Jumping and kicking in bush crickets

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Summary

Bush crickets have long, thin hind legs but jump and kick rapidly. The mechanisms underlying these fast movements were analysed by correlating the activity of femoral muscles in a hind leg with the movements of the legs and body captured in high-speed images.

A female *Pholidoptera griseoaptera* weighing 600 mg can jump a horizontal distance of 300 mm from a takeoff angle of 34° and at a velocity of $2.1\,m\,s^{-1}$, gaining 1350 µJ of kinetic energy. The body is accelerated at up to $114\,m\,s^{-2}$, and the tibiae of the hind legs extend fully within 30 ms at maximal rotational velocities of $13\,500\,deg.\,s^{-1}$. Such performance requires a minimal power output of 40 mW. Ruddering movements of the hind legs may contribute to the stability of the body once the insect is airborne. During kicking, a hind tibia is extended completely within 10 ms with rotational velocities three times higher at $41\,800\,deg.\,s^{-1}$.

Before a kick, high-speed images show no distortions of the hind femoro-tibial joints or of the small semi-lunar groove in the distal femur. Both kicks and jumps can be generated without full flexion of the hind tibiae. Some kicks involve a brief, 40–90 ms, period of co-contraction between the extensor and flexor tibiae muscles, but others can be generated by contraction of the extensor without a preceding co-contraction with the flexor. In the latter kicks, the initial flexion of the tibia is generated by a burst of flexor spikes, which then stop before spikes occur in the fast extensor tibiae (FETi) motor neuron. The rapid extension of the tibia can follow directly upon these spikes or can be delayed by as long as 40 ms. The velocity of tibial movement is positively correlated with the number of FETi spikes.

The hind legs are 1.5 times longer than the body and more than four times longer than the front legs. The mechanical advantage of the hind leg flexor muscle over the extensor is greater at flexed joint angles and is enhanced by a pad of tissue on its tendon that slides over a protuberance in the ventral wall of the distal femur. The balance of forces in the extensor and flexor muscles, coupled with their changing lever ratio at different joint positions, appears to determine the point of tibial release and to enable rapid movements without an obligatory co-contraction of the two muscles.

Key words: kinematics, joint mechanics, locomotion, motor neuron, motor pattern, *Pholidoptera*, bush cricket, kick, jump.

Introduction

Many insects have evolved elaborate mechanisms for displacing their body rapidly away from potential predators or as a means of increasing their forward speed of locomotion. The forces underlying these movements can be generated by different parts of the body. Click beetles jackknife their bodies at the junction between the pro- and mesothorax (Evans, 1972, 1973) whereas some other species of insects use their abdomens. The bristletail *Petrobius* depresses its tail (median caudal filament and paired cerci) and pivots on the end while contracting the anterior part of the abdomen, thereby raising and propelling the body rapidly forwards (Evans, 1975). Springtails rapidly unfurl a springing organ (the manubrium) at the posterior end of their abdomen to propel themselves forward (Brackenbury and Hunt, 1993). Some stick insects swing their abdomens forwards and then backwards in a jump, supplementing the momentum so generated with thrust produced by extension of the middle and hind pairs of similarly sized legs (Burrows and Morris, 2002). In fleas, the hind legs alone provide the thrust for jumping (Bennet-Clark and Lucey, 1967; Rothschild et al., 1972). Similarly, in orthopteran insects the legs have become the main propulsive mechanism, with the hind pair of legs showing the greatest specializations, most obviously in their large size relative to the others. The main thrust in these insects is provided by a rapid, co-ordinated extension of the two hind tibiae. Furthermore, rapid and powerful movements of an individual hind leg can also be used in defensive kicking.

Locusts are able to jump a horizontal distance of approximately one metre with a takeoff velocity of $3.2\,m\,s^{-1}$ (Bennet-Clark, 1975). The 1.5–2 g body is accelerated in 20–30 ms (Brown, 1967), requiring 9–11 mJ of energy. Three specializations of the hind legs enable this performance. First, the mechanical arrangements of the lever arms of the large extensor and smaller flexor tibiae muscles give maximal
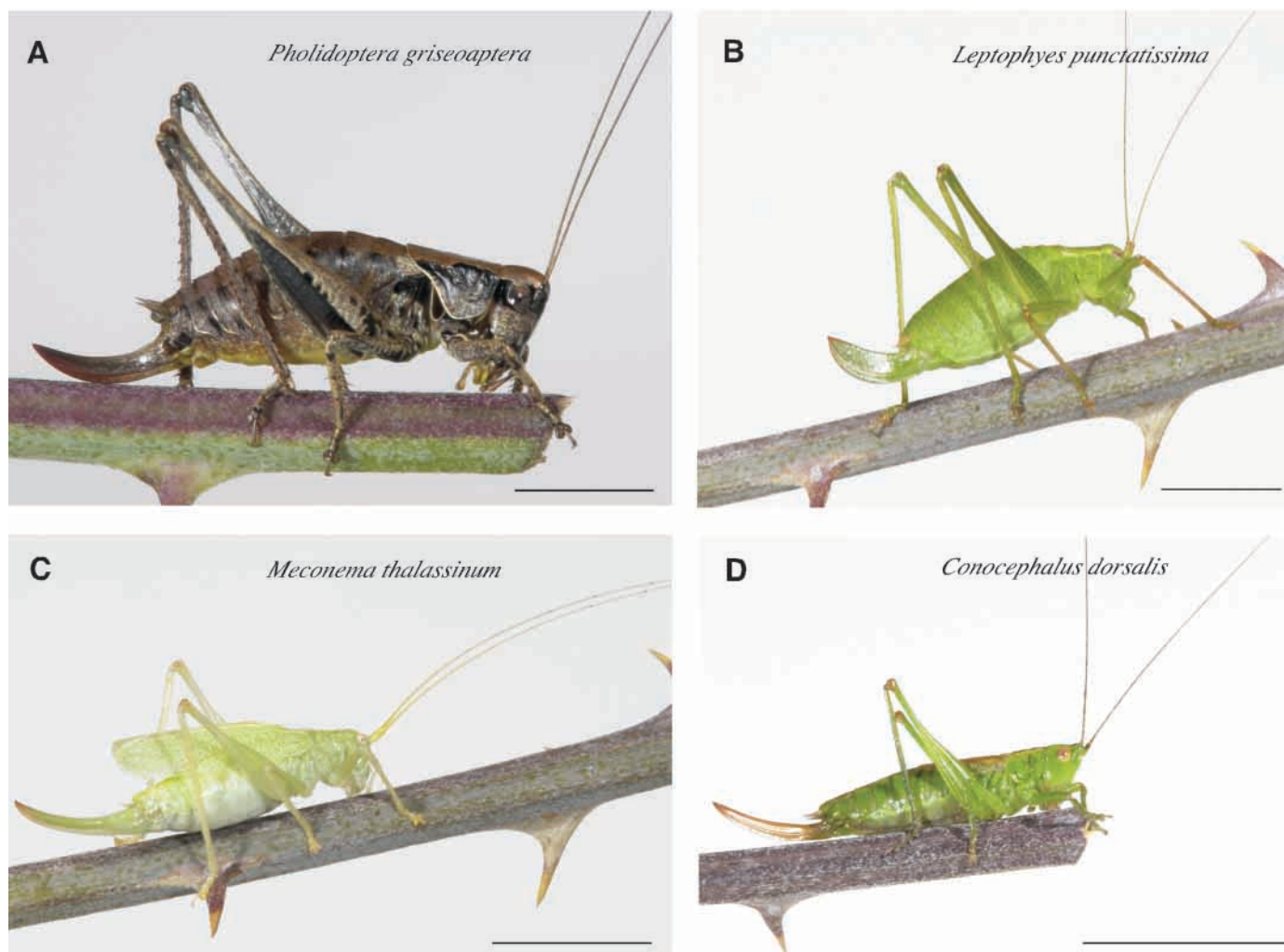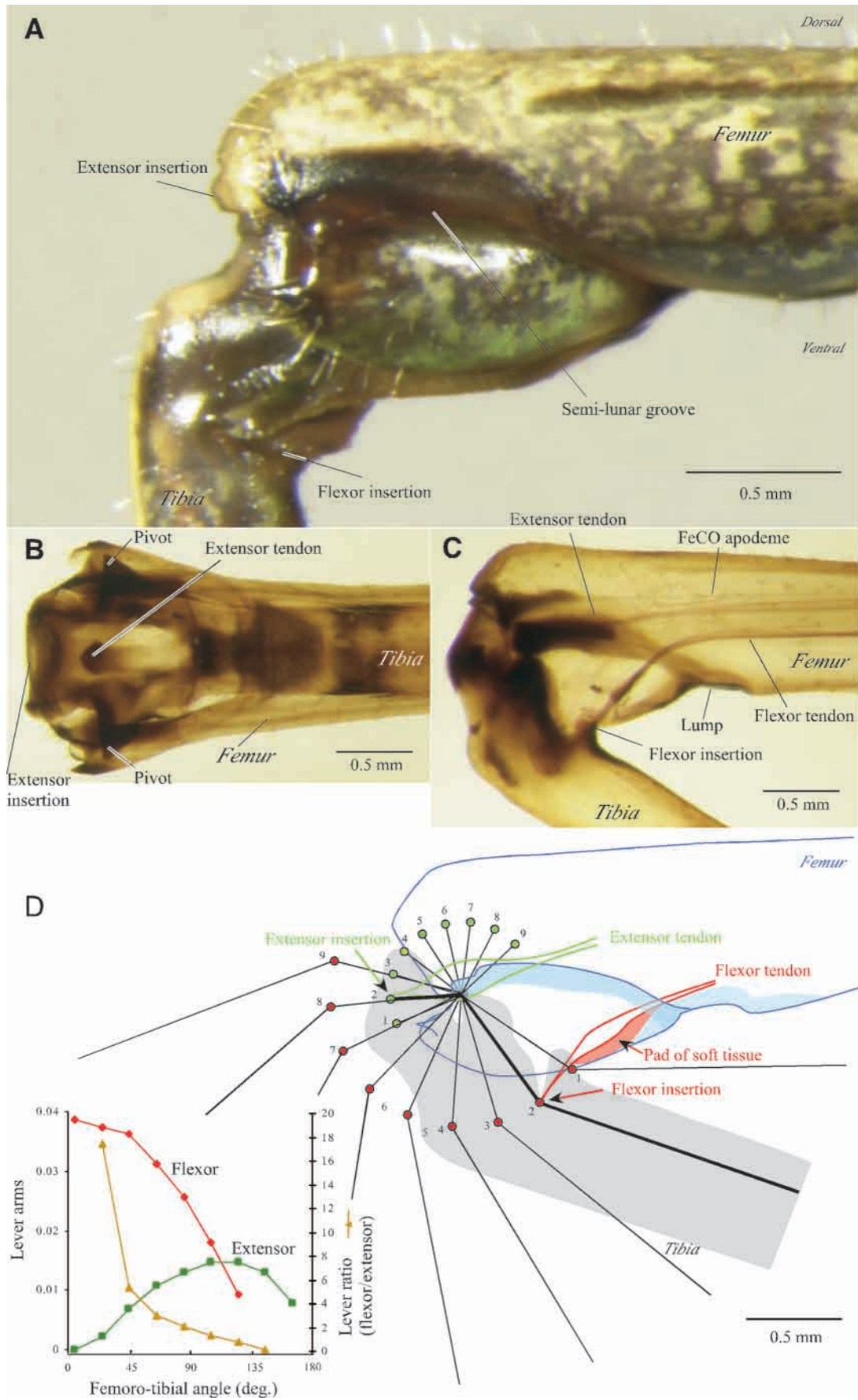
Fig. 1. Photographs of adult females of the four species of bush cricket used in this study: (A) *Pholidoptera griseoaptera*; (B) *Leptophyes punctatissima*; (C) *Meconema thalassinum* and (D) *Conocephalus dorsalis*. Scale bars, 10 mm (A–C); 15 mm (D).

advantage to the flexor when the tibia is fully flexed and to the extensor when the tibia extends (Heitler, 1974). The mechanical advantage of the flexor is further increased by an invagination, or femoral lump, of the distal ventral wall of the femur over which the tendon of the flexor tibiae muscle slides and becomes locked when the tibia is fully flexed (Heitler, 1974). Second, energy generated by muscular contractions must be stored before the rapid extension of the tibia. About half the energy is stored in distortions of the spring-like semi-lunar processes at the femoro-tibial joint (Bennet-Clark, 1975; Burrows and Morris, 2001) while the remainder is stored in the extensor tendon and cuticle of the femur. Third, a complex motor pattern is needed to generate the appropriate sequence of contractions by the muscles (Burrows, 1995; Godden, 1975; Heitler and Burrows, 1977). The main feature of this pattern is a period of co-contraction between the flexor and extensor muscles that can last several hundred milliseconds, during which the tibia remains fully flexed about the femur. The flexor motor activity is then inhibited, allowing the stored force generated by the large

extensor muscle to overcome the lock and the tibia to extend rapidly.

Fig. 2. Anatomy of the femoro-tibial joint of a left hind leg of an adult female *Pholidoptera*. (A) Photograph of the posterior (= medial) surface. The distal femur has a semi-lunar shaped groove. The flexor tibiae tendon inserts around a V-shaped rim of the ventral tibia. (B) A cleared leg viewed ventrally with the tibia almost flexed about the femur to show the black and opposed, flat regions of the femur and tibia that form the hinge joint. (C) The same leg as in B, viewed as in A to reveal the tendons of the flexor and extensor tibiae muscle and the apodeme of the femoral chordotonal organ (FeCO). The extensor tendon expands distally before inserting on the dorsal rim of the tibia. (D) Tracings from camera lucida drawings of the position of the tibia as it rotates about the femur. Nine positions of the tibia are shown as black lines with an outline of the tibia superimposed on a thicker line in position 2. The insertions of the flexor (red) and extensor (green) tibiae tendons are indicated. The structural reinforcing elements of the distal femur are in blue. Measurements made from this drawing were used to estimate the flexor and extensor lever arms at different joint angles, shown in the inset graph.

A

Dorsal

Femur

Extensor insertion

Semi-lunar groove

Ventral

Flexor insertion

Tibia

0.5 mm

B

Pivot

Extensor tendon

Tibia

Femur

Extensor insertion

Pivot

0.5 mm

C

Extensor tendon

FeCO apodeme

Femur

Lump

Flexor tendon

Flexor insertion

Tibia

0.5 mm

D

Femur

Extensor insertion

Extensor tendon

Flexor tendon

Pad of soft tissue

Flexor insertion

Tibia

0.5 mm

Lever arms

0.04
0.03
0.02
0.01
0

Flexor

Extensor

Lever ratio (flexor/extensor)

20
18
16
14
12
10
8
6
4
2
0

0   45   90   135   180
Femoro-tibial angle (deg.)

Analyses of other orthopterans reveal variations on these mechanisms and suggest possible ways in which the specializations for jumping might have evolved. *Prosarthria teretrirostris*, a false stick insect, jumps by using a very similar motor pattern to a locust that also involves a long period of co-contraction (Burrows and Wolf, 2002). It does not, however, use its much reduced semi-lunar processes to store energy but instead stores some energy in bending its curved hind tibiae. The femoral lump is also much reduced so that the mechanics of the joint are dependent on the changing lever ratios of the two muscles as the femoro-tibial joint rotates. House crickets (*Acheta domesticus*) have a variable motor pattern for kicking in which the period of co-contraction is much reduced (Hustert and Gnatzy, 1995). The pattern consists of a 12–20 ms period of so-called 'dynamic' co-contraction of the flexor and extensor muscles as the tibia is pulled into a flexed position, followed by a 'static' co-contraction of 3–12 ms when a few fast extensor motor spikes occur and during which the tibia does not move. The femoral lump is also small but its effect on the lever of the flexor muscle is enhanced by a soft pad of tissue on the tendon.

Bush crickets (Tettigoniidae), like locusts, kick and jump in defensive actions, in escape and as a means to take off into flight. Their similar body design might suggest that they use similar adaptations and mechanisms to effect these movements. We have, therefore, analysed their jumping and kicking movements with high-speed imaging to correlate the underlying motor activity with the joint movements of the hind legs. We show that the mechanisms are different from those in other orthopteran insects: the rapid tibial extensions in jumping and kicking do not require an initial full flexion; semi-lunar processes are not bent; and kicking movements can be generated without apparent co-contraction of the flexor and extensor tibiae muscles.

Materials and methods

Bush crickets were collected locally around Cambridge, UK: *Pholidoptera griseoaptera* (de Geer), the dark bush cricket (*N*=20); *Leptophyes punctatissima* (Bosc), the speckled bush cricket (*N*=2); *Meconema thalassinum* (de Geer), the oak bush cricket (*N*=4); and *Conocephalus dorsalis* (Latreille), the short-winged cone-head (*N*=7) (Fig. 1). They are orthopteran insects belonging to the suborder Ensifera (which also contains the true crickets and mole crickets), to the superfamily Tettigonioidea and the family Tettigoniidae. The descriptions and analyses are focused on *Pholidoptera* but are supplemented with observations on the other species to indicate the generality of the morphological features and physiological mechanisms. The morphology and mechanics of the femoro-tibial joint of the hind legs were analysed from photographs and drawings. Intact legs and legs cleared by boiling in 5% potassium hydroxide were also examined.

Images of jumping or kicking movements were captured with a high-speed camera (Redlake Imaging, San Diego, CA, USA) and associated computer at rates of 500–1000 s^{-1} with exposure times of 0.25–1 ms. In the figures, these images, and the measurements made from them, are aligned from the time when the tibia of a hind leg reached full extension in a kick or the animal first became airborne in a jump (*t*=0 ms). Selected images were stored as computer files for later analysis with the Motionscope camera software (Redlake Imaging) or with Canvas (Deneba Systems Inc., Miami, FL, USA). Jumping performance was measured in a circular arena with the insects jumping from the centre outwards.

Pairs of 50 μm stainless steel wires, insulated except for their tips, were inserted into the flexor and extensor tibiae muscles of a hind leg to record muscle activity during kicking movements. Crosstalk between the recordings from the extensor and flexor tibiae muscles was common because they are close together within a confined space, but identification of flexor and extensor motor neurons could still be achieved by comparing the relative amplitudes of their potentials at the two recording sites. In recordings from the extensor muscle during kicking and jumping, a prominent motor neurone was recorded that generated potentials very much larger than any others. This motor neurone was not active during slower movements of the tibia. In other acridids, gryllids (Wilson et al., 1982) and phasmids (Bassler and Storrer, 1980), two excitatory motor neurones innervate this muscle, one of which, the fast extensor tibiae (FETi), has the properties we observe here (Hoyle and Burrows, 1973). We have, therefore, tentatively called this motor neurone FETi. The electrical recordings were written directly to a computer with a CED (Cambridge Electronic Design, Cambridge, UK) interface running Spike2 software and sampling each trace at 5 kHz. They were synchronised with the video images on a second computer by pressing a hand switch to generate 1 ms pulses. These pulses were fed to a separate channel of the CED interface and simultaneously triggered light pulses on the images, thereby allowing movements and muscle activity to be correlated with the resolution of one image (1 ms or 2 ms).

All experiments were performed at temperatures of 27–36°C, with the lower temperatures used when recording muscle activity during kicking movements and the higher temperatures used when capturing images of jumping.

Results
Body structure

The characteristic features of all the bush crickets examined were the very long hind legs, long antennae and long ovipositors in females, which exaggerate the sexual dimorphism in body structure (Fig. 1). Adult female *Pholidoptera* had a mass of 602±42 mg (mean ± s.e.m., *N*=8), making them 45% heavier than adult males (mass 415±20 mg, *N*=12), and, with a body length of 33.2±0.8 mm (including the ovipositor), 53% longer than adult males (21.6±0.6 mm) (Table 1). The femur of a hind leg was more than four times the length of the femur of a front leg and more than three times the length of a middle femur, giving a ratio of femora lengths of 1:1.2:4.2 for the front, middle and hind legs, respectively. In

the other bush crickets, a hind femur was at least twice the length of that of a front femur. In *Pholidoptera*, the hind femur was longer than the hind tibia, but in *Leptophyes* the reverse was true. In all bush crickets, except for female *Conocephalus*, a hind leg (tibia plus femur) was 120–160% longer than the body. This means that the hind legs of bush crickets are longer relative to body length than in other jumping insects examined (Table 1). For example, in true crickets (e.g. *Gryllus bimaculatus*) the hind legs are 59–69% the length of the body, in locusts (e.g. *Schistocerca gregaria*) they are about the same length as the body and in a non-jumping stick insect (e.g. *Carausius morosus*) they are much shorter at only 39% of body length.

A hind femur of *Pholidoptera* is broad (3.5 mm) at the proximal end, which contains the main body of the flexor and extensor tibiae muscles, but tapers at 60% of its length to about a quarter of this width (0.8 mm) and continues at this diameter to the femoro-tibial joint. In cross section, the femur is almost oval, with the large extensor muscle occupying a cross-sectional area of approximately 4.4 mm^2 in females and the smaller flexor muscle an area of 1.08 mm^2. By contrast, the tibia has a uniform tubular construction with a diameter of 0.6 mm in its dorso-ventral axis along its length. On the dorsal surface are two rows, each of 23–26 spines with decreasing spacing distally, and on the ventral surface are two rows. each

of 9–11 smaller spines. The tarsi of the hind legs, but not the middle and front legs, have two proximal flanges that point ventrally and may assist with its grip on fine twigs or stems.

Structure of femoro-tibial joint

The tibia of a hind leg of *Pholidoptera* can be moved approximately 165° about the femur. The femoro-tibial joint itself shows few external specializations compared with the middle and front legs. The cuticle of the distal femur is deeply grooved on both the medial and lateral surfaces separating the body of the femur from the ventral flanges or coverplates (Fig. 2A). These semi-lunar shaped grooves are not heavily sclerotised and did not bend during kicking or jumping. At their distal extreme, the thickened cuticle forming these grooves turns inwards to form two flat edges that abut against similar edges on the tibia to form the pivot of the joint articulation (Fig. 2B). Each apposed surface is approximately 400 µm wide, and the two surfaces together make up 50% of the width of the femur at this level (Fig. 2B). A single distally protruding spine is present on the medial (posterior or inner) coverplate but not on the lateral coverplate.

The ventral surface of the femur at its distal end is invaginated to form a lump that protrudes dorsally into the femur, representing 130 µm (13.1±1.0%; N=5) of the thickness of the femur at this level (Fig. 2C). The tendon of the flexor

Table 1. *Body form in jumping insects*

Insect (N)	Body mass (mg)	Body length§ (mm)	Hind leg tibia Length (mm)	Hind leg femur Length (mm)	Max. width (mm)	Min. width (mm)	Ratio of femur lengths Front	Middle	Hind	Hind leg length as % of body length¶
Bush crickets *Pholidoptera* ♀ (8)	602±42	23.2(+10)±0.8	17.8±0.3	18.7±0.4	3.5	0.8	1	1.2	4.6	158
Pholidoptera ♂ (12)	415±20	21.6±0.6	15.6±0.2	17.1±0.2	3.2	0.8	1	1.2	4.2	152
Meconema ♀ (4)	174	18(+10)	11.5±0.5	10±0.5	1.9	0.5	1	1	2.1	125
Conocephalus ♀ (3)	250±15	22(+9)±1	11±0.5	10.5±0.5	2	0.5	1	1	2.1	95
Conocephalus ♂ (4)	130±5	17±1.1	10	10	2	0.5	1	1.1	3.8	118
Leptophyes ♀ (2)	285	20(+5)	17	15	2	0.6	1	1.2	2.7	160
Cricket *Gryllus bimaculatus* ♀ (4)	889±65	34±1	9±0.5	11±0.5	4	1.5	1	1	2.4	59
Gryllus bimaculatus ♂ (4)	738±24	29±2	9±0.5	11±0.4	4	1.5	1	1	2.4	69
Flea* *Spilopsyllus cuniculus*	0.45	1.5	0.4	0.45			1	1.5	2	57
Locusts *Schistocerca gregaria* ♀ (5)	2000±40	47.2±1.4	21.8±0.2	21.8±0.2	4.8	1.8	1	1.2	3.2	93
Schistocerca gregaria ♂ (5)	1600±35	41.4±1.2	20.2±0.4	20.2±0.4	4.6	1.8	1	1.2	3.2	98
Anacridium ♀ (6)	3550±58	44.3±0.5	18.9±0.4	20.9±0.4	4.6	2.0	1	1.2	3.4	90
Anacridium ♂ (7)	1840±44	58.4±0.4	24.6±0.9	27.6±0.9	5.6	2.3	1	1.2	3.9	89
False stick insect† *Prosarthria teretrirostris* ♀ (16)	1540±12	104.4±1.4	34.6±0.4	32.8±0.5	2.1	1.0	1	1	2.6	62
Prosarthria teretrirostris ♂ (10)	280±10	67.5±0.8	26.1±0.4	24±0.3	1.6	0.6	1	0.9	2.1	71
Stick insects‡ *Sipyloidea* sp. ♀ (18)	924±37.8	92±0.9	21±0.5	21±0.5	1.0	0.6	1	0.7	1	46
Sipyloidea sp. ♂ (10)	164±4.6	65±0.5	21±0.3	21±0.3	0.5	0.4	1	0.7	1	64
(Non-jumping) *Carausius morosus* ♀ (10)	1100±4	78±0.15	17	17			1	0.7	0.9	39

Numbers are means ± S.E.M.
*Bennet-Clark and Lucey (1967).
†Burrows and Wolf (2002).
‡Burrows and Morris (2002).
§Numbers in brackets represent length of ovipositor.
¶Length of ovipositor excluded; values calculated from individuals and then mean taken.

tibiae muscle has a pad of soft tissue on its ventral surface (Fig. 2D). The tendon of the extensor tibiae muscle broadens to insert on the U-shaped rim of the dorsal tibia about 250 μm from the joint pivot. The flexor tendon inserts around the V-shaped rim in the ventral tibia about 400 μm from the joint pivot (Fig. 2B–D).

At extended joint angles, the extensor muscle has a larger lever than the flexor muscle because the tendon inserts dorsal to the pivot whereas the line of action of the flexor muscle runs almost through the pivot (Fig. 2D). At flexed joint angles, the flexor has the greater lever, with the line of action of the extensor acting almost through the pivot. At the most flexed positions, the lever arm of the flexor is boosted because the soft pad of tissue on its tendon must ride over the ventral invagination in the femur. Morphological inspection suggests that the flexor lever arm exceeds the extensor lever arm for all joint angles up to 100° (Fig. 2D, inset). The functional lever ratio is, however, made more complex by the flexible and distributed sites of attachments of the two tendons on the tibia, as in locusts (Heitler, 1974) and *Prosarthria* (Burrows and Wolf, 2002). Comparison of the functional and morphological lever ratio in *Prosarthria* has shown that the latter tends to underestimate the extensor lever arm at all joint angles and to underestimate the flexor arm at extended tibial positions whilst overestimating it at flexed positions (Burrows and Wolf, 2002). Even when taking this into account, it is clear that the flexor and extensor lever arms balance at much more extended tibial positions in bush crickets (approximately 100°) than in *Prosarthria* (approximately 55°). Similar properties of the femoro-tibial joint of hind legs were found in the other species of bush cricket examined.

Kicking

A bush cricket could direct a rapid kick of one hind leg on its own (Fig. 3A) or both hind legs together (Fig. 3B) towards an object from a free-standing posture. The first movement of a hind leg was a forward rotation at the joint between the coxa and the body so that the tarsus was lifted from the ground. The tibia was

then flexed about the femur, before being unfurled rapidly to its fully extended position. In some kicks, the initial flexion of the tibia about the femur was complete so that the tibia was fully pressed against the femur along its length (Fig. 3A). Complete flexion of the tibia about the femur was not,
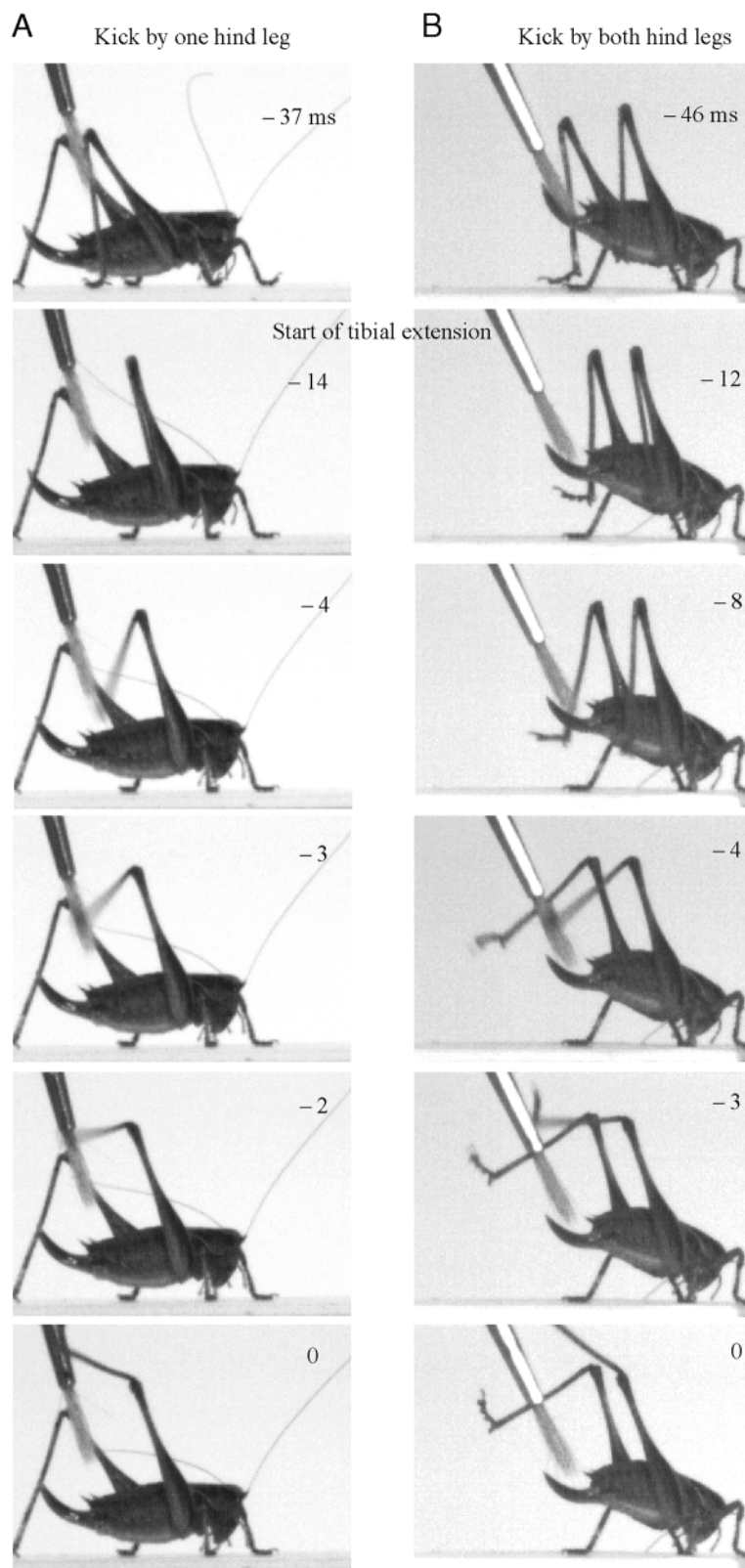
Fig. 3. Kicking movements of a female *Pholidoptera* illustrated by selected frames captured at 1000 frames s[-1]. (A) A kick by the right hind leg. At –37 ms, this leg was touched by a small paint brush (top left of frame). The right hind leg rotated forwards so that the tarsus was lifted from the ground and the tibia was fully flexed about the femur (–14 ms). From this position, the tibia was extended rapidly while the left hind leg remained in a constant position. Full extension was achieved at 0 ms. (B) A kick by both hind legs. At –46 ms, the ovipositor was touched by the paint brush and both hind legs rotated forwards but the tibiae were not fully flexed (–12 ms). From this position, the tibiae of both legs were then extended rapidly, with the right hind leg reaching full extension at 0 ms.

however, a prerequisite, and kicks could be generated from an initial femoro-tibial angle of approximately 30° (Fig. 3B).

The time taken for the tibia to extend fully in a kick and the maximum angular velocity of the tibial movements varied considerably in different kicks by the same animal and by different animals of the same species. Some kicks took only 7 ms from the start of tibial extension until maximum extension, while others took 25 ms (Fig. 4A). The mean time for tibial extension in male *Pholidoptera* was 10.1±0.72 ms (*n*=11 kicks by five animals) and in female*s* was 11.1±0.98 ms (*n*=16 kicks by four animals) (Table 2). In *Meconema*, tibial extension was faster, taking only 6.8±0.86 ms (*n*=10 kicks by four animals). The maximal rotational velocity of the tibia during extension in *Pholidoptera* ranged from 8000 deg. s^{-1} to 65 000 deg. s^{-1}. In males, the mean maximal velocity (26 400±3500 deg. s^{-1}; *n*=27 kicks) was lower than in females (41 800±3200 deg. s^{-1}, *n*=4 kicks) although both could achieve comparable maximum velocities. In the fastest kicks by either sex, the inertial forces were sufficient to cause the tibia to over-extend and then rebound in a series of flexion and extension movements of progressively diminishing amplitude. The same angular velocities of tibial movement could be produced from different initial angles of the femoro-tibial joint. For example,

in two kicks by an individual *Pholidoptera*, the same maximal rotational velocity of 65 000 deg. s^{-1} was first achieved from an initial fully flexed position and then from an initial femoro-tibial angle of 27° (Fig. 4A).

High-speed images of kicks with high angular velocities of tibial movements did not reveal any distortions of the femoro-tibial joint either preceding the release of the tibial movements or during the unfurling movements of the tibia itself (Fig. 4B,C). The lack of distortion evident in the end-on view of the joint is in direct contrast to the considerable distortion seen in the same view of this joint in a locust during a kick (Burrows and Morris, 2001). In the period before the kick when the tibia was flexed about the femur, the muscular contractions were not accompanied by any movement of the semi-lunar grooves in the femur or by any compression of the dorsal distal cuticle of the femur. Similarly, during tibial extension, no images indicated changes in the shape of the femur. This indicates that energy to power the kick is not stored in cuticular distortions at the joint.

Motor activity during kicking

The common features of the motor activity that characterized the variety of different velocities of kicks and the

Table 2. *Kicking and jumping performance*

Insect (*N*)	Body mass (g)	Jumping								Kicking	
		Distance (mm)	Extension time (ms)	Takeoff velocity (m s^{-1})	Takeoff angle (deg.)	Peak acceleration (m s^{-2})	Max. rotational velocity (deg. s^{-1})	Energy (µJ)	Power output (mW)**	Extension time (ms)	Max. rotational velocity (deg. s^{-1})
Pholidoptera ♀ (4)	0.6	296±14.7 *n*=57	32.6±0.95 *n*=25	2.12±0.33 *n*=4		143.8±28.8 *n*=4		1 380	40 (67)	11.1±0.98 *n*=16	41 800±3 200 *n*=4
Pholidoptera ♂ (5)	0.42	302±11.5 *n*=129	30.6±2.7 *n*=7	1.51±0.2 *n*=5	33.8±2.1 *n*=17	83.4±14.7 *n*=5	13 500	490	16 (38)	10.1±0.72 *n*=11	26 400±3 500 *n*=27
Meconema ♀ (4)	0.17		22.5±0.63 *n*=10	1.4 *n*=1				170	7.5 (45)	6.8±0.86 *n*=10	
Conocephalus ♂ (3)	0.25		21 *n*=2	1.0 *n*=2	56.8±12.3 *n*=17			125	6 (24)		
Leptophyes ♀ (2)	0.29	162±12.8 *n*=6			33.9±10.2 *n*=5						
Oecanthus ♀ (1)	0.07	107 *n*=3									
*Prosarthria** ♂ (10)	0.28	660	30	2.5	41	165	11 500	850	28 (100)	7	48 000
Schistocerca[†] (10)	1.5–2	1 000	25–30	3.2	45	180	9 000-11 000	333 (222)		3[§]	80 000[§]
Spilopsyllus[‡]	0.00045		0.75	1.0	50	1 330[‡]		0.225	0.3 (667)		
Sipyloidea[¶] (28)	0.270		90	0.6–0.8	10–35	10	4 000	96	1 (3.7)		

Numbers are means ± S.E.M. Means were calculated from data pooled from different animals. *N* = no. of animals; *n* = no. of observations.

*Burrows and Wolf (2002).

[†]Bennet-Clark (1975)

[‡]Bennet-Clark and Lucey (1967).

[§]Burrows and Morris (2001).

[¶]Burrows and Morris (2002).

**Numbers in brackets represent power output per gram body mass.
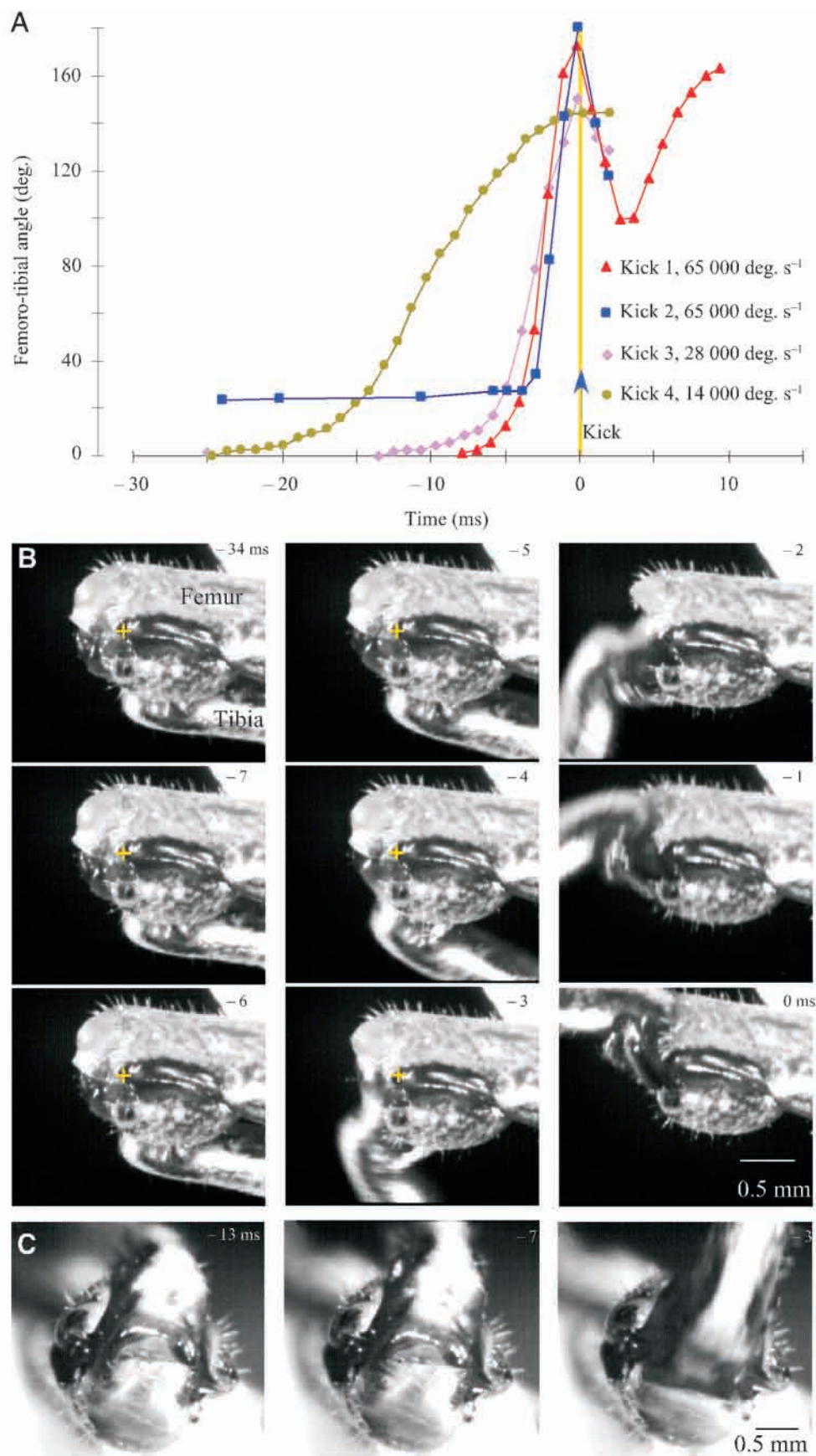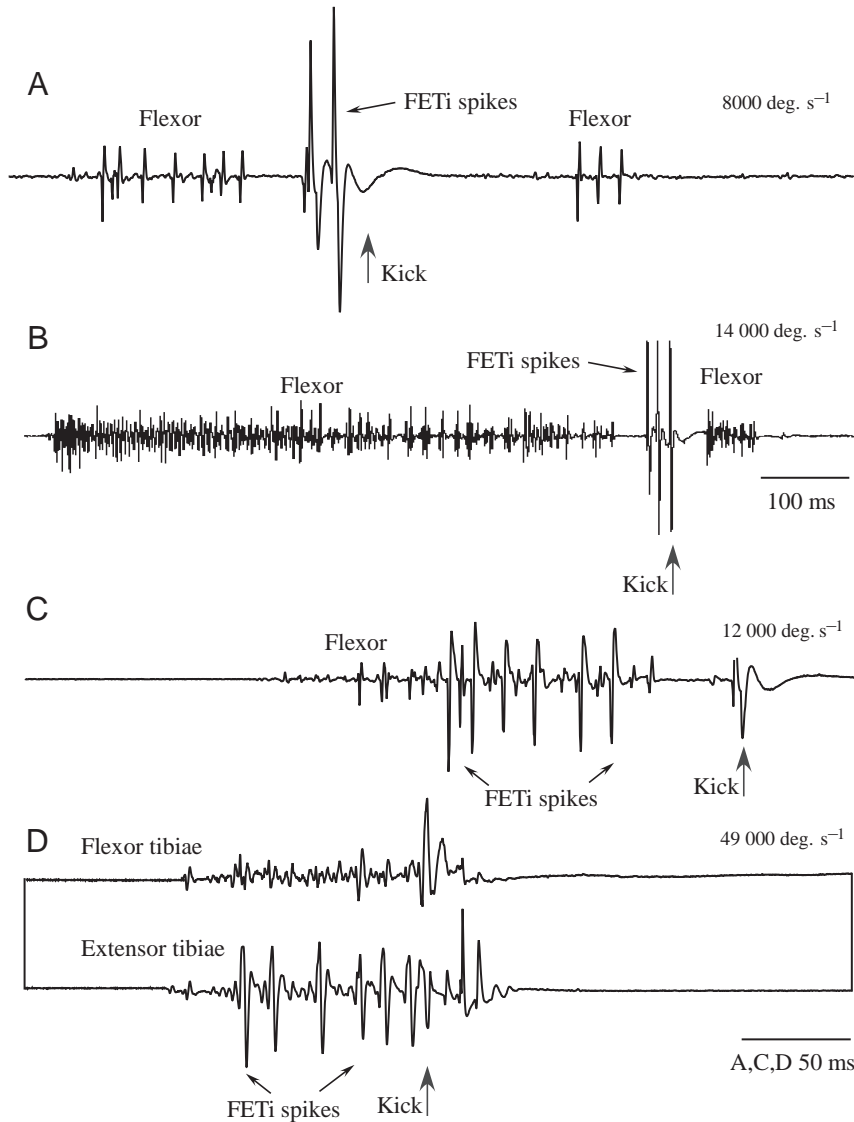
Fig. 4. Kicks of different velocities and from different femoro-tibial starting angles. (A) Changes of the femoro-tibial angle during four kicks by the same *Pholidoptera* aligned at the time of maximal extension (0 ms). Kick 2 started from a partly extended femoro-tibial angle but still achieved the same maximal rotational velocity ($65\,000$ deg. s^{-1}) as kick 1, which started from a fully flexed position. The rebound movement at full extension is plotted for kick 1. Kicks 3 ($28\,000$ deg. s^{-1}) and 4 ($14\,000$ deg. s^{-1}) are slower. (B) Movements of the femoro-tibial joint during a kick captured at 1000 frames s^{-1} and with an exposure of 0.25 ms. The tibia was fully flexed about the femur in the first frame (–34 ms). From the start of the first detectable extension movement (–7 ms) to full extension (0 ms) of the tibia took 7 ms. The crosshairs marking the anterior edge of the semi-lunar groove in the first six frames do not shift in position. (C) The femoro-tibial joint viewed end-on during a kick. There was no distortion of the distal femur either before (–13 ms) or during (–7 ms and –3 ms) the kick. The proximal part of the femur and the bush cricket itself were fixed in Plasticine.

Fig. 5. Variation in the motor pattern for kicking in *Pholidoptera*. The extracellular recordings are from the flexor and extensor tibiae muscles of restrained animals (A is from one animal, B–D from another). Images (not shown) of the movements of the tibia were captured to enable the peak angular velocity of the tibia (measured in deg. s^{-1}) and the timing of the kick (indicated by vertical arrows) to be determined. (A,B) Kicks involving no apparent co-contraction of flexor and extensor tibiae muscles. In A, a slow kick results from a few spikes in flexor tibiae motor neurones followed, after a delay, by two spikes in fast extensor tibiae motor neurones (FETi). In B, a prolonged flexion followed by three spikes in FETi results in a slightly faster extension of the tibia. (C,D) Kicks resulting from co-contractions. In C, the flexor motor neurones spike first and continue while six spikes of FETi occur. There is then a pause of almost 100 ms without motor activity before a slow tibial extension occurs. In D, a co-contraction of flexor and extensor tibiae motor neurones is followed immediately by a rapid extension of the tibia in a kick. In C and D, a movement artefact occurred at the time of the rapid extension of the tibia.

Brief periods of co-contraction lasting approximately 40–90 ms (*n*=10) between flexor and extensor muscles occurred during some kicks. For example, a 75 ms-long period of co-contraction followed by a 40 ms period when both muscles were silent led to the tibia being extended at a velocity no greater than in kicks that lacked co-contraction (Fig. 5C). By contrast, a similar period of co-contraction in another kick that was not followed by a period of silence in the two muscles led to a more rapid extension of the tibia (Fig. 5D).

The velocity of tibial extension in a kick was correlated with the number of FETi spikes (Fig. 6), but, because the period of muscle contraction varied only within narrow limits, the larger the number of FETi spikes, the higher was their frequency. As few as one FETi spike could lead to kicks with maximal angular velocities of 1000–30 000 deg. s^{-1}. Progressively more FETi spikes led to progressively faster tibial movements. Kicks with maximal angular velocities as high as 50 000 deg. s^{-1} could be produced by as few as three FETi spikes. Even the fastest kicks were associated with no more than 6–8 FETi spikes at peak instantaneous frequencies of 130 Hz.

The motor activity that led to a kick from a fully flexed tibia was similar to that from a partially flexed starting position and resulted in similar velocities of tibial movements (Fig. 7). For example, one kick from a fully flexed position involved a 40 ms co-contraction with six FETi spikes that began as the tibia was being flexed. These spikes were followed by a 30 ms period when only a few flexor motor spikes were detected but during which the tibia remained fully flexed. The tibia was then

variable starting angles of the hind leg femoro-tibial joints were the activity of the flexor and extensor tibiae muscles. The combinations of their activity were not, however, constant (Fig. 5). In low velocity kicks, the flexor tibiae muscle was activated by a small number and low frequency of motor spikes so that the tibia was pulled into a flexed position (Fig. 5A). The flexor motor spikes then stopped and, after a delay as long as 100 ms, a few spikes at 80–100 Hz then occurred in the fast extensor tibiae (FETi) motor neuron followed by tibial extension. The duration of the flexor motor activity varied fivefold (50–250 ms) in different kicks. In kicks with a longer period of flexor activity there could again be a pause before spikes occurred in FETi, which led to an extension of the tibia (Fig. 5B). In neither of these two patterns could flexor activity be detected during the spikes in the extensor, even with electrodes inserted into different regions of the muscle, suggesting that there was no active co-contraction of the two muscles. During the extensor spikes, some residual tension could have been present in the flexor resulting from preceding spikes in its motor neurons.
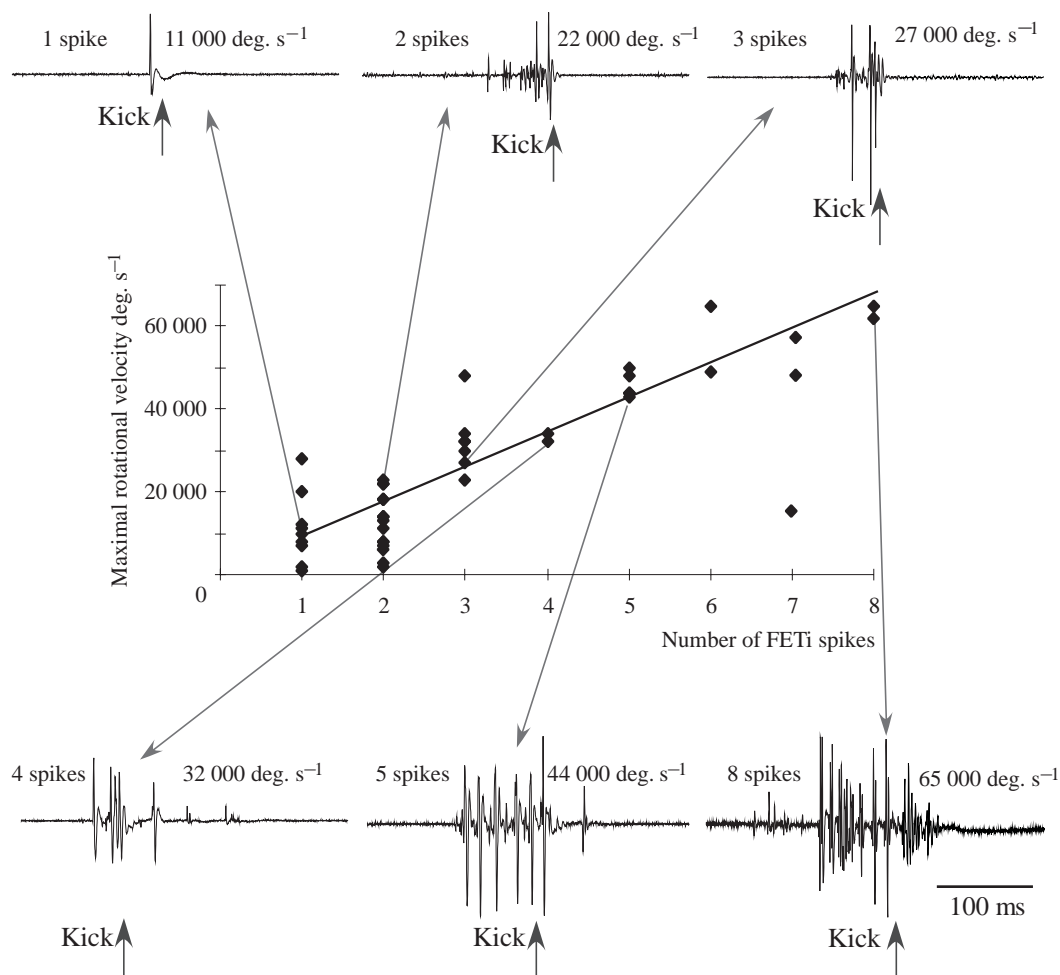
Fig. 6. Linear relationship between the maximal rotational velocity of the tibia during a kick and the number of spikes in the fast extensor tibiae motor neurone (FETi). The greater the number of spikes, the higher the speed of rotation, but there is variation in speed for a given number of spikes in different kicks. Data from 45 kicks by six *Pholidoptera* are pooled. The line was fitted by linear regression $y=0.83+8420x$ ($P<0.001$, $r^2=0.78$).

suddenly extended, even though no further FETi spikes occurred, reaching a maximal angular velocity of $65\,000\,\mathrm{deg.\,s^{-1}}$ (Fig. 7A). In a second kick by the same animal, the tibia was fully flexed by preceding flexor motor spikes but when the first FETi spike occurred the tibia extended by $27°$ (Fig. 7B). From this partially flexed and sustained position, FETi spikes continued for $70\,\mathrm{ms}$ before the tibia was suddenly extended, reaching the same peak angular velocity as in the first kick.

Jumping

Adult *Pholidoptera* jumped an average horizontal distance of $300\,\mathrm{mm}$ (males $302\pm11.5\,\mathrm{mm}$, $n=129$; females $296\pm14.7\,\mathrm{mm}$, $n=57$) (Table 2) or approximately 13–14 times their body length, although the maximum distance achieved by an individual was more than twice this at $660\,\mathrm{mm}$. A jump began with a forward rotation of the hind legs at their coxal joints and a flexion of the tibiae about the femora. The flexion of the tibiae was not always complete so that one (Fig. 8A) or both hind legs could begin their rapid extension movement from this already partially extended position. As the hind tibiae were extended, the body was raised from the ground and the forwardly directed antennae were swung backwards to point over the body (Fig. 8B). When viewed anteriorly, the hind legs

could be seen to rotate outwards at their joints with the coxae, and both the middle and front legs could be seen to depress at their coxal joints and extend at their femoro-tibial joints (Fig. 8C). The continuing elevation of the body eventually led to the front and middle legs losing contact with the ground before the hind legs, so that it was the hind legs that provided the thrust for the final 10–12 ms before the insect became airborne. The hind tibiae took $32.6\pm0.95\,\mathrm{ms}$ ($n=25$) in females and $30.6\pm2.7\,\mathrm{ms}$ ($n=7$) in males to reach full extension, achieving peak angular rotational velocities of $13\,500\,\mathrm{deg.\,s^{-1}}$. Once the hind tibiae reached their full extension, the insect became airborne at a mean takeoff angle of $33.8\pm2.1°$ ($n=17$, females and males). The mean takeoff velocity for females was $2.12\pm0.33\,\mathrm{m\,s^{-1}}$, with an acceleration during the last 5 ms before becoming airborne of $143.8\pm28.8\,\mathrm{m\,s^{-2}}$ ($n=4$), while in males the velocity was lower at $1.51\pm0.2\,\mathrm{m\,s^{-1}}$, with an acceleration of $83.4\pm14.7\,\mathrm{m\,s^{-2}}$ ($n=5$; Table 2).

These movements launched the insect into a parabolic trajectory (Fig. 9). At takeoff, all of the legs were parallel to each other and trailed below the body. As height was gained, they were all rotated upwards at their coxal joints so that towards the apogee of the jump they projected backwards and above the body. This posture of the legs is similar to that adopted by a tethered flying *Meconema* when exposed to a

Fig. 7. Comparison of the muscular activity and tibial movements underlying two kicks by the same *Pholidoptera*. (A) A kick from an initial position where the tibia was fully flexed about the femur (kick 1 in Fig. 4A). Spikes in fast extensor tibiae motor neurone (FETi) stop before the tibia extends rapidly ($65\,000\,\mathrm{deg.\,s^{-1}}$) in a kick. (B) A second kick by the same animal (kick 2 in Fig. 4A). The tibia is first fully flexed but then extends by 27°. It remains in this partially flexed position while FETi spikes continue, until it suddenly extends rapidly ($65\,000\,\mathrm{deg.\,s^{-1}}$) in a kick. The maximal angular velocity of the tibial movements was the same in both kicks. The electrical activity of the extensor tibiae muscle was recorded at the same time as the tibial movements that are plotted from sequences of images captured at $1000\,\mathrm{frames\,s^{-1}}$.
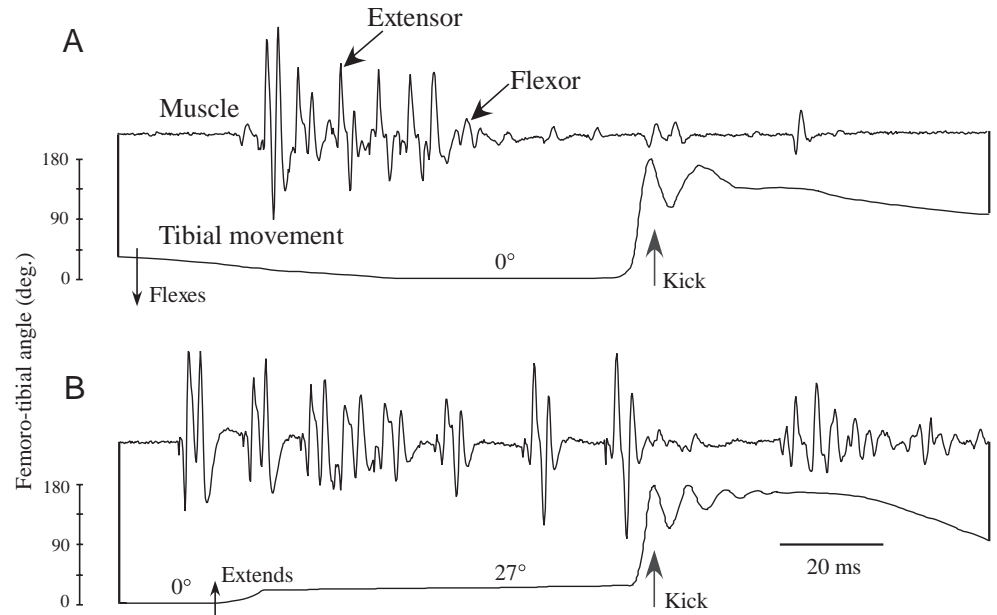
current of air (von Buddenbrock and Friedrich, 1932). It may represent a ruddering effect to aid stability of the body and to prevent the impulsive forces exerted by the legs on the ground causing the body to rotate when airborne.

The distance jumped by both sexes was similar (Table 2), implying a greater expenditure of energy by the heavier females that is partially offset by the greater mechanical advantage of their 12% longer hind legs (Table 1). The total energy required for the jump is the sum of the translational kinetic energy (E_k) at takeoff and the potential energy (E_p) due to the gain in height at takeoff:

$$E_k = mV^2/2\,, \tag{1}$$

where m is the mass (in kg) and V is the takeoff velocity (in $\mathrm{m\,s^{-1}}$), and:

$$E_p = mgh\,, \tag{2}$$

where m is the mass (in kg) of the body minus the legs that are still on the ground, g is acceleration due to gravity, and h is the height (in metres) gained before takeoff.

The insect did not spin once airborne, so rotational kinetic energy was assumed to be negligible. The translational kinetic energy of the jump by a female was $1350\,\mu\mathrm{J}$ (male, $470\,\mu\mathrm{J}$), and the potential kinetic energy was $30\,\mu\mathrm{J}$ (male $20\,\mu\mathrm{J}$), giving a minimal energy requirement of $1380\,\mu\mathrm{J}$ (male $490\,\mu\mathrm{J}$) (Table 2). The power output by a female was estimated to be approximately $40\,\mathrm{mW}$ (male $16\,\mathrm{mW}$) by assuming that energy expenditure was similar over the $30\,\mathrm{ms}$ duration of the propulsive phase of the jump.

Jumping by *Meconema*, *Conocephalus* (Fig. 10A,B) and *Leptophyes* had similar characteristics to those described above. The main thrust was provided by rapid extension of the hind tibiae and by depression and extension of the middle and front legs. Again, a hind tibia was not always fully flexed against the femur at the start of the jumping sequence. The hind legs were the last to leave the ground, thereby providing the final thrust before takeoff. The time taken for complete extension of the hind tibia in the most powerful jumps was shorter, and takeoff velocities ranged from $1\,\mathrm{m\,s^{-1}}$ to $1.4\,\mathrm{m\,s^{-1}}$ (Table 2). In *Conocephalus*, the takeoff angle was typically steeper at $56.8\pm12.3°$, but the body remained stable once airborne.

Discussion

Female bush crickets complete the rapid kicks of their hind tibia in $10\,\mathrm{ms}$, generating maximal angular rotational velocities of the femoro-tibial joint of $42\,000\,\mathrm{deg.\,s^{-1}}$. The tibia does not need to be fully flexed about the femur to achieve these rapid movements; slower kicks can be generated with or without co-contracting the flexor and extensor tibiae muscles. The underlying motor pattern in different kicks is variable and any periods of co-contraction tend to be brief. On average, bush crickets can jump a horizontal distance equivalent to 13–14 times their body length, but maximal distances can be twice as large. Females accelerate at $144\,\mathrm{m\,s^{-2}}$ to generate a takeoff velocity of $2.1\,\mathrm{m\,s^{-1}}$, requiring a minimal energy expenditure of $1380\,\mu\mathrm{J}$ and a power output of $40\,\mathrm{mW}$. Males are less powerful, accelerating more slowly to lower takeoff velocities despite a smaller mass. Their poorer performance may be partly explained by their shorter hind legs but also indicates that either the mass or performance of the muscles in their hind legs is lower.

Mechanisms for jumping and kicking

While our analyses have focused on *Pholidoptera*, its mechanisms for jumping and kicking appear to be common to
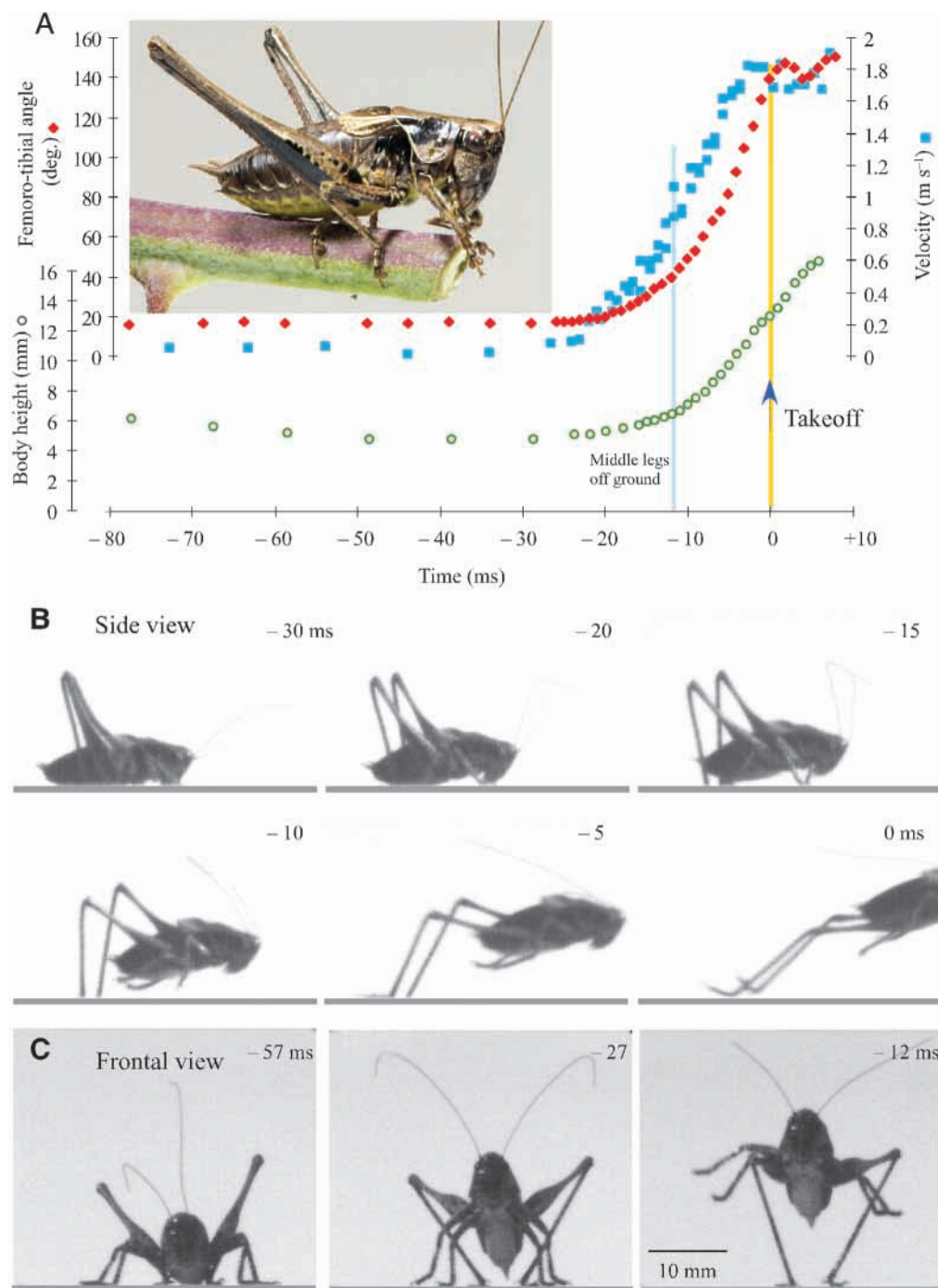
Fig. 8. Jumping in *Pholidoptera*. (A) Graphs of the changes in the femoro-tibial angle, body height and velocity of body movement during a jump by a male. The body was accelerated at $112\,\mathrm{m\,s^{-2}}$ during the last 5 ms before takeoff at a velocity of $1.75\,\mathrm{m\,s^{-1}}$. (B) Selected frames from the same jump viewed from the side. At the start, the tibia was not fully flexed about the femur but was then extended rapidly to push the body forwards and upwards. (C) A second jump by the same animal viewed head-on. The hind legs were first rotated outwards at the coxa joint with the thorax, and the tibia extends so that the body was raised from the ground. The front and middle legs left the ground before the hind legs.

the other bush crickets we examined. The specializations that generate these fast movements, as for other orthopterans, involve the design of the legs, the femoro-tibial joints of the hind legs, their associated tendons and muscles, and the motor patterns that drive the muscle contractions.

Leg length

The hind legs are approximately 1.5 times the length of the body and four times longer than the front legs. They are, therefore, relatively longer than the legs of other jumping insects (Table 1). Long legs allow the accelerating force to act on the substrate over a longer time, producing a higher takeoff velocity and greater jump distance. A long-legged insect, therefore, requires less force (working over a larger distance) to jump the same distance as a short-legged insect of comparable mass. A comparison of leg designs shows that reliance on a single pair of legs to generate the majority of force is met by an increase in the length of those legs. By contrast, in the stick insect *Sipyloidea* sp., in which leg and abdominal movements combine to generate a jump, the legs are all of similar size and structure (Burrows and Morris, 2002).
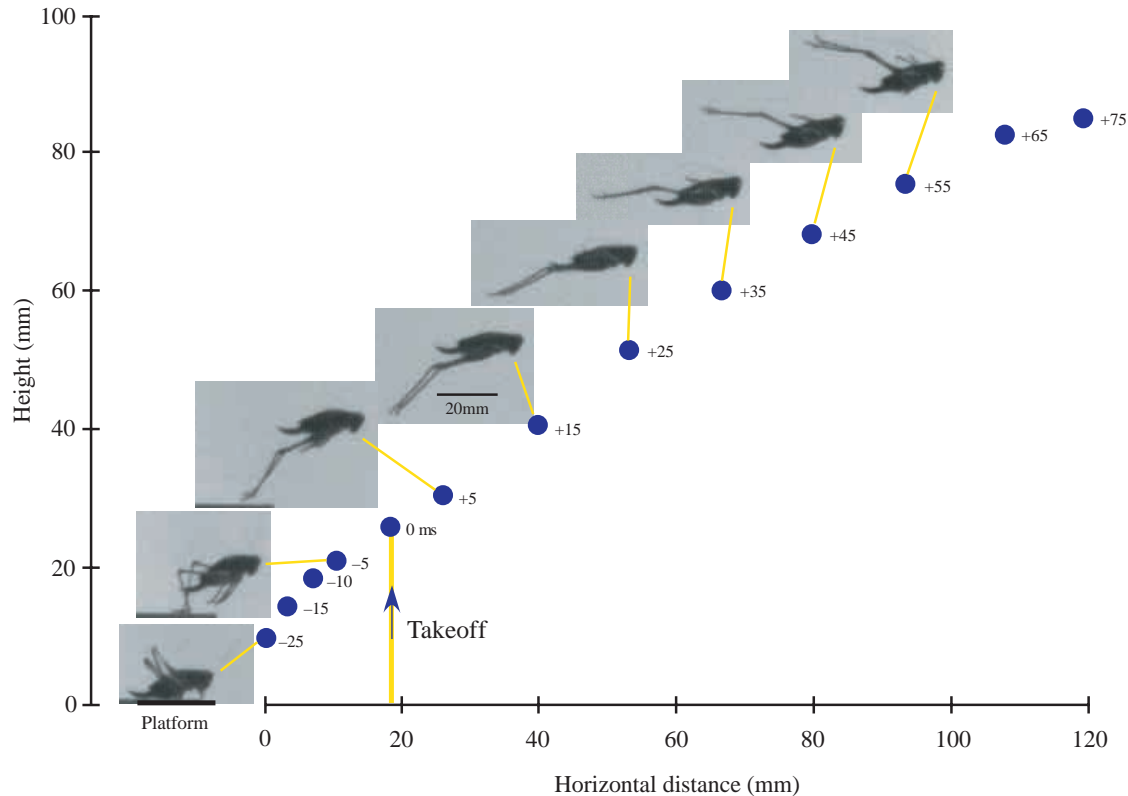
Fig. 9. The trajectory of a female *Pholidoptera* during a jump. The graph plots the upwards and forwards movement of the body, and the selected frames show the propulsive extension of the hind tibiae. After takeoff, the hind legs were swung forward so that they were above the body. The numbers give the time before and after takeoff at 0 ms.

Muscle lever arms and joint structure

The insertions of the extensor and flexor tendons relative to the pivot of a hind leg result in greater flexor lever arms at flexed joint angles and greater extensor lever arms at more extended angles. The femoral lump further enhances the line of action of the flexor tendon when the tibia is at or near full flexion. In locusts, the lump protrudes into the femur for 40% of its width (Burrows and Morris, 2001; Heitler, 1974), but in bush crickets, crickets (Hustert and Gnatzy, 1995) and *Prosarthria* (Burrows and Wolf, 2002) the comparable figure is 15–17%. In crickets and bush crickets, the smaller lump is offset by a pad of soft tissue on the flexor tendon that changes the line of action of the flexor tendon as it rides over the lump when the tibia is fully flexed.

In bush crickets, full flexion of the tibia does not have to precede a kick or a jump, and kicks of similar velocity can be generated from a partially flexed or from a fully flexed femorotibial angle. The changing lever ratios at different joint angles, combined with the balance of forces in the two muscles, must, therefore, determine the timing and velocity of tibial extension. If, for example, the tibia is fully flexed, the lever ratio of the flexor will be large, allowing a greater force to be generated by the extensor muscle before tibial extension occurs. If flexor tension is high, then the extensor force needed to produce a tibial extension will be proportionately greater, and the resulting extension faster, once the flexor relaxes. The flexor

force could result from the residual tension of a preceding flexor contraction or from a co-contraction of the flexor and extensor. A different balance of flexor and extensor forces could therefore result in kicks of similar velocities from different joint angles. By contrast, a locust cannot kick or jump if it is unable to flex its tibia fully, because the locking mechanism of the flexor tendon and the femoral lump can only be engaged in the fully flexed position and only then is the mechanical advantage of the flexor maximal. The small flexor muscle cannot restrain the force developed by the large extensor muscle unless these conditions are met. If the extensor muscle contracts when the tibia is not fully flexed and the lock is not engaged, the tibia will extend, but without the power needed for jumping or kicking.

Motor pattern

The differing starting angles from which a rapid tibial extension can occur and the wide range of angular velocities of the tibia in kicking are also reflected in the motor patterns. At one extreme, a few spikes occur in the fast extensor tibiae motor neuron after spikes in the flexor have ceased. At the other, a co-activation of extensor and flexor motor neurons leads to a co-contraction for 50–250 ms. The number of FETi spikes ranges from 1 to 8, with more spikes generating faster extensions. This brief and variable motor activity contrasts with the lengthy motor pattern with consistent features that
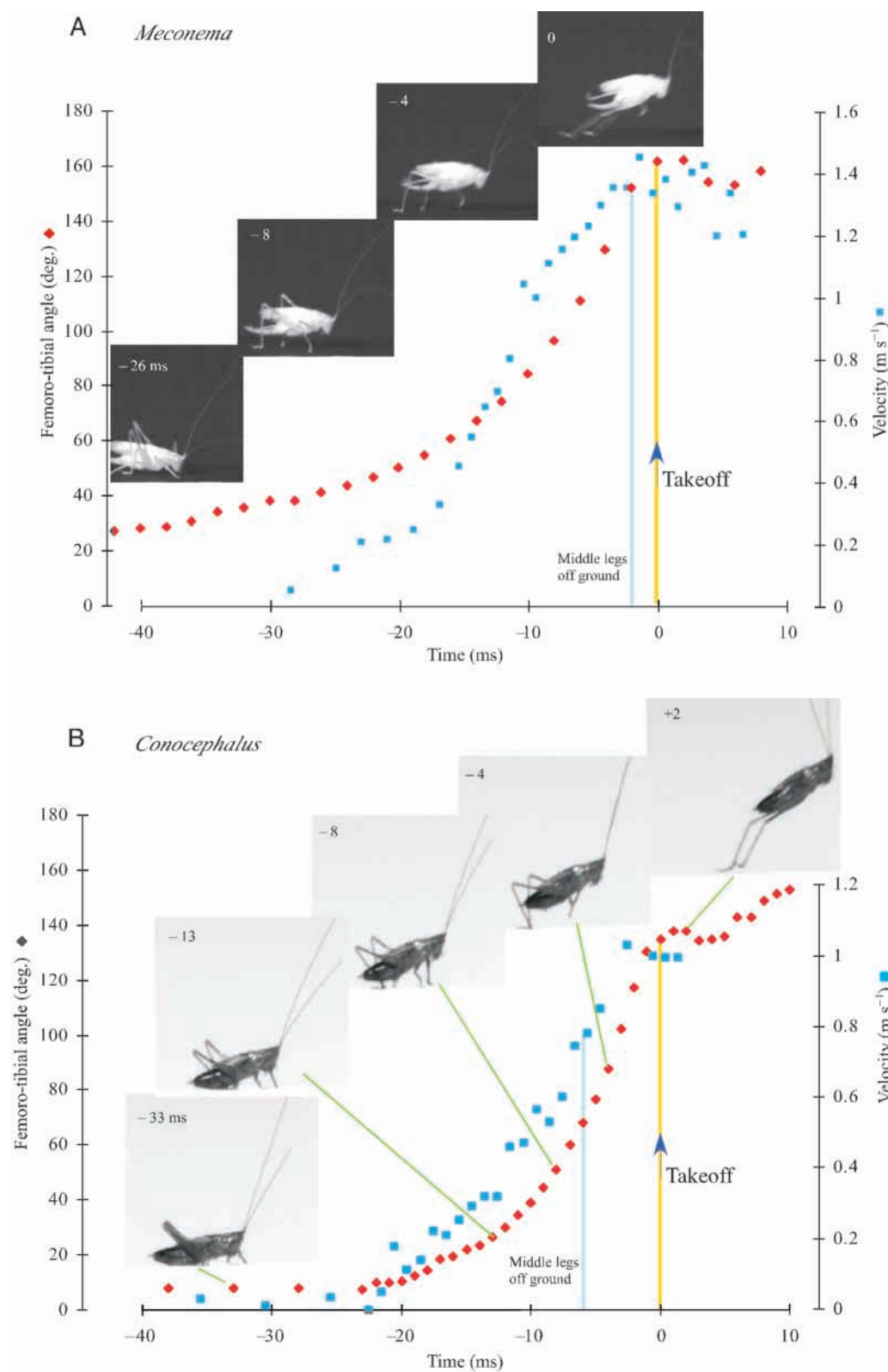
Fig. 10. Jumping in *Meconema* and *Conocephalus*. (A) Two jumps by the same female *Meconema*. Four selected images of one jump captured at 500 frames s^{-1} show the hind legs were not fully flexed before they were extended rapidly. The changes in the femoro-tibial angle and speed of body movement are plotted from a second jump with a takeoff velocity of 1.6 m s^{-1} captured at 1000 frames s^{-1}. (B) Selected images and plots of the femoro-tibial angle and speed of body movement from the same jump by a male *Conocephalus* taking off at a velocity of 1.0 m s^{-1} captured at 1000 frames s^{-1}.

generates kicking in locusts (Burrows, 1995; Heitler and Burrows, 1977) and in *Prosarthria* (Burrows and Wolf, 2002). In these insects, co-contraction of flexors and extensors can vary 20-fold, from 100 ms to 2000 ms, and can involve 2–50 FETi spikes, resulting in movements from slow and weak to fast and powerful (Burrows, 1995). The motor activity of bush crickets is, therefore, closer in structure to that of true crickets (e.g. *Acheta domesticus*) in which 1–4 fast extensor spikes are generated in a brief, 3–12 ms 'static' co-contraction (Hustert and Gnatzy, 1995). As for true crickets, the time from the

initiating sensory stimulus to full extension of the tibia in a kick is much shorter than for a locust. In crickets, the pattern is completed in 60–100 ms (Hustert and Gnatzy, 1995); in bush crickets it takes 50–250 ms, and in locusts it takes several hundred milliseconds. Consequently, crickets and bush crickets have a faster response time for their escape movements, offset by the shorter horizontal distance jumped or the reduced force in a kick.

Energy requirements and storage

Can bush crickets kick and jump as the result of the direct muscular contractions or do they have to store energy in advance? Bush crickets take approximately 10 ms at peak angular velocities of 41 800 deg. s^{-1} to extend a tibia fully in their faster kicks, *Prosarthria* takes 7 ms at velocities of 48 000 deg. s^{-1} but locusts take only 3 ms at velocities of 80 000 deg. s^{-1} (Table 2). These different performances and the different body masses are also reflected in the energy expended in jumping: locusts expend 9–11 mJ, male *Prosarthria* expend 850 μJ, whereas male bush crickets expend only 490 μJ. In both locusts and *Prosarthria*, the energy needed to kick rapidly or to jump can only be met by a preceding storage of energy and its rapid release. The power output during the acceleration phase of a jump greatly exceeds the maximum that can be produced by direct muscle action. For example, the peak power output of the locust extensor muscle is 450 mW g^{-1}, and each muscle in a female has a mass of 70 mg (Bennet-Clark, 1975). The combined power output of both extensors should be about 60 mW, but the measured power output during a jump is over five times greater at around 330 mW (Table 2). Assuming the extensor muscles of bush crickets account for a similar proportion of body mass (5 %) and have a similar specific power, we estimate that the hind leg extensor muscles of a 600 mg female *Pholidoptera* can generate a maximum power of 13.5 mW. This is less than half the 40 mW calculated from kinematic analysis (Table 2), implying energy storage prior to tibial extension, albeit not on the same scale as in the locust. Bush crickets do not appear to store energy in distortion of semi-lunar grooves (Fig. 4), so it is probable that the extra energy is stored in the extensor apodeme and elastic elements of the extensor muscle.

Jumping and kicking: objectives and adaptations

Jumping has two possible objectives: locomotion or escape. For the former, there is sufficient time to generate the force needed for a long jump; for the latter, speed of response may be critical when fleeing from a potential predator. This may be particularly true for nocturnal insects such as bush crickets and true crickets, which rely less on vision for early warning of approaching predators. Similarly, a defensive kick must be generated quickly following the stimulus. An insect, therefore, faces a trade-off between a rapid, relatively weak response that hits the offending object and a delayed, more forceful movement that may miss it altogether. The ability of both bush crickets (this paper) and true crickets (Hustert and Gnatzy, 1995) to produce rapid kicks without a prolonged co-

contraction is, therefore, significant. In crickets, a dynamic co-contraction supplements a short static co-contraction phase, enabling some energy storage to occur during the preparatory flexion that precedes the kick. Co-contraction can begin during the preparatory flexion in bush crickets (e.g. Fig. 7A), whereas in locusts the tibia must be fully flexed before the flexor muscle can withstand the force generated by the more powerful extensor, and activation of the extensor muscle is delayed accordingly. In bush crickets, the ratio of the flexor/extensor lever arm appears to be much higher than in locusts or *Prosarthria*. This adaptation enables jumps or kicks to be produced from a range of starting joint angles and shortens the response time by allowing build up of extensor tension without a preparatory full flexion.

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