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WIND-EVOKED ESCAPE RUNNING OF THE CRICKET *GRYLLUS BIMACULATUS*

I. BEHAVIOURAL ANALYSIS

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Summary

Spontaneous walking and escape running in response to wind puffs directed to the abdominal cerci were quantitatively studied in tethered walking crickets.

1. An apparatus for optically recording rotations of an air-supported sphere was developed to measure the intended locomotion of insects with high linear and temporal resolution but without mechanically imposed bias.

2. During spontaneous locomotion without sensory cues for orientation, alternate pauses of 0.35–2.2 s and walking phases of 0.5–6 s resulted in a highly variable pattern of locomotion on a meandering path.

3. A single air puff to one or both of the wind-sensitive cerci evoked a short run, whereas a continuous sequence of puffs caused sustained escape running with a tendency to turn away from the stimulus source. Escape running was characterized by a series of stereotyped running bouts and pauses, both significantly shorter than those recorded during spontaneous locomotion.

4. Forward speed and angular speed of escape running correlated linearly with the wind puff frequency between 5 and 10 Hz. This was caused by a shortening of the standing phases, while the durations of the running bouts were constant. The reflex-like running bouts and the pattern of escape running were largely independent of the duty cycle of the wind puff series and the wind speed. Neither individual steps nor running bouts were synchronized with the stimulus pattern.

5. The behavioural modes of spontaneous walking and escape running were maintained with a minor reduction in general activity in partly dissected specimens during intracellular recording in the prothoracic ganglion. Each impaled local interneurone with locomotion-related activity generated action potentials in the actual step rhythm of walking and running bouts, but did not show specific activity during escape running. Some of these local neurones, however, showed modulations of spike frequency before or during intended turns and may participate in the coordination of the prothoracic legs.

Introduction

Walking represents an essential form of locomotion in most terrestrial arthro-

Key words: insect locomotion, tethered walking, escape, wind stimuli, cricket, *Gryllus bimaculatus*.

pods. This largely stereotyped and repetitive behaviour has been studied by numerous researchers seeking to answer questions regarding leg coordination, the roles of individual muscles, sensory feedback from the periphery, central integration and control of movements by the central nervous system (for reviews, see Gewecke and Wendler, 1985; Delcomyn, 1985). In contrast, walking behaviour is flexible depending, for example, on surface structure (Franklin, 1985) and the anatomical integrity of the animal (leg amputation) (Hughes and Mill, 1974). Walking can also be looked at as a prerequisite for, and a component of, escape behaviour and orientation of the animal within its environment (Ritzmann, 1984).

Except for behavioural observations on unrestrained animals, all studies of walking arthropods require experimental manipulation of the individual and, therefore, reduce its freedom to move. Previous electrophysiological studies of insect walking have been made with extracellular recordings of muscle cell activity from animals free to walk in limited arenas (Pearson, 1972; Delcomyn and Usherwood, 1973; Orida and Josephson, 1978; Delcomyn, 1987) or on balls or treadmills (Delcomyn, 1973; Godden and Graham, 1983; Wendler *et al.* 1984). Intracellular studies were only made possible by using wheel-treadmills, which represent a rather abnormal surface during fast running and turning (Godden and Graham, 1984; Wolf, 1990), or by using extremely restricted individuals (Daley and Delcomyn, 1980*a*; Camhi and Nolen, 1981; Kien and Altman, 1984; Ramirez and Pearson, 1988), in which the walking behaviour could not be recorded. Quantitative studies on orientation behaviour have preferentially used either an actively driven walking compensator (the so-called 'Kramer sphere') to approach closed-loop conditions of sensory feedback (Götz and Wenking, 1973; Erber, 1975; Kramer, 1976; Weber *et al.* 1981) or different sphere-based systems, which passively track walking movements of the animal (Buchner, 1976; Dahmen, 1980; Brunner and Labhart, 1987; Doherty and Pires, 1987; Schildberger and Hörner, 1988). In the second type of experiment, the insect is fixed in three-dimensional space and, therefore, only intended translatory and rotatory movements of the individual are registered. This intended locomotion has no effect upon the strength and relative orientation of sensory stimulation, i.e. external stimuli are applied under open-loop conditions. In this paper we describe an improved design of an air-supported sphere as an unlimited, directionally unbiased walking surface. It allows simultaneous intracellular recording of neuronal activity from the central nervous system and registration of the intended movements with high resolution of time, distance and orientation.

As has been described previously for cockroaches (Camhi and Tom, 1978; Camhi *et al.* 1978; Ritzmann, 1984) and house crickets (Stabel *et al.* 1985), wind stimuli directed to the cerci, a pair of abdominal appendages carrying sense organs sensitive to air movements and vibration, can elicit vigorous escape running in orthopterous insects. Here we present results on the escape reaction of the field cricket *Gryllus bimaculatus* during open-loop wind stimulation of the cerci. We will show that this behaviour is based on a regular alternation of walking bouts and standing phases and combines reflex-like and variable components, the latter

depending on the actual stimulus frequency. The specific activity pattern is reflected in the activity of prothoracic local interneurones (this paper) and in the activity of ascending and descending interganglionic neurones, as discussed in the second part of this investigation (Hörner, 1992).

Materials and methods

Animals

We used adult crickets (*Gryllus bimaculatus* de Geer) of both sexes from a breeding colony in our laboratory held at 28°C under a dark/light regime of 12 h:12 h. The experiments were performed in the light phase, during which spontaneous walking activity is homogeneously distributed (Hörner, 1989). We rejected specimens which did not walk spontaneously using normal tripod leg coordination in the experimental apparatus. The bases of the forewings were fixed with wax to the prothoracic tergum. The posterior part of the abdomen and the cerci, however, were always free to move naturally.

Measurement of intended locomotion

Fig. 1A illustrates the set-up arranged around the walking apparatus. The insect was tethered at its neck and at the pronotum above a hollow styrofoam ball (diameter 120 mm, mass about 2.8 g), which was supported by a gentle permanent stream of air within a hemisphere milled into a block of polyvinylchloride (Carrel, 1972; Buchner, 1976; Dahmen, 1980; Brunner and Labhart, 1987; Schildberger and Hörner, 1988). Without a cricket attached to the apparatus, the air cushion stabilized the sphere in an almost constant position judged from visual inspection with a dissecting microscope. For lack of more precise equipment, we put the electromechanical pick-up system of a record player on the upper pole of the ball to get some estimate of the system's internal vibrations. We measured rather large signals of 50 and 100 Hz components, which were effectively reduced by connecting a water-filled vessel between the compressor and the experimental set-up. This served as a bubble column in the supporting air stream. We also observed a broad spectrum of higher vibrational frequencies with a probable maximum greater than 1500 Hz, as estimated from the signal reduction caused by a set of sequential low-pass filters with cut-off frequencies between 10 kHz and 10 Hz. A robust micromanipulator was used to lower the animal onto the ball's surface until all the legs approached a normal posture.

To record the intended walking movements of the cricket on top of the ball we measured the movement of the ball's surface using an optical method which avoided any friction of mechanical transducers (cf. Dahmen, 1980). Our system gave a high temporal and linear resolution of the translatory and rotatory components of locomotion. An array of 9×9 plastic light guides (0.5 mm diameter) was connected to a 150 W halogen bulb and illuminated a 9 mm×9 mm area of the ball at its equator in front of the cricket (Fig. 1B). Regularly intermingled with these light guides was an array of 8×8 measuring light guides, which were

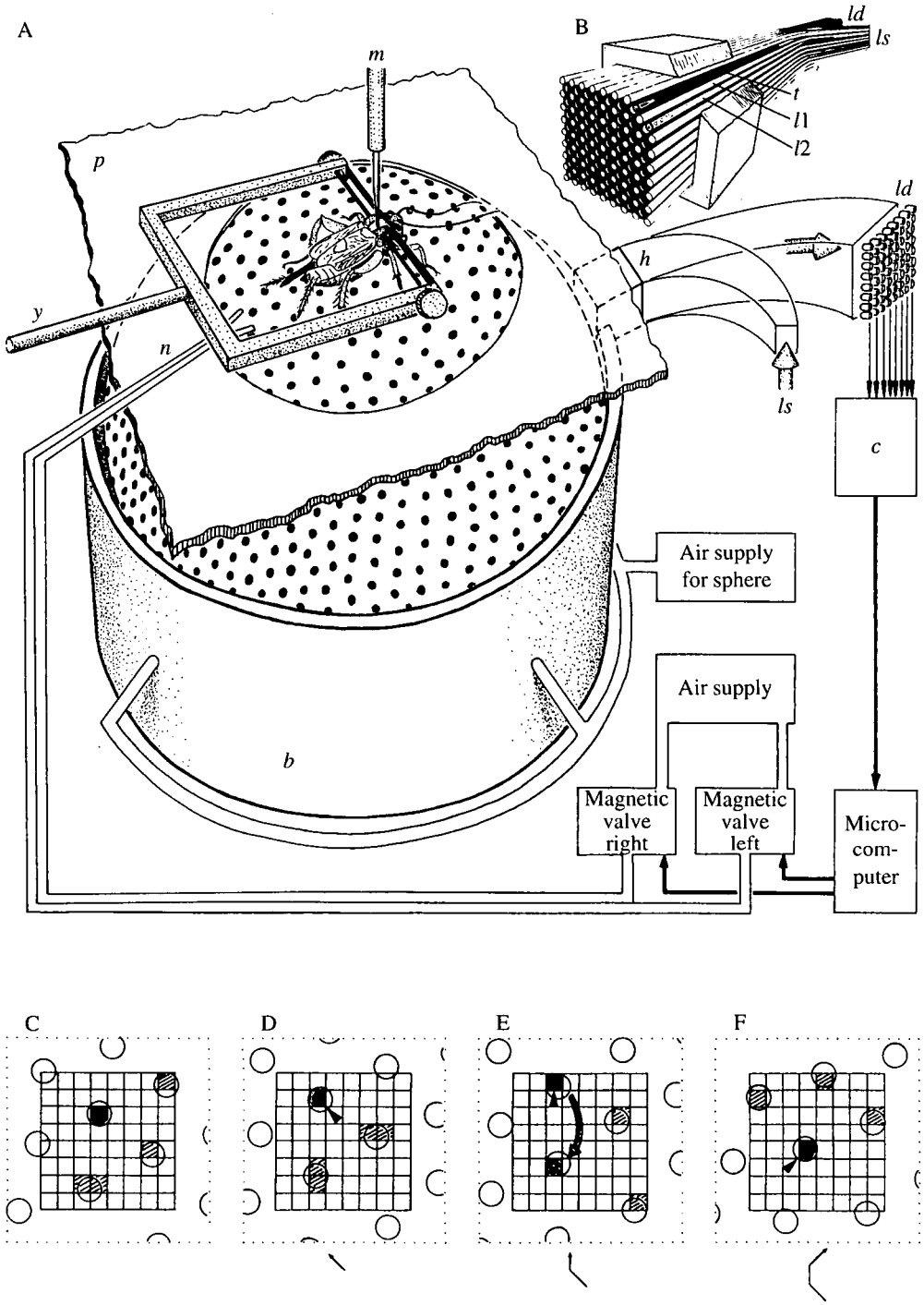
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Fig. 1

Fig. 1. Experimental apparatus used to measure walking activity of crickets. (A) Walking sphere and stimulus equipment. *b*, hemispherical bowl with styrofoam sphere; *p*, plate to protect the insect from air from the sphere's air cushion; *y*, yoke holding the cricket on top of the sphere; *m*, microelectrode; *ls*, light-source to illuminate the detector head stage (*h*); *ld*, light detector array with 64 phototransistors connected *via* 64 comparators (*c*) to the microcomputer, which also controls magnetic valves to stimulate the cricket's cerci through two nozzles (*n*). Ganglion holder and micromanipulators are omitted. (B) Enlarged, partly opened detector head to show the arrangement of illuminating light guides (*l*1) from the light source (*ls*) and measuring light guides (*l*2) to the light detector (*ld*), which are individually adjusted in steel tubes (*t*). (C–F) Examples illustrating the movement-detection algorithm. The square grid represents the 8×8 detector head, the circles represent individual dots on the sphere's surface. Each dot in front of the detector darkens at least one of the measuring light guides (hatched squares). One of these squares (black) is selected by the computer and followed during movements of the sphere. The arrowheads indicate the detected motion, the thin arrows below the drawings give the summed motion. When the selected dot reaches the border of the detector area (E), another dot inside the field is searched for and followed (arrow and square).

individually mounted in parallel steel tubes to transmit reflected light to 64 phototransistors (Telefunken BPW17N). Each phototransistor operated like a variable resistor in a voltage divider circuit, the output of which was fed to a comparator. As long as this output exceeded a predetermined voltage level, the comparator transmitted a 5 V (TTL) signal to one of eight eight-bit multiplexers (one attributed to each horizontal row of the 8×8 phototransistor array), which could be read by the microcomputer.

The ball's white surface was marked with a random pattern of black dots 1–1.5 mm in diameter. The distances between individual dots varied from 3 to 6 mm. The array of measuring light guides – positioned about 2 mm in front of the ball's surface – surveyed an area of about 7.2 mm×7.2 mm. At least one black dot was always detected by at least one photodetector. A program for the Apple IIe microcomputer (1 MHz, 128 kB RAM, timer card with 28-bit parallel interface) written in 6502 assembler language 'followed' this dot, i.e. the correlated pattern of darkened phototransistor(s) monitored by the 8×8 detector array (Fig. 1C–F). Whenever the position of the target dot was changed by a movement of the ball, the status of the corresponding photodetector was reversed from the dark to the light condition. It was expected that at least one of the eight neighbouring detectors would then be darkened by the same dot. To find this detector, the computer tested the eight elements surrounding the previous location until it found a 'dark' one. Because a fixed test sequence introduced a severe bias into the measurements, it proved necessary to change regularly between four contrasting sequences. Whenever the selected dot reached the edge of the array, another dot was searched for within the inner 6×6 centre of the detector and was followed as described above.

The resolution of recorded movement depends on the dimensions of the light guide array and was, in our apparatus, about 0.8 mm along the orthogonal axes

and about 1.1 mm along the diagonals of the array. The actual resolution attained was about 1 mm for translatory movements and about 1° for rotations. We calibrated the system with a dotted wheel rotating at a known speed in selectable orientation in front of the detector. This resulted in a calibration function measured in steps of 5°, which was applied to all data obtained with the sphere. Control experiments yielded a maximum error of 4 % for distance measurements and a maximum error below 2° for rotation measurements over 1 s intervals. Both errors were close to zero when averaged over intervals of 30 s.

The direction of elementary movement events was encoded in three bits and stored together with a timer reading (unit 1 ms) in the computer memory. The program generated an on-line graphic display of the intended walk, sampled and stored signals (action potentials, stimulus markers) from up to eight digital input lines and was able to control stimulus equipment *via* 16 digital output lines. By use of automatic data transfer to diskette, the system was suited to measure walks of infinite duration and of a velocity up to 3 m s^{-1}. Depending on walking activity and spike frequency, diskettes became filled and were exchanged every 15–60 min during an experiment.

Our method allowed vector measurement of movements in only two dimensions of the plane. Because the detector was positioned in front of the animal at the sphere's equator, we registered only intended movements of the cricket in the forward/backward direction, and rotations around the vertical axis, while any intended lateral movements were lost. Qualitative observations and quantitative measurements with the detector positioned at the 'south pole' of the ball indicated that such lateral crab-like movements do not occur during normal locomotion of the cricket.

After each experiment, the measuring program allowed some preliminary data inspection and evaluation. To perform more detailed analyses, a set of special computer programs was written. For statistical analysis, we used non-parametric tests (Wilcoxon–Mann–Whitney test, χ^2 test) with a critical probability of $P=0.05$.

To detect and illustrate possible correlations between the spike frequency of a neurone and the animal's concurrent translatory or rotatory speed and direction during an experiment, we arranged the data according to the scheme shown in Fig. 9D,E and in many similarly organized figures in the companion paper (Hörner, 1992). The histograms show the frequency distribution of instantaneous translatory and rotatory velocities measured during consecutive intervals of an experiment. The cricket is generally active only during 20–60 % of the experiment, which causes the large size of the zero bins in the histograms (note interrupted ordinate). The discontinuous form of the histograms results from an interference between the discrete linear resolution of the walking sphere and the fixed temporal measuring interval. The instantaneous spike frequency has been determined separately for each interval. These frequency values have been correlated with the speed attained within the same or the following time interval. During measuring intervals with the same actual speed value (sampled within the same histogram

bin), different instantaneous spike frequencies may occur, each of which is indicated by a dot below the histogram's respective bin. The specific relationship between both values is indicated in the resulting dot pattern: the dots become larger as more identical frequencies are observed during intervals with the same velocity. If the activity of a neurone correlates with an increased translatory or rotatory speed of walking, this is reflected in characteristic asymmetrical arrangements of the dot pattern, which is otherwise more or less homogeneous and influenced only by the general form of the histogram. Often such perturbations are most obvious near the margin of the dot-marked area or in its main orientation (parallel or oblique to the abscissa).

Stimulation

Wind stimuli were delivered to the cricket's cerci through two nozzles of 2 mm inner diameter placed about 6 mm away. Although the animal had some freedom to move its abdomen and the cerci, the actual wind direction was always from the left or from the right side with respect to the longitudinal axis of the insect. However, even during low-speed wind stimuli given through one air outlet, filiform hairs on both cerci were deflected, as could be observed under a dissecting microscope. All stimuli had an air velocity of 0.2–2 $m\,s^{-1}$, preferentially of 0.5 $m\,s^{-1}$, measured with a calibrated thermistor at the cerci. The acceleration of the wind puffs ranged from 10 to 15 $m\,s^{-2}$. The wind was pulsed through magnetic valves which allowed a maximum switching frequency of 10 Hz without distortion of the velocity profile or temporal shape of the air puff. Generally, we used puffs of 50 ms duration and frequencies of 2, 5, 7 and 10 Hz either given continuously for 15 s each by hand or given according to a predetermined time schedule under control of the microcomputer. The inter-stimulus interval was always 45 s. The acoustical background level during the experiments was 45–50 dB SPL. To reduce the probability of visual orientation (Scharstein, 1984), the set-up was surrounded by a semicircular screen of white fabric in front of the animal and was homogeneously illuminated from above by a 100 W bulb.

Electrophysiology

For intracellular recordings, the posterior margin of the cricket's head capsule was waxed to a U-shaped yoke placed around the ventral neck region. The animal was held dorsal side up. The pronotum was similarly waxed on both sides to metal hooks, with which – after this body segment had been opened by a longitudinal dorsal cut – the segment halves were spread slightly apart and fixed to the animal holder. Dorsolongitudinal muscles and fatty tissue were removed and the intestine was tied with fine thread to the outer cuticule of one side (see Schildberger and Hörner, 1988). The prothoracic ganglion was held by a silver platform and stabilized dorsally by a silver eyelet (Wolf and Pearson, 1987). Microelectrodes filled with 5% Lucifer Yellow dissolved in 0.1 $mol\,l^{-1}$ LiCl had resistances of 40–100 MΩ. After injection of Lucifer Yellow by hyperpolarizing current (3–10 nA) and standard histological processing, the anatomy of the recorded

interneurones was revealed using whole mounts or section series. To record from coxal depressor muscles of the forelegs, steel wires (25 μm in diameter, insulated with lacquer except at their tips) were inserted through holes punched in the cuticle and fixed with wax. After the experiment, ferric ions were electrolytically released from the wire tip and precipitated (Rowell, 1963) as a dark spot, the position of which was later determined by dissection. Neuronal signals were stored together with stimulus markers on magnetic tape (Racal SD7) for off-line evaluation. The signals were processed by window discriminators, and action potentials were registered on-line by the microcomputer, which simultaneously analysed the intended movements of the cricket.

Results

Upon the first tarsal contact with the walking sphere almost every cricket started leg movements which, in most cases, developed rapidly into the normal tripod pattern of locomotion. During the first 15 min of tethered walking, activity varied and grooming was often observed. The animals were therefore allowed to become accustomed to the set-up for 20 min before any behavioural experiments were started.

Spontaneous locomotion

During locomotion, the insects continually probed the surface of the sphere with their palps and antennae and walking activity was reduced if these mechanosensory organs were prevented from contacting the ground. Spontaneous walking of unstimulated crickets was characterized by an irregular sequence of pauses and locomotion without detectable orientation, thus resulting in a meandering path. We averaged the velocity of translatory (forward, backward) and rotatory (left, right) movements for 3 min intervals of spontaneous walking in 54 specimens (25 females, 29 males) to yield an average translation velocity of $35\pm1.1\,mm\,s^{-1}$ and an average rotation velocity of $0.94\pm5.1\,degrees\,s^{-1}$ (mean$\pm$S.E.M.). The mean forward speed during individual periods of 3 min was generally less than $60\,mm\,s^{-1}$. The large standard deviation of the small mean rotation reflects the frequent alternation of intended left and right turns and the absence of a preferred orientation. This means that our experimental set-up probably did not present the animal with any optical or mechanical cues that might be used for continuous orientation. However, even a slight asymmetry in mounting the animal in the holder or restriction of a leg's freedom of mobility introduced a rotational bias, which became especially obvious during fast running.

The distribution of walking-phase durations was homogeneous between 0.5 and 6 s (mean 2.51 ± 1.43 s), while most pauses lasted only 0.35–2.2 s (mean 1.05 ± 0.84 s) (Fig. 2). These results for the population of tested crickets also applied to the distributions computed for individual animals. We did not observe any qualitative or quantitative differences in walking behaviour between males

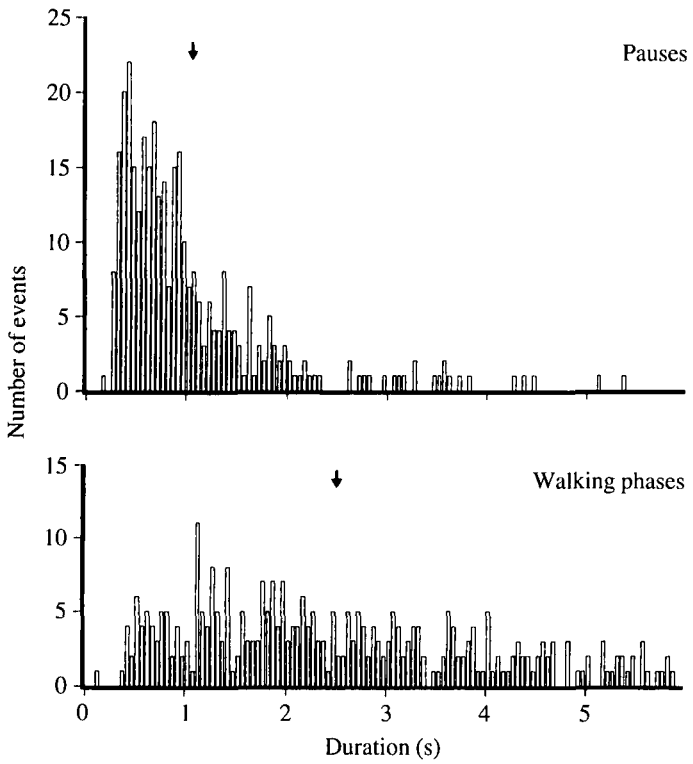

Fig. 2. Distributions of the durations of walking phases (N=371) and pauses (N=335) during spontaneous locomotion on the walking sphere. Arrows indicate the mean of each distribution. Data were pooled from 22 specimens.

and females. As was tested for some records of spontaneous locomotion, the duration of consecutive pauses and walking phases did not influence one another.

Escape running

An unmodulated stream of air applied for some seconds to one or both cerci of the cricket could evoke a short bout of running or continuous walking at a speed similar to that observed during spontaneous locomotion. Sometimes walking stopped at the termination of steady stimulation. This type of wind-evoked walking was extremely variable. In contrast, when stimulated with a single 50 ms wind puff, crickets responded with a single bout of running for 0.5–1 s. When similar wind puffs were presented in a continuous series, a sustained and reproducible running reaction was elicited. This distinct behaviour, the quantitative analysis of which is given below, proved to contain elements of the escape reaction of free-ranging crickets (see Discussion). Therefore, despite the unnatural stimulus conditions in our experiments, we will use the term 'escape running' for this specific mode of locomotion, which of course reproduces only a subset of

the behavioural patterns occurring during escape reactions of unrestrained *Gryllus bimaculatus*.

Because the specimen was held in a fixed position relative to the air outlets, its movements, representing an intended locomotion, did not modify the actual stimulus condition. This means that the responses of the cricket to invariant stimuli were studied under open-loop conditions. Fig. 3 shows an example from a record of wind-evoked running. Within the first 2 s of the 10 Hz stimulus the forward speed was increased from the low level of spontaneous walking to about 220 mm s^{-1} (Fig. 3A). Running slowed slightly to 140 mm s^{-1} during the 15 s of pulsed stimulation, but the escape behaviour persisted even during long-term stimulation for up to 30 s (not shown). At the end of the wind puff series the cricket either stopped immediately or slowed down gradually to its normal walking speed (Fig. 3A).

In most cases the escape reaction was oriented away from the wind direction: the irregular, unpredictable switching between left and right turns characteristic of normal walking was replaced by an intended rotation to the side of the less intensely stimulated cercus (Fig. 3B). Although the angular velocity during the escape reaction was rather variable, it was often higher than during spontaneous locomotion.

As a measure of the general escape behaviour of all tested specimens, we averaged the translatory and rotatory speed during each 15 s segment of repetitive wind stimulation. Fig. 4 shows the distributions of mean translational and rotational velocities during stimulation (10 Hz, 0.5 m s^{-1}) from the left and from the right side. There is no significant difference between the two histograms of forward speed (left stimulus, mean 113 mm s^{-1}, median 109 mm s^{-1}; right stimulus, mean 107 mm s^{-1}, median 102 mm s^{-1}). However, as escape running is oriented away from the wind source in most cases, the distributions of angular velocity are rather broad, but roughly mirror symmetrical. No individual has been observed consistently to orientate towards the wind stimulus but, because of the preferred walking direction of a few specimens, the distributions overlap asym-

Fig. 3. Comparison of spontaneous locomotion and wind-evoked escape running in a cricket. (A) The three graphs show, over a common time axis on the abscissa, from bottom to top, the translatory speed (forward, up; backward, down); the angular velocity (intended rotation to the left, up; to the right, down); and the total rotation since the beginning of the record. All values were obtained by integrating the elementary movements of the sphere over 1 s intervals. Black bars indicate unilateral wind puff stimulation preferentially to the left (first stimulus series) or to the right cercus (second stimulus series; 0.5 m s^{-1}; 10 Hz for 15 s, at approximately 20° from the animal's median plane). (B) The actual path of intended locomotion drawn in a coordinate system of forward distance (abscissa) and summed rotation (ordinate; left, up; right, down); in each case a forward distance of approximately 3.7 m is plotted. While continuous spontaneous walking for 180 s results in an unsteady path (middle trace), sequences of 15 s of spontaneous activity followed by 15 s of stimulation and then 15 s of spontaneous activity evoke an oriented escape reaction (top and bottom traces). Small crosses mark the periods of stimulation (0.5 m s^{-1}; 10 Hz; 50 ms).

metrically. Therefore, when normalized with regard to the direction of the stimulus, the two distributions are statistically different (P=0.038; left stimulus, mean 18.2 degrees s^{-1}, median 18.9 degrees s^{-1}; right stimulus, mean 16.0 degrees s^{-1}, median 15.3 degrees s^{-1}).

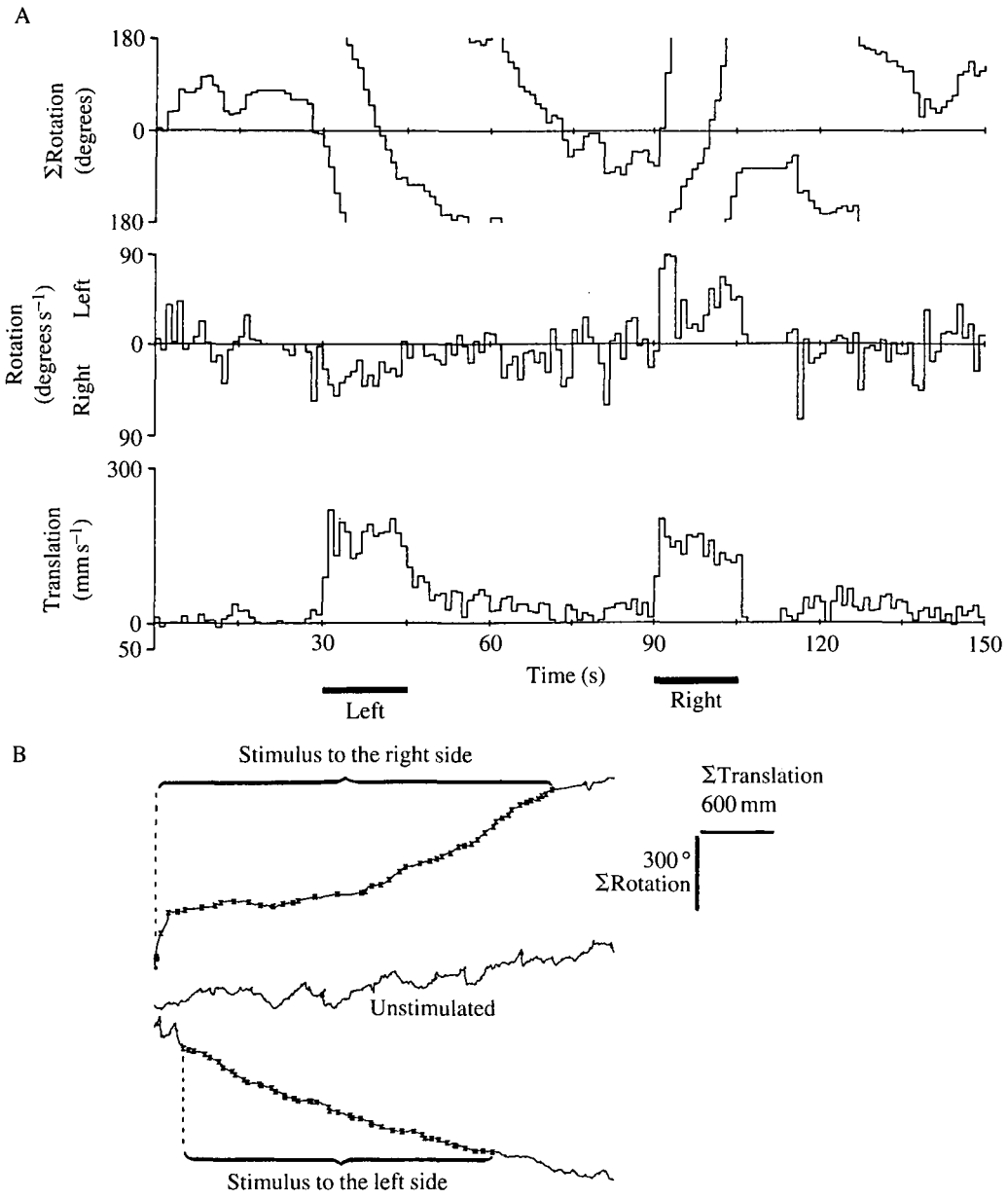

Fig. 3

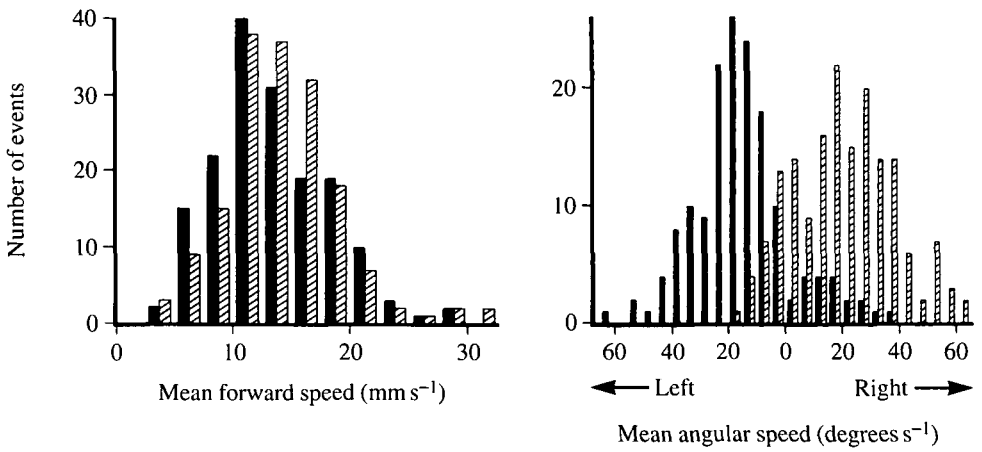

Fig. 4. Mean velocities of intended translatory and rotatory locomotion during 15 s sequences of 10 Hz wind puffs directed preferentially to the left or to the right cercus. The distributions of translatory speed are similar during stimulation from either side, but the distributions of turning speed are significantly different and represent the tendency of the insect to turn away from the stimulus source (solid bars, stimulus from right; hatched bars, stimulus from left).

Effects of stimulus frequency

We studied the effect of the repetition rate of 50 ms air puffs (wind speed 0.5 m s^{-1}) in another group of 34 crickets of both sexes. Both mean forward speed and mean angular velocity during a 15 s wind puff series depended on the stimulus frequency (Fig. 5). Some individuals did not respond consistently to stimuli given at 2 Hz, while others showed only brief behavioural reactions. The averaged velocities during 2 Hz stimulation were not significantly different from the velocities measured during spontaneous locomotion. Higher stimulus repetition rates resulted in an approximately linear increase in both forward and angular speed. A significant intended orientation away from the stimulus source was observed only in response to 7 Hz and 10 Hz stimulation (Fig. 5).

The correlation between stimulus frequency and mean velocity of escape is caused by a specific modulation of the temporal pattern of locomotion. In Fig. 6, segments of wind-evoked escape running are plotted with increased resolution for different stimulus frequencies. Generally, this behaviour is characterized by a periodic alternation of running bouts and short periods without locomotion. We will term these stops 'standing phases' to distinguish them from the more extended pauses during spontaneous walking. A similar pattern has been described by Stabel *et al.* (1985) for the cricket *Acheta domesticus* under open-loop stimulation. Recently, K. Hackenberg (unpublished observations) showed in our laboratory that free-ranging *Gryllus bimaculatus* respond to air puffs from a stationary nozzle (closed-loop stimulation from posterior) with only one or two short running bouts to escape from the stimulus, followed by inactivity or variable walking (see

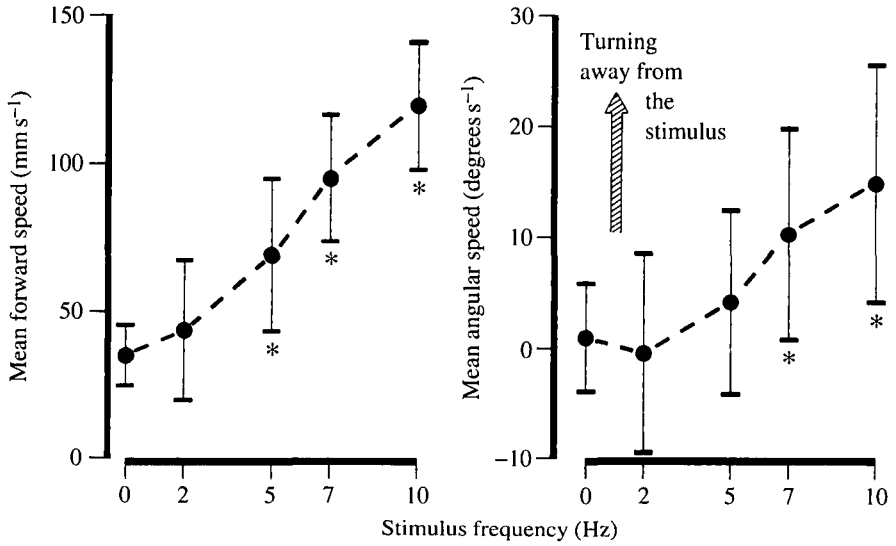

Fig. 5. Average translatory and rotatory activity during 15 s sequences of wind puffs ($0.5\,m\,s^{-1}$) given with different repetition rates and compared to spontaneous locomotion. Data were pooled from experiments with wind from the left and from the right side. Rotation is expressed relative to the side of the preferentially stimulated cercus. Each dot represents the mean of 204 time segments obtained in experiments with 34 specimens. Bars indicate the standard deviation; asterisks mark those values that are significantly different ($P<0.05$; two-tailed U-test) from spontaneous walking (0 Hz).

Discussion). In the same species, we found a repetitive stimulation of cercal afferents to be necessary and sufficient to elicit a sustained pattern of escape running, similar to the behaviour of *Acheta domesticus*. This characteristic rhythmic locomotion occurred neither spontaneously nor in response to any other kind of stimulation. Covering both cerci with Vaseline, which prevents the sensory hairs from detecting air movements, totally abolished the behavioural reaction to repetitive wind puffs. In contrast, one intact cercus was sufficient to elicit qualitatively similar escape behaviour.

We measured the duration of the individual running and standing phases in response to 5 Hz, 7 Hz and 10 Hz trains of stimuli (Fig. 7). These results differ from those found during spontaneous locomotion (cf. Fig. 2). However, statistical tests revealed no differences between the distributions of running duration for the three different stimulus frequencies. Furthermore, crickets achieved similar maximum running velocities as well as similar mean velocities (5 Hz, $204\pm62\,mm\,s^{-1}$; 7 Hz, $225\pm48\,mm\,s^{-1}$; 10 Hz, $213\pm39\,mm\,s^{-1}$) regardless of the applied stimulus repetition rate. In contrast, the distributions of standing phases during 5 Hz, 7 Hz and 10 Hz stimulation differed significantly from one another. Standing phases shortened with increasing stimulus rates. This combination of constant running bout lengths and variable standing phases is sufficient to explain

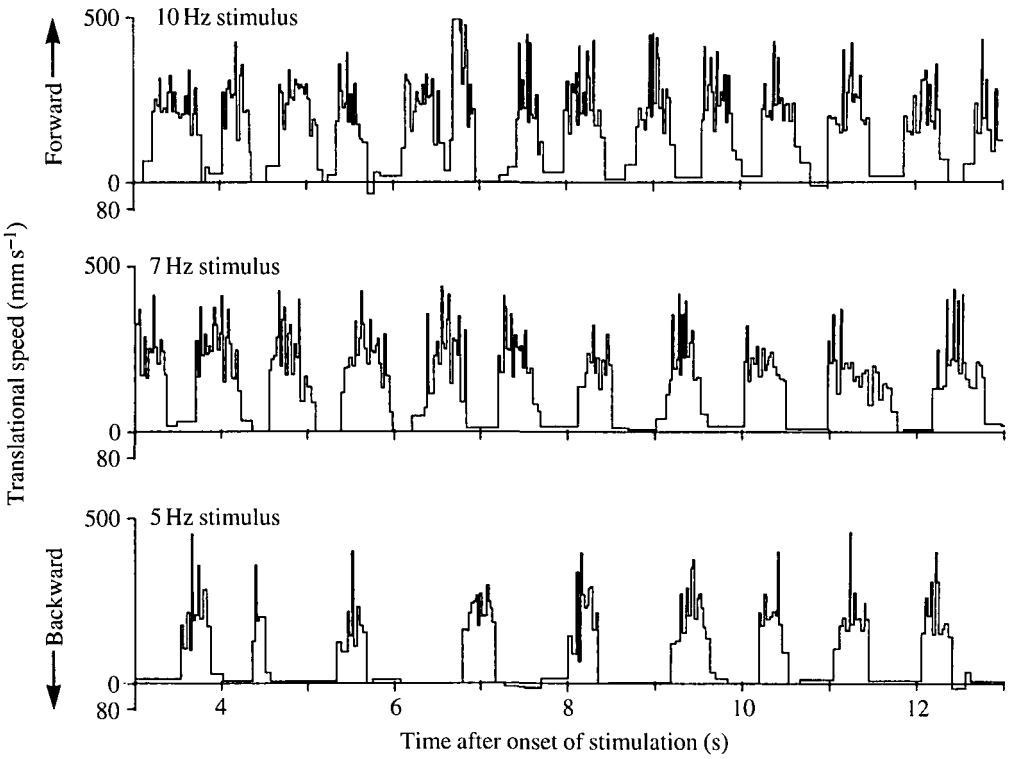

Fig. 6. High-resolution plots of translatory speed during escape behaviour evoked by wind puff (0.5 m s^{-1}; 50 ms each) sequences with different stimulus frequencies obtained from the same animal. The time segments start 3 s after the onset of the stimulus. The first 0.5–2 s of stimulation (not shown) is often more variable in instantaneous speed and pattern of runs and standing phases.

the correlation between wind puff frequency and the mean running speed during stimulation shown in Fig. 5.

In contrast to the constant wind puff duration of 50 ms, the interstimulus intervals varied with stimulus repetition rate. This caused reduced overall wind stimulation at low frequencies. However, control experiments with a 1:1 duty cycle of wind puff duration and interval evoked quantitatively identical escape behaviour, which apparently depends only on stimulus frequency. Wind speed variation in the range 0.2–1.5 m s^{-1} did not modify the running pattern, whereas a higher wind speed caused kicking or jumping of some animals (abrupt extension of hindlegs resulting in unusually fast movements or lifting of all six legs from the ball's surface). Furthermore, we analysed the latencies between the onset of individual running bouts and the preceding wind puff (six animals, N=165) and found an essentially flat distribution over the stimulus period. Therefore, the synchronization of stimulus sequence and running pattern can be excluded. The

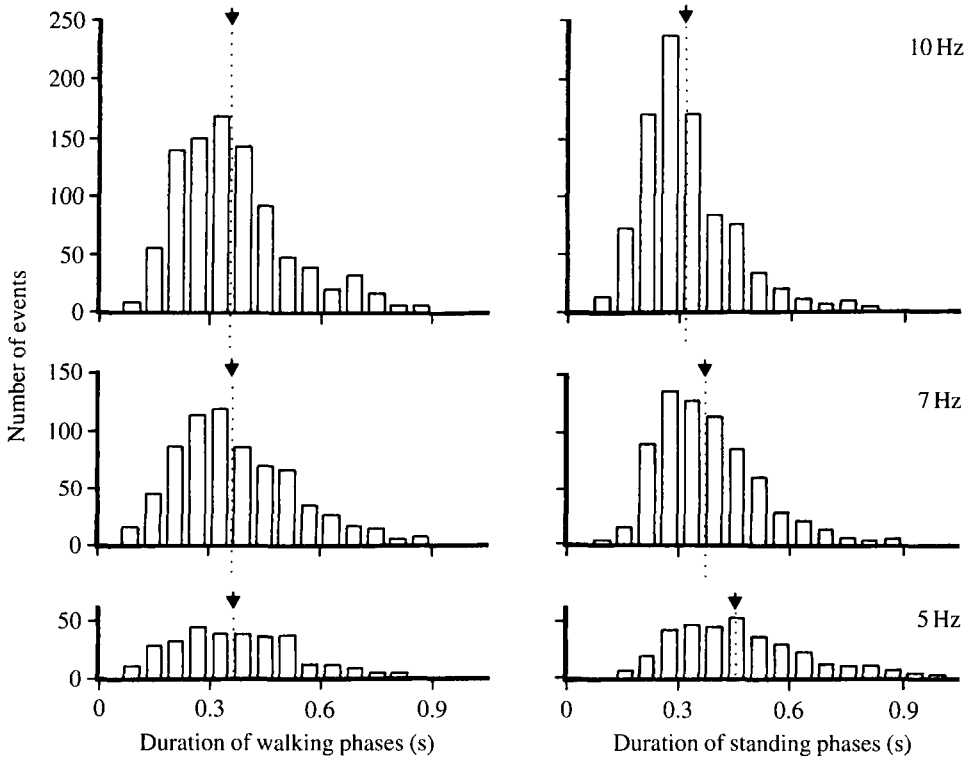

Fig. 7. Histograms of the durations of walking bouts and standing phases in response to different stimulus frequencies. Arrows indicate the mean of each distribution; data from 34 animals.

stereotyped form of individual running bouts is obviously not influenced by the temporal pattern of the stimulus sequence.

Recordings from leg muscles

To study the relationship between individual steps within the tripod walking gait and the wind-evoked running bouts, we recorded extracellularly from the coxal depressor muscles of both forelegs (muscle 77 according to Laurent and Richard, 1986*a*) while monitoring movements with an infrared reflection sensor. Spike bursts occurred during protraction of the ipsilateral foreleg (see Laurent and Richard, 1986*b*). Comparision of step frequency and walking velocity revealed a strict correlation between these variables, 2.9–15 steps s^{-1} producing a forward speed of 19.5–196 mm s^{-1}. The step frequency did not depend on burst duration nor was it synchronized with the air puff sequence. During spontaneous locomotion, only spikes of small amplitude were recorded, whereas each step of a running bout during escape was characterized by an additional spike of large amplitude (Fig. 8). In recordings from all 16 specimens tested this unit was active exclusively during running bouts in the course of escape behaviour.

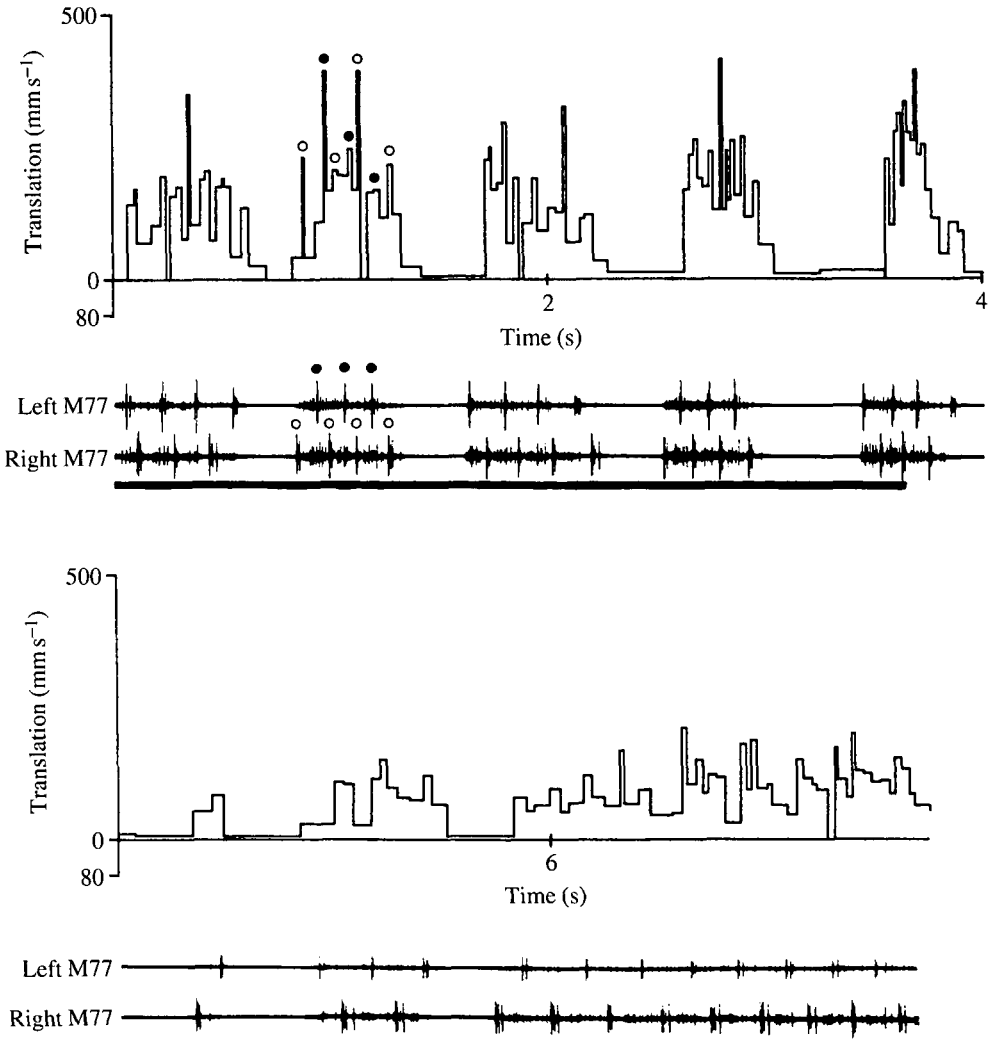

Fig. 8. Extracellular recordings of the coxal depressor muscles of both forelegs during escape running (upper part; solid bar, stimulus marker) compared with spontaneous locomotion (lower part of the continuous recording; traces from top to bottom, forward speed; activity of left and right M77; stimulus marker; wind pulses were directed to the left cercus; 50 ms; 10 Hz; 0.5 m s^{-1}). Notice large spikes as part of the alternating activity in the two muscles during escape. Each large spike corresponds to one step in the tripod walking pattern of the insect and can, therefore, be correlated with one transient maximum of forward velocity, as indicated for the second running bout (open and filled circles). In most cases the bilateral alternations of tripod walking are conserved between consecutive running bouts.

Analysis of the muscle recordings indicated another functional difference between spontaneous walking and escape running. The first step after a pause in spontaneous locomotion could be performed by either of the two triplets of legs,

regardless of the triplet used in the last step before the pause, i.e. the alternating pattern seemed to be reset by the pause. In contrast, during escape running, a continuously alternating pattern of tripod stepping was conserved in most cases in spite of the regular standing phases separating running bouts. Evaluation of standing phases occurring during escape running (cf. Fig. 7) of six specimens revealed that the step pattern was interrupted in only 25 of 163 cases, while 24 of 49 analysed pauses of more than 1 s during spontaneous walking (cf. Fig. 2) were followed by a change in the step pattern.

Intracellular recordings during locomotion

Previous descriptions of the walking and escape behaviour of *Gryllus bimaculatus* served as a reference for our intracellular studies of neuronal activity during locomotion (Hörner, 1989, 1992; Hörner *et al.* 1989; Gras *et al.* 1990). The present experiments focused primarily on ascending and descending fibres of the central nervous system or on central neurones with peripheral axons. We also found some units intrinsic to the prothoracic ganglion, which produced specific activities in the context of walking. Observations on one of these local neurones are presented to demonstrate the combination of intracellular recording techniques with simultaneous quantitative measurement of intended walking behaviour in semi-intact preparations.

About 80 % of the animals that had been prepared for intracellular recording walked with the normal tripod pattern, but with slightly less spontaneous activity. In control experiments, 26 dissected specimens were tested with the same standardized stimulus programme that had been used in the previous behavioural experiments. The crickets produced the characteristic pattern of escape running but attained only about 70 % of the mean forward speed of controls. The mean duration of running bouts was reduced in dissected crickets by about 6 % compared with intact specimens, while the standing phases were extended by about 22 %. Both effects resulted in a reduction in the frequency of running bouts from 1.5 Hz in intact to 1.4 Hz in dissected animals. Orientation away from the stimulus source and the angular velocities of turning were not impaired. Therefore, the general escape behaviour seemed to be unaffected by the operation necessary for intracellular recording.

Fig. 9A shows a prothoracic local interneurone with a ventral cell body whose primary neurite projected dorsally to the ipsilateral dorsal intermediate tract (DIT) and sent a collateral *via* dorsal commissure III to the contralateral side of the ganglion (neuroanatomical terminology according to Wohlers and Huber, 1985). All arborizations on the soma side of the ganglion were smooth, but the varicose branches at the level of the contralateral DIT had bulbous endings. In the resting animal, this neurone did not generate action potentials and was insensitive to external stimuli (sound, single wind puffs). During repetitive cercal stimulation, however, individual depolarizations summed and resulted in continuous spiking, which was not correlated with individual wind puffs (Fig. 9B). During spontaneous and wind-evoked locomotion, this neurone fired bursts of action poten-

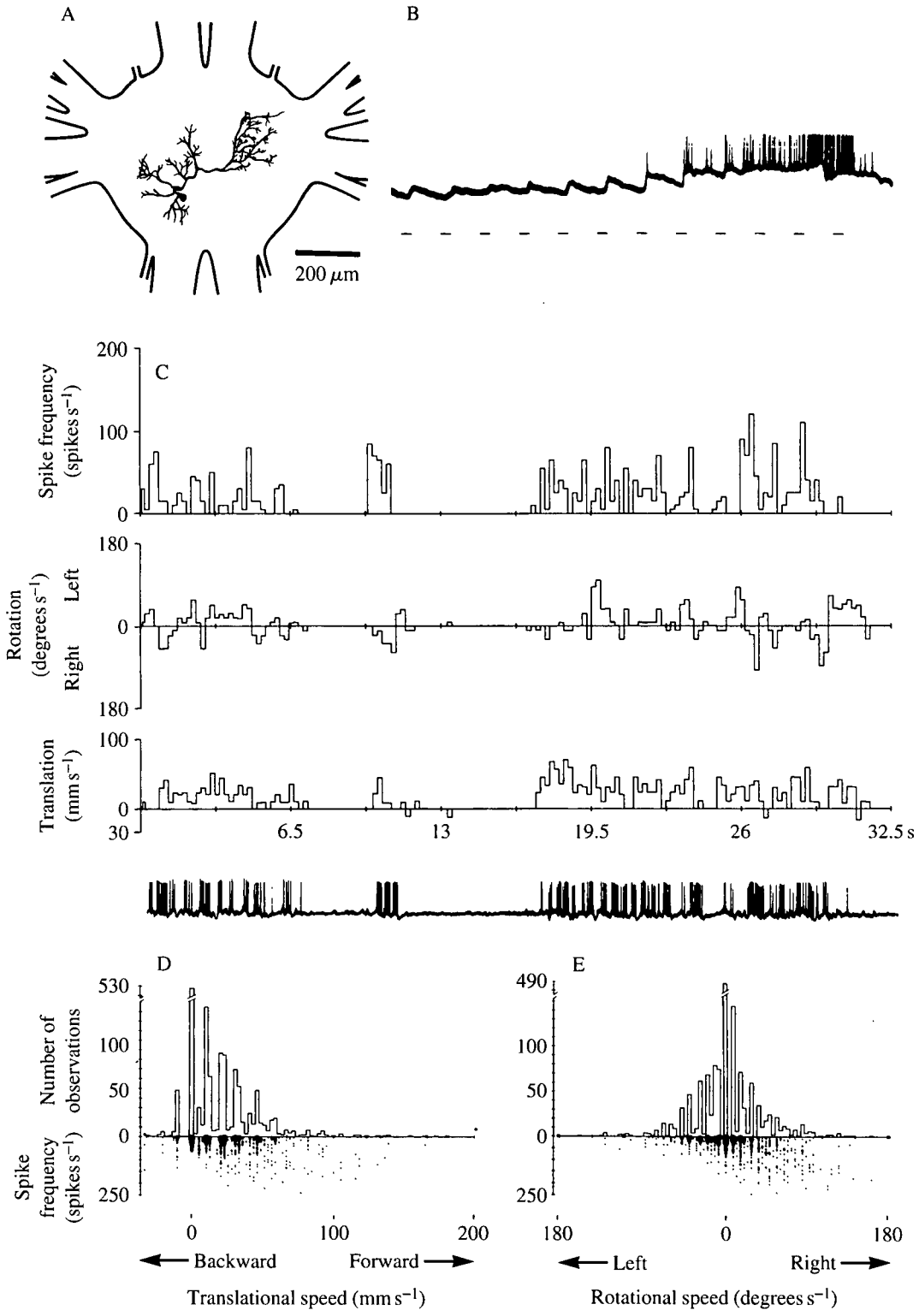
A
B
200 μm
C
Spike frequency (spikes s⁻¹)
200
100
0
Rotation (degrees s⁻¹)
Left
Right
180
0
180
Translation (mm s⁻¹)
100
0
30
6.5
13
19.5
26
32.5 s
D
E
Number of observations
530
100
50
0
Spike frequency (spikes s⁻¹)
250
0
100
200
Backward
Forward
Translational speed (mm s⁻¹)
490
100
50
0
250
180
0
180
Left
Right
Rotational speed (degrees s⁻¹)

Fig. 9

Fig. 9. Activity of a local interneurone during walking behaviour. (A) Drawing of the Lucifer-Yellow-filled neurone in the prothoracic ganglion. (B) In the course of a 7 Hz stimulus sequence, subthreshold depolarizations summate until the neurone begins to fire action potentials. (C) Although it is silent in the standing animal, the neurone generates rhythmic bursts of action potentials during spontaneous locomotion. Spike frequency is increased immediately before and during intended rotations to the right side (traces from top to bottom; spike frequency; angular speed; forward speed averaged over 200 ms intervals; intracellular recording). (D) Histogram of instantaneous translatory speed during 200 ms intervals computed from 221 s of spontaneous and wind-evoked locomotion and pauses. Each dot below the histogram indicates the frequency of spikes occurring 0–200 ms before an interval comprising a given speed. The size of the dots corresponds to the number of intervals with the same velocity and the same spike frequency (see Materials and methods). During about 60 % of the analysed time the cricket stood still (zero bin of the histogram) and the neurone was largely silent; dots below the zero bin of the histogram represent action potentials preceding short turns without a translatory component. Slow forward walking correlates with low spike activity, while up to 48 spikes per 200 ms are generated during faster running. (E) Histogram of instantaneous angular speed and correlated spike frequency displayed as in D. The distribution of turning speed is similar for rotation to the left and to the right sides. However, the asymmetrical dot pattern reveals that the spike frequency consistently increases with angular velocity to the right side, while neuronal activity is largely suppressed before fast turning to the left. Note the interrupted ordinate.

tials (Fig. 9C), often in synchrony with the step rhythm. The mean latency between the first spike and the onset of actual movement of the sphere was 102±10 ms. The burst duration was rather variable. Fig. 9D shows only a weak correlation between spike frequency and instantaneous forward speed during the following 200 ms time segment. However, there was a clear relationship between spike activity and turning behaviour. During intended rotations to the right side (i.e. the side contralateral to the neurone's soma) the spike frequency was increased. During rotations to the left, firing was suppressed compared to time segments without rotation (Fig. 9E).

Discussion

Since the pioneering study by Roeder (1948) on the neuronal basis of wind-evoked escape running of the cockroach, a comparable, specific escape behaviour triggered by cercal stimulation has been described in apterygote insects (Edwards and Reddy, 1986) and in orthopterans (cockroaches: Camhi and Tom, 1978; Camhi *et al.* 1978; Ritzmann, 1984; crickets: Gnatzy and Heußlein, 1986; Stabel *et al.* 1985). The functional sequence, from bending of filiform hairs on the abdominal cerci, stimulation of mechanosensory cells, conduction *via* giant fibres in the abdominal nerve cord to thoracic ganglia and to integrating centres of the brain, has been revealed in detail for these and other orthopterous insects (Boyan and Ball, 1990; Dagan and Parnas, 1970; Daley and Camhi, 1988; Edwards and Palka, 1974; Kanou and Shimozawa, 1985; Nicklaus, 1965; Ritzmann and Pollack,

1986; Tobias and Murphey, 1979; Westin, 1979). However, few data on escape running are available for crickets (Stabel *et al.* 1985), although the cercal and giant interneurone systems of crickets are anatomically and physiologically well understood and have often been used in studies of development and regeneration (Murphey, 1981, 1986; Roederer and Cohen, 1983*a*,*b*).

Measuring locomotion in tethered insects

The neurophysiological description of wind-evoked escape behaviour of *Gryllus bimaculatus* is facilitated if it can be reproducibly evoked and maintained for extended periods, while the actual behaviour is measured quantitatively. This is achieved by constant stimulation under open-loop conditions using the experimental apparatus described in our study. Experiments using a treadmill with simple mechano-optical transduction by friction disks (similar to the design developed by Dahmen, 1980) revealed that tethered crickets do not walk normally if there is any biased mechanical restriction of the walking substratum. The measuring technique applied in our present study avoids these problems and produces selectable high linear and temporal resolution, which allows precise correlation of neuronal and behavioural events. Of course, one should also be aware that our apparatus gives rise to restrictions and unnatural conditions of the walking substratum, which can probably be perceived by the insect.

The variables of spontaneous locomotion of crickets on the styrofoam sphere are similar to those observed in free-ranging specimens (K. Hackenberg, unpublished observations) and in untethered crickets walking on a compensated 'Kramer' treadmill (Weber *et al.* 1981). Although the tripod pattern of leg movements is conserved throughout, absolute and relative durations of walking phases and pauses as well as the forward speed attained are rather variable intra- and interindividually. Hörner (1989) found that unoriented females meandering on the styrofoam sphere consistently switched to precise intended tracking of a speaker emitting the conspecific calling song. This has also been shown for stationary walking under different experimental conditions (Weber *et al.* 1981; Schildberger and Hörner, 1988). Therefore, the walking substratum used in our study seems to represent a sufficiently natural condition for insect locomotion.

Characteristics of escape running

The regularly patterned sequence of running bouts and standing phases, which is typical of escape running by *Gryllus bimaculatus*, has not been observed in tethered animals, either during spontaneous locomotion or in response to any stimulus other than a wind puff series lasting some seconds and directed at the cerci (Hörner, 1989). The mean durations of running bouts and standing phases are quite similar under open-loop (350 ms and 310 ms, respectively, in response to 10 Hz wind puffs) and closed-loop cercal stimulation. In free-ranging crickets accidentally passing the outlet of a wind source modulated at 10 Hz only one or two running bouts with a mean duration of 347 ms are triggered (K. Hackenberg, unpublished observations). If two bouts are produced, they are separated by an

average standing phase of 285 ms. These values are significantly lower than the extremely variable durations of walking phases and pauses in the course of spontaneous locomotion in an arena (K. Hackenberg, unpublished observations) or on the styrofoam sphere (this study). We therefore presume that the running mode on the sphere does not represent an artefact caused by the repetitive air puff stimulation or unnatural loads and forces perceived by the cricket turning the styrofoam ball. Instead, it can be regarded as an extension and repetition of the phasic escape behaviour of unrestrained crickets stimulated under closed-loop conditions. Moreover, the two modes of locomotion seem to be quite distinct, because at the end of the wind stimulus the regular sequence of escape running usually stops immediately or switches to normal walking without a gradual transition. This has been concluded from high-resolution plots such as that in Fig. 8 but is obvious even in analyses with low time resolution as in Fig. 3.

The responses to cercal wind stimuli are largely suppressed in non-giant ascending fibres of the nerve cord in *Gryllus bimaculatus* during running (Hörner *et al.* 1989). This probably represents a protection from strong reafferent stimuli generated during motor activity. Running animals produce turbulence with their leg movements and, furthermore, they experience 'fair wind' during forward movement relative to still air. It is conceivable, therefore, that the sensitivity to the wind stimuli is reduced during the running bouts, while the interposed standing phases are used to probe for a lasting stimulus. As this behaviour is seen in tethered specimens, the presumed suppression of cercal information during intended running cannot result from a change in the position of the cricket relative to the stimulus source but must be caused by central mechanisms. This is in agreement with the results of Tomioka and Yamaguchi (1984) on flight. In contrast, cockroaches tested under identical open-loop conditions to the crickets in the present study are able to sense wind puffs during continuous escape running (Gras *et al.* 1989). Possible mechanisms of spike suppression are discussed in the companion paper (Hörner, 1992).

It has been shown in numerous studies that sensory input to the central nervous system of insects can specifically be suppressed or its functional relevance can be reduced during voluntary movements of the animal (Daley and Delcomyn, 1980*a*,*b*; Hedwig, 1986; Heitler, 1983; Wolf and von Helversen, 1986). The sensitivity of crickets to sound is markedly lower in walking than in inactive animals (Murphey and Palka, 1974; Orida and Josephson, 1978; Schildberger *et al.* 1988). Furthermore, most of the intersegmental interneurones recorded from the neck connectives of *Acheta domesticus* respond differently to multimodal (including mechanical) stimuli during flight and rest (Tomioka and Yamaguchi, 1984).

In crickets, the two distinct components of escape running make different contributions to adjust the overall behavioural response to different stimuli. The running bouts, which generally consist of 6–8 single steps, are constant in duration and attained speed (apart from a slight habituation), seem to be independent of actual sensory input and have features of a reflex-like all-or-nothing behaviour. The duration of the standing phases, in contrast, is a function of the repetition rate

of wind puffs aimed at the cerci. A summation of ascending signals evoked by consecutive wind puffs may be necessary to elicit the next running bout of a standing cricket. The reduction in standing phase durations together with constant walking phase durations results in an increase of the overall running speed in proportion to the stimulus frequency. In the tested range of other stimulus variables, velocity and direction of the wind puffs have no substantial effect on the temporal pattern of locomotion and the actual or mean running speed.

The orientation of escape running with respect to the direction of wind stimulation is not as precise as could be expected for a system optimized for escape from a potentially dangerous disturbance or an approaching predator. Instead, it shows a rather broad variability, indicating the erratic and unpredictable character of escape behaviour, which may be influenced by other sensory inputs which were not controlled in our experiments. Although the average turning tendency is away from the stimulus source in most cases, 20–30 % of all escape reactions contain no rotation or may even contain a turn towards the stimulus. This proportion is roughly similar to results obtained by Camhi and Levy (1988) in a study on the initial turning of the cockroach in response to a wind puff. During our experiments the crickets were free to move their cerci with respect to the air nozzles, thereby causing minor changes in the direction of the wind stream impinging on the cercal receptors. This variability, however, has presumably not impaired the precision of the turning reaction, since the abdominal interneurones, which process sensory information from the cercal filiform hairs and transmit it through the ventral nerve cord, employ a constancy mechanism which compensates for cercus position (Rozhkova, 1980). If a turning tendency during running was obvious in our experiments, it was retained for some seconds. This continuous intended rotation is presumably a consequence of the repeated open-loop stimulation, in contrast to the phasic turning at the beginning of escape in response to closed-loop stimulation of a free-ranging cricket.

Step pattern during escape running

The coxal depressor muscle 77 represents a muscle group consisting of eight individual muscles organized into three subgroups supplied by at least seven motor neurones (Laurent and Richard, 1986*a*), two of them activating the intrinsic coxal depressors that we recorded from in our experiments. These two neurones produce the small- and the large-amplitude potentials that served as indicators of individual steps during locomotion. Laurent and Richard (1986*b*) found the large unit to be active preferentially during fast walking, escape and seeking movements without tarsal contact, whereas it fired exclusively during escape running in our experiments.

Our observations indicate that the alternating tripod pattern of leg movement during escape running is conserved in spite of the standing phases interposed between running bouts. In most cases, the leg triplet which has finished the last step of the previous running bout with a swing phase will start the next bout with a stance phase. During spontaneous walking on the sphere (with its arrhythmic

sequence of variable phases of locomotion and pauses), however, the regular succession of steps is often not preserved between consecutive walking bouts. The internal rhythm of leg coordination seems to be reset or suspended by standing phases in the two types of behaviour. It is not known whether the probability of a change in the stepping pattern rises continuously with longer standing phases or increases abruptly beyond a critical duration of inactivity.

Intracellular recordings during intended locomotion

Schildberger and Hörner (1988) have obtained intracellular recordings from acoustic interneurones in tethered walking crickets. The intended orientation in response to sound stimuli was comparable in specimens dissected for recording and in controls. In our experiments, neither the dorsal preparation nor impaling the prothoracic ganglion with a microelectrode substantially modified the wind-evoked escape behaviour. With respect to the presumed reflex-like nature of the running bouts, it should be noted that dissected crickets often produced running bouts of slightly reduced speed and with distinctly longer standing phases. None of the local interneurones we recorded from in the prothoracic ganglion showed any activity characteristic of escape running, but a correlation with the step pattern of spontaneous walking and escape running in otherwise inactive interneurones was frequently observed. This contrasts sharply with ascending and descending interneurones, whose activity was never coupled to the step pattern but often reflected the more extended running bouts and standing phases, with a general modulation of sensitivity to various stimuli (Hörner, 1992). Bilaterally symmetrical prothoracic dorsal unpaired median (DUM) neurones, which send axons through segmental nerve roots and supply muscles (including leg muscles) of this body segment, represent a group of efferent neurones that do not evoke contractions but modulate the muscle's reaction to motor neurone activity (Evans, 1980). These neurones have recently been shown to spike preferentially before and during escape running without correlation to individual steps of tethered walking crickets (Gras *et al.* 1990). The individual local interneurones differed widely in their anatomical features. Neurones with arborizations in both halves of the ganglion may be particularly important in coordinating the prothoracic legs. This type of function is suggested by the increased spike frequency of the unit shown in Fig. 9 during and immediately before fast rotations to the side contralateral to the soma. Local interneurones, therefore, may play a similar role in the control of walking to that demonstrated by Reichert and Rowell (1986) for the flight system of the locust. These authors have shown that descending sensory information is alternately directed to motor neurones of the left or right ganglion hemisphere *via* sets of local interneurones that are under rhythmic control of the central pattern generator for flight activity.

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