Neural Control and Coordination of Jumping in Froghopper Insects

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Submitted 13 July 2006; accepted in final form 28 September 2006

Burrows M. Neural control and coordination of jumping in froghopper insects. J Neurophysiol 97: 320–330, 2007. First published October 4, 2006; doi:10.1152/jn.00719.2006. The thrust for jumping in froghopper insects is produced by a rapid, synchronous depression of both hind legs generated by huge, multipartite trochanteral depressor muscles in the thorax and smaller levator muscles in the coxae. A three-phase motor pattern activates these muscles in jumping. First, a levation phase lasts a few hundred milliseconds, in which a burst of spikes in the trochanteral levator motor neurons moves the hind legs into their fully cocked position and thus engages a mechanical lock between a coxa and a femur. Second, a cocked phase lasts a few seconds, in which a trochanteral depressor motor neuron spikes continuously at a frequency gradually rising to 50 Hz, although the hind legs remain stationary. Levator motor spikes are sporadic. Third, the jump movement lasts <1 ms, in which the spikes in the depressors stop abruptly and the legs rapidly depress. This pattern may vary in the speed of the initial levation and in the duration of the cocked phase. Recordings from the depressor muscles on both sides showed remarkable synchrony of their motor spikes. In one 4.9-long cocked phase all 174 spikes were synchronous and in another 27 s period of continuous spiking all but one of 1,176 spikes were synchronous. When a single hind leg moves rapidly, these depressor spikes are nevertheless independent of those of the other leg. These features of the motor pattern and the coupling between motor neurons to the two hind legs ensure powerful movements to propel rapid jumping.

INTRODUCTION

Froghopper insects (spittle bugs) are prodigious jumpers that achieve their prowess by a rapid and simultaneous depression of their hind legs (Burrows 2003; Burrows, 2006a). These movements accelerate the body at 5,400 m s⁻², to a take-off velocity of 4.7 m s⁻¹, so that the insect experiences a force equivalent to 550 times gravity. This jumping performance requires an energy output of 136 μJ and a power output of 155 mW, so that it ranks as the best among all insects. The enormous acceleration applied through the relatively short hind legs that is required to lift the insect into the air could not be provided by direct muscular contraction. Instead energy must be stored in advance of the jump and then released suddenly in a catapult-like mechanism. The hind legs have a number of characteristic features that are associated with their role in jumping (Burrows, 2006b). First, the main trochanteral depressor muscle generating the movement is located in the thorax so that the hind legs are light and can therefore be accelerated rapidly. Second, an elaborate locking mechanism between a femur and a coxa, involving protrusions covered with “Velcro-like” microtrichia, enables both hind legs to be held in a cocked position in advance of the jump and then released suddenly in a rapid movement that is accompanied by a characteristic click sound. Third, the lever arms of the trochanteral muscles favor the levator over the depressor when the leg is in its cocked position. This paper analyses the motor pattern and the coupling between the motor neurons to the muscles of the hind legs that control jumping.

In large insects such as locusts (Burrows 1995; Godden 1975; Hetler and Burrows 1977) and false stick insects (Burrows and Wolf 2002), which also use a catapult mechanism when jumping, the motor pattern consists of three phases: 1) a cocking phase in which the tibia is flexed about the femur of a hind leg; 2) a cocontraction phase in which the flexor and extensor tibiae muscles contract but the tibia remains stationary and firmly flexed about the femur, in consequence of which energy is stored in distortions of particular parts of the leg; and 3) a rapid extension or jump phase in which the flexor motor neurons are inhibited and the force stored by the prolonged contraction of the extensor is suddenly released to power the rapid extension of the tibia. In bush crickets the same general pattern is seen (Burrows and Morris 2003), but full flexion of the tibia is not a prerequisite and only brief periods of cocontraction may occur because of the greater leverage from their very long hind legs. In crickets that kick rather than jump, the movement can be powered by direct muscle contractions (Hus-tert and Gnatz 1995). The overall picture to emerge is that powerful and rapid movements require a slow contraction of a power-producing muscle, restrained by the action of other muscles and often aided by mechanical skeletal specializations. The much smaller size of other exceptional jumpers such as fleas (Bennet-Clark and Lucey 1967; Rothschild and Schlein 1975) precludes recordings being made so that nothing is known about motor patterns or muscle actions, and the jumping mechanisms have been inferred from the anatomical arrangements of the muscles and joints.

Froghoppers with a body length approaching 10 mm in larger species such as Aphrophora (Burrows 2006a) are bigger than fleas (1.5 mm) but considerably smaller than locusts (40–47 mm). Nevertheless, it has proved possible to make recordings from the muscles during jumping by taking advantage of the fact that when the body is restrained both hind legs can produce rapid and simultaneous movements that have all the characteristics of those during natural jumping. The only apparent difference is that, because the hind legs are not supporting the weight of the body, the final leg movements are faster. There is a strong analogy here with the jumping and kicking movements of locusts, bush crickets, and false stick insects. In kicking, which in these insects is usually performed by one hind leg that is not bearing the weight of the body, the underlying motor pattern has similar characteristics to those used in jumping (Burrows 1996).

This paper demonstrates that a motor pattern of three phases underlies jumping in froghoppers. In the first phase, the levator muscles move the legs into cocked positions and engage the

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Mechanical locks; in the second phase, lasting a few seconds, the hind legs remain stationary in their cocked position while the depressor muscles spike continuously but the extensors only sporadically. The final phase involves the sudden and rapid depression of the hind legs that powers the jump. Recordings from the depressor muscles of the left and right hind legs reveal a remarkable degree of coupling between their motor spikes that may contribute to the synchronous actions of the legs and thereby ensure that the jump propels the froghopper directly forward.

METHODS

Froghoppers, Philaenus spumarius (Linnaeus 1758), Aphrophora alni (Fallén 1805), and Cercopis vulnerata (Rossi 1807) were collected near Cambridge, UK. They belong to the order Hemiptera, suborder Auchenorrhyncha, and to the superfamily Cercopoidea. Aphrophora belongs to the family Aphrophoridae and Cercopis to the family Cercopidae. Recordings were made on the same day of collection, or after the insects had been kept in the laboratory for no more than a few days feeding on live Chrysanthemum plants.

The actions of the muscles controlling jumping were recorded by inserting pairs of 30-µm steel wires, insulated but for their tips, into the trochanteral depressor and levator muscles of the hind legs. The recording sites are indicated in the drawing of Fig. 1. Aphrophora or Cercopis were restrained on their backs in Plastocene with both hind legs free to move. Rapid and coordinated movements of the two hind legs occurred spontaneously or could be induced by the same mechanical stimuli used to promote unrestrained jumping. The sequence of movements evoked in this way was the same as that observed in unrestrained jumping (Burrows 2006a,b). Movements of a hind leg were recorded at the same time by fixing a 0.2-mm disc of reflective tape to a hind femur close to the femoro-tibial joint. A modified single-lens reflex camera with a concentric light around the lens was focused on the disc and the light it reflected was captured by a photocell in the film plane of the camera (Hedwig 2000). In some experiments the sound associated with the rapid extension of the leg was recorded with a microphone placed 5 mm laterally from one hind leg. In other experiments images of the movements of the legs were also captured at rates of 1,000 or 2,000 s⁻¹ with a high-speed camera (Redlake Imaging, San Diego, CA) and an associated computer. The camera was attached to a Wild M7A microscope viewing the insect from directly above. The electrical signals from the muscles were digitized at sampling rates of 8 kHz with a CED (Cambridge Electronic Design) interface running Spike2 version 5 software and were then written directly to a second computer. The resulting data files on the two computers were synchronized to a resolution of 1 or 0.5 ms depending on the image capture rate, by feeding a 0.5-ms-long electrical pulse to a separate channel of the CED interface that simultaneously triggered a light flash detected by the camera.

Two hundred and sixty-five jumps by 17 Aphrophora and 23 jumps by seven Cercopis were recorded and analyzed. Data are given as means ± SE. Temperatures ranged from 22 to 26°C.

RESULTS

Muscles powering a jump

The simultaneous and rapid depression of the two hind trochantera about the coxae provides the main force for a jump. These movements are also accompanied by the rapid extension of the tibiae about the femora (Burrows 2006a,b). The depression of a trochanter is controlled by a huge depressor muscle that occupies most of the space within each half of the thorax of the metathoracic segment (Figs. 1 and 2). The large trochanteral depressor muscle of a hind leg appears to be a special-
ization for jumping because the corresponding muscle of a middle or front leg is very much smaller.

**Muscles moving a hind trochanter**

The trochanteral depressor muscle of a hind leg consists of four parts that all insert on the same large tendon that attaches to the anterior and medial rim of the trochanter and extends through the coxa and into the thorax (Burrows 2006b) (Figs. 1A and 2). Two large parts of the muscle are within the thorax, a third smaller part extends through the coxa to the thorax, and a fourth small part is entirely within the coxa. The trochanteral depressor and levator muscles both seem similar in arrangement to comparable muscles in Orthopteran insects (depressor muscle 133 and levator muscles 131 and 132) (Snodgrass 1929, 1935) so that the same nomenclature will be used without necessarily implying homologies.

The first large part of the muscle (b) (Fig. 1A) lies laterally in the thorax and consists of pinnate sheets of fibers that arise from the anterior and lateral walls of the ventral metathorax. The fibers insert on both the anterior and posterior sides of a thin lateral arm of the tendon (Fig. 1B).

The second large part of the muscle (c) is more medial within the thorax and consists of a mass of parallel fibers that arise from the anterior and lateral walls of the ventral metathorax. The fibers insert on both the anterior and posterior sides of a thin lateral arm of the tendon (Fig. 1B).

The third small part of the muscle (d) consists of a small bundle of fibers, 300 μm long and 100 μm wide when the trochanter is fully depressed, that attach medially to the sternal apophysis just lateral and posterior to the metathoracic ganglion. The parallel fibers pass posteriorly into the coxa to insert on the dorsal surface of the tendon toward its medial edge.

The fourth part of the muscle (a), which lies entirely within the coxa, consists of a small bundle of short fibers, 200 μm long and 200 μm wide when the trochanter is fully depressed, that attach to the ventral wall of the coxa toward its medial and anterior edges. These fibers insert on the ventral surface of the main arm of the tendon.

The tendon of the trochanteral depressor is large and complex in structure (Fig. 1, A and B). It extends from its insertion on the medial rim of the trochanter, through the coxa, and into the thoracic cavity, a distance of almost 1 mm in Aphrophora. At its widest point it is 250 μm thick. The tendon is hard and rigid and does not appear to bend under the natural actions of its muscle or when manipulated experimentally. Its insertion onto the trochanter, however, is through tough but flexible membrane. As the trochanter moves through its complete angular range from the fully levated (cocked) to the fully depressed position, a fixed point on the tendon moves through a linear distance of some 360 μm.

The trochanteral levator muscles of the hind legs are much smaller than the depressors and consist of at least two parts (muscles 131 and 132) that attach to the walls of the coxae toward their anterior edges. They insert on two laterally facing horns of the trochanter, one ventral (Fig. 1B) and one dorsal.

**Muscles moving a hind tibia**

In contrast to the large trochanteral depressor muscle, the muscles moving a tibia are very much smaller. The extensor tibiae muscle within the femur is smaller than the flexor tibiae muscle (Fig. 1A). This is similar to the arrangement of the muscles in the femora of the front and middle legs of jumping Orthopteran insects such as grasshoppers, but a reversal of the arrangement in the hind legs, where the extensor muscle is huge, occupies most of the greatly enlarged femur and powers jumping.

**Pattern of muscle action during a jump**

The pattern of motor activity recorded from the depressor and levator muscles of a hind trochanter had three characteristic phases in all jumps of Aphrophora and Cercopis that were analyzed (Figs. 3 and 4).
First is a slow levation phase lasting a few hundred milliseconds, in which a burst of spikes occurred at high frequency in a trochanteral levator muscle, accompanied by a slow levation of a hind leg into its most elevated (cocked) position.

Second is a sustained, cocked phase lasting a few seconds, in which spikes occurred continually in a trochanteral depressor muscle gradually increasing in frequency, particularly toward the end, whereas those in the levator were sporadic. Despite
this sustained period of depressor activity, the leg remained locked in its cocked position and did not move.

Third is a rapid depression or jump phase (the movement launching the jump) lasting <1 ms, in which the spikes in the depressor stopped abruptly and the trochanter suddenly and rapidly depressed.

Variations in four aspects of this basic pattern were seen in different jumps by different Aphrophora and Cercopis, and even between successive jumps by the same individual insect of one species (Fig. 4). First, there were differences in the speed with which the leg was moved into the cocked position and therefore in the duration of the elevation phase. Second, the duration of the cocked phase and therefore in the duration of the continuous depressor activity was variable. Third, there were differences in the timing, number, and frequency of levator spikes during the cocked phase. Fourth, there were differences in the time before the leg was levated again after a jump. In contrast to these differences between different jumps, the rapid depression movements of the hind legs in the jump phase itself were remarkably constant.

**Elevation phase**

The burst of spikes in the levator muscles pulling the leg into its levated and cocked position appeared to derive from the activity of a few motor neurons (Figs. 3–5). The instantaneous frequency between successive spikes reached 200 Hz (Figs. 3 and 4), but these values do not necessarily represent the firing frequencies of individual motor neurons. The time taken to elevate the leg into its cocked position was $187.3 \pm 8.9$ ms ($n = 45$ jumps by one Aphrophora, range $88–353$ ms, median $183$ ms) (Fig. 5). No jumps were observed unless both hind legs were fully elevated, thereby engaging the femoral and coxal protrusions (Burrows 2006b). Slower levation and depression movements used during climbing did not involve the full levation and cocking of the hind legs.

**Cocked phase**

The first spikes in the depressor muscle (parts b and c) began only when the trochanter was fully levated with the dorsal protrusion on a femur engaged with the lateral protrusion of a coxa (Figs. 3–5). The spikes then continued throughout the sustained cocked phase, stopping only just before the jump occurred. During this phase, the spikes in the depressor muscle are most parsimoniously explained as being derived from a single motor neuron for the following reasons. First, placement of the electrodes at different positions within parts b and c of the depressor revealed the same pattern of activity. Even two pairs of electrodes placed simultaneously in different regions recorded the same pattern of spikes and failed to reveal the actions of additional motor neurons. Second, the shape and

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**FIG. 5.** Muscle activity initiating the levation phase of a jump. A and B: recordings from the depressor and levator of the left trochanter at the start of 2 jump sequences by the same Aphrophora. Trochanter is first levated by a burst of spikes in the trochanteral levator muscles. Rate of the levation differs in the examples shown. When the trochanter has been fully levated so that it is cocked, spikes in the depressor muscle begin but the trochanter does not move. Spikes in the levator muscle decline in frequency.
amplitude of the spikes were consistent in long sequences and there were no large discontinuities between spike amplitudes or shapes that would suggest the participation of different motor neurons. There were some small changes in amplitude but these would be expected given the likely movement of the extracellular electrodes relative to the muscle fibers during this powerful contraction. Third, the instantaneous frequencies do not exceed those expected from single motor neurons and the changes in frequency are explicable in terms of the activity of a single motor neuron. Fourth, if more than one motor neuron were active then they would have to be very tightly coupled. Larger spikes caused by the electrodes summing two simultaneous events were not recorded. Similarly there was no drift in the intervals between spikes leading to “beating,” as occurs between coupled oscillators, and which is seen in some insect muscles (e.g., spiracular closer muscles) innervated by two separate motor neurons that are closely coupled by their synaptic drive (Burrows 1978).

Assuming that the depressor spikes were from a single motor neuron, then the plots of the instantaneous frequency of these spikes show a gradual rise throughout the cocked phase from about 20 Hz at the start to just <50 Hz at the end (Figs. 3 and 4). Some pairs or triplets of spikes occurred sporadically at frequencies approaching 200 Hz.

The duration of the cocked phase in Cercopis, determined by the motor spikes in the trochanteral depressor muscle, was 2.85 ± 0.59 s for 18 jumps by seven animals (range 0.74 to 9.1 s, median 2.2 s). In Aphrophora the durations were similar at 2.9 ± 0.16 s for 160 jumps by six insects (range 0.47 to 9.9 s, median 2.3 s). In one example a continuous sequence of spikes lasted for 41 s but then stopped without leading to a rapid depression. Similar long sequences of motor spikes that would have been expected to lead to a jump, but are instead aborted, also occur in locust jumping (Burrows 1995; Heitler and Burrows 1977).

The activity of the trochanteral levator muscle was variable during this cocked phase both in repeated jumps by the same insect (Fig. 4) and between different insects. Analysis of all the jumps failed to reveal any indication of an underlying pattern to this activity. In most jumps there were no levator spikes after the initial burst moving the leg into the cocked position. In others, the initial burst of spikes continued at declining frequency into the cocked phase and then occurred at variable times and frequencies during this phase. This sporadic levator activity usually stopped before a jump was generated.

Jump phase

The rapid depression of the trochanter in the jump followed an abrupt end of the depressor spikes (Figs. 3, 4, and 6, A–C). The time from the last spike and the start of the leg movement was 35.3 ± 2.3 ms for 103 jumps by six Aphrophora (range 1.9 to 172 ms, median 34.6 ms). There was no reduction in the frequency of the depressor spikes as the time for the jump approached, but simply a sudden cessation.

In recordings from two animals made with electrodes in the coxa, a burst of spikes was recorded at the time that the leg rapidly depressed (Fig. 6). All other recordings from similar sites in the coxa did not reveal such activity, although normal, rapid leg movements still occurred. The muscle in which these spikes were generated is unknown, but the spikes have the following characteristics. They were of smaller amplitude than those attributed to the levator muscle as the trochanter was elevated into its fully cocked position. Some of the apparent spikes appeared simultaneously in the recording from the depressor muscle and had a shorter time course, suggesting that
they might be movement artifacts associated with the rapid movements of the jump. The spikes also occurred at different times relative to the rapid depression movement even when jumps were recorded sequentially from the same site in the same individual (open arrows in Fig. 6, A–C). The mean time that elapsed from the first spike to the start of the movement in one individual was 5.5 ± 1.2 ms, n = 8 (range 2.1 to 11 ms, median 3.9 ms) (Fig. 6D). Much of the activity occurred after the jump.

**Spikes in trochanteral depressor muscles**

The large spikes recorded in the trochanteral depressor muscle (parts b and c) during a jump were not recorded during slower movements of the legs (Fig. 7). In the example shown, the large-amplitude spikes described above showed their typical pattern of activity during the cocked phase and stopped just before the jump phase. After the jump, the leg then levated, but not into its fully cocked position, by the action of the levator muscle. A series of slow depression and levation movements then followed, with each levation accompanied by a burst of levator activity but each depression marked by an absence of depressor spikes comparable to those during the cocked phase of the preceding jump. These observations suggest that the motor neuron recorded when the leg was cocked and preparing for a jump is restricted in its action and that slower depression movements are mediated by other depressor motor neurons not recorded by these electrode placements or by the other parts of the depressor muscle.

Simultaneous recordings from the left and the right trochanteral depressor muscles showed that their patterns of spikes were remarkably similar (Fig. 8). The spikes on one side sometimes started before those on the other, as in the example shown, but then the overall frequency profile of the spikes on the two sides was the same throughout the cocked phase (Fig. 8A). Transient changes in frequency caused by the occurrence of groups of a few spikes were also reflected on both sides. Finally, the last spikes in the left and right depressor muscles always occurred at the same time. Plotting the time of occurrence of spikes on one side against those on the other side revealed a linear relationship with only a few spikes that occurred independently. In the example shown (Fig. 8B), five spikes at the start of the cocked phase occurred on one side but not the other, and during the remainder of the phase only two spikes occurred on one side that were not accompanied by a simultaneous spike on the other.

When spikes in the depressor muscles during the cocked phase were displayed on an expanded timescale and analyzed in detail, the vast majority of spikes on one side were matched by a spike on the other side occurring at the same time (Fig. 9A). Triggering on a fixed point on the rising phase of spikes on one side and overlaying spikes of both sides showed that all 174 spikes during a 4.9-s cocked phase preceding a jump were synchronous (Fig. 9B). No examples were found where spikes on one side led those on the other by a measurable interval.
Occasional depressor spikes occurred on one side without a matching spike on the other (Fig. 9, C and D). Most remarkably during a 27-s-long cocked phase that was aborted and did not result in a jump, all but one of 1,176 spikes were synchronous on the two sides. These motor neurons can nevertheless act independently on the infrequent occasions when the two legs moved rapidly but independently (Fig. 9E). The large spikes then occurred in separate bursts on either side and the electrodes on the inactive side recorded no reflected spikes arising from cross talk from the active side.

**DISCUSSION**

**Pattern of muscle action**

Jumping in froghoppers is propelled by a sequence of movements by the hind legs and an associated motor pattern that consists of three phases. First is a *levation phase* lasting a few hundred milliseconds in which the trochantera are slowly elevated about the coxae and into their cocked position. This is accomplished by a brief burst of spikes in motor neurons to the trochanteral levator muscles that ensures that a mechanical lock between protrusions on the dorsal femora and ventral coxae are engaged (Burrows 2006b). The result is that both hind legs adopt a position with the femoro-tibial joints pointing anteriorly and tucked between the abdomen dorsally and the middle legs ventrally. Second is a *cocked phase* in which the hind legs remain motionless for almost 3 s, whereas the trochanteral depressor muscles contract continuously. Motor neurons generating large potentials in these muscles spike continuously at a frequency that gradually rises to 50 Hz toward the end of the phase. The spikes to the left and right muscles are tightly coupled. Motor spikes in the levator muscle are sporadic during this phase and follow no distinctive pattern in different jumps. Third is the *jump phase* in which the trochantera of both legs are suddenly and rapidly depressed and the tibiae extended about the femora. The motor spikes to the depressor muscle stop and the resulting movement is completed in <1 ms.

The motor pattern recorded from the muscles is directly reflected in the movements of the hind legs. The speed with which the legs are moved into their cocked position is related...
powerful thrust applied to the trochantera. In that the extension of the tibiae may be the passive result of the extensor tibiae muscles. This suggests the extensor tibiae muscles are much smaller and are even smaller of the space within the metathoracic cavity. By contrast, the trochanteral depressor muscles are enormous and occupy most rapid depression of both hind trochantera about the coxae, Muscles feedback loop would take much longer.

FIG. 9. Synchrony of spikes in the left and right trochanteral depressor muscles of the hind legs of Aphrophora. A: section of a recording from the 2 muscles during the cocked phase of a jump. Spikes occurred simultaneously in both muscles. B: spikes in the left muscle were used to trigger the sweeps when they reach a selected level, and the sweeps were then overlaid. All 174 spikes during the 4.9 s of the cocked phase were synchronous on the 2 sides. C: section of a recording from a prolonged cocked phase of the hind legs that subsequently did not result in a jump. A single spike was not matched on the 2 sides. D: all but this one spike (arrow) of the 1,176 spikes during a period of 27 s were exactly matched. E: independent spike activity in the 2 muscles during rapid but independent fast movements of the left and right hind legs.

to the frequency of motor spikes and the duration of the burst in the levator muscle. The jump does not occur unless the hind legs have been fully cocked. Similarly the duration of the cocked phase is determined by the duration of the continuous stream of spikes in depressor motor neurons. The jump does not occur until spikes in the depressor have stopped. No jumps were observed in which the depressor spikes continued into the jump phase of the movement itself, as would be expected if the spikes were curtailed by proprioceptive feedback resulting from the depression movement itself. The jump movement is complete in <1 ms; the flow of sensory information in a feedback loop would take much longer.

Muscles

The main propulsive force for a jump phase comes from the rapid depression of both hind trochantera about the coxae, accompanied by extension of the tibiae about the femora. The trochanteral depressor muscles are enormous and occupy most of the space within the metathoracic cavity. By contrast, the extensor tibiae muscles are much smaller and are even smaller than their antagonists, the flexor tibiae muscles. This suggests that the extension of the tibiae may be the passive result of the powerful thrust applied to the trochantera. In Philaenus the mass of the trochanteral depressor muscles represents almost 12% of the body mass. This huge investment in jumping muscles (locusts invest only half as much; Bennet-Clark 1976) enables froghoppers to perform jumps that are exceptional relative to their body mass with a power output of ≈74 W/g muscle.

Each trochanteral muscle is complex both in the attachments of its four parts to different parts of the skeleton, in the arrangement of their constituent fibers, and in their insertions on the large and elaborate depressor tendon. The two largest parts in the thorax (b and c) would seem to be responsible for generating most of the force. The most lateral part (b) consists of pinnately arranged fibers inserted onto a thin lateral arm of the tendon and the bulkier more medial part (c) consists of many parallel fibers that insert on the main body of the tendon. Recordings during a jump from electrodes placed in these two parts of the muscle are dominated by the spikes of what appears to be the same motor neuron. A contribution of different motor neurons was not revealed. The parallel arrangement of the fibers in one part and the pinnate arrangement in the other, however, suggests a different contribution to the force that is generated.

Recordings have not revealed whether the two smaller parts (a and d) of the depressor muscle have independent actions during a jump and evidence may be hard to obtain in this way because of the surrounding activity of the very much larger parts of the depressor muscle. Instead, anatomical studies presently under way of the neurons innervating the depressor muscle should indicate whether the different parts of the muscle are separately innervated and thus whether they could act independently. The small mass relative to that of the whole muscle and the different attachments and insertions of these two parts of the muscle suggest that their primary action is not to add appreciably to the overall force. Instead, their role may be to stabilize the tendon during the massive forces generated by the other larger parts of the muscle, to influence the line of action of the tendon or, perhaps, to provide some efferent control of as yet unknown proprioceptors monitoring the buildup of the large forces.

Energy storage

The energy developed by the prolonged contractions of the trochanteral depressor muscles in advance of the jump must be stored in such a way that it can be delivered rapidly to power the rapid movements of the legs. Previous reports (Gorb 2004; Rothschild et al. 1975; Sander 1957) indicated the presence of resilin in the metathoracic skeleton. In addition, some thoracic skeletal elements of the metathorax, such as the pleural folds, are also much larger than in the other thoracic segments. Contraction of the trochanteral depressor muscles would therefore distort the thoracic cuticle enabling energy to be stored in the highly elastic resilin. There do not appear to be any energy-storage devices at the femoro-tibial joints equivalent to the semilunar processes of locusts (Bennet-Clark 1975; Burrows and Morris 2001).

Release and triggering

The slow but powerful contraction of the trochanteral depressor muscles during the cocked phase of a jump does not produce any movement of the coxo-trochanteral joints that they control, so that the hind legs remain stationary. What prevents movement of a hind leg?

A possible mechanism would be a cocontraction of the trochanteral depressor and levator muscles. The recordings do not, however, show a consistent pattern to the sporadic activity of the levator muscles and there is no sustained activity to indicate that a cocontraction is responsible. Thus froghoppers are not using the same mechanism as in locusts, in which a
cocontraction enables the small flexor tibiae to restrain the powerful contraction of the extensor tibiae muscle, thus allowing stored force to be delivered suddenly in a jump when its motor neurons are inhibited (Burrows 1995; Heitler and Burrows 1977).

Could differences in the lever arms of the depressor and levator muscles be an adequate explanation? In the fully elevated and cocked position, the lever arm of the depressor muscle is at its smallest (Burrows 2006b). It comes close to the pivot of the joint but direct observation shows that it apparently does not go over center as previously claimed from models of its action (Gorb 2004). In this position the force developed by the depressor muscle would require the least restraint to prevent it extending the hind leg. Residual tension in the levator lingering from the preceding levation phase seems unlikely to suffice because the cocked phase can last several seconds and would need to be reinforced by an active contraction of the levator under direct motor control. This is at best sporadic during the cocked phase.

Restraint could also be provided by the mechanical engagement of the femoral and coxal protrusions of a hind leg (Burrows 2006b). A combination of some residual tension in the levator, the weak lever arm of the depressor tendon, and the engagement of the femur and coxa might be sufficient to prevent depression until sufficient force is generated that would allow all the stored energy to be delivered suddenly. Additionally the small parts of the depressor muscle may contribute. It was previously suggested (Gorb 2004) that the small part of the depressor (133a) that lies entirely within the coxa can bend the tendon, thus moving it from being overcenter to a point when it will have a positive mechanical advantage. There are two problems with this suggestion. First, the depressor tendon is hard and does not bend. Second, the tendon does not appear to go over center when a hind leg is cocked. Nevertheless, contraction of this part of the muscle might be able to improve the mechanical advantage of the tendon if it were capable of moving the tendon medially under the huge force applied axially by the thoracic parts (b, c) of the muscle. Whatever the mechanism of release it must operate with an accuracy of \( \frac{1}{10^2} \) ms to ensure that both hind legs move at the same time to propel the insect directly forward.

A few recordings show a burst of muscle activity at the time of the jump. Some of this appears to result from movement artifacts associated with the powerful contractions of the depressor and the rapidity of the jump movement. Moreover, the timing of this activity is variable and begins on average only 5.5 ms before the rapid jump movement. A skeletal muscle of an insect, such as the locust extensor tibiae, takes some 50 ms to reach peak tension in a twitch contraction (Hoyle and Burrows 1973). A locust flight muscle has a rise time to twitch tension of 14 ms (Neville and Weis-Fogh 1963) and even the fast muscle used by katydids in singing has a rise time of 7 ms, falling only when body temperature is raised by a warm-up period (Josephson 1973). The fastest vertebrate muscles, such as those used to move the rattle in rattle snakes (Schaeffer et al. 1996) or the syrinx in doves (Eleman et al. 2004), have twitch half times of 10 ms. This suggests that in froghoppers the possible activation of a muscle by a burst of spikes at the times recorded would be too late to develop a force that could influence the timing of the rapid jump movement.

Synchronization of both hind legs

When using their hind legs to propel jumping animals must synchronize the movements of both legs. In locusts the synchronization between both hind legs is no better than a few milliseconds but can be tolerated because it takes 30 ms to accelerate the body to take-off (Bennet-Clark 1975; Brown 1967). Froghoppers accelerate their bodies in \(<1\) ms (Burrows 2003; Burrows 2006a) so have a much smaller tolerance. There are two possible mechanisms for simultaneous release of the hind legs. First, a trigger muscle on each side might be responsible (Gronenberg 1996), as previously suggested for fleas (Bennet-Clark and Lucey 1967) and froghoppers (Gorb 2004). For this mechanism to work, the necessary forces must be produced within 1 ms on each side. Second, the forces developed by the depressor muscles could reach levels that overcome resistance to depression. Again this must be achieved within 1 ms of each other on the two sides. Both mechanisms would require tolerances that would challenge the biological control mechanisms. A simpler mechanism might be a mechanical linkage between the two hind legs such that a movement of one leg would directly trigger a similar movement of the other hind leg. The linkage between the medial walls of the coxae provided by microtrichial fields has been proposed as a mechanism synchronizing jumping (Gorb 2001, 2004), but the coxae are not responsible for delivering the force that generates a jump. Other parts of the hind legs of froghoppers do not touch, so that a mechanical coupling would have to result from distortions of the thorax caused by the powerful contractions of the depressor muscles. A movement of one hind leg would therefore trigger a closely synchronized movement of the other hind leg.

Synchronization of depressor spikes

The motor spikes in the left and right trochanteral depressor muscles are tightly coupled during the cocked phase of a jump but can act independently when one hind leg moves quickly on its own. During a jump, the spikes occur in the two muscles without any detectable time difference between the two; moreover, coupling is so strong that during many seconds of spiking at frequencies \( \leq 50 \) Hz all spikes on one side can be accompanied by synchronous spikes on the other. Occasional spikes are missed on one side and together with complete independence during movements by a single hind leg, provide strong evidence that the synchronous spikes do not result from cross talk in the recordings. This degree of synchrony between motor spikes is rare even for motor neurons innervating the same muscle and is not reported for motor neurons to different sides of the body. What mechanisms could explain this synchrony?

First, common motor neurons with bifurcating axons could innervate the left and right depressor muscles, as in the thoracic spiracular closer muscles of the locust (Burrows 1978; Miller 1960). The two spiracular motor neurons with axons in the median nerve are driven by many common synaptic inputs so that their patterns of spikes are similar but not synchronous (Burrows 1978). By contrast, the trochanteral depressor muscles of froghoppers are innervated by lateral nerves so it is likely that each side of the body is innervated by different motor neurons. The only efferent neurons that have axons innervating muscles on both sides of the body are the dorsal
unpaired median (DUM) neurons (Plotnikova 1969) that release octopamine to effect various changes at the presynaptic terminals of the motor neurons or on the muscle fibers (Evans and O’Shea 1977; O’Shea and Evans 1979). No evidence indicates that they release a fast-activating transmitter that could cause contraction of muscle fibers.

Second, independent motor neurons to the left and right sides could be electrically coupled so that a spike to one side is reliably reflected by a spike to the other side. The left and right lateral giant fibers of crayfish are coupled in this way (Watanabe and Grundfest 1961), thus ensuring symmetrical movements of the abdomen in tail flips. The branches of the left and right motor neurons would have to overlap so that electrical junctions could occur. Most insect motor neurons have neurites on only one side of a ganglion so that direct synaptic connections are not possible, but there are some rare exceptions (Tyrer 1983). Both the first and second mechanisms require that spikes to one side can be gated to allow the occasional failures and the independence of action when one leg alone moves.

Third, independent motor neurons to the left and right sides could be driven by common synaptic inputs from the same set of presynaptic interneurons. This form of control is widespread, particularly for motor neurons that innervate the same muscle (Burrows 1975, 1980; Burrows and Horridge 1974). Common synaptic inputs drive membrane potentials toward a similar probability of spiking, but the different properties of the individual motor neurons mean that spikes are not tightly coupled. Existing examples of this type of coupling thus do not show the sort of synchrony between spikes that occur in the froggopher depressor muscles. To achieve the level of synchrony observed, the common synaptic drive would have to be both powerful and itself synchronous, thus pushing the explanation to an earlier stage in the central processing.

To resolve the mechanisms underlying the bilateral synchrony of these motor spikes, it will be necessary to stain the motor neurons to reveal their structure and then to record from them to reveal the physiological basis of any coupling between them.

Acknowledgments

The author thanks Cambridge colleagues for many helpful suggestions during the course of this work and for comments on the manuscript. I am particularly grateful to B. Hedwig for suggesting and then helping to make the photoelectric method for recording leg movements during a jump. I am also most grateful to D. Crick of CED (Cambridge) for providing the scripts that made possible the analysis and display of the coupling between depressor motor spikes.

References
