

Ballistic movements of jumping legs implemented as variable components of cricket behaviour

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Accepted 5 August 2010

SUMMARY

Ballistic accelerations of a limb or the whole body require special joint mechanisms in many animals. Specialized joints can be moved by stereotypic or variable motor control during motor patterns with and without ballistic components. As a model of variable motor control, the specialized femur–tibia (knee) joints of cricket (*Acheta domestica*) hindlegs were studied during ballistic kicking, jumping and swimming and in non-ballistic walking. In this joint the tendons of the antagonistic flexor and the extensor muscles attach at different distances from the pivot and the opposed lever arms form an angle of 120deg. A 10:1 ratio of their effective lever arms at full knee flexion helps to prepare for most ballistic extensions: the tension of the extensor can reach its peak while it is restrained by flexor co-contraction. In kicks, preparatory flexion is rapid and the co-contraction terminates just before knee extensions. Therefore, mainly the stored tension of the extensor muscle accelerates the small mass of the tibia. Jumps are prepared with slower extensor–flexor co-contractions that flex both knees simultaneously and then halt to rotate both legs outward to a near horizontal level. From there, catapult extension of both knees accelerates the body, supported by continued high frequency motor activity to their tibia extensor muscles during the ongoing push-off from the substrate. Premature extension of one knee instantly takes load from the lagging leg that extends and catches up, which finally results in a straight jump. In swimming, synchronous ballistic power strokes of both hindlegs drive the tibiae on a ventral-to-posterior trajectory through the water, well coordinated with the swimming patterns of all legs. In walking, running and climbing the steps of the hindlegs range between 45deg flexion and 125deg extension and use non-ballistic, alternating activity of knee flexor and extensor muscles. Steep climbing requires longer bursts from the extensor tibiae muscles when they support the extended hindlegs against gravity forces when the body hangs over. All ballistic movements of cricket knees are elicited by a basic but variable motor pattern: knee flexions by co-contraction of the antagonists prepare catapult extensions with speeds and forces as required in the different behaviours.

Key words: Motor control, ballistics, kick, jump, swim, run, cricket.

INTRODUCTION

Many insects have evolved specialized appendages for specific tasks such as catching, digging, swimming or jumping, but these limbs are also involved in less specialized behaviour. If they impede ordinary movements, they are often kept out of the way: locusts raise their hindlegs from the substrate before their rapid body turns and only the other four legs rotate the body behind small stems or grass leaves (Hassenstein and Hustert, 1999), and desert mantids (e.g. *Eremiophila* sp.) keep their specialised catching forelegs raised while running rapidly with just their middle- and hindlegs (R.H., unpublished observation).

In the saltatory orthopteran insects the hindlegs are elongated and their femur–tibia joints (knees) are specialized for ballistic extension in jumps or defensive kicking. Their basic knee biomechanics and motor programs have been described for locusts during kicking and jumping (Heitler, 1974; Heitler and Burrows, 1976; Burrows, 1995; Burrows, 1996). These insects use a lever advantage of the flexor muscle and a locking (catch) mechanism in their knees. Crickets (Hustert and Gnatzy, 1995), some other grasshoppers (Burrows and Wolf, 2002) and bushcrickets (Burrows and Morris, 2003) have no locking device in the knees of their jumping legs. In their preparation for ballistic extensions, the lever advantage for the flexor tibiae muscle causes initial knee bending while the antagonistic extensor tibiae co-contracts and increases isometric tension during this restraint.

Here we focus on the cricket *Acheta domestica*: the strong and elongated jumping legs participate fully in almost all locomotive or defensive movements. The knee specializations for catapult-like extension of their tibia (Hustert and Gnatzy, 1995) impose no stereotypic movement patterns on the hindlegs, which can perform ballistic behaviour with high variability. The different types of motor control of the antagonistic knee muscles was studied using electromyogram (EMG) recordings and high-speed video recording during voluntary behaviours: ballistic kicking, jumping and active swimming as compared with the non-ballistic behaviours, walking and climbing. We could estimate only the role of the more proximal coxa–trochanter and thorax–coxa joints, which are less visible but have important stabilizing function in hindleg movements and also support ballistic extension in jumping and swimming and in targeting of kicks.

MATERIALS AND METHODS

Male or female house crickets (*Acheta domestica* Linnaeus) from a laboratory stock were used for all experiments and preparations. They were anaesthetised by chilling to 0–4°C before and during preparations. All results presented in this paper are based on a set of at least five experiments for each type of measurement.

Geometrical changes of the effective lever arms due to the femorotibial joint angles were determined in freshly prepared legs with the femur waxed to a microscope slide while the tibia could

be moved freely and parallel to the surface of the slide. The cuticle was removed on the distal femoral surface without changing the functional properties of the joint. That made it possible to see the joint axis, the lever arms where tendons attach to the tibia and the angles at which they pulled when the tibia was positioned at the different knee angles. The dynamics of joint movements were observed in similar preparations: the leg on the microscope slide was mounted vertically and all muscle fibres were removed. Fine wires, attached to the flexor and extensor tendon were used to load the flexor side with different weights and the extensor tendon could be pulled progressively until kicks were released.

The two motor units of the tibia extensor muscle could be stimulated *via* separate motor nerves with suction electrodes at the cut ends of efferent nerves 3B and 5A [numbering adapted from Campbell (Campbell, 1961)], because the fast and slow motor axon of the extensor tibiae run separately in these nerves. Stimulation was coupled by using two stimulators (Grass SD9; Quincy, MA, USA), one of them with a delay.

Muscles forces in response to stimulation were measured with calibrated transducers (strain gauges mounted on steel spring tongues; made in the electronic workshop of our institute). The same transducer monitored the instant of takeoff in free jumps from the platform underneath.

Electro-myograms (EMGs) of freely moving crickets were recorded chronically from the extensor and flexor tibiae muscles at their femoral attachments with 30 µm diameter stainless steel (or 40 µm copper) wires coated except at the tips. The coating was stripped for 1–2 mm from the tip of the common indifferent electrode, which was inserted in the femur distally so that it pierced the septum that separates ventral and dorsal haemolymph compartments of the femur. Many recordings from femoral muscles showed cross-talk from their antagonist, however, the single fast unit of the extensor tibiae was identified easily by the high and uniform amplitudes. The only other excitatory unit is the slow unit with much lower amplitudes that often increase because of facilitation. Also, it often coincided with the fast motor unit of the muscle. Extensor EMG recordings were used only if they could be distinguished clearly from the more complex flexor EMGs recorded simultaneously from the flexor tibiae. The EMGs from the flexor tibiae were taken from the proximal and the medial part containing up to 12 excitatory motor units (Nishino, 2003; Nishino, 2004). Data with regular coincidence of spikes in flexor and extensor EMGs were regarded to be the result of electrical crosstalk artefacts and discarded.

The EMGs (and also force measurements) were recorded initially on magnetic tape (Racal Store 7, Weybridge, UK) and later with computer software (Datapac 2K2, Mission Viejo, CA, USA).

For voluntary jumps from a defined area, the crickets were released on a small dry platform in the middle of a water-filled Petri dish of 12 cm diameter. The animals first explored the platform and then tried to jump off with long jumps. To measure the takeoff time of jumps, the platform was coupled with a strain gauge and movements were video-recorded under pulsed red LED light, which crickets cannot see (pulses: 0.1 ms duration, frequencies up to 1000 Hz). Simultaneous video-recording of jumps or kicks with corresponding EMGs (visualized on an oscilloscope screen) were combined on single frames by a video mixer (Panasonic WJ-AV E5 with input from two Kappa CF15 cameras).

Movement variability in the different movement types of free kicking, swimming, jumping and running were recorded separately with the high-speed mode of a digital camera (Casio EX-F1) at frame rates of 600 Hz.

RESULTS

Biomechanical basics of the cricket knee

The knee of the hindleg is a hinge-joint where femur and tibia flex and extend between 10 deg and 150 deg and the proximal leg joints provide an additional range of trajectories for the whole leg. In resting animals the knees point 30 deg or more laterally from the body and femur and tibia perform normal anterior–posterior walking movements in that plane. In the knee joint the tibia pivots about two lateral condyles (Fig. 1B) which are embedded at the inside of the two lateral ('semilunar') processes of the distal femur. The latter are composed of very hard cuticle that never deforms, even under heavy strain [other than the homologous semilunar processes of locusts (Bennet-Clark, 1975)]. The thick and very hard proximal rim of the tibia has a semicircular profile (Fig. 1B). From the rim towards the centre stretches a thin, tough and flexible arthroal membrane (syndese), like a drumhead, with the hard cuticular tendon of the extensor tibiae muscle embedded in the middle. The arthroal membrane contains resilin, which can be identified by its blue fluorescence using UV illumination (see Neff et al., 2000).

The attachment of the flexor tendon at the tibia is fortified laterally with a 'fork' of hard cuticle that joins the tibia about 0.7 mm away from the pivot axis of the knee (Fig. 1C). The insertions of extensor and flexor tendons, with the pivot axis of the joint in between, constitute a lever with its two arms at an angle of 120 deg (Fig. 1A). That differs from knee mechanics in the middle- and forelegs which are provided with a straight (180 deg), two-armed lever. In the hindleg, the flexor tendon has its optimal angle and leverage of attack when the knee is at a 15 deg angle, while for the extensor tension the angle is at 85 deg of knee flexion (Fig. 1D–F). Between these angles, joint extensions increase the effective leverage (momentum) of extensor tendon and flexions increase the effective leverage of the flexor tendon. For the latter, its angle of attack is improved further by sliding over a ridge of the distal femur (Fig. 1A) and by an embedded cushion (wrapped in tough, resilin-containing tissue) that also slides over the ridge and further moves the tendon dorsally (Hustert and Gnatzy, 1995). This additionally improves the angle of attack for the flexor tendon (Fig. 2B). The accessory flexor muscle is attached to the cushion region (Fig. 2, inset) (Nishino, 2003) and its force can ease sliding of the cushion over the ridge during knee flexion.

Myograms and the ballistic kick

Kicks are the fastest catapult movements of the cricket tibia for they accelerate only the mass of the tibia and last about 2–6 ms. The momentum for the kicks, developed during the previous 18–40 ms of dynamic co-contraction of the antagonistic extensor and flexor tibiae, is caused mainly by the potential energy from isometric tension of the extensor tibiae muscle. Very strong kicks require high counter-force by the restraining flexor during the co-contraction period (Fig. 2A) which in turn is superseded by increased extensor force caused by up to six final spikes of the fast extensor motor unit (Fig. 2C). Individual crickets can have a preference for slow force kicks or for vigorous kicks in response to similar tactile stimuli. Vigorous kicks against a firm object can hurl the cricket itself away for several body lengths. Occasionally, kicks are released early from incomplete knee flexion (Fig. 2B) because the extensor tension overrides the prevailing flexor tension early at the momentary ratio of effective leverage. In natural behaviour, such 'incomplete' kicks can intervene during running or in repetitive kicking.

Just before the release of kicks all excitatory motoneuron activity to both extensor and flexor tibiae terminates (Fig. 2C). The accessory flexor tibiae muscle discharges late during the co-contraction phase and its more dorsoventral angle of attack eases slipping of the

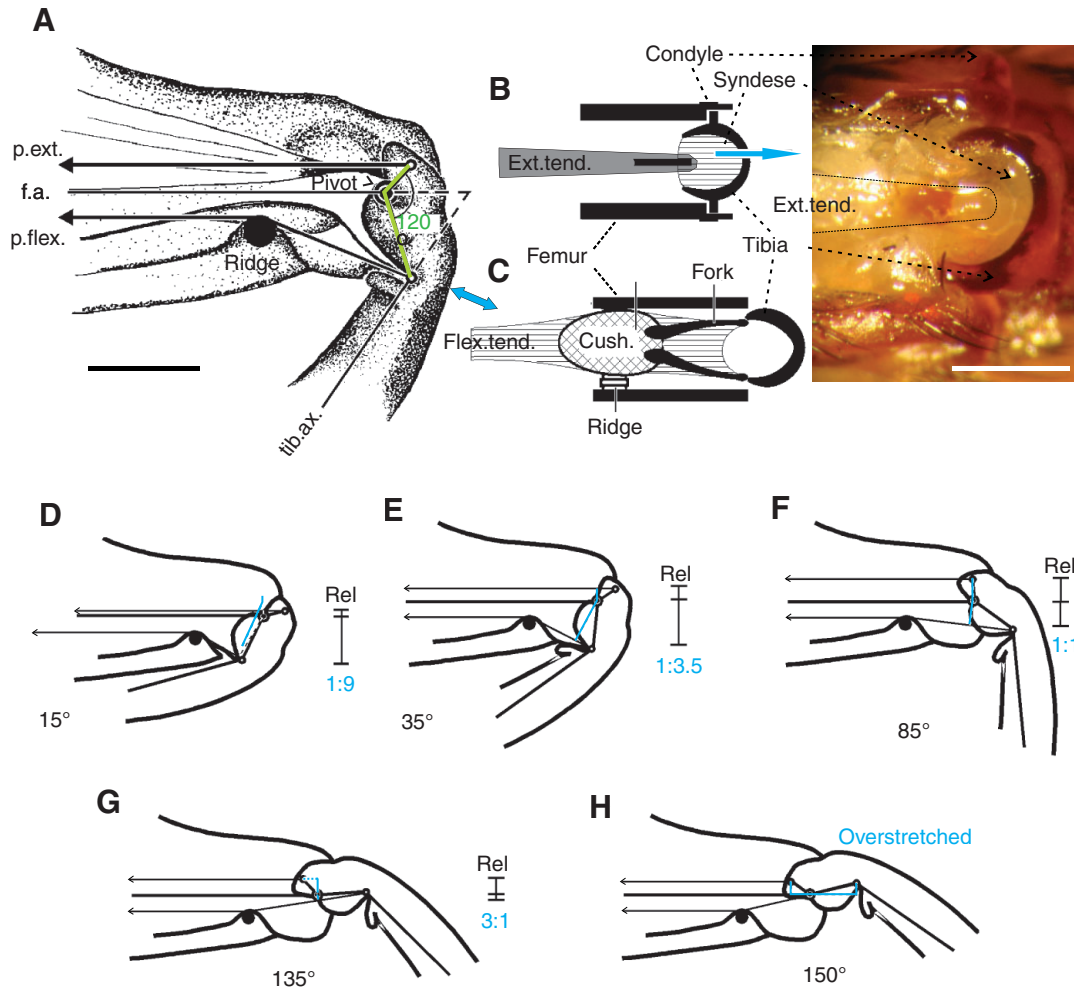


Fig. 1. Biomechanics and knee angles related to tendon attachments of the cricket hindleg. (A) Lateral view of the joint with the lateral cuticle of the femur removed and extensor and flexor muscle attachments at the tibia exposed. Superimposed schematically are the pulling vectors of their tendons (p.ext.; p.flex.), the femur long axis (f.a.) and the two-armed lever (green) that mainly influences effective leverage. Scale bar, 1 mm. (B) Schematic dorsal view of a flexed femur-tibia joint (80 deg) showing the insertion of the hard extensor tendon (Ext.tend.) at the tibia mediated by a drumhead-like syndese. Right: a view of the actual joint with a piece of the dorsal femoral cuticle removed (tendon is outlined); scale bar, 0.5 mm. (C) Schematic horizontal cross section of the flexed femur-tibia joint (80 deg) where the flexor tendon inserts also with its lateral fortifications (fork) as a hinge-like attachment at the tibia. More proximally on the tendon lies the cushion (Cush.) that slides in the bending knee over the ridge of the femur. (D-H) Geometry and effective leverage (blue bars) of tendon insertions between the extreme angles (15 deg vs 150 deg) of the knee with the effective lever ratio (Rel) indicated in blue numerals and the bars below (based on camera lucida drawings of dissected leg).

cushion on the flexor tibiae tendon over the ridge. In our EMGs, the main flexor activity usually decreased during final discharges of the extensor fast unit (Fig. 2C, Fig. 3A). That may be different in different compartments of the flexor muscle (Nishino, 2003; Nishino, 2004) and therefore may be not represented in our recordings with a single focal EMG electrode from the long multi-unit flexor muscle.

Force and pattern of muscle contractions

The tension of the extensor tibiae muscle develops slowly during preparatory co-contraction in kicks and is driven mainly by the slow unit (Fig. 2C). The following, superimposed fast-unit activity increases tension rapidly and finally releases ballistic extensions, once all antagonistic forces are overcome. If then the tibia hits, with high intensity, a resisting object, the rebound from the object can hurl the insect itself for several centimetres. Repetitive fast unit firing increases the peak force to levels that may be used in strong kicks or jumps (Figs 3, 4).

The relationships of forces developed by the combined activity of the slow and the fast unit of the extensor tibiae muscle, such as in kicks, was mimicked in a nerve-muscle preparation with a combined pattern of slow and fast unit stimulation (Fig. 3A). That was only possible because the motor axons of the fast extensor and slow extensor run in the two separate leg nerves, 3B and 5B, where they can be stimulated selectively to measure the resulting tension developed in the extensor tibiae. To provide near natural efferent patterns similar to those during kicks and jumps, the slow units were first stimulated alone *via* nerve 5B for 48 ms at 400–500 Hz and after a delay of 30 and 50 ms fast unit stimulation *via* nerve 3B was superimposed at 200 Hz. The slow motor unit increases extensor tension moderately after about 12 ms and peaks about 60 ms later. The first superimposed fast muscle potential causes, within a few milliseconds, a steep rise in tension that peaks after about 25 ms. This is required for the rapid build-up of muscle tension and the chance for release of ballistic extension in natural movements. The time course and the amplitudes of forces may be different in intact

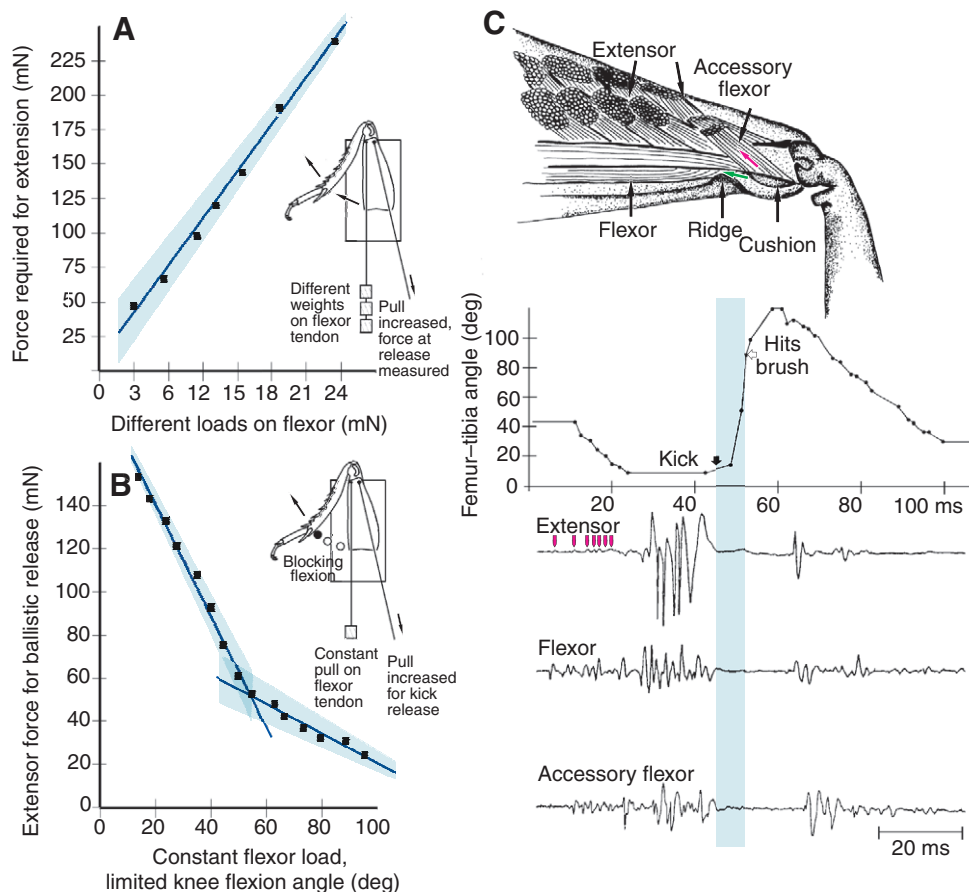


Fig. 2. Muscles and forces of knee movements. (A) Diagram of forces measured at the release of kicks with different pre-set loads at the flexor tendon. The inset shows the experiment with a freshly mounted hindleg (femur vertical, tibia mobile) and the knee bent completely (shown less flexed here) while at the flexor tendon different weights pull constantly with 3–24 mN. The extensor tendon is pulled with increasing force until the ballistic knee extension is released and the threshold force required for the release is recorded. Extensions under different loads exhibit a fairly constant 10:1 ratio of forces due to just the knee biomechanics (purple line: averaged regression line taken from five tested preparations and corresponding extent of variation as blue shading). (B) Extensor force threshold for eliciting kicks from different pre-set angles of knee flexion. The constant flexor force equals 15 mN. The inset shows the setup (similar to A): a constant flexor load is applied while the initial angle (α) of joint flexion is varied. The threshold forces required to elicit kicks follow a curve composed of two inclinations (blue lines: averaged regression curves for the two sections taken from five tested preparations, with variation ranges in blue shading), that indicates altered geometrical relations due to the flexor cushion. (C) Activity and co-activation of the antagonistic femur-tibia muscles (main and accessory) during a moderately strong kick of a freely moving cricket. The sequence of video-recorded knee joint angles (diagram) is time matched with the three subjacent EMG traces (no crosstalk between them). The ballistic movement time between kick (black arrow) and hit (hitting of the stimulating paintbrush) is marked by the blue shading. The knee muscles receive no further excitation during knee extension but their previous activity patterns show the typical co-contraction (pink arrows point to slow extensor units). Large drawing above: internal view of the locations and distal attachments of flexor and extensor tibiae muscle bundles with insertion on the tendons. Arrows show effects of flexor contractions: green for main flexor and red for the accessory flexor that lifts the cushion over the ridge.

animals with normal haemolymph and oxygen supply for the leg muscles.

Acceleration in jumps

Voluntary jumps of the cricket *Acheta domestica* (mass ~0.5 g) reach distances of up to 50 cm. Takeoff velocity is 1–3 m s⁻¹ in jumps of different length. All spontaneous jumps of our crickets from a small platform were strictly in a frontal direction and had typical takeoff angles between 20 deg and 30 deg (extremes at 15 deg and 45 deg). Escape jumps are different: the crickets turn rapidly away from a tactile or wind stimulus and jump off immediately to one side or high up in the air. Voluntary jumps have three main phases (Fig. 3B). (1) The tibiae of both hindlegs are drawn forward with flexing of the knees by co-contraction and their tarsi are set near the first abdominal segments under the body. (2) The static co-contraction of knee muscles is maintained for 10–120 ms while the

motor unit activities may decrease, sometimes as if the animal hesitates to jump (Fig. 4D). That makes the extensor/flexor burst length subject to considerable variation, specifically in shorter jumps (Fig. 4B). (3) The final preparation for a jump (up to 50 ms) involves spreading the flexed femur and tibia of both legs laterally (a 'delta'-shape from above) with the knees pointing near horizontal and perpendicular to the body long axis (Fig. 3B). That rotation is by means of the proximal joints and tilts the substrate contacts of the hindlegs to the lateral distal spurs of the tibia and the claws of the tarsus. (4) Ballistic release and acceleration of the jump require high frequency firing of extensor motoneurons that continues far into the push-off period when the tibial spurs and the tarsi are still on the ground (Fig. 3B, Fig. 4D).

The knee angle extends from 10 deg to 150 deg within 8 ms in long-distance jumps and up to 30 ms in the short-distance jumps. Depression of the femur before and during a jump is accomplished

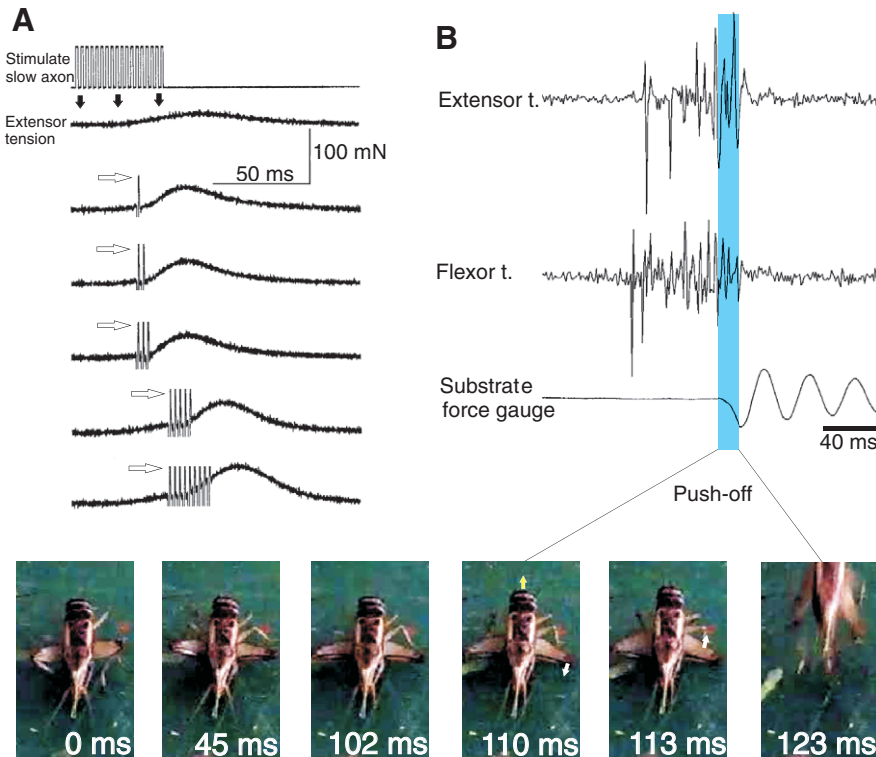


Fig. 3. (A) Muscular forces developed in a preparation by selective nerve stimulation of slow and fast motor units of the extensor tibiae. Electrical stimulation of the slow extensor tibiae motor unit alone (first trace) causes extension force at the tibia (at 30% distal from the knee joint, second trace). Additional stimulation of its fast motor unit (arrows in traces 3–7; stimulus artefact superimposed on tension trace) causes steep rising of tension. (B) EMG of extensor and flexor tibiae in a hindleg during a voluntary jump (20 cm), with the timing measured at the resilient (steel spring) substrate. The push-off period is marked by blue shading and is related to high-speed video frames of a long jump. Frames: 0 ms, cricket stops walking; 45 ms, complete flexion of knees; 102 ms, flexed knees rotated down; 110 ms, flexed legs rotated backwards (white arrow) by proximal joints and body moves forward (yellow arrow); 113 ms, knees start ballistic extension (white arrow); 123 ms, cricket leaves substrate.

by the proximal joint muscles that serve also to stabilize the proximal joints when the forces of the extending femur–tibia joint are transferred to the whole body. Depressing the coxa can contribute to the acceleration of the body before and during the push-off period of jumps. Depression of the coxa without knee extension is often seen to move the body forward and up for 5–10 ms before the knee of a hindleg starts ballistic extension (Fig. 3B). For the knee muscles, frequency distribution and burst duration in extensor and flexor EMGs varies for repeated jumps – even for the same jump distance of the same cricket (Fig. 4B,C), but more so for short jumps. Also, in all jumps the activity of the flexor motor units continues for 10–25 ms into the push-off phase after the ballistic release of the tibia (Fig. 4D, Fig. 5) but it often persists also until the end of knee extension. Generally, there is a slight trend for longer co-contraction time and jump preparation in long-distance jumps, while push-off times become shorter and firing frequency of the fast extensor unit is higher (Fig. 4A,C). So it is unpredictable for jumps of the same trajectory and distance how the two phases will combine: (1) the strength and preparatory time of the ballistic component, and (2) the power for the acceleration during the push-off phase by the extensor muscle. Just after takeoff the body decelerates slightly (Fig. 5) when the hindlegs leave the ground and their slower mass constitutes a negative momentum that decelerates the body.

In the normal bilateral jump with two hindlegs the two parallel catapults are released at the same time. A major delay between both would cause oblique jumps or body rotations in the air – as is observed in jumps of animals that have lost one hindleg. In voluntary cricket jumps, extensor bursts in both hindlegs terminate fairly simultaneously and tibia extension is synchronous (Fig. 4D, Fig. 5).

Influences on jump distance

The preparatory energy storage of the extensor tibiae is similar in jumps and kicks: after knee bending the remaining flexor tension

can briefly act as a holding force. For the release of jumps, the residual flexor tension plus the weight of the body must be overcome by the extensor force (Fig. 3B, Fig. 4D). Major influences on jump distances of between 8 and 50 cm are: (1) at high flexor tension during preparatory co-contraction, a proportionally high extensor discharge tension is needed to release a jump which in turn has a proportionally higher momentum at the release of the ballistic extension, and (2) during knee extension (push-off period), the fast extensor units continue to fire while the legs have contact with the substrate. Our EMG recordings from the flexor tibiae show that, before jumps are released, its activity does not terminate early as in kicks (Fig. 3B, Fig. 4D). We could not determine all of the details of the neural control for this muscle because of the many excitatory motor units (over 12) supplying this muscle. The junction potentials of these motor units superimpose heavily in EMGs, whereas other motor units may not be represented (Nishino, 2003; Nishino, 2004).

EMGs from the extensor tibiae show high efferent frequencies of bursting of the fast unit from the onset of jump preparation until the cricket is airborne (Fig. 3B), but bursts remain variable in frequency distribution even for jumps of the same cricket with the same jump distance (Fig. 4B,C) as if the animal could regulate the motor program at will and according to the prevailing conditions. Decreasing efferent frequencies near the end of flexor bursts favour the release of tibial extension. A possibly increased support of flexor relaxation by inhibitory motoneurons could not be elucidated in the EMGs.

Repetitive leg movements

Walking

In normal walking and running (step frequency up to 12 Hz), crickets use their hindlegs mainly for steps that push straight backwards mainly by knee extensions between 45 deg and 120 deg. In continuous walking the motor activities of the extensor and flexor tibiae muscles alternate, sometimes with a short overlap, but they never co-contrast as in ballistic movements. Hindlegs usually

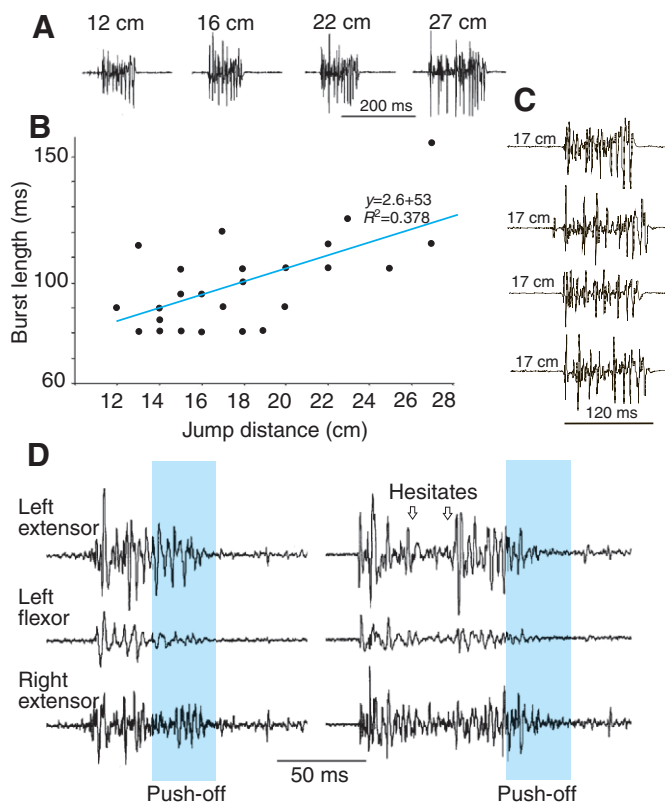


Fig. 4. Variability of jumps recorded by EMGs from extensor and flexor tibiae in freely moving crickets performing jumps of different lengths. (A) Examples of extensor activity with increasing preparatory burst lengths of the fast extensor tibiae for longer jumps. (B) High variability of fast extensor burst durations related to jumping distances of a single animal. Trend line in blue (y , inclination; R^2 , regression coefficient). (C) Extensor burst variability for 17 cm jumps of one animal. (D) Variability of motor patterns of tibia extensor muscles of both legs and of one flexor tibiae during preparatory co-contraction and push-off period for two short 12 cm jumps of one cricket. The first compact preparatory burst differs from the second, which is almost subdivided (hesitates). Extensor bursts of both hindlegs terminate similarly in the long push-off periods (shading; movement was video monitored).

participate in the tripod gait of all legs, but rapid defensive kicks may intervene when a cricket is touched from the rear while the animal continues walking. The hindlegs touch the ground mainly with their tibial spines and the spines of the last tarsomere when running. They push backwards with step amplitudes corresponding to those of middle- and forelegs even when climbing steeply. The extensor tibiae motor patterns of hindlegs change to higher burst frequencies of the fast unit, followed by slow unit discharges that serve to support the body while the other hindleg swings forward. Burst durations become longer when crickets climb up on the flat surface of wooden boards with increasing inclination (Fig. 6). During climbing, high frequency discharges in EMGs of the extensor tibiae correspond with the main function of hindlegs: to push the body upwards while the forelegs mainly pull and the middle legs rotate in a 'rowing' manner. More vertical climbing (80–90 deg) alters the pattern seen in hindleg extensor EMGs into two more-or-less distinct fast extensor bursts per step, one apparently for the dynamic knee extension and the second for more static holding of the extended knee to prevent the whole animal toppling over backwards after leg extension [compare: locust climbing (Duch and Pflüger, 1996) and cockroach climbing (Goldmann et al., 2006)].

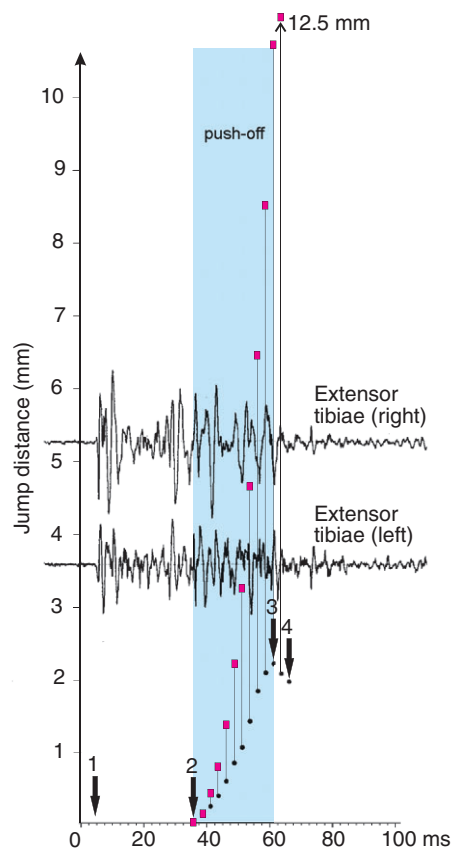


Fig. 5. Jump acceleration of the body during the push-off with corresponding EMGs from both extensor tibiae muscles inserted. Video recording of body acceleration under a LED strobe light (400 Hz) during a 14 cm jump with a takeoff angle of 35 deg. Black dots in the movement graph mark the flash by flash progress, and red squares the absolute progress of a reflecting mark on the body. Blue shading marks the push-off period in this jump. Numbers on arrows indicate: 1, simultaneous start of muscle activity in both hindlegs (co-contraction); 2, start of body acceleration; 3, peak velocity at takeoff; 4, airborne cricket leaves video frame.

Swimming on water

Adult crickets float on the surface of water because of their specific weight of $0.7\text{--}0.8\text{ g cm}^{-3}$, partly dependent on the prevailing volume of all tracheal air sacks of the body, which in turn depends on internal factors such as compression by heavier food or genital products. Surface tension of the water can provide additional support, and in clean crickets the space between the hydrophobic cuticle and the multiple bristle hairs on the body and the legs can trap air, visible as a silvery underwater coat, that is preserved for minutes and increases buoyancy. Crickets with a soiled and wet cuticle sink deeper. So crickets can sink between 20% and 80% of their body height below the water level. The proximal and distal leg segments dimple and partially penetrate the water surface, while middle parts of the legs are often in the air. When first floating on water, crickets struggle with their fore- and middle legs and reach down with their hindlegs in search of contact with the ground. With nothing solid to grasp they swim freely, but prefer to steer towards visual or tactile (antennae) targets. Unrestrained forward swimming of *Acheta domesticus* (Fig. 7A), observed with high-speed video recordings (600 f.p.s.), is similar to that in tethered *Gryllus bimaculatus* (Matsuura et al., 2002): bilateral rowing of all legs with mainly the

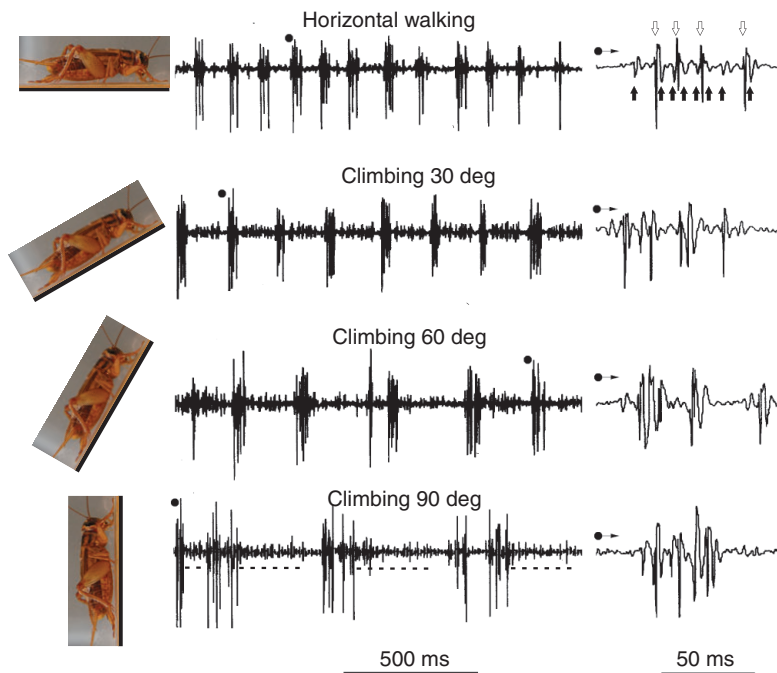


Fig. 6. EMG traces of extensor tibiae burst patterns, recorded from a freely moving cricket that walked horizontally and uphill with different inclinations (traces 1–4, insets) on the surface of a wooden board. For each angle a single burst (marked by a dot) is shown at a larger timescale on the right. In the first trace filled arrows mark slow units, empty arrows mark fast units. When climbing, the extension with the use of high-amplitude fast spikes is followed by slow extensor activity (marked in the 90 deg trace by dotted lines) to maintain tension against the downhill drag until the knee flexes for the next intervening leg swing (gaps without spikes).

tibia and tarsus below the water surface and at frequencies up to 8 Hz. But in *Acheta* foreleg and middle leg strokes never cross, other than as described by Matsuura et al. (Matsuura et al., 2002). Generally, the power strokes are performed with the whole legs under water (in hindlegs most of the femur remains over the water) whereas for the return strokes the legs are lifted and move partly through the air. The sequence of leg strokes usually starts after short intervening gliding periods with the middle legs initiating their power stroke while the forelegs are held forward. During the mid-leg stroke the knees of the stretched hindlegs start bending (Fig. 7B) for 60–120 ms and then rotate the flexed knee almost to the water surface (duration 20–60 ms) by action of the proximal joints. Then the ballistic power stroke extends the tibia under water down and backwards for 15–45 ms. The long and hairy tibial spurs (Fudalewicz-Niemczyk, 1980) and the spines increase their effective

surface to push water backwards. Knee extensions of the hindlegs in swimming are driven only by the momentum and residual tension of the extensor tibiae that was developed previously in the co-contraction period, since no extensor tibiae motor units are active during the tibia extension period. The cricket then briefly glides with extended hindlegs, and the power stroke of the previously extended forelegs follows. When after another 60–120 ms the middle and forelegs have returned forward simultaneously, the next stroke sequence can begin. In rapid escape swimming the acceleration of the extending knee can suck large air bubbles below the water surface (Fig. 7A). They are caught by the spines and spurs of the tibia, drawn backwards with the extension stroke and then released to float behind briefly. The rapid and synchronous extension of both hindleg tibiae and tarsi through the water provide the main thrust for swimming.

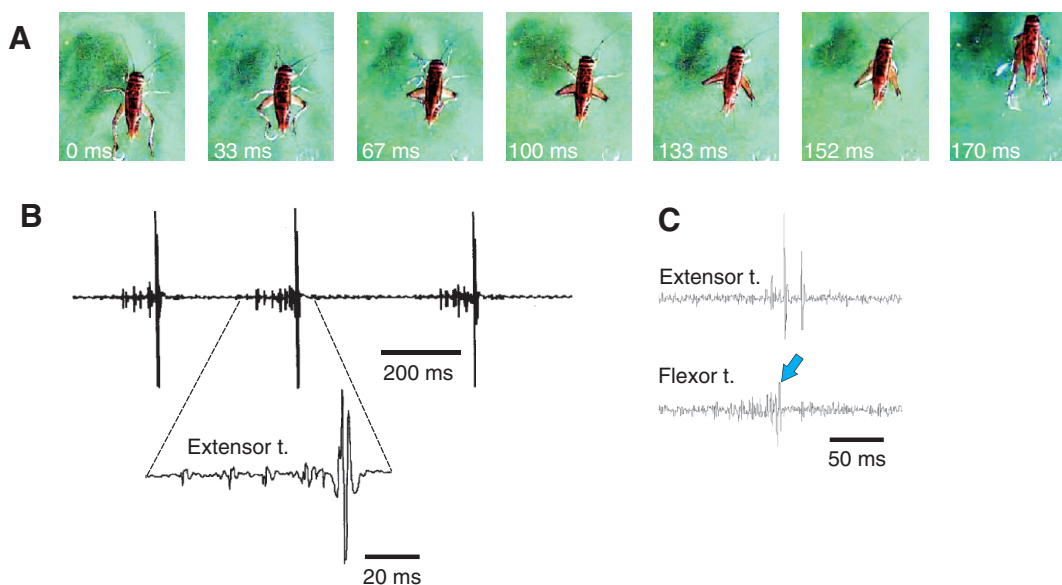


Fig. 7. Strokes of hindlegs during swimming. (A) Frames begin with flexion (0–100 ms), transit to femur depression (100–133 ms) and powerful extension (152 ms; before air bubble formation), stroke ends with complete extension (170 ms; silvery air bubbles are pushed backwards). (B) EMG of extensor swimming strokes at a moderate speed with just one fast spike releasing the ballistic extension. Expanded trace of the middle burst is shown below. (C) Extensor and flexor tibiae coordination in a stroke show typical early termination of flexor activity (arrow).

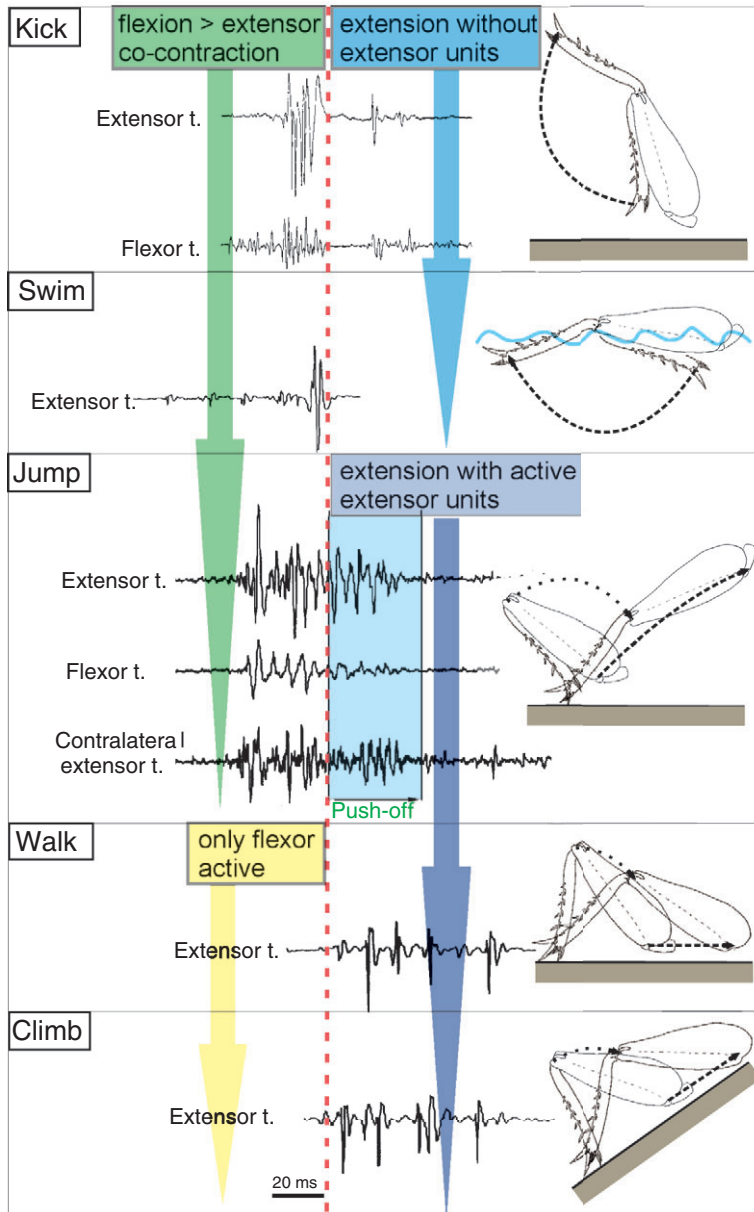


Fig. 8. Motor control of flexion–extension sequences in the femur–tibia joint, compared for different behaviours with ballistic and non-ballistic components in the hindlegs. EMGs are aligned to the point where extension of the knee starts (red hatched line). All activities during flexions in the different behaviours appear on the left and all extension activities appear on the right (sketches show the corresponding types of knee extension).

EMG recordings from hindlegs show that swimming strokes are mainly ballistic. They are prepared by dynamic flexor–extensor co-contraction, in which a series of slow extensor discharges is followed by one to three final fast extensor discharges (Fig. 7B). The efferents to the flexor have terminated about 20 ms before the end of extensor bursts (Fig. 7C) and enable the release of the subsequent ballistic extension of the tibia.

DISCUSSION

Comparison of the ballistic movement types

The mechanical design of the femur–tibia joint in the cricket hindleg requires the same preparatory step for all types of ballistic knee extension: co-contraction of flexor and extensor tibiae muscle that causes knee flexion and simultaneous rise of catapult tension in the extensor muscle (overview: Fig. 8). A release of the catapult by tibia extension follows whenever the torque by the extensor tension overrides the antagonistic forces at the flexor moment arm. For ballistic extensions from a fully flexed knee the effective lever ratio must exceed 10:1. In kicks and swimming strokes only the (residual)

tension in the flexor muscle must be overcome, but in jumps the inertia of the whole body also resists knee extensions. Once an extension is released, other knee mechanisms contribute to acceleration of the tibia: (1) the progressive advantage of the extensor lever arm during leg extension, (2) the effective lever arm of the flexor tibiae decreases, specifically after the cushion has slid from the cuticular ridge at an early stage of knee extension (Hustert and Gnatzy, 1995). These features resemble the kicking mechanisms of bushcrickets (Burrows and Morris, 2003). In locusts, ballistic knee movements of hindlegs follow the same basic mechanical rules but without a cushion on the flexor tendon, and with a catch mechanism of the flexor tendon instead (Heitler, 1974). Elastic energy storage before extension should have only a small role in the cricket hindleg: the hard femoral semilunar processes are unable to store energy, unlike in locusts (Bennet-Clark, 1975), and the stiff tibia does not deform, unlike in the long hindlegs of the acridid grasshopper, *Prosarthria* (Burrows and Wolf, 2002). Although resilin is present in the cricket arthrodial membrane and the cushion of the flexor tendon, these structures are not arranged to store much energy to

contribute significantly to acceleration of the tibia. Here, resilin seems to mitigate impacts that otherwise may injure strained tissue or cuticle.

In crickets, jumping is the most 'modified' ballistic behaviour whereas kicking is the 'purest' ballistic movement (Fig. 8). Major differences in the motor control of the three different ballistic movement types performed by cricket hindlegs require both preparatory knee flexion by co-contraction of extensor and flexor tibiae muscles and rapid ballistic extension.

(1) Kicks start with the shortest preparatory knee flexion (below 30 ms), beginning with activity of the slow extensor motor unit that develops the basal tension of the muscle (Fig. 2E) (Hustert and Gnatzy, 1995). One or two fast motor unit spikes at the end of the flexion cause the rapid switch from flexion to extension. The peak tension of the extensor muscle should be reached 10–15 ms after release of the last fast motor unit (Fig. 3A), which is early during the ballistic extension movement. Kicks are purely ballistic since after their release the catapult accelerates only the tibia: that can move (within 1–3 ms) through the air unimpeded for hitting a target. The thrust of the tibia is sufficient to hurl away small intruders (insects) and to warn larger ones when they get hit by the tibial spines. That movement is normally stopped by a heavy, resisting object, and even the cricket itself can be hurled away. Aiming of the kicks is performed by the levator muscles of the proximal joints in the preparatory phase (Hustert and Gnatzy, 1995).

(2) Swimming strokes begin with a relatively slow flexion of the hindlegs by flexor–extensor co-contraction with a low-frequency activity of just the slow extensor motor unit. Then, in contrast to kicking, the flexed hindlegs are rotated backwards and down to the water surface, and there a final volley of one to three fast spikes initiates the ballistic extension. That differs from swimming strokes of locusts (Pflüger and Burrows, 1978) in which fast extensor units fire throughout the co-contraction period. Extension is slowed by the water resistance during the stroke. Therefore, it is surprising to find stroke durations of 25–40 ms in which the tibia extends without continued neural drive to the extensor tibiae muscle. That may be explained by the long persistence of muscle tension in the extensor tibiae after fast unit spikes (see also Fig. 2E). It is also specific to swimming that the flexor activity decreases 10–20 ms before the last fast extensor potential of a stroke appears – which is similar to locust swimming (Pflüger and Burrows, 1978). In crickets, this decrease of opposing force helps trigger the power stroke by the drive from just one fast extensor spike to the extensor muscle. One may also interpret this type of coordination as a transition to alternating activity of flexor and extensor, such as in walking. Swimming strokes resemble kicks, but between flexion and extension an interval is required for the depressor muscles of the proximal joints to rotate the femur to the water level. From that starting position the power stroke can move the complete tibia through the water. In shallow water the tarsi can hit the ground and speed up propagation of the floating body.

(3) Jumps start, similar to kicks, with knee flexion by dynamic co-contraction of flexor and extensor tibiae, but the flexion draws the hindleg tarsi under the body and co-contraction holds the knees fully flexed for 20–140 ms, a period that seems not absolutely necessary for jump performance, as very long jumps can be preceded by short or long halts with flexed knees. Just before jump release, the flexed hindleg often rotates laterally and downwards, forming a delta-shape of both legs. Depressor and abductor muscles of the proximal joints perform these lateral rotations. That is different from kicking or swimming, but similar to the (less pronounced) rotations described for jumping bush crickets (Burrows and Morris, 2003). The fast extensor tibiae units increase their final frequency and raise muscle tension until the release of the jump. Unlike in

kicking or swimming, high frequency firing of the fast unit continues further into the push-off period and promotes further body acceleration as long as tibia and tarsus can push against the ground. The jumps of locusts show no extensor motor unit activity during the push-off period in natural jumps (Fotowat and Gabbiani, 2007). This means that locust jumps are more ballistic because all energy is stored before knee extension, unlike in crickets.

If jump distances are planned in voluntary jumps the necessary extensor force must be reached before the ballistic release. That requires (1) avoiding the release of premature short jumps by sufficient flexor co-activation in the preparatory period and (2) a balanced control of the restraining flexor tension during the final preparation for long jumps, to reach the targeted isometric extensor tension. Unfortunately our EMGs did not reveal such a correlation, probably because the more than 12 excitatory motor units of the flexor tibiae muscle (Nishino, 2003) are not represented by our rather focal EMG electrodes (30 µm conducting tip diameter).

In EMGs from the extensor tibiae it often seems as if the initial preparatory co-contraction is not sufficient to power the 'intended' jump and requires a concluding high frequency burst of fast extensor units to release the appropriate jump. Such variations in frequency and duration of motor unit discharges in the static phase of co-contraction before the release of jumps indicate sensory feedback control of the jump preparation. This may explain also, why in voluntary jumps extensor burst durations and patterns appear to be not well correlated to the final jump distances (Fig. 3B). This partly contradicts the fact that push-off periods must become shorter in longer jumps. One sensory-controlled activity during co-contraction may be the lateral abduction of the flexed hindlegs by the proximal leg joints to adjust the whole leg for the takeoff angle of a successive jump. That is quite different from observations in jumping locusts (Sutton and Burrows, 2008) which mainly use their forelegs for the control of takeoff angles. Generally, the mechanosensory control of jump distances which concerns preparation and push-off performance during jumps remains unresolved. Afferent monitoring may use the strain recorded by campaniform sensilla in the leg cuticle during extensor and flexor co-contraction (Burrows and Pflüger, 1988; Höltje and Hustert, 2003). That may also apply for the campaniform sensilla at the base of tibial spurs (Fudaliewicz-Niemczyk et al., 1980) which provide the main substrate contact during jumps. Other proprioceptors might also control joint positions and movements and be crucial for ballistic acceleration of the cricket hindlegs: the chordotonal organs, multipolar receptors and hair plates which in crickets are similar to the sensory supply of locust legs (Fudaliewicz-Niemczyk et al., 1980).

The typical voluntary jumps of the cricket *Acheta domestica* have takeoff angles of 20–30 deg and they usually aim at dark horizontal structures. Chances to reach these are better with low jumps although for the same distance they must develop more force than in jumps with the optimal ballistic takeoff angle of 45 deg. In escape jumps (Tauber and Camhi, 1995), neural control for jumping must vary in response time and type, e.g. in reaction to the approach of a grasping hand almost vertical escape jumps are seen (R.H., unpublished observation). Parameters of leg coordination that influence the angle at takeoff are: (1) how the tarsi are positioned below the centre of gravity of the animal, (2) how the proximal leg joints are held and extend actively during takeoff, and (3) to which jaw angle the body is held by the middle and forelegs, a mechanism that is more crucial in jump preparations of locusts (Santer et al., 2005).

Lateral leg rotation and depression by the proximal joints before jumps can also contribute to the release of the jump in the knee joint: that moves the body mass forward and up and thereby decreases the load for the knee catapult, causing its release. That

contribution of the depressor muscles to jumping is difficult to determine since their more-or-less continuous activity in EMGs also reflects general support of the body by the legs.

Each of the three ballistic behaviours, kicking, swimming and jumping are in themselves very variable. These basic motor patterns are modified in the CNS to: (1) take aim in advance, (2) determine the forces for accelerations, or (3) shape an ongoing movement by sensory control of coordination. The proximal joints help to aim the ballistic knee movements: the femur is raised for targeting in kicks, depressed to the water surface for power strokes, or rotated laterally in jumps. A similar motor variability is seen in grooming movements of locust hindlegs (Berkowitz and Laurent, 1996).

Common inhibitors to muscles of the cricket hindleg should also influence rise times and amplitudes of muscle tension in the extensor and flexor tibiae. That was shown in detail for the locust kick in preparations (Burrows, 1995), but common inhibitor activity cannot be recorded in freely behaving crickets. So it remains obscure how these and other relaxing or modifying effects on muscle contractions influence the different types of ballistic extension of the hindlegs.

Bilateral co-ordination in jumps

All jumps involve both hindlegs and their coordination is fairly synchronous. That leads to straight jumps and stable head-on flight positions after the crickets are airborne. Crickets that have lost one hindleg can jump but then tumble through the air (M.B. and R.H., unpublished observation). For the straight bilateral jumps the synchrony of left and right side motor commands in a jump need not be very precise: if the ballistic extension of one hindleg is released a few milliseconds earlier on one side, left-right mechanical coupling across the body immediately decreases the opposing force also for the contralateral catapult, namely the contralateral extensor tibiae muscle, which is released promptly and executes ballistic knee extension. Its acceleration meets lower counterforce and catches up with the slower other hindleg during the push-off period. This prevents unbalanced bilateral acceleration of both extensor muscles and ensures straight jumps. That mechanism may also be important when the animal jumps from an uneven substrate with different relative positions of the hindlegs. During spontaneous jumps only minimal differences in timing or frequency of left and right extensor tibiae motor units were detected, both during the final jump preparation and during the subsequent push-off period. In escape jumps, the cricket *Gryllus bimaculatus* first turns away from a strong wind stimulus and then also jumps straight forward (Tauber and Camhi, 1995).

Walking and climbing

In walking and climbing, knee flexion and extension of the hindlegs alternate regularly. Variable speeds of locomotion (stepping frequencies 0.5–12 Hz) and features of the terrain require coordination patterns that cover a wide range of limb trajectories, accelerations and recruitment of motor units (for an overview see Fig. 6). Sensory control of these movements is crucial. The bursts of flexor and extensor motor units in walking alternate, often with a little overlap. The specific mechanisms in the knee do not impede alternating movements because they avoid extreme flexion angles where extreme moment arms of extensor and flexor leverage may interfere.

Although cricket hindlegs are specialised for kicking and jumping, in walking all legs follow the typical tripod gait. That differs from walking in locusts and bushcrickets (katydids) whose jumping legs often take longer strides than the anterior leg pairs (Duch and Pflüger, 1995).

The motor control of the legs is influenced by the unique gravity system of the crickets, the clavate hairs on the abdominal cerci (Funke, 2004). In mature crickets, the centre of gravity is located in the first abdominal segment, and continuous support of the abdomen by the hindlegs is required during climbing when the cricket must avoid toppling over backwards. Our recordings of motor patterns during steep climbing [compare with cockroaches (Goldmann et al., 2006)] indicate that after knee extension an additional ventral pressure towards the vertical substrate is provided during the stance period of each hindleg. That apparently requires altered extensor coordination for fast extensor bursts in each step cycle which are separated into two phases (Fig. 6). This may correspond to the altered activity of the flexor tibiae muscle as seen in the hindlegs of locusts (Duch and Pflüger, 1995) climbing vertically.

ACKNOWLEDGEMENTS

We thank Matthias Könen for his contribution to the biomechanics of the knee joint.

REFERENCES

- Bennet-Clark, H. C. (1975). The energetics of the jump of the locust *Schistocerca gregaria*. *J. Exp. Biol.* **63**, 53–83.
- Berkowitz, A. and Laurent, G. (1996). Local control of leg movements and motor patterns during grooming in locusts. *J. Neurosci.* **16**, 8067–8078.
- 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: Oxford University Press.
- Burrows, M. and Morris, O. (2003). Jumping and kicking in bush crickets. *J. Exp. Biol.* **206**, 1035–1049.
- Burrows, M. and Pflüger, H.-J. (1988). Positive feedback loops from proprioceptors involved in leg movements of locusts. *J. Comp. Physiol. A* **163**, 425–440.
- Burrows, M. and Wolf, H. (2002). Jumping and kicking in the false stick insect *Prosarthria teretirostris*: kinematics and motor control. *J. Exp. Biol.* **205**, 1519–1530.
- Campbell, J. I. (1961). The anatomy of the nervous system of *Locusta migratoria migratorioides* R&F. *Proc. R. Zool. Soc. Lond.* **137**, 403–432.
- 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.
- Fotowat, H. and Gabbiani, F. (2007). Relationship between the phases of sensory and motor activity during a looming-evoked multistage escape behaviour. *J. Neurosci.* **27**, 10047–10059.
- Fudalewicz-Niemczyk, W., Olesky, M. and Roscizewska, M. (1980). The peripheral nervous system of the larva of *Gryllus domesticus* L. (*Orthoptera*). Part III. Legs. *Acta Biologica Cracoviensis. Series: Zoologica* **Vol. XXII**, 52–63.
- Funke, F. (2004). *Steuerung der Beinmotorik von Grillen durch ein Paar gravizeptiver Interneurone*. Dissertation, Georg-August-Universität Göttingen.
- Goldman, D. I., Chen, T. S., Dudek, D. M. and Full, R. J. (2006). Dynamics of rapid vertical climbing in cockroaches reveals a template. *J. Exp. Biol.* **209**, 2990–3000.
- Hassenstein, B. and Hustert, R. (1999). Hiding responses of locusts to approaching objects. *J. Exp. Biol.* **202**, 1701–1710.
- Heitler, W. J. (1974). The locust jump. Specialisations of the metathoracic femoral-tibial joint. *J. Comp. Physiol. A* **89**, 83–104.
- Heitler, W. J. and Burrows, M. (1976). The locust jump. I. The motor programme. *J. Exp. Biol.* **66**, 203–220.
- Höltje, M. and Hustert, R. (2003). Rapid mechano-sensory pathways code leg impact and elicit very rapid reflexes in insects. *J. Exp. Biol.* **206**, 2715–2724.
- Hustert, R. and Gnatzy, W. (1995). The motor program for defensive kicking in crickets: performance and neural control. *J. Exp. Biol.* **198**, 1275–1283.
- Matsuura, T., Kanou, M. and Yamaguchi, T. (2002). Motor program initiation and selection in crickets, with special reference to swimming and flying behavior. *J. Comp. Physiol. A* **187**, 987–995.
- Neff, D., Frazier, S. F., Quimby, L., Wang, R.-T. and Zill, S. (2000). Identification of resilin in the leg of cockroach, *Periplaneta americana*: confirmation by a simple method using pH dependence of UV fluorescence. *Arthropod Structure and Development* **29**, 75–83.
- Nishino, H. (2003). Local innervation patterns of the metathoracic flexor and extensor tibiae motor neurons in the cricket *Gryllus bimaculatus*. *Zool. Sci.* **20**, 697–707.
- Nishino, H. (2004). Motor output characterizing thanatosis in the cricket *Gryllus bimaculatus*. *J. Exp. Biol.* **207**, 3899–3915.
- 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.
- Santer, R. D., Yamawaki, Y., Rind, C. F., Peter, J. and Simmons, P. J. (2005). Motor activity and trajectory control during escape jumping in the locust *Locusta migratoria*. *J. Comp. Physiol. A* **191**, 965–975.
- Sutton, G. P. and Burrows, M. (2008). The mechanics of elevation control in locust jumping. *J. Comp. Physiol. A* **194**, 557–563.
- Tauber, E. and Camhi, J. M. (1995). The wind-evoked escape behaviour of the cricket *Gryllus bimaculatus*: integration and behavioural elements. *J. Exp. Biol.* **198**, 1895–1907.