THE WIND-EVOKED ESCAPE BEHAVIOR OF THE CRICKET *GRYLLUS BIMACULATUS*: INTEGRATION OF BEHAVIORAL ELEMENTS

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Summary

The wind-evoked escape behavior of freely ranging crickets (*Gryllus bimaculatus*) was studied using high-speed video and film analysis. The escape response can be of three types: a turn, a jump or a turn + jump. Any of these can be followed by running.

The turn is similar to that of the cockroach, in terms of the details of body and leg movements. A jump occurs only when the cricket has its back to the wind, either because the stimulus came approximately from behind or because the cricket had first turned away from the wind and then jumped.

The jump, like that of locust, requires some form of energy storage and quick release to obtain the necessary power. Locusts use long-term co-activation of antagonistic leg motor neurons to produce mechanical energy storage. By contrast, crickets do not appear to co-activate antagonistic leg motor neurons. Possible alternative energy storage and release mechanisms are discussed.

Key words: cricket, escape behavior, jump, locust, *Gryllus bimaculatus*.

Introduction

The mechanisms of escape behavior in orthopteroid insects, such as the cockroach, locust and cricket, have been extensively studied over the past 30 years (Camhi, 1993; Ritzmann, 1993; Heitler, 1974; Pearson, 1982; Miller *et al.* 1991; Gras and Hörner, 1992). Several orthopteroids show an evasive locomotory response to wind stimuli, which are detected by filiform hair receptors on the cerci, consisting of two caudal antenna-like appendages.

Cockroaches, for instance, detect weak air displacement such as that caused by an approaching predator and respond by turning away and running rapidly (Camhi and Tom, 1978; Camhi *et al.* 1978). The wind-activated cercal receptors excite a group of giant interneurons (GIs) that are important mediators of the turn (Comer, 1985; Levi and Camhi, 1994; Kolton and Camhi, 1995; Liebenthal *et al.* 1994). The mean behavioral latency can range from 14 to 58 ms, depending on the cockroach's behavior at the time of stimulation (Camhi and Tom, 1978; Camhi and Nolen, 1981).

Locusts, which cannot run quickly, escape by means of a very impressive jump; vaults up to 80 cm high are common (Hoyle, 1955; Bennet-Clark, 1975). It is unclear whether a wind stimulus by itself can evoke a jump, and such stimuli are not known to induce an evasive turn. Correspondingly, the locust's cerci are considerably less developed than those of the cockroach. Other threatening stimuli, most notably visual, can

trigger a jump. But, the jump occurs only after a very long latency (200–500 ms), during which specific movements of the hind legs prepare for the impulsive leg extension (Heitler and Burrows, 1977; Pearson, 1982).

Crickets, the subject of the present study, have features in common with both the cockroach and the locust. Like cockroaches, they are fast runners and have well-developed cerci, which are covered with filiform hairs that excite giant interneurons (Edwards and Palka, 1974; Walthall and Murphey, 1986; Miller *et al.* 1991; Theunissen and Miller, 1991). Moreover, in response to a wind stimulus, crickets initially turn away with a short latency (Stabel *et al.* 1985; Olberg and Miller, 1991; Gras and Hörner, 1992; Gras *et al.* 1994). However, crickets also have good jumping hind legs that resemble those of a locust much more than those of a cockroach (Fig. 1).

By examining the wind-evoked escape behavior of crickets, we show that it incorporates elements of turning, jumping and running. Their escape movements thus constitute a complex, highly integrated behavioral program. We also examine the kinematics, and to some extent the mechanics, of both the turn and the jump. We compare the cricket's turn with that of the cockroach, in which the initial turn involves highly specialized movements, with at least five of the six legs pushing simultaneously against the
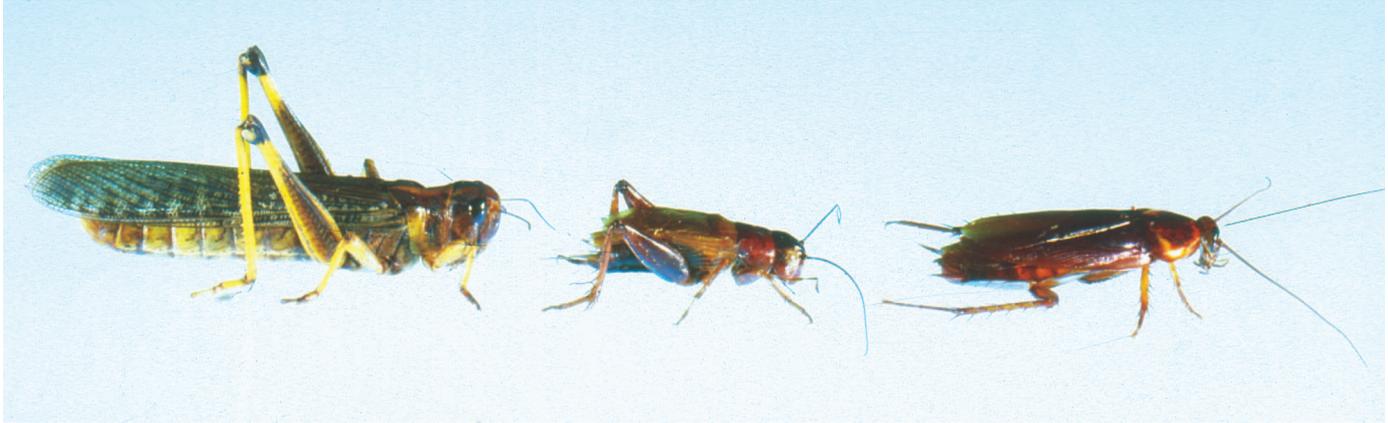
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Fig. 1. Three orthopteroid insects, all adults. Left, the locust *Locusta migratoria*; middle, the cricket *Gryllus bimaculatus*; right, the cockroach *Periplaneta americana*. The hinds legs of the locust and cricket, designed for jumping, are clearly different from those of the cockroach, which are designed for running.

ground, an action different from that used in running (Camhi and Levy, 1988). Specifically, the two pairs of front and middle legs of the cockroach move in the medial–lateral axis in the same direction, while the hind leg on the inside of the turn remains on the ground as a pivot. The overall result is a pure rotation of the body, which pivots about a point near its posterior end. We find that the cricket's escape turn is remarkably similar.

We compare the cricket's jump with that of the locust. The locust's impressive jump requires that mechanical energy be developed at a much higher rate than can be provided by the contraction of its leg muscles (Hoyle, 1955; Heitler, 1974; Bennet-Clark, 1975). To achieve this, antagonistic muscles co-contract at the femorotibial joint of each hind leg, and energy is stored in the elasticity of skeletal elements. The large, fast motor units of the antagonistic muscles are thus simultaneously activated. It is this co-contraction period that requires the 200–500 ms pre-jump delay. The stored energy is suddenly released when the femoral flexor muscle is inhibited, resulting in rapid extension (Bennet-Clark, 1975; Heitler and Burrows, 1977).

The jump of the cricket *Gryllus bimaculatus* is not as remarkable as that of the locust and does not involve a long preparatory delay. We show that there is no co-activation, at least of the large, fast motor units, of the antagonistic leg muscles. The cricket does, however, appear to use an energy-storage mechanism to produce its jump.

Materials and methods

We used adult crickets (*Gryllus bimaculatus* de Geer) of both sexes from our laboratory culture. This same species has been used in one previous study of cricket escape behavior (Gras and Hörner, 1992). The other studies used *Acheta domesticus* (Stabel *et al.* 1985; Olberg and Miller, 1991). We raised the crickets at 30–31 °C on a 12 h:12 h L:D cycle. We fed them rat chow, cabbage and water *ad libitum*. We also carried out a few tests on adult locusts, male and female

Locusta migratoria and male *Schistocerca gregaria*, both *phasis gregaria*.

The arena for behavioral testing has been described before (Camhi and Levy, 1988). Briefly, crickets walked freely within an enclosed circular arena, 1 m in diameter, whose surface we roughened with a mixture of sand and water-based paint, to increase friction. We performed the experiments during the dark half of the crickets' photoperiod, under the illumination of three 75 W lamps. We placed 1–4 crickets at a time in the arena and permitted them 15 min to become accustomed to the environment. Then, if a cricket entered a specified rectangular region in the center of the arena, measuring 17 cm×7 cm, we presented a wind stimulus.

The wind stimulus was produced by a motor that depressed a plastic sheet, which closed off one end of a wind channel. This end of the channel, which was rectangular in cross section, measured 25 cm×30 cm. This resulted in an air puff being expelled from the channel's opposite, open end, which was a slit 2 cm high and 25 cm wide (Fig. 2A). The wind channel was fixed at a downward slanting angle of 45 ° relative to horizontal.

The wind stimulus within the specified rectangular region, measured at the same height above the platform as the cricket's cerci, had an air speed that increased, over a period of approximately 200 ms, to a peak of $2.3 \, \text{m s}^{-1}$ (Fig. 2B). This is very similar to the stimulus previously used in this laboratory to study cockroach escape behavior (Camhi and Levy, 1988). We measured the wind speed using a hot-wire anemometer with a frequency response of approximately 0–100 Hz (Datametrics VTP 800, Watertown, MA, USA). The wind signals were highly laminar, at least for the first 150 ms, which included the onset time of the behavioral response. During experiments, we monitored the wind signal using the same type of anemometer, by placing its miniature probe inside the wind channel. Our recordings of the cricket's behavior included this anemometer readout.

We calibrated the interval from the onset of the wind puff inside the channel to its onset at the cricket's position, and
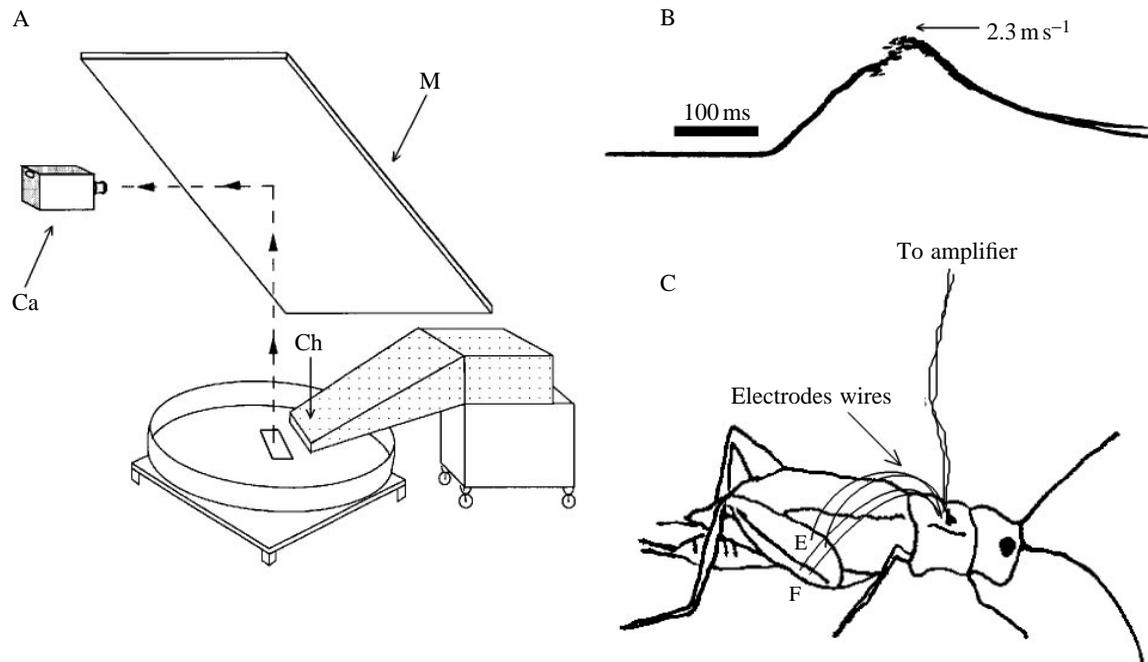
Fig. 2. The experimental set-up. (A) Arrangement of the behavioral testing arena. Ca, camera; M, mirror; Ch, wind channel. The rectangle in the center of the arena is the region within which the cricket was located at the time of the stimulus. Not drawn to scale. (B) The wind stimulus: seven superimposed recordings with a hot-wire anemometer from within the rectangle shown in A at cercus level (5 mm) above the ground. (C) Arrangement of EMG electrodes. F, flexor muscle electrodes; E, extensor muscle electrodes.

found it to be less than 1 ms. This is to be expected, though at first sight it might not seem so. Even at our peak wind speed of $2.3 \, m \, s^{-1}$, for any given air molecule to move from our anemometer inside the wind channel, to the cricket (a distance of about 23 cm) would take about 100 ms. However, the time difference of onset, at two different locations, of air displacement caused by a moving object is not determined by the wind speed, but approximates the speed of sound, $330 \, m \, s^{-1}$. (It is like the near-field component of sound produced by a single, outward movement of a speaker's membrane.) This would give an interval, from wind onset at our anemometer to its arrival at the cricket, of less than 1 ms, which corresponds with our measured interval. Given this small time interval, we used the anemometer inside the wind channel, recorded at very high gain, to determine the moment when the wind first arrived at the cricket. The error of this measurement was no greater than 4 ms based on the filming speed (see below). In contrast, the upper limit of the anemometer's frequency output did not contribute significantly to the measurement error of wind onset time; its output, recorded at high gain, was subject to an error of probably well under 1 ms.

We recorded the behavior of free-ranging crickets using a Locam cine camera (Redlake Corp., Santa Clara, CA, USA) operated at $250-350 \, frames \, s^{-1}$. We filmed the image reflected from a mirror above the behavioral arena, oriented downwards at $45°$. We then projected the film frame-by-frame onto a digitizing pad (Hipad, Houston Instruments, Austin, TX, USA). For each frame, we digitized the positions of the six tarsi, the front edge of the head at its midline and the rear edge of the abdomen at its midline. These digitized data provided the basis for the following behavioral measures, plotted as a function of time: (1) body angle relative to the direction of the wind stimulus; (2) whether each tarsus moved, during a given inter-frame interval, relative to the ground (indicating whether this leg was in its swing or stance phase); and (3) the medial–lateral and the anterior–posterior position of each tarsus relative to the body. The calculated tarsal positions were normalized to body length, permitting comparison among animals.

We analyzed only those trials which met the following criteria: (1) the cricket's cerci were within the specific rectangular region of the platform at the time when the wind arrived; and (2) all six tarsi were clearly visible on the film. Out of 167 stimuli, the crickets gave a total of 80 behavioral responses, of which 46 (in 27 crickets) fulfilled the above criteria. Our data are thus based on these 46 responses.

In some experiments, we recorded electromyograms (EMGs) from hind-leg muscles in response to the same wind stimuli. For these data, we recorded the behavior with a high-speed video camera (NAC, Tokyo) operated at $250 \, frames \, s^{-1}$. We projected the EMG recording onto the video monitor, using a wave inserter (NAC). We recorded the EMGs from the extensor and flexor tibiae muscles of one hind leg. The recording electrodes for each muscle were a pair of $50 \, \mu m$ diameter copper wires, insulated except at their tips. A 25 cm length of these wires led upwards from the cricket to a holder (Fig. 2C). This permitted the animal a walking range of roughly 18 cm radius on the platform, which included the rectangular stimulation region. The load introduced by the

electrodes and their leads did not exceed 10 % of the cricket's body mass.

In restrained crickets, we inserted the EMG electrodes just under the cuticular surface, in the thick region of the femur. We amplified the EMG recordings with RC-coupled amplifiers (Grass P-15) and stored the data on a video recorder (Neurocorder DR-886), which had a frequency response of 0–20 kHz. We analyzed these data using the software package Computerscope (R. C. Electronics, Santa Barbara, CA, USA).

For statistical comparisons of leg movements in different experimental groups, we used a method we have developed previously (Levi and Camhi, 1994). Specifically, for a given experimental group, we plotted the direction and distance of the initial movement of a given leg on each trial. Using the program JUMP on a Macintosh Quadra computer, we calculated, on the assumption of a normal distribution of points, three ellipses: an outer ellipse that would statistically include 95 % of all the data points; a middle one that would include 50 %; and an inner one that would include 20 %. This was done for each leg. Next, we assigned a score to each data point: 3 for each point that fell in the central ellipse, 2 for each falling in the middle ellipse, 1 for each in the outer ellipse and 0 for each point outside the outer ellipse. We carried out the above procedure initially on one group of crickets. We then superimposed the three ellipses from each leg of this initial group of crickets onto the data from a second group of animals that we wished to compare with the initial group. For both the initial and the second group of animals, we scored each movement of each leg. Finally, we compared, for each leg, the scores of the initial group with those of the second group of animals, using a Mann–Whitney *U*-test.

Results

Stimulus–response relationships in cricket escape behavior

Escape behavior fell into the following three categories. (1) *Turn response* (Fig. 3A). The cricket turned away from the wind puff without jumping; that is, at least one leg remained on the ground at all times. The turn involved a pivot roughly about the rear end of the body, as in cockroaches. This cockroach-like escape occurred in 16 of the 46 wind-evoked responses. The mean latency to the onset of the body turn was 87±56 ms (s.d.), considerably longer than for the cockroach (14–58 ms, depending on the experimental situation; Camhi and Tom, 1978; Camhi and Nolen, 1981). (2) *Jump response* (Fig. 3B). The cricket jumped without taking any prior steps. That is, all its legs left the ground. This locust-like escape behavior occurred in 6 of the 46 responses. The mean latency to the onset of the power stroke of the hind legs was 94±51 ms. (3) *Turn + jump response* (Fig. 3C). The cricket first turned, taking at least one step in doing so, and then jumped. This type of escape, not seen in cockroaches or locusts, was the most common, occurring in 24 of the 46 trials analyzed. The mean latency from wind onset to the onset of the body turn was 52±42 ms, and from wind onset to the onset of the hind legs' power stroke the mean latency was 191±33 ms. Given the wide
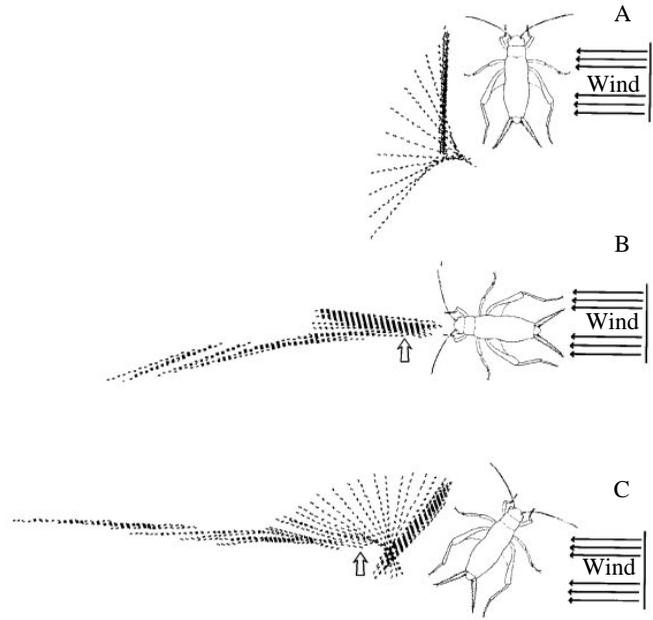

Fig. 3. Three representative escape responses of the cricket *Gryllus bimaculatus* to a wind stimulus. Dashed lines represent the body axis at 4 ms intervals. (A) Turn response (cockroach-type escape). (B) Jump response with no prior turning (locust-type jump). (C) Turn + jump response (a type not seen in cockroaches or locusts). Open arrows in B and C point to the position of the rear of the abdomen at the initiation of the jump (i.e. at the beginning of the power stroke of the hind legs). Each example shows the first 100 ms of the response. Each response type was often followed by running (not shown).

range of latency values within each type of escape behavior, there were no significant differences among the latencies of the three categories (ANOVA).

The angle of turn is plotted as a function of the initial stimulus direction in Fig. 4A, for all three types of response. Turn angle is highly correlated with stimulus direction ($r=-0.68$; $P<0.01$). Since this correlation could result from a simple left–right discrimination by the cricket, we recalculated the correlation in a way that eliminates this left–right discrimination from the analysis. Taking the data shown in Fig. 4A, we first multiplied both the *x*- and the *y*-values of points from turns in response to wind stimuli from the left (all points in the left half of Fig. 4A) by −1. As a result, all turns away from the side of the wind stimulus appeared in the bottom right-hand quadrant and all 'wrong turns', towards the wind stimulus, appeared in the upper right-hand quadrant. Turn angle was still highly correlated with stimulus direction ($r=-0.39$, $P<0.01$). Thus, the cricket discriminates not just wind from the left *versus* wind from the right, but also wind from near the front *versus* wind from near the rear.

The absolute values of the mean stimulus angles that evoked, respectively, turns, turn + jumps and jumps, were 144±27 ° (*N*=16), 123±32 ° (*N*=24) and 58±32 ° (*N*=6), respectively. The difference between the stimulus angles for jump and for the other two categories was highly significant ($P<0.001$, Mann–Whitney *U*-test), and between turns and turn

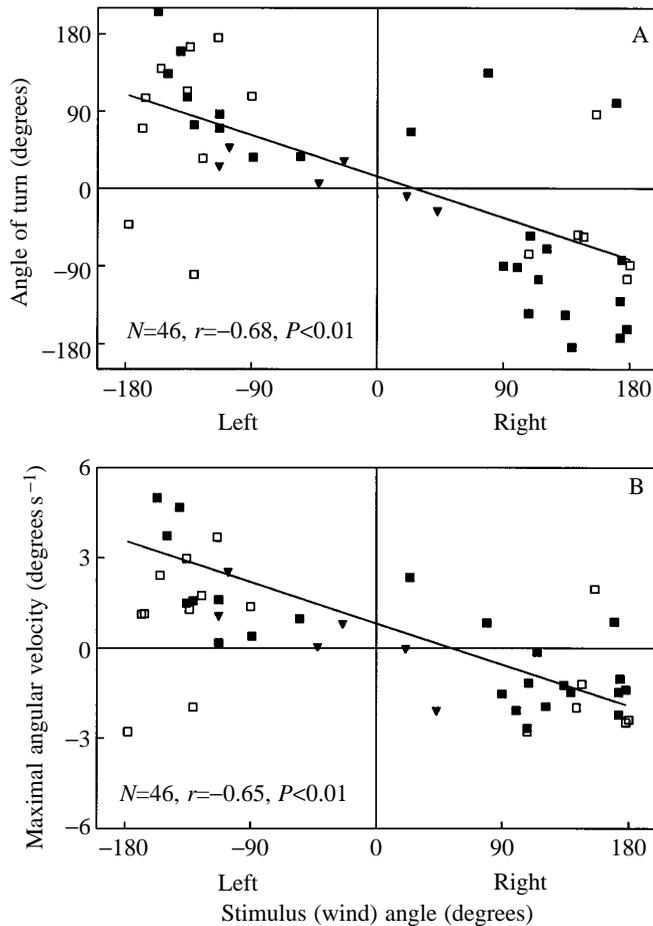Fig. 4. Directionality of escape behavior. (A) Angle of turns *versus* stimulus angle. A stimulus of 0° represents a wind stimulus from behind, and −180° or +180° represent wind from the front. A turn angle of 0° represents straight forward movement, and of + or −180° represents a 180° turn to the right or left, respectively. Open squares, turn responses; filled squares, turn + jump responses; triangles, jump responses. In the case of jump or turn + jump responses, any turning occurring during take-off was included in the measurement, and any turning occurring during the jump itself was included until the animal left the field of view of the camera. (B) Maximal angular velocity *versus* stimulus angle. Same format as in A. Both angle of turn and maximum angular velocity are highly correlated with stimulus direction.
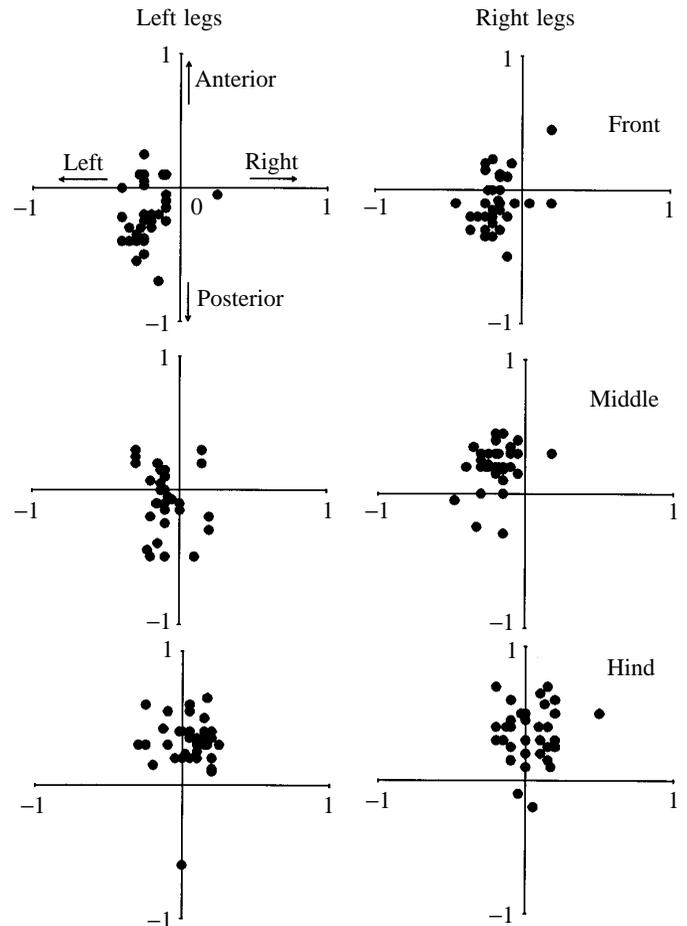

Fig. 5. Initial movement of each leg, relative to the body, in right turns (left turns have been mirror-reversed). For each plot, the point (0,0) represents the initial position of the leg on each trial. Each point is for a separate recording.

+ jumps was marginally below significance level (*P*=0.06). Thus, the probability of evoking a jump tends to decrease as the wind angle increases (i.e. becomes more frontal).

We also determined angular velocity using frame-by-frame analysis. Fig. 4B, which plots the maximal angular velocity achieved on each trial *versus* stimulus direction, shows a highly significant correlation (*P*<0.01).

Mechanics of the turn

The behavioral response to a wind stimulus usually began not with turning movements of the body, but rather with a simultaneous forward swing of both hind legs, caused largely by a closing of the femorotibial joint, as though in preparation for a jump. This closing occurred in 35 of the 40 turn and turn + jump trials, but was not followed by a jump. Rather, the tarsi of the two hind legs were placed on the ground, after which all six legs usually remained on the ground during the initial 8–16 ms of the turn (30 of 40 trials).

We analyzed in detail the first movement of each leg from the moment the turn began. Lasting only 8–16 ms, these initial leg movements were probably executed in an open-loop manner. Fig. 5 summarizes the direction of initial movement of each leg relative to the body, starting at the onset of the turn. The (0,0) position for each leg in this figure represents the leg's initial position on each trial, and a given point represents the position where the movement ended, relative to the body, on a given trial. The turns are all to the right (i.e. left turns have been mirror-reversed for this figure). Thus, a leg that moves to the left relative to the body would contribute to producing such a right turn.

Although the variation among the trials is quite large, the following generalizations can be made. For the front and middle pairs of legs (hereafter called the T1 and T2 legs, respectively), the movement is consistently directed to the left,

with left legs moving laterally and right legs medially. The anterior–posterior component of the movements in these two pairs of legs is less consistent, although the left T1 and T2 legs generally moved backwards and the right T2 leg generally moved forwards. In contrast, the hind (T3) legs moved consistently forwards, either medially or laterally. This refers not to the initial forward swing movement of the hind legs that preceded the turn, but to the movements of these legs from the moment the turn began. Since the legs push against the ground in their stance phase, they would move the body in the opposite direction. Thus, body torque to the right would be produced by the front and middle legs, whereas the hind legs appear not to produce body torque. This set of leg movements presumably accounts for the body's rotation about its rear end (Fig. 3A,C).

These initial leg movements of the cricket may be compared with those of an escaping cockroach, in response to a wind stimulus coming from roughly the same range of left–front directions (Camhi and Levy, 1988). Almost all legs moved in very similar directions in the two insects. For instance, in both species, the T1 and T2 legs all moved to the left, and the left T1 and T2 legs moved more posteriorly then their right homologs. Also, the right T3 leg moved forwards in both cases. The only consistent difference was that in the cricket the left T3 leg also moved forwards, whereas in the cockroach this leg was in a forward swing phase on about half the trials, and in a rightward and backward stance phase in the other half. We compared statistically the movements of all legs except the left T3 in turns of crickets with those of cockroaches from the two studies (see Materials and methods). There was no significant difference for any leg.

After the initial movement of each leg, subsequent movements varied substantially from trial to trial, and it was difficult to define a consistent pattern, with the exception of two features. First, during the time that the T1 and T2 legs took 2–3 steps, the T3 legs took only one step. Second, the T3 leg contralateral to the wind consistently initiated its swing phase before the ipsilateral T3 leg. Then, towards the end of the turn, the ipsilateral T3 leg also swung forwards. At this point, with both hind legs forward, a jump could be initiated (turn + jump trials).

A digression on the locust jump

Before describing the cricket's jump or turn + jump responses to a wind simulus, it is useful to consider the much better understood jump of the locust. It appears to be accepted that the locust jump is evoked by wind stimuli sensed by cercal receptors (Boyan *et al.* 1989; Pearson, 1982), although we are not aware of any specific study that showed this. We therefore carried out high-speed video recordings of the responses of nine adult locusts (*Locusta migratoria, phasis gregaria*; four males and five females) to the same wind stimuli that were used for the cricket.

In 61 out of 98 trials, the locust showed some movement response. By far the most common response was flexion of the hind legs into a position preparatory for a jump, but without producing a jump. Jumps occurred in only 10 trials. After 1 or
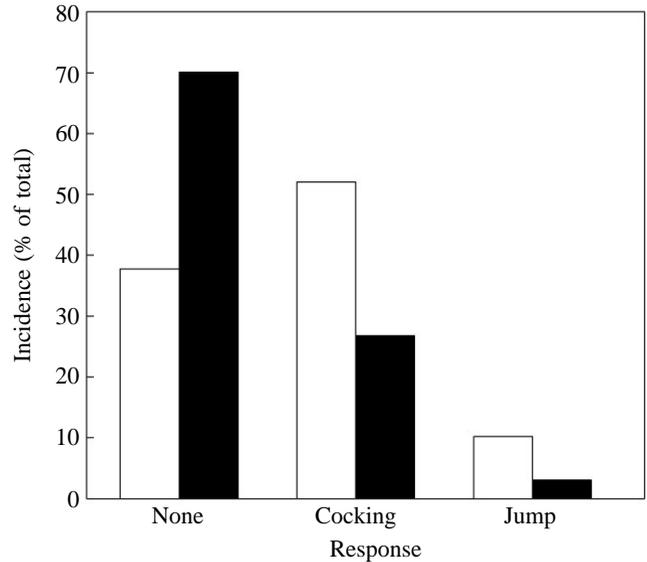

Fig. 6. Responses of *Locusta migratoria* to wind puffs. Incidence of hind leg flexion ('cocking'), jumping and no response, in intact locusts (open bars) and those whose cerci had been covered with Vaseline (shaded bars).

2 days, we covered both cerci of these same locusts with Vaseline and immediately retested them (Fig. 6). The rate of response was significantly decreased ($P<0.05$, Wilcoxon one-tailed test; $N=10$). In a separate group of nine locusts, we carried out identical procedures except that, as a control, we covered the pronotum, rather than the cerci, with Vaseline. The Vaseline treatment and associated handling of the animals did not significantly affect the percentage of animals responding or the type of response ($P=0.63$, Mann–Whitney U-test; $N=9$).

In all the jumping responses we obtained from all the locust groups described above (a total of 14 responses), the locusts jumped directly from their resting position, with no turning component. We also examined the responses of five adult males of a different locust, *Schistocerca gregaria, phasis gregaria*. In general, these were less sensitive to wind than *Locusta migratoria* and simply responded with hind leg flexion but no jumping responses. Thus, locusts do respond to cercal wind stimuli, although the incidence of jumping is much lower than in crickets and involves no turning.

The jump response of the cricket

We defined the cricket's behavior as a jump if all the legs were simultaneously in the air (i.e. it was moving relative to the ground between film frames). Whereas in adult locusts a jump usually leads to flight, this never occurred in the cricket, whose wings were never seen to open.

A jump began only when the cricket was oriented more or less away from the wind source. This may be seen by comparing Fig. 7A, depicting the angle of the body to the wind source at the start of all 46 responses, with Fig. 7B, depicting the angle of the body to the wind source at the moment of onset of all jumps.

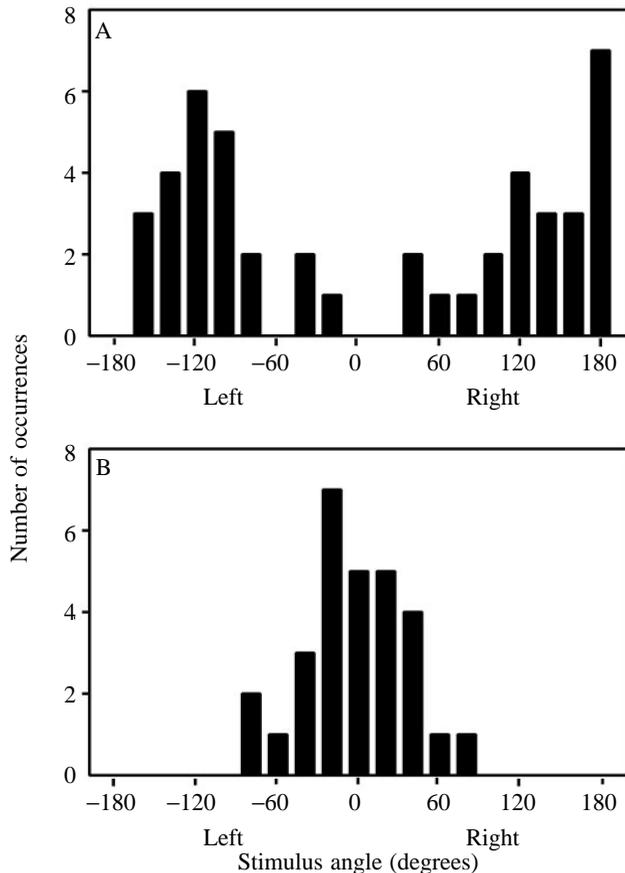The six jump responses all began with a preparatory stage

Fig. 7. Distribution of initial wind angles and wind angles at the moment of the jump. (A) Distribution of initial wind angles relative to the body. (B) Distribution of wind angles relative to the body at the moment that the jump began, in all jump and turn + jump trials. The cricket jumped only when the body was positioned with the wind from the rear ±90˚. If it was not so positioned initially, it first turned its body into this position.

in which the hind legs simultaneously moved forwards, bringing the tibia to full flexion. In the turn + jump responses, a similar hind leg flexion occurred as the outset of the movement response to the wind stimulus, but this did not lead to a jump. Rather, a second hind leg flexion occurring, as described above, at the end of the turn gave rise to the jump.

Fig. 8 summarizes the movements of all the legs relative to the body during jumping. In contrast to the turning depicted in Fig. 5, all six legs move backwards, with no clear medial–lateral preference. The movements of each leg during turns (Fig. 5) were significantly different from those during jumps (Fig. 8) ($P<0.05$, Mann–Whitney U-test; $N=26$–37, for each legs in each behavior).

We noted that the onset of the power strokes in the two hind legs were not necessarily synchronous. The mean time difference was 6 ± 11 ms (S.D.). Since all six legs are on the ground and moving backwards during take-off, presumably they all contribute force to the jump. However, in all the trials, the T1 and T2 legs became fully extended before the T3 legs, which then continued to extend, while on the ground, for a further
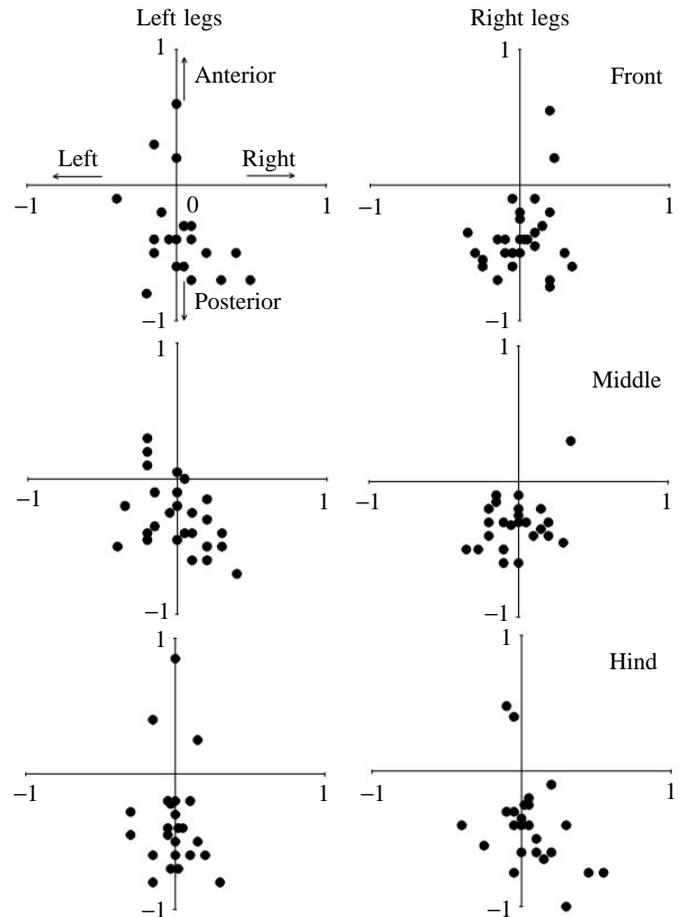

Fig. 8. Initial movement of each leg, relative to the body, in all jumps, from both jump responses and turn + jump responses. Same conventions as in Fig. 5. The movement of each leg was calculated from the moment that the first of the hind legs began its power stroke, till the end of each individual leg's own power stroke movement. Trials in which the wind stimulus was from the left are plotted directly, and those in which wind was from the right have been mirror-reversed. Almost all movements are backwards, with considerable medio-lateral scatter.

24–28 ms. Given their greater duration on the ground during take-off, and their larger size, the cricket's hind legs clearly supply more of the power for the jump than does either of the other leg pairs, as is the case in the locust (Bennet-Clark, 1975).

During the turn + jump response, although most of the rotation was produced before the take-off, some rotation could also be produced during the take-off. In 10 of these 24 trials, rotation was enhanced during take-off compared with that just beforehand. In 7 of these 10 trials, the enhanced turn was in the same direction as that before the jump (two such examples are shown in Fig. 9). Since the T3 legs left the ground last, they may be largely responsible for this enhanced rotation during take-off.

The energetics of cricket jumping

The remarkable jumping performance of the locust is achieved largely by special mechanical and neural mechanisms that store and suddenly release mechanical energy for the jump
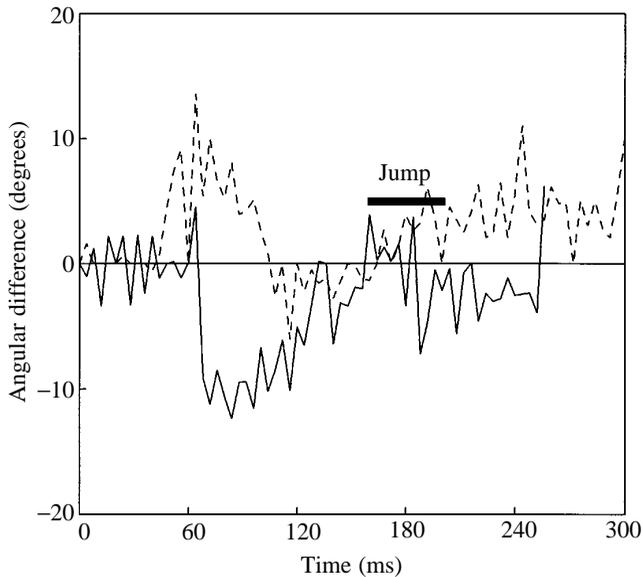
Fig. 9. Directional jumps. The frame-by-frame change in body angle is shown for two examples of turn + jump responses. Rotation almost ceased prior to the jump and then began anew with the onset of jumping. In these two trials, the re-initiation of turning was in the same direction as that prior to turning.

(Hoyle, 1955; Bennet-Clark, 1975; Heitler and Burrows, 1977). This energy-storage process occupies 0.2–0.5 s, during which the hind legs are cocked in the fully flexed position prior to take-off. In our observations, crickets have no such prolonged period of hind-leg flexion prior to the jump; instead, take-off begins immediately after the final flexion of the hind legs has been completed. Does the cricket, then, not require energy storage for its jump?

To test this, we recorded 20 jumps in eight crickets using the high-speed video camera with the insect facing perpendicular to the camera's line of sight. Jumps that occurred out of this plane were not analyzed. The optical distortion was less than 5 %. For each frame, we digitized the position of a fixed point on the pronotum, giving us the trajectory of the jump. We then weighed each animal, and dissected out and weighed its extensor tibiae muscles.

Fig. 10 plots position and velocity in the vertical direction against time for a single, typical jump. During take-off, the velocity increases to a peak, at which time the cricket leaves the ground, 28 ms after the start of the jump. By differentiating the velocity over time, we obtained the peak instantaneous acceleration for all jumps analyzed. We then calculated peak instantaneous force (after weighing the crickets), as the product of mass and peak acceleration, and peak power, as the product of peak force and peak velocity. Table 1 lists the mean values of these and other parameters and compares them with those calculated for a locust jump (Bennet-Clark, 1975).

The energy requirement of the jump can be estimated using the data of Table 1. A 12 cm jump by a 0.7 g cricket would utilize 0.82 mJ of kinetic energy. Assuming that most of the work is done by the hind leg extensor tibiae muscles, each
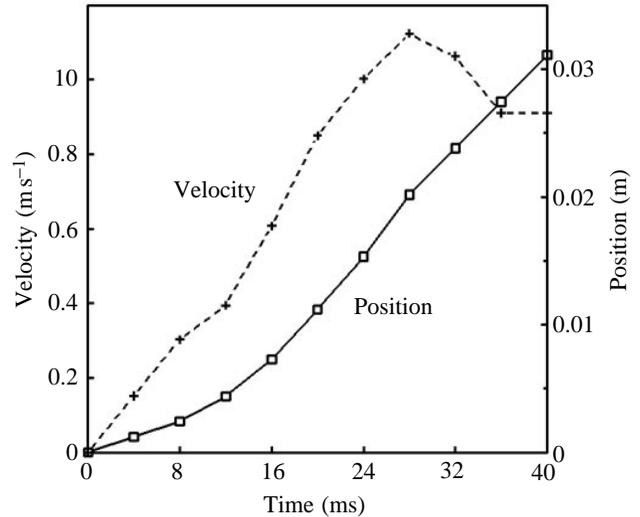

Fig. 10. Kinematics of the jump of *Gryllus bimaculatus*. The vertical position and velocity during a representative jump. See text for details.

Table 1. *Comparison of jump energetics between the cricket* Gryllus bimaculatus *and the locust* Schistocerca gregaria

	Cricket	Locust
Mass, female (g)	0.7±0.1	2.5–3.5
Height of jump (cm)	12±6	50–70
Peak force (N)	0.04±0.03	0.3
Peak power (W)	0.03±0.02	0.75
Muscle mass (mg)	9±4	70
Specific power (W g^{-1})	3.8±2.2	5.3

Values for the cricket are means ± S.D. (*N*=20 jumps in eight crickets).

Data for the locust are taken from Bennet-Clark (1975).

weighing 9 mg, each produces about 0.41 mJ, which amounts to 46 J kg^{-1}. Striated muscles of arthropods should be able to produce and store up to 175 J kg^{-1} (Bennet-Clark, 1975). Thus, these muscles can produce sufficient energy to account for the cricket's jump. The problem is delivering this energy sufficiently quickly; that is, delivering sufficient power.

The jumps of crickets are weaker than those of locusts in terms of both distance and force. Yet the jumping muscles (extensor tibiae of the hind legs) of crickets are much less massive than those of the locust. It is for this reason that the peak power production during the jump, divided by the mass of one hind-leg jump muscle (the specific power), is similar for the two species (3.8 *versus* 5.3 W g^{-1}).

The specific power (power/mass) produced by the locust's jump muscles, during tetanic stimulation, is 0.45 W g^{-1} (Bennet-Clark, 1975). This is roughly similar to that for numerous other muscles tested; e.g. 0.37 W g^{-1} for frog jump muscles (Lutz and Rome, 1994), 0.19 W g^{-1} for locust flight muscles (Neville, 1965) and 0.86 W g^{-1} for pigeon flight muscles (Pennycuick and Parker, 1966). But the specific power

of the locust's jump muscles is approximately ten times smaller than the maximal power production during its jump. The excess power during the jump is provided by its energy-storage and quick-release mechanism (Bennet-Clark, 1975). The cricket's jump also produces power that is approximately ten times greater than the specific power produced by the locust's jumping muscles during tetanic stimulation (3.8 *versus* 0.45 W g^{-1}). Though the comparable tetanic measurement has not been made for the cricket's jumping muscles, nothing about their general appearance suggests that they might produce ten times the power of the locust jumping muscles. This suggests, then, that the cricket also uses an energy-storage and quick-release mechanism. As seen in the next section, we have found evidence for such a mechanism.

EMG recording during the jump

Given that the cricket appears to require some energy-storage and release mechanism, and that one possibility would be co-excitation of the main power muscle for the jump (tibial extensor) and its antagonist (tibial flexor), we recorded EMGs from these muscles during the jump. Though we did not expect to find prolonged co-activation as in the locust, one possibility was to find a briefer period of co-activation. We analyzed 23 jumps in 18 crickets, from simultaneous recordings of the EMGs and behavior using the high-speed video camera. As seen in a sample recording (Fig. 11A), there is very little overlap between the activity of large flexor and large extensor units; instead, they alternate, as would occur in running. In all 23 jumps, there was a second flexor burst after the extensor burst had ended, as seen in Fig. 11.

During the entire initial flexor burst, there are small ripples on the extensor trace. These could represent activity in very small extensor units, but it seems more likely to us that this is cross-talk from the flexor muscle. It should be noted that very similar ripples occur in the extensor trace during the second flexor burst, at which time one would not necessarily expect flexor–extensor co-activation. (In fact, there are even larger ripples on the flexor trace during the extensor burst.) However, even if the extensor ripples during the first flexor burst are caused by small extensor units, it seems unlikely that these could be effective in bucking the simultaneous activity of the large flexor units. For comparison, in the locust, which is known to use flexor–extensor co-activation to prepare for a jump, the extensor activity that occurs simultaneously with that of the flexors consists of very large and clear EMG spikes (Heitler and Burrows, 1977; Pearson and Robertson, 1981).

The paucity of overlap between the initial flexor activity and the extensor activity is seen for all 23 trials in Fig. 11B. In 12 of the 23 trials, there was no overlap at all and in a further five trials there was just one extensor spike before the end of the flexor burst (as shown in Fig. 11A).

When we correlated the time of onset of flexion and extension movement of the legs with the contraction of the corresponding muscles, we found a significant difference for the two muscles (Figs 11A, 12). Whereas flexion begins close
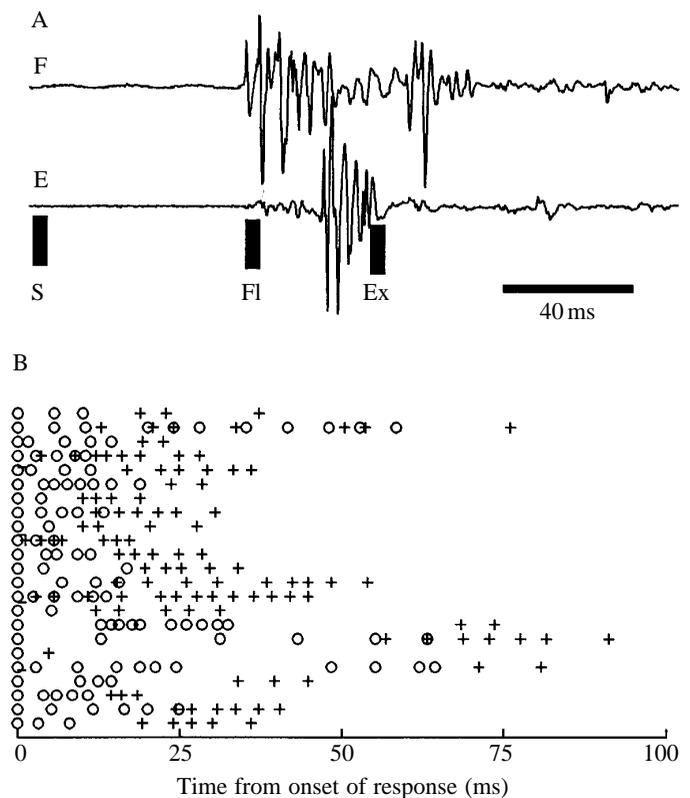

Fig. 11. EMG recordings from tibial flexor and extensor muscles of a hind leg during a jump. (A) A representative example. F, flexor recording; E, extensor recording; S, onset of wind stimulus; Fl, onset of joint flexion; Ex, onset of joint extension. (B) Raster display of flexor and extensor impulses that were clearly above the noise and cross-talk level, recorded from the hind legs in all 23 trials. Circles, flexor impulses; crosses, extensor impulses. There is very little overlap between the activity of the two muscles.

to the onset of flexor muscle activity, extension begins only towards the end of the extensor muscle burst. The mean delay from the onset of the burst of EMG activity in the flexor muscle to the start of joint flexion was 6.7 ms. By contrast, the corresponding parameter for the extensors was 15.8 ms, which was significantly different from that for flexion ($P<0.05$, Mann–Whitney U-test; $N=18$ for flexors, $N=23$ for extensors). In fact, in five of the 23 trials, the extensor burst had actually terminated before the onset of joint extension. These findings are compatible with some form of energy storage during most of the period of extensor muscle contraction, although simultaneous electrical activity in the flexor muscles is apparently not required for this storage mechanism.

Although, in approximately half the trials, the flexors showed no continuing EMG activity at the time of onset of the extensor burst, their contractile activity could well remain effective for tens of milliseconds after the end of electrical membrane activity. Thus, even though electrical co-activation is limited, co-contraction could be considerable and could contribute to energy storage. The subsequent relaxation of the flexors could then contribute to determining the moment of onset of the jump.
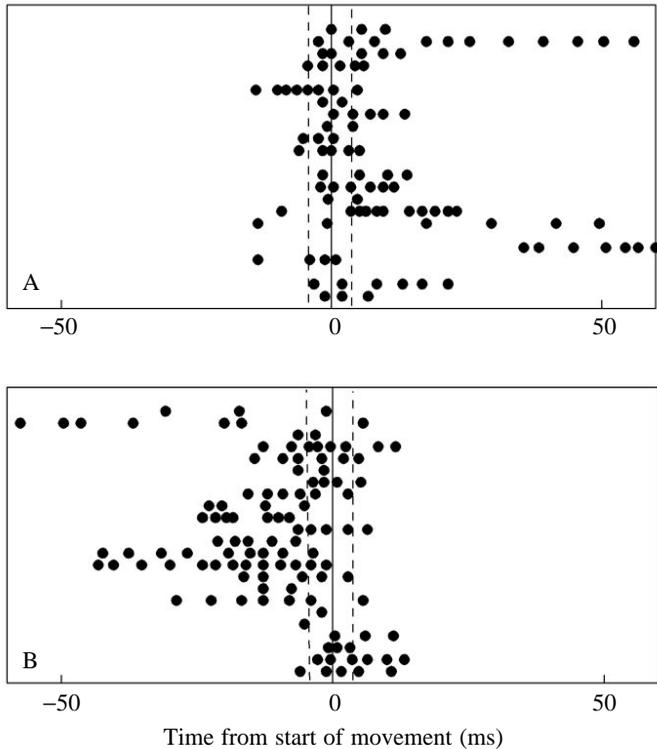
Fig. 12. Raster displays of the timing of impulses from EMG recordings, relative to the time of onset of the corresponding movement of the femorotibial joint. (A) Flexor muscle *versus* joint flexion. (B) Extensor muscle *versus* joint extension (i.e. power stroke of the jump). Two dashed vertical lines in each panel indicate a measurement error of ±4 ms, caused by the frame rate of the high-speed video camera.

Discussion

We have shown here that the evasive behavior of the cricket is composed of two distinct elements, a turn and a jump. These may either occur separately, or they may both occur, in the sequence turn + jump (Fig. 3). Any of these categories can be followed by running. For each of these behavioral elements, the cricket uses a different consistent pattern of leg movements (Figs 5, 8).

Turning and jumping escape responses are characteristic of cockroaches and locusts, respectively. The cockroach first maximizes the angle of its body relative to a wind source and then runs. Although such pivoting is time-consuming, this strategy appears to be adaptive in escaping from natural predators (Camhi *et al.* 1978). Locusts, although less responsive to wind stimuli, escape using a non-directional jump. The advantages offered by the jump are its explosive, or rapidly accelerating, quality and the use of movement in three dimensions, thus incorporating an additional degree of freedom for escape. Crickets appear to be able to utilise the advantages of both these strategies.

The existence of more than one escape strategy implies more than one motor circuit, which may be activated individually or in sequence. A similar situation has been found in crayfish escape behavior, where rapid abdominal flexion is mediated by the activation of the giant interneurons, then re-extension is mediated by a feedback loop, and the subsequent swimming is mediated by a non-giant circuit activated in parallel to the tail flexion command, but with a longer delay (Reichert, 1988).

What determines whether a cricket will respond to a wind puff with a turn, a jump or a turn + jump? The wind angle is a key factor: jump responses were evoked only by wind approximately from behind, and the mean wind angle evoking turn + jump responses tended to be lower than that evoking turn responses (Fig. 4). That is, the closer the wind is to the rear, the greater the likelihood of a jump, with or without a prior turn. Moreover, in turn + jump responses, the turn first repositioned the cricket so that the wind source was almost behind it at the time that the jump occurred (Fig. 7).

What determines the timing of the jump? First, all three response types began with a closing of the femorotibial joint of the hind legs, which is the preparatory stage for a jump. Only in the jump responses did this lead directly to a jump. In the turn + jump responses, towards the end of the turn there was a second closing of this joint, which then led to the jump.

In these latter cases, the jump could be initiated by feedback received during the turn component, as for the tail re-extension following its initial flexion in crayfish escape behavior (Reichert, 1988). Or the jump could be initiated by a parallel excitatory pathway from the sensory input, as in the subsequent swimming in crayfish escape behavior (Reichert, 1988). Although we have no physiological data to determine which mechanisms operate, further analysis of our behavioral data provided some insights.

It is clear that the cricket does not execute a fixed-size turn and then jump, as the size of the pre-jump turn was a function of stimulus angle (Fig. 13A). In fact, as shown by the slope of 0.98 (close to 1) of this curve, together with the rather low scatter, the crickets first turned to align themselves fairly accurately away from the wind source, and then jumped. Fig. 13B indicates that the duration of the pre-jump turn varied widely, suggesting that the crickets did not achieve their alignment away from the wind source by controlling their turning interval. We did not attempt to determine whether the size of the pre-jump turn was achieved ballistically or by feedback either from the continuing wind stimulus or from other sources. What is clear, however, is that completion of a turn away from the wind source is a good predictor of when the cricket will jump.

The turn response

The crickets turned consistently away from the wind source (Fig. 4). This involved not only a left/right discrimination of wind direction, but also a discrimination of different wind angles on a given side. This is seen both in terms of the size of the initial turn (Fig. 4A) and in terms of the maximal angular velocity (Fig. 4B). In spite of the correlation of these two parameters of the turn with wind angle, there is much scatter in the turning response. Recently, in another species of cricket, it has been shown that the wind-activated giant interneurons
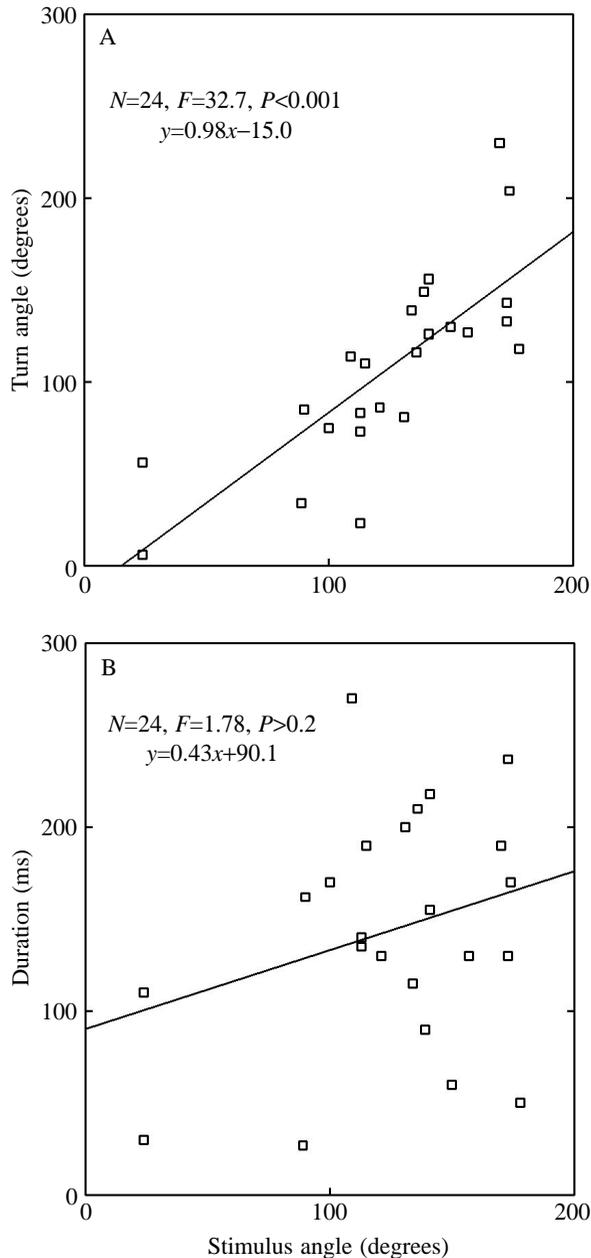
Fig. 13. Analysis of the turn + jump responses of the cricket to a wind stimulus. (A) The turn angle prior to jumping as a function of the angle of the wind stimulus to the body. Absolute values of both parameters are plotted. The data include three 'wrong' turns, towards the wind source. (B) Duration of the turning component as a function of stimulus angle.

register wind direction with an accuracy of less than $8°$ (Theunissen and Miller, 1991; Miller *et al.* 1991). Since the wide scatter we observe in the turning behavior does not seem to be consistent with such fine directional discrimination, one wonders whether under specific conditions, such as darkness or some combination of environmental and behavioral factors, the crickets would turn with considerably less scatter. We did not investigate this point. Similar scatter is seen in the escape turns of cockroaches.

The cricket's escape turn is very similar to that of the cockroach. This similarity includes the following parameters (Camhi and Tom, 1978): (1) rotation of the body about a pivot at its posterior end; (2) a simultaneous initial push by at least five legs to produce the initial turn; (3) similar directions of initial leg movements in each of five legs.

Turns studied in other insects, not executing an escape behavior, have an entirely different basis (courtship turns of the cockroach *Blatella germanica*, Franklin *et al.* 1981; circling in bees, Zolotov *et al.* 1975). The resemblance between turning in the cricket and cockroach escape behavior could result from convergent adaptation based both on similar needs for a rapid turn and on similar biomechanical constraints. Alternatively, the resemblance could express a common phylogenetic origin, suggesting that these are homologous behaviors. Our data do not permit us to discriminate between these two possibilities.

The jumping response

For some types of movement, the power required (that is, the rate of force development) is greater than can be supplied by ordinary contraction of the muscles. For the jumping locust, as well as other jumping insects (Bennet-Clark and Lucey, 1967; Evans, 1975; Frantsevich, 1981), various mechanisms have evolved to overcome this limitation, all based on storage and quick release of mechanical energy, as with the shooting of an arrow or the snapping of the fingers. In locusts, energy is stored during a prolonged interval (0.2–0.5 s) during which the jump muscle of each hind leg contracts isometrically, opposed by co-activation of the antagonistic muscle and the mechanical locking of the joint (Heitler, 1974).

This time-consuming process is hardly adaptive for an escape behavior that must begin quickly after the onset of a threatening stimulus. The cricket jump, in fact, occurred much more quickly, 94 ms after the wind arrived at the cerci. Thus, if crickets use an energy-storage mechanisms, it must be rapidly executed.

Our energetic analysis suggests that, unless crickets have jumping muscles capable of power production roughly 10 times greater than that of the locust extensor tibiae muscles, which would seem unlikely, the cricket must also have some energy-storage mechanism. This requirement may appear surprising, since the cricket jumps to a much lower height and over a shorter distance than the locust; however, its jumping muscles are also much smaller (Table 1). As shown by the EMG recordings from extensor and flexor tibiae muscles during the jump (Fig. 11), there is practically no overlap between the spike bursts of large, fast motor units from these antagonistic muscles, and perhaps none from small, slow motor units. Thus, co-activation such as that in locusts appears not to be employed by the cricket. However, as the contractile force of a muscle can last tens of milliseconds after the end of electrical activity, it is possible that the flexor remains contracted during at least part of the extensor burst. This could be a case of co-contraction without electrical co-activation. In

support of this idea, the actual leg extension began only towards the end of the extensor burst. Thus, the extensors work isometrically at first. This suggests that the system stores energy during this isometric period and releases it later, at the time of extension.

Additional factors could contribute to the storage of energy during the onset of extensor contraction. The joint could be locked by some anatomical arrangement and then quickly released. Alternatively, with the leg in its flexed position, the extensor tibiae tendon could be positioned centrally with respect to the femorotibial joint, such that contraction of the extensor muscle would cause no joint movement or only very slight initial joint extension or flexion. Energy could initially be stored in elastic elements, to be released quickly when leg extension begins in earnest. If the extensor tibiae tendon is initially centrally positioned with respect to the femorotibial joint, then the onset of leg extension would require the activation of a different muscle to pull the tendon away from its initial position, thus translating the extensor tibiae contraction to leg extension. A similar mechanism has been described for the jump of the flea (Bennet-Clark and Lucey, 1967). In the cricket, one possibility, rather than activation of a different hind leg muscle to pull the tendon away from its initial position, would be for the initial forward push to be given by the front and middle legs. With the hind legs resting on the ground, this could move the joint such that contractile force in the extensor muscle could produce leg extension.

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