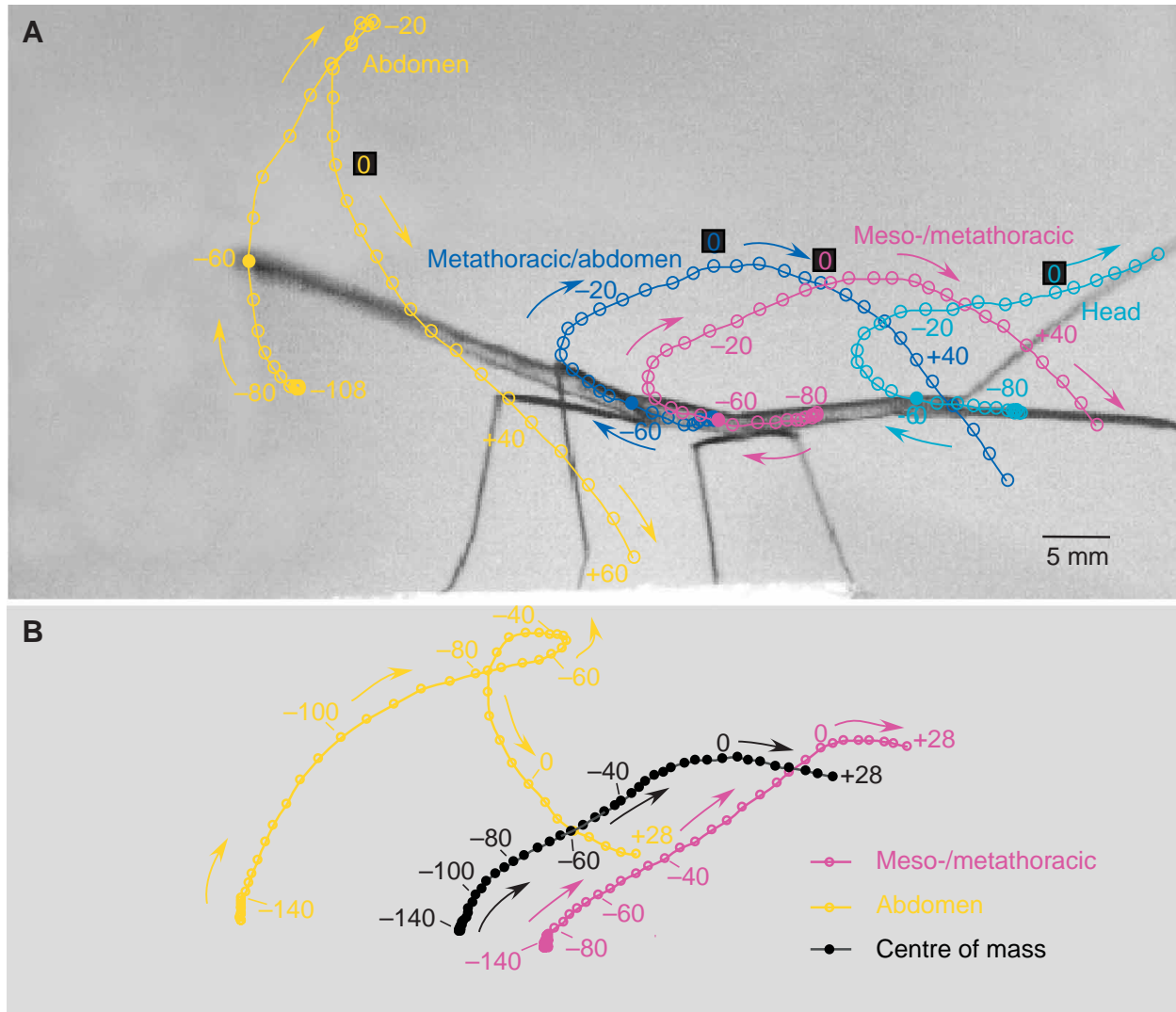


Fig. 4. Movements of the body during jumping. (A) A single frame at time  $-60$  ms is shown from the jump by a nymph starting at  $-108$  ms and ending at  $+60$  ms with take-off at  $0$  ms (highlighted in black boxes) and with each frame separated by  $4$  ms. The positions of four fixed points on the body are superimposed onto this frame: the tip of the abdomen (yellow), the joint between the metathorax and abdomen (dark blue), the joint between the meso- and metathorax (pink) and the position of the head (light blue). As the abdomen is thrust upwards and forwards, the insect rocks backwards. When the abdomen reaches the peak of its forward movement and reverses to move backwards, the body is accelerated forwards. The take-off trajectory is forwards and downwards. (B) Changes in the centre of mass of a male during a jump plotted in relation to the movements of the tip of the abdomen and the joint between the meso- and metathorax. The sequence lasts from  $-140$  to  $+28$  ms, with take-off at  $0$  ms. At  $-44$  ms, the middle legs are fully extended; at  $-16$  ms, both hind legs are fully extended. The scale is the same as in A.

took a weighted average of the positions of the main three body regions (the head plus pro- and mesothorax, the metathorax and the abdomen) during a jump. In the normal resting posture, the centre of mass lies posterior to the metathoracic coxae, approximately 12% along the length of the abdomen. As the abdomen was swung forwards between 140 and 50 ms before take-off, the position of the centre of mass also moved forwards and upwards so that it came to lie above and just behind the articulation of the mesothorax with the metathorax. The abdomen was then swung backwards so that for the last 40 ms before take-off the centre of mass moved backwards relative to the articulation between the meso- and metathorax. This means that, at take-off, the centre

of mass was behind and just below the articulation between the meso- and metathorax. The insect did not spin when it became airborne, indicating that the forces at take-off were acting through the centre of mass.

#### Jumping and flying

Adult males jumped using characteristic abdominal flicking movements and leg movements to launch themselves into flight (Fig. 5A,B). The hind wings began to open and elevate as the body first flexed at the joint between the meso- and metathorax. The elevation continued as the abdomen was thrust forwards by a  $70^\circ$  flexion at the joint between the metathorax and abdomen that lasted 60 ms at a maximum

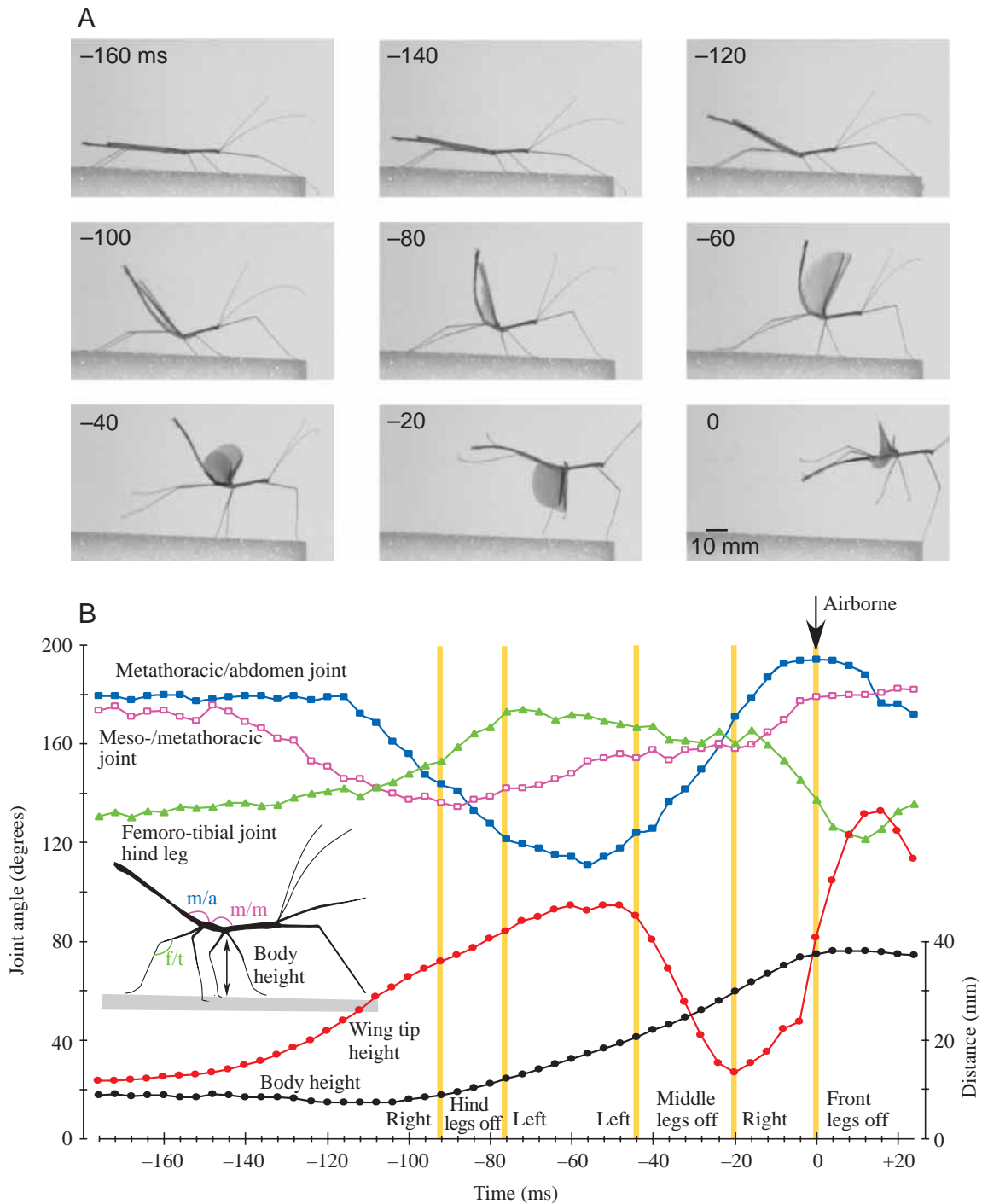


Fig. 5. An adult male jumping and launching into flapping flight. (A) Selected images from the jump sequence. The abdomen is curled forwards as the wings are elevated and then moves backwards as the wings are depressed. (B) Graphs of the changes in the angles of the joints between the meso- and metathorax (m/m), between the metathorax and abdomen (m/a) and between the femur and tibia (f/t) of a hind leg. The height of the tip of a hind wing and the height of the body above the ground are also plotted. The take-off velocity was  $0.6 \text{ m s}^{-1}$  at an angle of  $10^\circ$ , so that the trajectory was forwards and upwards.

angular velocity of  $1800^\circ \text{ s}^{-1}$ , and with the tip of the abdomen moving at a linear velocity of  $0.9 \text{ m s}^{-1}$ . During this time, the femoro-tibial joint of one of the hind legs, having started from an initial angle of  $130^\circ$ , extended by only a further  $20^\circ$  before this leg lost contact with the ground. Both hind legs left the

ground before the wings reached their most elevated position. The wings then started to depress, the abdomen reversed its direction to move backwards and one of the middle legs lost contact with the ground. When wing depression was complete, the other middle leg lost contact with the ground, and the insect



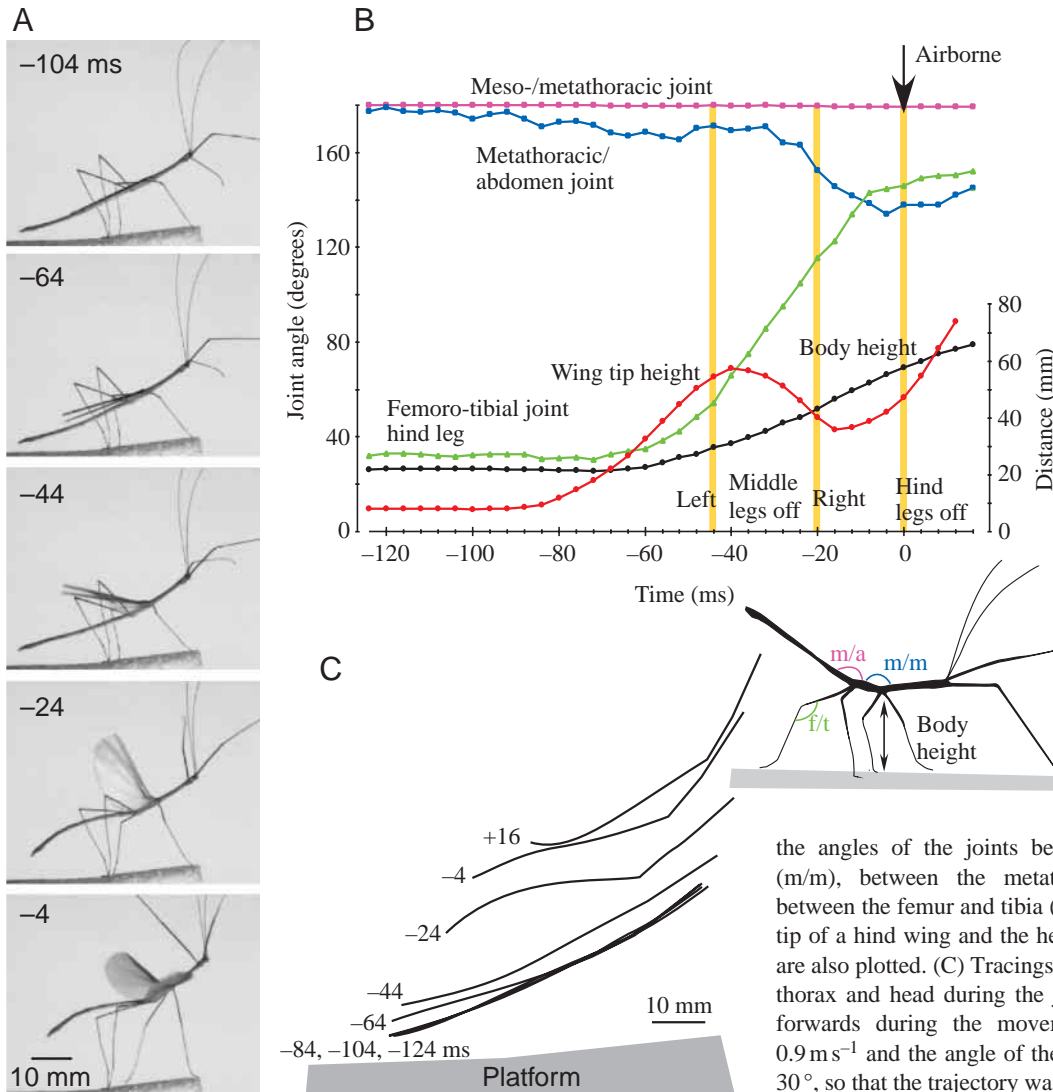


Fig. 6. A male taking off and flying without jumping. (A) Selected images of the take-off starting from an initial position in which the long axis of the body is inclined upwards by  $25^\circ$ . (B) Graphs of the changes in the angles of the joints between the meso- and metathorax (m/m), between the metathorax and abdomen (m/a) and between the femur and tibia (f/t) of a hind leg. The height of the tip of a hind wing and the height of the body above the ground are also plotted. (C) Tracings of the movements of the abdomen, thorax and head during the jump. The abdomen is not flicked forwards during the movement. The take-off velocity was  $0.9 \text{ m s}^{-1}$  and the angle of the thorax relative to the ground was  $30^\circ$ , so that the trajectory was forwards and upwards.

became airborne 150 ms after the start of all these movements with a take-off velocity of  $0.6 \text{ m s}^{-1}$  and at a shallow take-off angle of  $10^\circ$ . The translational kinetic energy of the jump was  $25 \mu\text{J}$ . Repetitive flapping of the wings at a frequency of approximately 14–15 Hz enabled the insect to continue gaining height. In jumps by males that were wing-assisted in this way and led directly to flapping flight, the result was a gain in height; in the larger and heavier females, the trajectory was downwards, even though the wings were flapped. In the wing-assisted jumps analysed, the angle of the anterior thorax relative to the horizontal just before take-off and when the wings were fully elevated was  $7 \pm 1.6^\circ$  (mean  $\pm$  S.E.M.,  $N=9$ ) and was therefore similar to that in jumps that did not involve the wings.

#### Take-off and flying without jumping

Adult males could take off and fly without launching themselves by jumping (Fig. 6A–C). The first movement was elevation of the hind wings, and it was only when this was

half-completed that the tibiae of the hind legs began to extend. As the hind wings were elevated further, the femora of the middle legs were depressed, the tibiae were extended and the body was elevated further. No movements of the abdomen occurred until the wings began to depress. No change occurred in the angle between the meso- and metathorax, but a flexion at the joint between the metathorax and abdomen resulted in a small dorsal curvature replacing the formerly ventral curve. This curvature increased until midway through the second cycle of wing elevation, when the tibial extension of the hind legs was also completed and the insect became airborne. In the example shown, take-off velocity was  $0.9 \text{ m s}^{-1}$ , and the continued flapping of the wings enabled the insect to gain height. The angle of the anterior thorax relative to the horizontal just before take-off and when the wings were fully elevated, was much greater at  $28 \pm 2.6^\circ$  (mean  $\pm$  S.E.M.,  $N=10$ ) in take-offs into flight in which jumping was not involved than in jumps alone or in jumps accompanied by flapping wing movements.

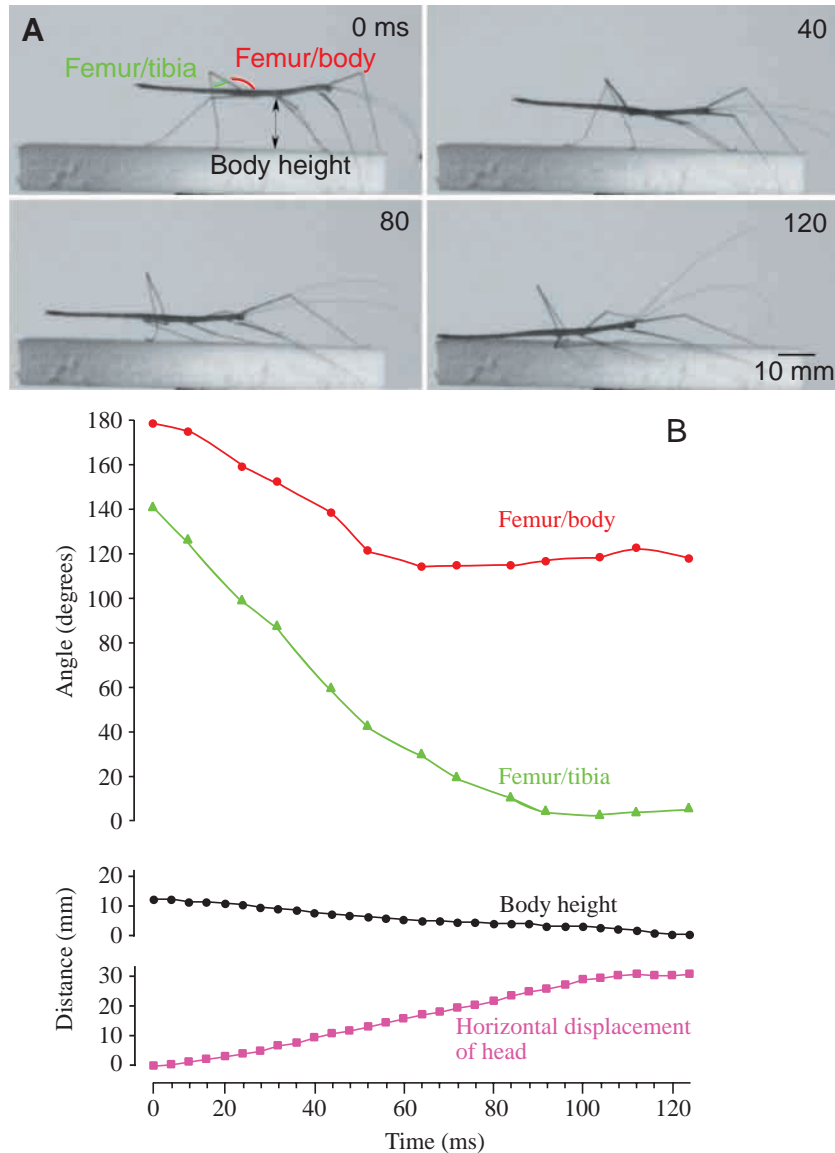


Fig. 7. Rapid backward movement of a nymph following a tactile stimulus to the head. (A) Selected frames from the whole sequence. In the first frame, at 0 ms, the insect stands erect and then starts to collapse backwards so that at 120 ms the abdomen rests on the ground. (B) Graph of the changes in angle between a hind femur and the body and between the femur and tibia of a hind leg. The angles are marked in the first frame of A. The height of the body and the horizontal, backward displacement of the head are also plotted.

#### Backward evasive movements

If, while standing on a horizontal surface, a stick insect was touched lightly on the head, the anterior part of the body or the front legs, it rapidly moved away from the stimulus (Figs 7, 8). These backward movements by nymphs and males lasted  $88 \pm 5.9$  ms and propelled the insect backwards by  $33 \pm 3.4$  mm at velocities of  $0.4 \pm 0.2$  m s<sup>-1</sup> (means  $\pm$  S.E.M.,  $N=21$ ). The movements did not involve flicking movements of the abdomen. The response most frequently observed was a backward movement combined with the body collapsing onto the substratum (Fig. 7A,B). During these movements, the

thorax and abdomen remained in their initial posture throughout, but the angles of the hind femora with the body decreased so that the hind legs were rotated forwards as the body height decreased. The femoro-tibial angle of the hind legs also decreased so that the flexion movement appeared to pull the insect backwards. Rotation of the middle legs also accompanied these movements. The height of the body from the substratum decreased throughout these leg movements so that, eventually, it came to lie with the abdomen prostrate. The net result was to displace the head from its original position backwards by approximately half a body length, with the head moving downwards.

Some movements from the same initial posture launched the insect into a backward jump from the platform with a consequent greater displacement (Fig. 8A). Similar sequences of leg movements occurred in such movements, but the body was not lowered. The propulsion was insufficient to elevate the body so, when the legs lost contact, the insect started to fall, often bumping into the edge of the platform on its backward and downward path.

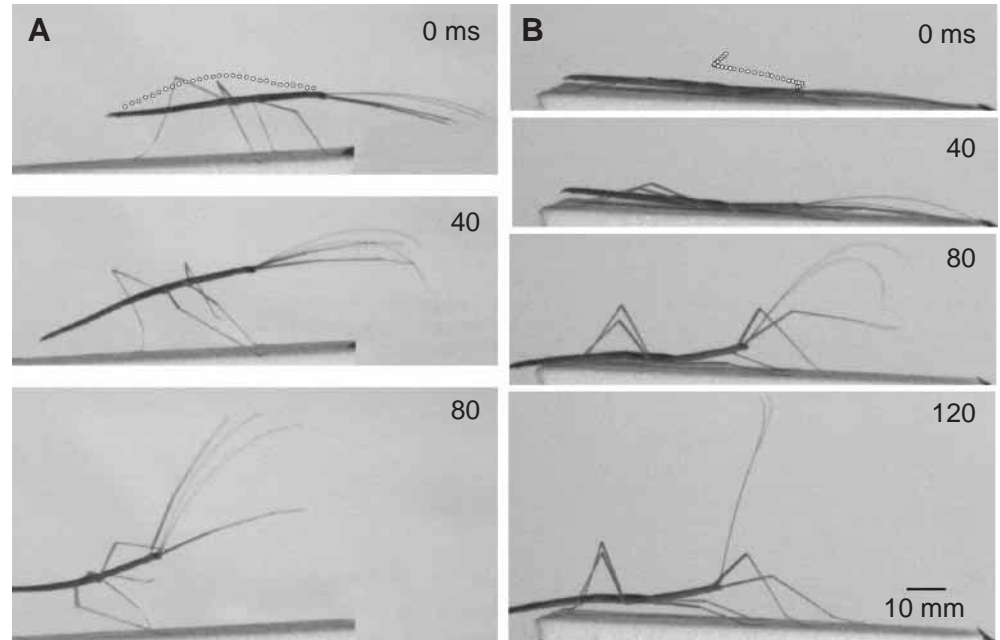
The same backward darting movements also occurred from cataleptic postures when the body was prostrate and with the legs held parallel to the long axis of the body (Fig. 8B). The first movements were a rotation of the hind legs so that they were raised and moved forward by a rotation at the joint with the thorax. The tibiae of the hind legs were then flexed at their joints with the femora, and the body moved backwards. The joint between the meso- and metathorax was also flexed so that the anterior thorax and head were raised and supported by the middle legs.

#### Jumping from a vertical posture

When standing vertically on a twig or a pillar with the head up, stick insects produced two types of movement that paralleled those shown from a horizontal posture. In response to a stimulus to the abdomen from below ( $N=26$ ), they jumped upwards and outwards from the pillar before falling backwards to the ground (Fig. 9). When stimulated on the head from above ( $N=14$ ), they pushed backwards and fell straight down from the pillar (Fig. 10B).

The upward jumping movements had all the characteristics of jumps from a horizontal posture. The abdomen was curled dorsally (upwards) by flexions at the joints between the meso- and metathorax and between the metathorax and the abdomen. At the same time, the femoro-tibial joints of the hind legs were extended. The whole body moved upwards and continued to do so even when the hind legs lost contact with the pillar. The dorsal movements of the abdomen then slowed and reversed

Fig. 8. Variations on backward movements by nymphs. (A) The insect stands erect and then moves rapidly backwards without lowering its body height so that it launches into a backward and downward jump from the platform. The position of the head in each frame from this 80ms sequence is plotted in frame 0ms. (B) The initial posture (0ms) is a mimic of a twig in which all the legs are held parallel to the long axis of the prostrate body. The body is then pulled backwards away from a tactile stimulus to the head. The circles in the first frame (0ms) measured from each frame in the 120ms sequence show the backward movement of the head.



and, some 40 ms after the hind legs had left the pillar, the middle legs also lost contact so that the insect became airborne. The jump propelled the insect laterally and allowed it to fall a few body lengths horizontally away from the original perch. The horizontal displacement could be increased when the jump was accompanied by flapping flight, but rarely resulted in a gain in height (Fig. 10A).

The backward falling movements also had the characteristics of the backward movements from a horizontal position in that neither abdominal nor wing movements contributed (Fig. 10B). The middle and hind legs pushed downwards and then lost contact with the pillar so that the head moved closer to the pillar as the insect fell. At the end of its fall, the insect was now much closer to the base of the pillar than when the abdomen had been flicked upwards and backwards or when the wing movements were also used.

### Discussion

The Thailand winged stick insect *Sipyloidea* sp. jumps from a horizontal or vertical posture by flicking its abdomen forwards and then backwards while extending the tibiae and depressing the femora of the hind and middle legs. From a horizontal standing position, the net result is a jump with a low take-off angle and a low take-off velocity that, nevertheless, propels the insect forwards and initially upwards. The forward momentum, unless assisted by flapping flight, carries the insect only a few body lengths horizontally away from the take-off point. Normally, however, the insect will be perched on vegetation so that the jump ensures its rapid fall to the ground, displaced in a horizontal direction from its take-off position. From a vertical posture, similar abdominal and leg movements propel the insect upwards and horizontally

away from its perch, ensuring that when it falls to the ground, it is again displaced both horizontally and vertically. Tactile stimuli to the anterior of the insect cause a rapid backward movement that does not involve movements of the abdomen and that can propel it backwards from its perch. This insect therefore has the ability to jump in different directions, in contrast to other well-known jumping insects, which can usually only jump over a narrow range of angles and directions.

### Body design for jumping

The body shape of *Sipyloidea* is typical of stick insects in that it is long and thin with long thin legs and long antennae. Movements of the abdomen and the hind and middle legs are involved in jumping. The adult female abdomen accounts for 44% of the body mass and the adult male abdomen for 35%, exceeding by many times the mass of the legs. This contrasts with the body design of a locust, in which the abdomen comprises just 28% of the total body mass. The abdomen of *Sipyloidea* can be flexed at the joint with the metathorax, which in turn can be flexed at its joint with the mesothorax. These movements, together with movements at the abdominal segments, allow the abdomen to be curled forwards by as much as 80–90°, so that its tip comes to lie vertically above the metathorax. The forces generated by the rhythmic dorsal and ventral flexion movements of the abdomen during struggling can be much greater than the body weight. During a jump, the abdomen is first curled forwards and then straightened in a backward movement, thereby increasing the forces transmitted to the ground through the tarsi of the middle and hind legs. Once airborne, these forces would cause the insect to rotate, but the movements of the abdomen also change the position of the centre of mass. The abdominal movements would therefore appear to have two actions. First, they add momentum to the

jump. Second, they allow the forces at take-off to act through the centre of mass of the body and ensure that the body does not spin when airborne.

The legs alone do not appear to be responsible for generating all the forces needed in jumping for three reasons. First, all three pairs of legs are of similar length so that they resemble the legs of non-jumping stick insects such as *Carausius*. The design of the legs is different, therefore, from that of powerful jumping orthopterans such as the locust, which have large hind legs that are much longer than the other two pairs of legs, so that the ratio of leg length is (front:middle:hind) 1:1.3:3.2. Even the false stick insect *Prosarthria teretrirostris* (an orthopteran), which jumps powerfully despite having spindly legs, has long hind legs and a leg length ratio in females of 1:1:2.6 (Burrows and Wolf, 2002). The thin femora of the hind legs of *Sipyloidea* suggest that they do not contain muscles powerful enough to launch the body into a jump. Furthermore, the front legs often do not support the body weight and in many jumps are not in contact with the ground.

Second, the femoro-tibial joints of the hind legs have no specialisations that would allow the slow development of force by the extensor muscles, the storage of energy and then the sudden release of this energy to power the jump. This again contrasts with the design of this joint in locusts (Bennet-Clark, 1975; Burrows and Morris, 2001; Heitler, 1974).

Third, before a jump, the tibiae of the hind legs are not fully flexed about the femora and often start at a position that allows only a few degrees of further extension. The large variation in the initial starting angles of the femoro-tibial joints suggests that the force contributed to the jump is also variable. Depression of the femora and extension of the tibiae of the meso- and metathoracic legs may nevertheless contribute to the jump by raising the body from the ground and shifting its angle of attack. In backward evasive movements, in which the abdomen is not curled, the legs provide the only thrust.

In nymphs, which have no wings, the abdominal and leg movements are the only means of generating the forces for a jump. In adults, the front wings are scarcely more than stubs, but the large hind wings can be opened and flapped to generate lift and thrust. Even in adults, however, many jumps are produced without the assistance of the wings. When they are used, the wings are opened at the same time as the abdomen is thrown forward and then depressed as the abdomen swings backwards so that flapping flight assists the jump. Adult males can gain height from such a wing-assisted take-off, but the heavier females still lose height. Use of the wings may nevertheless provide greater stability during a jump, as it does for flea-beetles when they use their wings (Brackenbury and Wang, 1995).

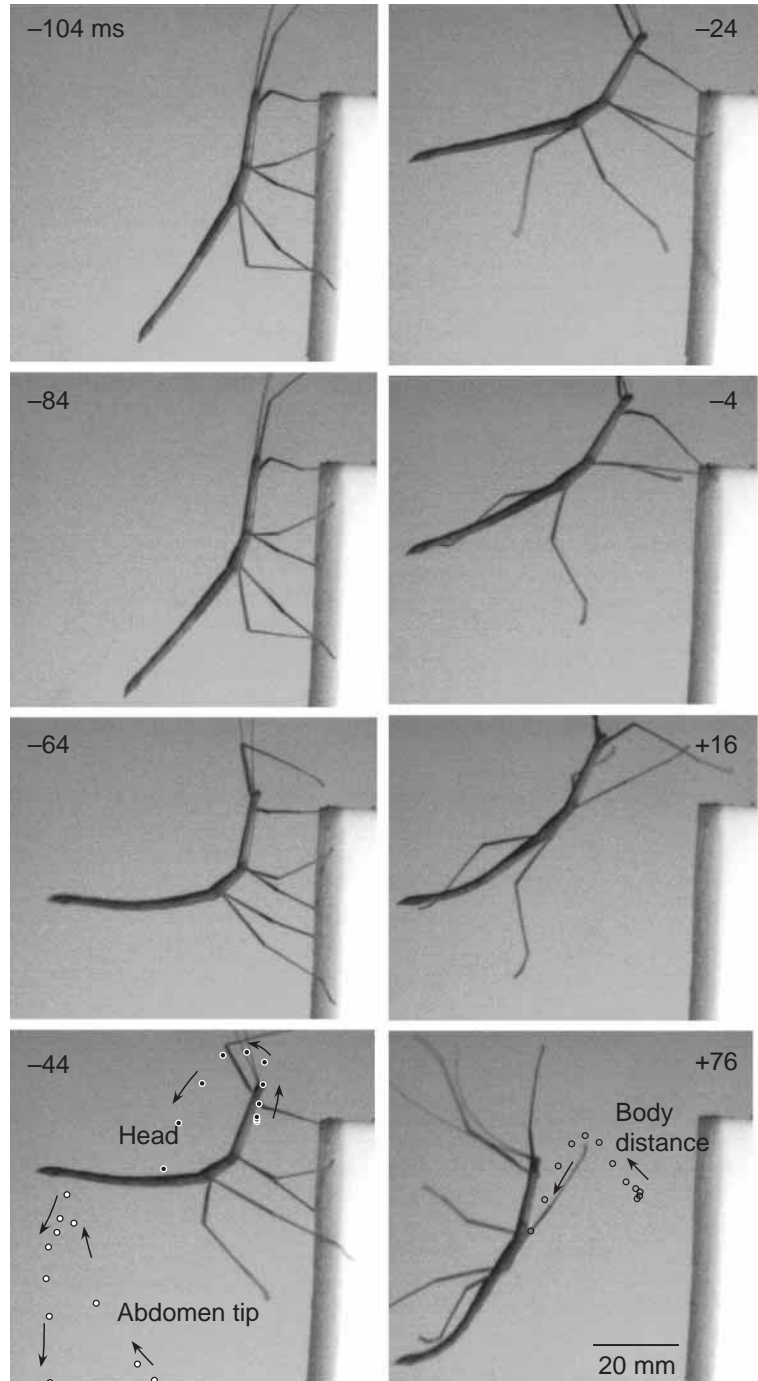


Fig. 9. A backward jump by a nymph from an initial vertical posture. Selected frames from the sequence in which take-off occurred at 0 ms are arranged in two columns. The position of the head and the tip of the abdomen and the distance of the body from the vertical pillar are plotted in the bottom two frames. The abdomen is flicked forwards and the body moves upwards before the legs lose contact with the pillar and the insect falls in a trajectory away from the pillar.

#### Jumping mechanisms in other animals

Locusts (Bennet-Clark, 1975), false stick insects (Burrows and Wolf, 2002) and fleas (Bennet-Clark and Lucey, 1967) all use rapid extension of the hind legs to propel their jump. Male

locusts weighing 1.5–2.0 g can take off in 25–30 ms at velocities of  $3.2 \text{ m s}^{-1}$  and at peak accelerations of  $180 \text{ m s}^{-2}$  to jump a distance of 0.8–0.95 m (20 body lengths). The energy required can be as great as 11 mJ and is generated by muscle contraction in advance of the jump and stored in cuticular deformations. Male false stick insects (*Prosarthria*) weigh only 0.28 g and take off in 30 ms at velocities of  $2.5\text{--}3.0 \text{ m s}^{-1}$  and at peak accelerations of  $165 \text{ m s}^{-2}$  to jump a distance of 0.9 m (13 body lengths) (Burrows and Wolf, 2002). Again, the energy requirement of  $850 \mu\text{J}$  can be met only by muscle contraction in advance of the jump, but is achieved without bending of the semi-lunar processes that provide almost half the energy storage for the locust. The flea *Spilopsyllus cuniculus* weighs only 0.45 mg and can jump 3–5 cm into the air at a take-off velocity of approximately  $1 \text{ m s}^{-1}$ . The energy required is again produced by a prior contraction of the enlarged depressor muscle in the hind leg and then stored in a pad of resilin. The stored force is released suddenly by the contraction of a small muscle that changes the point of action of the depressor muscle so that the femur can be depressed rapidly.

In contrast to these performances, the jumping of *Sipyloidea* is much more modest. The time during which the insect is accelerated in a jump is almost three times as long as in a locust, and the take-off velocities, acceleration and energy requirements are much smaller. Our estimate of 1 mW for the mean power output during a jump is well within the bounds of direct muscle action (Weis-Fogh and Alexander, 1977), so that there is no need to invoke storage mechanisms to power the jump, as in many other jumping insects. This stick insect combines the kinetic energy provided by abdominal movements with the forces generated by two pairs of legs, thereby extending the time over which the acceleration is applied. In these respects, it has features in common with jumping spiders and jumping ants.

The salticid spider *Sitticus pubescens* jumps a distance of some 7 cm or up to 10 body lengths at a take-off velocity of approximately  $0.7 \text{ m s}^{-1}$  (Parry and Brown, 1959). The thrust for the jump is

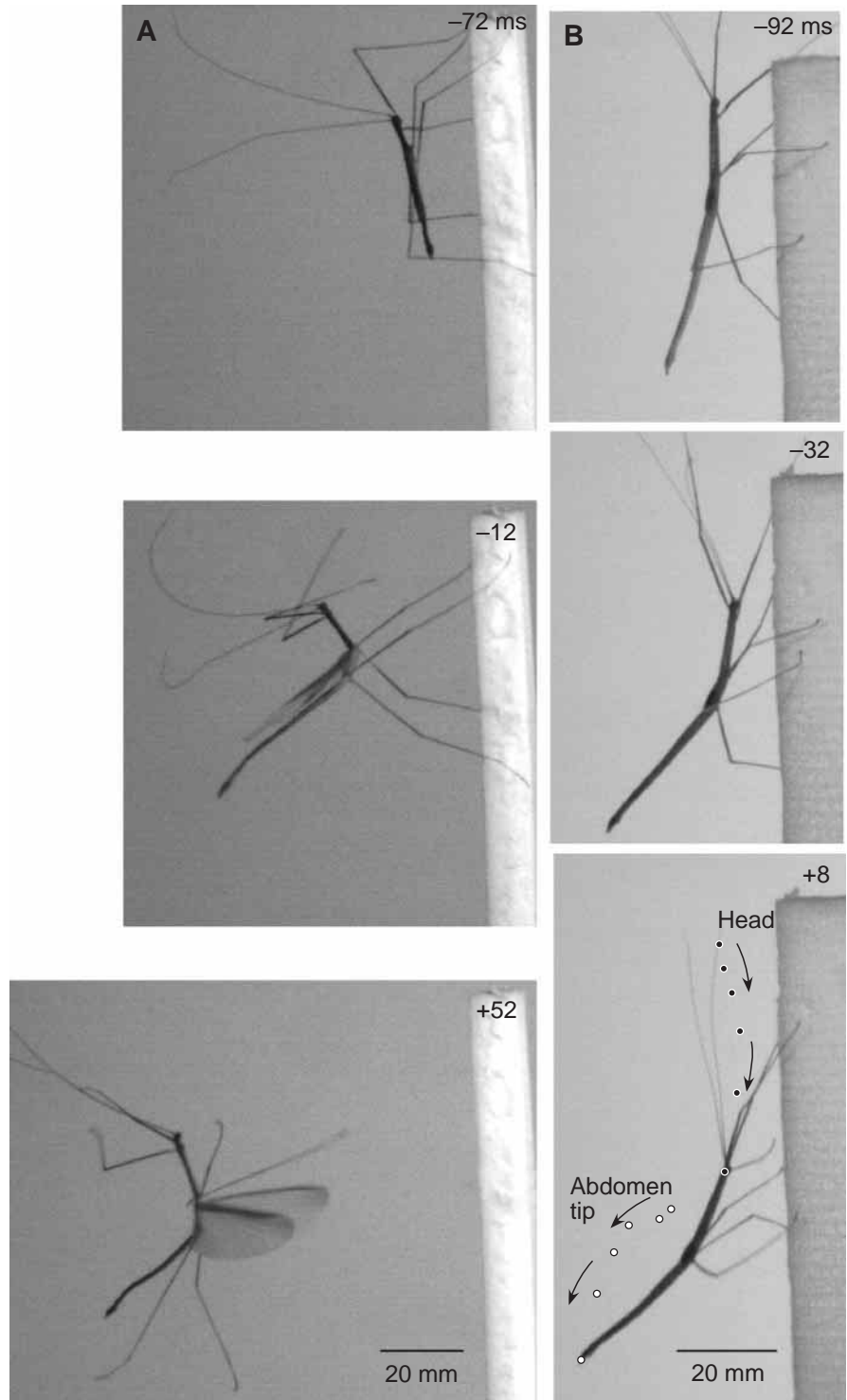


Fig. 10. Variations in backward jumping from a vertical posture by an adult male. (A) Jumping is accompanied by flapping movements of the wings. Three frames are shown from the selected sequence in which take-off occurred at 0 ms. The wing movements propel the insect further from the pillar as it falls. (B) The insect falls, but the abdomen is not flicked forwards. The movements of the tip of the abdomen and the head are plotted in the bottom of three selected frames from the whole sequence.

provided mainly by the fourth pairs of legs, which are extended fully by depression of the femur and extension at the

femur/patella joint. The third pair of legs extends by only a small amount before the legs lose contact with the ground, and the first two pairs of legs are lifted from the ground before the jump even starts. Other jumping spiders may use the simultaneous extension of two pairs of legs. The ant *Harpegnathos saltator* jumps to escape from predators and to hunt prey by the rapid extension of both the middle and hind pairs of legs (Baroni et al., 1994; Tautz et al., 1994). The jump, which takes some 15–25 ms from the time the head is first raised to when the legs leave the ground, propels the body forwards some 3–4 cm at an angle of approximately 40°, but with a low take-off velocity of 0.6–0.7 m s<sup>-1</sup>. The centre of mass of these ants is anterior to the mesothoracic legs so that the body does not spin during a jump. In *Gigantiops destructor*, however, it is behind the hind legs and, to compensate, the gaster (part of the abdomen) is moved forwards at the same time as the legs are extended and is held in the forward position as it becomes airborne. As in *Sipyloidea*, the abdominal movements may also provide kinetic energy to propel the body forward (Tautz et al., 1994).

#### *Lines of defence*

How effective behaviourally is the jumping of *Sipyloidea*? Broadly, two main strategies are used to avoid predation: first, it adopts cryptic postures to minimise detection and, second, it moves away from potentially harmful stimulation. Its cryptic body shape and coloration, helped by an ability to sustain a particular posture for a long time without moving, make it hard for potential predators to detect. Tactile stimulation leads to a number of behavioural responses. First, it may withdraw rapidly from a stimulus and then freeze, so that the predator may lose contact and then has to go through the recognition process again. Second, it may walk rapidly away, so that the predator has to pursue it. Third, it may jump from its perch, thus propelling itself quickly and some distance from the predator to land amongst the leaf litter, where its cryptic posture and coloration will again make it difficult to detect. Use of the abdomen to provide forward or upward momentum, depending on the initial starting posture when jumping, may have evolved from the abdominal curling movements seen in defensive postures by other stick insects. Finally, the jump may be combined with flapping flight to put a large distance between the insect and the predator, making pursuit possible only for aerial predators. The ability to jump rapidly, if only for short horizontal distances, could therefore be an important survival strategy.

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