

COORDINATED RIGHTING BEHAVIOUR IN LOCUSTS

A. A. FAISAL AND T. MATHESON*

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

*Author for correspondence (e-mail: tm114@hermes.cam.ac.uk)

Accepted 24 November 2000; published on WWW 1 February 2001

Summary

A locust placed upside down on a flat surface uses a predictable sequence of leg movements to right itself. To analyse this behaviour, we made use of a naturally occurring state of quiescence (thanatosis) to position locusts in a standardised upside-down position from which they spontaneously right themselves.

Locusts grasped around the pronotum enter a state of thanatosis during which the limbs can be manipulated into particular postures, where they remain, and the animal can be placed upside down on the ground. When released, thanatosis lasts 4–456 s (mean 73 s) before the animal suddenly becomes active again and rights itself within a further 600 ms. Thanatosis is characterised by very low levels of leg motor activity.

During righting, one hind leg provides most of the downward force against the ground that rolls the body around a longitudinal axis towards the other side. The driving force is produced by femoral levation (relative to the body) at the trochanter and by tibial extension. As the animal rolls over, the hind leg on the other side is also levated at the trochanter, so that it does not obstruct the movement. The forelegs and middle legs are not required for successful righting but they can help initially to tip the locust to one side, and at the end of the movement they help

stop the roll as the animal turns upright. Individual locusts have a preferred righting direction but can, nevertheless, roll to either side.

Locusts falling upside down through the air use both passive and active mechanisms to right themselves before they land. Without active movements, falling locusts tend to rotate into an upright position, but most locusts extend their hind leg tibiae and/or spread their wings, which increases the success of mid-air righting from 28 to 49% when falling from 30 cm.

The rapid and reliable righting behaviour of locusts reduces the time spent in a vulnerable upside-down position. Their narrow body geometry, large hind legs, which can generate substantial dorsally directed force, and the particular patterns of coordinated movements of the legs on both sides of the body are the key features that permit locusts to right themselves effectively. The reliability of autonomous multi-legged robots may be enhanced by incorporating these features into their design.

Key words: locust, *Schistocerca gregaria*, righting, behaviour, thanatosis, escape, motor pattern, struggling, video analysis, computer model, muscle activity, legged robot.

Introduction

When terrestrial animals that use their legs for support and locomotion fall over, it is important that they can right themselves so that they can regain foot contact with the ground. Amongst vertebrates, righting strategies differ markedly between genera, with some animals being more effective at righting themselves than are others. Righting movements of insects have received little attention, but those of cockroaches have been described as ‘uncoordinated’ and are often unsuccessful on a smooth surface (Camhi, 1977). Our aims were (i) to describe the rapid and reliable righting behaviour of desert locusts; (ii) to interpret this with reference to the contrasting mechanical constraints imposed by different animal body plans; and (iii) to use these comparative observations to suggest design features that may improve the righting of autonomous robots.

The body plan of an animal affects both its stability when standing upright and the position in which it falls. Each body

plan places different biomechanical constraints on the animal’s limb movements and its moment of inertia when righting. Righting may occur on the ground (contact-righting), or it may occur as an animal falls through air (air-righting) or floats in water. Each situation also imposes additional mechanical constraints, such as the presence or absence of a solid surface on which to rotate, or different fluid viscosities that impede limb movements or body rotation. Contact-righting has been described in detail in rats, cats, toads, turtles and cockroaches (Arabayan and Tsai, 1998; Pellis et al., 1991b; Bisazza et al., 1996; Ashe, 1970; Full et al., 1995). Even these few descriptions reveal three different righting strategies that relate to the different body plans of these animals.

The broad flat bodies of cockroaches and many turtles mean that when these animals fall over they lie in a stable upside-down position. Mechanical constraints mean that their feet

cannot touch the ground unless the animal first rolls to one side. This initial roll must therefore be generated by some mechanism other than direct action of the feet or legs on the ground. Turtles right themselves by twisting their neck through 180° and bending it dorsally so that their chin rests on the ground beneath the carapace and their head faces backwards. Elevation of the head lifts the front of the body to permit rotation around a longitudinal axis. If the turtle can get a firm purchase on the ground with its front claws (e.g. on grass), the righting movements are often successful, but on a smooth or slippery surface they usually are not (Ashe, 1970; S. Currie, personal communication). Cockroaches flex their body into an inverted U-shape that touches the ground only at its rostral and caudal ends. From this unstable position, the animal tips to one side, from where the feet can push on the ground to flip the animal over (Sherman et al., 1977; Full et al., 1995). Movements of the legs of a cockroach during righting are similar in many respects to those used for walking (Sherman et al., 1977), but the forces produced are close to the maximal possible leg force (Full et al., 1995). On smooth surfaces, the cockroach *Gromphadorhina portentosa* often fails to right itself, even after 30 min or more (Camhi, 1977).

Rats and cats can twist their bodies axially, and their relatively long thin body plan means that if they fall over they are unlikely to land upside down. Instead, they generally fall onto one side, and their feet may already be able to touch the ground. Rats right themselves by first rotating their shoulders to turn the neck and head to an upright position, and then rotating their body to bring the hind legs into contact with the ground (Pellis et al., 1991a).

Toads have a short, relatively inflexible vertebral column, which prevents them from using axial rotations to right themselves. Instead, they use dorsal movements of their large hind legs to push off from the ground on one side so that the body rotates to the other side (Robins et al., 1998). Alternatively, they may throw a hind leg rapidly across the centre of gravity to generate momentum, which then rotates the body. The same leg brakes the movement when the animal turns upright. When submerged in water, toads use a foreleg to control rotation into an upright posture (Bisazza et al., 1996). In both situations, toads show an individual preference to right towards a particular side.

Locusts, unlike cockroaches, jump and fly readily, perhaps making them more prone to falling upside down. Their body is longer and more slender than that of a cockroach (length:width ratios: locust, 14:2; cockroach, 5:2), but it cannot be rotated axially like that of a rat or cat. Locusts have large hind limbs that can touch the ground when the animal is upside down, somewhat like those of a toad. Do these anatomical features permit effective righting in this insect? Can locusts right themselves on smooth surfaces, such as the broad expanses of sand that dominate their natural habitat? Can they right themselves in mid-air if they tumble during a jump, perhaps pre-empting the need to right on the ground?

Understanding the interplay between body plan and righting strategies of different animals may help to guide the design of

autonomous robots that, for example, would be able to right themselves in remote locations such as on the surface of Mars (Lauback, 1999). To our knowledge, no current hexapedal robot can right itself independently, although some computational models of robots can recover from stumbles during walking (e.g. Cruse et al., 1998), and a quadrupedal robot, the AIBO dog, can right itself from a position lying on its side (Taylor, 1999).

To analyse righting in locusts, we first induced thanatosis, which permitted us to manipulate the animals into a standard upside-down position on the ground from which they voluntarily righted themselves. Thanatosis is a quiescent state that has previously been described in detail in stick insects (e.g. Godden, 1974; Bässler and Foth, 1982) and crickets (Nishino and Sakai, 1996) but, because it has not previously been described in locusts, we first give a brief description for this species. Some of these data have been published in abstract form (Faisal and Matheson, 1999).

Materials and methods

Experiments were performed on adult male and female locusts, *Schistocerca gregaria* (Forskål) from our crowded culture. Righting was carried out on a hard flat table top.

Induction of thanatosis

To induce thanatosis, gentle pressure was applied to the pronotum of a locust gripped between the tips of a thumb and a forefinger (for details of the method in crickets, see Nishino and Sakai, 1996) while the legs were manipulated into a standardised posture (see Fig. 1B,D). The front and middle legs were rotated anteriorly so that the femora lay at right angles to the body axis, and the femoro-tibial joints were set to 90°. The femora of the hind legs were held close to the body and the tibiae flexed. The locust was gently placed onto its back on the ground, and the hind legs were adjusted so that the distal end of the femora touched the ground symmetrically to stabilise the animal. The grip around the pronotum was released, and the animal was left undisturbed until it righted itself. In over 1000 trials in 60 animals, thanatosis was always induced within 1 min. Between any two trials, a locust was given 10–180 s in which it was gently encouraged to walk or kick.

Video recording

Righting movements of four locusts were videotaped at 25 frames s⁻¹ from lateral, dorsal and posterior views. Images from the three cameras (JVC TKC-1380) were combined by a video splitter (FOR-A MV40-PS) and stored together with a timing signal on VHS tapes (Panasonic NV-HS900 recorder). Sequences of images were digitised using a Miro Video (DC30 plus) capture card and software, then converted into AVI files using Adobe Premiere software. To analyse the most rapid movements in greater detail, a high-speed digital video camera (Redlake PCI Motionscope 2000) was used to record righting behaviour at up to 500 frames s⁻¹.

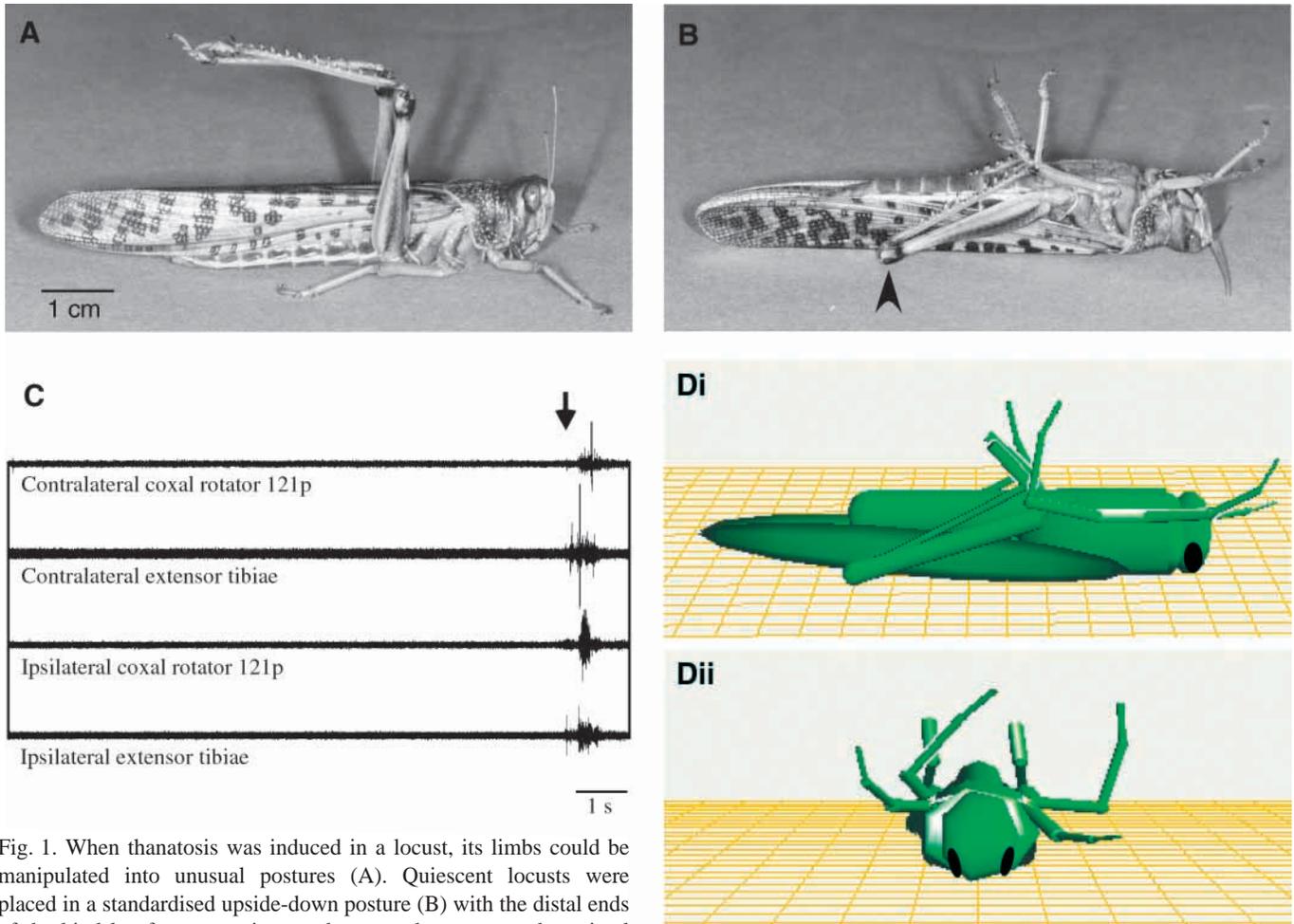


Fig. 1. When thanatosis was induced in a locust, its limbs could be manipulated into unusual postures (A). Quiescent locusts were placed in a standardised upside-down posture (B) with the distal ends of the hind leg femora resting on the ground to support the animal (arrowhead). None of the legs touched another leg or the body. Myograms showed that during thanatosis there was little or no motor activity in the coxal or tibial motor neurones of either hind leg (C). At the end of thanatosis (arrow), abrupt bursts of activity in all the recorded muscles accompanied righting movements. (D) An anatomically accurate interactive computer model of a locust was used to generate images of righting locusts based on measured joint angles that could be viewed from any viewpoint. (Di) Computer image of the video frame shown in B, viewed from the same perspective. (Dii) The same data viewed from anterior to the animal.

Analysis, description and illustration of righting movements were facilitated by entering all limb joint angles and body coordinates measured from selected sequences of video images into a custom-designed computer model of a locust. The model generated a three-dimensional image for each video frame, which could then be viewed from any angle. For example, measurements taken from a locust lying on its back (see Fig. 1B) were used to generate an image that could be viewed from a virtual camera located at a similar point in space to one of the original cameras (Fig. 1Di), or from a different virtual camera located in front of the animal (Fig. 1Dii). This program is available from the following address (<http://www.zoo.cam.ac.uk/zoostaff/matheson/index.htm>).

Force measurements on photoelastic gel

To detect forces applied to the ground during righting behaviour, locusts were placed on a photoelastic gelatine substratum illuminated from below by linearly polarised light

and videotaped from above by a camera fitted with a linear polarising filter (Harris, 1978; Harris and Ghiradella, 1980; Full et al., 1995). This method could detect only the largest forces present during righting.

Righting on horizontal and inclined substrata

The preferred righting directions of 18 locusts were established on a horizontal surface. Four locusts were subsequently tested on a surface inclined at an angle of 5 or 10° to the left or right. To prevent external biases, animals were released alternately by the experimenter's left and right hands, and the entire experimental apparatus was rotated periodically through 180°.

Behaviour in free fall

Locusts were gripped from the ventral side by forceps placed between the middle and hind legs, close to the centre of gravity. This did not induce thanatosis. The locust was turned upside

down and released from heights of 30, 45 or 60 cm. Behaviour during the fall was videotaped at 25 frames s^{-1} . The falling height for each trial was varied systematically.

Electrophysiology

Myograms were recorded from the coxal, trochanteral and tibial muscles of the hind legs during righting behaviour of 15 locusts. The righting movements were videotaped so that muscle activity could be related precisely to specific leg movements. Myogram electrodes were made from pairs of 63 μm diameter insulated steel or copper wires which passed from the recording sites to the pronotum, fixed at intervals by drops of wax. From the pronotum, the wires passed posteriorly to leave the animal between the tips of the wings so that they did not impede righting behaviour. Motor activity was identified using standard criteria (see Bräunig, 1982; Field and Burrows, 1982; Burrows, 1995; Burrows, 1996; Duch and Pflüger, 1995).

Signals were amplified ($\times 1000$) and bandpass-filtered, then either displayed on an oscilloscope and stored on tape (Racal Store-4 or Store-7 FM recorders) or captured directly to computer using a Cambridge Electronic Design micro-1401 AD/DA interface and Spike 2 software (Cambridge Electronic Design). To correlate the videotaped movements with motor activity, a synchronising signal was recorded both on the videotape and together with the electrophysiological signals.

Results

Thanatosis

When a locust was held by applying gentle bilateral pressure to the pronotum, ventilatory movements of its abdomen decreased and movements of all its limbs ceased, usually within 60 s. Once quiescent, locusts could be placed on the ground in any stable position and released gently without disturbing their thanatosis (Fig. 1A,B). They then remained immobile for 4–456 s (mean 73 s, 60 trials in 10 animals), with the exception of ventilatory movements of the abdomen, which resumed within a few seconds of the animal being released. During thanatosis, the limbs could be manipulated into unusual positions without otherwise disturbing the animal (e.g. Fig. 1A) where they then remained until the end of thanatosis. Myograms showed that during thanatosis there was little or no motor activity in any of the hind leg muscles recorded (e.g. Fig. 1C).

The first visible signs of arousal from thanatosis were often small movements of the antennae. Within 1 s of the start of these movements, locusts began moving their limbs, often jumping or, if they had been placed upside down, righting themselves. Strong tactile, auditory or visual stimuli could also arouse a quiescent animal. Animals that were placed upside down in thanatosis and then given a foam ball to grasp immediately started walking. Animals that were tethered at the pronotum and held upside down without contact with any substratum attempted either to fly or to kick out at the tether. They did not attempt the full sequence of righting movements

that we describe below, regardless of whether thanatosis had been induced or not.

Righting behaviour

Locusts placed on their sides or upside down on the ground quickly turned themselves upright. To analyse the movements that comprise this righting behaviour, thanatosis was induced as described above and locusts were placed in a standardised upside-down posture (Figs 1B,D, 2A), with the distal ends of both hind femora touching the ground and the middle and fore leg tibiae pointing away from the body. Spontaneous righting behaviour at the end of thanatosis consisted of a stereotypic sequence of leg movements that quickly flipped the animal back onto its feet. Fig. 2 illustrates this sequence for a roll to the animal's right. Throughout this paper, we refer to the legs on the side over which the animal rolls as 'ipsilateral', i.e. the right-hand legs in Fig. 2.

Five components of righting behaviour were present in all trials. First, there was levation of the contralateral hind leg femur to begin a rotation of the whole animal towards the ipsilateral side. Second, there was contact of the contralateral hind leg tarsus with the ground so that tibial extension could contribute further to the rotation. Third, the ipsilateral femur was levated to move the ipsilateral leg under the body so that it too could continue to propel the animal in the direction of rotation. Fourth, there was depression of the ipsilateral femur once the tarsus had reached the ground. The final element of righting occurred when the contralateral tarsi touched the ground to halt the animal's rotation.

At the end of thanatosis (Fig. 2A), the contralateral hind leg femur began to levate (short curved arrow in Fig. 2B), so that the distal end of the femur pressed down against the ground (straight arrow in Fig. 2B). This caused locusts to roll slowly ($< 5^\circ$ in 80–120 ms) to the other (ipsilateral) side (long curved arrow in Fig. 2B). The femur continued to levate, and the tibia extended rapidly from 15 to 120° by 100–250 ms after the beginning of righting (curved arrow in Fig. 2C; Fig. 2D) so that the full length of the extended tibia and the tarsus came into contact with the ground (straight arrow in Fig. 2F). Locusts pivoted about the distal end of the ipsilateral femur and the dorsal surface of the head and thorax (arrowheads in Fig. 2F).

After 300 ms, the ipsilateral hind leg femur had been levated from 30° (at 0 ms) to 90° (curved arrow in Fig. 2F), and locusts had rolled by 90° (Fig. 2F,G). Rotation of the body about the pivot points, together with this levation of the ipsilateral hind leg femur, meant that the distal end of the ipsilateral femur passed beneath the body after 200–250 ms, and the ipsilateral tarsus touched the ground (arrowhead in Fig. 2G). The tibia of the ipsilateral hind leg was extended and the femur depressed (short curved arrow in Fig. 2H), contributing to rotation of the body, which then lifted the contralateral tarsus from the ground and over the body (long curved arrow in Fig. 2H; Fig. 2I). The ipsilateral middle and fore leg tarsi then came into contact with the ground, forming new pivot points for the remainder of the body rotation (arrowheads in Fig. 2H).

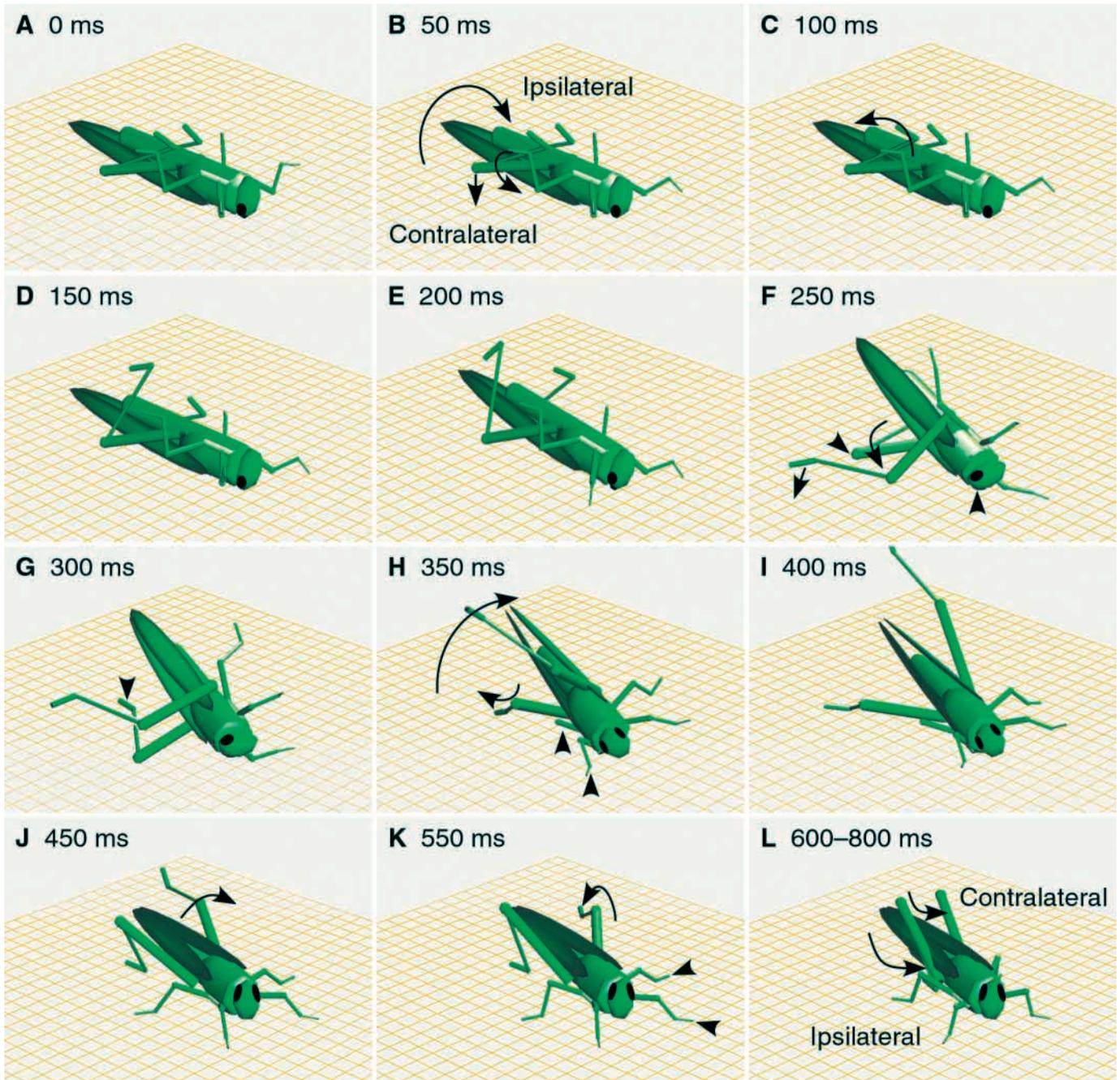


Fig. 2. Computer visualisation of the sequence of leg movements used during righting behaviour. The locust was righting towards its right-hand side (defined as ipsilateral). Images are at the times indicated (in milliseconds) from the start of the movement. Arrows indicate movements, and arrowheads indicate key points of contact with the ground, all of which are referred to in the text.

Between 250 and 500 ms, the contralateral hind leg tibia remained extended beyond 120° as the leg was carried across the midline by body movement and femoral rotation. The femur was abducted from the body by approximately 10° (curved arrow in Fig. 2J) and depressed to $15\text{--}30^\circ$ (curved arrow in Fig. 2K) as the animal continued pivoting about its ipsilateral tarsi. These movements together carried the contralateral tarsus in an arc of decreasing radius around the longitudinal body axis. The tarsus touched the ground

simultaneously with the contralateral middle and fore leg tarsi as the animal reached an upright position (arrowheads in Fig. 2K). This marked the end of righting behaviour at 550–600 ms.

Following righting, locusts usually assumed their normal resting posture with the hind leg femora levated to approximately 40° and the tibiae fully flexed (curved arrows in Fig. 2L). Locusts remained in the resting position, walked or jumped away.

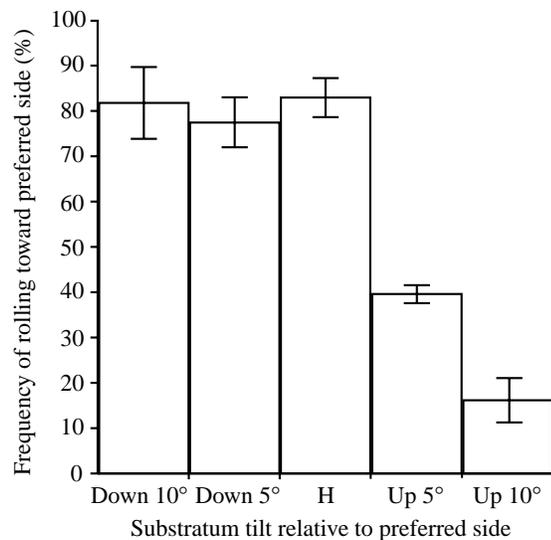


Fig. 3. The slope of the ground affected righting direction. On a horizontal surface (H), locusts had an individual preference to roll towards one side. When the surface was tilted so that righting to this preferred side required an uphill roll ('Up 5°' or 'Up 10°'), locusts were less likely to roll to that side. Reversing the slope so that righting to the preferred side required a downhill roll ('Down 5°' or 'Down 10°') did not increase the frequency of rolling to that side. $N=800$ trials in 18 animals on horizontal ground and 307 trials in four animals for other surface orientations. Error bars indicate the standard deviation.

The sequence of righting behaviour lasted 585 ms (median; range 440–1430 ms, 35 trials in eight animals). The mean angular velocity of body rotation was therefore 308°s^{-1} , but the fastest angular velocities of 680°s^{-1} occurred 200–400 ms after righting began, starting when the tibia of the contralateral hind leg was extending rapidly and its tarsus was in contact with the ground.

Righting preference and effects of leg lesion

Most locusts had a preferred direction of rotation when righting on level ground, but this could be either towards the left or towards the right in different animals. On average ($N=18$ animals), locusts rotated towards their individually preferred side in 81% of trials (Fig. 3). This preference was statistically significant ($r^2=8.27$; $P<0.005$). The handedness of folding of the wings (left wing over right wing or *vice versa*) was not correlated with the preferred righting direction. Individual locusts could have preferences of more than 90% in sequences of 20 righting trials, and these preferences could be maintained over at least 2 days.

The direction of righting was influenced by the angle of the ground. Locusts righted towards their preferred side less frequently if they had to roll uphill, for surfaces inclined at 5 or 10° (Fig. 3). There was no change in frequency of righting towards the preferred side if this entailed rolling downhill (Fig. 3).

The direction of righting could also be influenced by adjusting the initial position of the hind legs. For example, a

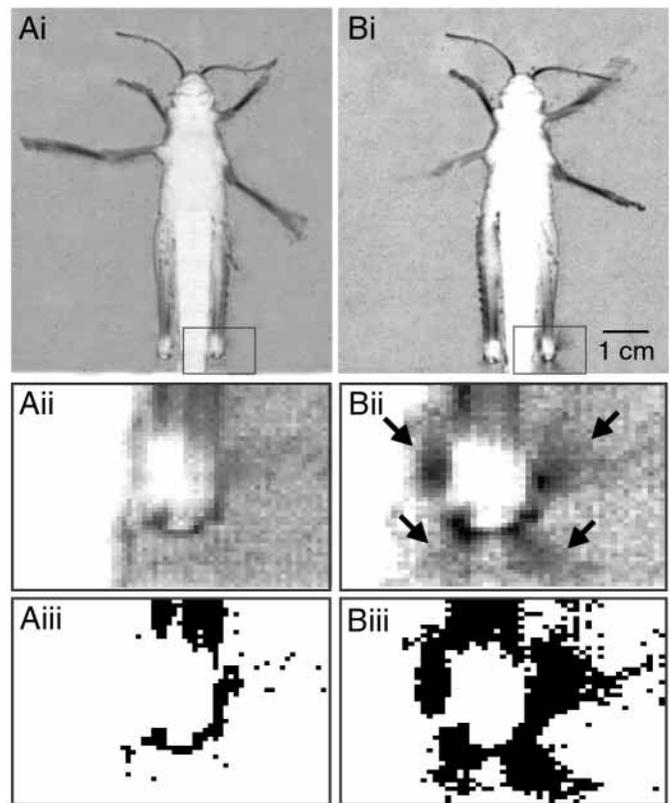


Fig. 4. Force visualisation of the beginning of a righting movement to a locust's right-hand side. Aii and Bii are enlargements of the regions marked with boxes in Ai and Bi. Aiii and Biii are processed versions of Aii and Bii in which a threshold function has been applied to discriminate between pixels darker or lighter than an arbitrary cut-off value. Before the start of movement (A), little force was detectable at any point of contact between the locust and the substratum (the background is a uniform grey in Ai,ii, and few pixels other than the outline of the femur are black in Aiii). At 20 ms after movement had begun (B), the distal end of the hind leg femur on the animal's left-hand side (the 'contralateral' leg) evoked symmetrical light patterns in the photoelastic gel (Bi, iii, arrows in Bii).

locust that preferentially rolled towards its left in 73% of trials ($N=67$), rolled instead to the right in 100% of trials ($N=10$) when its left hind leg was initially abducted 20° laterally so that the tip of the femur rested on the ground approximately 3 mm further lateral than that of the right femur. Conversely, when the locust was placed with the right leg abducted by 20°, it rolled to the left in 70% of trials ($N=10$).

Progressive removal of hind limb segments (tarsi, tibiae then femora) showed that locusts could right themselves reliably as long as the femur of one hind leg was present ($N=2$ locusts). Locusts with intact fore and middle legs but missing hind legs could not right themselves; instead, they made erratic movements of their fore and middle legs, and rocked from side to side. Conversely, a locust missing its fore and middle legs reliably righted itself using its intact hind legs.

Forces during righting

During the first 80 ms of righting (as locusts rotated from

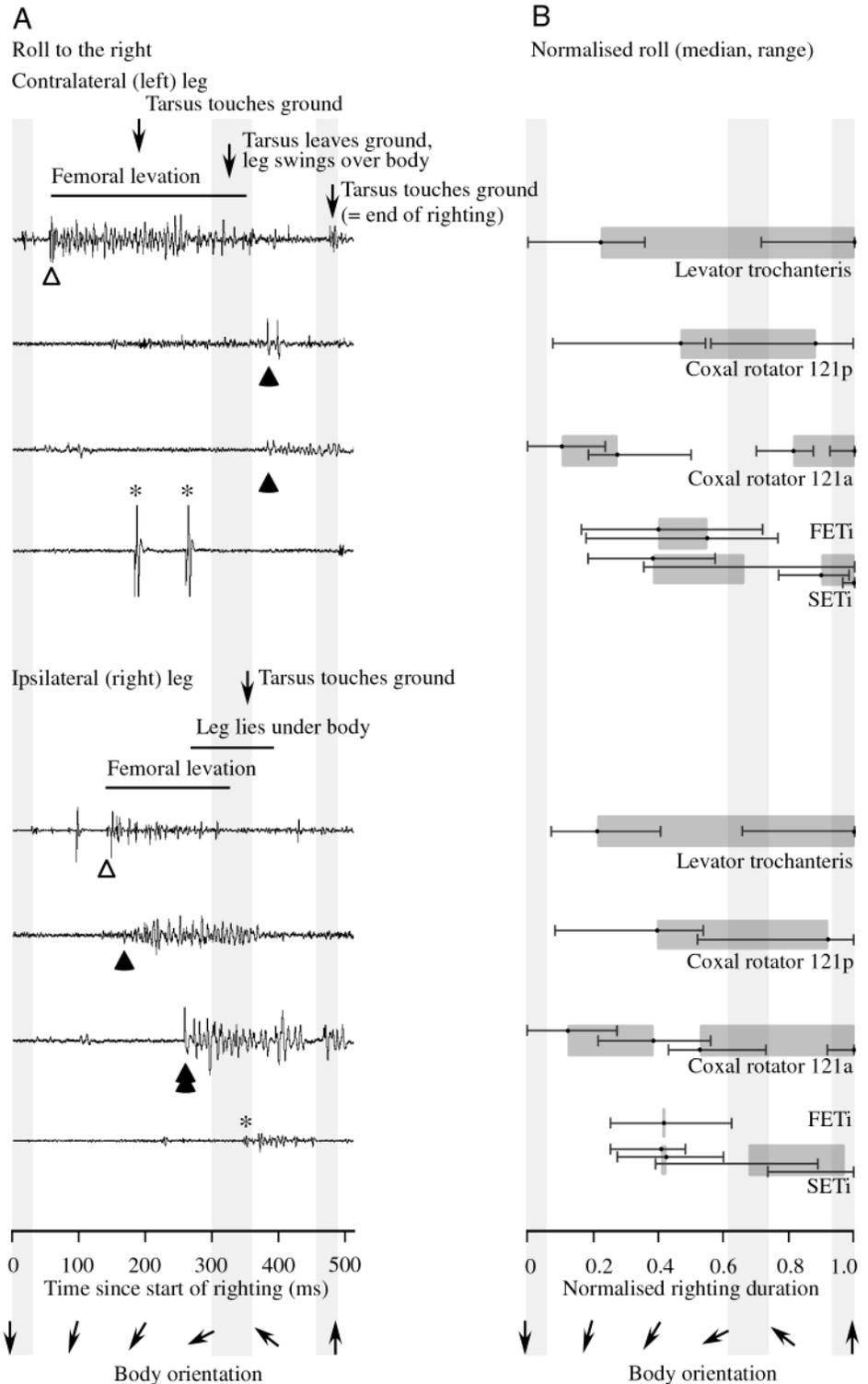


Fig. 5. Myograms of coxal, trochanteral and tibial muscle activity of both hind legs of a locust righting to its right (A), and schematic representation of normalised burst durations (B). (A) The upper panel of four traces contains recordings from muscles of the contralateral (left) hind leg, which provided the main force to roll the locust towards the right. In this example, the righting duration was 480 ms. The timing of femoral levation and times when the tarsus touched and lifted from the ground are indicated above the traces. The lower panel of four traces contains recordings from the corresponding muscles of the ipsilateral (right) hind leg. Femoral levation and the period during which the animal rolled over the ipsilateral leg are indicated above the traces. Body orientation is indicated by arrows at the bottom of the figure (arrows point dorsally) and by light grey vertical columns indicating when the animal was upside down, lying on its side or standing upright. All traces have the same vertical scale. The asterisks and open and filled arrowheads refer to events described in the text. (B) Start and end points of motor bursts (median \pm range) for 27 rightings in four animals, normalized for the measured duration of each righting movement. Activity of the fast (FETi) and slow (SETi) extensor tibiae motor neurones, visible as large and small potentials, respectively, in the extensor muscle recordings in A, is represented separately in Fig. 5B.

180 to 135°), the distal end of the contralateral hind leg femur was pressed down against the substratum, generating approximately symmetrical light patterns in the photoelastic gel (Fig. 4A,B). These forces were recorded in five out of six animals in 19 trials. One animal did not generate sufficient force to be detected, despite making apparently normal righting movements.

At the end of righting, i.e. during the last 30° of rotation, the contralateral middle leg tarsi of three animals reliably generated detectable pressures when they landed on the photoelastic gel (not shown). In another three animals, these pressures were below the detection threshold. The contralateral front and hind tarsi did not generate detectable pressures in any of the six animals tested (19 righting movements in total).

Leg motor activity

To examine further the contributions made by the movements of particular hind leg joints to righting behaviour, myograms were recorded from selected coxal, trochanteral and tibial muscles in freely moving animals that righted themselves normally from the standard upside-down position described above. The movements were videotaped, and the timing of muscle activity was related precisely to the observed movements. The following description and recordings illustrated in Fig. 5A are from animals rolling to the right, for consistency with the movements illustrated in Fig. 2. The right legs are again 'ipsilateral'. Vertical grey columns in Fig. 5 indicate the approximate times when the locust was upside down, lying on its side or standing upright (also see arrows labelled 'body rotation' at the bottom of the figure) to provide a visual reference against which the timing of activity in the different muscles can be compared. The variability of motor activity driving righting in four animals was analysed by determining the start and end times for bursts of motor activity in each muscle (median \pm range), normalized for the measured duration of each righting movement. These data are summarised in Fig. 5B.

Movements of the contralateral hind leg were driven by the following sequence of muscle activity (top panels of four traces in Fig. 5A,B). Initial femoral levation was accompanied by a burst of large- and small-amplitude potentials in the levator trochanteris muscles (open arrowhead in Fig. 5, top) and a cessation of activity in the anterior rotator coxae muscle 121a. Muscle 121p was silent (some small-amplitude crosstalk from another muscle is visible in Fig. 5A). Tibial extension to the point where the contralateral tarsus touched the ground (see Fig. 2F) was driven solely by slow extensor tibiae (SETi) motor activity (Fig. 5B, not visible in the particular recording illustrated in Fig. 5A), but at this point the fast extensor tibiae (FETi) was usually (88%) recruited to fire 1–5 times (asterisks in Fig. 5A, top) while the levator trochanteris muscles remained active. FETi activity drove a rapid extension of the tibia (see Fig. 2C,D). As the leg lifted from the ground and was abducted as it swung over the rotating body (see Fig. 2H), activity resumed in both coxal rotators 121a and 121p (filled arrowheads in Fig. 5A, top). Activity in the levator trochanteris muscles declined as the femur was depressed (see Fig. 2J) and the tibia flexed to bring the tarsus back into contact with the ground. SETi spiked again as the tarsus touched down (Fig. 5A,B).

Movements of the ipsilateral hind leg were driven by a different pattern of motor activity in the same muscles (bottom panels of four traces in Fig. 5A,B). Femoral levation began 80–100 ms after that of the contralateral leg, but was similarly driven by a burst of activity in the levator trochanteris muscles (open arrowhead in Fig. 5A, bottom). In the ipsilateral leg, however, this levation was accompanied by a prolonged burst of large-amplitude potentials in the posterior rotator coxae muscle 121p (filled arrowhead in Fig. 5A, bottom). The anterior rotator coxae muscle 121a was sometimes active at the start of righting, but this activity ceased as activity started

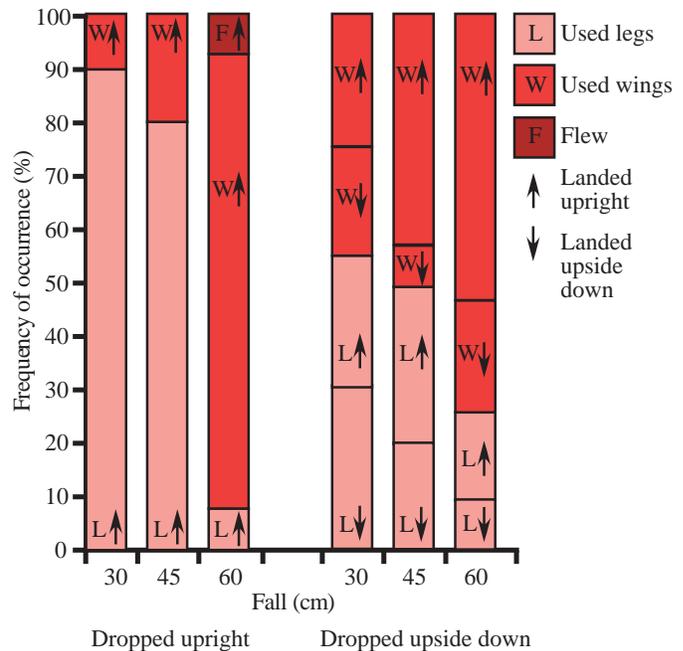


Fig. 6. Landing orientation and falling behaviour depended on free fall height. Locusts dropped upright (left half of figure) always landed upright (upward-pointing arrows) irrespective of their behaviour (L and pink columns, extended legs; W and red columns, extended wings; F and brown column, flew). When dropped upside down (right half of figure), locusts landed either upright (upward-pointing arrows) or upside down (downward-pointing arrows). $N=30$ trials from three animals dropped upright, and 50 trials from 10 animals dropped upside down.

in muscle 121p (Fig. 5B). As the animal rolled further onto its ipsilateral side so that this leg was under the body (see Fig. 2F), there was always a burst of activity in muscle 121a (double filled arrowhead in Fig. 5A, bottom). Once the ipsilateral tarsus touched the ground (see Fig. 2H), there was a burst of slow extensor tibiae activity (asterisk in Fig. 5, bottom). In 39% of normal righting movements, the ipsilateral FETi also fired (Fig. 5B), but it produced at most a single spike. If a locust slipped on the ground during righting, the FETi motor neurones of both hind legs often fired several times.

Righting during free fall

Locusts that were dropped from an upright position maintained this orientation to land upright in every trial (Fig. 6; three animals, 10 trials each). Locusts that were dropped from an upside-down position also landed upright in many cases, and successful mid-air righting was more likely for greater falling heights (30 cm, 49.1% landed upright; 45 cm, 72.7% landed upright; 60 cm, 70.7% landed upright; 10 animals, five trials each at each height; Fig. 6). Locusts that did not land upright always started righting behaviour on the ground within 30 ms of landing, as described above.

Behaviour during each free fall trial was classified into one of three categories: (i) 'leg extension', in which the locust

extended its hind leg tibiae but did not unfold its wings; (ii) 'wing extension', in which the locust extended and perhaps flapped its wings, but landed less than 20 cm from the vertical; and (iii) 'flight', in which the animal flew or glided so that it landed more than 20 cm away from the vertical. Regardless of starting orientation or height, locusts either extended their legs or extended both their wings and legs. For both starting orientations, however, more animals extended their wings when dropped from the greater heights (Fig. 6). A few animals flew for more than 20 cm, but only when dropped upright from 60 cm (Fig. 6).

Dead locusts that were dropped upside down also landed upright in many cases, with the probability of landing upright increasing with the height of the fall (30 cm, 28% landed upright; 45 cm, 52% landed upright; 60 cm, 68% landed upright; five animals, five trials at each height).

Discussion

We have shown that locusts placed upside down on a smooth surface perform a characteristic and asymmetrical sequence of leg movements that reliably turn the animal upright within a few hundred milliseconds. Locusts dropped from heights of more than 45 cm can right themselves in mid-air using both passive and active mechanisms.

Contact righting is driven by the contralateral hind leg

The considerable flexibility afforded by the complex subcoxal and coxo-trochanteral joints in the locust means that the hind legs can reach far dorsally and laterally so that their contact with the ground is maximally effective in driving rotation of the body. The front and middle legs are not required for righting, although they can assist initial destabilisation and, at the end of righting, they help stop the locust's rotation and stabilise its posture. The main torque necessary for contact righting in locusts is therefore provided by the large hind legs, especially the contralateral hind leg, which acts against the ground during femoral levation and tibial extension.

The relatively long femoral and tibial segments of the hind legs mean that the contralateral leg can act as an effective lever to generate high rotational velocities, but the ipsilateral leg (on the downward side) must be moved as the animal rolls over it so that it does not obstruct the rotation. During the roll, the contralateral hind tarsus is moved in an arc of decreasing radius as the leg swings over the body. This causes the tarsus, and thus the centre of mass of the entire leg, to move closer to the centre of rotation of the whole animal, decreasing the inertia of the body and contributing to the increased angular velocity of the roll between 200 and 400 ms.

Motor patterns in righting, walking, kicking and jumping

Hind leg movements used during righting in locusts are asymmetrical, with each leg playing a different role in the behaviour. The movements occur in a single non-repeating sequence rather than a rhythmical pattern and thus differ at a gross level from hind leg movements made during walking,

which are both symmetrical and rhythmical, from those used during jumping, which although non-rhythmical are symmetrical and ballistic, and from those used during kicking, which although asymmetrical are non-rhythmical and involve the hind leg on only one side of the body. The motor activity underlying a single righting movement is also different from that underlying a single step cycle (see Duch and Pflüger, 1995), a kick or a jump (Heitler and Burrows, 1977) both in timing and in recruitment of motor neurones.

The large hind leg tibial extensor muscle can produce powerful and rapid contractions that are essential for jumping and kicking in locusts (see Burrows, 1996). A characteristic feature of these behaviours is co-contraction of the tibial extensor and flexor muscles during which the fast extensor tibiae motor neurone fires for 150–500 ms at frequencies of up to 100 Hz. During walking, FETi is usually inactive, and such co-contractions do not occur (see Burrows, 1996). During righting, FETi of the ipsilateral leg is generally inactive, and there is no co-contraction in either hind leg. FETi of the contralateral leg fires just 0–5 times at frequencies usually in the range 5–20 Hz, but sometimes reaching 65 Hz for one or two spikes. This use of FETi in righting is therefore intermediate between the powerful activation seen in jumping or kicking and the lack of activation seen in walking.

The patterns of activity in hind leg coxal rotator muscles M121a and M121p also differ between walking and righting. Muscle 121a is innervated by a single excitatory motor neurone which may be weakly active on both the left and right sides of the animal at the start of righting, but then stops firing. The ipsilateral motor neurone begins firing again at up to 120 Hz as the animal rolls over the ipsilateral leg, and the contralateral motor neurone begins firing at a similar rate approximately 100 ms later as the contralateral leg lifts off the ground and passes over the animal. During walking, however, the motor neurone to M121a fires almost continuously on both sides at frequencies up to 50 Hz, although the spike rate is highly variable and its pattern of activity is unrelated to the step cycle (Duch and Pflüger, 1995). At the start of righting, the single motor neurone to M121p is also inactive on both sides. The ipsilateral motor neurone produces a burst of approximately 20 spikes at up to 130 Hz as the ipsilateral femur is levated, whereas the contralateral motor neurone produces just a few spikes as the contralateral leg lifts off the ground. During walking, the motor neurone to M121p is either inactive or fires only a few times during each cycle of leg protraction. During upside-down walking, it fires a burst of 20 spikes at up to 40 Hz during protraction (Duch and Pflüger, 1995). Modulation of the activity of both coxal rotator muscles M121a and M121p is therefore stronger and more precisely timed during righting than during walking. During righting, the patterns of activity on the two sides are different and can be related precisely to the asymmetrical movements made by the legs.

The motor patterns driving hind leg movements in walking and grooming locusts also differ from one another, with tibial extension occurring during femoral levation in grooming, but during femoral depression in walking (Berkowitz and Laurent,

1997). The marked differences between the motor patterns used for righting, stepping and grooming in the locust contrast strongly with the reported similarity between cockroach motor patterns for these three behaviours (Reingold and Camhi, 1977). In cockroaches, leg muscle burst durations, interburst intervals and the phasing of antagonist muscles differ only a little between behaviours.

Righting strategy is correlated with body plan

In those animals whose righting has been studied in detail, including toads (Robins et al., 1998), turtles (Ashe, 1970), cockroaches (Camhi, 1977; Full et al., 1995), rats (Pellis et al., 1991a), cats (Magnus, 1924) and locusts (this study), contact-righting always involves rotation around a longitudinal axis. These animals are relatively long and narrow, so the observed rotation requires a minimum of torque. This may also explain why locusts generally keep their wings folded throughout righting. Opening them would increase the width of the animal and thus its drag and inertia, could impede leg movements and would increase their risk of being damaged. Despite this overall similarity in righting between animals, there are consistent differences in the patterns of movements used by each, which can be related to their body plans.

Cockroaches, unlike locusts, are poor at righting themselves (*Gromphadorhina portentosa*, Camhi, 1977; Sherman et al., 1977; *Blaberus discoidalis*, Full et al., 1995). This can be attributed primarily to their broad flat body and their leg geometry, with the coxae relatively nearer to the midline than those of a locust. When cockroaches are upside down, the lateral margins of the body and wings prevent large-amplitude dorsal (downwards) movements of any of the legs, so that, even when the tarsi touch the ground, they are often unable to exert sufficient force to rotate the animal. In striking contrast, the body geometry of a locust means that its contralateral hind leg provides a long lever that generates most of the required force to pivot the animal about the ipsilateral legs and body surface. The quick and reliable righting behaviour of locusts would clearly be advantageous to these animals that might often land upside down after jumping or flying.

Turtles placed upside down face similar problems to cockroaches because they also have a broad flat body and relatively short legs that cannot easily touch the ground. Like cockroaches, they are poor at righting on smooth substrata (Ashe, 1970). To right themselves, they extend their head and sometimes their tail dorsally to lift the carapace so that the whole animal rolls to one side. Twisting of the neck and tail, together with movements of the lower ('ipsilateral') legs that push against the ground, then flip the animal over. This strategy is therefore similar to that used by cockroaches and differs from that used by locusts.

Toads placed upside down right themselves using movements of their hind legs (Robins et al., 1998) that resemble those used by locusts. Both animals have large hind legs specialised for jumping, and in the initial phase of righting use the contralateral hind leg to push off from the ground (Robins et al., 1998; this study). Toads can also use an

alternative mechanism in which the contralateral hind leg is thrown across the body to generate rotational momentum and to shift the centre of gravity. We did not observe any similar movements in locusts, perhaps because the hind leg is too light to generate sufficient momentum. In toads, the ipsilateral hind leg is largely passive during righting; in locusts, it is used actively. Femoral depression and tibial extension contribute to the ongoing rotation, and activation of anterior rotator coxae muscles in the ipsilateral leg as it passes under the animal suggests that lateral (downwards) force is also applied to the ground by the femur, which would contribute further to the rotation.

A wingless stick insect (*Eurycantha calcarata*, 15 cm length, weighing 30 g) also rights itself using rapid levation of its contralateral hind leg, but this movement is combined with dorsal levation of the contralateral front leg and a strong dorsal arching movement of the abdomen, which together lift and tip the animal over. The ipsilateral front leg is levated as the body rolls over it, and this leg then contributes to the second half of the roll. Unlike in the locust, however, the ipsilateral hind leg is not levated to move it out of the way, and it often impedes the roll, ending up folded underneath the standing animal (T. Matheson and O. Morris, personal observation). The use of the abdomen and forelegs presumably helps to overcome the large mass of this stick insect and compensates for the inability of the relatively short hind legs to generate sufficient dorsally directed force to roll this heavy insect past the point of no return.

Rats and cats make use of their considerable axial flexibility to right themselves by first rotating their shoulders to carry the neck and head into an upright position, and then rotating the body to bring the hind legs into contact with the ground (rats, Pellis et al., 1991a; cats, Magnus, 1924). Such a strategy is not possible for the locust, in which all the legs arise from the relatively rigid thorax.

Locusts show handedness

Individual locusts right preferentially towards one side, but there is no overall general preference for either the left or the right, unlike toads which are usually right-handed (Robins et al., 1998). It is not known whether cockroaches have a preferred righting direction, but because their righting begins with an erratic destabilisation of their body position this seems unlikely. The preference of a locust to right towards one side is diminished when the animal has to roll uphill on an inclined substratum, suggesting that the lateralisation is subject to external mechanical factors. This interpretation is reinforced by the observation that manipulating the starting position of a hind leg can also influence the direction of righting. In particular, locusts preferentially roll away from the side on which a hind leg has been positioned laterally (this leg therefore becomes the 'contralateral' leg that drives the roll). This strategy has clear mechanical advantages because the lateral position of the driving leg would enable it to provide more torque around the longitudinal axis, and the ipsilateral leg, being already close to the body, would be less likely to

impede the movement. The contralateral hind leg always begins levating before the ipsilateral leg, suggesting that the asymmetry is present in neuronal circuits driving the movement and is not simply a reflection of differing muscle strength on the two sides. Coordination between the legs of walking stick insects may also be 'handed' (Foth and Graham, 1983). Phase coupling between the contralateral legs of a single body segment acts in both directions, but the leg on one side can exert a stronger effect on its counterpart than it, in turn, receives. This dominance is thought to be partly inherent to the animal but also partly dependent on external factors (Cruse, 1990). The asymmetric nature of locust righting must also be flexible, because individual locusts can right towards either side with equivalent sequences of movements, regardless of their preferred direction.

Locusts right themselves in mid-air

In contrast to righting on a solid substratum, righting behaviour in mid-water and mid-air allows an animal to rotate around all three body axis with fewer mechanical constraints. As there is no solid surface from which to push off, animals must generate a rotation in some other way. Cats and other mammals (e.g. Magnus, 1924; Pellis et al., 1991b) solve this elegantly with zero-torque rotations of their body (Arabyan and Tsai, 1998) in which an appendage such as the tail is rotated around their longitudinal body axis in a direction counter to the rotation of the body. Other animals, such as arthropods, exploit aerodynamic or hydrodynamic surfaces to generate the necessary torque. Lobsters (*Nephrops norvegicus*) use asymmetrical movements of their swimmerets and uropods to roll back upright with rotation about the longitudinal body axis. Alternatively, if their initial orientation is exactly inverted, lobsters use symmetrical beating of their swimmerets to swim forwards in a head-down looping trajectory in which rotation is therefore about a transverse (pitch) axis as they turn upright (Newland and Neil, 1987).

Locusts are able to land upright if dropped upside down from heights above 30 cm, partly because of the passive aerodynamic properties of their anatomy and partly because of their active use of the aerodynamic properties of their wings. Locusts clearly employ different righting strategies when falling or when righting on the ground. In contrast, the cockroach *Gromphadorhina portentosa* makes the same righting movements as soon as its tarsi lose contact with the ground, regardless of the animal's orientation (Camhi, 1977). Some turtles also make righting movements when suspended upright in air with their feet clear of the ground (Ashe, 1970) or when exposed to zero gravity (Wassersug and Izumi-Kurotani, 1993).

Thanatosis and sensory signals that influence the initiation of righting

Thanatosis in *S. gregaria* is similar to that described in the cricket *Gryllus bimaculatus* (Nishino and Sakai, 1996): it can be induced in a similar way by lateral pressure applied to the pronotum, and it can be terminated by sudden mechanical,

visual or auditory stimuli. Its duration, however, is shorter in locusts (mean 73 s) than in crickets (mean 187 s; Nishino and Sakai, 1996). Thanatosis does not affect the sequence of movements used in subsequent righting behaviour. Locusts turned themselves upright immediately upon arousal irrespective of whether thanatosis was induced before or after they had been turned into the upside-down position.

Sensory mechanisms that signal loss of contact between the tarsi and the ground and those that signal the inverted posture of the animal must either remain active throughout thanatosis or be reactivated immediately on arousal. Locusts that were placed upside down and given a foam ball to grasp did not initiate righting when thanatosis ended, but walked instead, indicating that there is a strong inhibitory interaction between tarsal sensory systems signalling loss of contact and those signalling body angle of rotation.

Design principles

Locusts, rats, cats and toads all right themselves quickly and reliably, whereas cockroaches and turtles are less adept at righting. To our knowledge, no current hexapedal robot design incorporates a righting strategy. For example, a computational algorithm that generates robust hexapedal walking gaits (Cruse et al., 1998) recovers well from stumbling, but cannot turn itself over if it falls upside down (H. Cruse, personal communication). What can be learned from comparisons of the righting strategies used by different animals?

The righting problem may be separated into the problem of generating sufficient angular momentum to roll over and the problem of coordinating the limbs to prevent damage or obstruction of the roll. What features of locust righting may be valuable in improving robot design? First, the body should be long and narrow to reduce angular inertia for a roll about the longitudinal axis, but the limbs must provide sufficient stability to prevent the machine from tipping over in the first place. This would require relatively long limbs, so it may be advantageous to fold all but the driving limb out of the way, at least until the robot passes the point of no return during a roll. It may also be advantageous for the other limbs to have different dimensions, perhaps optimised for locomotion. Second, the limbs that drive a roll must be able to make large-amplitude dorsal movements to act downwards against the ground. Third, these movements must generate sufficient force and, therefore, angular momentum to carry the whole machine through the point of no return once the driving limb leaves the ground. Lighter robots and those with most of their mass near the centre of rotation will require less force. The stick insect strategy of using the ipsilateral front leg to complete the roll once the contralateral hind leg leaves the ground may be useful for heavier or slower robots. Finally, the robot must have sensors that detect loss of limb contact with the ground and signal body orientation with respect to gravity so that it can calculate the most favourable direction to roll, even on a sloping surface.

We thank M. Burrows, V. Dürr, B. Hedwig, O. Morris and P. Riewe for valuable comments on a draft of the manuscript.

This work was funded by a studentship from the Studienstiftung des Deutschen Volkes and a scholarship from the Cambridge European Trust to A.A.F., grants from the Royal Society and BBSRC to T.M. and a grant from the BBSRC to M. Burrows.

References

- Arabyan, A. and Tsai, D.** (1998). A distributed control model for the air-righting reflex of a cat. *Biol. Cybernetics* **79**, 393–401.
- Ashe, V. M.** (1970). The righting reflex in turtles: a description and comparison. *Psychon. Sci.* **20**, 150–152.
- Bässler, U. and Foth, E.** (1982). The neural basis of catalepsy in the stick insect *Cuniculina impigra*. I. Catalepsy as a characteristic of the femur–tibia control system. *Biol. Cybernetics* **45**, 101–105.
- Berkowitz, A. and Laurent, G. J.** (1997). Local control of leg movement and motor patterns during grooming in locusts. *J. Neurosci.* **16**, 8067–8078.
- Bisazza, A., Cantalupo, C., Robins, A., Rogers, L. J. and Vallortigara, G.** (1996). Right-pawedness in toads. *Nature* **379**, 408.
- Bräunig, P.** (1982). The peripheral and central nervous organization of the locust coxo-trochanteral joint. *J. Neurobiol.* **13**, 413–433.
- Burrows, M.** (1995). Motor patterns during kicking movements in the locust. *J. Comp. Physiol. A* **176**, 289–305.
- Burrows, M.** (1996). *The Neurobiology of an Insect Brain*. Oxford, New York, Tokyo: Oxford University Press.
- Camhi, J. M.** (1977). Behavioral switching in cockroaches: transformations of tactile reflexes during righting behavior. *J. Comp. Physiol. A* **113**, 283–301.
- Cruse, H.** (1990). What mechanisms coordinate leg movement in walking arthropods? *Trends Neurosci.* **13**, 15–21.
- Cruse, H., Kindermann, T., Schumm, M., Dean, J. and Schmitz, J.** (1998). Walknet – a biologically inspired network to control six-legged walking. *Neural Networks* **11**, 1435–1447.
- Duch, C. and Pflüger, H.-J.** (1995). Motor patterns for horizontal and upside-down walking and vertical climbing in the locust. *J. Exp. Biol.* **198**, 1963–1976.
- Faisal, A. A. and Matheson, T.** (1999). Locusts show characteristic righting behaviour. In *Proceedings of the 27th Göttingen Neurobiology Conference* (ed. N. Elsner and U. Eysel), p. 238. Stuttgart, New York: Georg Thieme Verlag.
- Field, L. H. and Burrows, M.** (1982). Reflex effects of the femoral chordotonal organ upon leg motor neurones of the locust. *J. Exp. Biol.* **101**, 265–285.
- Foth, E. and Graham, D.** (1983). Influence of loading parallel to the body axis on the walking coordination of an insect. II. Contralateral effects. *Biol. Cybernetics* **48**, 149–157.
- Full, R. J., Yamauchi, A. and Jindrich, D. L.** (1995). Maximum single leg force production: cockroaches righting on photoelastic gelatin. *J. Exp. Biol.* **198**, 2441–2452.
- Godden, D. H.** (1974). The physiological mechanism of catalepsy in the stick insect *Carausius morosus* Br. *J. Comp. Physiol. A* **89**, 251–274.
- Harris, J.** (1978). A photoelastic substrate technique for dynamic measurements of forces exerted by moving organisms. *J. Microsc.* **114**, 219–228.
- Harris, J. and Ghiradella, H.** (1980). The forces exerted on the substrate by walking and stationary crickets. *J. Exp. Biol.* **85**, 263–279.
- Heitler, W. J. and Burrows, M.** (1977). The locust jump. I. The motor programme. *J. Exp. Biol.* **66**, 203–219.
- Lauback, S.** (1999). Mars rover: July 4, 1999, and beyond. *ACM Crossroads* **4** (3), 3–7.
- Magnus, R.** (1924). *Körperstellung*. Berlin: Springer.
- Newland, P. L. and Neil, D. M.** (1987). Statocyst control of uropod righting reactions in different planes of body tilt in the Norway lobster *Nephrops norvegicus*. *J. Exp. Biol.* **131**, 301–321.
- Nishino, H. and Sakai, M.** (1996). Behaviourally significant immobile state of so called thanatosis in the cricket *Gryllus bimaculatus* DeGeer: its characterization, sensory mechanism and function. *J. Comp. Physiol. A* **179**, 613–624.
- Pellis, S. M., Pellis, V. C. and Teitelbaum, P.** (1991a). Air righting without the cervical righting reflex in adult rats. *Behav. Brain Res.* **45**, 185–188.
- Pellis, V. C., Pellis, S. M. and Teitelbaum, P.** (1991b). A descriptive analysis of the postnatal development of contact-righting in rats (*Rattus norvegicus*). *Dev. Psychobiol.* **24**, 237–263.
- Reingold, S. C. and Camhi, J. M.** (1977). A quantitative analysis of rhythmic leg movements during three different behaviors in the cockroach, *Periplaneta americana*. *J. Insect Physiol.* **23**, 1407–1420.
- Robins, A., Lippolis, G., Bisazza, A., Vallortigara, G. and Rogers, L. J.** (1998). Lateralised agonistic responses and hindlimb use in the toad. *Anim. Behav.* **56**, 875–881.
- Sherman, E., Novotny, M. and Camhi, J. M.** (1977). A modified walking rhythm employed during righting behavior in the cockroach *Gromphadorhina portentosa*. *J. Comp. Physiol. A* **113**, 303–316.
- Taylor, D.** (1999). AIBO: AI that works like a dog to entertain you. *IEEE Intell. Syst. App.–Intelligencer* **14**, 7–8.
- Wassersug, R. and Izumi-Kurotani, A.** (1993). The behavioural reactions of a snake and a turtle to abrupt decreases in gravity. *Zool. Sci.* **10**, 505–509.