J. comp. Physiol. 81, 23—52 (1972)

A Behavioural Analysis of the Temporal Organisation of Walking Movements in the 1st Instar and Adult Stick Insect (*Carausius morosus*)

D. Graham

Dept. of Biology, Case Western Reserve University, Cleveland, Ohio, U.S.A.

Received June 29, 1972

Summary. The coordination of protraction leg movements in free walking first instar and adult stick insects has been examined by film and video-tape analysis. The first instar insect uses two alternative modes of walking which differ in the step frequency dependence of the time required to complete one metachronal cycle of protractions and the duration of the protraction cycle (Figs. 2, 4). The adult uses only one of these modes and its step patterns show a persistent right-left asymmetry in the timing of leg movements (Fig. 7). Two alternative methods of changing direction were found (Figs. 5, 9) and they appear to be related to the two modes of walking used by the animal. A model based on inhibitory interactions between oscillators representing leg activity has been constructed to explain the step pattern changes in both modes of walking and the temporal asymmetry of the adult pattern. This model appears to be applicable to the walking behaviour of other insects including the cockroach.

Introduction

In studies of walking behaviour in *Blatta* by Hughes (1952), *Periplaneta* by Delcomyn (1971a), *Carausius* by Wendler (1964a) and a number of hexapods by Wilson (1966) it has been shown that there is a significant difference in the temporal pattern of stepping at opposite ends of the speed range in a given insect. At high speed the walk is best described by the simultaneous movement of three legs forming a tripod of support for the body. At low speed at least four legs are in contact with the ground at any time and the legs on each side of the body step with a metachronal rhythm. Legs on opposite sides of the body in the same segment step alternately and the timing of leg movements is symmetrical about the body axis.

In the work to be described the step patterns of starts and turns have been examined as extensively as those of straight walking for they provide a useful insight into the organisation of the walking system as a whole. In contrast to earlier work on the adult stick insect by Wendler (1964a), using a treadmill, evidence is presented for two asymmetries in the timing of leg movements when the adult walks freely on a horizontal surface.

The existance of asymmetry in a coordinated set of movements suggests that one part of the system is dependent upon the performance of the other and this idea has been used to devise a model for the walking behaviour.

The objectives of the work were as follows:

1) To abstract from the walking behaviour of the stick insect a small number of parameters which describe the sequence of leg movements during walking.

2) To examine first instar nymph and adult walking in terms of these parameters and quantify differences in the walking behaviour of the insect at these two stages of development.

3) To search for relationships between the timing of leg movements in straight walking and turning which might show how the recovery of legs in preparation for new steps is organised.

From these studies a model has been constructed and the performance of the model is compared with that of the walking insect.

Method

Carausius morosus were obtained from the department of Zoology Cambridge University, and the Max-Plank-Institute, Seewiesen. In all experiments first instar nymphs varied in age between 12 hours and 3 days (body length 1 cm), and adults were used within the two weeks following their final moult (body length 7 cm).

The walking behaviour of the insects was recorded on 8 mm and 16 mm film or video tape under artificial illumination at framing rates from 18 to 70 per second. The unconstrained insects walked freely on a horizontal surface covered with graph paper which could be moved horizontally beneath the camera lens. All undamaged insects easily grasped such a surface and did not slip.

Twelve animals were filmed for the first instar study giving a total of 274 cycles of leg movement or 547 metachronal sequences of protractions. Four of these animals exhibited both types of walking pattern described in the text and the data characterising the first instar walk includes measurements on these 4 animals and 6 of the others (Figs. 2, 4).

Seven animals were used in the adult study and a total of 480 cycles of leg movement were recorded. This gave timing information on 960 metachronal sequences including right and left sides. Six of the animals provided records of 47 leg cycles each on average and one animal was filmed for 200 cycles to give the data characterising the walking behaviour of the adult (Figs. 4, 7).

The terminology and symbols used in the present work are defined as follows:
protraction–the forward movement or recovery stroke of a leg;
retraction–the rearward movement or propulsion stroke of a leg;
protraction time–the time taken for the forward movement (t_p);
retraction time–the time taken for the rearward movement (t_r);
period–the time taken for a complete cycle of leg movement,

$$P = t_p + t_r;$$

stride–the distance moved by the leg tip during protraction or the distance between the footprints of one leg;

lag–the time interval between the beginning of protraction in one leg and the immediately following beginning of protraction in another. Legs are numbered 1, 2, 3 posteriorly and the prefixes R and L are used to identify the right and left sides respectively. The lag between R3 and L3 is written $_{R3}L_{L3}$. The term $_3L_2$ defines a lag between legs 3 and 2 on the same side;

phase–the lag between two legs divided by the period of the first. Phase is a measurement of the temporal relationship between the cyclic movement of two legs. The phase of L2 relative to R3 is written L2:R3.

Results for the First Instar Insect

Leg Coordination during a Straight Walk

A typical step pattern for the first instar nymph is shown in Fig. 1. Walking is achieved by the simultaneous movement of a tripod of three legs alternately protracting and retracting. Legs 1 and 3 on one side step at the same time as leg 2 on the other side and the lags $_3L_2$ and $_2L_1$ are of equal duration. Legs of the same segment have a relative phase of 0.5 and these criteria define the pattern of leg movements known as the tripod gait. As an alternative to the statement that certain legs step simultaneously an equally effective description of this walk is given by the definition $_3L_1=P$ where the lag $_3L_1$ is the time interval for the completion of a sequence of protractions beginning with leg 3 and ending with leg 1 on the same side. This metachronal description of the tripod gait will be used in preference to that of simultaneous protraction in legs 3 and 1 because it simplifies the comparison of this particular gait with other walking patterns used by the stick insect.

The simultaneous use of three legs at a time in the tripod gait permits a temporal analysis of the force developed by the legs during one cycle of leg movement and a velocity profile of body movement is shown below

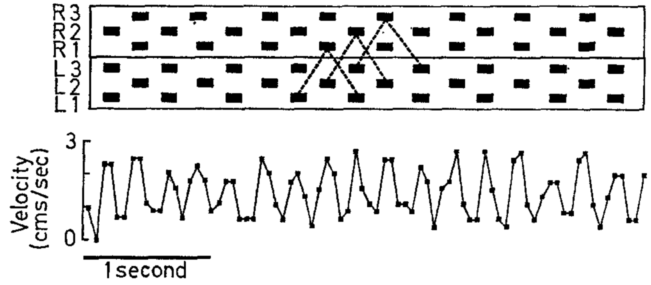

Fig. 1. Straight walk step pattern for a first instar stick insect. Protractions are shown by black bars with time increasing from left to right. Legs on the right (*R*) and left (*L*) are numbered 1, 2 and 3 from front to rear. Velocity was derived from the insect body displacement between frames and is plotted on the same time scale as the step sequence. Dashed lines stress the phase of legs in the same segment

the step pattern in Fig. 1. A rapid acceleration of the body during the first half of each retraction stroke suggests that the propulsive motor output to the retracting legs is a maximum at this time. During the second half of this stroke the body quickly decelerates. This is probably caused by a decrease in the propulsive force of the retracting tripod and an inertial reaction to the throwing forward of the other three legs during their protraction stroke. This jerking method of progression is typical of the tripod coordination pattern in this insect and it gives this walking behaviour the appearance of a military march.

Frequency Dependence of the Step Pattern in Straight Walking

The relationship between step pattern and period during a straight walk is illustrated in Fig. 2, where the average value of lag ${}_3L_1$ is plotted as a function of period P. This representation of the walking data is used in preference to one of phase versus period in order to show how the duration of the metachronal sequence depends upon period.

To avoid the inclusion of atypical lags caused by rapid step frequency changes the measurements of ${}_3L_1$ used in this graph were selected by the

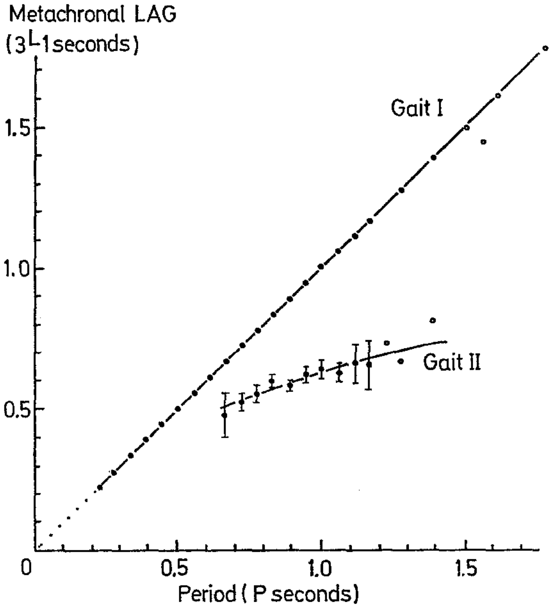

Fig. 2. Metachronal lag (${}_3L_1$) versus period (P) for 10 first instar stick insects. Closed circles represent the mean value of ${}_3L_1$ for a given mean period and open circles single observations. Error bars denote the error of the mean where this is larger than the symbol

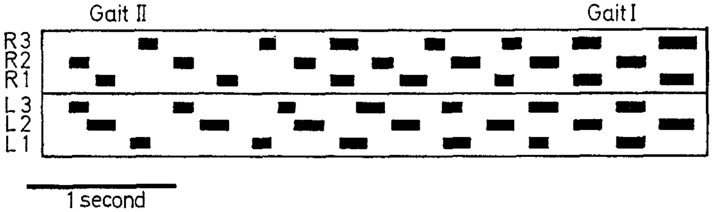

Fig. 3. Step pattern for a first instar stick insect starting in gait II and transferring from gait II to gait I

criterion that values of lag were only included in the average if the preceding period equalled the period of measurement to within one film frame. This selection process discarded 30% of the metachronal sequences in a typical straight walk.

The theoretical relationship between lag and period for a tripod gait is represented by a straight line of unit slope passing through the origin. The values of $_3L_1$ which conform to this relationship show that the nymph can use the tripod gait at any walking speed. The nymphs most frequently walked in this manner but not every walk followed this pattern At low speeds in the range of step period from 0.6 to 1.4 seconds an alternative gait was occasionally seen in which $_3L_1$ was significantly less than the step period.

When using the tripod gait the simultaneous protraction of three legs was easily observed and the insect gave the impression of marching towards a distant objective. The antennae were held in the horizontal plane at 40° to the body axis well above the walking surface. When using the alternative gait the head moved from side to side, the antennae swept the walking surface, the step pattern had a disordered appearance and frequent changes in heading were observed.

Fig. 3 shows a spontaneous starting pattern in which the nymph began to walk with a lag versus period relationship typical of gait II. After a few steps it accelerated and converted its walk into the pattern associated with gait I. The recording of such a sequence was quite rare as the nymphs normally used one gait or the other throughout a given walk but visual observation of the insect behaviour over a period of a few hours showed that transitions could take place in either direction. A transition from gait I to gait II generally occurred at the end of a long period of walking in gait I.

Another useful distinguishing feature of these two gaits is the dependence of the duration of protraction (t_p) on the step period. Fig. 4 shows the mean value of the protraction time for mesothoracic legs plotted

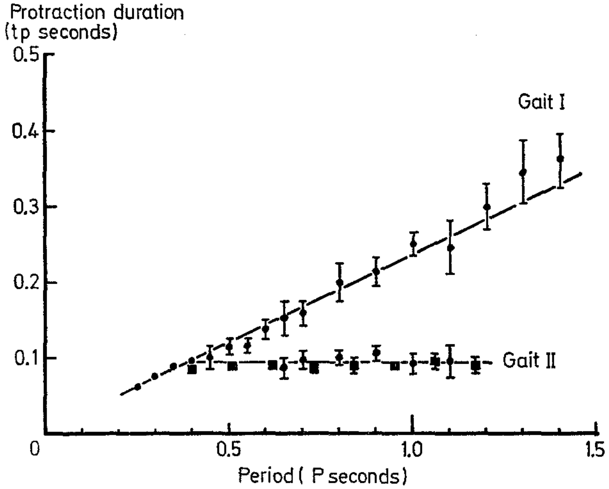

Fig. 4. Protraction time t_p as a function of period P for the mesothoracic legs of first instar and adult insects. Closed circles are average values of t_p for a first instar insect. Closed squares are average values of t_p for an adult insect. Error bars denote the error of the mean where this is larger than the symbol

against period for gait I and gait II. In gait I t_p increased with period so that $t_p = (0.23 \pm 0.02)$ P while in gait II t_p was independent of P within experimental error and had a constant value of 100±20 msec.

Phase Relations between Legs in Straight Walking

Fig. 2 can be used to calculate the phase relations for legs on the same side and clearly these will differ depending upon the gait being used by the insect. The phase relations between legs on opposite sides of the body in gait I can be deduced from Figs. 1 and 2. The insect consistently maintained a phase of 0.5±0.05 for legs on either side of the same segment and this parameter was independent of the step period over the range examined.

In contrast to this well defined behaviour in gait I the phase relationship between legs of the same segment in gait II was extremely variable. Although brief sequences of straight walking were recorded, such as that shown at the beginning of Fig. 3 in which the phase of right legs on left was 0.7, the typical behaviour in gait II consisted of frequent turns to right and left. In general the frequency of stepping on right and left sides differed and this continuous turning behaviour made it impossible to draw any inferences on the true nature of the temporal relationships between right and left sides other than to remark on the apparent rarity of full coupling between the two sides. Thus the present analysis of gait II is limited to the dependence of lag and protraction duration on period.

Leg Coordination during Changes in Speed and Direction

In order to increase its speed of movement the insect has two alternative options. It can either increase the stroke of its leg movements by taking longer strides, keeping the step frequency the same, or, alternatively, it can increase its step frequency keeping stride length constant.

In changing its walking direction the same considerations apply and a turn can be achieved either by a brief change in stride on one side or keeping stride length constant the step frequency may be altered on right and left sides. These examples are extreme assumptions and, in reality, one might expect the insect to use a combination of both methods in changing speed and direction.

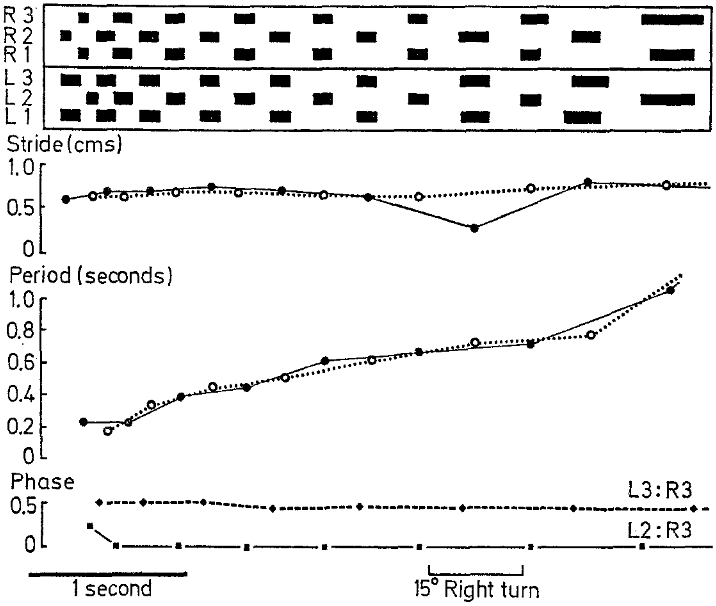

Fig. 5. Typical straight walk and turn sequence for a first instar stick insect. Step pattern, stride and period of the mesothoracic legs, and the phases of L3:R3 and L2:R3 are plotted simultaneously as a function of time. Stride is the distance moved by the leg tip during protraction for legs R2 (closed circles) and L2 (open circles) and is plotted at the mid point of protraction. Phase for L3:R3 is the time from the onset of a protraction by leg R3 to the next protraction of leg L3 divided by the period of leg R3 and is plotted at the onset of the protraction of leg L3. Similarly for L2:R3

In Fig. 5 a step sequence is shown in which the insect decelerated in a straight walk and then turned and walked in a straight path with a new heading 15° to the right of the original direction. The measurements of stride, period and phase show that step frequency increased with speed in straight walking and compensated for a slight decrease in stride with increased speed. During the change of direction stride decreased momentarily on the inside of the turn while the step frequency, phase and, therefore, the step pattern remained the same and showed no indication that the turn had taken place.

Thus in gait I turns can be produced by stride changes rather than step frequency changes and a typical walk consists of a series of straight line segments connected by rapid turns. No turns have so far been observed in gait I that produce a breakdown in the regular tripod step pattern.

No good examples of deceleration or acceleration were found in the rare sequences of straight walking associated with gait II but the frequent observation of turns associated with differences in step frequency on the right and left sides of the body suggest that changes in direction in this gait are produced by alterations in both step frequency and stride length.

Starting Step Patterns

During the filming of walking behaviour in the first instar nymph spontaneous starts were observed on four occasions. In three of these starts the insect began walking in a fully coordinated tripod but on one occasion the sequence of steps shown in Fig. 3 was recorded. The insect began its protraction movements by simultaneously recovering legs R2 and L3, this was followed by the pair R1 and L2 and the insect walked in a brief sequence of gait II in which legs of the same segment stepped consistently with a phase of 0.7 for right on left. Then right and left sides became temporarily uncoupled changing their timing with respect to each other until the typical coordinated tripod walk appeared. In 8 stimulated starts produced by touching the abdomen of the insect it immediately adopted a fully coordinated gait I step pattern.

Results for the Adult Insect

Leg Coordination during a Straight Walk

The tripod step pattern which is the dominant mode of locomotion in the first instar nymph is relatively rare in the adult and only occurred at the highest walking speeds.

At slower speeds the adult step pattern is similar to gait II of the first instar nymph and legs protract in pairs. However, long sequences

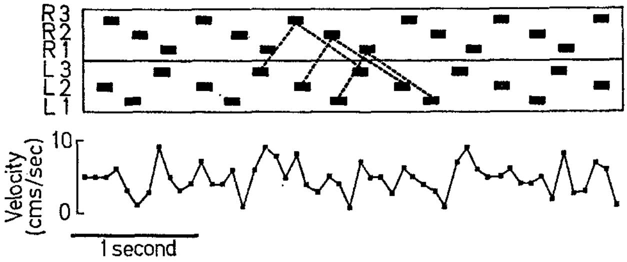

Fig. 6. Straight walk step pattern for an adult stick insect. Legend as in Fig. 1

of coordinated leg movements are common and right and left sides appear to be strongly coupled.

Fig. 6 shows a typical step sequence for the adult insect. The organisation of individual steps into successive metachronal sequences is evident. The gait may be termed bi-quadrupod for the legs protract in diagonal pairs and retract in sets of four. Thus at least four legs are in contact with the walking surface at all times. At the highest walking speeds the metachronal sequences overlap and the pattern then resembles gait I in which legs 3 and 1 on the same side step simultaneously.

One important feature of the low speed walk is the bilateral asymmetry of the step pattern. Right legs protract shortly after left legs in the same segment and the phase of right on left is 0.3 in the example of Fig. 6. A symmetrical alternative is theoretically possible in which the phase of right on left would be 0.7 and leg pairs R1-L2 and R2-L3 would protract simultaneously but walks in which this pattern of stepping occurred were rare in the present study.

As in the first instar nymph the speed of the body varied during a constant step frequency walk but the acceleration and deceleration were less extreme. This may be explained by the difference in the step pattern because in the bi-quadrupod gait two pairs of legs are in different stages of retraction at any instant of time and the impeding effect of the leg pair in protraction will be less noticeable.

The walk shown in Fig. 6 was considered to be a straight walk because contralateral legs maintained a fixed phase relation throughout the walk and certainly over a short distance the walk appeared to follow a straight path. However, when such a walk was observed over a distance of 1 metre the track was found to be slightly curved to the left with a change in heading of 10–20° over the total length of the track. This slight curvature was not found in first instar straight walks and in references to the adult the word straight will be enclosed in inverted commas.

Frequency Dependence of the Step Pattern in 'Straight' Walking

A plot of lag ${}_3L_1$ as a function of P for the adult insects is shown in Fig. 7. Consistently different lag values were obtained for right and left sides at each period. This was especially evident for short periods where the curves for right and left legs diverged. This difference between the mean values of lag on right and left sides was only significant (see Table 1) for the shortest step periods although the mean value of ${}_{R3}L_{R1}$ was less than ${}_{L3}L_{L1}$ at all periods examined.

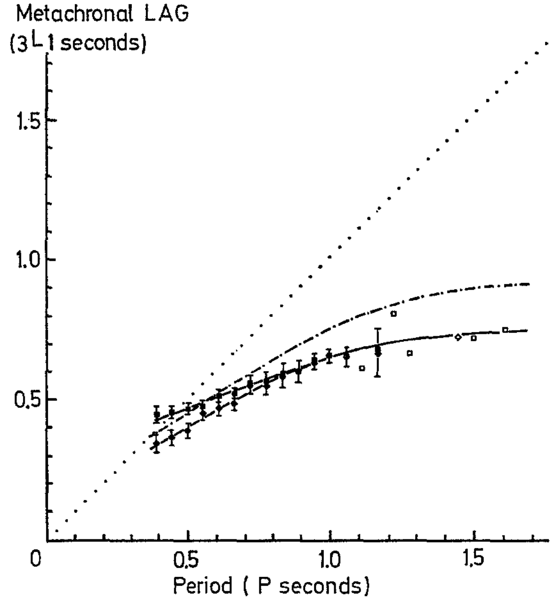

Fig. 7. Metachronal lag (${}_3L_1$) versus period (P) for one adult insect. Squares represent left leg steps. Diamonds represent right leg steps. Open and closed symbols and error bars have the same meaning as in Fig. 3. The —·—·— line is derived from the published results of Wendler (1964a) for an adult insect walking on a treadmill. The ···· line represents gait I for the first instar stick insect

A comparison of Figs. 2 and 7 shows that the adult gait is similar to gait II (${}_3L_1 < P$) of the first instar nymph but the adult is able to extend this gait to higher step frequencies. A second similarity between the adult walk and gait II in the nymph is the frequency dependence of the duration of protraction. Fig. 4 shows that in both cases protraction time t_p is independent of step period.

Table 1. Lag versus period for an adult insect

Period (P) (frames)	Right side			Left side			
	Mean lag $_{R3}L_{R1}$ (frames)	Sample size	Standard deviation	Mean lag $_{L3}L_{L1}$ (frames)	Sample size	Standard deviation	Probability[a] (t test)
8	6.63	16	1.26	8.21	19	0.86	<0.001
9	7.00	21	1.34	8.38	16	0.88	<0.01
10	8.15	20	0.81	8.53	19	1.02	<0.10
11	8.40	10	0.70	9.22	9	1.09	<0.05
12	8.75	8	1.03	9.29	7	0.77	>0.10
15	10.30	10	0.67	10.44	9	1.02	>0.10

One frame = 55 msec at 18 frames/sec.

[a] Probability that such extreme samples arise from only one population.

Phase Relations between Legs in 'Straight' Walking

The temporal relationship between certain pairs of legs in 'straight' walks of the adult are shown by phase histograms in Fig. 7. The data were obtained from a series of runs of one animal but the results are representative of all the adult stick insects so far examined. There is a strong tendency for simultaneous protraction of the diagonal leg pairs L1-R2 and L2-R3. Legs of the same segment do not step with a mean relative phase of 0.5 but instead show a preference for a phase of 0.35 for right on left (see also Fig. 6). This asymmetry becomes less noticeable as the step frequency increases until at maximum speed the legs in the same segment have a phase of 0.5. As the insect most frequently walks at speeds below the maximum the histograms are skewed.

Leg Coordination during Changes in Speed and Direction

In the adult insect speed and direction are altered by varying step frequency rather than stride length. An adult walking sequence which includes an acceleration, deceleration and a turn to the left is illustrated in Fig. 9. At first sight the step pattern appears to be rather disordered but an analysis of the walk shows that this is the result of rapid changes in step frequency and a temporary uncoupling of the leg movements on right and left sides. Measurements of stride for L2 and R2 showed that this parameter remained unchanged throughout the walk. The periods of legs L2 and R2 increased after 0.5 seconds (deceleration) and then decreased to their original value (acceleration). The heading of the insect and the phase of L2:R3 and L3:R3 remained unchanged during this

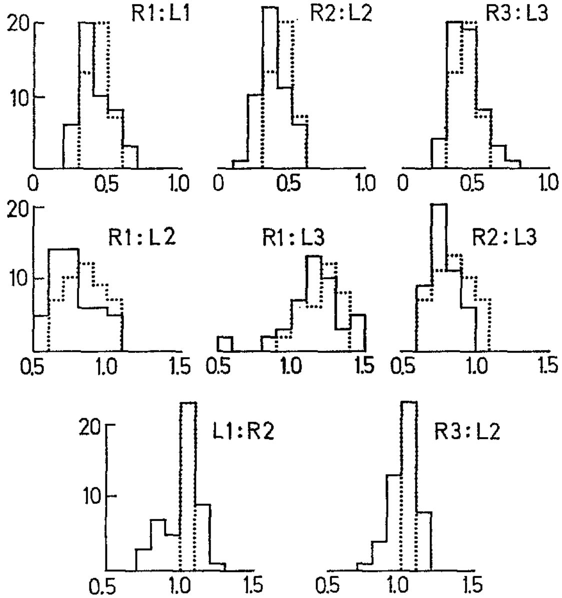

Fig. 8. Phase histograms of straight walking sequences selected from the data for the adult insect used in Fig. 7. The line histograms represent the experimental data. The broken line histograms are derived from the model described in the discussion

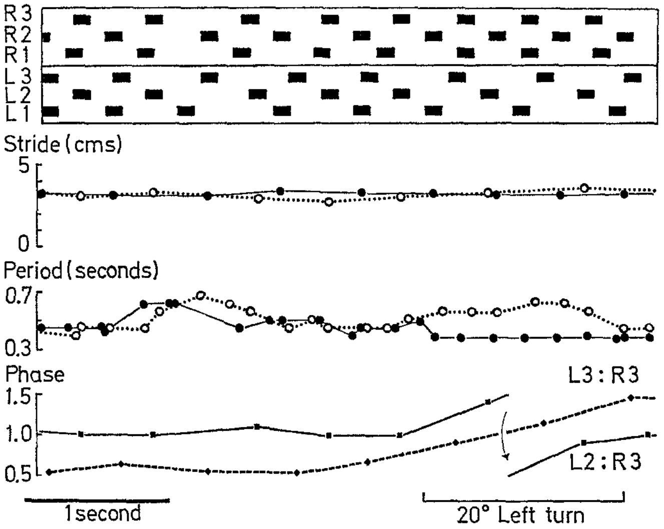

Fig. 9. Typical straight walk and turn sequence for an adult stick insect. Step sequence, stride, period and phase for an adult insect. For details of the measurement of these parameters see Fig. 2

manoeuvre. After 2.5 seconds the period of R2 decreased while that of L2 increased. These periods then remained at values of 0.4 and 0.6 seconds respectively for 1.5 seconds before they became equal again. During this time a change in the relative timing of legs on opposite sides occurred (see phase plot Fig. 9), and the insect turned to the left and changed its heading by 20° in 1.5 seconds. The alteration in phase between right and left sides can easily be detected visually in any free walking adult because at this time legs of the same segment step momentarily in synchrony. Thus, in Fig. 9, the 6th protraction of R3 was almost synchronous with the 6th protraction of L3 and this was also true of the following leg pairs R2-L2 and R1-L1. This 'gallop' walk was only temporary and its momentary appearance suggests that the right and left sides of the insect were uncoupled during the turn. In general this gait is only associated with turning step patterns but it has been observed for a number of successive steps in one starting sequence.

Starting Step Patterns

Three examples of the beginning of a walk, produced by touching the abdomen of the insect, are shown in Fig. 10a. Most commonly the normal step pattern appears immediately the animal starts to walk (Fig. 10a) but on one occasion a reversal of the normal stepping sequence on the right side of the insect occurred (Fig. 10b). On another occasion the right and left sides began stepping in almost perfect synchrony (Fig. 10c)

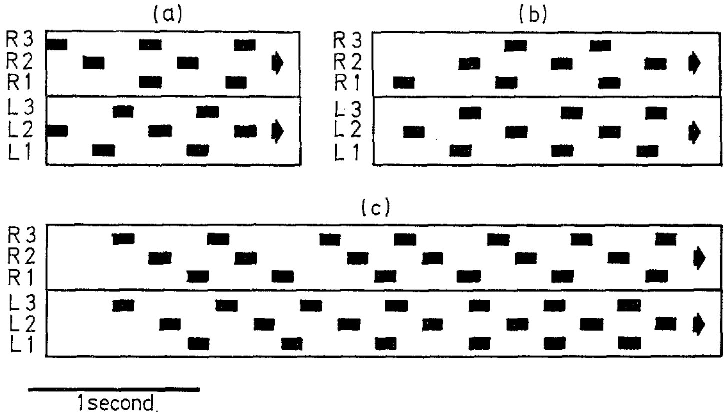

Fig. 10a—c. Starting step patterns for an adult insect. a) Typical start step sequence for an adult stick insect. b) Rare start sequence. This may be considered as a reversal of the normal sequence on the right or the absence of an R3 protraction. c) Rare 'gallop' start sequence in which the legs of the same segment step in synchrony followed by a gentle turn to the right

and maintained this pattern for four consecutive step periods before the insect began a gentle turn to the right. This maintained gallop shows that right and left sides can be uncoupled or perhaps coupled in a different manner for an appreciable period of time under certain circumstances. Finally, in connection with the adult behaviour, I must mention a number of errors that occurred in the normal metachronal sequence of protractions. No such errors were found in any of the step sequences of first instar nymphs using gait I.

Deviations from the Normal Stepping Pattern

The deviations most commonly observed in the adult walking behaviour fall into one of two categories.

The first is equivalent to the absence of a protraction from the normal stepping sequence of a prothoracic leg. As a result the leg continues to move backwards until the appropriate time for the next protraction occurs. This phenomenon was observed in one animal twice in 400 steps of a prothoracic leg. The incidence of these lost protractions can be increased by persuading an insect to walk along a straight path with right and left sides operating at different step frequencies. This can be achieved by placing the insect on a table so that the left legs, for

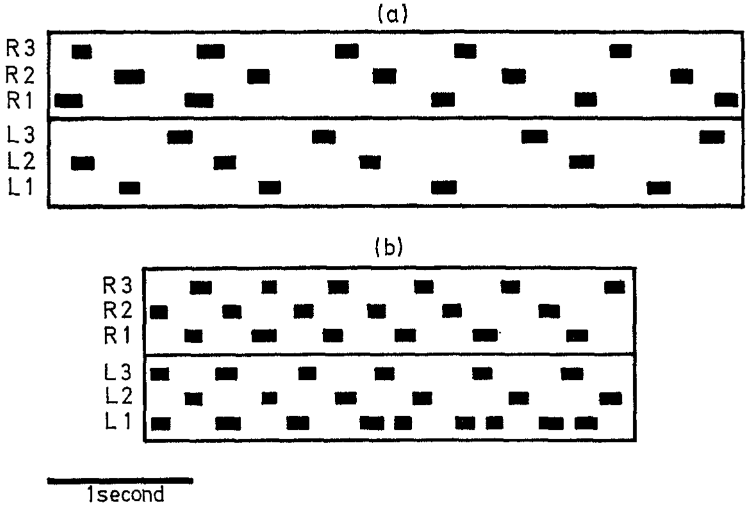

Fig. 11a and b. Deviations from the normal metachronal step sequence observed in the adult stick insect. a) An example of the step pattern produced by an adult insect walking with its right legs in contact with an edge. b) An example of the step pattern produced by an adult insect where 'extra' protractions of the leg L1 occur. Notice that additional or missing protractions do not reset the leg rhythm example, contact the edge while those on the right walk on the flat surface. As a result the left legs step at a higher frequency than those on the right and a protraction of the left prothoracic leg will fail to occur approximately once in every five steps. An example of such a walk is shown in Fig. 11a.

The second type of deviation is the occurrence of double protractions. These can occur in any leg but are most often seen in the prothoracic legs and consist of a normal protraction, i.e. one which occurs at regular intervals with the same period as other legs on the same side, followed by another forward movement of the leg instead of the retraction normally expected at this time. This type of deviation was observed 5 times for R1 and 3 times for L1 in 400 leg cycles of one adult insect. A higher incidence is usually associated with clearly discernable damage to the tarsus of the leg concerned. This behaviour is equivalent to the insertion of an additional protraction into the normal walking sequence and it should be noted that the extra protraction does not reset the timing of the subsequent steps (Fig. 11b).

Discussion

Some of the results of the present work are similar to those described by Wendler (1964a) who examined the step patterns of adult *Carausius morosus* walking on a treadmill. Measurements of the lag ${}_3L_1$ for walks on the treadmill are consistently greater than those for free walks (Fig. 7) but perhaps this difference can be explained by the body support given to the insect in the treadmill experiments. Indeed, the addition of small weights to the body of a free walking adult stick insect increases the step period for a given value of ${}_3L_1$. Thus decreasing the effective body weight might be expected to alter the dependence of lag on period in the manner shown in Fig. 7. Differences in the lag ${}_3L_1$ between right and left sides and the temporal asymmetry of the 'straight' walking step pattern which exist in the free walking animal appear to be suppressed when the insect walks on a treadmill. It is possible that the edge contact required by the treadmill experiment may account for some of the differences between this data and the data presented herein as it has already been shown that edge contact can produce unusual changes in the relative step frequency of right and left sides in the free walking insect.

Turns, starts and other examples of walking behaviour which might have given rise to differences in step pattern between right and left sides were not possible in the treadmill study but in series of free walking experiments on *Cantharis fusca* larvae Wendler (1964b) showed that right and left sides of this insect normally operate at slightly different step frequencies and turns are produced by accentuating this difference. The only other reference to turning behaviour in insects known to the author is the work of Roeder on *Mantis religiosa* (1937). He mentions that turning is achieved by changes in step frequency on the two sides and also describes a gait in which legs of the same segment step synchronously with a phase between adjacent legs on the same side of 0.5. This type of walk is similar to the gallop gait shown in the starting pattern of Fig. 10c, however, most of the time mantids appear to use a gait similar to that of the adult stick insect in which diagonal pairs of legs protract simultaneously.

The walking behaviour of the stick insect nymph most closely resembles that of the cockroach. Hughes (1952) and Delcomyn (1971) have shown that the cockroach characteristically uses a tripod gait over a wide range of step frequencies. At the lowest frequencies the step pattern is one in which the lag ${}_3L_1$ is less than P but this pattern blends uniformly into a tripod gait as the step frequency increases. There is no evidence of two alternative step patterns at low speed as seen in the first instar stick insect. Unfortunately no data is available on turning behaviour in the cockroach but the absence of any examples of the synchronous protraction of legs in the same segment suggests that turns may be achieved by the method described for the stick insect nymph in which the mesothoracic leg of the retracting tripod makes a shorter retraction stroke than the other legs.

Finally, in both insects the protraction time increases with step period so that $t_p \simeq 0.23\,P$ for the first instar nymph using gait I while $t_p \simeq 0.30\,P$ for the cockroach in the step period range 0.05 to 0.10 seconds. This is quite different from the adult stick insect behaviour and that of the nymph using gait II where the protraction time appears to be independent of step period.

Stick Insect Walking Behaviour

The existence of two different types of walking behaviour has been established in the present work. These two gaits differ in almost every respect and some of the basic features of the step patterns are summarised below in order to illustrate these differences.

Gait I.

1. ${}_3L_1 \simeq P$ for legs on the same side.

2. The phase of L:R $\simeq 0.5$ for legs on opposite sides of the same segment. Values of the lag ${}_3L_1$ are not significantly different on right and left sides.

3. Coupling between right and left sides is fixed and inflexible during starts, turns and straight walking.

4. Turns are produced by a decrease in the retraction stroke of a mesothoracic leg on the inside of the turn.

5. Protraction duration is proportional to the period.

6. No errors in metachronal step sequence have been observed.

The first instar nymph using gait II turns frequently and legs on right and left sides seldom step with any fixed phase relationship. Thus it is only possible to make quantitative measurements of lag and period on each side. However, all the features of gait II have been observed in the adult walking behaviour and this suggests that these patterns are formed by the same underlying mechanism. The only difference is that gait II in the first instar occurs over a more limited range of period and is complicated by frequent changes in heading. For these reasons gait II has been summarised in terms of information gained from the study of the adult insect. An asterisk indicates that a given observation has been experimentally confirmed in the first instar nymph.

Gait II.

1. ${}_3L_1 < P^*$ for most of the period range except at the highest step frequency where ${}_3L_1 \simeq P$.

2. A phase of 0.5 for legs of the same segment is found at the highest step frequency. At lower speeds the timing of leg steps is asymmetrical and the phase of R3:L3 is typically 0.35. The lag ${}_3L_1$ measured on the right differs significantly from that measured on the left at high step frequency.

3. Coupling between right and left sides is labile* and permits slow changes to a typical coupling or complete uncoupling in which right and left sides appear to operate independently.

4. Turns are produced by step frequency changes* rather than alterations in the leg stroke.

5. Protraction duration is independent of period*.

6. Errors in step sequence, such as missing or additional protractions, occur but they do not reset the timing of subsequent steps.

In gait I the absence of stepping errors, the inability of the insect to uncouple the leg movements of right and left sides and the frequency independence of the step pattern make the problem of determining a universally acceptable mechanism for tripod coordination particularly difficult. Many models of equal merit could be constructed and there is little hope of establishing any one model on the basis of externally observed behaviour alone. Gait II, however, provides much more information about the organisation of the walking system as a whole. In addition, changes between gait II and gait I are possible and a model of gait II must be capable of generating gait I. This provides a valuable constraint on models of gait II.

Gait II has a number of rather unusual features. The first and perhaps one of the most interesting is that right and left sides of the animal can operate independently as shown by the turning behaviour of the adult insect. This has been more rigorously confirmed in a treadmill experiment by providing two separate walking surfaces for right and left legs (flat belts of mylar film running on light rollers). The adult insect was supported above the treadmills by a stick glued to the dorsal surface and was frequently seen to walk with the legs of one side stationary.

Another feature of gait II which requires explanation is the asymmetrical phase relation between legs in the same segment. The phase of R:L is typically 0.35 for 'straight' walks at low speeds (see Fig. 6) but on rare occasions a phase of 0.5 or even 0.7 is possible although this last observation only occurred three times in measurements on a total of 7 adult insects. This asymmetry appears to be present in most adult stick insects as no example of an adult walking with a mean phase of R3:L3 $=0.65$ has been found. Many examples of right left asymmetry occur in other invertebrates and Wilson (1968b) has shown that motor output asymmetries frequently occur in the flight system of the locust although there does not appear to be a consistent asymmetry in this insect. However, parthenogenic reproduction may be responsible for the one handed asymmetry found in all the stick insects so far examined. In addition to this phase asymmetry there is also a difference in the lag versus period relation for right and left legs such that ${}_{\mathrm{R3}}L_{\mathrm{R1}}$ is consistently less than ${}_{\mathrm{L3}}L_{\mathrm{L1}}$ for a given value of P (see Fig. 7).

It appears that the major difference between turning and 'straight' walking in the adult is that in turns the right and left sides are uncoupled and operate independently but in a 'straight' walk one side interacts with the other to maintain a stable asymmetrical step pattern. This interpretation is an appealing one because the phase asymmetry can then be explained in terms of a slight difference in motor activity between the right and left sides of the insect.

Using the behavioural data for the adult and a system of interacting relaxation oscillators to represent the action of individual legs a model can be constructed which has the asymmetrical properties of the adult gait, shows how turns and changes in speed could be achieved and suggests a possible mechanism for the transition between gait II and gait I in the first instar stick insect.

A Model of Walking Behaviour in the Stick Insect

I must first admit to a bias in favour of a central mechanism for the coordinated timing of protractions in insect walking for reasons which will be discussed later. However, I have attempted to model the timing of leg movements in a sufficiently abstract form that the model can be expanded, in detail, from either a central or peripheral reflex point of view. I have used relaxation oscillators to represent the action of individual legs as they can be given a simple mathematical formulation and may be replaced by central pacemakers or peripheral reflex loops activating each leg. Similarly coupling between legs can have either a central or peripheral pathway.

The operation of a relaxation oscillator can be described most easily by the use of a water clock analogy in which a reservoir (pivoted bucket in stable equilibrium) is filled by an input (water flow). When the input fills the reservoir to threshold (a level determined by the bucket and pivot design) the oscillator is reset to its original state (bucket tips, empties itself and returns to its original position) and is again open to the input. This cycle of operation will be repeated with a frequency determined by the input rate.

Oscillators of this kind may be coupled together to form fixed phase relationships by using the reset of one to affect the threshold of another. In the stick insect the lag between two legs is a function of step frequency and the simple direct coupling of leg oscillators is incapable of describing the frequency dependence of the step pattern. To generate a lag between two oscillators that depends upon their common input I have used the concept of a single cycle oscillator. I have called this unit a delay oscillator because it is used to represent the delay or lag between the protraction of two legs. This unit functions in the same manner as the relaxation oscillator already described with the addition that the resetting of the oscillator (emptying of the bucket) also turns off its own input. Thus the delay unit only completes one cycle each time its input is turned on.

Using these components and the behavioural data for the adult stick insect a model capable of generating the timing of leg movements can be constructed as follows.

The independent operation of right and left sides during turning suggests that the walking system may be conveniently divided into separate right and left halves. Considering the left side first I have assumed that the metachronal sequence is produced by the oscillator system shown in Fig. 12. An input E_{L} to the left side of the model causes oscillators L3, L2 and L1 to begin activity. When L3 resets after a period determined by the input rate E_{L} the delay oscillator DL3 is turned on and using the same input E_{L} completes one cycle of activity. During the operation of this delay unit the threshold of L2 is temporarily increased. After a few cycles of activity the coupling between L3 and L2 will establish a constant phase relationship provided that the natural frequency of L2 is slightly greater than L3 (see appendix).

This form of coupling is similar to the concept of forward inhibition proposed by Wilson (1966, 1968a) as a possible mechanism for the forma-

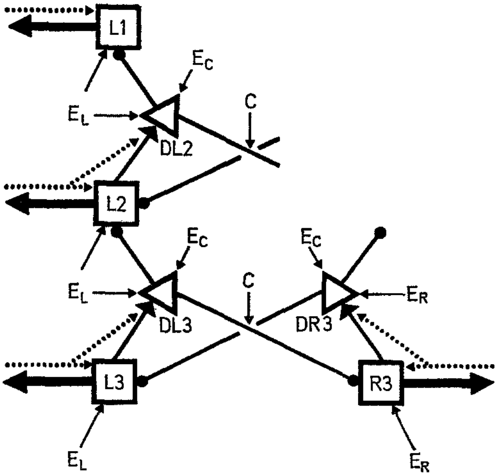

Fig. 12. Model for the walking system of *Carausius morosus.* ◻ Leg 'relaxation' oscillator driven by an input (E_L or E_R). ◀ Timing signal from the leg oscillator. This occurs only at reset and indicates the time for protraction of a given leg. ← Timing output to delay oscillator. This occurs at reset and initiates one cycle of the delay oscillator. ⇠ Possible proprioceptive input to leg and delay oscillators. ◁ Delay 'relaxation' oscillator producing lags, e.g. $_3L_2$. ●— Inhibitory command suppressing the reset of a leg oscillator by raising its threshold. E_L → Leg oscillator input on the left side. C → Command controlling the coupling between right and left sides. E_c → Delay oscillator input responsible for producing the unique dependence of lag on period for a particular walking gait

tion of a metachronal sequence of leg protractions in a walking insect. Oscillators L2 and L1 are coupled in the same manner and when a stable metachronal sequence is formed the period of all three oscillators is equal to the natural period of L3 and the lags between them correspond to the periods of the appropriate delay oscillators. Increasing or decreasing the input E_L causes a corresponding change in the step frequency of the system as a whole but the phase relationship (step pattern) is independent of E_L.

Fig. 13a shows how a metachronal sequence of protractions can be generated by the model. In this example the front leg oscillator has been activated first and the result is a starting sequence of the kind shown in Fig. 10b.

Since diagonal leg pairs such as L2-R3 step simultaneously it is assumed that the delay units which produce the metachronal rhythm on each side can also influence the opposite leg oscillator in the same

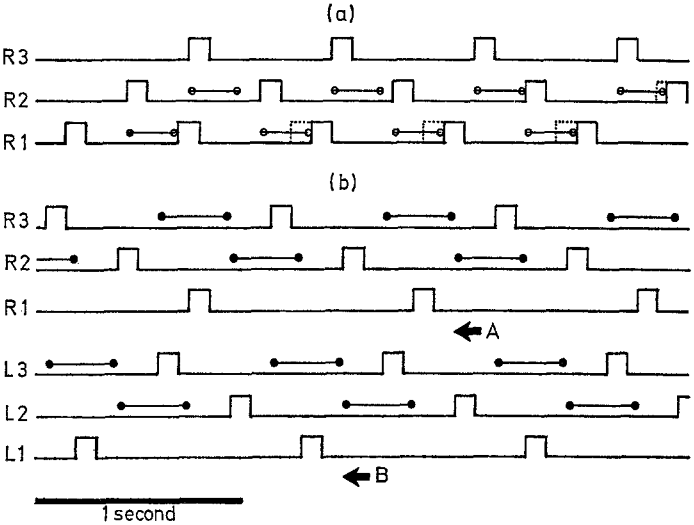

Fig. 13a and b. Model simulation of the step pattern for the adult stick insect. a) Simulated protraction pattern for one side based on the relationship between parameters derived in the appendix. The duration of the ipsilateral delay is represented by the symbol •——•. Oscillator 1 begins activity first followed by 2 and then 3. The resulting sequence of protractions is similar to that of the legs on the right side for the starting pattern shown in Fig. 10b. b) Simulated protraction pattern for both sides showing only the duration of the contralateral delays produced by the delay oscillators generating the metachronal rhythm on the opposite side. An increase in E_R moves the protraction pattern for the right legs in the direction of arrow A and produces a stable configuration in which the phase of R on L is 0.3. An increase in E_L moves the pattern on the left in the direction of arrow B and produces a phase of R on L equal to 0.7. These are the two alternative stable patterns permitted by the model in Fig. 12 when ${}_3L_1 < P$

segment and thereby couple the right and left leg systems in a 'straight' walk. This is illustrated in Fig. 13b. Only the delays across the body are shown but they occur at the same time as those producing the metachronal rhythm and are assumed to originate from the same source (the delay oscillators). It should be noticed that the model limits coupling to the meso- and metathoracic segments. These delays across the body form the only mechanism for coupling the right and left metachronal rhythms and when these pathways are suppressed by control C (see Fig. 12) the two sides are permitted to function independently.

The inputs E_L and E_R have been assumed equal in constructing Fig. 13b but it is unlikely that these inputs will always be exactly equal and the step pattern is inherently unstable. A stable pattern can only be produced by making E_L and E_R slightly different. A reduction in the step period on the right causes protractions to occur at a slightly earlier time in each step and as a result the step pattern for the right side moves in the direction of the arrow A. This gentle turning behaviour will continue until the delays initiated by the leg oscillators L3 and L2 interact with the oscillators R3 and R2. When this happens the right side is forced to operate with the same period as the left and walking continues with R3 : L3 = 0.3. The left side can be called the 'driving' side for it constrains the right side to operate at its own lower frequency. The right side which takes its timing from the left will be termed the 'driven' side.

An alternative stable protraction pattern is possible if E_L is greater than E_R, for the sequence on the left side in Fig. 13b will move in the direction of arrow B, the phase of R3 : L3 will become 0.7 and the leg pairs R2-L3 and R1-L2 step synchronously. In this configuration the right side of the model becomes the 'driving' side.

A further important asymmetry in the adult gait is the difference between the mean value of the lag ${}_3L_1$ for right and left sides at a given period. These differences appear to be a consequence of forcing the 'driven' side to adopt the timing of the 'driving' side. The coupling across the model affects the period of all three legs on the driven side but does not affect the lag ${}_2L_1$.

In the model I have assumed a unique relationship between ${}_3L_1$ and P which is defined by the characteristics of the leg and delay oscillators. However, this relationship can only be observed experimentally on the 'driving' side. On the 'driven' side ${}_3L_1$ will have a value corresponding to a shorter period but the measured period on this side is established by cross coupling from the opposite side. Thus the lag measured for the 'driven' side will always be less than that for the 'driving' side as a function of period. This explains the difference between ${}_{R3}L_{R1}$ and ${}_{L3}L_{L1}$ in Fig. 7 in terms of a higher level of activity on the right side and is consistent with the left curvature of long tracks in 'straight' walking.

As presently constructed the model generates gaits of constant pattern which may be represented on a lag versus period graph by straight lines radiating from the origin. They are of this form because the delay and leg oscillators both depend in exactly the same way on the inputs for each side. Fig. 7 shows that at long period the lag may approach a constant value which implies that in very slow walking the delay oscillators are independent of the leg oscillator inputs but possess a constant low level input of their own. If a constant symmetrical input E_c (see Fig. 12) is provided for all the delay oscillators and its magnitude is small compared to the typical inputs E_R and E_L required for high speed walking then the resulting relationship between ${}_3L_1$ and P will be of the form observed experimentally for the adult insect in Fig. 7.

In this new configuration the model provides an explanation for the decreasing difference in ${}_3L_1$ for right and left sides as the step period increases because the operation of the delay oscillators becomes progressively less dependent upon the input to the leg oscillators and more dependent upon the constant symmetrical input E_c.

It is this input E_c which offers a simple means of converting the action of the model from gait II to gait I. When E_c equals zero a linear relationship between ${}_3L_1$ and P of unit slope can be constructed to represent gait I. In this mode of operation, where ${}_3L_1=P$, the delays acting across the body lock the step timing into a symmetrical pattern in which legs of the same segment can only step with a phase of 0.5. If E_c is made greater than zero a curvilinear relationship in which ${}_3L_1$ is less than P occurs at slow walking speeds. This is a gait II type walk in which the previously described asymmetrical step patterns can exist. A configuration in which E_c is the only input to the delay oscillators is similar to the metachronal rhythm generator proposed by Wilson (1966) in which the lag ${}_3L_1$ is independent of step period.

As a preliminary test of the performance of the model for the adult stick insect the phase relations between the legs for the periods used to plot the lag versus period curve were calculated from the model and are shown in Fig. 8. The theoretical histograms show the same phase characteristics as the experimental observations.

Finally, a brief mention should be made of a published model of walking behaviour in the stick insect put forward by Wendler (1968) which at first sight appears to bear some resemblance to the model presented here. The Wendler model was devised to explain the step patterns produced by insects walking on a treadmill but under these conditions the consistent asymmetries whose explanation has formed an essential basis for the model described in this paper were not observed. Unfortunately, no details are given of the nature of the coupling between the legs used in the model, and no reference is made to the source or frequency dependance of the delays occuring between nearest neighbour legs. However, a basic assumption of his model appears to be that all leg oscillators must have identical natural frequencies and in this respect his model seems to differ fundamentally from that presented here.

Developmental Changes in Walking Behaviour

The model shows how speed and direction might be controlled and suggests a simple mechanism for changing rapidly between gait I and gait II by an alteration in the level of input E_c to the delay oscillator.

So far as developmental changes in behaviour are concerned the first instar nymph only appears to be capable of making the input E_c greater than zero at relatively low levels of activity when the animal wishes to carefully explore the surface on which it walks. However, the model suggests that intermediate values of E_c should be possible and further examination of later instars and first instar nymphs walking under different conditions may provide examples of gaits having different lag versus period characteristics.

During growth the change in walking behaviour from gait I to gait II may result from the increase in size of the insect relative to its surroundings. A first instar nymph feeds on leaves and stems which are large compared to the body length of the insect and under these conditions gait I is both fast and reliable. However, the adult insect is 10 times the length of the first instar nymph and continuously faces obstacles (leaves and stems) of half its own length. Under these conditions gait II has the advantage that four legs are always in contact with the walking surface over most of the speed range and a tripod pattern is still available at maximum speed if circumstances permit.

Application of the Model to the Walking Behaviour of Other Insects

It has already been shown that the model can be used to generate step patterns for the adult and first instar stick insect by a simple change in magnitude of the input parameter E_c. This same parameter permits the simulation of step patterns for other insects such as the cockroach.

Hughes (1952) and Delcomyn (1971) have shown that at low speeds the lag ${}_3L_1$ becomes significantly less than the step period P. Thus the walking behaviour of the cockroach can be described as a gentle transition from a step pattern of the gait I type to that of gait II as the walking speed decreases. This small reduction in the lag ${}_3L_1$ with increasing step period can be simulated in the model by using a small but non zero value for the parameter E_c. In this configuration a tripod gait will dominate the walking behaviour over a wide range of step frequencies and only give way to a gait II type pattern at very low step frequency. The model suggests that the phase relation between legs of the same segment should be 0.5 over most of the speed range with slight departures from this average value at the lowest speeds.

The model also appears to be capable of simulating locust and grasshopper step patterns. One long legged grasshopper is of particular interest because it often walks with an unusual step pattern in which the rear legs step at approximately half the frequency of the pro- and mesothoracic leg pairs. Fig. 14 shows a typical step pattern for this katydid *Neocono-*

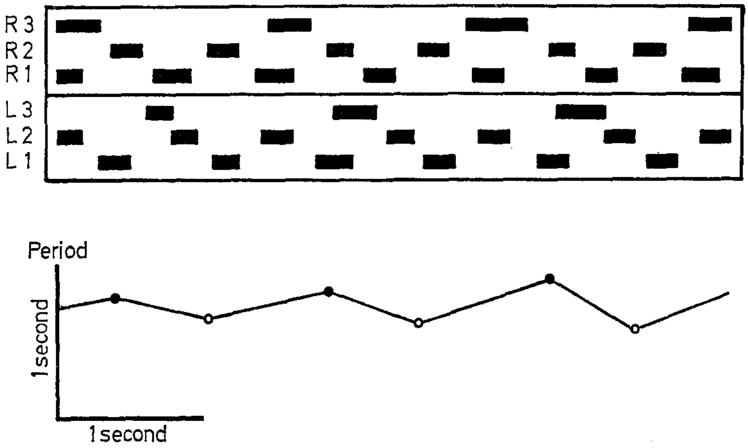

Fig. 14. Step pattern and step period of the right mesothoracic leg for the Katydid, *Neoconocephalus robustus*. Period is plotted at the end of the retraction concerned and it can be seen that the step period of R2 during which leg R3 protracts is always greater than the following period

cephalus robustus. Simulation of such a step pattern by the model suggested that a rear leg oscillator should only influence the natural period of the mesothoracic leg on the same side once in every two cycles of this leg. Thus the period of the oscillator timing the protraction of leg R2 should alternate between its natural period and that imposed on it by oscillator R3. Fig. 14 shows that the step period of the mesothoracic leg of this grasshopper does indeed vary in the manner predicted by the model.

Central and Peripheral Interpretations of the Model

The proposed model can be most easily incorporated into our present knowledge of insect walking by considering it to be a central generator providing timing signals for the onset of protractions. It can be used to drive the sinusoid motor pattern generator constructed by Delcomyn (1969, 1971b) or that of Pearson and Iles (1970) in place of their unspecified command system and protraction pacemaker or bursting interneuron. As suggested by both these models it may be assumed that retraction is an ongoing process whose input is derived from E_R and E_L and protraction is produced by coordinated motor output bursts which also inhibit the continuous retraction of the legs at appropriate intervals.

The model is most easily interpreted in neuronal terms by resorting to central pacemakers and direct interneuron connections between them, however, it is equally permissable to postulate peripheral reflexes as the basis for the oscillatory behaviour of the legs and postulate sense organs which respond to protraction as the source of coupling between the legs. Thus the behavioural model proposed here is not dependent upon a central or peripheral hypothesis and it is possible to use central pacemakers, peripheral reflex oscillators or hybrid systems as the components of the model. However, it does depend heavily upon the assumption that inter-leg coordination is a dynamic process in which leg oscillators influence the action of one another. Thus my use of the word central denotes the suggested anatomical location of the neural components responsible for timing leg movements rather than the concept of an inflexible motor score or tape as suggested by some earlier uses of this word (Hoyle, 1964).

A number of observations made during the present study suggest that the division of walking into central and peripheral components is a useful one. Extra protractions, missing protractions and difficulties in demonstrating intersegmental reflexes (Wilson, 1965; Delcomyn, 1969) seem to be most easily explained by assuming that sensory structures in the leg are relatively unimportant in directly coordinating the action of legs on one side of the animal, although they do appear to have a role in coordinating motor activity across a segment (Usherwood, Runion and Campbell, 1968). These observations suggest that the mechanism for timing whole leg movements may be relatively independent of the detailed action of the leg in propulsion and support. Thus a central timing system could be used to generate protraction commands which bring legs into the appropriate coordination but these commands may be usurped by individual legs under certain circumstances via a reflex arc. As an example, if a leg fails to grip the walking surface and slips the leg protracts a second time without disturbing the central rhythm and it is occasionally found that a leg appears to miss its timing command altogether and fails to protract at the appropriate time.

Another example of this two level type of behaviour is turning in the first instar stick insect. Throughout the turn in gait I the tripod step pattern is rigidly maintained but the motor activity of the mesothoracic leg is momentarily reduced.

Davis (1969) in his study of the swimmeret system of the lobster has identified a central command system for timing the beats of a swimmeret and a peripheral reflex organisation for modulating motor output to deal with load variations. This is an excellent example of the kind of two level system that appears to be appropriate for the analysis of walking behaviour. A high level or central system controls the timing of whole leg movements while a low level or peripheral system coordinates intra-leg muscle activity and inter-leg muscle activity within one segment to produce propulsion, leg recovery and body support. This separation into two levels does not imply complete isolation of the upper system from the lower for it would be surprising if the sensory information from the periphery were not used to provide a subtle influence on the operation of the central oscillators individually or as a group. For example, leg proprioceptors could be used to lower an oscillator threshold in the event of extreme leg extension and the influence of the periphery on the group as a whole is shown by the removal of both mesothoracic legs. The step pattern is significantly altered as shown by Wendler (1964a) and it must be concluded that some form of sensory input is essential to the maintenance of certain coupling pathways between the leg oscillators.

In conclusion, a model has been proposed in this discussion which is consistent with the observations of Bethe (1921) and von Holst (1935) that synchronous stepping of diagonal pairs of legs is a dominant feature of the free walking adult stick insect gait. It presents an explanation of the observed asymmetries in the adult gait and suggests mechanisms for direction and speed control, and transitions between different coordinations patterns. The model appears to have a more general application to at least two other insects and provides one possible framework on which to assemble more detailed studies of the neuronal mechanisms controlling the coordination of leg movements in the walking insect.

Appendix

Parameters of the Protraction Generator

The limiting values of the natural periods of the oscillators used in the model step sequence in Fig. 13 were derived as follows. Assume a period for the leg L3 appropriate to the velocity of interest.

$$P_{\mathrm{L3}} = 0.7 \text{ seconds.}$$

Consideration of Fig. 7 shows that the equation

$${}_{\mathrm{L3}}L_{\mathrm{L1}} = 0.33\,P + 0.30$$

is an adequate approximation for the left leg data in the period range 0.3 to 1.0 seconds. This expression is used to determine the lag at the period of interest.

$${}_{\mathrm{L3}}L_{\mathrm{L1}} = 0.5 \text{ seconds.}$$

Then as ${}_{\mathrm{L3}}L_{\mathrm{L2}} = {}_{\mathrm{L2}}L_{\mathrm{L1}} = {}_{\mathrm{L3}}L_{\mathrm{L1}} \div 2$ within experimental error.

$${}_{\mathrm{L3}}L_{\mathrm{L2}} = {}_{\mathrm{L2}}L_{\mathrm{L1}} = 0.25 \text{ seconds.}$$

To create a metachronal rhythm in the model certain conditions for the choice of the oscillator frequencies must be fulfilled.

Condition I. The oscillator frequencies must be in ascending order from the rear. Therefore, $P_3 > P_2$ and $P_2 \geqslant P_1$. Notice that if $P_3 < P_2$ and $P_2 < P_1$ no metachronal rhythm can occur with inhibitory coupling.

Condition II. If an oscillator pair such as 3 and 2 are to lock into a fixed phase relationship then oscillator 2 must have a period greater than

$$P_3 - {}_3L_2$$

or it will continuously advance in phase relative to the oscillator 3 (consider the construction of Fig. 13b). This behaviour of the model will occur for values of $P_2 < P_3 - {}_3L_2$ until $P_2 = P_3 \div 2$ or more generally $P_2 = P_3 \div N$, where N is a positive integer. Phase locking will occur in a small range of P_2 immediately below each harmonic value of P_2 identified by the integer N.

As we are not interested in the harmonic examples for the stick insect $N = 1$ and

$$P_3 - {}_3L_2 < P_2 < P_3,$$

and by the same argument

$$P_2 - {}_2L_1 < P_1 < P_2.$$

Now given P_3 and ${}_{\mathrm{L3}}L_{\mathrm{L1}}$ we can suggest appropriate values of P_2 and P_1 i.e. 0.65 and 0.55 seconds respectively.

The conditions outlined are sufficient to produce the normal metachronal rhythm and a simple extension of these rules creates the condition for harmonic stepping where, for example, one might have front and middle legs stepping at twice the frequency of the rear legs. In this case every step of a middle leg would provide the timing for a front leg and the lower step frequency of the rear legs would define the protraction of middle legs once every two cycles.

So far I have only considered the differences in oscillator period on one side. By a similar argument to that already used one can derive the condition that right and left sides lock into a fixed phase relation. Assuming that the left side is driving it is

$$P_{\mathrm{L3}} - {}_{\mathrm{L3}}L_{\mathrm{L2}} < P_{\mathrm{R3}} < P_{\mathrm{L3}}.$$

Consideration of this inequality shows that the large difference in the natural frequency of the right and left sides when the adult is walking with a period of 0.4 seconds is well within the limiting condition of the model and does not cause a breakdown in the metachronal rhythm on the right side.

This work was supported by a Public Health Service grant NB-06054 to Dr. R. K. Josephson and a fellowship F03-GM-42337 to the author.

I would like to thank Drs. P. N. R. Usherwood, F. Delcomyn, C. Walther, M. D. Burns and W. Winlow for their criticism of earlier drafts of this manuscript and I am particularly indebted to Dr. R. K. Josephson for his encouragement in this project.

References

Buddenbrock, W. V.: Der Rhythmus der Schreitbewegungen der Stabheuschrecke Dixippus. Biol. Zbl. **41**, 41–48 (1921).

Davis, W. J.: Reflex organisation in the swimmeret system of the lobster. I Intrasegmental reflexes. J. exp. Biol **51**, 547–563 (1969).

Delcomyn, F.: Reflexes and locomotion in the American cockroach. Ph. D. Thesis. University of Oregon (1969).

Delcomyn, F.: The locomotion of the cockroach *Periplaneta americana*. J. exp. Biol. **54**, 453–469 (1971a).

Delcomyn, F.: The effect of limb amputation on locomotion in the cockroach *Periplaneta americana*. J. exp. Biol. **54**, 453–469 (1971b).

Holst, E. von: Die Koordination der Bewegung bei den Arthropoden in Abhängigkeit von zentralen and peripheren Bedingungen. Biol. Rev. **10**, 234–261 (1935).

Hoyle, G.: Exploration of neuronal mechanisms underlying behaviour in insects. Neural theory and modelling, p. 346–376. Reiss, R. Stanford University Press 1964.

Hughes, G. M.: The coordination of insect movements. I. The walking movements of insects (*Blatta orientalis*). J. exp. Biol. **29**, 267–284 (1952).

Pearson, K. G., Iles, J. F.: Discharge patterns of coxal levator and depressor motor neurons of the cockroach, *Periplaneta americana*. J. exp. Biol. **52**, 139–165 (1970).

Roeder, K. D.: The control of tonus and locomotor activity in the praying mantis (*Mantis religiosa*). J. exp. Zool. **76**, 353–375 (1937).

Usherwood, P. N. R., Runion, H. I., Campbell, J. I.: Structure and physiology of a chordotonal organ in the locust leg. J. exp. Biol. **48**, 305–323 (1968).

Wendler, G.: Laufen und Stehen der Stabheuschrecke *Carausius morosus*. Z. vergl. Physiol. **48**, 198–250 (1964a).

Wendler, G.: Über die Fortbewegung der Larven von *Cantharis fusca*. Z. vergl. Physiol. **48**, 283–294 (1964b).

Wendler, G.: Ein Analogmodell der Beinbewegungen eines laufenden Insekts. ‚Kybernetik 1968‘, Beih. Elektronische Rechenanlagen **18**, 68–74. München: Oldenbourg 1968.

Wilson, D. M.: Proprioceptive leg reflexes in cockroaches. J. exp. Biol. **43**, 379–409 (1965).

Wilson, D.M.: Insect walking. Ann. Rev. Entomol. **11**, 103–122 (1966).

Wilson, D. M.: Stepping patterns in Tarantula spiders. J. exp. Biol. **47**, 133–151 (1968a).

Wilson, D. M.: Inherant asymmetry and reflex modulation of the locust flight motor pattern. J. exp. Biol. **48**, 631–641 (1968b).

Dr. D.Graham
Department of Biology
Case Western Reserve University
Cleveland, Ohio U.S.A.
Present address:
Department of Zoology
University of Glasgow
Glasgow, Scotland