

STEPPING PATTERNS IN ANTS

I. INFLUENCE OF SPEED AND CURVATURE

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Summary

The locomotory behaviour of workers of 12 ant species belonging to four different genera (Formicinae: *Cataglyphis*, *Formica*, *Lasius*; Myrmicinae: *Myrmica*) was studied by filming individuals walking on smoked-glass plates. Subsequent multivariate analyses of footfall positions and walking kinematics revealed a set of constant features characterizing ant locomotion. The alternating tripod gait prevails over a wide range of speeds. The temporal rigidity of tripod coordination is paralleled by spatially rigid footfall patterns. Tripod geometry is preserved irrespective of speed and curvature. When walking around curves, tripods are rotated relative to the walking trajectory. Whereas stride length on the inner side of the curve is shortened, that on the outer side is independent of curvature.

Introduction

During recent decades, terrestrial locomotion of insects has become the subject of a steadily growing number of studies focusing on the neural background and the morphological and mechanical constraints of locomotion. There is now detailed knowledge of how temporal and spatial coordination of the legs is brought about in some insects (*Carausius morosus*: Bässler, 1985; Cruse, 1985*a,b*; Cruse and Schwarze, 1988; Cruse and Knauth, 1989; Dean, 1989; *Periplaneta americana*: Delcomyn, 1985, 1991*a,b*) and important insights into the functional relationship between walking mechanics, gait patterns and body morphology have been obtained (*Acheta domestica*: Harris and Ghirardella, 1980; *Blatella germanica*: Franklin, 1985; *Carausius morosus*: Cruse, 1976; Jander, 1985; Dean, 1991; *Periplaneta*: Full and Tu, 1990, 1991; Full *et al.* 1991; Carabidae: Evans, 1977).

The studies presented here focus on interleg coordination patterns in ants. Ants appear to be especially well suited for comparative studies, as this taxon exhibits a high degree of inter- and intraspecific variability, with respect to both morphology and behaviour. The

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analyses shed some light on three different, but mutually connected, aspects of insect locomotion.

Part I of the studies provides a basic description of the constant and variable components of spatiotemporal interleg coordination. Part II (Zollikofer, 1994a) analyzes the role of body morphology (size, species, caste) and mechanical constraints on walking kinematics, and part III (Zollikofer, 1994b) deals with alterations in the locomotory behaviour observed in ant workers carrying loads.

Materials and methods

Animals

Colonies of four species of *Cataglyphis* from Tunisia (*C. bicolor*, *C. bombycina*, *C. albicans* and *C. fortis*) were held in the laboratory under constant conditions (30 °C, 50% relative humidity, 14h:10h light:dark cycle). Individuals belonging to the genera *Formica* (*F. pratensis*, *F. lefrancoisi*, *F. rufa*), *Lasius* (*L. niger*, *L. fuliginosus*, *L. flavus*) and *Myrmica* (*M. ruginodis*) were collected at different sites and kept in boxes.

Data acquisition and analysis

Data sampling consisted of filming the ants walking on smoked-glass plates. This method, first used by Manton (1952) in semiquantitative analyses of arthropod stepping patterns, still provides an elegant means of measuring tarsal imprints and body position simultaneously.

A video camera (50 half-frames s⁻¹) was placed above the walking area (30 cm × 30 cm Perspex box). Smoked-glass plates (7 cm × 10 cm or 9 cm × 12 cm) were calibrated with a reference point grid using an *x,y*-plotter and were then positioned beneath the visual field of the camera. During the tests, the ant was allowed to move in any direction and to stop and to resume walking at any point of its path. Each individual had to perform at least 15 runs, the glass plates being replaced after 1–2 runs. At the end of the test series, the ants were killed and weighed to the nearest 0.1 mg (body mass *m*). The position of the centre of mass was determined by suspending the ant on a nylon fibre glued to the thorax and moving the point of attachment until the ant assumed a horizontal position. The influence of leg positions was accounted for by repeating centre of mass determination with the legs cut off at the coxae. Morphological dimensions (Table 1) were measured to the nearest 0.1 mm.

Video data sampling was performed by copying frame-by-frame the position of the head of the ant and the direction of the longitudinal axis of the body onto a tracing foil overlay placed on the monitor screen. The reference points imprinted on the glass plates were sampled for later calibration. The successive body positions (frame interval 20 ms) were digitized (MOP digitizer; 0.1 mm resolution) and transmitted to a Cromemco Minicomputer. Image distortions due to the video system were corrected for by referring the coordinate values of each sampled data point to the nearest reference grid points. For further analyses, the original data (head position and body axis vector) were replaced by the coordinates of the centre of mass.

The footprints, as well as the calibration marks, were identified on photographic replicas of

Table 1. A list of the variables describing body morphology, footfall geometry and walking kinematics

Variables describing body morphology	
$L1, L2, L3$	Length of fore-, mid-, and hindlegs (mm)
m	Body mass (mg)
Th	Thorax length (mm)
Variables describing footfall geometry	
Tripod shape [distance between tarsal positions (T) of a tripod]	
$d12$	Distance between T1 and contralateral T2
$d13$	Distance between ipsilateral T1 and T3
$d23$	Distance between contralateral T2 and T3
Tripod position (lateral distances from longitudinal axis of the body)	
$l1$	Lateral distance of T1
$l2$	Lateral distance of T2
$l3$	Lateral distance of T3
Distances from midleg to succeeding tripod	
$i21$	Distance from T2 to next ipsilateral T1
$i23$	Distance from T2 to next ipsilateral T3
$s2$	Distance from T2 to next ipsilateral T2, stride length of the midleg
Distances from a fore- or hindleg to succeeding tripods	
$c31$	Distance from T3 to next contralateral T1, contralateral span
$i13$	Distance from T1 to next ipsilateral T3
$i32$	Distance from T3 to next ipsilateral T2
$s1$	Distance from T1 to next ipsilateral T1, stride length of the foreleg
$s3$	Distance from T3 to next ipsilateral T3, stride length of the hindleg
Variables describing walking kinematics	
c	Curvature=1/radius of curvature (mm^{-1})
f	Stepping frequency (s^{-1})
s	Stride length= $(s1+s2+s3)/3$
v	Speed (mm s^{-1})

Leg lengths ($L1$, $L2$ and $L3$) are measured from the coxofemoral joint to the tips of the tarsal claws.

The description of the footfall geometry is based on distances between the tarsal imprints of the fore- (T1), mid- (T2) and hindlegs (T3), respectively.

The variables are grouped according to the results of an intercorrelation analysis.

The basic footfall pattern is the alternating tripod gait; each tripod consists of the simultaneous footfalls of the ipsilateral fore- and hindlegs and the contralateral midleg. Tripod shape is determined by the distances between the tarsal imprints belonging to one tripod ($d12$, $d13$ and $d23$); tripod position is determined by the lateral perpendicular distances of the tarsal imprints from the longitudinal axis of the body ($l1$, $l2$ and $l3$); stride lengths are defined as the distances between two successive footfall positions of the same leg ($s1$, $s2$ and $s3$). All remaining variables indicate distances between tarsal positions of successive ipsilateral ($i21$, $i23$, $i13$ and $i32$) and contralateral ($c31$) footfalls. Variables describing walking kinematics are explained in Materials and methods

the glass plates (enlargements 2:1–5:1). The smoke layer put onto the plates was sufficiently fine to be pierced by the tarsal claws and basal bristles of the distal tarsal segments, yielding individually discernible footprints. Digitizing followed similar procedures to those described for body positions. Both body and tarsal position data were then match-merged into a common coordinate system by referencing to the calibration grid. The accuracy of the tarsal data was checked by making direct measurements of the distances between tarsal imprints on the glass plates themselves and comparing the results with data obtained by digitizing. The sampling error of the video data was estimated by analyzing repeated measurements of a single test run. The tolerance of positional information was ± 0.15 mm for tarsal distances, and the reproducibility of velocity values was at least $\pm 3\%$.

The geometry of stepping patterns was sampled by a set of 14 variables specifying the distances between footprints as well as their orientation relative to the walking trajectory. Variables were defined without presuming the existence of any regular coordination (e.g. tripod) pattern, but were systematically grouped and named according to the results of the intercorrelation analysis presented below (Table 1). It should be pointed out that stride lengths are defined on purely geometric criteria, i.e. as the distance between successive imprints of a given tarsus. Stride length s (the mean value of the stride lengths of the legs that act in phase) measures the distance travelled in a full stride (Alexander, 1977).

The movement of the centre of mass was described by speed (v , determined from two consecutive positions of the centre of mass) and the local radius of curvature (r , determined from three consecutive positions). Average values of v and r were attributed to each stepping cycle. Calculations of averages were based on the consecutive body positions (time intervals 20 ms) situated within the polygon outlined by the tarsal positions belonging to one cycle.

Further data handling and statistical analyses were performed with SAS (Statistical Analysis Software) utilities and procedures. The test runs of each animal were analyzed with SAS procedure VARCLUS. This procedure performs a covariance analysis on the correlation matrix of all variables (in this case a 14×14 matrix) and subsequently cluster-analyzes the results to specify groups of highly intercorrelated variables.

The fact that stride length increases with increasing speed suggests that speed may act as a strong correlator on intertarsal geometry. In order to eliminate speed effects, the analyses are based on partial correlations, i.e. correlations between any variables, but keeping constant speed.

Results

The analysis of interleg coordination follows a three-step procedure. First, the temporal correlation of footfalls is investigated. Second, the spatial correlations between footfall positions are screened for constant patterns. Third, the influence of walking speed and curvature on spatial patterns is examined.

Temporal coordination of the legs

The temporal pattern of interleg coordination of worker ants is simple: at speeds ranging from slow walking to high-velocity running, ants exhibit a fairly strict alternating

tripod pattern (Fig. 1) (Hughes, 1952). The fore- and hindlegs of one body side together with the contralateral midleg move in phase relative to each other and in antiphase relative to the opposite legs, yielding the footfall pattern L1R2L3 alternating with R1L2R3, where L is the left and R is the right side and 1, 2 and 3 represent the fore-, mid- and hindlegs, respectively.

At very low speed, when resuming locomotion after a stop or when walking on strongly bent trajectories, the tripod gait is replaced by metachronal coordination.

Spatial coordination of the legs

A graphic examination of the stepping pattern geometry (Fig. 2) reveals that the spatial arrangement of the legs is highly regular and reflects the rigidity of the temporal patterns. The analysis of intercorrelations between the variables describing footfall geometry yielded tree diagrams of the correlative fit for each individual ant. As no substantial differences between individuals or between species could be revealed, the following results apply to worker ants in general. An overall outcome of the analysis is that geometric tripods between legs L1R2L3 and/or R1L2R3 are shown to be spatially constant entities. Furthermore, the size and the shape of tripods depend neither on the distance between them nor on their orientation relative to the walking direction.

In quantitative terms, these results are expressed as follows. Each individual tree diagram consists of four subsets comprising variables which are highly intercorrelated to each other ($r^2 > 0.6$; $P < 0.02$). Each subset of variables characterizes a distinct geometric property of the footfall patterns (see Table 1). (1) Subset A, all variables describing the size and shape of a tripod (L1R2L3 and R1L2R3); (2) subset B, all variables describing the position of a tripod relative to the trajectory (inclination and lateral shift); (3) subset C, distances from a midleg tarsus (R2 or L2) of a given tripod to tarsal positions of the subsequent tripods; (4) subset D, distances from foreleg and hindleg tarsi (L1 and L3, or R1 and R3) to subsequent tripods.

Whereas subsets A and B describe intratripod geometry, subsets C and D represent distances between subsequent tripods. Moreover, subsets C and D correspond to distances measured from opposite body sides of a given tripod. This indicates decoupling of right and left leg movements, a point that will be discussed under curve-walking.

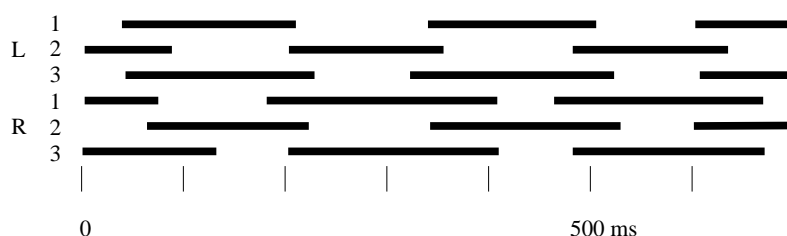


Fig. 1. Tripod gait pattern in *Cataglyphis bicolor* (mean speed 60 mm s^{-1} ; slow walk). Adjacent and opposite legs swing in antiphase (black bars represent stance phases; L, left, R, right body side; 1, 2 and 3, fore-, mid- and hindleg).

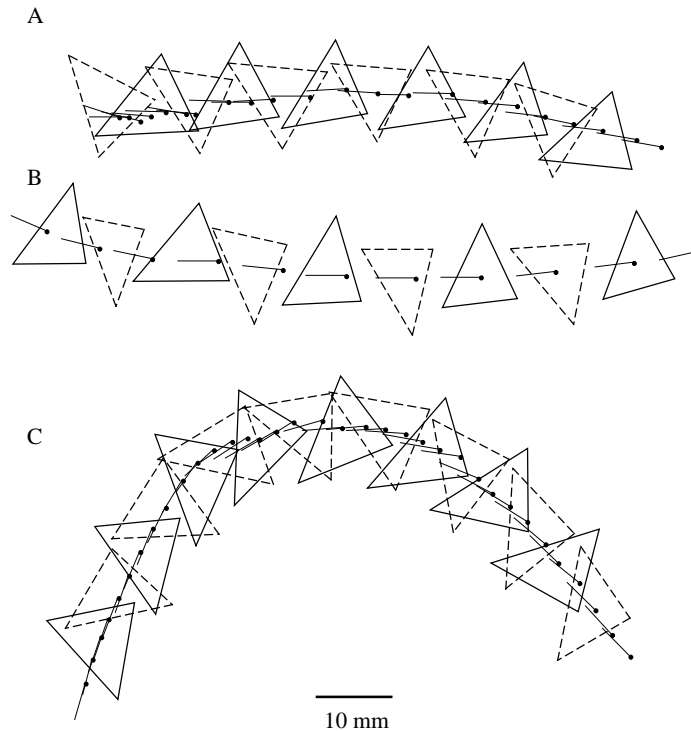


Fig. 2. Locomotion in *Cataglyphis bombycina* (body mass 17.9 mg) at a mean velocity of 17 mm s^{-1} (A), 43 mm s^{-1} (B) and 15 mm s^{-1} (C); the mean radius of curvature in C is 30 mm. Solid-line triangles, tripods R1L2R3; dashed-line triangles, tripods L1R2L3; the longitudinal axis of the body is indicated from head position (dot) to centre of mass (end of line); time intervals are 20 ms; walking direction is from left to right.

Effects of speed and curvature on stepping pattern geometry

This analysis tests the correlation of footfall geometry with speed and curvature, based on linear regression models. Each individual was analyzed separately. The results presented here (Table 2) refer to workers of all species, as scale effects or species-specific differences could not be detected.

Speed

Speed is positively correlated with all variables indicating distances between subsequent tripods (subsets C and D of the above analysis; Fig. 3A). However, there is no correlation between speed and any of the variables describing tripod shape and position (subsets A and B; Fig. 3B). Thus, speed has no influence on the spatial relationship between the legs acting together as a tripod (Table 2, tripod shape and position). With increasing speed, the tripods are simply placed further apart from each other (Table 2, stride lengths; Fig. 2A,B), without any shape alteration.

Curvature

When walking along curved paths (Fig. 2C), the tripod L1R2L3 supporting the body

during a left turn is geometrically similar to R1L2R3 in a right turn, as in both cases the tarsus of the midleg is placed on the concave (inner) side of the curve. Correspondingly, tripod L1R2L3 in right turns is equivalent to R1L2R3 in left turns. Data have been

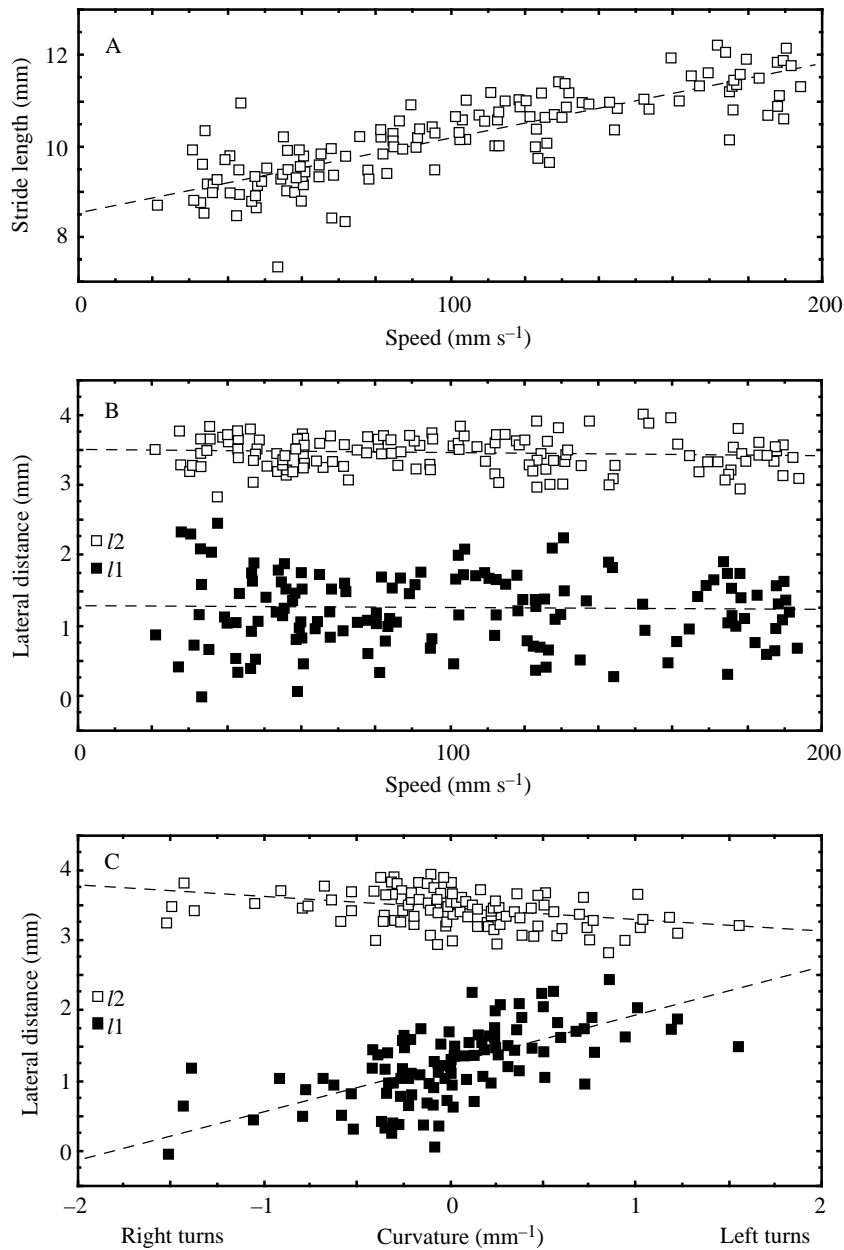


Fig. 3. Correlation of footfall geometry with speed (v) and curvature (c) (*Cataglyphis albicans*, body mass 2.8 mg). Stride length (s) is extended with increasing speed (A). Tripod position, measured by the lateral distances of the foreleg (I1) and midleg (I2), does not depend on speed (B), but does depend on curvature (C). Dotted lines indicate linear regressions.

Table 2. *Influence of speed (v) and curvature (c) on the footfall geometry*

	Variables describing footfall geometry										
	Tripod shape		Tripod position			Stride lengths					N
	d12	d13	l1	l2	l3	s	s1	s2	s3		
v	-0.05	0.05	-0.03	0.09	-0.01	0.70	0.63	0.55	0.59	142	
c (T2 out)	0.01	0.00	-0.52	-0.13	0.49	-0.04	-0.31	0.07	-0.51	70	
c (T2 in)	0.05	0.03	0.44	-0.31	-0.49	-0.25	0.08	-0.42	0.00	72	

Figures represent mean values of individually calculated correlation coefficients ($r > 0.20$ is different from 0 at $P < 0.01$; N , average number of observations per individual).

To demonstrate the influence of curvature, data were grouped according to the position of the tarsus of the midleg (T2), outside or inside the curve. Tripod shape was determined by the distances from the position of the foreleg tarsus to the midleg tarsus ($d12$) and to the hindleg tarsus ($d13$), respectively. Tripod position was determined by the lateral distances of the front- ($l1$), mid- ($l2$) and hindleg tarsi ($l3$) from the longitudinal axis of the body. Tripod shape is independent of speed (v) and curvature (c), but tripod position is dependent on c . Stride length (s) is strongly correlated with speed. Although stride lengths of the fore- ($s1$), mid- ($s2$) and hindleg ($s3$) on the inner side of the curve are shortened ($r < 0$), they remain constant on the outer side ($r \approx 0$).

Further explanations of the variables are given in Table 1.

categorized according to this criterion. Correlations of curvature (inverse of the radius of curvature) with the tarsal constellation were studied after speed effects had been eliminated by calculating partial correlation coefficients (Table 2).

The size and shape of the tripods are not altered with respect to curvature. Conversely, intertripod distances as well as tripod positioning vary with curvature; stride length of the legs acting on the inner side of the curve is shortened, whereas stride length on the outer side does not depend on curvature. This finding confirms the decoupling of the left and right body sides, as stated earlier. With increasing curvature, the forelegs on the concave side of the curve are placed closer to the body axis and the hindlegs are placed farther from it. The opposite situation is found on the convex side (Table 2, lateral distances of the tarsi $l1$, $l2$, $l3$; Figs 2C, 3C).

These findings demonstrate that, depending on the curvature, footfall positions change relative to the longitudinal axis of the body, yet the spatial arrangement of the legs belonging to one tripod is always held constant.

Discussion

Gait patterns

The alternating tripod gait has been thoroughly studied in a variety of insect species (Coleoptera, Dermaptera, Hemiptera, Blattariae, Orthoptera: Hughes, 1952; Delcomyn, 1971; Graham, 1972; Manton, 1972; Burns, 1973; Evans, 1977; Kozacik, 1981). The alternating tripod gait is a widespread interleg coordination pattern for walking at moderate to high speed. Tripod coordination is generally lacking during slow walking (*Periplaneta americana*, Spirito and Mushrush, 1979; *Carausius morosus*, Graham,

1972; *Neoconocephalus robustus*, Graham, 1978) or, obviously, in species using less than six legs in locomotion (*Mantis religiosa*, Roeder, 1937; *Romalea microptera*, Graham, 1972). As has been demonstrated in this paper, tripod coordination in ants predominated over a wide range of speed and curvature. Moreover, tripods proved to be highly constant spatial entities. Given the above evidence, it is assumed that the spatiotemporal constancy of this gait pattern may be a general feature of fast-running insects (*Periplaneta americana*, Delcomyn, 1971; Carabidae: Evans, 1977).

In vertebrates, Taylor *et al.* (1980) observed that the specific cost of locomotion increases with decreasing body mass. This is mainly due to the higher number of stepping cycles a small animal has to perform in order to cover a given distance. Following this argument, increasing levels of energy consumption result because muscular efficiency is inversely proportional to contraction speed. Hence, in order to minimize the cost of locomotion, an animal should minimize the number of stepping cycles and maximize stride length.

For insects, from a geometric point of view, there are two strategies for maximizing stride length. First, to extend the ranges of action of the legs simultaneously (from anterior to posterior extreme position); second, to extend the spans between temporally successive legs. Maximum spans between successive legs are attained if the temporal onset of retraction of a given leg is maximally shifted relative to the onset of retraction of a neighbouring leg. This is the case when adjacent legs are moving in antiphase. From a static point of view, stability must be maintained by supporting the body with at least three legs.

The alternating tripod gait represents an optimal pattern with respect to both geometric and static demands. The antiphase relationship between contralateral as well as adjacent legs yields longer strides than any other coordination pattern. At the same time, three-point supports are established. More generally, every antiphase relationship between adjacent legs will yield maximum stride length, e.g. alternating tetrapods in Arachnidae (Wilson, 1967; Ward and Humphreys, 1981; Land, 1972) and Scorpionidae (Bowerman, 1975) and even in sideways-walking crabs (*Uca pugnax*, Barnes, 1975; *Ocyrode ceratophthalma*, Burrows and Hoyle, 1973). The above argument suggests that the prevalence of symmetrical gait patterns may reflect kinetic rather than neuronal constraints.

Apart from the constant phase relationships, the results presented here show that the legs belonging to one tripod build up a spatially constant entity. This implies that, depending on speed and curvature, the tarsal positions of a tripod may vary considerably relative to the body axis and to the position of the succeeding tripod while remaining constant within tripods. Except for some qualitative descriptions given by Manton (1972), spatial constancy of tarsal positions has not yet been described in insects, although it may be a common feature of the terrestrial locomotion of arthropods.

What is the neural basis of spatiotemporal constancy? The emergence of gait patterns in walking insects is attributed to the action of central pattern generators (CPGs) and/or to the influence of sensory input (Cruse, 1985a; Delcomyn, 1985). In *Carausius morosus* (Cruse, 1985a,b; Cruse and Schwarze, 1988; Cruse and Knauth, 1989), interleg coordination patterns can be explained by a series of well-defined coupling mechanisms

that control the timing of protraction of adjacent and of opposite legs, and there is no evidence for the action of CPGs in this slow-walking species (Cruse, 1985a). In fast-running insects, however, CPGs may play an important role. In *Periplaneta americana* (Delcomyn, 1985, 1991a,b), the amputation of a leg altered the phase relationship and the consistency of the bursting activity of motor neurones. These effects were drastic at low speed but disappeared at high walking speeds. Thus, while sensory feedback seems to be essential for interleg coordination during slow walking, CPGs become increasingly important with increasing speed (Delcomyn, 1991b). Following this argument, the rigidity of tripod gait patterns observed in ants indicates that CPGs are dominant over sensory input at medium to high walking speeds. Tripods have been shown to be spatiotemporal entities that are invariant over a wide range of speeds and curvatures. Thus, CPGs appear to generate both the patterns of temporal coordination and of spatial arrangement of the legs belonging to a tripod.

Walking around curves requires path differences between the legs of the left and the right body sides. To achieve this, insects use different strategies. In *Apis mellifera* (Zolotov *et al.* 1975), in *Geotrupes stercorosus* and in *G. stercorarius* (Frantsevich and Mokrushov, 1980), the legs on the inner side walk backwards, whereas in *Blattella germanica* a slightly modified tripod pattern is used (Franklin *et al.* 1981). In both *Apis mellifera* (Zolotov *et al.* 1975) and *Carausius morosus* (Jander, 1985), the stride frequency is lowered on the inner side, resulting in the uncoupling of the stepping rhythms on each side of the body. Stride length reduction on the inner side is reported for every species cited above.

During curve-walking, ants use comparatively conservative strategies. Distances between successive footfalls on the inner side are shortened, whereas on the outer side they remain unchanged. Uncoupling of the two body sides has been demonstrated by the loose correlative fit between intertripod distances on the two body sides. The spatial tripod pattern, however, is maintained even when ants walk around narrow curves. Thus, the footfall positions of legs belonging to one tripod are held constant relative to each other, although they may vary relative to body position.

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