

ROTATIONAL LOCOMOTION BY THE COCKROACH *BLATTELLA GERMANICA*

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Abstract—Locomotion on complex substrata can be expressed in a plane by two geometric components of body movement: linear locomotion and rotational locomotion. This study examined pure rotation by analysing the geometry of leg movements and stepping patterns during the courtship turns of male *Blattella germanica*. Strict rotation or translation by an insect requires that each side of the body cover equal distance with respect to the substrate. There are three mechanisms by which the legs can maintain this equality: frequency of stepping, magnitude of the leg arcs relative to the body and the degree to which legs flex and extend during locomotion. During the courtship behaviour of *Blattella germanica* selected males executed turns involving body rotation along with leg movements in which the legs on the outside of the turn swung through greater average arcs than those on the inside of the turn. This difference should have resulted in a translation component. However, legs on the inside of the turn compensated by flexion and extension movements which were greater than those of opposing legs. The net effect was that both sides of the body covered equal average ground. These cockroaches used a wide variety of stepping combinations to effect rotation. The frequency of these combinations was compared to an expected frequency distribution of stepping combinations and further to an expected frequency of these stepping combinations used for straight walking. These comparisons demonstrated a similarity between interleg coordination during straight walking and that during turning in place.

Key Word Index: Locomotion, rotation, walking, arthropod, turning

INTRODUCTION

ETHOLOGISTS and neurophysiologists favour the terrestrial locomotion of arthropods as a model for studying the generation and control of movements (HOYLE, 1976). Much of this work has centred on straight walking by insects (for review see: HUGHES and MILL, 1974; HOYLE, 1976; DELCOMYN, 1977). But travel over varied substrata, such as insects are likely to encounter in nature, requires complex paths of movement (ETIENNE, 1977; MURPHEY and ZARETSKY, 1972; BAILEY and THOMSON, 1977). The two distinct geometric components of these paths are translation and rotation; various combinations of translation and rotation produce a continuum of body movements possible during locomotion. Straight walking lies at one end of this continuum; at the other end is the rotational pattern about which almost nothing is known (ROEDER, 1937; GRAHAM, 1972).

When walking straight, the legs on each side of an insect's body cover equal distances on the ground. Any systematic difference in the ground covered by strides of legs on opposite sides of the body (i.e. bilateral differences) will introduce a curvature into the trajectory of the animal (JANDER and WENDLER, 1977), resulting in some degree of body rotation. Any combination of the following three features of leg movement can result in this curvature: (1) frequency—legs on one side of the body can step more frequently than those of the other side; (2) arc—legs on one side

of the body can swing through relatively greater arcs with respect to the body; (3) functional length—legs on one side may flex and extend farther, thus increasing their functional or effective length with respect to the contralateral legs.

The curved paths of insects consist of translation and rotation superimposed. To identify the leg movements responsible for the rotational component a pure rotational locomotion, such as turning in place, must be studied. Pivoting or turning in place imposes at least two constraints on the leg movements of an insect. First, legs on opposite sides of the body walk in opposite directions. Typically legs on the outside of the turn (left side of a right pivot) move as they do in forward walking and legs on the inside of the turn walk backwards (ZOLOTOV *et al.*, 1975). Second, as in straight walking, legs on each side of the body must also cover equal distances. If the legs are of equal functional length and swing through equal arcs then the centre of rotation will fall on the body long axis between the points of articulation of the middle legs. In this case the middle legs rotate the animal with changes in angle relative to the body. No changes in functional length are required. The fore- and hind-legs articulate at some distance from the rotational centre and must therefore cover a relatively greater distance than the middle legs. The distance to be covered is proportional to their distance from the centre of rotation. The methods by which these legs cover this additional distance depend on where the animal positions them with respect to its body. If the fore- and hind-legs are held nearly parallel to the body long axis

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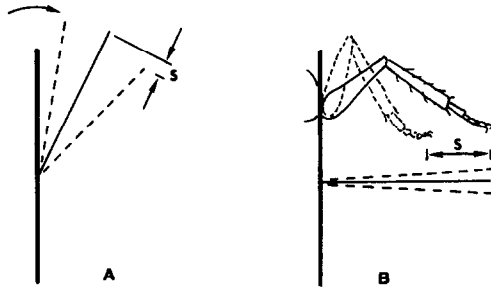


Fig. 1. The movements of legs distal to the centre of rotation combine arc magnitude and functional length in proportion to their position relative to the body. (A) A leg (thin solid line) held near to parallel with the body long axis during stepping covers ground mainly by the arc through which the leg swings (dotted lines). There is little change in functional length (S). (B) When stepping from a position orthogonal to the body long axis, ground is covered by relatively larger changes in functional length than in (A) and with smaller changes in the arc through which the leg swings.

during stepping, then they cover ground by relatively large changes of angle and with a minimum of flexion and extension (Fig. 1A). On the other hand, if the legs operate from a position orthogonal to the body axis they will cover ground principally by large changes of functional length with little accompanying change in angle (Fig. 1B). Within these extremes the animal may vary the relationship between its arc swing and functional length, combining them in varying ways to cover a given amount of ground. In addition an insect may vary the stepping frequencies of legs relative to one another and superimpose them on the capabilities outlined above.

Pure rotation is an extreme form of locomotion for insects which has been reported in specific contexts such as predation (ETIENNE, 1977) and courtship (BELL and SCHAL, 1980). Synthesis of a contact pheromone (BURGSTÄHLER *et al.*, 1975, 1977) has provided the means for eliciting courtship turning movements in the cockroach *Blattella germanica* (BELL, VUTURO and BENNETT, 1978; BELL *et al.*, 1978). These 180° pivots are the rotational pattern reported on in this paper. The turns use the same basic geometry of

leg movements and coordinated stepping with which these animals walk straight. However, these characteristics of walking appear to have been reorganized into a more complex pattern for turning. Clarification of this complexity may eventually lead to a more complete understanding of the functional organization of the elements of nervous systems which generate and control locomotion.

METHODS AND PROCEDURES

Blattella germanica mate by the female mounting the dorsal surface of the male's abdomen when he is facing away from her. This position is the result of a sequence of actions initiated by the male's detection of a contact pheromone on the surface of the female's cuticle (BELL *et al.*, 1978). The male positions himself head to head with the female and then pivots 180°, raises his wings and presents the dorsal surface of his abdomen to her. Should the male not receive any sensory contact from the female on his dorsal abdomen within several seconds of having turned, he will counter-turn (turn back in the reverse direction), presumably to relocate the female (BELL and SCHAL, 1980). The initial turns occur as uninterrupted patterns of stepping through 180°. However, the counter-turns, which occur after an unsuccessful mating attempt, are searching movements. In this case the animals frequently pause and seek, with their antennae, information regarding the position of the female. This behaviour suggests caution in making comparisons between the types of turns.

Numerous induced courtship turns were filmed at high speed (50 frames/sec). From these films, turns were selected by the following criteria: (1) animals were required that turned and then counter-turned each in the same respective directions; and (2) the longitudinal axis had to move only by rotation (a difficult criterion to meet since most turns contained a small yet significant amount of translation). Turns by three animals met these requirements.

The films of these turns were inspected frame by frame to analyze the locomotory activity of the animals' legs. The observational unit for this study is the step of each of the six legs, characterized by the

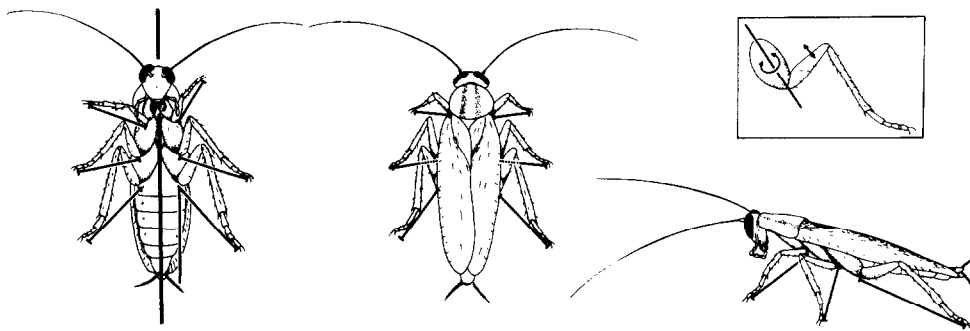


Fig. 2. Three views of a male *Blattella germanica*. Superimposed on the views are lines indicating the geometric parameters which were investigated in this report. (A) Angular movements of limbs relative to the body long axis. (B) Span or functional length of each leg as represented by the length of a line extending from the tip of each tarsus to each coxa/trochanter articulation point. This latter reference point served as well as the base of the coxa since all the coxae moved only by rotation about their long axis (inset). Thus the relationships between the coxa and the trochanter with respect to the body were the same.

following parameters. The geometry of each leg movement was measured in each frame by (1) the angle formed between the body long axis and a line drawn from the tip of the tarsus to the base of the leg, as shown in Fig. 2; and (2) the length of the line joining the tarsus and the leg base, referred to as the functional or effective length of the leg. The coordinated stepping was recorded by noting, in each frame, whether a leg was executing a power or a return stroke. Since the legs were photographed from above, the movements of the coxae were not directly visible. By visual inspection of ventral views of freely moving animals, using a glass substrate, mirror and dissecting microscope, it was determined that during pure body rotation the coxae moved only by rotation about their long axes (see inset, Fig. 2). Therefore, the coxa/trochanter joint, which was visible when filmed from above, provided a reliable reference point with respect to the body long axis from which to record angular change and functional length (as shown in the ventral and dorsal views of Fig. 2). This unusual movement of the coxae was further verified by examining the coxal movements of tethered males on a smooth, even substrate. The motions of their legs as they struggled to escape confirmed that these animals can use three degrees of freedom for coxal movement. These movements by cockroaches have been studied and reported in more detail by DRESDEN and NIJENHUIS (1953).

RESULTS

A. Geometry of leg movements

The three initial turns took almost the same length of time to perform (1, 1.05, 1 sec) while the counter-turns varied a bit more (1.5, 1.75, 1.2 sec). The combined initial (right) turns consisted of a total of 92 steps taken by all legs (see Table 1); the left or counter-turns consisted of a total of 79 steps.

The average amplitudes of the arcs through which legs cycled are presented as the shaded areas around

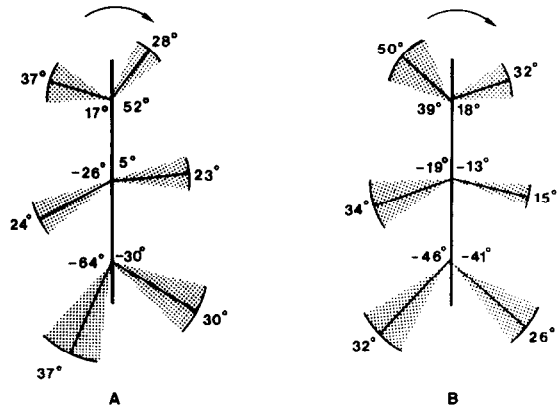


Fig. 3. Midpoints of the legs of *Blattella germanica* during three right (A) and three left (B) turns (shown in mirror image) and the mean arcs through which the legs swung. Values near the intersection of the legs (straight thin lines) with the body are mean deviations in degrees from a position orthogonal to the body long axis. Values near the arcs at the tips of the legs are mean degrees of arc covered during locomotory oscillations. Data from all three turns of each type were grouped for the calculations. The left or counter-turn values are shown in mirror image to facilitate comparison.

the lines representing each leg in Figs 3A, B. Both turn types are represented and the counter-turns (Fig. 3B) are shown in mirror image to facilitate comparison. The averages were calculated from the grouped steps for each type of turn. The lines representing each of the legs are drawn from the body long axis to the midpoint of each of the respective arcs. The positions of these legs are expressed in degrees of deviation from a line orthogonal to the body long axis.

The midpoints differ somewhat but not radically from geometric data available for other species of insects walking straight (CRUSE, 1976; BURNS, 1973; HUGHES, 1952). Note, however, that the leg midpoints for the initial turns are canted 30° in a direction opposed to that of the turn. While there are no reported results for the geometry of leg movements of straight walking *Blattella germanica*, observations of these animals walking freely indicate that their legs are positioned much as they are by other Orthopteran insects.

The rotational centre of each turn was found by superimposing the body long axis in the successive frames of film of each turn. Their intersections formed a cluster of points along the body axis line; its centre of mass was the average point of rotation. For the initial turns all three points were located slightly caudal to the points at which the middle legs of the animals attached to their bodies. The points of rotation for the counter-turns were more variable in their placement, ranging from near the bases of the hind-legs to a position somewhat rostral to the bases of the middle legs.

The measurements of the rotational centres and the average arc amplitudes for the initial turns substantiate the geometric illustration of turning presented in the Introduction. Since the pivot points of the turns are quite near the bases of the middle legs, these legs need not cover as much curvilinear distance as the fore- and hind-legs. Consequently the mean arc

Table 1. Numbers of steps in the turns

A. Initial turns

Animal No.	R1	L1	R2	L2	R3	L3	Total steps per turn
1	7	5	6	7	5	7	37
2	6	6	4	4	4	4	29
3	6	5	3	4	4	4	26
Total	20	16	13	15	13	15	92

B. Counter-turns

Animal No.	R1	L1	R2	L2	R3	L3	Total steps per turn
1	6	7	5	4	3	3	28
2	4	6	4	6	4	3	27
3	5	4	3	6	3	3	24
Total	15	17	12	16	10	9	79

R = leg on right side of the body; L = leg on left side of the body; 1 = fore-leg; 2 = middle leg; 3 = hind-leg.

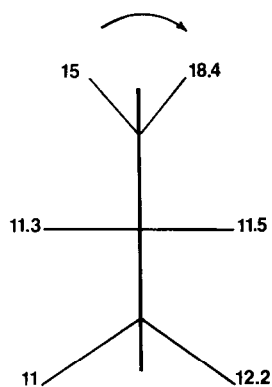


Fig. 4. Average functional length of the legs of *Blattella germanica* males during three right turns. Values are expressed in mm, taken from an image magnified to twice its normal size.

swings of the latter two are greater than the former, as illustrated in Fig. 3A. The variable nature of the behaviours of these animals makes the comparison less clear for the counter-turns (Fig. 3B).

The results for both types of turns illustrates that the average arc magnitudes of legs on the outside of the turns (left side of the body) are greater than those on the inside (right side of the body). These differences are significant at the 0.05 level for the fore- and hind-legs of the initial turns and for all three leg pairs of the counter-turns when analyzed with a Mann-Whitney U test. This outcome is surprising since, all other factors being equal, it indicates that the legs contralateral to the turns cover more distance than the ipsilateral legs. This should result in translation superimposed on rotation. However, these turns were carefully selected to consist only of rotational body movements. Therefore, if the introductory geometric propositions are correct, some method of compensation should be evident to ensure that the different activity of the legs on each side of the body results in equal distances being covered. There are two possibilities: (1) a relatively higher stepping frequency by legs on the inside of the turn or (2) a larger average functional length for these legs. The figures from Table 1 show no systematic differences in number of steps by legs on each side of the body. In fact, for the initial turns, the sum of all the steps taken by legs on each side are exactly equal (46). Figure 4 does show for the initial

Table 2. Time spent on the substratum as a percent of total cycle time (initial turns)

R1	L1	R2	L2	R3	L3
79.1	82.8	86.3	87.8	85.6	84.5

(Nomenclature of legs as in Table 1.)

turns, however, that there are systematic differences in mean functional length between leg pairs across the body. The differences between sides for the fore- and hind-legs are significant at the 0.05 level (Mann-Whitney U test). Legs contralateral to the turn swing through relatively larger arcs by comparison with the ipsilateral legs which flex and extend more. This same pattern of differences is shown by all three segmental pairs of legs during counter-turns ($P \leq 0.05$, Mann-Whitney U test). Leg swing and flexion/extension in varying proportions on different sides of the body are used by these insects to cover the same net distance. A possible explanation for this seemingly unnecessary complexity is presented in the Discussion section.

B. Stepping patterns

Given the geometric constraints cited in the Introduction and the necessity of supporting the body off the ground, there are a wide variety of ways in which *Blattella germanica* could use their legs singularly and in combinations to turn on the spot. For analysis of these coordinated movements only the steps of the initial turns have been considered for reasons cited in the Methods section.

Table 1A presents the number of times each of the six legs stepped during the three right (initial) turns. There is a slight tendency for the fore-legs to step more frequently than the middle or hind-legs. The total number of steps taken by legs on the outside of the turn were exactly the same as those taken by legs on the inside (46) for the three turns examined. However, the total number of steps taken by all six legs in each of the three turns was different despite the fact that they covered the same angle of rotation.

A further characteristic of stepping which can influence the coordinated use of legs is the proportion of the entire cycle time that each leg spent in its return phase. Table 2 illustrates the percent of the total cycle time that each leg was on the ground, averaged over

Table 3. Predicted and observed relative frequency of different numbers of legs stepping in combination*

Legs in combination	Observed frequency	Observed relative frequency	Expected relative frequency
0	5	0.078	$p(0) = 0.3513$
1	41	0.465	$p(1) = 0.4015$
2	33	0.380	$p(2) = 0.1912$
3	10	0.155	$p(3) = 0.437$

* Summation of the predicted probabilities will not add to 1 since the use of 4, 5 and 6 legs at a time have not been considered. The expected frequency distribution is generated by multiplying 'c' times 'p' times 'q' where

'c' = number of possible combinations of a specified number of legs stepping,

'p' = the probability of a leg stepping (0.16) raised to the power of the number of legs stepping, and

'q' = the probability of a leg not stepping (0.84) raised to the power of the number of legs left on the ground.

Thus the expected frequency for doublets is: $p(2) = 15(0.16)^2 \times (0.84)^4 = 0.1912$. However, $p(0)$ is simply $(0.84)^6 = 0.3513$.

the three turns. The proportions for each of the six legs are quite similar, about 84%.

The frequency distribution of the return strokes of one (singlets), two (doublets) and three (triplets) legs at a time, given in Fig. 5, quantifies the diversity of coordination. Since *Blattella germanica* stepped with approximately equal frequency with all of their legs and used the legs for about the same amount of time in return strokes (16%) it is possible to construct an expected frequency distribution of the different stepping patterns. By comparing the observed and the expected outcome it may be determined whether there is, in addition to postural, another deterministic component underlying the coordination of the legs. In Table 3 a Chi-square analysis indicates that the distributions are significantly different ($p \leq 0.0001$).

Interpretation of the outcome of this statistical test might be ambiguous considering that some doublets and triplets could be the result of overlap of the cycles of two and three legs, and not a coordinated effort by the animal. However, the way in which the expected frequencies were generated accounts for this possibility. These frequencies include all possible sources for doublets and triplets occurring by chance, including chance overlap. Therefore, during turns, these animals used two and three legs in combination more frequently than would be expected of an animal stepping randomly. While these cockroaches used single legs approximately as expected, the relative

amount of time spent not stepping at all, $P(0)$ (all legs on the ground), was lower than expected.

An explanation for the non-random component of the stepping pattern analysis involves the use of a tripod coordination pattern such as these animals use when walking straight (HUGHES, 1952; WILSON, 1966; DELCOMYN, 1971). Given the constraints of body support all possible combinations of steps using one, two and three legs at a time are shown in Fig. 5. The number above each pattern indicates the total number of times that particular combination occurred in the three right turns. Of all the triplets shown in Fig. 5, the most frequently used combination was the alternate tripod involving the left front/right middle/left rear legs. The complementary alternate tripod did not occur at all. However, the most frequent doublets are those composed of legs that are subsets of the complementary missing tripod. This suggests that *Blattella germanica* may use these subsets or 'incomplete triplets' during turning in addition to the regular tripod triplets. The doublets in Fig. 5 have been divided into two categories: those that are not subsets of tripods (5A) and those that are (5B). If the usage of doublets were uniformly distributed over both of these categories then 60% of the total frequency of occurrence of doublets should fall into the non-subset category and 40% in the subset category.

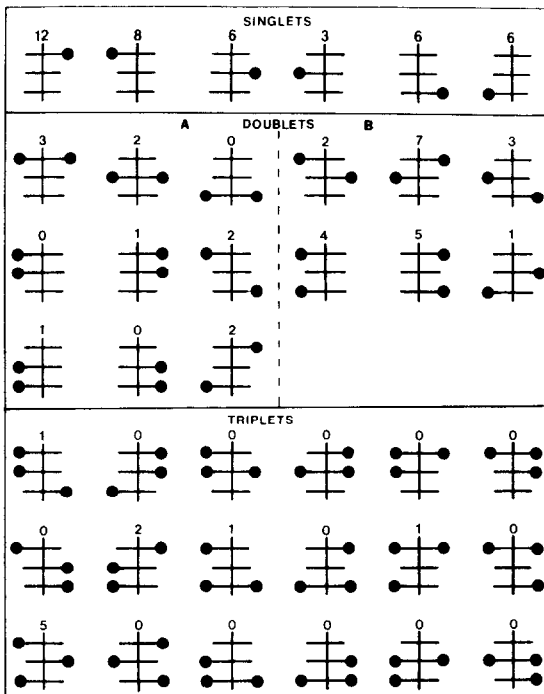


Fig. 5. A schematic representation of all the stepping combinations a cockroach can perform and still support its body off the substrate. The dark circles represent legs executing a return stroke. The doublets are further divided into two subsets. (A) Those doublets formed from combinations which are not part of the normal alternate tripod stepping pattern found in straight walking insects. (B) Those that are part of the normal stepping pattern.

	Non-tripod subsets	Tripod subsets
Observed	11.0	22.0
Expected	19.8	13.2

As these figures show, this is clearly not the case. The number of times tripod subsets were used was greater than expected by chance ($p \leq 0.002$).

These results demonstrate a similarity between the coordination of legs as they are used for straight walking and for sharp turning. The alternate tripod coordination pattern, in its complete or incomplete form, represents the deterministic component in an otherwise apparently random set of stepping combinations.

DISCUSSION

The leg and body movements of *Blattella germanica* males differ in some respects from those suggested by the geometric constraints presented in the Introduction. For example, the actual position of the rotational centre of turning males lies behind, rather than at the bases of, the middle legs as proposed in the Introduction. If we assume that functional length is a reflection of the morphological length of an animal's legs, then *Blattella germanica*, whose fore-legs are considerably shorter than its hind-legs, should shift its rotational centre more toward the fore-legs than towards the hind-legs. Since the longer hind-legs can cover greater distances per step than the fore-legs, shifting the point of rotation forward reduces the distance that the shorter fore-legs must travel during a turn. In moving the rotation point forward, toward its fore-legs, the male also shifts its whole body closer to the female and thus may hit her with its abdomen at the end of its initial turn. Shifting this point back

along its body axis enables the animal also to shift the final position of the abdomen slightly away from the female and reduces the risk of butting her, an act which is interpreted as aggression by other species of cockroaches (BARTH, 1960; ZIEGLER, 1972) and so might chase her away.

The caudal shift in the position of the rotational centre imposes on the fore-legs the necessity of covering an even greater distance than if the centre were at the bases of the middle legs. They can do this in three ways: by increasing their stepping frequency or their arc swing and/or functional length relative to the other pairs of legs. The results indicate that these mechanisms are not mutually exclusive (nor independent) and the animals used two in concert. The sum of all the steps taken by the fore-legs in the three right hand turns is greater (36) than those taken by the middle (28) or the hind-legs (28) as shown in Table 1A. Thus these animals may use relative differences in segmental stepping frequency to cover relatively greater distances. Use of a second mechanism for this purpose appears in the results of Fig. 4 where the average functional length of the fore-legs is greater than either the middle or hind-legs. However, no similar, systematic difference between legs of a segment is in evidence when the mean swing amplitudes are compared (Fig. 3A). In view of the close interaction between arc magnitude and functional length, presented in several contexts in this report, the discovery that differences in mean functional length account for increased coverage of distance by the fore-legs (in cooperation with frequency of stepping) and not mean arc amplitude is surprising.

The bilateral differences in mean arc magnitude, shown in Figs. 3A, B are seemingly inappropriate to the geometry of pure rotation. One explanation for this complex interaction of arc and functional length, suggested by the turns of the Walking Stick insect, is that when *Blattella germanica* traverses curved paths it may do so by using bilateral differences in the swing of its legs. The motor programme which generates these differences for gradual turns may be expressed by the animals during pure rotation despite the fact that they are not necessary for executing pivots. Compensatory flexion and extension movements by intrasegmental partners eliminate the potentially maladaptive disorientation that the bilateral differences in arc might create and thus the angular component, apparently part of turns of any degree, remains in pure rotational locomotion.

It is not altogether surprising to find the alternate tripod leg coordination of straight walking as a deterministic component in the stepping patterns of turning cockroaches. There is evidence of this same leg coordination pattern as an element of righting responses (CAMHI, 1977; SHERMAN *et al.*, 1977) and of grooming (REINGOLD and CAMHI, 1977) by other cockroaches. The Walking Stick insect, also an Orthopteran insect, walks in a wide arc with a well organized alternate tripod leg coordination which deteriorates as the curvature of the turn increases (i.e. changes the ratio between rotation and translation). Further, the suppression of stepping of individual legs by Orthoptera during straight walking, resulting in doublets, has been explored in a somewhat different

geometric context by BURNS (1973) and GRAHAM (1972, 1978a,b). These three sets of evidence suggest that: (a) straight walking coordination has been used as the basis or at least a component of the leg coordination of related motor patterns and (b) turning on the spot, one end of a continuum of locomotion, involves some loss of intersegmental coordination, so that a previously fairly predictable walking pattern becomes more stochastic in nature during sharp turning. For turning on the spot there are no geometric or postural constraints that would preclude walking in opposite directions on either side of the body with the highly determined alternate tripod coordination pattern analogous to that of straight walking. In fact, spiders perform these turns with the same interleg coordination that they use for walking straight (LAND, 1972). This relative lack of organization in the leg movements by *Blattella germanica* males during turning may reflect a behaviour pattern which is still in the process of evolving to a more highly determined form.

On the other hand, the turns have obviously reached a point of evolutionary success as they are; the amount of order in the stepping patterns of turns is sufficient to accomplish mating. Several studies of arthropods have reported successful walking using stepping patterns which are not highly coordinated; for example, the Water Strider (BOWDAN, 1978) and the crab *Uca pugnax* (BARNES, 1975). Since little is known as to how other insects turn on the spot it is not possible, by comparison, to further elaborate these arguments.

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