STEREOTYPIC LEG SEARCHING MOVEMENTS IN THE STICK INSECT: KINEMATIC ANALYSIS, BEHAVIOURAL CONTEXT AND SIMULATION

VOLKER DÜRR*

Abteilung für Biokybernetik und Theoretische Biologie, Fakultät für Biologie, Universität Bielefeld, Postfach 10 01 31, D-33501 Bielefeld, Germany

*e-mail: volker.duerr@biologie.uni-bielefeld.de

Summary

Insects are capable of efficient locomotion in a spatially complex environment, such as walking on a forest floor or climbing in a bush. One behavioural mechanism underlying such adaptability is the searching movement that occurs after loss of ground contact. Here, the kinematic sequence of leg searching movements of the stick insect *Carausius morosus* is analysed. Searching movements are shown to be stereotypic rhythmic movement sequences consisting of several loops. The typical loop structure allows the mean tarsus trajectory to be calculated using a feature-based averaging procedure. Thus, it is possible to describe the common underlying structure of this movement pattern. Phase relationships between joint angles, analysed for searching front legs, indicate a central role for the thorax–coxa joint in searching movements. Accordingly, the stereotyped loop structure of searching differs between front-, middle- and hindlegs, with leg-specific patterns being caused by differing protraction/retraction movements in the thorax–coxa joint. A simple artificial neural network that had originally been devised to generate simple swing movements allows two essential features of empirical searching trajectories to be simulated: (i) cyclic movements and (ii) the smooth transition into a search trajectory as a non-terminated swing movement. It is possible to generate several loops of a middle-leg search, but the precise size and shape of the loops fall short of a real-life approximation. Incorporation of front-leg retraction or hind-leg protraction during searching will also require an extension to the current model.

Finally, front-leg searching occurs simultaneously with antennal movements. Also, because leg searching movements are a local behaviour, the legs remaining on the ground continue their stance phase, causing a forward shift of the body, including the searching leg. As a result of this shift, the centre of the searched space is close to the anterior extreme position of the tarsus during walking, representing the location of most likely ground contact according to past experience. Therefore, the behavioural relevance of searching movements arises from the combined actions of several limbs.

Key words: leg movement, searching, stick insect, *Carausius morosus*, artificial neural network, motor control.

Introduction

When walking on a natural substratum, for example the leaf-covered floor of a forest, animals frequently encounter obstacles, changes in slope or gaps. If these surface irregularities are small compared with the size of the animal, they may not involve large changes in the locomotor pattern in order to adapt to them. Rather, known leg coordination mechanisms are sufficient to explain several adaptive properties of the locomotor system (Cruse et al., 1995b). In some instances, however, in particular when encountering gaps, complete extension of the leg may not lead to ground contact, and a correction movement is required to re-establish a foothold. In insects, repeated corrective leg movements have been described in locusts (*Locusta migratoria*; Pearson and Franklin, 1984) and have been termed searching movements because of their active effort to find support. Similar cyclic searching movements have been described in other

invertebrates (e.g. Delcomyn, 1987; Karg et al., 1991) and vertebrates (e.g. Gorassini et al., 1994). Because leg searching movements do not necessarily involve sensory anticipation, e.g. from visual input, but are initiated locally after a lack of ground contact, quantitative analysis of searching movements has been limited to stationary walking animals or even to fixed animals. In insects, the studies of Karg et al. (Karg et al., 1991), Bässler et al. (Bässler et al., 1991) and Bässler (Bässler, 1993) on the stick insect *Cuniculina impigra* have contributed to a good understanding of the sensory control of searching movements and their involvement in the transition from swing to stance phase, but all these studies were limited to a two-joint preparation on a single leg. Despite the fact that the re-establishment of a foothold may, to some extent, be solved locally, i.e. by the leg itself, the functional interpretation of leg searching movements in behaviour requires the concerted

actions of the neighbouring limbs, possibly even of the entire body, to be considered. This is because several limbs may contribute to the efficiency of corrective movements to find a new foothold.

The aim of the present study was to extend our understanding of the functional role of leg searching movements in freely walking stick insects. This involves a quantitative three-dimensional description of tarsus trajectories in body coordinates, and also of the searched space in external coordinates, for all six legs of the animal. Furthermore, I will describe how front-leg searching movements and concurrent ipsilateral antennal movements act in parallel to increase the efficiency of spatial sampling. Finally, the observed movement trajectories of individual legs are simulated by means of an artificial neural network (ANN). In particular, I will investigate the extent to which a small ANN that is part of an existing distributed controller of hexapod walking (Cruse et al., 1998) can explain two major aspects of the empirical data: the cyclic structure of the search and the smooth transition from swing to search by means of a single controller. An earlier attempt to incorporate leg searching movements into a model of hexapod walking relied on separate controllers of the swing and searching movements (Espenschied et al., 1996).

The emerging picture will increase our understanding of limb coordination during walking on rough terrain, and the quantitative description of unrestrained behaviour will assist modelling studies on legged locomotion. Preliminary results of this study have been published previously in abstract form (Dürr, 1999; Dürr, 2000).

Materials and methods

Behavioural analysis

Experiments were carried out on adult female stick insects, *Carausius morosus* Brunner 1907, kept in a parthenogenetic colony at the University of Bielefeld, Germany.

Front-leg searching movements and antennal movements were studied in freely walking animals on a 32 mm wide cardboard bridge of length 350 mm; 185 walks of nine animals were recorded. Between trials, animals were left to walk in pseudo-randomly varied directions along the bridge to minimise learning effects. Care was taken to vary the starting point of the walk. Because front-leg searching movements were studied under normal daylight conditions, a control experiment was performed to investigate the effects of visual input. In this experiment, one animal was blindfolded by reversibly covering its eyes with Protemp II (ESPE) and a superficial layer of black camera varnish (Tetenal). Front-leg joint angles and antennal direction were calculated only for the right side of the animal, because only one laterally placed mirror was used in this experiment, often leaving the left front coxa and the femur–tibia joint invisible. However, the left front tarsus was usually visible, so that three-dimensional measurement of left tarsus trajectories could be compared with right tarsus trajectories.

Experiments on middle- and hind-leg searching movements were carried out on two 40 mm wide cardboard bridges, separated by a gap of variable width; 345 walks of 18 animals were recorded. Typically, the width of the gap was set to 16–17 mm, but some trials were recorded using a gap of 21 mm. To minimise visual input, the immediate environment was black and was illuminated by an infrared spotlight. Mirrors were placed on both sides of the animal for this experiment to provide complete lateral views of both sides.

In both experiments, animals were video-recorded from above and, simultaneously, *via* the mirrors, in lateral view. The video system consisted of a CCD camera (Fricke GmbH, CCD-7250, 1 ms shutter, 50 Hz), a frame code generator (Magnasonic, VTG 200) and an sVHS video recorder (Blaupunkt RTV-925 or similar). Filming distance was 900 mm, and the spatial resolution was 0.32 mm per pixel. For spatial analysis, video sequences were either displayed on a NEXT computer or captured as non-compressed AVI files (Microsoft video format) to an IBM-compatible computer *via* a graphics card (Elsa Victory Erazor) and manually digitised using a custom-written program (Borland Delphi). Digitising error, as estimated from repeated analysis of the same sequence, was less than 1 mm. In each frame, the positions of the end of the coxa, the femur–tibia joint and the tibia–tarsus joint of the leg of interest were digitized in both camera views, along with the base of the antennae and the point mid-way between the hind-leg coxae, to define the body axis.

For front-leg searching movements, the position of the tip of the ipsilateral antenna was also digitized. The resulting three-dimensional pixel coordinates of each point were converted into metric values and used to calculate body coordinates with reference to the current body axis. To calculate leg joint angles, the plane defined by the three joint coordinates per leg was determined. The thorax–coxa joint angle α was defined as the forward rotation of this plane with respect to the sagittal plane of the body (protraction/retraction). The coxa–trochanter angle β and the femur–tibia angle γ were calculated within the plane of the leg (see Fig. 8A). Note that these measures deviate slightly from standard inverse kinematics (e.g. Cruse and Bartling, 1995), mainly because they do not depend upon the definition of a joint axis for the thorax–coxa joint. Rather, a second degree of freedom in the thorax–coxa joint is determined, which has not been calculated in earlier studies: the pronation of the leg plane. However, because pronation is dependent upon protraction and is of relatively small amplitude in stick insect leg movements, it is often neglected by defining a fixed slanted joint axis for inverse kinematics. Because these methodical differences have no impact on the results of the present study, further detailed comparison of the two algorithms will be presented elsewhere (V. Dürr, in preparation). Data analysis was performed using custom-written programs and Origin (MicroCal).

Neural network simulation

The computer simulation of searching movements was based on an artificial neural network (ANN) called SwingNet, which is a module of a distributed controller for hexapod

walking (Cruse et al., 1998). SwingNet controls the angular velocity in three joints during mechanically uncoupled leg movement, i.e. movement without ground contact. The simulation program was written in Pascal (Borland Delphi) and run on an IBM-compatible computer. It included a WindowsNT graphics interface for educational purposes, a study version of which can be downloaded (http://www.uni-bielefeld.de/biologie/Kybernetik/staff/volker/programs.html). A detailed description of the ANN is given in the Results section. The network was trained to approximate empirically measured tarsus trajectories in body coordinates. This was accomplished by means of a random-search algorithm, using the following evaluation function:

$$E = \sqrt{\frac{1}{n}\sum_{i=1}^{n} d_i{}^2}, \qquad (1)$$

where d is the Euclidean distance between corresponding points on the simulated trajectory and its empirical counterpart, and n is the number of corresponding pairs of points. Thus, E represents the mean deviation between the simulated and empirical trajectories. Corresponding pairs of trajectory points were defined such that the empirical sequence with n data points (time base 20 ms) was assigned a sequence of model iterations with a fixed interval $q \in \{1, 2, 3\}$. Simulated trajectories therefore consisted of $q{\times}n$ iterations. For training, starting values of all weights were set at random. In each trial, weights were altered at random by a statistically varying learning rate. All weights were selected with equal probability, and altered weights were accepted if $E(t) < E(t{-}1)$, where t is the trial number. Training was aborted after 300 trials without learning success. Two kinds of training conditions were used: either a single empirical trajectory served as the template, or a set of 10 empirical trajectories was used in parallel. In the latter case, equation 1 was applied separately for each trajectory in the set and the average value of E was used for evaluation. Training involved several thousand random searches for each type of leg. The best results were obtained for middle-leg trajectories, using single trajectory templates, $q{=}2$ and small starting weights (<0.5).

Results

Stereotypic searching movements of the front legs

Front-leg searching movements were investigated in a situation in which the stick insects reached the end of the bridge on which they were walking and stepped across the edge. There was no observable transition from the swing movement that led to the experience of 'lack of ground contact' and the subsequent search. Rather, the front leg engaged in rhythmic searching movements in a smooth continuation of the preceding swing movement, leaving it unclear whether searching is the result of a distinct motor pattern or is part of a non-terminated swing movement.

In total, 35 front-leg searches by five animals were analysed with a sampling interval of 20 ms. Analysis started with the last

posterior extreme position (PEP) before stepping across the edge and ended with the first contact of the leg with either the bridge or the mirror of the video system. Data for 25 searches of right front legs included measurements of joint angles and the direction of the ipsilateral antenna. Ten of these sequences also included one complete preceding step cycle to allow comparison of searching movements with normal stepping movements. For 10 searches of left front legs, only the coordinates of the body axis and the tibia–tarsus joint were measured.

Three-dimensional analysis of the tarsus trajectory in subsequent trials revealed that front-leg searching movements take the form of a rather stereotyped sequence of loops with a fairly constant spatial layout (Fig. 1). The swing movement of the preceding step continued through the fictive anterior extreme position (AEP), i.e. the location where ground contact would have occurred during normal walking, to continue ventro-medially, often crossing the sagittal plane (in 19 of 25 right-leg, and seven of 10 left-leg searches). Having reached this innermost position, the leg was drawn back and the tarsus moved dorso-laterally, often closely following its previous inward trajectory. The tarsus was then moved inwards again to draw a second loop across a more proximal, ventro-medial area. This second loop was often followed by a third, even more proximal, loop and occasionally by further loops. Despite the variability in the tarsus coordinates among trials, searching trajectories always consisted of 2–4 conspicuous loops (Fig. 1), appeared symmetrical for the right and left legs and looked similar in different animals.

Apart from the stereotyped leg movement, a complete description of searching behaviour must include the concerted action of all the legs and the antennae, because their simultaneous movement determines the size and location of the space searched. This will be briefly outlined here and treated in more detail below. During a search, the legs remaining on the ground continue their stance phase, thus shifting the body further across the edge (see Fig. 7). Eventually, the contralateral leg terminates its stance phase and joins the search. The antennae also alter their typical movement pattern (Dürr et al., 2001) and aid the search in the dorsal area (see Fig. 4).

As soon as the searching front legs or an antenna touch a solid object, the behaviour changes immediately, and the insect usually attempts to climb onto the object detected. If the search does not lead to contact with an object, leg searching movements slow down after the third loop, and the movements of the legs and antennae either freeze at their current position or the animal slowly adopts the typical thanatosis posture. In this posture, both front legs are fully extended and protracted to point forward, parallel to the antennae, seemingly extending the body axis and thereby causing twig mimesis (see p. 4 in Bässler, 1983).

Because all searching trajectories recorded here were well described by a series of loops, it was possible to use these loops as common features to reduce each data set to the location and timing of its characteristic features. These reduced data sets allowed an average searching trajectory, representing the
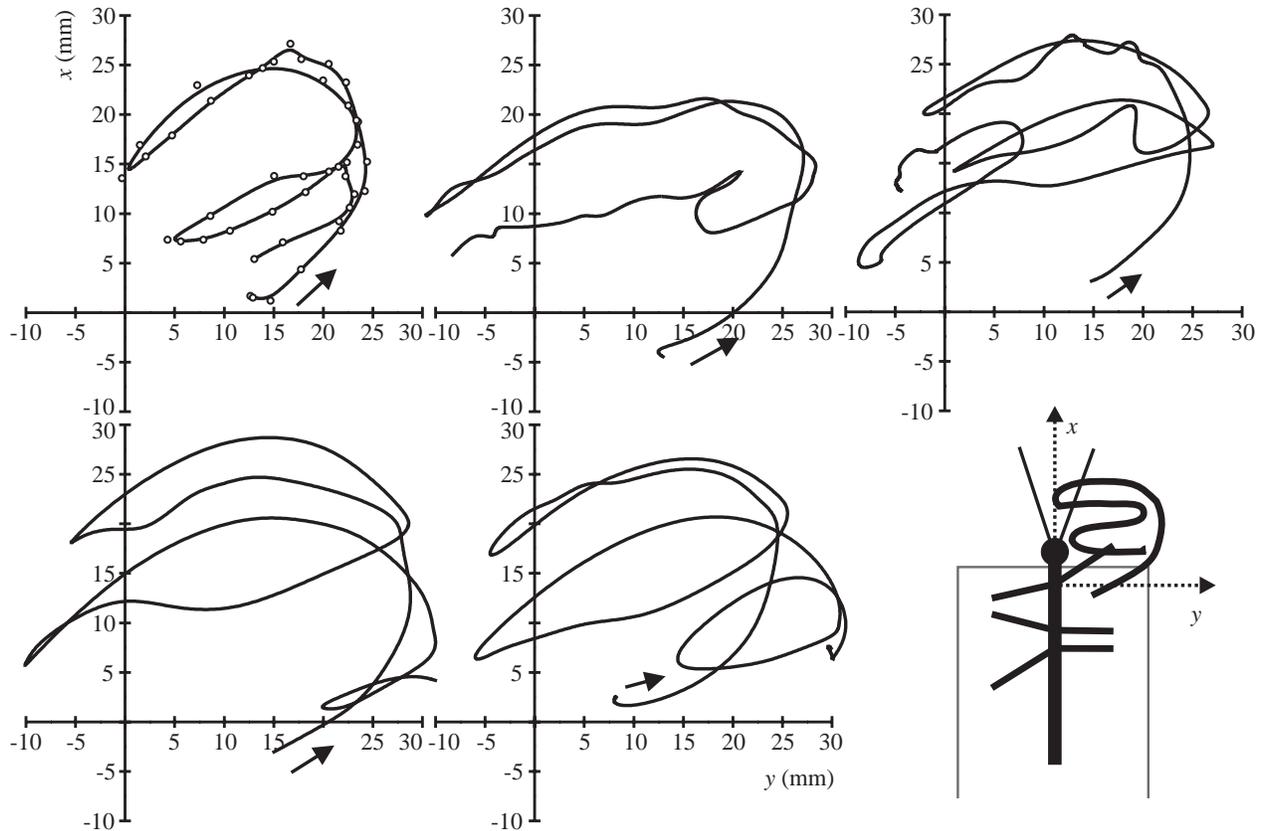
Fig. 1. Top view of tarsus trajectories during searching movements of the front leg. The diagrams show five individual searches by the same animal. The horizontal components of the searching trajectories are plotted in body coordinates with the end of the right front coxa at the origin. The long axis of the body and the orthogonal line within the horizontal plane of the animal define the x- and y-axes, respectively. Open symbols in the top left-hand diagram depict measured data points at 20 ms intervals. The trajectories in all diagrams are B-spline interpolations of measured data points (see Dierckx, 1995) calculated using Origin. The bottom right inset is a top view of the experimental arrangement showing an insect stepping across the edge with its right front leg; the body coordinate system and a schematic trajectory within this coordinate system are also shown.

template underlying all trajectories, to be calculated. Apart from illustrating the basic movement pattern, another purpose of the average trajectory is to simplify the comparison of the behavioural data with the artificial trajectories generated by computer simulation. Here, a feature-based average trajectory was calculated by reducing each three-dimensional trajectory to the six local extreme points (LEPs) of each loop (Fig. 2). Thus, a loop was represented by three pairs of LEPs, equivalent to its dorsal/ventral, rostral/caudal and medial/lateral boundaries, together with the timing of each LEP, to allow temporal reconstruction. The average LEP coordinates were calculated as the arithmetic mean of all LEPs of a kind. The resulting three-dimensional coordinates defined the spatial layout of the average trajectory. To recover the temporal sequence of average LEPs, the median delay with respect to the dorsal LEP of the same loop was determined (Fig. 2A). The median was used instead of the mean because the distributions were rather asymmetric. Arrangement of the average LEPs according to their median timing allowed the average time course of the tarsus position to be recovered (Fig. 2B).

The examples shown in Fig. 2A,B are based on 25 searches

of the right front leg, taken from five animals. The average time course of the three coordinates reveals that the y- and z-coordinates oscillate almost in phase, indicating that the tarsus is moved back and forth diagonally between a ventro-medial and a dorso-lateral extreme position. Superimposed on this diagonal movement is a retraction of the tarsus along the x-axis with low-amplitude oscillations. The tarsus is thus retracted towards the position from where its last swing movement had been initiated.

An example of a feature-based mean searching trajectory is displayed in Fig. 2C, in which the five single trajectories of Fig. 1 were averaged. To allow a detailed comparison of the sequence of LEPs in a single animal (Fig. 2C) with that of a group of five animals (Fig. 2A,B), LEPs are labelled and loops are colour-coded. Close inspection reveals that two LEP pairs occur in reverse order (C1 and M1, L3 and D3) and that V3 occurs before the pair C3/M3 in Fig. 2A but after this pair in Fig. 2C. These observations can be explained by the fact that the ventral, medial and caudal LEPs can occur within a rather short period, such that small phase shifts can lead to a reversal in the timing of these LEPs in small samples (Fig. 2C,D).
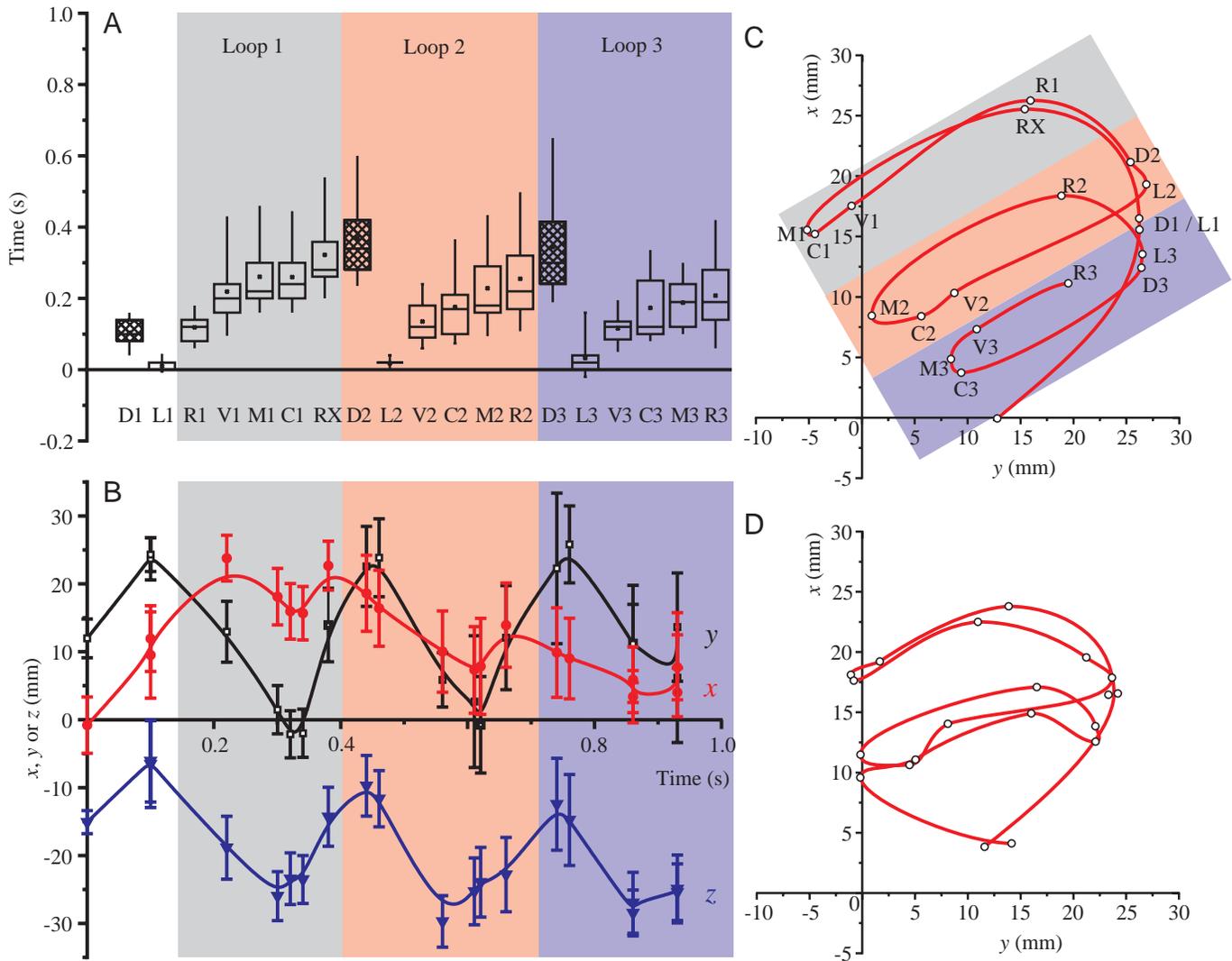
Fig. 2. Calculation of a feature-based average searching trajectory. Each trajectory is reduced to the body coordinates and the delay of six features, the local extreme points (LEPs) per loop, with 1–3 loops per search. (A) The temporal sequences of 25 LEPs of the right front leg of five animals are shown as box-and-whisker plots of their delays. Colour shading identifies the three loops. The LEP delays of subsequent loops were measured with respect to the dorsal LEP of the same loop (hatched boxes). The delay of the dorsal LEP of loop 1 (grey) was measured relative to the last posterior extreme position (PEP). Points are labelled D, V, R, C, L and M for dorsal, ventral, rostral, caudal, lateral and medial, respectively, and numbered 1–3 according to the loop from which they were taken. RX is an additional rostral LEP that always occurs in loop 1. Whiskers denote the fifth and ninety-fifth percentiles. Filled squares denote the mean value. (B) Time courses of LEP coordinates according to their median delays shown in A. The red, black and blue lines are B-spline interpolations of the mean LEPs for the x, y and z components of three-dimensional points. Symbols and error bars depict means and standard errors of the mean (S.E.M.) LEP coordinates. Colour shading as in A, but with a different abscissa. (C) Average trajectory of the five searching movements shown in Fig. 1. The symbols depict the locations of the labelled LEPs. The trajectory is drawn with horizontal, vertical and sloping tangents in the rostral/caudal LEPs, lateral/medial LEPs and dorsal/ventral LEPs, respectively. (D) Average trajectory of five searching movements of the same animal as in C, but after blindfolding.

As a control for the effects of visual input during searching movements, the average searching trajectory was determined in a blindfolded animal (Fig. 2D). Locomotion of a blind stick insect appears to be slower and seemingly more cautious than it is in a seeing animal. Accordingly, the front-leg searching movement of a blind animal is slower than normal (median duration of loops 1–3: 0.34, 0.31 and 0.16 s in Fig. 2C, for a seeing animal; 0.7, 0.64 and 0.36 s in Fig. 2D, for a blind animal), but still shows the conspicuous loop structure of

searches in seeing animals. Therefore, the feature-based averaging procedure was applicable to blindfolded animals. Comparison of Fig. 2C with Fig. 2D, both of which are from the same animal, reveals that the location and size of the first two loops are similar in the seeing and the blind animal, but the third loop shows considerable variation; in particular, the rostral and caudal LEPs occur in reverse order. The observed differences indicate that vision has a considerable effect on the animal's behavioural state. Nevertheless, judging from the

similarities between the first two loops, vision is not necessary for the control of searching movements.

Coordination of joint angles during front leg searching

The average time course of tarsal position during a searching movement (Fig. 2) neglects the role of the leg joints that ultimately control tarsus position. To describe the coordinated action of the three main leg joints, the phase relationship of their movement cycles was determined. To do this, the normalised flexion/extension cycle of the femur–tibia joint (which moves the tarsus in and out) was used as a time base and reference cycle (maximum flexion at phase $\varphi_{Fle}=0$ or $\varphi_{Fle}=1$, maximum extension at phase $\varphi_{Ext}=0.5$). The phase lags of the protraction/retraction cycle of the thorax–coxa joint (which moves the tarsus forwards and backwards) and the levation/depression cycle of the coxa–trochanter joint (which moves the tarsus up and down) within the reference cycle were analysed for each search and are plotted as histograms of minimum and maximum joint angles (Fig. 3).

Because the swing movement of a front leg step begins with a brief retraction, maximum retraction is reached shortly after lift-off [$\varphi=0.09\pm0.05$; mean angle ± mean angular dispersion according to Batschelet (Batschelet, 1965), normalised to the interval (0, 1) with $\varphi_{Ext}=0.5$ and $\varphi_{Fle}=1.0$]. Maximum levation occurs at phase $\varphi_{Lev}=0.22\pm0.12$, i.e. half-way to maximum extension. During walking, maximum extension is equivalent to the time of ground contact, i.e. the anterior extreme position

(AEP). During a search, the levation/depression cycle, on average, maintains a 90° phase shift with respect to the flexion/extension cycle, as indicated by the central locations of the peak values in the depression and levation histograms ($\varphi_{Lev}=0.26\pm0.11$; $\varphi_{Dep}=0.79\pm0.12$; Fig. 3B). In contrast, the mean phase of retraction differs considerably during the initial swing and the subsequent search. The thorax–coxa joint continues protraction of the leg well into the search, reaching maximal protraction shortly before maximal flexion. After that, mean retraction and protraction lead mean extension and flexion, respectively, by a small phase shift ($\varphi_{Ret}=0.49\pm0.14$; $\varphi_{Pro}=0.88\pm0.1$; Fig. 3C). This corresponds to an almost reversed timing compared with normal walking, in which maximal extension and flexion occur at around the end of the swing phase (protraction, $\varphi_{Pro}\approx0.5$) and stance phase (retraction, $\varphi_{Ret}\approx1.0$), respectively.

Simultaneous antennal searching

If a stick insect steps across an edge, searching movements of the front legs are accompanied by a change in the pattern of movement. During forward walking, stick insects move their antennae in a characteristic way that is spatio-temporally coupled to the movement of the ipsilateral front leg (Dürr et al., 2001). As soon as a stick insect begins a searching movement with a front leg, the ipsilateral antenna ceases its regular 'walking' pattern and sweeps increasingly through the space immediately ahead of the animal. To illustrate the

Fig. 3. Joint angle coordination in the front legs during searching. (A) Schematic diagram of the movement sequence of a searching right front leg. The body coordinate system is indicated by dotted lines, and the solid line depicts the long axis of the body. The filled circle marks the front end of the body axis. Levation of the femur (tarsus moves up) leads extension of the tibia (tarsus moves out), and depression of the femur (tarsus moves down) leads flexion of the tibia (tarsus moves in). Depression of the femur does not result in ground contact, so protraction of the leg continues almost until maximal flexion of the tibia. Retraction is then concurrent with extension, and protraction is concurrent with flexion. (B) Phase shift of the levation/depression cycle (coxa–trochanter joint) relative to the normalised flexion/extension cycle (femur–tibia joint, $\varphi_{Ext}=0.5$ and $\varphi_{Fle}=1.0$, bin width 0.05 cycles), expressed as histograms of phase lag (φ) to maximum levation (white or grey) and maximum depression (black). (C) Phase shift of the protraction/retraction cycle (thorax–coxa joint) relative to the normalised flexion/extension cycle, expressed as histograms of phase lag to maximum retraction (white or grey) and maximum protraction (black). PEP (posterior extreme position) indicates the last ground contact and the start of the swing phase and subsequent searching. Grey columns indicate the maximum angles reached during the last swing phase preceding the actual search. Arrows and values indicate the median time of each femur–tibia joint half-cycle. Data are from 25 searches of right front legs taken from five animals.
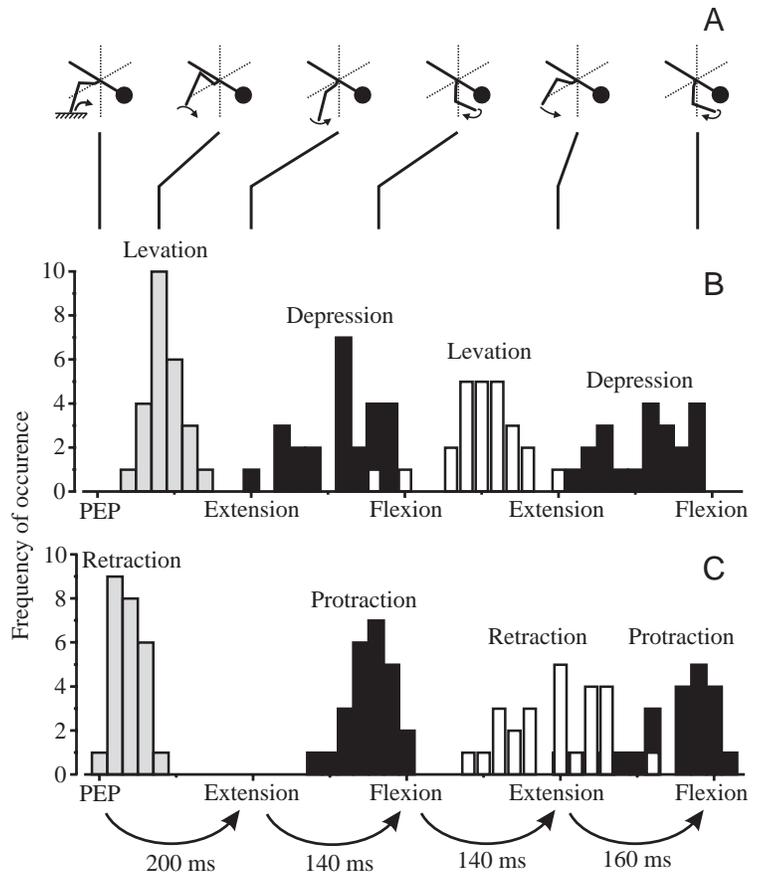
Table 1. *Probability of each leg stepping into a gap*

	Front leg (%)		Middle leg (%)		Hind leg (%)	
	Left	Right	Left	Right	Left	Right
Relative frequency	49.0±2.7	58.8±2.6	40.3±2.6	36.5±2.6	22.6±2.3	21.4±2.2
Cruse (1979)	65.2±2.2		47.7±2.3		24.8±2.0	

Relative frequencies (±95 % confidence intervals, N=345 steps by 18 animals) for all six legs of stepping into a gap 16–17 mm wide. Data from Cruse (1979) for a gap of 15 mm are also shown (means ± S.D.).

changes in sampling probability of the ipsilateral antenna, Fig. 4 presents density plots from 15 step cycles during normal walking and from 25 searches. In addition, the changes in antennal and leg movement trajectories are illustrated by a representative single pair of sequential step and search patterns.

During a normal step cycle of a front leg, the ipsilateral antenna completes a single retraction/protraction cycle (back and forth) and two levation/depression cycles (up and down). During a search, the ipsilateral antenna is depressed soon after 'lack of foothold' and remains in the frontal region for a second upstroke. Although the antennal movement pattern appears to be more variable during searching than during walking, it is evident from the density plots that the probability of the antenna pointing into the frontal 30° sector is increased by almost 20 % with respect to the step cycle (see histograms in Fig. 4). The probability of the antenna pointing into the 30–60° sector decreases accordingly. Interestingly, the antennal tip hardly ever crosses the sagittal plane during a search, whereas the ipsilateral tarsus does so 14 % of the time. The density plots of the searching tarsus and the ipsilateral antennal tip overlap in the region where the leg typically touches the ground during walking, i.e. at the AEP. The altered antennal movement shows that searching behaviour, in spite of the stereotyped movement of a searching front leg, is not limited to a single leg, but also involves the actions of other appendages. The ipsilateral antenna extends the search space of the ipsilateral front leg to an adjacent dorso-anterior sector.

Differences between the front, middle and hind legs

The searching movements of the front legs were shown to follow a stereotyped pattern, so it was of interest to determine whether the same or a similar pattern of movement could be observed in the legs of the meso- and metathorax, i.e. the middle and hind legs. To make the stick insects initiate searching movements with their middle and hind legs at a defined location,

two bridges were used, separated by a gap of variable width. In total, 345 gap crossings by 18 animals were filmed. The frequency with which a front leg stepped into the gap is slightly lower than the ratio of average step length to gap width (16/24=0.667, compared with 0.49 and 0.588 for left and right front legs, respectively). This may be because the long tarsus decreases the effective width of the gap by a few millimetres. The relative frequency with which a middle leg stepped into the gap was lower than for the front legs and even lower for the hind legs (Table 1), indicating ipsilateral transfer of information. The conditional probabilities that adjacent legs will step into the gap (ipsilateral coincidences) and those for bilateral coincidences are listed in Table 2. The fact that the relative frequency that both front legs will step into the same gap is only slightly lower than would be expected for independent events [P(left)×P(right)= 28.8 %; P(contra/ipsi)=26.4±2.3 %] suggests little heterolateral exchange of information. Interestingly, the relative frequencies with which both middle legs or both hind legs step into the same gap are significantly lower than the expected frequencies for independent events (the difference is larger than the confidence interval of the binomial distribution). This may indicate the presence of heterolateral exchange of information for the middle and hind legs.

The middle legs and hind legs always performed a cyclic searching movement after stepping into the gap. The tarsus trajectories of the middle leg typically consisted of one or two loops before the tarsus touched the posterior edge of the gap. Hind-leg searching movements were also cyclic, but a strong forward component increased the chance of the tarsus touching the front edge of the gap before completion of the first loop. Therefore, only few hind-leg trajectories contained a whole loop. The cyclic nature of middle- and hind-leg searching trajectories allowed the same feature-based averaging procedure as used for the front legs to be applied. Detailed analysis of trajectories and joint angles included 22 middle-leg searching movements by four animals and 17 hind-leg

Table 2. *Conditional probabilities that pairs of legs will step into the same gap*

	Front leg (%)		Middle leg (%)		Hind leg (%)
Ipsilateral pairs	21.4±2.2	24.6±2.3	17.4±2.0	13.3±1.8	–
Contralateral pairs	26.4±2.3 (28.8)		4.9±1.1 (14.7)		0.6±0.4 (4.8)

Mean relative frequencies (±95 % confidence intervals) that pairs of neighbouring legs will step into the same gap are shown.
Values in parentheses show the expected probabilities for independent contralateral events.
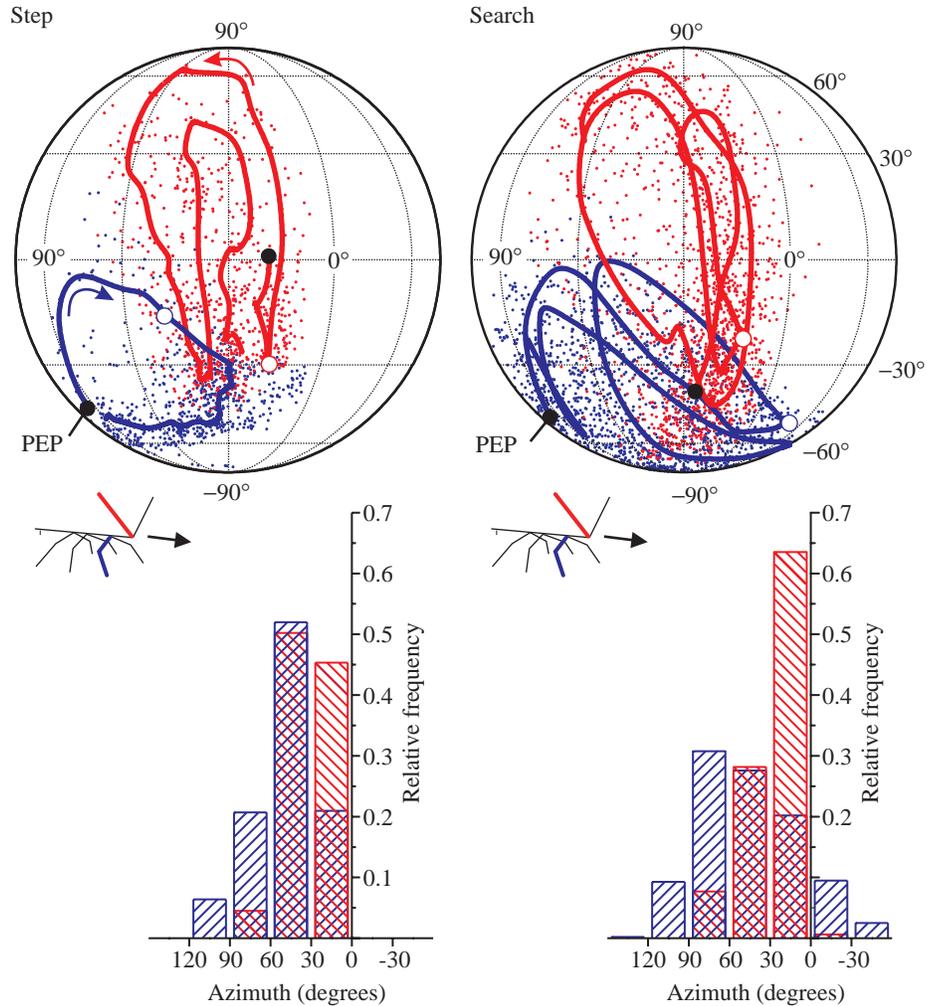N=345 steps by 18 animals.

Fig. 4. Sphere plots of polar coordinates (azimuth and elevation) of the right antennal tip (red) and the right front leg tarsus (blue) with the centre of the sphere located at the base of the antenna and the end of the right front coxa, respectively. Spheres are rotated medially by 30°. Insets indicate the orientation of the body axis, which defines the zero coordinates. Small dots show the locations of 735 (left) and 1432 (right) data points measured in 15 normal steps (left) and 25 searches (right). Blue and red lines depict representative coincident trajectories of the antenna and front leg, respectively. Step and search trajectories show immediately consecutive episodes. Black circles indicate the starting points of each trajectory, corresponding to the posterior extreme position (PEP) in the case of the front leg. Open circles indicate coincident locations on the antennal and tarsus trajectories. The histograms show the relative frequencies with which the antenna (red) and leg (blue) point into a given 30° sector of the sphere, delineated by the meridians.

searching movements by four animals (the selection criteria were at least 1.5 completed loops per middle-leg search or one complete loop per hind-leg search; at least two searches on both sides per animal). Data from the right and left legs were pooled (see legend to Fig. 5).

The resulting average trajectories in a body-fixed coordinate system are shown in Fig. 5, for all 35 front-leg searches. Corresponding to the number of loops per search, the area covered by the trajectories is largest for front-leg searches and smallest for hind-leg searches. The first loop is largest for the front legs and smallest for the hind legs. The average front-leg search shows increasing retraction from loop to loop, causing each loop to lie posterior to the preceding one, but the average middle-leg search does not show such retraction. As a consequence, the two loops of the middle-leg trajectory are superimposed. All the legs show the cyclic ventro-medial to dorso-lateral cycle of the tarsus trajectory, as described above for the front leg. Because of the upward inclination of the body axis during walking, tarsus trajectories are further below the body horizon in the front legs than in the middle and hind legs.

The main difference between the searching movements of different legs was related to retraction and protraction, and Fig. 6 presents the changes over time of all individual traces

of the thorax–coxa joint angle α during searching. The different y offset of the thorax–coxa joint angle in different legs reflects the different locations of their working range relative to the frontal plane through the coxae (thorax–coxa angle 0°). The variability among individual traces is fairly low during the initial swing movement, i.e. the fast forward protraction of the leg, and increases during searching. The working range of the thorax–coxa joint during searching is largest for the front legs. The average time course for each kind of leg, corresponding to its most probable thorax–coxa joint angle at any given time, shows virtually the same slope and amplitude for the initial swing movement. However, the time course then takes on a negative slope for the front leg, a positive slope for the hind leg and an intermediate value for the middle leg (Fig. 6). This difference in slope reflects an average retraction of the front legs, zero retraction of the middle legs and continuous protraction of the hind legs.

So far, leg movements have been described either in body coordinates or as joint angles, to explain *how* the stick insect searches. However, a functional evaluation of searching behaviour must involve a description of the searched area in external coordinates, to explain *where* the stick insect searches. When plotted in external coordinates, the tarsus trajectories of
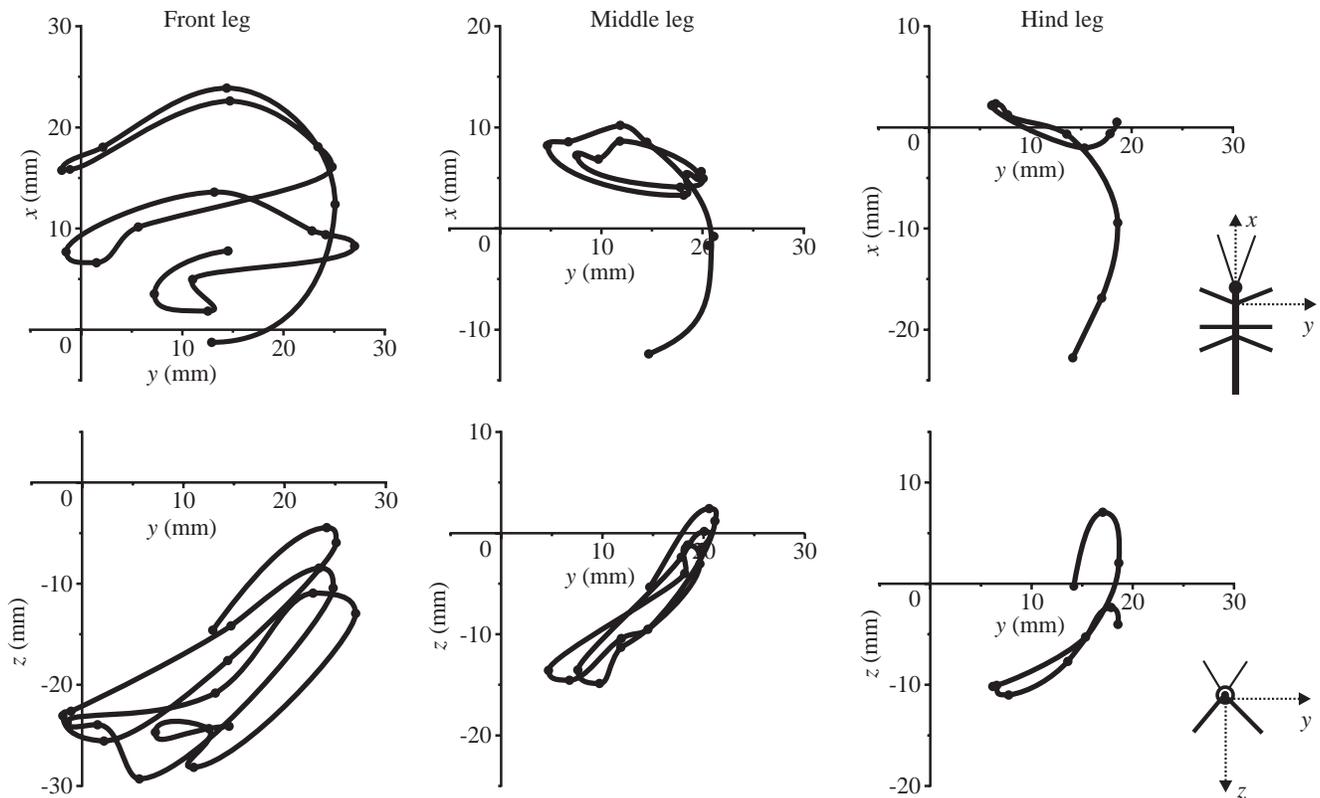
Fig. 5. Average searching trajectories of the front leg (left-hand panels), middle leg (middle panels) and hind leg (right-hand panels). The positions of the tarsus were measured in the body-fixed coordinate system relative to the respective coxa and are plotted as *x,y* coordinates (top view, top panels) and *y,z* coordinates (hind view; bottom panels), as indicated by the insets on the right. Front-leg searches were recorded after an animal had stepped across the end of the bridge. Middle- and hind-leg searches were recorded as the animal stepped into a 16 mm wide gap in the bridge. Data from left and right leg searching movements were pooled. Front leg, *N*=10+25 (5); middle leg, *N*=10+12 (4); hind leg, *N*=8+9 (4); where numbers denote left+right searches and the number of animals (in parentheses). Filled circles are local extreme points (LEPs) calculated according to the feature-based averaging procedure described in Fig. 2. Trajectories were drawn to have their vertical, horizontal and intermediate tangents in the LEPs according to the boundaries set by the respective LEPs.

searching front legs appear rather compressed in the walking direction of the animal (Fig. 7B) relative to the body-centred system (Fig. 5). This is because the legs remaining on the ground continue their stance movements, thereby pushing the body, including the searching leg, forwards. In spite of the continuous retraction of the front leg during searching, the
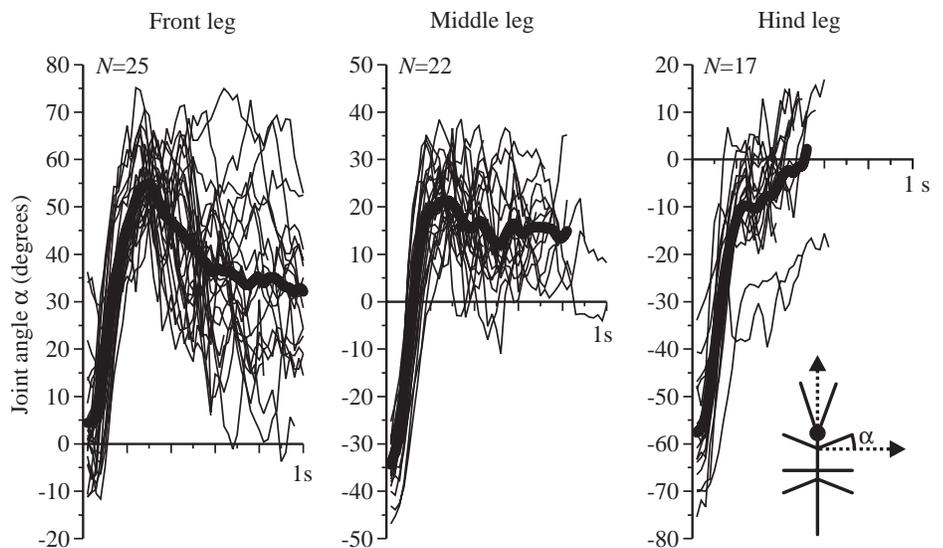

Fig. 6. Protraction/retraction of the front leg (left), middle leg (middle) and hind leg (right), i.e. the thorax–coxa joint angle α (see inset), during swing and subsequent searching. Thin lines show individual measurements. Thick lines show the mean values for all traces (at least five traces per point) to emphasize differences among legs. Only the right leg trajectories were included for the front leg because joint angles were not analysed for the left front legs.
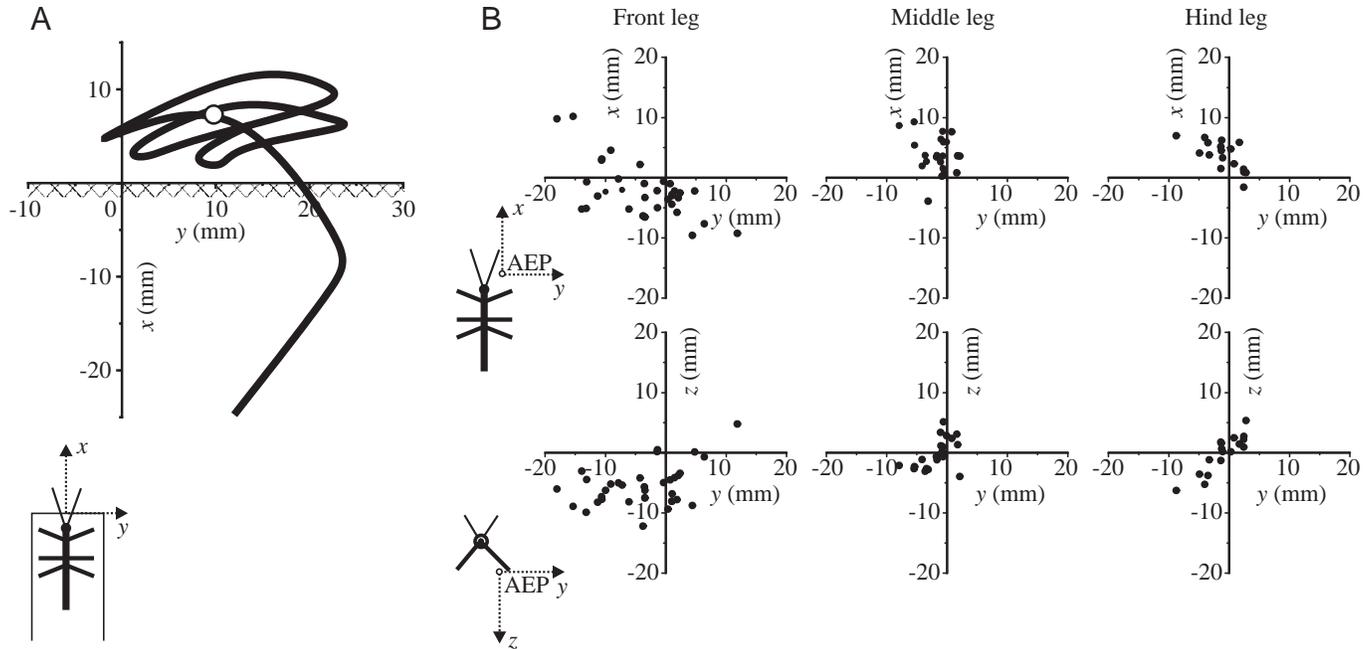
Fig. 7. External searching space in relation to the anterior extreme position (AEP). (A) Top view of the average front-leg tarsus trajectory in the external coordinate system (compare Fig. 5, top left), i.e. after adding the average forward movement of the body. The open circle marks the location of the AEP. The *x*-axis is aligned with the long axis of the body, whereas the *y*-axis is chosen arbitrarily as the edge of the bridge (see inset). (B) Location of the centre of the searched space relative to the fictive AEP, i.e. the location where the tarsus traverses the plane of the walking surface. The coordinate systems of external space are aligned with the body coordinate system but centred on the fictive AEP (top, top view; bottom, hind view; as shown in the insets). Centre points were calculated as the average tarsus position vector for an entire search, starting with the fictive AEP. Same data sets as in Fig. 5.

tarsus actually sweeps across an area approximately centred on the fictive AEP. To investigate this further, all searching movements were analysed with respect to the location of the fictive AEP, which was defined as the coordinate position where the tarsus would have touched the surface if there had not been a gap. Fig. 7B shows the centres of all tarsus trajectories relative to the location of the fictive AEP, calculated as the average coordinate vector of all tarsus positions after having passed the fictive AEP.

For the front leg, the centres of searched areas are most often located proximal to and below the fictive AEP. The medio-lateral coordinates of the centre points are more variable than the dorso-ventral or antero-posterior coordinates. Middle-leg and hind-leg searches have their centre points mostly distal to the fictive AEP, whereas their dorso-ventral and medio-lateral coordinates are scattered around zero. Front-leg searches therefore have a backward tendency, whereas middle- and hind-leg searches have a forward tendency. Despite the marked protraction in hind-leg searches (Figs 5, 6), the forward shift of the centre of the search area is similar to that of the middle legs. This is probably because of the early tarsus contact with the far edge of the gap, leaving little time for the motion of the body to cause a pronounced shift.

Neural network simulation

Rather than using separate controllers for swing and searching movements (as used by Espenschied et al., 1996),

the following simulation study attempts to use a single controller to generate both types of leg movement. Furthermore, the study investigates the extent to which the observed behavioural data can be modelled by an existing leg controller (Fig. 8). The artificial neural network (ANN), on which the simulation will be based, is a module of WalkNet (Cruse et al., 1998), a distributed ANN controller of hexapod walking specifically designed to model stick insect walking behaviour. In WalkNet, leg movements without ground contact are controlled by a network of three neuroids, each of which drives the angular velocity of one of three leg joints. The modelled angles are those of the thorax–coxa joint, the coxa–trochanter joint and the femur–tibia joint, labelled α, β and γ respectively, according to their proximal-to-distal sequence along the leg (Fig. 8A). Because each of these joints, at least to some extent, can be moved independently, three control elements are needed to control the leg. Each control element may be simulated as an integration controller, as drawn in Fig. 8B, where the weighted sum of an internal reference value, α target (or α_T), and a sensory input about the current joint angle α drive the protractor/retractor muscle system, which in turn changes the angular velocity $\dot{\alpha}$ and, as a consequence, the current joint angle α. Three analogous versions of this control element can be networked into the ANN drawn in Fig. 8C. If all weights except those connecting the external reference and the sensory input to the respective neuroid are set to zero, three independent joint controllers of
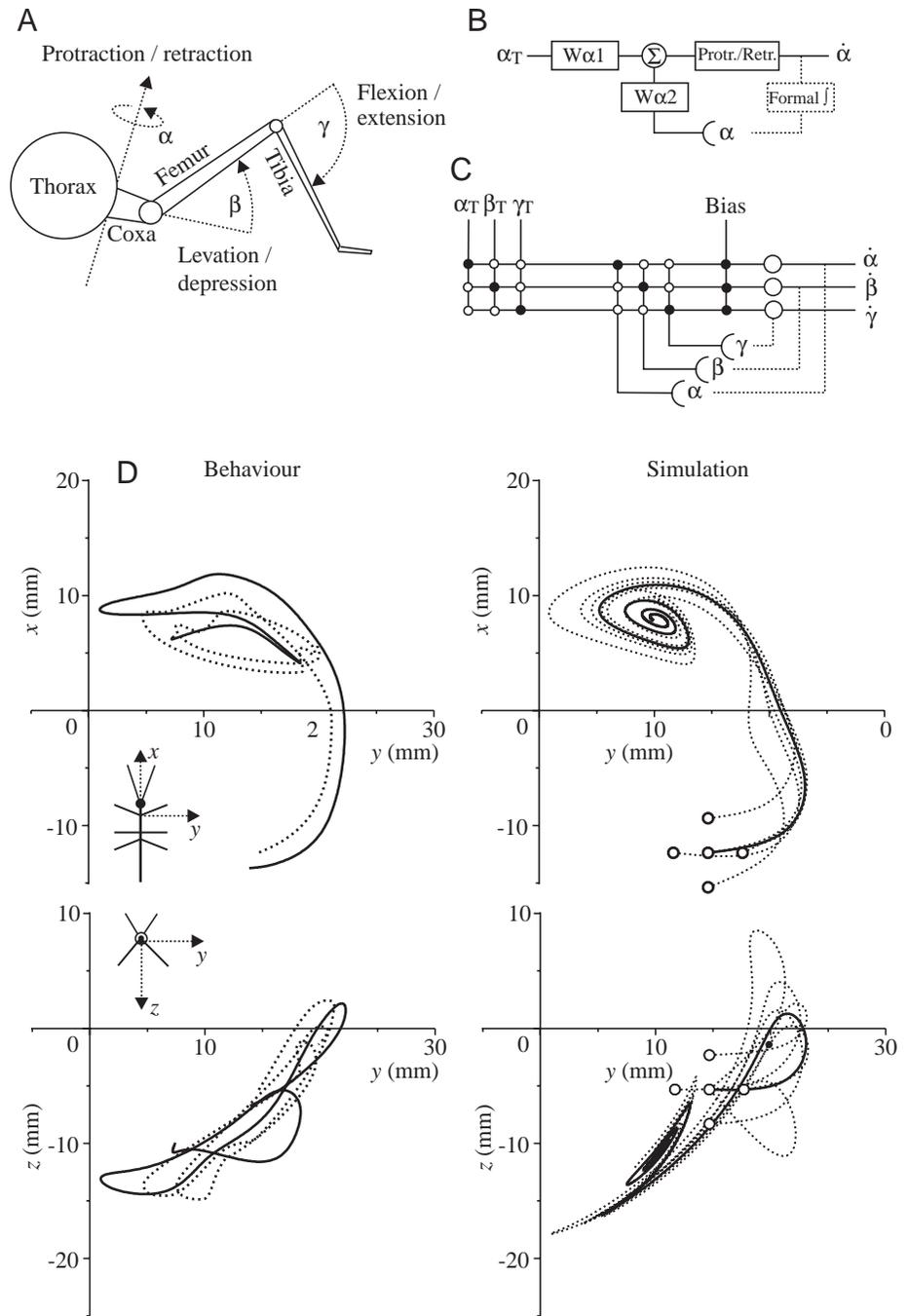
Fig. 8. Artificial neural network (ANN) model for searching movements and a simulation example. (A) Schematic drawing of a stick insect leg with three main joints, each of which allows rotation with one degree of freedom (α, thorax–coxa joint; β, coxa–trochanter joint; γ, femur–tibia joint). (B) Control circuit for a single joint (using α as an example). An internal target angle α_T and the afferent external value of α are weighted by $W_{\alpha 1}$ and $W_{\alpha 2}$, respectively, and summed so as to drive the protractor/retractor muscle system (Protr./Retr.). Muscle contraction causes changes in angular velocity $\dot{\alpha}$ and, as a consequence of movement, a change in joint angle α (by formal integration, $\int$). (C) SwingNet is an artificial neural network consisting of three neuroids, each of which represents a single-joint controller as in B (with target values α_T, β_T and γ_T, afferent inputs α, β and γ and movement outputs $\dot{\alpha}$, $\dot{\beta}$ and $\dot{\gamma}$). Filled circles depict the weights of joint-specific input/output connections. Open circles depict the weights of interjoint connections. A bias input, constantly set to 1, allows an activation offset to be introduced. (D) Comparison of behavioural measurements and simulation results using SwingNet as shown in C. Left: a searching trajectory of a middle leg (solid line) and the average trajectory as shown in Fig. 5 (broken line). Right: an example of a tarsus trajectory generated by SwingNet after training to the single trace on the left (solid line) and four trajectories of the same ANN with different starting points (dotted lines).

the kind described in Fig. 8B will run in parallel. To allow modelling of interactions between two or more joints, further weights are introduced to connect all inputs with all neuroids. Moreover, a bias term allows individual thresholds for each neuroid to be introduced. Training this ANN to generate the empirically measured tarsus trajectories can be managed by a random search algorithm (see Materials and methods).

A result of the simulation is illustrated in Fig. 8D, together with a single trajectory of a middle-leg searching movement that it was trained to approximate. The average trajectory of middle-leg searching movements is also redrawn from Fig. 5 for comparison. The example shows that the WalkNet module

is capable of generating cyclic searching movements together with the preceding swing movement. Both a targeted swing movement and the cyclic searching movement can be explained by the properties of the same networked control circuit. Moreover, starting from different PEPs shows that the ANN is capable of generalisation. Interestingly, an anterior shift of the PEP would lead to a physiologically impossible trajectory into the ground, with the result that the ANN could only commence a swing movement behind a certain position. This is reminiscent of the position control of the PEP (Bässler, 1977; Cruse, 1985). Nevertheless, the simulation has obvious shortcomings. Typically, physiologically meaningful solutions

of the simulation lead to weight matrices that generate either a plain swing trajectory with no terminating loops or a trajectory with a terminal spiral of loops. Although the shape of the swing trajectory and the location of the spiral centre can be varied by different sets of weights, the size of the spiral is typically smaller than for the empirically observed loops. Also, the spiral is a useful approximation of the average middle-leg trajectory, with its superimposed loops, but it falls short of generating the continued retraction or protraction observed in the front and hind legs. Trajectories with different starting conditions take slightly differing routes but terminate in spirals located in the same region (Fig. 8D). Thus, despite the shortcomings mentioned above, the simulation shows unequivocally that cyclic searching movements of the middle leg can be modelled as a non-terminated swing movement to become a robust feature of a simple ANN controller. There is no need for separate control structures for swing and search. Still, the ANN has yet to be extended to explain front- or hind-leg-like movements.

Discussion

Leg searching movements of the stick insect *Carausius morosus* have been shown to be stereotypic, rhythmic movements consisting of several loops (Fig. 1). The location and timing of local extreme points of individual tarsus trajectories allows a feature-based average trajectory (Fig. 2), describing the common underlying structure of this movement pattern, to be calculated. In a searching front leg, the movement cycles of the femur–tibia and coxa–trochanter joints have a similar phase relationship to those during walking, whereas the cycle of the thorax–coxa joint undergoes a marked phase shift after passing through the expected AEP by intermitting prolonged protraction phase (Fig. 3). Front-leg searching is accompanied by an altered movement pattern of the ipsilateral antenna (Fig. 4). A comparison of the searching trajectories of different legs reveals a stereotyped loop structure for all legs, but with the size and antero-posterior location of the loops differing (Fig. 5). The leg-specific patterns are caused by differing protraction/retraction movements in the thorax–coxa joint (Fig. 6). Because searching movements are performed while the legs remaining on the ground continue in stance phase, the tarsal trajectories appear compressed in external coordinates, with the centre of the searched space occurring close to the expected AEP (Fig. 7). The mean location of search centres differs among legs. Finally, a simple ANN, originally devised to generate swing movements, allows empirical searching trajectories to be simulated to some extent (Fig. 8). While it is possible to generate several loops for a middle-leg search as a non-terminated swing movement, the exact size and shape of the loops fall short of a real-life approximation, particularly for the front and hind legs.

Stereotypic searching movements as non-terminated swing movements

The leg searching movements of insects were first studied by Pearson and Franklin (Pearson and Franklin, 1984) in the locust *Locusta migratoria*, and front-leg searches were described as a sequence of several rapid elevation/depression cycles with marked extension of the distal joints. The speed of searching cycles in the locust (up to $8\,\text{cycles}\,\text{s}^{-1}$) was approximately twice the speed observed in the stick insect ($3–4\,\text{cycles}\,\text{s}^{-1}$). As for stick insects, locust leg searching movements were terminated upon contact with an object. Karg et al. (Karg et al., 1991), using a preparation of the stick insect *Cuniculina impigra* in which movement was restricted to the two distal joints of a single front leg, were the first to give a quantitative description of joint angles during leg searching movements in insects. The searching movements of the remaining leg segments were found to follow a stereotypic pattern, with femoral depression leading tibial flexion during the downward phase and a rapid extension of the femur–tibia joint accompanied by slower levation of the coxa–trochanter joint. Thus, the phase relationship in their preparation is different from that described in Fig. 3, where the depression/levation cycle of the coxa–trochanter joint always leads the flexion/extension cycle of the femur–tibia joint. For a direct comparison of joint angle coordination during searching, the results of Karg et al. (Karg et al., 1991) and those from the present study are plotted in Fig. 9. Searching movements of *Cuniculina impigra* are executed within a narrower range of joint angle β and a wider range of joint angle γ than searching movements of *Carausius morosus*, but include the range assumed at the end of the swing phase in *Carausius morosus*. The ablation experiments of Karg et al. (Karg et al., 1991) resulted in altered leg movements, so it is likely that the difference illustrated in Fig. 9 is not solely a species difference but is also a consequence of the fixed thorax–coxa joint and the altered sensory input caused by the restriction in this preparation.

In a follow-on study of the one-legged *Cuniculina impigra* preparation, extracellular recordings from the protractor and retractor nerves (nl2 and nl5, respectively) revealed weakly modulated activity during searching, with maximum activity in nl5 at maximum elevation (Bässler et al., 1991). The same study reported the same result for comparative experiments on *Carausius morosus* middle legs. Therefore, the phase relationship between attempted protraction/retraction of the immobilised leg and the movement cycle of the coxa–trochanter joint resembled that described in Fig. 3 for the unrestrained animal. Moreover, nl2 activity in *Cuniculina impigra* was pronounced during the grasping reaction that occurs after interruption of a downward movement. This intended forward movement of the leg is reminiscent of the forward force exerted by a *Carausius morosus* leg at the swing–stance transition (Cruse, 1976; Bartling and Schmitz, 2000). On the basis of this finding and other similarities between searching and swing movements, Bässler et al. (Bässler et al., 1991, p. 513) concluded that 'the swing phase of walking and searching are the same behavioural element with the only difference that the swing phase is terminated by touching the ground'. Moreover, the prolonged protraction
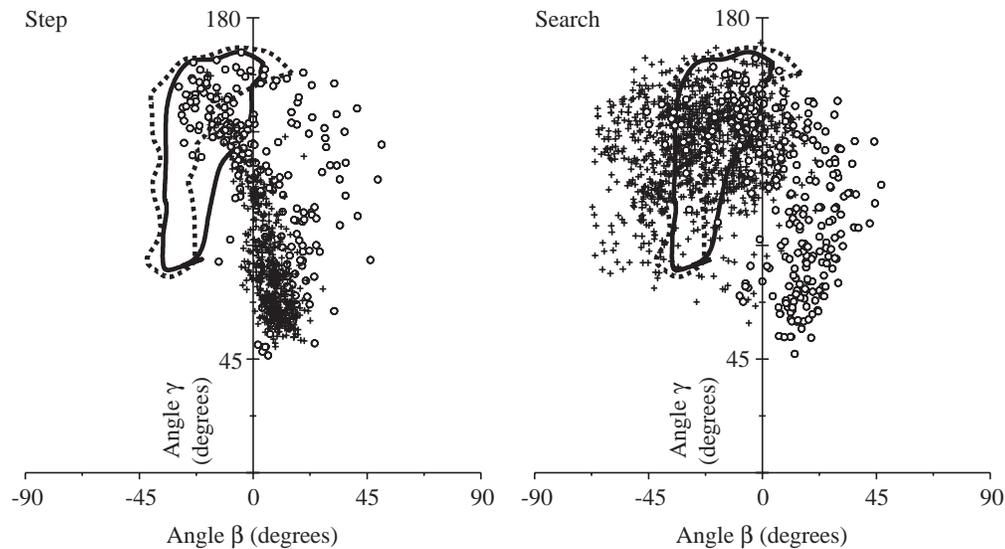
Fig. 9. Comparison of the joint angles of *Carausius morosus* and *Cuniculina impigra* during searching and normal steps. The relationship between angle γ (tibial extension/flexion) and angle β (femoral levation/depression) for single frames was analysed for 15 front-leg steps cycles (left) and 25 front-leg searches (right). Open circles depict pairs of angles during swing movements, and crosses depict those during the subsequent stance (left) or searching movement (right). For comparison with the results of Karg et al. (1991) for the front legs of *Cuniculina impigra*, solid and broken lines delimit the data range of their Fig. 4 for upward and downward searching movements, respectively. Note that angle γ is plotted as the inner angle between the femur and tibia, following Karg et al. (1991), not as shown in Fig. 8A. Therefore, γ=180° indicates complete extension of the leg.

in the early phase of searching (Figs 2, 3) together with the finding that the forces exerted during the final third of a swing movement show no sign of expected ground contact (Cruse and Bartling, 1995) suggest that protraction is probably not a consequence of ground contact but is instead dependent on the current joint angles and/or on central input. Finally, the absence of any sign of a kinematic transition from swing to search in the measured trajectories (e.g. Fig. 1) and the finding that both swing and searching can be modelled with the same ANN controller (Fig. 8) show that the cyclic search does not need to be produced as a distinct motor pattern but can be explained as the terminal part of a swing movement.

On the basis of observations on the coxal extensor burst cycle during leg movements of the cockroach, Delcomyn (Delcomyn, 1987) concluded that searching is the result of a different motor pattern from that for walking. Provided that there is a hierarchically superior neural structure that selects either swing or stance as one of two mutually exclusive motor actions (Schmitz and Haßfeld, 1989), the results of Delcomyn (Delcomyn, 1987) agree with the interpretation that a swing movement continues into the motor pattern of searching unless the swing/stance selector switches to stance and continues the walking motor pattern. However, this opposes the claim made by Delcomyn (Delcomyn, 1987) that righting cockroaches can produce a motor pattern similar to walking. Because righting, like searching, is a movement pattern devoid of sensory signals provided by ground contact and/or a mechanical load, Delcomyn concluded that there are two centrally generated motor patterns in cockroaches (walking/righting and searching).

The view of searching as a non-terminated swing phase is also supported by results on vertebrates, in which the extensor muscle motor pattern shows a decline in activity independent of ground contact (humans, Melvill-Jones and Watt, 1971; cat hind leg, Gorassini et al., 1994). From studies on spinalised (Hiebert et al., 1994) or decerebrate (Hiebert et al., 1995) cats, it is known that the swing/stance transition in cats is induced by extensor group 1 afferents. Afferent activity causes exit from a pre-programmed spinal motor program that would otherwise, i.e. in the absence of ground contact, perform a corrective movement reminiscent of the searching movements of insects.

Differences among legs

In spite of their morphological similarities, each pair of legs of the stick insect have different ranges of action (Cruse, 1976), exert different forces (Cruse, 1976; Bartling and Schmitz, 2000) and show differing inherent walking directions (Bässler et al., 1985). Furthermore, an ANN simulation study required a different weight matrix for each leg to make the swing movements generated match the empirical data (Cruse et al., 1995a). The latter finding indicated the need for specific interactions between neighbouring joints in each leg (see below). On the basis of the interpretation that searching movements are non-terminated swing movements, it was of interest to determine the whole swing movement sequence, i.e. including the terminal search, for each leg.

Searching movements of the middle and hind legs were studied in an experimental situation equivalent to that used by

Cruse (Cruse, 1979), and the description of the stick insect behaviour given by Cruse was confirmed: stick insects step into the gap less often with the middle leg than with the ipsilateral front leg and even less often with the hind leg. The systematically larger relative frequencies given by Cruse (Cruse, 1979) may be due to different walking surfaces (styrofoam, Cruse, 1979; cardboard in the present study), which are known to influence step length (T. Kindermann, unpublished observations) and, as a consequence, alter the probability that a leg will step into a gap of a given width. Table 2 lists the conditional probabilities of a leg stepping into a gap after another leg has already stepped into it. These data suggest that the probability of both front legs stepping into a gap can be predicted by considering the two legs to act independently. For the middle and hind legs, some heterolateral influence on the execution of the trailing leg movement may exist, but ipsilateral coordination mechanisms (Cruse, 1990) could also contribute to this effect.

When the expected foothold is absent, all legs perform cyclic searching movements, but the trajectories of these movements differ in their spatial properties (Fig. 5). The middle legs are protracted during swing and remain at that level of protraction throughout the search. In contrast, the front legs are retracted, sometimes almost returning to the thorax–coxa angle at the PEP, whereas the hind legs are continuously protracted. In other words, all legs search towards the centre of the body. This tendency could be due either to a different motor program for different legs or to a hitherto undescribed coordination mechanism acting on legs in the swing phase. Further experiments are required to distinguish between these alternative hypotheses. So far, coordination mechanisms have been described as being active only during the stance phase (e.g. Cruse, 1990; Cruse et al., 1995b), but recent results on the grasping reaction at the end of a swing phase (Cruse et al., 1998) have provided the first evidence of a coordination mechanism active during swing movements.

Because the thoracic ganglia and legs of insects have evolved as metameric structures, the existence of common properties of searching movements among different legs suggests the presence of similar control structures. Thus, the loop structure of a non-terminated swing movement is likely to arise from similar properties of the movement controller of each leg. Conversely, differences among legs indicate functional adaptations of a common pattern to improve functioning as a whole. A possible functional role for front-leg retraction and hind-leg protraction during searching could be to direct the searching effort towards locations where the present foothold of other legs signals the likelihood of finding a foothold for the searching leg.

Neural network simulation

Computer simulation of limb kinematics is a powerful tool to probe the limits of our current understanding of motor control. The simulation part of the present study served two main purposes. First, it tested the hypothesis that searching movements can be modelled as non-terminated swing movements. So far, searching movements have been modelled using a specialized search reflex (Espenschied et al., 1996). Second, it was necessary to test the ability of the existing ANN SwingNet to generate searching movements. SwingNet was introduced by Cruse et al. (Cruse et al., 1995a) as part of a modular ANN controller for hexapod walking. A basic feature of SwingNet is the generalisation of performance with variable starting and target points, much as in the searches generated in Fig. 8D. Moreover, Cruse et al. (Cruse et al., 1995a) demonstrated an overshoot of the generated trajectories beyond the target point, a feature required to avoid early termination of movement for steps into a pit. Cruse and Dean (Cruse and Dean, 1997) illustrated trajectories with a terminal 'hook' that could be interpreted as a primitive searching movement. Preliminary results had also indicated the possibility of cyclic terminations, similar to searching movements (M. Dreifert, unpublished results), but the absence of empirical data did not allow numerical training to such features. In subsequent modelling studies (e.g. Cruse et al., 1998), the weight matrices were simplified by setting several weights to zero; however, this led to a complete loss of any terminal curvature in the swing trajectories.

An important difference between the ANN used in the present study and the older versions is that the ANN used here does not require a non-linear velocity compensation, which had been introduced into the original version to reduce velocity changes during swing movements. The training procedure used in the present study may have made this compensation redundant because at least every third trajectory point was evaluated during training, rather than only two points per whole trajectory as in earlier studies. From the results presented in Fig. 8, one can conclude that a simple ANN such as SwingNet may serve as a multi-purpose controller, capable of transitions from swing movement to searching movement. SwingNet therefore not only renders a specialised search controller redundant but also does not require a decision about whether or not to engage in searching, i.e. no motor pattern needs to be transformed or switched on. Furthermore, it implies that cyclic searching movements can be modelled as damped oscillations of a networked integration controller that assumes a steady state for a set of joint angles in the vicinity of the input target vector.

However, all the training results show evident discrepancies with respect to the empirical data. First, the loops are not as large as in real searching and, second, continuous protraction or retraction could not be achieved. Rather, the trajectories of all physiologically plausible solutions converge to a stable point. To overcome these limitations, searching probably needs to be modelled by a more complex ANN. The introduction of an antagonist neuroid for each joint may help to improve the current model (H. Cruse, C. Linder and H. Cruse, in preparation), because this would allow the weights of sensory inputs and target values to be asymmetric for actions in opposite directions. A further helpful extension of the current model might be the

introduction of a dynamically changing target input. Because, as a general rule, one could claim that all legs search towards the centre of the body, a dynamic target vector could be determined by weighted position information from all other legs remaining on the ground.

Functional significance of searching movements

Most earlier studies on searching movements in insects (Delcomyn, 1987; Karg et al., 1991, Bässler et al., 1991) and cats (Gorassini et al., 1994; Hiebert et al., 1994; Hiebert et al., 1995) have focused mainly on aspects of neural motor control. In insects, Pearson and Franklin (Pearson and Franklin, 1984) studied leg searching movements in a behavioural context, yet restricted their analysis to single legs.

In the following, I want to argue that the stereotypic execution of leg searching movements (Figs 1, 2, 5), the simultaneous action of antennal movements (Fig. 4) and the differences between the three pairs of legs (Figs 5–7) may be important aspects of overall locomotor efficiency.

First, pre-programmed movement sequences require little information processing and guarantee quick execution; as a consequence, they save behavioural cost in terms of the computational effort required and reaction time. Second, the searching movements of the front legs take advantage of the range of action of the neighbouring antennae, which greatly alter their normal movement pattern (Dürr, 1999; Dürr et al., 2001) to search the anterior region of the immediate environment. Finally, leg searching movements in *Carausius morosus* exploit past experience. Because the body coordinates of the AEP are rather constant during forward walking, the AEP may reflect the location of expected touch-down. To search around this location is a simple, yet efficient, strategy because the spatial layout of the environment usually offers support in the vicinity of the current substratum (e.g. a branching or bending twig). If the leg is likely to find a foothold slightly lower than in previous steps, slightly more laterally or a tarsus length further ahead, searching around the AEP means taking advantage of previous experience in an environment with nearby alternatives. Accordingly, the backward bias of the front leg and the forward bias of the other legs reflect the likelihood of finding a foothold in the direction where the other legs are standing. Because centering the searched area near the AEP in external coordinates requires body movement to be taken into account, the results presented in Fig. 7 suggest an interaction between the searching leg and the legs remaining in stance. According to this view, leg searching movements are stereotyped, locally controlled actions that take on their behavioural relevance when acting in concert with the rest of the body.

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