

THE MOTOR PROGRAM FOR DEFENSIVE KICKING IN CRICKETS: PERFORMANCE AND NEURAL CONTROL

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Summary

Crickets can repulse sources of mechanical touch to their wings, legs or to the posterior body by kicking backwards ipsilaterally with one hindleg. The main component of a kick is the rapid extension of the femoro-tibial (knee) joint. A kick as a defence against predators must occur instantly after the moment of touch. The cricket kick is completed within 60–100 ms, whereas in locusts 500–2000 ms elapses between the stimulus and the end of the kick. The rapid movement of the cricket hindleg was recorded with a high-resolution video technique. Cricket kicking is based on a dynamic co-contraction of the extensor and flexor tibiae muscles during the pre-kick knee flexion period, thus differing from the static co-contraction period seen in locusts. Biomechanically, the knee joint is specialized for

kicking and jumping by the specific leverage of tendons inserting at the knee, by a femoral ridge that modifies the angle of attack for flexor muscular forces and by a cushion-like swelling on the flexor tibiae tendon. Because of these structural specialisations for rapid kicking, the neural control of the motor pattern of the muscles participating in the tibial movement can vary considerably, but still produce efficient kicks. Kicking is also an element of other complex behaviours.

Key words: ballistic movement, biomechanical basis, high-resolution video recording, defensive kicking, motor coordination, cricket, orthopteran insect, *Acheta domestica*.

Introduction

The long specialized hindlegs of most orthopteran insects participate in walking, in several other specific locomotor patterns, and (in locusts, crickets and bushcrickets) in the ballistic movements of jumping and kicking. Kicking is a behaviour with components of coordination also apparent in swimming and jumping of locusts (Pflüger and Burrows, 1978; Gynther and Pearson, 1986; Heitler and Bräunig, 1988), but it differs considerably from the simple pushing of objects with a hindleg that may also occur. Kicking with one hindleg is a behavioural response to weak ipsilateral mechanical stimuli that crickets often use rapidly to repel approaching objects, conspecifics or intruders. This response can be a successful general defence (Huber, 1965; Dumpert and Gnatzy, 1977) or it can be directed against specific predators such as parasitic digger wasps (Gnatzy and Heußlein, 1986). During the short period between recognizing the attack and the response kick, the cricket's central nervous system must select a specific behavioural reaction from its behavioural repertoire. It may decide (i) to ignore, (ii) to avoid, (iii) to escape, (iv) to wait for another stimulus, (v) to kick, (vi) to perform a head stand while turning the abdomen towards the location of the stimulus, (vii) to stilt stand, or (viii) to push slowly with one hindleg.

Kicking requires a further decision for aiming with the appropriate hindleg using a trajectory that will hit and remove the stimulus. At the same time, the coordination for counterbalancing the body with the other legs during the kick must be organized by accompanying motor programmes.

Specific coordination of the other legs is required when preceding motor programmes, such as a stilt stand or head stand, position the body for more efficient defensive kicking (Gnatzy and Heußlein, 1986). This preparatory behaviour may follow warning signals emitted by the approaching intruder, such as a touch by its antennae or air currents evoked by its movements that stimulate cercal thread hairs (Gnatzy and Kämper, 1990). The following kick is even quicker, better aimed and, thus, more efficient in repulsing the intruder.

The kick itself, however, cannot be interrupted after it has started. It is initiated within a few milliseconds after the mechanical stimulus and the programme for coordinating all the legs (one leg kicks and the others support the movement) must be determined in advance.

We have studied the time course, coordination and aspects of spatial orientation of the unilateral defensive kick. Specific attention was paid to the preparatory period, when energy storage by co-contraction of the extensor and flexor tibiae

muscles develops. In locusts, the kick is prepared during an extensive static period of antagonistic muscle co-contraction for energy storage (Heitler, 1974). For crickets, with their extremely rapid performance of a complete kick, we expected to see major differences from locusts in motor activity before and during kicking. A preliminary account of this study was given by Hustert and Gnatzy (1989).

Materials and methods

Adult male and female *Acheta domesticus* (L.) from our laboratory culture were kept in a small rectangular arena with a wooden base and glass sidewalls for observation. In the dark or under red light, the animals rarely tried to escape. The kicking movements and other reactions were elicited by touching tactile sensilla of the animal's body and appendages with a single paintbrush bristle. In some animals, repeated touch aroused additional preparatory defence behaviours such as the head stand and stilt stand. For optical tracking of the rapid kicking movements, the lateral femur and tibia were marked with spots of white paint (TippEx).

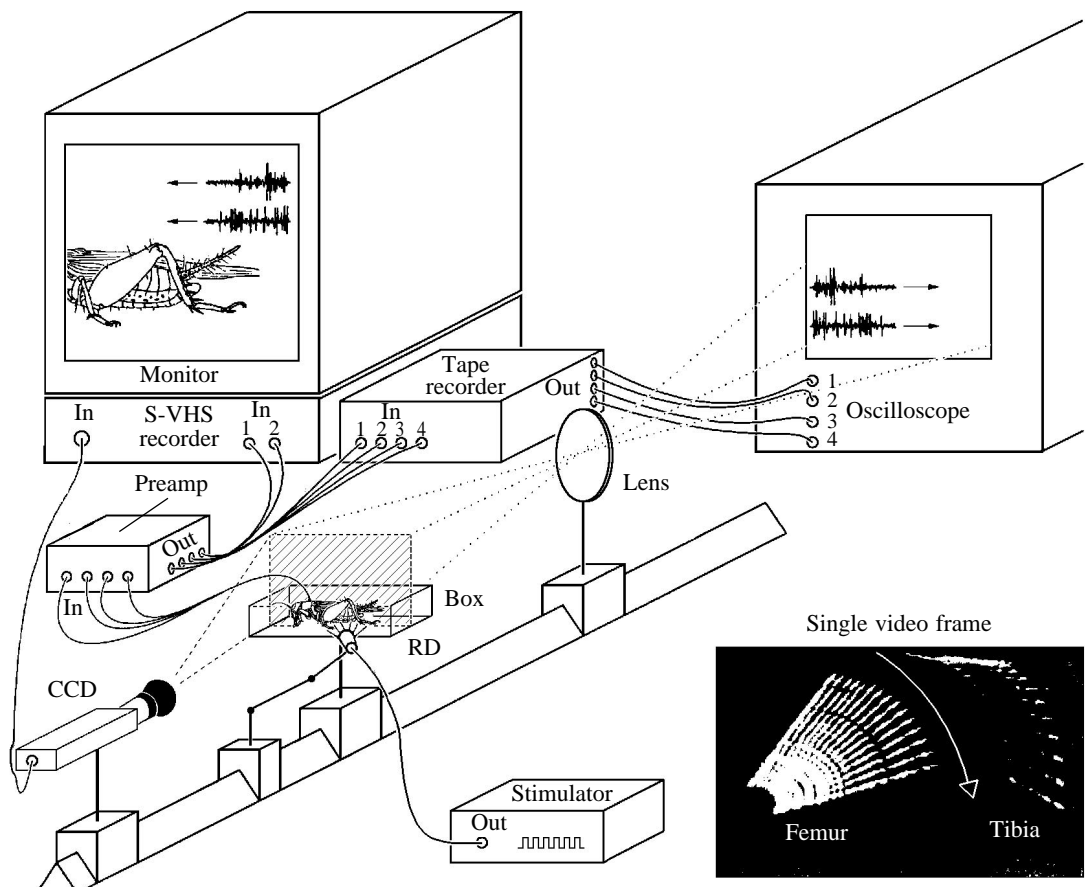
In a system for simultaneous movement and myogram recording (Fig. 1), leg movements were observed from a lateral aspect using a CCD monochrome video camera (Sony AV-D1), with close-up lens, and recorded with a Sony U-matic video recorder. The camera was sufficiently red-sensitive to detect movements of the animal, which was illuminated just by

the light of a red light-emitting diode (LED) with maximum brightness of 500 mcd. This was pulsed by the symmetrical rectangular output of a function generator at 500–800 Hz. Later, the illumination was improved by using brighter and shorter (0.1 ms) light pulses repeated at the same frequencies. Each video frame is exposed for 20 ms, thus capturing a 20 ms section of the movement. The previous frame was erased totally before exposure of the following one. During each frame, the light pulses flashed (typically) at 1.25–2 ms intervals (see Fig. 1, inset) and traced the progress of movement, resulting in 10–16 exposures on each frame. At these frequencies of intermittent flashing, the trajectories of pre- and post-kick movements and of normal leg movements are represented clearly, whereas the tracks of rapid tibial extension during the kick are seen only faintly. Both the trajectory and the average speed of the leg segments can be measured at 2 ms illumination intervals.

Myograms from the leg muscles were simultaneously recorded with chronically implanted 30 μm stainless-steel wires. The animals could move freely in a glass-walled observation arena (20 mm \times 50 mm).

The myogram traces, displayed on an oscilloscope screen 50 cm behind the arena, were projected with a collecting lens (50 cm focal length) to a level above the arena and video-recorded together with the corresponding leg movements of the cricket, as viewed laterally. The myogram traces from the extensor and flexor tibiae muscles were also recorded on tape,

Fig. 1. Experimental apparatus for simultaneous recording of movements and myograms from leg muscles during cricket kicking. The animal is placed in a transparent box. The chronic myogram wires are connected to a preamplifier (Preamp) and then split to a video recorder, a tape recorder and an oscilloscope. Pulsed red light (RD), invisible to the animal, is timed by the stimulator and reflected preferentially by white paint markings on parts of the hindleg. A CCD camera records a composite picture of both the cricket in the box and the oscilloscope display of myograms projected to a level above the cricket with a lens (see monitor). The inset shows a single video frame of the return movement (post-kick) made by the knee joint (femur, tibia) at a light pulse frequency of 800 Hz.



both on the stereo channels of the video recorder and on a data recorder, where up to four myograms could be stored. A preliminary estimation of the time during a movement at which specific muscles receive their neural input was achieved by driving the stroboscopic LED with amplified myogram signals. When the signals exceeded a preset voltage threshold, they triggered rectangular pulses of 2 ms duration, thus illuminating the leg or whole animal during the periods of muscular activity.

The analysis of single video frames was mainly carried out using printouts from a video printer (Sony UP-104) or by measuring slides taken of the screen. In these, the visible section of oscilloscope traces and corresponding leg position and movements recorded on a single video frame represented the same 20 ms period (Fig. 1). These data could subsequently be correlated precisely to the myograms from the video recorder voice channels and the magnetic data tape. Several hundred kicks were recorded on video tape. Our results were taken from four animals from which their good-quality movements, myograms and stimulation measurements were recorded.

Throughout this paper the femoro-tibial joint is termed the 'knee'.

Results

The basic movements

Cricket kicks with their ipsilateral hindleg in response to delicate tactile stimulation of mechanosensory hairs on their rear body surface and legs, particularly to the large guard hairs (Hustert, 1985) and the filiform hairs of the cerci (Gnatzy and Hustert, 1989). These kicks are very rapid and are completed (i.e. the tarsus is returned to the ground) within 60 ms from the first visible leg movement. Kicking may start from any given femoro-tibial angle and may even occur during slow walking. Three main phases (Fig. 2A) constitute a complete kick: the pre-kick, the kick and the post-kick.

For 6–10 ms before the pre-kick, there are synchronous bursts of excitation in the flexor and extensor tibiae and in many other leg muscles, but no visible movement (Fig. 3). The following tibial flexion of the pre-kick usually ends when the knee joint, ready for the actual kick, is almost completely flexed so that the ventral femoral and tibial surfaces make contact in a postero-ventral groove of the femur. A large protruding sensory hair of the tibial contact surface (Fig. 2) is usually bent when approaching the femur during flexion. The levation caused by the proximal joints during the pre-kick period mainly determines the direction in which the kick of the whole leg will be aimed. The duration of the pre-kick period is proportional to the initial angle between the femur and tibia and it can last from 12 ms to more than 20 ms.

The kick itself follows the pre-kick after a still period of 3–12 ms and is a rapid extension of the knee joint lasting 6–10 ms. The profile of the tibial angular velocity is very similar in different kicks. The major component of this movement is femoro-tibial extension accompanied by a small depression of the femur at the coxo-trochanteral joint. The tip of the tibia therefore moves through a large radial arc rather

than in a straight line (movement in a single joint would always cause movement in an arc, whereas the movement of two or more joints is required for a linear trajectory). Maximal joint extension is not always reached, for instance when the tarsus actually hits the object (Fig. 3). The kick is sometimes followed by further pushing against a resisting object.

The post-kick period is the return movement mainly of the tibia, by which the whole leg is returned to a normal position on the substratum. When another behaviour (e.g. a repeated kick, head stand, stilt stand, walking away or an escape) immediately follows, the tarsus is held above the ground. The post-kick may last 20–60 ms. The main components of return movements are flexion of the knee joint and depression of the whole leg at the proximal joints.

The transfer of muscular forces in the knee joint

The efficiency and force of a kick are mainly due to the rapidly accelerated tibial extension at the knee joint. Biomechanically, the cricket hindleg knee joint possesses both general orthopterous and cricket-specific features. The basic mechanism of the femoro-tibial joint is known from locust hindlegs: the joint movements are limited to uniaxial rotations about the two bilateral joint condyli. Antagonistic pull from the tendons of the tibial flexor, located ventrally in the femur, and tibial extensor, located dorsally, controls joint position and movement (Fig. 2B–D). The insertions of the extensor and flexor tendons are not in line with the pivotal axis, as in a simple two-armed lever, but are eccentric and at different distances from the point of rotation. Therefore, the effective levers and the ratio of extensor and flexor leverage change with different angles of the knee joint. In crickets, the effective leverage ratio of flexor to extensor is about 1:1 when the femoro-tibial angle is 90°. The greatest extensor leverage is also reached at this angle. With full flexion, the extensor leverage approaches zero, for then the extensor tendon attachment is almost level with the joint's pivotal axis. Only the distal dorsal muscle bundles of the extensor (the 'accessory extensor') have a different angle of attack on the tendon and could exert forces in support of knee extension when the joint is fully flexed.

The effective flexor leverage is near zero when the tibia is fully extended. It would be maximal at a femoro-tibial angle of about 40° and decrease for smaller angles, but two specific mechanisms increase the angle of attack continuously until maximal flexion is reached (Fig. 2B–D). (i) An angular pulley mechanism by which the flat proximal part of the flexor tendon slides around a wide inward-bulging ridge of femoral cuticle. This bends the tendon progressively when the tibia is flexed, that is, when the tibial insertion of the tendon moves towards the ridge ('pulley'). This mechanism alone would shift the maximum effective leverage of the flexor to a femoro-tibial angle of about 25°. (ii) The mechanism is further enhanced, so that extreme (10°) flexions have the most effective flexor leverage because the tendon thickens into a ventrally bulging elastic cushion that slides onto the cuticular ridge when the knee is flexed below 90°, which pushes the tendon further

dorsally (Fig. 2C). Additional support for this movement is given by the ventral arthrodistal membrane, which progressively restrains the distal flexor tendon from progressively stretching ventrally during knee flexion.

The combination of femoral ridge, elastic cushion and restraining arthrodistal membrane is most effective when the knee bends to angles of less than 90°. Sliding of the flexor tendon's cushion on the cuticular ridge should be supported

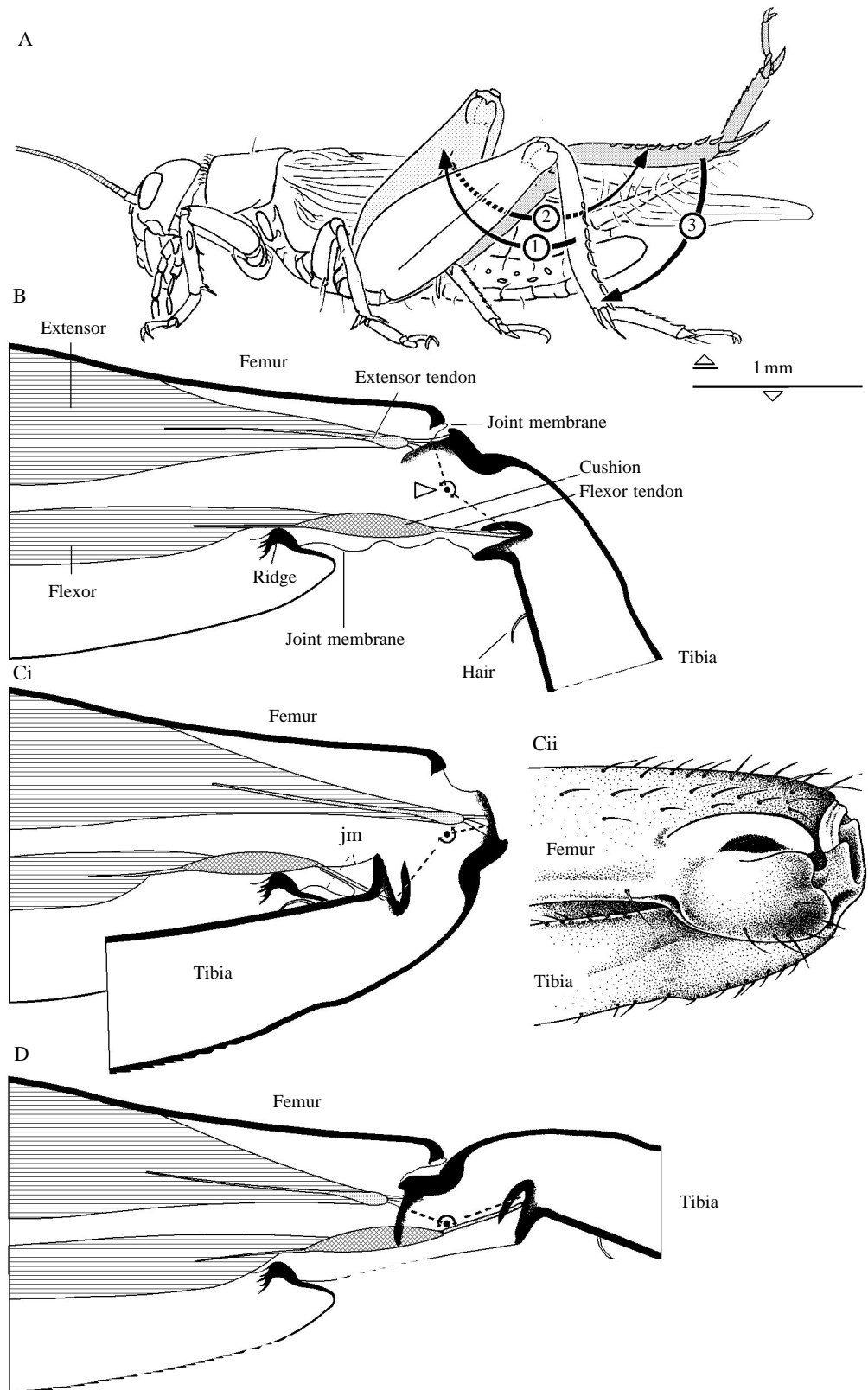


Fig. 2. Mechanics of cricket kicking. (A) Transition between the main stages of a kick, viewed laterally. The pre-kick knee flexion (1) starts from the normal stance of the hindleg with the femur being levated and the tibia being flexed. The actual kick (2) is a rapid tibial extension to a knee angle of 150° with femur depression. From there, the return movement (3) of the post-kick usually returns the leg to stance again. (B–D) The internal knee mechanics during normal stance (B, femur and tibia at an angle of 105°), during complete flexion (Ci; 15° angle) and during complete extension (D, 150° angle). The longitudinal axis of the femur is horizontal. The axis of knee rotation (pivot axis, marked by a white triangle in B) lies at an angle (dashed lines) to the insertions of the extensor tendon and the flexor tendon. The angles of attack for the tendons change with tibial rotations. That of the flexor is also influenced by a ventral femoral cuticular ridge, a cushion enlargement of the flexor tendon, and an inward bulge of the joint membrane (jm) that restrains and bends the tendon during strong flexions. A view of the medial (=posterior) cuticular surface of the completely bent knee is given in Cii.

particularly by the anterior and posterior accessory flexor muscles because of their more oblique angles of attack at their tendon insertions lateral to the cushion.

The cushion, being squeezed between the tendon's downward pressure and the distal face of the ridge, may also store energy that produces forces helping it to slide down and back from the ridge when the flexor tension is released after extreme flexions. This could serve to support the initial knee extension during a kick.

The basic motor pattern in the hindleg

In the hindleg of a normal standing cricket, the pre-kick is preceded by synchronous activation of slow motor units in the flexor and extensor tibiae muscles (Fig. 3). After a short delay of 6–10 ms, the first externally visible movement is the knee flexion of the pre-kick movement, indicating an advantage of the effective flexor force over extensor force. The movement usually stops when the femur and tibia make contact after 12–22 ms, depending on the initial knee angle. During this flexor contraction, tension in the antagonistic extensor muscle fibres also increases as a result of their own neural excitation

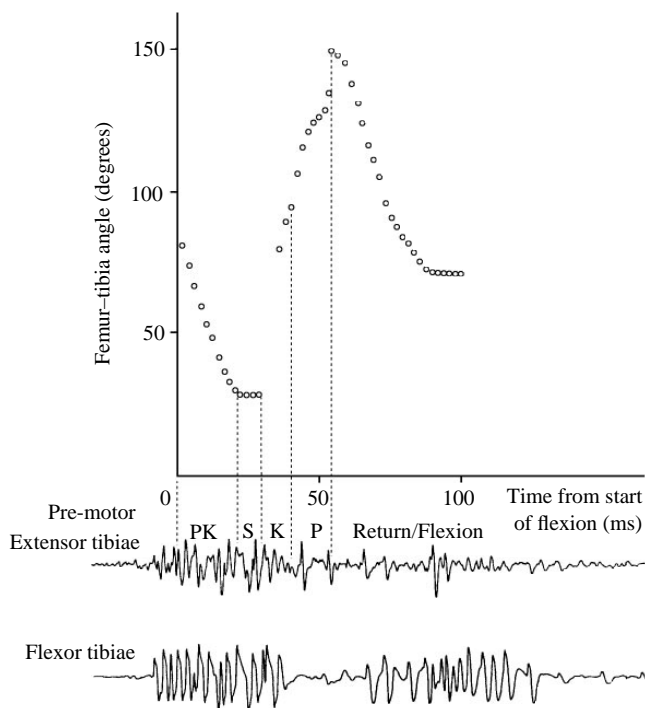


Fig. 3. Correlation between femur-tibia angle and extensor and flexor myograms (on the same time scale) during a kick that hits and pushes an object. The EJPs in both muscles precede the movement (pre-motor period) and, during the muscles' co-contraction in the pre-kick period (PK), flexor forces override extensor forces, resulting in flexion movement only. The extensor effects start to prevail after the short still (S) period and release the kick (K), during which EJPs subside in both the flexor (completely) and extensor (partially). After the object is touched, pushing against it (P) completes tibial extension. The tarsus briefly slips on the object (last dashed line). Resumed flexor activity supports the return movement that ends with the leg in a normal stance with a knee angle of 75°.

and passive stretch caused by the tibial flexion. This we term dynamic co-contraction of the extensor muscle, in contrast to the static co-contraction seen in the hindleg of locusts (Heitler, 1974), which locks the tibia in a flexed position for a longer period before a kick is possible. In crickets, static co-contraction occurs briefly in the still period of 3–12 ms that separates the pre-kick flexion from the extension that constitutes the actual kick. In the cricket, the kick is apparently triggered by the discharge of 1–4 additional spikes of the extensor tibiae fast motoneurone (best seen in Figs 4–6 because of the favourable recording site for the myogram).

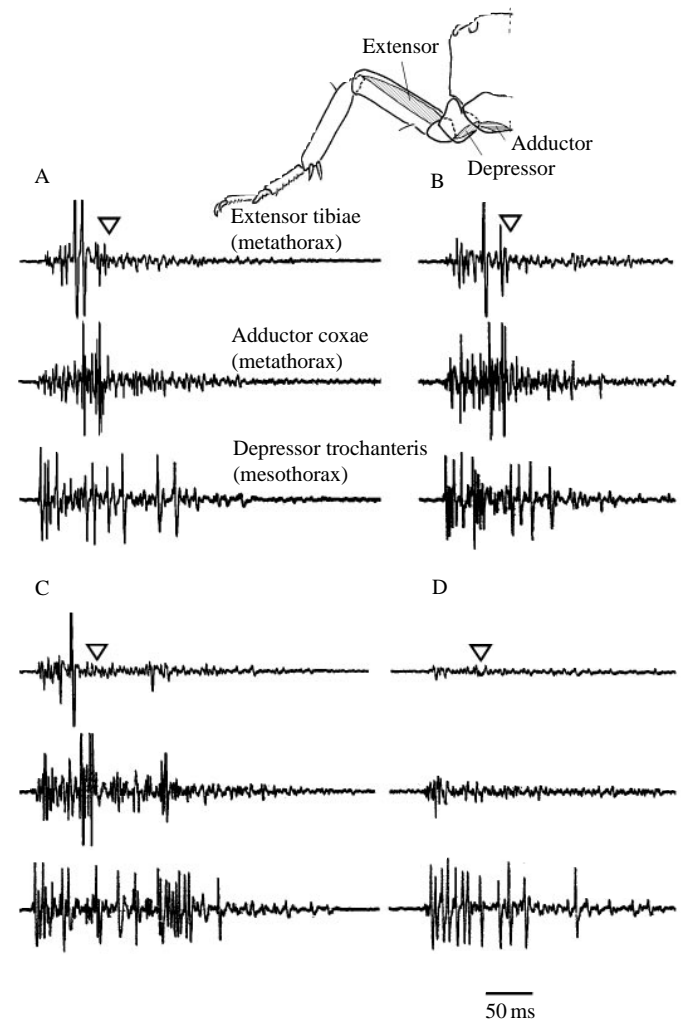


Fig. 4. The variability of hindleg neural control of three muscles in different kicks. (A–C) The variability of metathoracic extensor tibiae activation in otherwise indistinguishable kicks of the same animal. The metathoracic adductor coxae provides support during pre-kick stabilisation and after the kick, braking the movement in the subcoxal joint. The mesothoracic depressor trochanteris develops additional force for body support when a hindleg leaves the ground for kicking. (D) The importance of this mesothoracic support function, shown by the EJPs of the depressor muscle when the contralateral leg kicks. Kicks are marked by arrowheads; in D, the arrowhead denotes the timing of a contralateral kick. Inset: schematic view of the muscles recorded. Muscles are shown for the mesothoracic segment, but their locations are similar in the metathorax.

Both extensor and flexor tibiae activity decrease rapidly before and during the initial phase of the kick and then usually cease completely. The kick lasts for only 5–10 ms.

The post-kick period, beginning about 10–25 ms after the end of the pre-kick, is a return flexion of the knee that is supported by resumed flexor activity and is occasionally accompanied by extensor discharges. It usually ends when the tarsus returns to the ground.

In general, the myograms represent the timing of extensor and flexor discharges that precede the actual movements (Fig. 3). They do not represent all neural activity in a muscle, since they only show the excitatory junction potentials (EJPs) in the muscle fibres near the recording myogram wires. The extensor tibiae is known to be supplied by two excitatory, one common inhibitory and one dorsal unpaired median efferent neurone, whereas the flexor is supplied by at least eight excitatory motoneurons (and possibly by inhibitory neurones, as in locusts). Extensor myograms more often reveal slow motoneurone EJPs and low-amplitude fast EJPs, apparently because each motoneurone does not innervate all the fibres of the muscle. In flexor discharges, single units can only be distinguished during low general excitation that is not typical for kicking programmes.

The kicking motor programme is very variable. No two myogram recordings from the same animal show exactly the same pattern during kicking movements (Fig. 4). Even the most constant component, the rapid extension, is produced by variable patterns of excitation in the extensor tibiae, which can be seen in the burst duration and discharge patterns of its two excitatory motor units. It remains uncertain whether this variability represents a neural fine control mechanism, i.e. an adaptation of the kick for the location or the intensity of the eliciting stimulus.

Supporting motor programmes

For a cricket standing on a horizontal surface, the centre of mass lies between the six legs, which extend laterally. Lifting any one leg adds more load to other legs. This also applies when a hindleg is raised for kicking. The radial trajectory of the hindleg tibia during the knee flexion of the pre-kick period would cause the tarsus to rub along the ground unless there was femoral levation at the proximal joints (Fig. 4A–C) or elevation of the body by means of the other legs (Figs 4–6). A stimulus applied to the cricket body that elicits a kick, triggers an almost synchronous onset of activity in the weight-supporting muscles of the standing legs and in the muscles involved in the kicking movement. This activation prestretches elastic elements in the postural muscles and increases their tension, thus counterbalancing the ‘expected’ lifting and kicking of the hindleg. Nevertheless, in many kicks, the whole body jerks forwards or backwards, but without the legs losing contact with the ground.

The mesothoracic depressor trochanteris muscle is representative of the load-compensating muscles that reach high levels of activity very early. Located in the coxo-trochanteral joint, it is situated close to the animal’s centre of

gravity and is especially important for body support. High-frequency discharge of depressor motor units is characteristic for the early pre-kick period, sometimes superimposed on an ongoing discharge when the body has previously been raised (see Figs 5, 6). During a kick, the contralateral hindleg also develops tension for the support of the posterior half of the body (Fig. 4D).

Aimed kicking

The kicking motor programme of crickets depends on (i) the location and intensity of touch to mechanosensory hairs on the body, and (ii) the type of preparatory behaviour preceding the kick.

Qualitative experiments have shown that the trajectory of the tarsus during a kick always covers the area of the eliciting stimulus, on whichever segment or appendage behind the mesothorax it may occur. Most kicks have their trajectory in a plane that is roughly parallel to the body’s long axis. Kicks directed further laterally were observed after the outside of a hindleg femur had been touched. The control of trajectory relies on the muscles of the thoraco-coxal and the coxo-trochanteral joints, for these determine the position of the femur at the end of the pre-kick period. Stimulation of the cerci elicits kicks directed posteriorly. Stimulation of the wing surface or the dorsal surface of a hindleg elicits kicks directed more dorsally because of the high levation of the femur during the pre-kick. In these kicks, the tibia extends through a similar arc, but the overall direction of tarsal movement is determined by the proximal leg joints. Stimulation of the dorsal

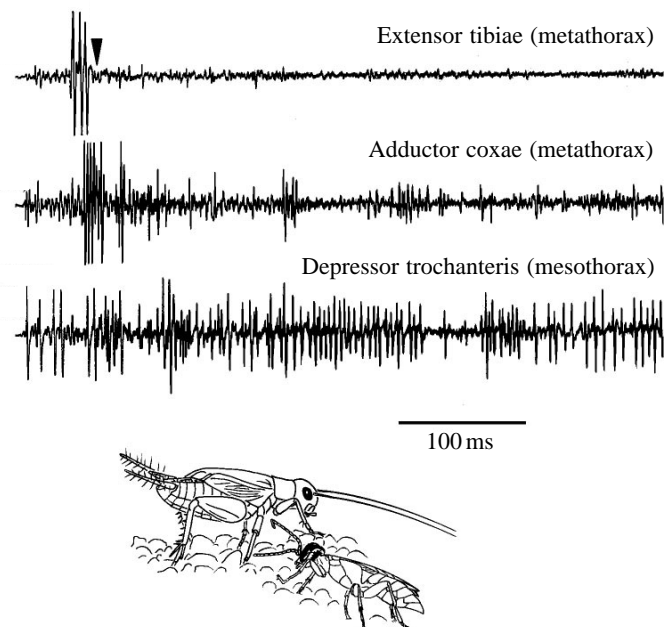


Fig. 5. The overlap of two behaviours seen in chronic myograms. The stilt stand requires continuous activity in the trochanter depressor muscle of the mesothorax to raise the whole body. The ipsilateral hindleg muscles are active mainly during the kick (arrowhead). The inset demonstrates a stilt stand of an alerted cricket as a defence against a parasitic wasp.

mesothoracic or pronotal regions may elicit either a kick aimed dorsally, due to extreme femoral levation and protraction, or just a rapid metathoracic femoral levation without the components of a kick (Fig. 2A). This type of defence was termed wiping in locusts (von Rekowski and Hustert, 1991).

The animal's slowest defensive response to touch is pushing, a gradual extension of the hindleg against an object to remove it from the location of touch. In this behaviour, extension of the knee joint starts directly from the prevailing leg position without initial knee flexion.

Additional defensive behaviours

When crickets are alerted by an imminent attack or previous contact, they often assume specific body positions in which the hindlegs are relieved from body support and point at the intruder, presumably allowing a more rapid and effective response. These positions can be a stilt stand, with the body raised on all legs (Fig. 5), a head stand with the hindlegs off the ground (Fig. 6) or just a turning manoeuvre with the whole body (Gnatzy and Heußlein, 1986).

One common feature of the head stand and stilt stand is that the middle legs help to raise the body above its normal level. The depressor trochanteris muscle of the coxo-trochanteral joint is primarily responsible for this. Therefore, myograms from this muscle are a very reliable indicator for the timing

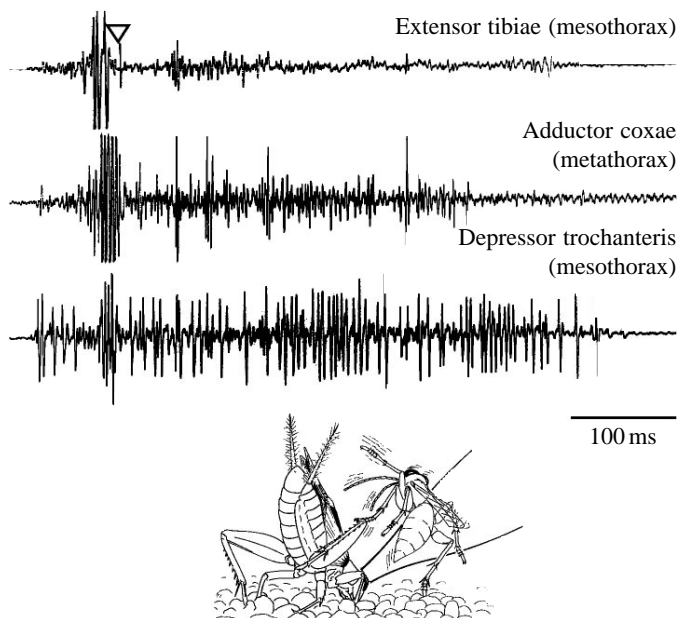


Fig. 6. The head stand as recorded with chronic myograms demonstrates the strong support of the body required from the depressor trochanteris in the middle leg before and for some time after a kick (arrowhead) of the hindleg. This position keeps the abdomen raised high, gives the hindleg more freedom and shortens the pre-kick duration for rapid kicking, when the leg is kept off the ground continuously. The tonic activity in the mesothoracic depressor trochanteris ceases after the head has taken over more of the body weight. The inset demonstrates a head stand with a successful kick warding off a parasitic wasp.

and intensity of these behaviours. Its activity starts early in every pre-kick phase in both ipsilateral and contralateral kicks and generally continues before and after a kick in the head stand or stilt stand (Figs 5, 6). After a kick, several types of behaviour may follow: standing, repeated kicking, a maintained head stand or a stilt stand. Kicks may occur during walking, but they rarely disturb the progress of locomotion.

Discussion

Ballistic movements of appendages are used by many insect species to strike, hit, catch, whip or kick (whereas in jumping, the movement propels the whole body). The target may be a conspecific opponent, a prey, a predator or a molesting object. The long hindlegs make the kicking behaviour particularly effective in locusts, crickets and bushcrickets. In these animals, unilateral kicking can be evoked reliably in 'standard situations', for example by something tickling the posterior parts of the animal. Similarities with kicking are visible in swimming and jumping of these insect groups (Pflüger and Burrows, 1978), although these behaviours use both legs simultaneously.

In kicking, the hindleg tibia undergoes a very rapid acceleration along a short trajectory for power and speed (by a rotatory movement with a small radius). The knee and, to a lesser extent, the proximal leg joints contribute most to the movement. To enable the main acceleratory muscles to contract suddenly after developing their full force, the serial elastic elements are first stretched against the load of a large mechanical resistance. When released from this resistance, the tibia is immediately subject to the maximal acceleration driven by the extensor muscle, as in a catapult.

Jumping insects, such as the flea or locust, that have sufficient time to prepare catapult-like catch mechanisms of joints or tendons, often gradually store potential energy in their muscles and elastic cuticular elements (Bennet-Clark, 1975; Heitler, 1974). When, for example, visual anticipation of imminent danger leaves time to make the decision to crouch, to kick or to jump, then the antagonistic tibial extensor and flexor muscles have considerable time for a static co-contraction period before the final rapid hindleg action. For a cricket, in contrast, the response time for a successful kick after a touch to the body mechanoreceptors is extremely short: a time-consuming static co-contraction period before a kick would frequently be fatal. The problem is solved by a 20–80 ms dynamic co-contraction during knee flexion of the pre-kick period that precedes the actual kick. The complete kick is thus performed 5–10 times faster in a cricket than in a locust. This solution requires adaptations at the level of neural control, the muscular performance or the biomechanical design of the knee and tendons.

The mechanical design

The knee of the cricket hindleg shows biomechanical specialisations for kicking and jumping that are not seen in the forelegs and middle legs. These are the cushion of the flexor

tibiae tendon and the cuticular ridge, both of which progressively improve the vector of the flexor tendon's pull during knee flexion. The same design is seen in the hindlegs of most bushcrickets, but not in non-jumping Jerusalem crickets (Stenopelmatidae), mole crickets or other, non-jumping orthopterans such as cockroaches and stick insects (R. Hustert, unpublished observations). Only acridid grasshoppers have a comparable cuticular specialisation of the flexor tendon ('Heitler's lump', Heitler, 1974), but they lack a cushion. These specialisations of the knee hint that crickets share a closer common ancestry with bushcrickets than with other orthopteran groups (see also Sharov, 1971).

The differences between the knee biomechanics of the hindlegs of locusts and crickets could be attributed to the duration and release mode of their kicks and jumps: crickets react instantly to tactile stimuli to the body by jumping or kicking, even during walking. They therefore need a very rapid pre-kick flexion and release of the actual kick, which does not allow for an extended period of mechanical locking of the flexor tendon, as seen in locusts (Heitler and Burrows, 1977a). Locusts, in contrast, can use their good vision to anticipate a predator and thus to prepare a jump or kick (Riede, 1990). The source of a tactile stimulus that is not accompanied by a visual input is usually small and probably innocuous, which leaves time to prepare a kick if necessary.

The lever and pulley mechanisms of the cricket knee joint are basically the same as in locusts: the effective leverage of the flexor muscle increases progressively with knee flexion, whereas that of the extensor muscle decreases. With knee extension, the situation reverses progressively in favour of extensor muscle leverage. The flexor tendon's cushion increases the effective ratio of leverage and prevents the tendon from locking. This is just the opposite of the locking device of the locust's flexor tendon that seems to favour static muscular co-contraction during an extended pre-kick period lasting for 500–1000 ms.

Motor control

The onset of a unilateral kick starts with almost synchronous excitation of many leg muscles (Figs 4–6), including the extensor and flexor tibiae muscles of the kicking hindleg. The mechanical result is an initial flexion of the knee joint. The advantage of flexor activation is due to (i) the amount of excitation (frequency and recruitment of the 6–8 excitatory motor units) it receives in contrast to just one motor unit initially active in the extensor; and (ii) to the mechanics of the knee joint, which favours flexion at the prevailing angles of a standing cricket (45–110°).

The transition from pre-kick to kick is based on a decreased ratio of flexor to extensor force. After the increase of extensor force by the later recruitment of the fast motor unit (1–4 EJPs preceding a kick), the actual kick follows several milliseconds later, usually coinciding with decreasing flexor and extensor activity (Figs 3–6). The interposed still period (basically a static co-contraction) may represent the time required after the pre-kick flexion for the extensor muscle to develop sufficient

force to overcome the flexor force at the extremely flexed position of the knee, and thus to release a kick.

It was surprising to see how, in apparently very similar kicks, the motor pattern of the main power muscle (extensor tibiae) shows very different discharge frequencies. The only explanation is that the mechanics of the knee joint is primarily responsible for shaping the femoro-tibial component of the kicking movement (Könen and Hustert, 1993).

Experiments on the energetics of the locust jump (Bennet-Clark, 1975) have demonstrated that the functional performance of the kick lags 10–20 ms behind the EJPs recorded in the leg muscles, but in the cricket kick (admittedly with less load than in a jump), the leg muscles seem to respond much sooner.

The high angular velocity of the femoro-tibial joint has three principal causes: (i) release of the activated contractile apparatus from resistance; (ii) conversion of potential energy in serial elastic elements into kinetic energy; and (iii) the mechanical design of the joint, which favours extensor force over residual tension of the flexor with progressive extension in the joint.

The amplitude of the kick itself is limited by the extensibility of the knee joint and sometimes by the resistance of the object that is being kicked. The force underlying the rapid extension may be exhausted early in the kick, leaving the continuing movement to inertia. The reason for this may be that orthopteran extensor tibiae sarcomeres have their most effective length at a knee angle of 30° and their lowest power output at angles above 150°, and because of the decrease in effective leverage (Bennet-Clark, 1975).

After the tibial extension during a kick, the flexor activity is resumed in order to return the leg to a normal flexed position on the ground. Alternatively, a leg may remain raised when the animal immediately assumes the defensive positions of a stilt stand or head stand.

Supporting motor control

Every kick from the preparatory period onwards is balanced by the standing legs. For the redistribution of body mass when the hindleg is lifted (e.g. mesothoracic depressor trochanteris activity), and for compensation of the ballistic forces, there is counteracting muscular force at the base of the hindleg (e.g. metathoracic adductor coxae activity) and in the muscles of the other legs. The coordination of a kick therefore requires the transmission of neural commands throughout the thoracic central nervous system. An example seen in myograms is pushing of the contralateral hindleg against the ground to support the body while the other leg kicks. It would be interesting to see whether the laterality of the kick is also reflected in ganglia other than the metathoracic ganglion, or whether there is only one general motor programme to accompany any of the various modes of a kick. There is a difference in their activities when the different defensive positions (head stand or stilt stand) are assumed by a cricket: during the head stand the weight-supporting muscles of the

middle leg decrease their activity after most of the body weight has been transferred to the head.

Sensory control

Sensory influences on the performance of the cricket kick are largely unknown, although many proprioceptors supply the hindleg, most of them homologous to those known in the locust (Gnatzy and Hustert, 1989). Only Brunner's organ which, in locust hindlegs, signals the complete knee flexion that is a prerequisite for static co-contraction of flexor and extensor muscles (Heitler and Burrows, 1977a,b) is not present in crickets. One possible functional equivalent of Brunner's organ is a long tibial hair pointing into the bending area of the knee joint of the cricket. It is bent by the approaching femur when the knee becomes almost completely flexed in the pre-kick period. Tibial strain, signalled by the tibial campaniform sensilla, as during the locust co-contraction (Burrows and Pflüger, 1988), could not contribute to the kick performance. For this sensory system, and possibly for all other proprioceptive ones, the axonal conduction times and synaptic delays in the central nervous system would delay the sensory information until well after the kick had been performed.

References

- BENNET-CLARK, H. C. (1975). The energetics of the jump of the locust *Schistocerca gregaria* *J. exp. Biol.* **63**, 53–83.
- BURROWS, M. AND PFLÜGER, H.-J. (1988). Positive feedback loops from proprioceptors involved in leg movements of the locust. *J. comp. Physiol. A* **163**, 425–440.
- DUMPERT, K. AND GNATZY, W. (1977). Cricket combined mechanoreceptors and kicking response. *J. comp. Physiol. A* **122**, 9–25.
- GNATZY, W. AND HEUBLEIN, R. (1986). Digger wasp against cricket. I. Receptors involved in the antipredator strategies of the prey. *Naturwissenschaften* **73**, 212–215.
- GNATZY, W. AND HUSTERT, R. (1989). Mechanoreceptors in behavior. In *Cricket Behavior and Neurobiology* (ed. F. Huber, W. Loher and T. E. Moore), pp. 198–226: Ithaca: Cornell University Press.
- GNATZY, W. AND KÄMPER, G. (1990). Digger wasp against cricket. II. A signal produced by a running predator. *J. comp. Physiol. A* **167**, 552–556.
- GYNTHNER, I. C. AND PEARSON, K. G. (1986). Intracellular recordings from interneurons and motoneurons during bilateral kicks in the locust: implications for mechanisms controlling the jump. *J. exp. Biol.* **122**, 323–343.
- HEITLER, W. J. (1974). The locust jump: specialisations of the metathoracic femoral-tibial joint. *J. comp. Physiol. A* **89**, 93–104.
- HEITLER, W. J. AND BRÄUNIG, P. (1988). The role of fast extensor motor activity in the locust kick reconsidered. *J. exp. Biol.* **136**, 289–309.
- HEITLER, W. J. AND BURROWS, M. (1977a). The locust jump. I. The motor programme. *J. exp. Biol.* **66**, 203–219.
- HEITLER, W. J. AND BURROWS, M. (1977b). The locust jump. II. Neural circuits of the motor programme. *J. exp. Biol.* **66**, 221–241.
- HUBER, F. (1965). Brain controlled behaviour in orthopterans. In *The Physiology of the Insect Nervous System* (ed. J. E. Treherne and J. W. I. Beament), pp. 233–246. London: Academic Press.
- HUSTERT, R. (1985). Multisegmental integration and divergence of afferent information from single tactile hairs in a cricket. *J. exp. Biol.* **118**, 209–227.
- HUSTERT, R. AND GNATZY, W. (1989). Defensive kicking of crickets: release, trajectories and coordination of the motor programmes. In *Dynamics and Plasticity in Neuronal Systems: Proceedings of the 17th Göttingen Neurobiology Conference* (ed. N. Elsner and W. Singer), p. 120. Stuttgart, New York: Thieme.
- KÖNEN, M. AND HUSTERT, R. (1993). The defensive kick of crickets: motor control and biomechanical requirements. In *Gene–Brain–Behavior: Proceedings of the 21st Göttingen Neurobiology Conference* (ed. N. Elsner and M. Heisenberg), p. 183. Stuttgart, New York: Thieme.
- PFLÜGER, H.-J. AND BURROWS, M. (1978). Locusts use the same basic motor pattern in swimming as in jumping and kicking. *J. exp. Biol.* **75**, 81–93.
- RIEDE, K. (1990). Optically and acoustically evoked escape behaviour in grasshoppers. In *Rhythmogenesis in Neurons and Networks: Proceedings of the 18th Göttingen Neurobiology Conference* (ed. N. Elsner and G. Roth), p. 207. Stuttgart, New York: Thieme.
- SHAROV, A. G. (1971). *Phylogeny of the Orthopteroidea*. Reprint. Israel Program for Scientific Translations, Jerusalem.
- VON REKOWSKI, C. AND HUSTERT, R. (1991). Sites of tactile stimuli on the body of locusts determine defensive reactions. In *Synapse–Transmission–Modulation: Proceedings of the 19th Göttingen Neurobiology Conference* (ed. N. Elsner and H. Penzlin), p. 67. Stuttgart, New York: Thieme.