STICK INSECT LOCOMOTION ON A WHEEL: PATTERNS OF STOPPING AND STARTING

By JEFFREY DEAN* AND GERNOT WENDLER

Zoologisches Institut, Universitaet zu Koeln, F.R.G.

SUMMARY

The relationship between standing and steady walking was investigated for stick insects walking on a wheel. Normal hexapod coordination patterns ensure that each point in the gait cycle has static stability. Nevertheless, stick insects show preferred stopping sequences: the final protraction in ipsilateral metachronal sequences is most often by a front leg and least often by a rear leg (Fig. 1, Table 1). The associated preferred stance is one in which front, middle, and rear legs are spread apart (Fig. 2). This preferred stance does not conform precisely to those of steady walking, necessitating small adjustments to the walk in the final steps. First, the final leg protraction often occurs in the absence of strong retraction by the supporting legs. Second, the insect often takes advantage of the left/right asymmetry, letting rear and middle legs on the leading side retract beyond their normal endpoints while completing the metachronal sequence on the trailing side. Walking typically resumes with an initial retraction by all legs. Stances are close enough to leg configurations of steady walking that metachronal rhythms are often continuous across pauses, a feature which suggests that leg coordination is affected by peripheral parameters, such as leg position.

INTRODUCTION

Unlike quadrupeds, animals with six or more legs normally walk in such a way that they retain static stability at all times over a wide range of speeds (McGhee & Sun, 1974). Even during fast walking in which the support phase of each leg lasts only half the step cycle, an insect can always rely on at least three legs for support. For insects walking fast, the classical tripod coordination ensures that the three supporting legs always form a stable support. For insects walking more slowly, four legs or more may be simultaneously in contact with the substrate, providing even more stability.

This inherent static stability throughout the step cycle raises several questions concerning the relationship between walking and standing. First, given that all leg configurations in the step cycle provide adequate support, is an insect in fact equally likely to stop walking at any point in the cycle? Second, are leg configurations assumed by a stationary insect also present during walking or are they specific to standing? Third, if these preferred stances differ from those used during walking, how is the

* Present address: Fakultaet fuer Biologie, Universitaet Bielefeld, Postfach 8640, D-4800 Bielefeld 1, F.R.G.
Key words: Insect walking, behaviour, coordination.

transition made between walking and standing and what features of walking are unaffected by pauses? This transition has been the subject of several studies with humans and quadrupeds (reviewed in Wetzel & Stuart, 1976). The present study investigates these three questions for a six-legged walker, the stick insect.

METHODS

Data were obtained from adult female stick insects (*Carausius morosus*) walking on a wheel. Each insect was glued dorsally to a metal rod which was clamped in position above a walking wheel of light construction (Wendler, 1978). The insect walked along the 3·0 cm wide rim of the wheel and experienced an inertial mass of 1·5 g. The wheel was mounted on a fixed axis and had a radius of 16·4 cm.

Recordings were made of intervals of walking which included pauses. If the insect did not spontaneously begin or resume walking, it was stimulated to do so either by air puffs or by light pressure on its abdomen. The insect was allowed to stop of its own accord. The findings presented here derive mainly from four animals for which a total of 104 intervals were recorded showing step sequences preceding and following a pause of 2 s or more. From these same animals, a further 27 intervals showing starting only and 44 intervals showing stopping only were included in some analyses. Data from 12 more animals were used to corroborate these findings, providing a database of between 250 and 310 intervals for the analysis of contiguous stops and starts or for that of stops and starts considered separately.

Two kinds of data were recorded (Wendler, 1978). One system registered the absolute motion of the wheel in 1 mm units. The second system recorded the anterior–posterior position of each leg by using a photoelectric method to determine the angle between femur and body axis. This measurement primarily reflects protraction and retraction of the coxal-subcoxal joint. It is approximately proportional to anterior–posterior tarsus position as long as the tarsus steps on the wheel rim, but as Baessler (1972) has shown for free-walking insects, the deviation between tarsus position and femur angle increases for extreme leg positions. Leg positions were measured at a rate of 88 samples s^{-1} (interval between samples approx. 11·3 ms).

These measurements were recorded on tape and then later processed with a PDP 11/40 mini-computer to obtain two kinds of data files. One file was an image of the raw data; it contained the sequential leg positions and the record of wheel movement. The second file, referred to below as the step file, contained a fit of protraction and retraction phases for each leg together with general step parameters – stride length, step period, and walking speed – based on steps of the right rear leg.

These two files provided the basis for the following analysis, which consisted of three stages. First, the step file was used to calculate mean protraction and retraction endpoints for sustained walking. This calculation included regular steps only, that is, those in which the period of the right rear leg differed by less than 20 % from that of both the preceding and following steps. Second, the raw data were plotted and used to tally protraction sequences before and after pauses in locomotion. Third, for the four animals which were analysed in detail, intervals of raw data were printed to determine the exact leg positions during halts. Then the ensuing two steps were retrieved from the step file to permit both an accurate determination of the sequence

leg protraction and a calculation of protraction and retraction endpoints for the first step following the pause.

RESULTS

The results to be presented here all relate to one basic event: the behaviour of a stick insect as it first ends a walk and then resumes walking. Fig. 1 shows several examples of such sequences from one animal in which this transition was particularly abrupt. The following analysis examines various features of this behaviour.

Stopping sequences

The first question to be answered was whether stopping occurs with equal frequency at all points in the step cycle or whether there are preferred step sequences used in stopping. (If each stopping sequence is directly determined by stability influences, then our experimental situation was actually less stringent than free-
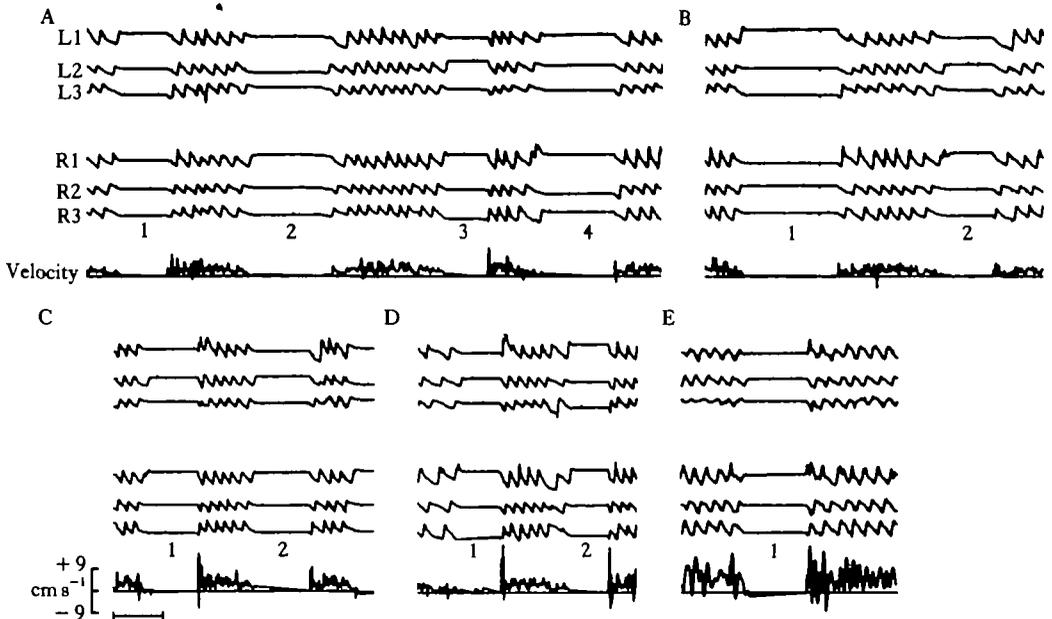

Fig. 1. Examples of starting and stopping sequences. All examples are from an animal which when stimulated made short walks with particularly abrupt transitions between walking and standing. In each record the lowest trace shows the wheel velocity; the six upper traces depict the forward and backward motion of the six legs – left (L) and right (R) front, middle and rear (1, 2 and 3, respectively). Protraction corresponds to upward movement of the trace. The time bar at the lower left represents 5 s for parts A–D and 2·5 s for part E. (A) Four sequences, three of which illustrate continuity in metachronal rhythm for interruptions after: a front leg protraction (1, L and R; 2 and 3, R; 4, L), a middle leg protraction (3, L), and a rear leg protraction (4, R). The left side in sequence 2 shows an omission of the L1 protraction expected as the second in the start sequence. (B) Two sequences showing departures from metachronal continuity. In 1, L1 precedes L2 but appears to be shortened by the L2 protraction. In 2, the L1 protraction expected at the start is omitted. (C) Two sequences showing shortened protractions as walking starts (L3 in 1; L2 in 2). (D) Two further examples of adjustment in step amplitude. In 1, L1's initial retraction is shortened as the leg adapts to the metachronal rhythm. As walking slows and stops in 2, R1 omits a protraction, causing both R2 and R3 to make small protractions. (E) The final protraction by R1 is resumed with little or no intervening retraction after a pause. Similarly, the almost simultaneous protraction of L1 shows minimal retraction at the start of walking.

walking: because the insect's position above the wheel was fixed and required ◀ support from the legs, unstable leg configurations would not have caused it to fall.)

Observation immediately revealed one trivial category of halting configuration that did not occur: no leg remained raised in mid-protraction; all legs grasped the wheel during pauses. More significantly, almost all protractions continued to near their normal endpoints, even when the supporting legs had virtually stopped retraction and no wheel motion was evident. Thus, it did not appear that legs remained in a state of protraction during a halt. In rare instances (<2 % of all stops, but ranging from 0 to 6 % for different individuals), a protraction was obviously shortened before the halt and then resumed at the start of walking (Fig. 1E, R1). Front, middle and rear legs all showed such protractions. In most of these cases, slight retraction and associated wheel motion were discernible preceding the resumption of protraction.

Since halts generally do not interrupt protractions, the next question was whether each leg is equally likely to make the last protraction. Only ipsilateral step relationships will be considered. For this purpose, ipsilateral leg protractions can be grouped in triplets composed of successive protractions by rear, middle and front legs. (This metachronal description has often been applied in the past, but it does not necessarily correspond to any internal coordinating entity, von Holst, 1939; Cruse, 1979.) As Table 1 shows, front, middle and rear legs were not equally likely to make the last protraction before a pause. In general, the front leg was most likely (65 % of stops) and the rear leg was least likely (12 % of stops) to make the last protraction.

For each individual insect, this order of preference was strong on one side of the body and less pronounced on the other, but only in one case – the left side of animal 1 – were final protractions more often made by a leg other than the front leg. Some lateral difference would be expected from the fact that the triplet sequences on the two sides normally are not in phase. This factor should reduce the probability of segmental partners each making the last protraction on their respective sides. Nevertheless, the adult stick insect often completes both metachronal sequences, in part because contralateral phase relations are not exactly antiphasic (Wendler, 1964; Graham, 1972). This asymmetry means that the interval between protractions of left and right front legs is longer in one half of the cycle than in the other. As a result, stopping after the front leg protraction of the trailing side should be more conducive to achieving a final triplet sequence of rear–middle–front on both sides. Although contralateral

Table 1. *Leg making the final protraction before a pause, tallied separately for left and right sides*

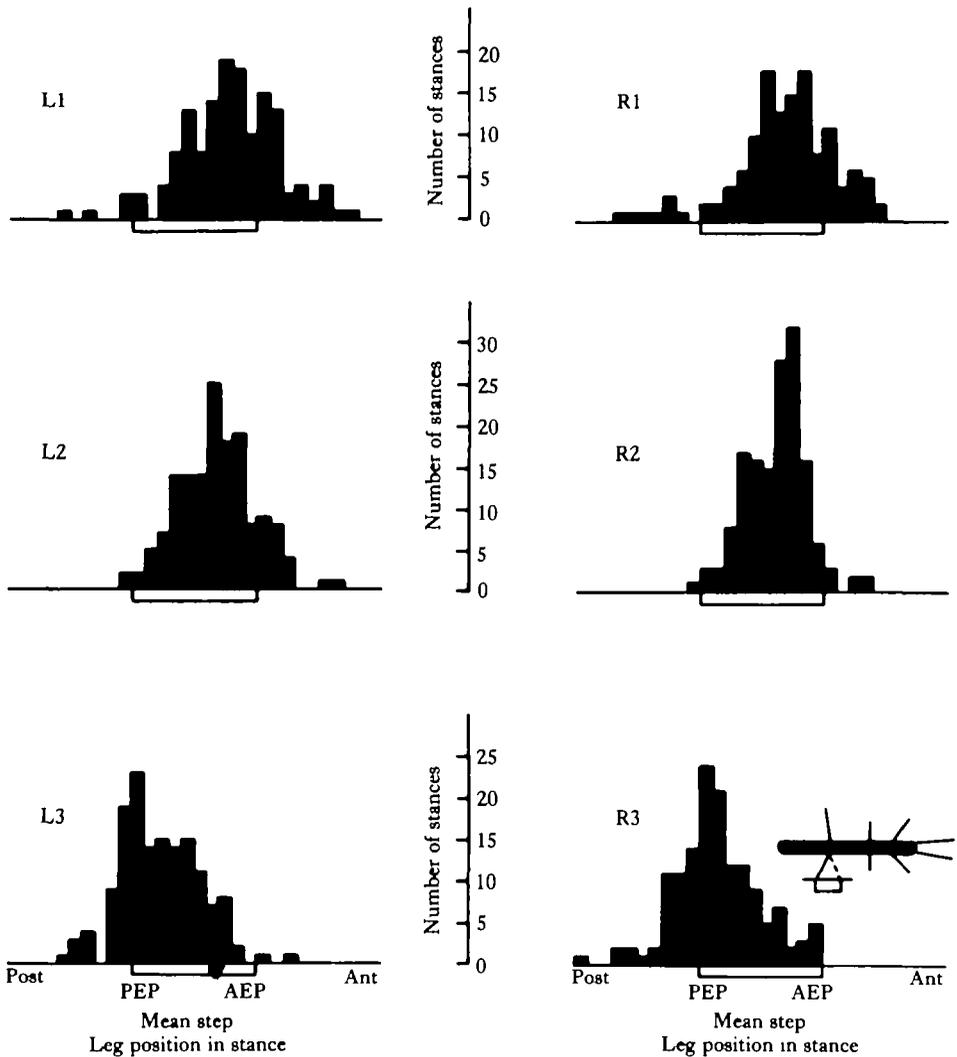|	R3	R2	R1	L3	L2	L1
			Four individual animals			
A1	3	5	25	3	20	10
A2	1	5	18	2	7	11
A3	3	9	26	8	4	30
A4	7	0	17	1	1	18
			Combined totals for all animals			
All	30	63	204	27	61	154
	13%	20%	66% $N=308$	11%	25%	64% $N=2$◀

Fig. 2. Histograms of leg positions during stances. The six histograms show the three ipsilateral leg positions for left and right sides. Data from four animals are combined. For each leg the average protraction length during sustained walking was normalized and the class width was set to 0·1 of this length. PEP, posterior extreme position; AEP, anterior extreme position.

phase relations in the final steps before a pause were not calculated directly, inspection of final gait sequences indicates that stopping preferentially occurred in this part of the cycle.

Stance configurations

Since the step sequence is not interrupted randomly, it is unlikely that the stances assumed during pauses are random. This expectation is confirmed in histograms showing leg positions during pauses in relation to the range of positions during walk-(Fig. 2). The more consistently one leg made the last protraction on its side, the

more frequently it assumed stances in the anterior part of its range. The preceding █
in the triplet sequence, which usually made the next to last protraction, finished in the
middle of its range, while the third leg, having protracted ahead of the other two,
ended in the posterior part of its range. Therefore, the most frequent stopping con-
figuration left the front, middle and rear legs in anterior, middle and posterior
positions, respectively. For individual animals, the phase difference between the left
and right sides again led to an asymmetry corresponding to that found in Table 1.

These findings show that stick insects have preferred stopping points in the
ipsilateral triplet sequence and that they assume preferred stances when stationary;
they do not yet establish whether these preferred stances are themselves normal
walking configurations. Before this question could be answered, it was necessary to
find a method of representing the leg configurations which occur during steady walk-
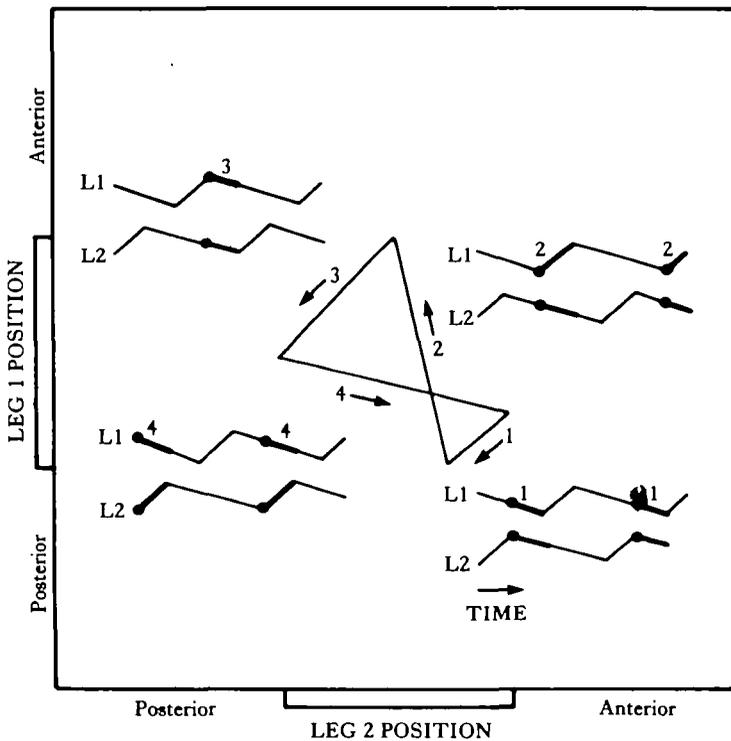ing. The method chosen here is based on a geometrical graphing of simultaneous leg

Fig. 3. Schematic diagram showing the relation between temporal and spatial representations of
ipsilateral walking coordination. The figure illustrates the basis used in Fig. 4 for the comparison of
stances with leg configurations of steady walking. The geometrical representation graphs the path
traced out by successive positions of two legs. The abscissa and ordinate show leg position with the
lower left corner of the square representing posterior for both legs. The open bars for each axis extend
from the leg's mean retraction endpoint to its mean protraction endpoint; this mean step range is
normalized for each leg. The small arrows beside the path indicate the direction of the progression
for forward walking. Each of the four line segments corresponds to the thick-lined interval in the
associated inset; these insets depict the position of the two legs *versus* time in a conventional manner.
The four corner points are the mean leg positions when one leg or the other switches between
protraction and retraction (black points in the insets). See text for further details.

■itions for each ipsilateral leg pair (Fig. 3). For the cyclic, phase-shifted stepping of two legs, this procedure generates Lissajous-like figures (Scharstein & Horsmann, cited in Wendler, 1978). The progression of successive positions traces hour-glass figures which are shifted and distorted as the legs take stances that are closer together or farther apart. The top and bottom of the hour-glass, non-intersecting segments of positive slope, represent intervals of joint retraction by the two legs; the progression in time is toward the lower left. Of these two more or less parallel segments for adjacent legs, the segment at the lower right corresponds to the interval between the protraction of the posterior leg and the subsequent protraction of the anterior leg. During this interval, the two legs are closest together. The two intersecting segments of the figure, both usually with negative slope, represent intervals in which one leg protracts and moves rapidly forward while the other leg continues its slower retraction. Neither time nor walking speed explicitly appears, but the latter can be envisaged as the speed with which the successive leg positions advance along the path. This representation would be most useful if the form of the path were constant for different walking speeds, but for adult stick insects this is not quite the case. One reason is that protraction duration does not lengthen in proportion to retraction duration as step period increases. In fact, protraction duration remains generally constant (Wendler, 1964; Graham, 1972). Therefore, as walking speed decreases, each leg changes its position less during the protraction phase of the second leg. This factor should cause the angle between the intersecting segments to approach a right angle for slow walking.

Fig. 4 uses this geometrical representation to compare the stationary stances for one animal with its leg configurations during steady walking. For this figure, the path describing the mean relation between leg pairs was constructed by first determining the mean protraction and retraction endpoints for each leg and the corresponding mean position of its partner. Then, these four points were joined to form the mean step path (see Fig. 3). In order to interpret the results, the initial expectation was that an insect stopping suddenly during walking would stand with a leg configuration on or near this path. Clusters of points would indicate preferred stances; their location in relation to the mean cycle should reflect any divergence between stopping and steady walking. If stances were closely related to walking, three different clusters might be expected differing according to which leg made the final protraction.

The example illustrated in Fig. 4 and similar plots for the other three individuals show that stances generally lay close to leg configurations present during walking, but they were not restricted to any small part of the walking path. The dimensions of the distributions were usually as large as the length of a joint retraction segment. Discrete clusters of stances related to final protractions by different legs in the triplet sequence could be discerned for only a few leg pairs.

Despite the spread of points, several features illustrate specific characteristics of the relationship between walking and standing. First, the stances were not randomly distributed over the whole field of walking configurations; instead, they were more concentrated in the upper left half of the path. Of the two joint retraction phases, this is the one in which the two legs are farther apart and therefore provide a more stable supporting platform. This concentration corresponds to the preference for stopping ■er a completed triplet sequence. For the one animal in which the majority of halts
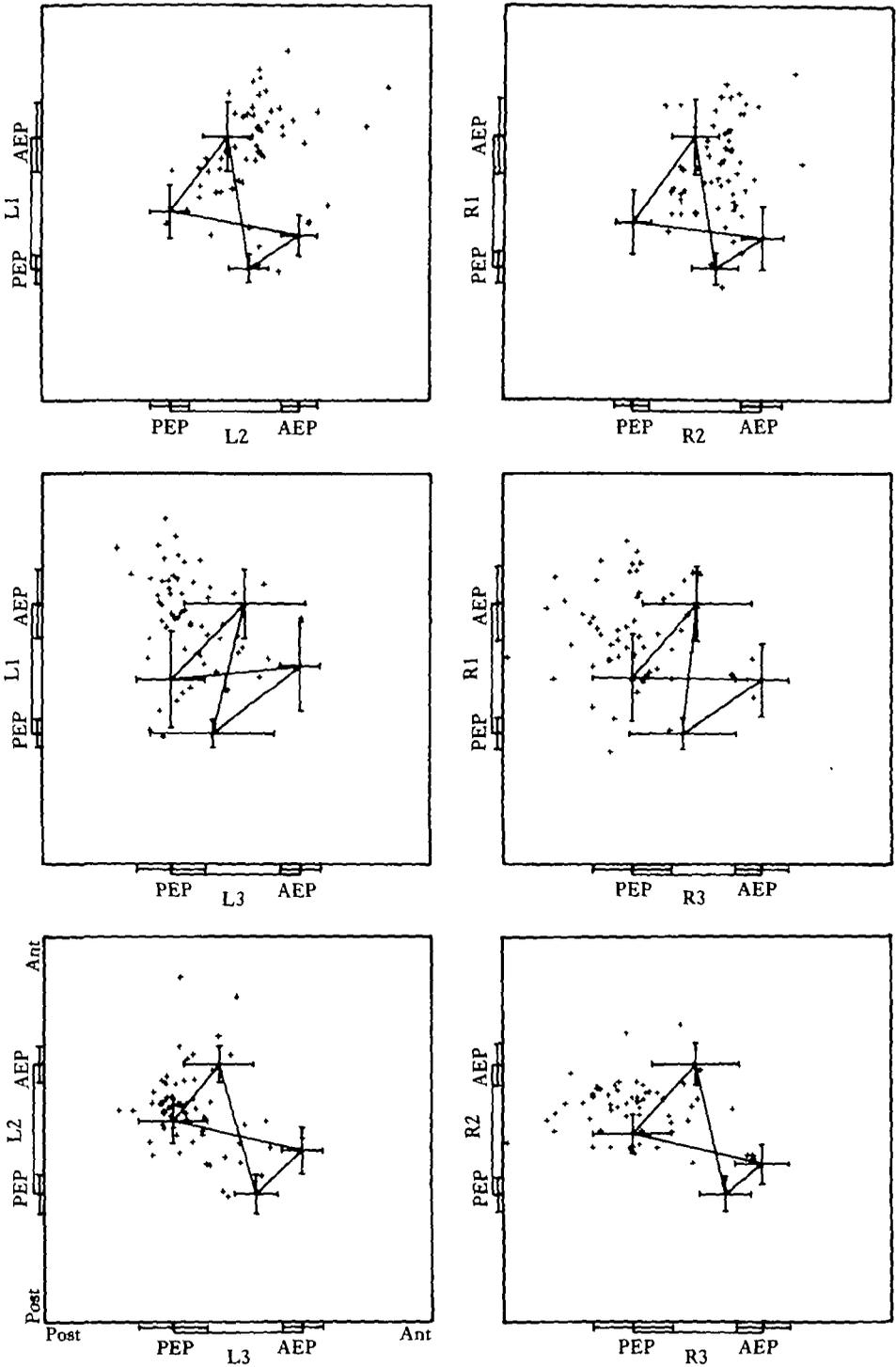
J. DEAN AND G. WENDLER

Fig 4

▎the left side followed middle leg protractions, the stances for the left middle and front leg pair were distributed along the joint retraction segment at the lower right. Second, the stance points tend to be distributed along the upper left retraction segment, indicating that the relative stances conform to relationships that obtain during steady walking. Third, the location of the distribution relative to this segment of joint retraction in the mean path reveals slight changes peculiar to stopping. Displacement perpendicular to the segment is determined at the protraction endpoint of the last leg to protract. The amount of joint retraction then displaces the final position parallel to this segment.

For rear leg–middle leg pairs, the distributions showed no consistent shift above or below this joint retraction segment: for each animal one pair was evenly distributed around this line; three of the contralateral pairs were shifted below and one was shifted above this segment. Absence of consistent perpendicular displacements indicates that normal spatial relationships are maintained at least until the middle leg finishes its protraction. The distribution along this segment was more concentrated: all eight such pairs assumed stances posterior to the segment's anterior end (upper right) and five of the eight had stances concentrated in the posterior half of the joint retraction. Thus appreciable joint retraction of middle and rear legs usually occurred before stopping; often this retraction continued beyond the point at which rear leg protraction would normally begin in steady walking.

In contrast to the rear leg–middle leg pairs, the distribution of middle leg–front leg stances did not coincide with the joint retraction segment but lay below it for all eight pairs. In addition, six of the eight showed significantly more frequent stances lying anterior to the segment midpoint and four of the eight lay anterior to its mean starting position. This divergence points to an alteration in spatial configuration which accompanies stopping. Such a change would result if the final protraction of the front leg occurs with little or none of the normal retraction by the middle leg. This interpretation was supported by inspecting records of wheel velocity in relation to the final leg protraction (see Fig. 1). When the front leg made the last protraction in the metachronal sequence before a stop, this protraction coincided with or even followed the cessation of wheel motion in one-third to one-half of all cases. (A similar relation was observed for middle legs in the less frequent instances in which a middle leg made the final protraction. Terminal protractions by rear legs were still less common, but these

Fig. 4. Leg configurations during standing, shown in relation to leg configurations for steady walking. Crosses indicate the relative position of leg 1 (ordinate) and leg 2 (abscissa) during pauses in walking. Posterior is down and to the left. The bar on each axis is the normalized mean step range. The hour-glass figures represent the mean path of successive leg configurations during steady walking. The horizontal and vertical bars at each corner are standard deviations for leg positions when one of the legs switches between the protraction and retraction phases. These orthogonal bars do not accurately represent the fact that for some points, x and y are correlated and the actual distribution is elliptical. In both graphs of middle leg *versus* rear leg positions (bottom row), the stances are clustered in the posterior half of the upper joint retraction segment. On the right side, many stances are to the rear of the normal retraction endpoint for the rear leg. In front leg *versus* rear leg plots (middle row), the stances show the front leg generally farther forward than would normally be the case during steady locomotion: the points lie above the upper joint retraction segment. In front leg *versus* middle leg plots (upper row), the cluster indicates that the middle leg is shifted rostrally, indicating the absence of normal retraction during the final protraction of the front leg. PEP, posterior extreme position; AEP, anterior extreme position.

were more often completed before wheel velocity slowed.) Because these final protra▮tions generally are full length while the wheel slows down as the supporting legs omit or reduce their usual thrust to the rear, the protracting leg steps into a configuration slightly different from those which normally occur during walking.

Starting sequences

These results show that stationary stances are similar to leg configurations of steady walking. Therefore, an insect should be able to begin walking simply by resuming the interrupted sequence of protractions. Most starts (70–90 %) were organized in triplets. Therefore, the frequency with which a particular leg made the initial protraction upon resumption of walking suffices for an initial characterization of starting sequences. In all animals, walking most often began with a protraction by the rear leg (Table 2). This would be expected both from the leg's stance – usually near the posterior limit of its normal walking range – and from its position in the triplet sequence – following the protraction of the ipsilateral front leg which most often terminated walking. Even for the left side of one animal in which most final protractions were by the middle leg rather than the front leg, it was still the rear leg which most often made the initial protraction. More typically, however, the percentage of final front leg protractions was larger and it generally equalled or exceeded the percentage of initial rear leg protractions (compare the percentage of initial rear leg protractions in Table 2 with the percentage of final front leg protractions in Table 1). This discrepancy suggests that the triplet sequence is not strictly maintained across a pause.

Sequential stops and starts

More direct information on continuity is revealed by an examination of sequential stopping and starting sequences. For three of the four individuals tested, more than 85 % of the sequences showed a clear triplet organization of both stop and start; for the fourth, the corresponding figure was 65 %. However, continuity of these triplets across a pause varied considerably among animals and between sides of the same animal. The right side of the animal illustrated in Fig. 1 showed the greatest continuity: 93 % of its starting sequences simply continued the sequence interrupted by the pause. If the front leg made the final protraction, then walking began with a rear leg protraction (e.g. Fig. 1A: sequence 1). In this animal, there were no obvious

Table 2. *Leg making the initial protraction in the triplet sequence following a pause, tallied separately for left and right sides*

	R3	R2	R1	L3	L2	L1
			Four individual animals			
A1	25	3	4	15	4	13
A2	11	4	2	10	2	6
A3	17	8	14	27	9	12
A4	11	7	2	14	2	1
			Combined totals for all animals			
All	172	52	87	133	23	57
	55%	17%	28% $N=311$	62%	11%	27% $N=2$▮

Table 3. *Changes in spatial parameters of initial step following pause*

	R3	R2	R1	L3	L2	L1
			Retraction endpoints			
A1	−48*	−22*	9	−48*	−24*	−37*
A2	−66*	−33	−117*	−69*	−48*	−64*
A3	−214*	−66*	117*	−179*	−114*	100*
A4	−169*	−41	−107	−199*	31	87
			Protraction endpoints			
A1	−50*	−7	32	−13	−27*	−3
A2	−117*	36	−30	−2	−2	−24
A3	−94	−60	60	−68*	79*	321*
A4	−236*	25	198	−83*	15	147

* Difference significant at *P* < 0·05, *t*-test.
For both protraction and retraction, the table shows the difference between mean endpoints during steady walking and mean endpoints for the leg's initial step as walking resumes. Negative differences indicate that values for initial steps were more caudal. The measurement units from the walking wheel differ from animal to animal; in these units, mean step amplitudes generally ranged from 177 to 344 for A1 and from 529 to 1249 for A2 to A4.

differences according to which leg made the last protraction, but the number of such occurrences for the middle and rear legs was small (e.g. Fig. 1A: sequence 3 and sequence 4, respectively). The least continuity was shown by the right side of animal 3 with only 26 % of the starts resuming the triplet sequence broken off at stopping. In all, the percentage of continuous metachronal sequences across pauses exceeded 50 % in six of the eight sides examined. The most common deviation was an additional step by a front leg (as in Fig. 1E); such sequences together with strictly continuous ones comprised more than 50 % of the sequences for all eight cases. Omissions of single protractions (e.g. Fig. 1B: sequence 2; Fig. 1A: sequence 2) also occurred, again most often for front legs. In summary, a pause often left the basic temporal step sequence unaffected but this was not always the case.

A pause also affected spatial characteristics of the following steps. Fig. 1C illustrates two instances in which protractions were obviously shortened in starting. Protraction and retraction endpoints of the initial step following a pause were altered as shown in Table 3. For the rear legs, both protraction and retraction endpoints were significantly to the rear of those measured during sustained walking. For the middle legs, the retraction endpoints were also shifted posteriorly. No clear changes were evident in either the protraction endpoint of the middle leg or protraction and retraction endpoints of the front legs. However, all these values were subject to interactions with the order of the leg's first protraction in the resumed metachronal sequence. Both middle legs and front legs tended to retract farther to the rear the later their initial protraction in the ipsilateral starting sequence. Both middle and rear legs tended to protract farther forward if they were not the first to protract.

DISCUSSION

In the faster, dynamically stable gaits of quadrupeds, abrupt stops are only possible particular points in the gait cycle and stopping normally is achieved over several

step cycles (Roberts, 1967). For hexapods, the criterion of static stability is m█ throughout the normal gait cycle. Although stick insects may gradually slow down over several step cycles, especially when the initial walk is fast, the largest part of the deceleration generally requires only part of a step cycle. Nevertheless, the results presented above show that adult stick insects do not stop randomly in their step cycle. Although there is no single invariant sequence of final steps, rear legs rarely make the last protraction before walking ceases, while front legs often do so. The preferred stopping sequence places the legs in a preferred stance, a stationary configuration providing the insect with the widest and most even spread of the three legs on a side and therefore one conferring the greatest stability. This preferred stance does not represent a radical departure from steady walking: a similar ipsilateral configuration occurs during slow walking when each metachronal triplet is completed before rear leg protraction begins a new one.

Nevertheless, the alternation of the two sides means that the preferred stance is not simultaneously present on both sides. Therefore, in stopping, the insect must either leave one side in a less than optimal stance or modify the leg relationships of steady walking. The result usually is a compromise based on two minor modifications. The more obvious is a change in the amount of thrust during the final protraction. When an insect is walking, leg protraction is accompanied by an increase in propulsive motion by the other legs (Graham, 1972, 1981). In contrast, in about half the stopping sequences, the final protraction occurs with little or no retraction of the supporting legs. The second modification is for some legs to retract beyond their normal retraction endpoints. The asymmetry in contralateral phase relationships means that the two sides are closer to the preferred stance in one half of the step cycle than in the other. By allowing the leading side a more extended retraction, the stick insect can complete the metachronal sequence on the trailing side.

The overall pattern of adjustment may be summarized as follows. When an adult stick insect stops, its rear and middle legs move into appropriate positions during retraction, a time in which they are coupled to other supporting legs, while front legs reach their position with a protraction in the absence of strong retraction by the supporting legs. For most stops, the modifications described above are sufficient to achieve a stationary stance without departing from normal ipsilateral gait sequences, changing step lengths or readjusting leg positions after stopping.

In starting, the initial movement is almost always a joint retraction by all six legs. This quick production of forward motion is analogous to that derived by humans from the controlled unbalancing which initiates walking (Carlsoo, 1966; Herman, Cook, Cozzens & Freedman, 1973; Cook & Cozzens, 1976). This starting thrust may represent the most efficient way to set up and activate peripheral reflex mechanisms which contribute to the smooth coordination of protraction, the subsequent step phase for all legs. In spinal cats, one function performed by the activity in the midbrain locomotor trigger area is to switch reflex responses into forms appropriate for locomotion (Shik, Orlovskii & Severin, 1966).

In adult stick insects, the initial protraction usually is by a rear leg, a feature reported by Muybridge (1957) in his early studies of quadrupeds. However, in our results, this preference appears to relate to the preceding step sequence ending walking and the consequent position from which the leg resumes walking. A similar eff█

leg position in determining the initial protraction has been suggested for quadrupeds by Howell (1944).

Immediate metachronal organization is characteristic of most starts by stick insects on a wheel; Graham (1972) states that this is also true for free-walking insects. Some modifications in gait and spatial parameters which do occur can be attributed to interactions between gait and spatial parameters. The most common gait deviation is the addition or omission of front leg protractions. For the one animal in which omissions were especially common, they were associated with unusually anterior positions of this leg during standing. (The origin of extra front leg protractions is less clear; it may lie in the function of the front legs in locating supporting substrates to allow walking to continue.) On the other hand, timing may affect spatial parameters: when a leg must wait until later in the metachronal sequence to make its first protraction, its initial retraction endpoint is caudal to those of steady walking.

Discrepancies between leg configurations typical of standing and those of steady walking are also revealed in other spatial parameters. The posterior shift of the initial retraction endpoints for rear and middle legs may derive from stance positions already caudal to normal step endpoints or from the initial joint thrust to the rear by all legs. The changes in the protraction endpoints of middle and rear legs are probably brought about by the guiding behaviour (Cruse, 1979; Dean & Wendler, 1983) as adjustments to the more caudal position of the adjacent, rostral leg.

It is evident that stick insects have no single stopping or starting sequence; there is only a preferred stance and associated final step sequence. The gait sequence for resuming walking reflects the stance position and therefore continues from the final protraction sequence. This behaviour is found even though the insects in our experiments were not supporting their own weight. Load factors cannot contribute to either the step sequence performed or the stances taken, but for free-walking animals they might increase the regularity of the behaviour. Curiously, one pattern of contralateral coordination which is obviously unstable and yet occurs infrequently in free-walking animals (Graham, 1972) did not appear more frequently under the less stringent conditions of wheel walking. This pattern is the 'gallop' with simultaneous protractions by segmental legs. A similar pattern, the bilateral sequence of 3–2–1, frequently occurred in our data but with one side delayed slightly to avoid simultaneous segmental protractions (e.g. Fig. 1A: sequence 1).

This gait continuity across pauses in walking is similar to that shown by jumping spiders interrupting turns. In describing this spider behaviour, Land (1972) proposed a qualitative model in which leg protraction is strictly determined by geometrical parameters of leg position. Such a model simplifies the requirements for a central control system. It removes the need to store the final state of the system, since this information is held in the leg positions themselves. Regardless of the length of the interruption, the system can resume proper coordination on the basis of the current leg positions. Such simplicity is also a feature of the 'peripheral oscillator models' proposed for insects (Wendler, 1968, 1978; Graham, 1977; Cruse, 1980). The observations reported here are consistent with such a model although the considerable variability would not fit with a rigid mechanistic programme for stopping and starting. However, some of the deviations from gait continuity also point to the interaction of temporal and spatial parameters in determining coordination. Both parameters are

subject to adjustments in order to meet the slightly different demands of standing a▇
steady walking.

REFERENCES

BAESSLER, U. (1972). Zur Beeinflussung der Bewegungsweise eines Beines von *Carausius morosus* durch Amputation anderer Beine. *Kybernetik* 10, 110–114.

CARLSOO, S. (1966). The initiation of walking. *Acta Anat.* 65, 1–9.

COOK, T. & COZZENS, B. (1976). Human solutions for locomotion. III. The initiation of gait. In *Neural Control of Locomotion*, (eds R. M. Herman, S. Grillner, P. S. G. Stein & D. G. Stuart), pp. 65–76. New York: Plenum Press.

CRUSE, H. (1979). A new model describing the coordination pattern of the legs of a walking stick insect. *Biol. Cybernetics* 32, 41–48.

CRUSE, H. (1980). A quantitative model of walking incorporating central and peripheral influences. II. The connections between the different legs. *Biol. Cybernetics* 37, 137–144.

DEAN, J. & WENDLER, G. (1983). Stick insect locomotion on a walking wheel: interleg coordination of leg position. *J. exp. Biol.* 103, 75–94.

GRAHAM, D. (1972). A behavioural analysis of the temporal organisation of walking movements in the 1st instar and adult stick insect (*Carausius morosus*). *J. comp. Physiol.* 81, 23–52.

GRAHAM, D. (1977). Simulation of a model for the coordination of leg movement in free walking insects. *Biol. Cybernetics* 26, 187–198.

GRAHAM, D. (1981). Walking kinetics of the stick insect using a low-inertia, counterbalanced pair of independent treadwheels. *Biol. Cybernetics* 40, 40–57.

HERMAN, R., COOK, T., COZZENS, B. & FREEDMAN, W. (1973). Control of postural reactions in man: The initiation of gait. In *Control of Posture and Locomotion*, (eds R. B. Stein, K. G. Pearson, R. S. Smith & J. B. Redford), pp. 363–388. New York: Plenum Press.

HOLST, E. VON. (1939). Die relative Koordination als Phaenomen und als Methode zentralnervoeser Funktionsanalyse. *Ergebn. Physiol.* 42, 228–306.

HOWELL, A. B. (1944). *Speed in Animals*. Chicago: University of Chicago Press.

LAND, M. F. (1972). Stepping movements made by jumping spiders during turns mediated by the lateral eyes. *J. exp. Biol.* 57, 15–40.

McGHEE, R. B. & SUN, S.-S. (1974). On the problem of selecting a gait for a legged vehicle. Proc. IV IFAC Symposium on automatic control in space. USSR. pp. 53–62.

MUYBRIDGE, E. (1957). *Animals in Motion*. New York: Dover.

ROBERTS, T. D. M. (1967). *Neurophysiology of Postural Mechanisms*. New York: Plenum Press.

SHIK, M. L., ORLOVSKII, G. N. & SEVERIN, F. V. (1966). Organization of the locomotor synergism. *Biophysics* 11, 1011–1019.

WENDLER, G. (1964). Laufen und Stehen der Stabheuschrecke *Carausius morosus*: Sinnesborstenfelder in den Beingelenken als Glieder von Regelkreisen. *Z. vergl. Physiol.* 48, 198–250.

WENDLER, G. (1968). Ein Analogmodell der Beinbewegungen eines laufenden Insekts. In *Kybernetik* 1968, (eds. H. Marko & G. Faerber), pp. 68–74. Muenchen, Wien: Oldenbourg.

WENDLER, G. (1978). Erzeugung und Kontrolle koordinierter Bewegungen bei Tieren. In *Kybernetik* 1977, (eds G. Hauske & E. Butenandt), pp. 11–34. Muenchen, Wien: Oldenbourg.

WETZEL, M. C. & STUART, D. G. (1976). Ensemble characteristics of cat locomotion and its neural control. *Prog. Neurobiol.* 4, 1–98.