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The kinematics and neural control of high-speed kicking movements in the locust

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Summary

The tibiae of locust hind legs can be extended fully in a kick in 3 ms with peak angular velocities of at least 80 ° ms^{-1}. If the mass of the distal part of the leg is halved, then the extension is complete in less than 1 ms with angular velocities of more than 200 ° ms^{-1}. The high velocities and the associated power are generated by a preceding storage of energy and its sudden release produced by a specific motor pattern and specialisations of the femoro-tibial joints. To understand the dynamics of these rapid movements and the interrelations between joint mechanics and the motor pattern, kicks were analysed with high-speed video images coupled to simultaneous intracellular recordings from identified leg motor neurones. The first movement is a full tibial flexion followed by co-contraction of the extensor and flexor tibiae muscles for 0.3–1 s, during which the distal end of the femur is flattened dorso-ventrally and expanded laterally. The two semi-lunar processes on the distal femur are bent when the fast extensor tibiae motor neurone spikes so that their tips move ventrally by up to 0.6 mm. The inward projections of these processes into the femur form the proximal part of the hinge joint with the tibia, so that the pivot of the joint also changes and the tibia therefore moves proximally and ventrally, widening the gap between it and the femur. Extension of the tibia begins on average 34 ms after the flexor motor neurones are inhibited at the end of the co-contraction phase. The tibia then begins to extend slowly, reaching peak velocities only when it has extended by 60–70 °. The semi-lunar processes do not start to unfurl until the tibia has extended by 55 °, so they cannot provide the initial energy for extension. An audible click is produced when the semi-lunar processes unfurl. The peak velocity of tibial extension is correlated with the amount of bending of the semi-lunar processes and with the number of fast extensor motor spikes, but the same amount of semi-lunar bending can be produced by both short and long co-contractions. When the tibia reaches full extension, inertial forces may cause it to bend by as much as 33 ° at a plane of weakness in the proximal tibia, thus allowing further extension of the distal end.

Key words: kinematics, joint mechanics, locomotion, motor pattern, locust, *Schistocerca gregaria*, kicking.

Introduction

The conflicting requirements of muscle to produce contractions that are both rapid and powerful has led to specialisations of joint mechanics or motor patterns when movements necessitating both these characteristics must be generated. Such muscular requirements are widespread in the behaviour of animals, but are exemplified in the prodigious jumping and kicking movements of locusts and grasshoppers. Rapid extension of the tibiae of both hind legs provides the propulsive force by which these insects jump to avoid predators and to initiate flight or, as larvae, to increase their speed of locomotion by hopping. Rapid and powerful extensions of individual hind legs are also used to kick at predators or conspecifics.

During jumping, the hind tibiae are extended in 20–30 ms (Brown, 1967) so that a locust can take off at a velocity of 3.1 m s^{-1}. Each extensor tibiae muscle in the hind legs can generate peak force only slowly, in 350–500 ms, but the power output of 0.5 mW kg^{-1} is high (Bennet-Clark, 1975). Kicking to repel adversaries involves an even more rapid extension of the hind tibiae, often independently, but with a tarsus lifted from the ground and the leg rotated at the coxa so that it can be aimed effectively. We do not, however, know the velocities of movements involved or the relationships between muscle actions and joint movements in kicking.

The high velocity and power output required for these ballistic movements can only be produced if the leg muscles contract slowly before the movement to store force in deformations of the cuticle (Bennet-Clark, 1975; Brown, 1967; Godden, 1975; Heitler and Burrows, 1977a). Successful kicks and jumps therefore result from a complex interplay between the neurally generated motor pattern and the mechanics of the joint, muscles and apodemes. Neither the neural nor the mechanical specialisations are present in the other two pairs of legs. The motor pattern consists of three phases (Burrows, 1995; Heitler and Burrows, 1977a): (i) an initial cocking phase during which the tibia is fully flexed about the femur; (ii) co-contraction of the flexor and extensor tibiae muscles, and (iii) a triggering phase during which inhibition of the flexor motor neurones allows a rapid and powerful tibial extension. The required force is generated during the co-contraction phase by a slow and almost isometric contraction of the large extensor tibiae muscle once the tibia has been locked in the fully flexed position. Co-contraction of the smaller flexor is able to counter the contraction of the extensor because of the mechanical advantage it enjoys over the extensor when the femoro-tibial joint is fully flexed and the engagement of the flexor tendon in a specialised lock (Heitler, 1974). More than half the energy is stored in distortions of the semi-lunar processes of the femur at the joint with the tibia (4 mJ in one leg at peak stresses of 15 N), just under half (3 mJ) in the apodeme (tendon) of the extensor tibiae muscle and a small amount (0.3 mJ) in the walls of the femoral cuticle of each hind leg on which the extensor muscle fibres insert (Bennet-Clark, 1975). We do not, however, know when these stored forces are delivered to power the extension of the tibia or whether they all act at the same time.

To determine the critical sequence of events that leads to these high-velocity and powerful movements, high-speed video images with a resolution of 0.5 ms were captured of kicks to show the tibial movements and distortions of the femoro-tibial joint. These were synchronised with simultaneous intracellular recordings from the leg motor neurones involved in generating the required forces in the muscles that move the tibia. This paper shows for the first time the detailed anatomy of the femoro-tibial joint of the hind legs, the sequence of joint distortions and movements that occurs during a kick and how these are effected by the actions of known motor neurones.

Materials and methods

Mature adult locusts, *Schistocerca gregaria* (Forskål), of either sex and at least 2 weeks after their final moult were used from our crowded laboratory culture. They were fixed ventral surface uppermost in Plasticine with the tibiae and tarsi of both hind legs free to move throughout their full range. All experiments were performed at room temperatures of 20–22 °C. During a kick, high-speed images were made either of the movements of one entire hind leg or of the proximal tibia and the semi-lunar processes at the femoro-tibial joint. The high-speed camera (Red Lake Imaging, San Diego, CA, USA) and associated computer enabled images to be captured at rates of 500–2000 s^{-1} with exposure times of 1–0.25 ms. Unless stated otherwise, kicks were captured at 1000 images s^{-1} and with an exposure time of 0.5 ms. In the figures, the images are timed from the point (0 ms) when the tibia reaches full extension. Lighting was provided by two Schott 1500 cold light sources and fibre-optic guides. Selected images were stored as computer files for later analysis with the Motionscope camera software (Red Lake Imaging, Morgan Hill, CA, USA) or with Canvas (Deneba Systems Inc, FL, USA). One hundred and forty-four kicks by 17 locusts evoked by touching hairs on the proximal part of the abdomen or hind legs were recorded, and 51 of these were analysed.

Intracellular recordings were made from identified motor neurones of hind-leg muscles during kicks. The meso- and metathoracic ganglia were stabilised on a wax-coated platform, and the thorax was perfused with a continuous flow of locust saline. The sheath of the metathoracic ganglion was treated with a 1 % (w/v) solution of protease (Sigma type XIV) for 1–2 min to facilitate penetration of the somata of motor neurones. Glass microelectrodes were filled with 2 mol l^{-1} potassium acetate and had resistances of 50–80 MΩ. Motor neurones were characterised by correlating spikes recorded intracellularly in their somata with the movement of a leg joint caused when such spikes were evoked by intracellular injection of current. As an aid to further identification, pairs of 50 μm diameter stainless-steel wires, insulated but for their tips, were inserted into particular muscles to stimulate the axon terminals of their motor neurones and evoke antidromic spikes. These wires were also used to record the electrical activity of the muscles. Evoking a spike in the fast extensor tibiae (FETi) motor neurone caused a characteristic monosynaptic depolarising synaptic potential in flexor tibiae motor neurones (Burrows et al., 1989). These procedures gave unequivocal identification of FETi but did not distinguish between the nine different flexor tibiae motor neurones.

Recordings were always made from two motor neurones, one of which was FETi and the other a flexor. The electrical recordings were written directly to a computer with a CED (Cambridge Electronic Design, Cambridge, UK) interface running Spike2 software and sampling each trace at 5 kHz. To enable these electrical recordings to be synchronised with the video images, which were written to a second computer, two sets of synchronising signals were generated and were fed to separate channels on the CED interface and to the video. First, the spikes recorded intracellularly in FETi triggered 1 ms pulses from a window discriminator and these, in turn, were used to generate light pulses recorded on the video. Second, pressing a hand switch at random intervals generated 1 ms pulses that were used to trigger a second series of light signals on the video. Events recorded on the video images could therefore be related to the electrical activity of the motor neurones at the resolution of one image.

The sound generated by a leg when kicking was recorded by placing a microphone 30 mm from the dorsal surface of the proximal tibia. At 20 °C, the sound would take approximately 0.09 ms to travel from the leg to the microphone. Simultaneous intracellular recordings and video images were made during 88 kicks by 10 locusts. Sound and motor neurone or muscle activity were recorded for a further 29 kicks in five locusts, of which eight were analysed in detail.

The mass of the tibia was altered by the addition of small Plasticine weights or by removing distal sections of the tibia in nine animals during 44 kicks, of which 30 were analysed.

Results

Structure of the femur and tibia

The distal part of the femur has features that are not present on the other legs and that are presumably part of the specialisations for kicking and jumping (Fig. 1). Especially prominent on the distal femur are two black, highly sclerotised, longitudinally laminated semi-lunar processes, one on the anterior and one on the posterior surface (Fig. 1A–D). Each weighs approximately 1.3 mg (Bennet-Clark, 1975) and is approximately 2.7 mm long and 0.8 mm wide at its widest point. The ventral distal parts of both semi-lunar processes are lighter in colour and bow outwards to form ventral domes at their most distal ends (Fig. 1A,C). The blacker dorsal and distal parts curve into the cavity of the femur to form peg-like projections some 0.5 mm long and with flat proximal edges (Fig. 1D). A V-shaped area of flexible membrane separates the distal end of a semi-lunar process ventrally from a thin, double-walled cover plate (Fig. 1A). This and the dorsal distal part of the femur are compressed during a kick. Ventrally, between the two cover plates, the femur is grooved to accommodate the proximal end of the tibia when it is fully flexed. When viewed anteriorly (laterally) or posteriorly (medially), therefore, the cover plates obscure the proximal tibia when it is fully flexed about the femur. Towards the proximal end of the ventral groove in the femur, the surface is invaginated to form a lump (Heitler, 1974) that projects dorsally inside the femur by approximately 0.7 mm (or approximately 30 % of the width of the femur at that point) and over which the tendon of the flexor tibiae muscle must slide. The extensor tibiae muscle inserts on the inner rim of the semi-circular most dorsal part of the tibia (Fig. 1B–D). Just ventral to this are two lateral curved horns with flat dorsal edges that are black and heavily sclerotised. The flexor tendon bifurcates to insert on either side of a groove on the ventral surface of the tibia.

The femoro-tibial joint

The joint between the tibia and the femur is a hinge that allows movement in one plane through approximately 160 °. The main part of the hinge is formed by the close apposition of the flat edges of the inward projections of the semi-lunar processes into the femur and the flat edges of the medial part of the tibial horns (Fig. 1B,D). These flat cuticular edges are each 0.5 mm long and are held tightly together by a stiff membrane. The width of the tibia from the lateral tips of the horns is almost 2 mm, more than double that of the remainder of the tibia, thus making a hinge joint that is wide, stable and strong. Further stability is provided by the lateral tips of the two tibial horns, which locate and rotate within the ventral domes of the two semi-lunar processes. As the joint progressively flexes, the curved horns of the tibia are accommodated in these domes of the semi-lunar processes, and the ventral part of the tibia moves between the two cover plates into the ventral femoral groove. In this way, the tibia can be pressed tightly against the femur along most of its length.

Movements of the tibia during a kick

Full tibial extension in a kick was completed on average in 6 ms, during which the tibia reached peak rotational velocities of 54.5±1.3 ° ms^{-1} (mean ± S.E.M., N=42 kicks). The fastest kicks took only 3 ms, with peak rotational velocities of at least 80 ° ms^{-1}. If the mass of the tibia was halved (from approximately 21 to 10 mg) by removing the tarsus and the distal part of the tibia, full tibial extension was completed in less than 1 ms, with peak angular velocities of 200 ° ms^{-1}. This experiment also reduced the surface area of the leg, and the increased velocity could therefore have been caused by reduced drag. If the mass of the tibia was increased by adding Plasticine weights to the same distal point to simulate the loading that would be experienced during jumping, peak velocities fell to 25 ° ms^{-1} but were sustained at this level when the loading was increased to 10 times the tibial mass.

The first movement in preparation for a kick was always a full flexion of the tibia about the femur without which only much slower extension movements of the tibia could occur. When the flexor muscle had pulled the tibia into its flexed position, the extensor and flexor tibiae muscles began to co-contract for periods usually of 200–1000 ms (Burrows, 1995; Heitler and Burrows, 1977a) – the co-contraction phase. When the flexor muscle relaxed, the tibia was rapidly extended – the kick movement. The following sequence of femoral distortions and tibial movements was seen during this sequence (Fig. 2, Fig. 3, Fig. 4).

The semi-lunar processes began to bend when the tibia was held fully flexed about the femur and continued to bend progressively throughout the co-contraction phase (Fig. 2A,B). The distal tip of a semi-lunar process moved on average by 0.4 mm, but in some kicks the movement was 0.6 mm so that the tips of the semi-lunar processes disappeared behind the dorsal edges of the cover plates. There were four consequences of the bending of the semi-lunar processes. First, the V-shaped gap formed by the flexible membrane between each semi-lunar process and its cover plate was obscured. Second, because the distal parts of the semi-lunar processes form the hinge about which the tibia articulates, the pivot of the joint also moved ventrally and proximally (Fig. 2A,B, Fig. 3A). Third, the progressive movement of the pivot resulted in a 0.3 mm ventral movement of the tibia and a 0.4 mm proximal movement so that the gap between it and the femur widened along their previously closely apposed surfaces (Fig. 2A,B). Fourth, the distal dorsal part of the femur was compressed by 20 % dorso-ventrally and expanded in width by 20 % laterally (Fig. 2B,D).

At the end of the co-contraction phase, the tibia began to accelerate slowly, extending through approximately 20 ° in the first 3 ms (Fig. 2A,C, Fig. 3B). During the initial extension, the semi-lunar processes did not move. It was not until the femoro-tibial angle reached 55.5±2.4 ° (mean ± S.E.M., N=6 kicks, images captured at 2000 s^{-1}) that they started to unfurl, and the velocity of extension increased to a peak that was sustained for an average of 3 ms (N=42 kicks) until the tibia slowed as it reached full extension. When the semi-lunar processes unfurled, the dorso-ventral compression of the femur was relieved, allowing it to return to its original shape. The energy stored in the bent semi-lunar processes could not therefore contribute to the initial extension of the tibia and could only

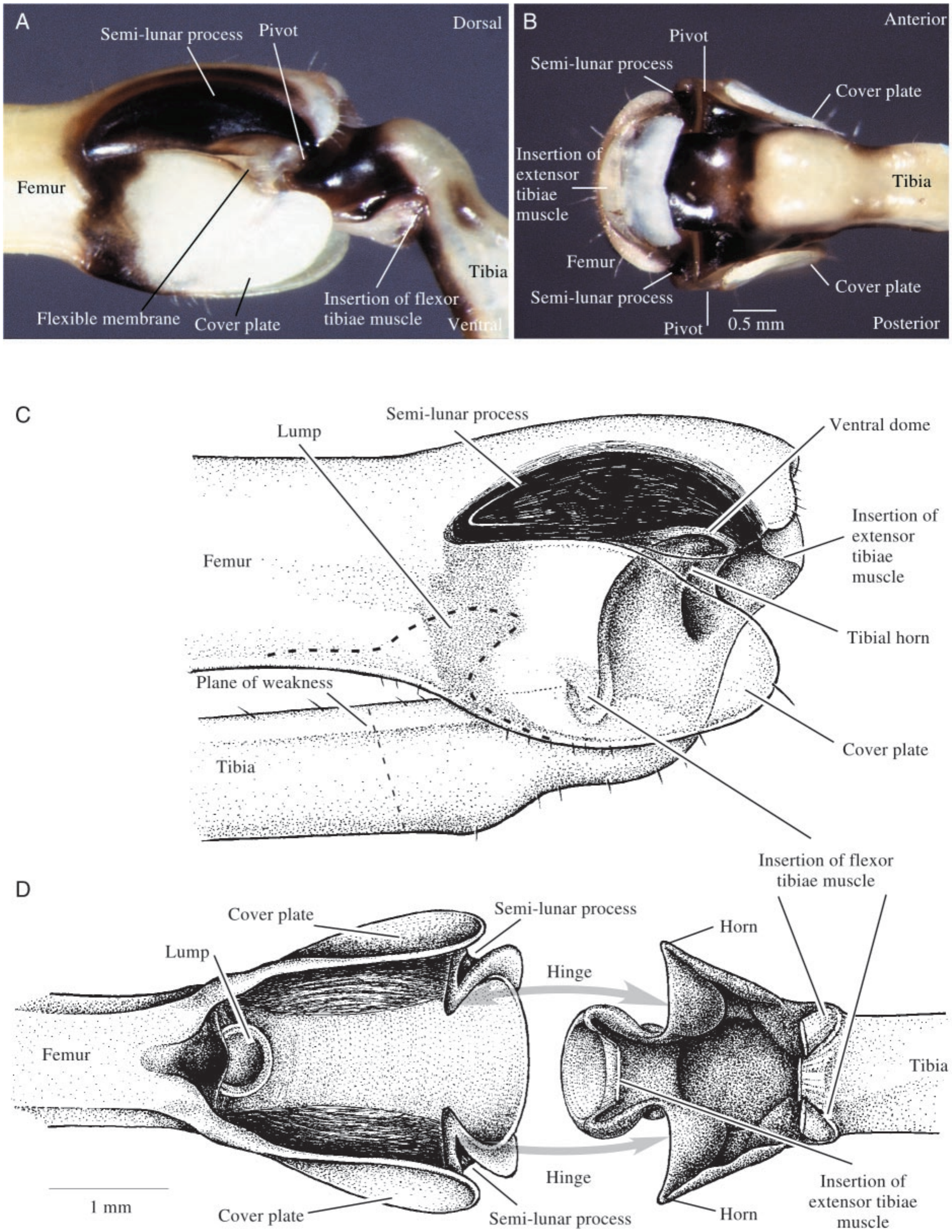

Fig. 1. Anatomy of the femoro-tibial joint of a left hind leg of a mature locust. (A) Photograph of the anterior (=lateral) surface. The semi-lunar processes and the proximal part of the tibia are black and heavily sclerotised. The curved horns of the tibia are engaged in the domes of the more lightly sclerotised ventral parts of the semi-lunar processes. (B) End-on photograph with the tibia held at an angle of approximately 90° relative to the femur. The hinge apposition of the flat surfaces of the two semi-lunar processes and the horns of the tibia are shown. (C,D) Drawings of the femoro-tibial joint. (C) Anterior surface with the tibia flexed about the femur. The anterior cover plate is drawn as though transparent to show a tibial horn engaged in the ventral dome of a semi-lunar process. The extent of the inwardly projecting process from the ventral wall of the femur, Heitler's lump, and the plane of weakness about which the tibia bends are indicated by dashed lines. (D) Ventral view of the distal femur and proximal tibia with the joint membrane and muscles removed to show the invaginations of the semi-lunar processes. The tendon of the extensor tibiae inserts on the dorsal wall of the tibia and that of the flexor, after splitting into two, on the ventral wall. The opposing surfaces of the femur and tibia that form the hinge joint are indicated by the curved arrows.

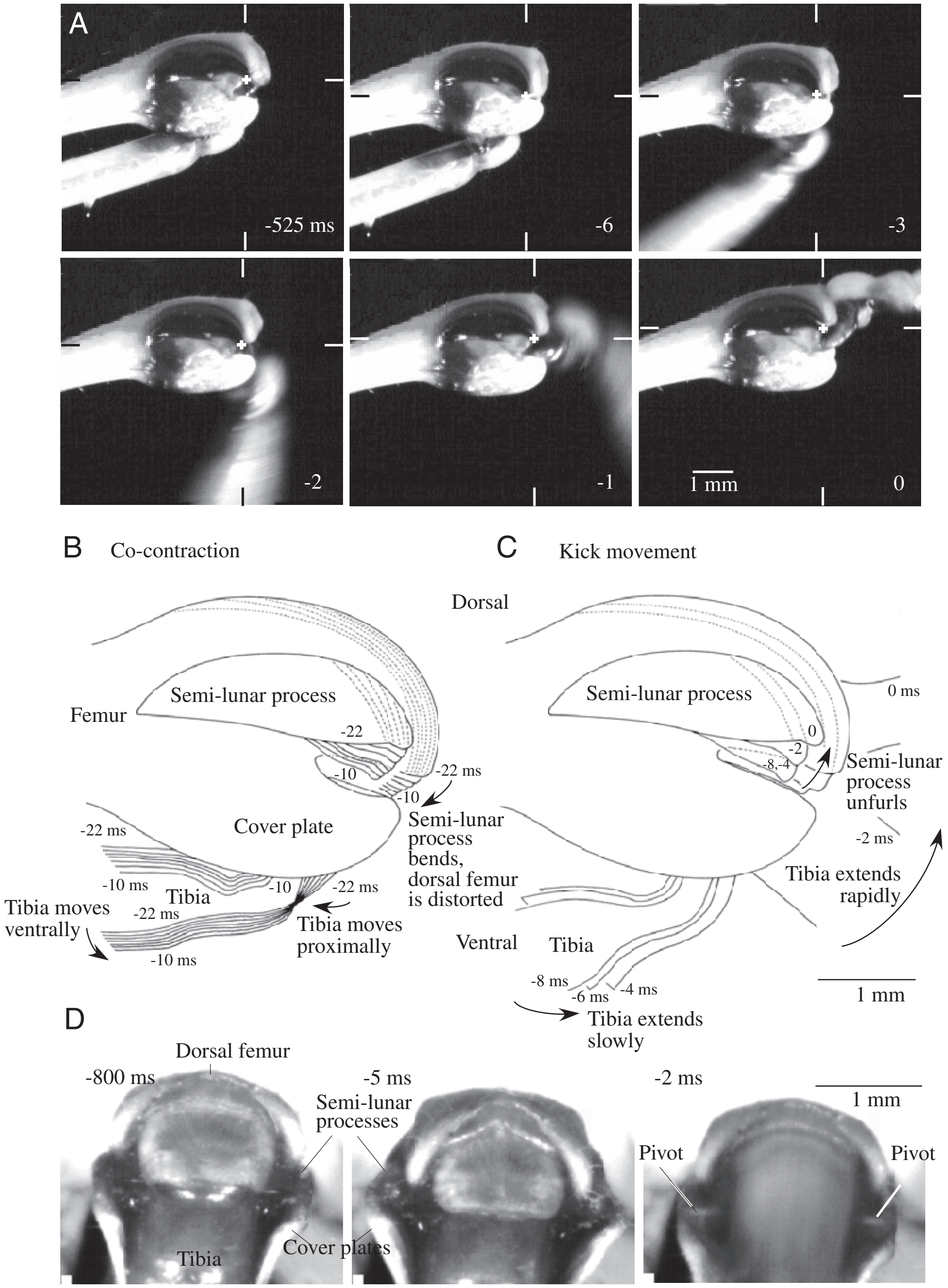

Fig. 2. Distortions of the femur and movements of the tibia during a kick. (A) Selected images taken at 1000 s^{-1}. At the start of co-contraction (–525 ms), the semi-lunar process is not distorted, but at the end of co-contraction (–6 ms) it is bent. The proximal movement of the tibia, seen by reference to the tibial spine in the first two images, results in a widening of the gap between the femur and tibia. As the tibia begins to extend, the semi-lunar process remains fully bent (–3 ms) and begins to unfurl only when the tibia has already extended by 58.5 ° (–2 ms). As the tibia extends further, the semi-lunar process unfurls to its original state (–1, 0 ms). The cross hairs here and in Fig. 5 and Fig. 6 are aligned on the distal tip of the semi-lunar process. (B,C) Superimposed tracings of individual images from a kick taken at 500 s^{-1} and with an exposure time of 1/2000 s. (B) Co-contraction. The anterior semi-lunar process is progressively bent from –22 to –10 ms and the dorsal and distal part of the femur is compressed. The tibia also moves progressively ventrally and proximally in its fully flexed position. (C) The rapid extension movement. From –8 to –4 ms, the tibia begins to extend gradually, but the semi-lunar process only begins to unfurl at –4 ms when the tibia is moving at its maximum velocity and appears as a blur (the outlines of the tibia show the extreme positions of its leading and trailing edges during this image). (D) Selected images of an end-on view of the femoro-tibial joint from a kick captured at 1000 s^{-1}. At the start of co-contraction (–800 ms), the tibia is fully flexed but the femur is not distorted. At the end of co-contraction (–5 ms), the femur is compressed dorso-ventrally and expanded laterally. As the tibia extends rapidly (–2 ms), the femur returns to its original shape.

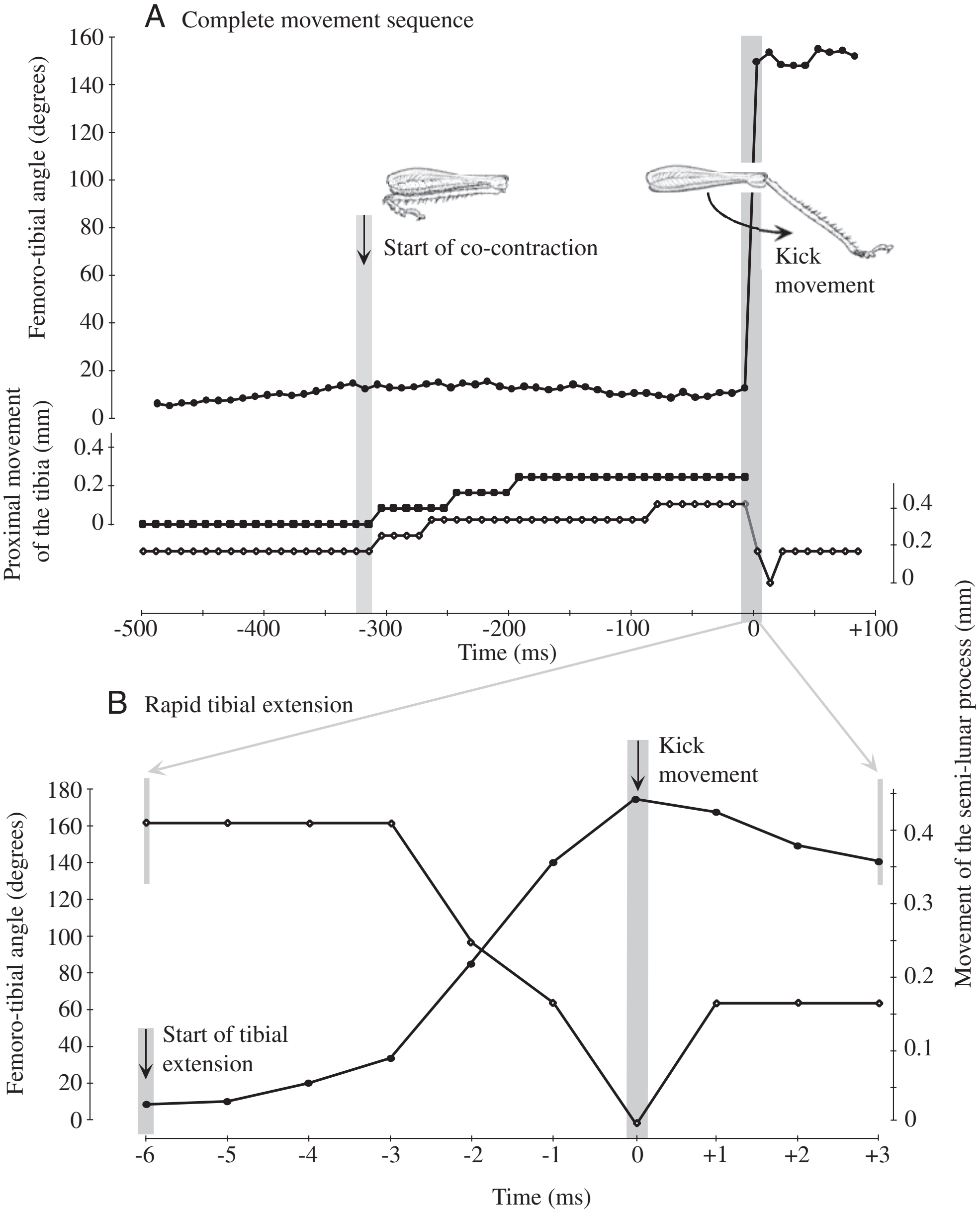

Fig. 3. Graphs of the movements of the tibia and of the distortions of the semi-lunar process during a kick captured at 1000 images s^{-1}. (A) The distortions of the semi-lunar process and the movements of the tibia during the complete sequence are measured from every tenth image (10 ms intervals). (B) An expanded portion during the rapid tibial extension in which measurements from each image (1 ms intervals) are plotted. The semi-lunar process unfurls only when the tibia has already begun to extend. Circles, femoro-tibial angle; squares, proximal movement of the tibia; diamonds, movement of the semi-lunar process.

power the rapid extension once the movement was already under way.

To determine whether distortions of the semi-lunar processes correlate with the velocity of tibial movements, differing velocities of tibial extensions were analysed, and three that represented the range observed were plotted against the extent of any accompanying distortions of semi-lunar processes (Fig. 4). A slow tibial extension (extension 1 in Fig. 4), took 20 ms to complete, reached a peak angular velocity of 11 ° ms^{-1}, but involved no distortion of the semi-lunar processes. In a second movement (kick 1), extension was completed in 12 ms and reached a peak velocity of 21 ° ms^{-1}. In this kick, the initial co-contraction distorted a semi-lunar process, but the maximal movement of its tip was only 0.15 mm. In the fastest movement of this series (kick 2), tibial extension took just 7 ms, with a peak velocity of 33 ° ms^{-1}, and the semi-lunar process was bent so that its tip moved by 0.4 mm. When data for 44 kicks in 10 locusts weres analysed, the extent of the distortion of a semi-lunar process and the peak velocity of tibial movement showed a positive correlation (r=0.653, N=47, P<0.01, Spearman rank correlation test): the greater the bending of the semi-lunar processes, the faster the tibial extension.

Motor pattern

High-speed images showed that the first spikes in an impaled flexor motor neurone were associated with the initial full flexion movement of the tibia but did not cause any distortion of a semi-lunar process (Fig. 5). Bending of a semi-lunar process started only after the first FETi spike and increased progressively during the period of high-frequency spiking of both the extensor and flexor motor neurones that marked the co-contraction phase. The result was that the semi-lunar process bent progressively so that, by the end of this phase, the gap between its distal tip and the cover plate was closed. In this particular kick, there was a pause in the sequence of FETi spikes during the co-contraction, and this was accompanied by a pause in the bending of the semi-lunar process that resumed only when the frequency of FETi spikes had risen once again. The end of the co-contraction phase was marked by rapid inhibition of the flexor motor neurone followed 23 ms later by the start of tibial extension. In eight other kicks from five locusts analysed with accompanying high-speed images, the delay between the intracellularly recorded inhibition of a flexor motor neurone and the first extension movement of the tibia averaged 34 ms (range 21–47 ms). In the example shown, FETi spikes stopped before those in the flexor so that 50 ms elapsed between its last spike and the start of the tibial movement. In the other kicks analysed in this way, the timing of the last FETi spike varied so that on some occasions it occurred only after the flexor spikes had been inhibited, while on others it occurred before. In all these examples, nevertheless, the FETi spikes stopped at least 15 ms before the start of the tibial movement.

The semi-lunar processes did not begin to unfurl until both motor neurones had stopped spiking and the tibia had begun to extend. In the kick illustrated in Fig. 5, the semi-lunar process remained fully bent until the tibia had extended to an angle of 50 °. Unfurling then occurred quickly during the rapid extension from 50 to 160 °, which was accomplished in 3 ms and when neither motor neurone was active.

The following features of the motor pattern were analysed in several kicks to determine whether they were correlated with each other and with the velocity of tibial movements; the duration of co-contraction and the number of FETi spikes during the whole co-contraction and during the last 100 ms of the co-contraction. The amount of distortion of the semi-lunar processes was not dependent upon the duration of the co-contraction because similar distortions could be produced by both short (approximately 200 ms) and long (approximately 800 ms) co-contractions. The number of FETi spikes during the whole co-contraction was positively correlated both with the amount of distortion of the semi-lunar processes (r=0.528, N=47, P<0.01) and with the peak velocity of a kick (r=0.562, N=47, P<0.01). If there were only a few FETi spikes, then the distortion of the semi-lunar processes was small and the tibia was extended slowly. The number of FETi spikes during the last 100 ms of the co-contraction was positively correlated with the degree of distortion of the semi-lunar processes (r=0.614, N=47, P<0.01) but only weakly with the peak velocity of the tibial movements (r=0.372, N=47, P<0.05). This suggests that the build-up of force during the whole co-contraction is important in the final outcome of the kick.

Tibial bending

The final angular velocity of the tibia in a kick was so great that when the femoro-tibial joint reached its maximal excursion inertial forces caused the tibia to bend at a proximal plane of weakness approximately 3 mm from the pivot of the femoro-tibial joint (Fig. 6) (Heitler, 1977). The result was that the distal part of the tibia extended further by as much as 33 °. This over-extension was then followed by a series of 2–4 cycles of damped oscillations of the tibia in which it first flexed though 20–40 ° and then extended again, in the absence of any motor spikes in the respective flexor and extensor muscles, to reach a final resting position near full extension. The tibial bending and the rebound movements are thus passive and the consequence of the preceding rapid extension. Active flexion of the tibia occurred later and at variable times, often to a fully flexed position in preparation for another kick.

Sound

Each kick was accompanied by an audible click (Fig. 7). This proved to be a reliable characteristic of a kick and depended upon the execution of the motor pattern for kicking,

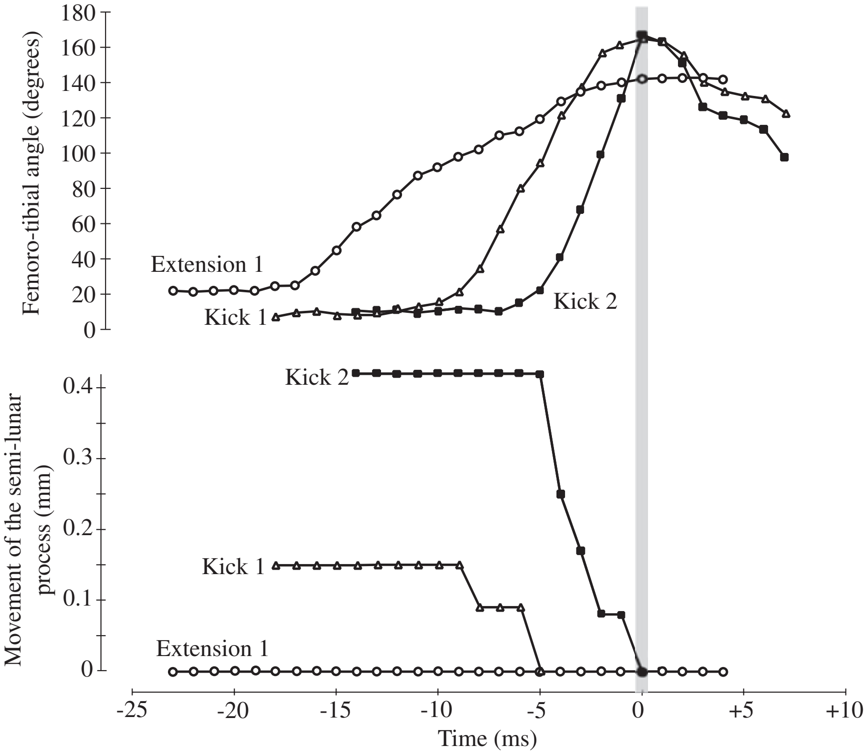

Fig. 4. Correlations between distortions of the semi-lunar processes and the velocity of tibial movements. Three tibial extensions of different velocities are plotted. Extension 1, open circles; there was no distortion of the semi-lunar process and the tibial extension was slow. Kick 1, open triangles; there was a small distortion of the semi-lunar process and the resulting tibial extension was more rapid. Kick 2, filled squares; there was a large distortion of the semi-lunar process and the resulting tibial extension was even faster. The curves are aligned at the time (0 ms) when maximal tibial extension is achieved.

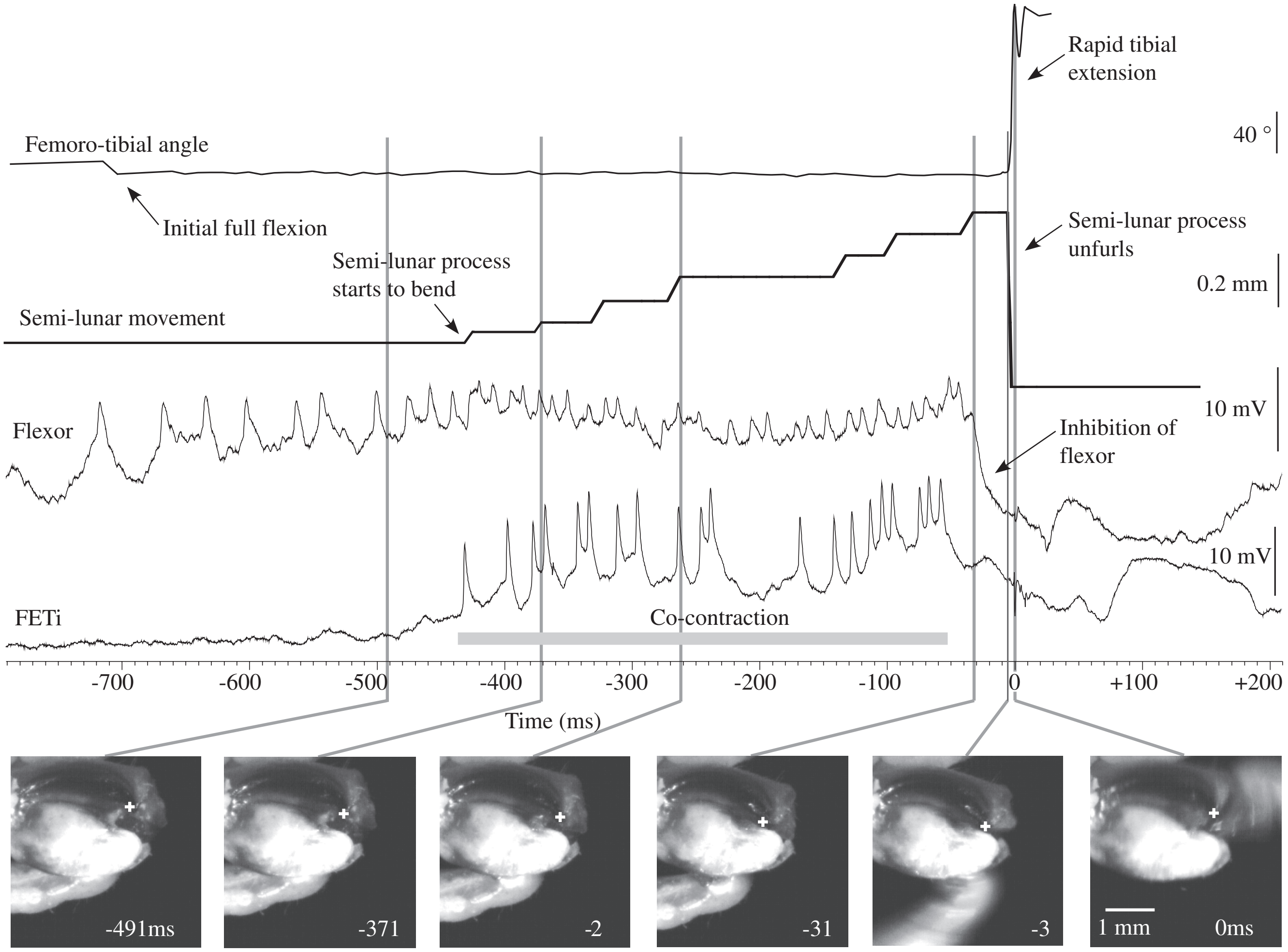

Fig. 5. The activity of leg motor neurones during a kick and the consequent distortions of the semi-lunar processes and tibial movements. Intracellular recordings are from the fast extensor tibiae motor neurone (FETi) and from a fast flexor tibiae motor neurone. The first spikes in the flexor motor neurone move the tibia into the fully flexed position. When the FETi motor neurone starts to spike, so that the extensor and flexor muscles are now co-contracting, the semi-lunar process begins to bend. The bending continues until the flexor motor neurones are inhibited and the semi-lunar processes unfurl during the rapid extension. The apparently stepwise bending of the semi-lunar process is an artefact of the limited resolution of the measurements of each image. The cross hairs in the images show the progressive bending during FETi spiking and the rapid unfurling once tibial extension has started.

as determined by intracellular recording from motor neurones or by myograms, and the accompanying distortion of the semi-lunar processes. The sound did not accompany an extension of the tibia lacking the normal kicking motor pattern and distortions of the semi-lunar processes. To determine when the sound occurred relative to the events so far described, kicks were induced but tibial extension was stopped at different femoro-tibial angles (Fig. 7A). The mechanical stop was made of compressible rubber so, as the tibia struck it, no detectable sound was produced. No sound was detected if the tibia was allowed to extend by only 20 °. If the tibia was allowed to extend to 50–60 °, then only a low-intensity click was produced. As the tibia was allowed to extend to progressively larger angles, the sound intensity increased until it reached its maximum at angles of approximately 130–140 °. To determine the relationship between the sound and distortions of the semi-lunar processes, high-speed images were made of joint movements while also recording the sound (Fig. 7B). The sound pulse began only after the semi-lunar processes had started to unfurl, and its peak occurred when the unfurling was complete and the tibia was almost fully extended. This suggests that the sound might be produced by the rapid unfurling of the semi-lunar processes or by events that occur at the same time as this unfurling process. The sound does not appear to be caused by the rapid movement of the tibia through the air because a sound was still generated when the tarsus and distal two-thirds of the tibia were removed.

Discussion

This analysis has shown that an average kick movement of a locust is completed in 5–6 ms, with the fastest kicks taking

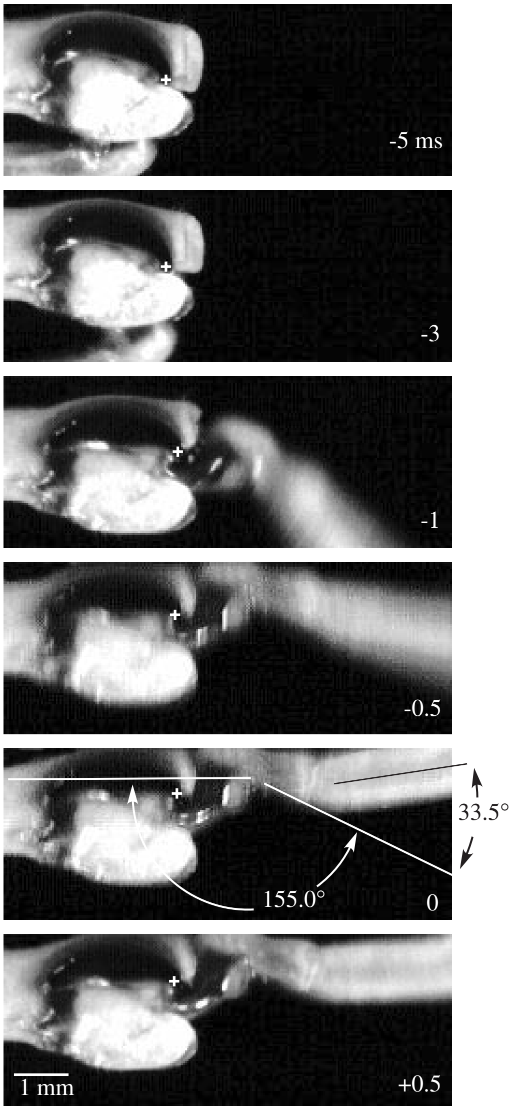

Fig. 6. Tibial bending during a kick. Selected images from a kick captured at 2000 images s^{-1} and with an exposure time of 1/4000 s. Before the extension movement (–5 ms), the semi-lunar process is fully bent. The semi-lunar process remains fully bent during the initial part of tibial extension (–3 ms) and only unfurls when the tibia is partially extended and moving rapidly (–1 to –0.5 ms). At full extension (0 ms), inertial forces cause the tibia to bend at its proximal plane of weakness. As the tibia rebounds from full extension (+0.5 ms), it is still bent.

only 3 ms, during which the tibia rotates about the femur at angular velocities as high as 80 ° ms^{-1}. The movement is powered sufficiently so that increasing the mass of the tibia by 10-fold has only a small effect on the velocity, but reducing the mass and wind resistance can result in kicks that are completed in 1 ms. This presumably reflects the need for the similar extension movements of the tibia that are used in a jump to lift the weight of the body. The body mass of a mature female is 2 g and that of the smaller males is 1.6 g; when they jump, extension of the tibia takes approximately 30 ms, by which time the insect is airborne. The large forces needed to power these very rapid movements result in considerable distortions in the hind legs; before the tibia can be extended, the distal femur is distorted and the semi-lunar processes are bent; at the end of the movement, the tibia is bent when the femoro-tibial joint reaches its maximal excursion. The high-speed images together with the recordings of motor activity have allowed the sequence of the various events to determined precisely.

Distortions of the hind legs during kicking

The co-contraction of the flexor and extensor tibiae muscle bends the tips of the semi-lunar processes by up to 0.6 mm and distorts the distal femur so that it is flattened dorso-ventrally and expanded laterally by up to 20 %. These distortions increase progressively during the co-contraction phase while the tibia remains firmly flexed about the femur. They are fully reversible when the tibia extends. The semi-lunar processes form the hinge joint with the tibia, so their distortion shifts the pivot of the joint ventrally and results in an initial proximal and ventral movement of the tibia. Spikes in the fast extensor tibiae muscle are correlated with these distortions when the tibia is held by the flexor in a fully flexed position. The tibia can therefore be extended at a range of different velocities, with the high-speed kicks representing a specialised mechanism. Nevertheless, the velocity of kicks can also be varied depending on the force generated by the muscles.

The severe distortions of the distal femur during a kick suggest that sense organs must monitor their extent to prevent excessive muscle contractions exceeding the safety factor of the cuticle and causing irreversible damage. The need would be even greater during maturation of a locust following a moult, when the cuticle is initially soft and achieves its final hardness only after a period of many days (Norman, 1995; Norman, 1996). What sense organs could be involved? Of those that are known, the most obvious candidates would be the two multipolar neurones that form the ventral- posterior-lateral receptor (Coillot and Boistel, 1968; Coillot and Boistel, 1969). These neurones are now more widely known as the lump receptor (Heitler and Burrows, 1977b) because of their association with the inward projection of the ventral wall of the femur – Heitler's lump. These neurones are activated when tension is applied to the flexor tendon if the tibia is held in the fully flexed position, but we do not know their action during a kick or during distortions of the distal femur. Other receptors may also provide feedback, but again we do not know whether their signals can limit the action of motor neurones during the co-contraction phase of the motor programme and therefore regulate muscle force. There is certainly time for the feedback to be effective in limiting the amount of force that is generated because co-contraction can take 100–1000 ms.

At the end of a kick, when the tibia reaches the limits imposed by the femoro-tibial joint, bending occurs at a proximally located plane of weakness (Heitler, 1977). The amount of tibial bending can be considerable, allowing a further extension of its distal end by as much as 33 °. This is then followed by a series of damped oscillations that are the result

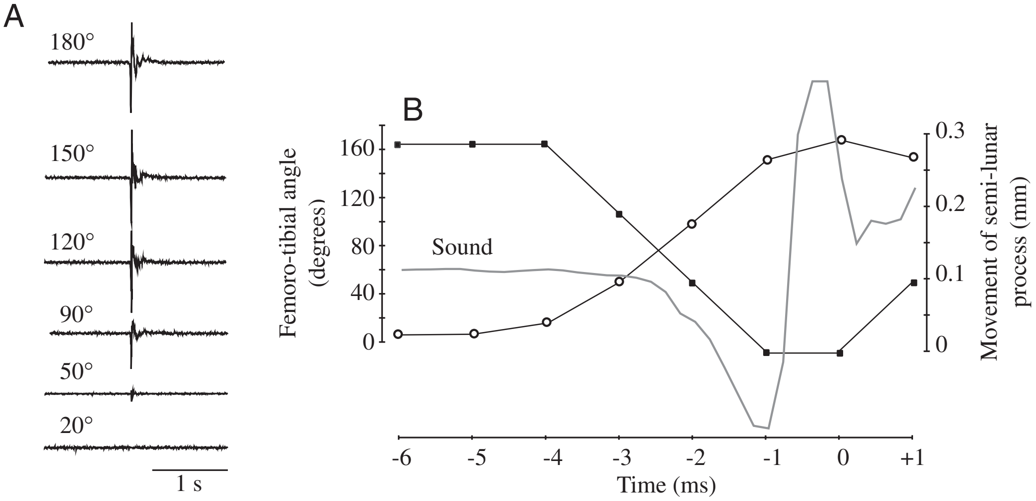

Fig. 7. A pulse of sound is generated during a kick. (A) Recordings to show the level of sound that is generated in different kicks by a single locust if the tibia is allowed to extend only to the angle indicated. No sound is produced if extension is prevented at 20 °, and only a faint sound occurs when extension is prevented at 50 °. (B) The timing of the sound pulse relative to movements of the tibia (circles) and distortions of a semi-lunar process (squares) in an individual kick. The sound begins only when the semi-lunar process is unfurling and when the tibia is already extending. Measurements were made from images captured at 1000 s^{-1}.

of inertial forces as they are not powered by active contractions of the muscles or spikes in either the flexor or extensor motor neurones. The most likely role for this bending is to act as a shock absorber to decelerate the tibia without rupturing the femoro-tibial joint. When kicking freely, the femur would also move to absorb some of the kinetic energy of the tibial extension. The bending occurs at a region of the tibia that is richly endowed with mechanosensory receptors, including the subgenual organ and several campaniform sensilla, but these could have no limiting effect on the amount of extension.

Energy storage during kicking

Three sites for the storage of energy during the slow co-contraction for rapid deliverance during tibial extension have previously been identified, with the semi-lunar processes contributing half (Bennet-Clark, 1975). At the start of a kick, the tibia extends slowly and there is no unfurling of the semi-lunar processes. Instead, they only begin to unfurl and deliver their stored energy when the tibia has extended by 55 ° and is approaching its maximum velocity of movement. It would seem, therefore, that the other energy stores in the extensor apodeme and the walls of the femur and not the semi-lunar processes power the initial part of the kick.

A by-product of the rapid unfurling of the semi-lunar processes is an audible click that is an identifying characteristic of a kick. Other extension movements that are not preceded by a co-contraction show no bending of the semi-lunar processes, are less rapid and are not associated with a click. The sound still occurs if the tarsus and a substantial part of the tibia are removed, so it cannot be caused by motion through the air. It is, however, abolished if the tibia is prevented from extending by more than 20 ° and is of only low intensity if the tibia is allowed to extend by 50–60 °. This suggests that the sound may be produced by the sudden unfurling of the semi-lunar processes or by some other as yet unidentified event that occurs at the same time.

Motor actions and kick movements

The high-speed images have shown that there are strong correlations between the actions of the various motor neurones innervating the muscles in the femur, the distortions of the femoro-tibial joint and the peak angular velocity of tibial movements. Bending of the semi-lunar processes is caused by spikes in the fast extensor motor neurone, with changes in the amount of bending being correlated with the pattern of motor spikes and their number. The same amount of bending can, however, be produced by both short and long co-contractions. The velocity of tibial movement is similarly correlated with the number of fast extensor spikes during the whole of the co-contraction phase and with the amount of bending of the semi-lunar processes. Slow extensions occur when there are only a few extensor spikes, no co-contraction with the flexor and no distortions of the semi-lunar processes. Progressively faster extensions occur with more extensor spikes, prolonged co-contractions and progressive bending of the semi-lunar processes.

Mechanisms for the production of rapid movements

An underlying design principle for the production of rapid movement that emerges from studies on a number of different animals is a reliance on the slow increment of force in a joint that is locked in one position, the storage of this force in specialisations of the skeleton and a sudden release of the force so that acceleration is applied over only a very short period. The flea beetle *Blepharida sacra* has a spring formed by the curling and chitinisation of the extensor tibiae tendon (Furth et al., 1983; Maulik, 1929). The tibia is probably locked into the flexed position when a small triangular plate at the femoro-tibial joint is moved by contraction of the flexor muscle, so enabling the extensor to generate isometric force. The lock is probably released through changes in the force in the flexor, and the stored energy is delivered rapidly as the spring snaps back to its original shape. The click beetle *Athous haemorrhoidalis* propels itself vertically into the air by jack-knifing its body at the junction between the pro- and mesothorax (Evans, 1972; Evans, 1973). The joint between these segments is first locked, allowing a large dorsal intersegmental muscle to contract isometrically and store energy that is then released suddenly, accompanied by an audible click, when the joint position is shifted by unknown mechanisms. The requirements for the jump of the flea *Spilopsyllus cuniculus* are again met by a prior contraction of a large depressor muscle, with energy being stored in a pad of resilin (Bennet-Clark and Lucey, 1967; Rothschild et al., 1972). 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. Mantid shrimps strike at prey or predators with the rapid extension, lasting only 4–5 ms under water, of a highly specialised mouthpart appendage and involving a mechanism remarkably similar to that used in a kick by a locust (Burrows, 1969). The joint is first locked in the flexed position by the contraction of two small flexor muscles, and the flexor and extensor muscles then co-contract for as long as 1 s before the flexor motor neurones stop spiking and the stored energy is delivered suddenly. A cocking and rapid release of stored energy are also used by the ant *Odontomachus bauri* when closing its jaws on prey (Gronenberg, 1995a; Gronenberg, 1995b; Gronenberg et al., 1998). Contact with a potential prey leads to the prolonged contraction of a closer muscle that is unable to close the jaws from their opened position. When two long hairs on the jaws touch the prey, they induce the contraction of a small muscle that alters the mechanics of the joint, allowing the stored force to be delivered rapidly, and the jaws to snap shut in 0.3 ms.

Rapid movements can nevertheless be achieved without these complex mechanisms, but there is then a price to paid in reduced power and performance. In the few species of ant that jump, extension of the legs does not appear to require the preceding storage of energy, so that there is no co-contraction of the femoral muscles (Tautz et al., 1994). Crickets perform well-directed kicks with a single hind leg but do not jump. The rapid extension of a tibia is accomplished by a brief co-contraction of the flexor and extensor tibiae muscles that lasts no longer than 20 ms, with the velocity and force of extension depending on the balance of forces produced by the two muscles (Hustert and Gnatzy, 1995). This design enables a cricket to respond rapidly to a tactile stimulus, but does not enable it to generate sufficient force to lift its body in a jump.

The hind legs of locusts represent an extreme specialisation for the production of the rapid and powerful movements needed in kicking and in lifting a heavy body off the ground in jumping. It will now be informative to analyse from an evolutionary perspective, with the same correlative analysis of joint mechanics, neuronal activity and kinematics, and the mechanisms used by other orthopterans such the false stick insects and the bush crickets. These insects jump and kick but have spindly hind legs lacking well-developed semi-lunar processes at the femoro-tibial joints. Their hind legs therefore more closely resemble the construction of the other walking legs.

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