

UNUSUAL STEP PATTERNS IN THE FREE WALKING GRASSHOPPER *NEOCONOCEPHALUS ROBUSTUS*

II. A CRITICAL TEST OF THE LEG INTERACTIONS UNDERLYING DIFFERENT MODELS OF HEXAPOD CO-ORDINATION

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SUMMARY

The free walking behaviour of the tettigonid *Neoconocephalus robustus* provides a unique quantitative description of the interactions that can occur between a rear and middle leg on the same side of the body in an insect. The rear legs step at approximately half the frequency of the anterior legs, and right and left sides of the body can function almost independently. Relative co-ordination produces a slow drift in the timing of the rear and middle leg protractions so that all the possible values of inter-leg phase may be observed.

A statistical examination of this behaviour shows that the duration of the middle leg step cycle is increased by the presence of a rear leg protraction, only when it occurs in the last half of the retraction stroke of the middle leg. If it occurs in the earlier part of the cycle there is no corresponding contraction of the middle leg step period. This and several other features of the walk exclude a 'magnet effect' or an 'excitatory' interaction between homologous points in the leg cycle and provide a verification of the ascending 'inhibitory' interaction proposed by Wilson (1966).

Co-ordinated walking in this insect appears to be a discrete process in which the performance of a protraction stroke activates a co-ordinating influence and, in conjunction with a frequency hierarchy, maintains the required time relationship between the legs.

INTRODUCTION

In the preceding paper (Graham, 1977c) I have described the general characteristics of the step patterns of the long legged grasshopper *Neoconocephalus robustus*. One of the unusual features of these patterns is that the rear leg often steps at a lower frequency than the anterior legs and I suggest that this apparent reduction in frequency might be produced by a failure of the leg to protract at the correct time. The rear leg is then forced to await the next cycle of a central command, producing a stride of twice the normal amplitude.

In this paper I wish to describe the effect of these low frequency stepping move-

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ments of the rear leg on the timing of the middle legs. Before doing so I must stress that the observations I shall make regarding this interaction are entirely independent of the mechanism responsible for the so-called 'absences'.

Our knowledge of the co-ordinating mechanisms in insect walking has been somewhat unsatisfactory in the past as it has tended to be based upon circumstantial evidence for the nature of the interaction between the legs. Many attempts have been made to misinform the C.N.S. about the behaviour of a leg either by damage to the sensory organs (Wendler, 1964; Wilson, 1966) or by reversing the information they provide, Bässler (1967), and thereby identify the interactive pathways. Such peripheral changes have produced only minor alterations in leg amplitude or changed the angles between segments of the leg, and apart from amputation have left the co-ordination of the legs unchanged. Yet removal of all sensory input (Pearson & Iles, 1973) appears to remove most of the normal walking co-ordination, so there appears to be both a central and a peripheral component in inter-leg co-ordination.

A further indication that the peripheral component may be important in defining the exact timing of leg movements is the loss of co-ordination upon restraint of the middle legs in first instar stick insects, Graham (1977*a*). In these experiments the legs were held in their normal resting position alongside the thorax with no distortion of the legs which might activate the campaniform sensilli in the trochanter in the manner suggested by Pearson & Iles (1973) for cockroach. Yet in both cases co-ordination between front and rear legs is only possible when normal middle leg movements are permitted or the restrained middle legs are amputated.

The failure of the search to find any one sense organ specifically responsible for inter-leg co-ordination suggests that either co-ordination is primarily central or there is considerable redundancy in sensory input and that the C.N.S. uses an assembly of sensory cues to decide what is happening at the periphery. A test of the importance of peripheral information in the interaction between the legs must therefore be tackled indirectly using 'natural' movements of the leg as peripheral sensory input. The experimenter must either take over the control of a leg, thereby simulating a leg movement at a slightly different frequency to that of the neighbouring legs, or find an animal that makes incongruous or unusual steps which interact with the other legs in new ways. In such preparations it should be possible to examine the direct influence of one leg upon another that might be expected in a peripheral interaction. The first approach is perhaps the ideal one but in its temporary absence *N. robustus* presents a natural experimental example illustrating the second approach.

This preparation is made particularly important, in this context, by the unique combination of the following three features: (1) Coupling across the body is often very weak and right and left sides operate almost independently. (2) Relative co-ordination is present between the middle and rear legs on the same side of the body. Under this condition the phase changes with time and permits the rear leg to take up all possible time relationships with the leg immediately in front. (3) Each alternate step of the middle leg acts as a standard of comparison for evaluating the influence of a rear leg protraction on the duration of a middle leg step. A statistical examination of the relationship between rear leg phase and the step period of the middle leg provides a critical test for some of the models describing the walking co-ordination of insects.

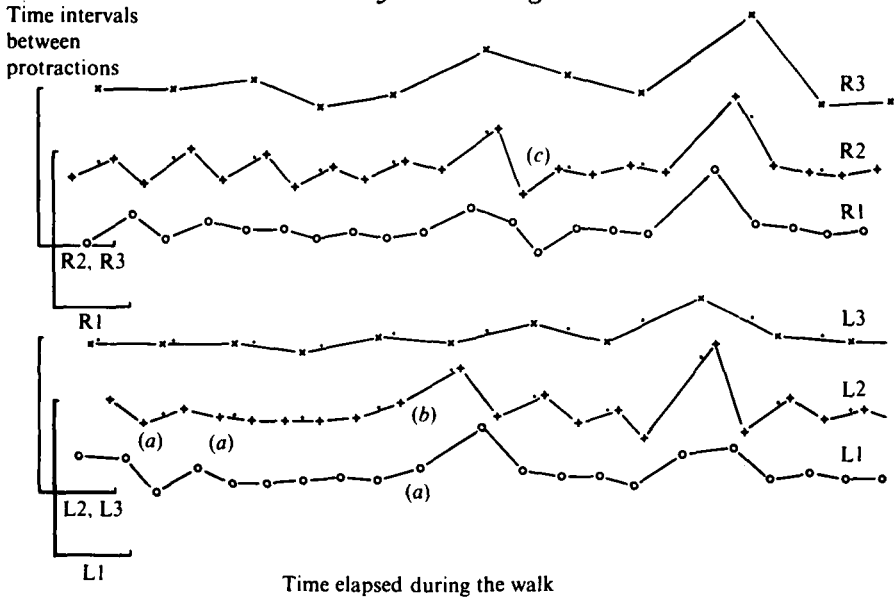


Fig. 1. Step pattern for *N. robustus* performing a systematic absence walk. The abscissa is elapsed time and the ordinate shows the interval between the onset of successive protractions. The plots for front legs are displaced vertically to avoid overlap with middle legs. Lines join successive protractions for each leg. Time bars represent 1 s. R and L represent right and left and legs are numbered from front to rear. (a) Shows protractions which occur simultaneously (within 20 ms) in legs of the same segment. (b) A cycle of the rear leg containing only one protraction of the middle leg on the same side. (c) A cycle of the rear leg containing three protractions of the middle leg on the same side. Dots show the timing of protractions of other relevant legs: the dots on L3 record show protraction of R3 and those on R2 and L2 show the protractions of R3 and L3 respectively.

METHOD

Insects, and the recording of step patterns, were as described in the previous paper (Graham, 1977c).

RESULTS

Fig. 1 shows a plot of the onset of protraction in all six legs for *N. robustus* walking with the systematic absence pattern previously described (Fig. 2c of Graham, 1977c). This is the beginning of a walk which continued for 35 s and is representative of several walks by two animals. The protractions of R2 and L2 are occasionally simultaneous (a) and show that there is weak coupling across the body. This also occurs for R1 and L1 in this figure and later in this record it occurs for R3 and L3.

The period of R2 oscillates strongly in the first part of the record. When R3 protracts just before R2 the step period of R2 is long. When it occurs earlier or is not present the period of R2 is short. Similarly in the second half of the record the step period of L2 is long when L3 protracts just before it and is short when it does not. In the first part of the record for left legs we see that L2 does not show this oscillation in period and we notice that the protraction of L3 does not precede L2 by a short interval but is at a phase of ~ 0.5 . Only when the phase of L3 on L2 increases to values greater than 0.5, as it does towards the end of the record, can we find

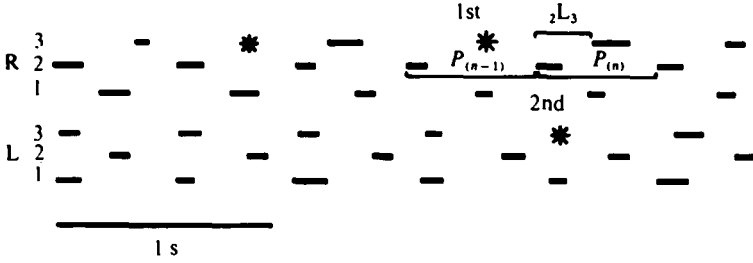


Fig. 2. Typical step pattern showing single and paired absences. Protractions are shown by the black bars. An asterisk shows the approximate position of a missing protraction. $P_n - P_{n-1}$ is defined for the first of a pair of absences and the corresponding phase of leg 3 on leg 2 is given by the lag ${}_2L_3$ divided by P_n .

co-ordinated oscillations in the step period of the middle leg on the left side. This variation in the phase continued throughout all the walks.

The normal sequence of two protractions of leg L2 for each rear leg cycle is disrupted at (b) where only one step of L2 occurs for one step of L3. This occurs three times during this walk, of which approximately one third is shown here. This shows that the protractions of leg L2 are moving to the right, along the time axis, relative to those of L3. A similar examination on the right side shows that leg R2 is drifting to the left, in time, compared to R3, and occasionally on this side three protractions of R2 occur during one cycle of R3. This disruption of the normal sequence is shown at (c).

To summarize the drift relations, the two rear legs operate at almost the same frequency. L2 steps at slightly less than $2 \times$ the rear leg frequency and R2 steps at slightly more than $2 \times$ the rear leg frequency. Similar behaviour occurred in other walks by the same animal. In some of the walks of another animal both middle legs stepped more quickly than $2 \times$ the frequency of the rear legs.

Fig. 1 shows that when leg 3 protracts just before leg 2 the period of leg 2 is longer than the preceding period which contained no protraction of leg 3. Ideally we would like to quantify not only this behavioural record but also include the data for all the absences including the intermediate walks of the kind shown in Fig. 2, to see if similar changes in the period of leg 2 occur and if such changes are significantly correlated with phase.

To examine these results statistically I have plotted the difference between the step period of the n th step and the $(n-1)$ th step for a middle leg, against the phase of the rear leg protraction on the n th step of the middle leg. Thus by definition an n th step always contains a protraction of the rear leg. These parameters are shown in Fig. 2. $P_n - P_{n-1}$ in this figure is the change in period for the first of a pair of absences. To form such a plot I select only those steps of the middle leg which have a rear leg protraction in them and consider each as an n th step. Then I measure the period of the n th step and subtract from it the period of the $(n-1)$ th step and plot the change in period ΔP against the phase of leg 3 on the n th step of leg 2.

To demonstrate such a plot I have first analysed the data for a 'complete' walk with no absences as a control. Fig. 3(a) shows that the 'centre of gravity' of the data is at $\Delta P = +7$ ms, phase $3:2 = 0.66$. This shows that there is no significant alternation in step period in a 'complete' walk and gives a phase value in agreement with the

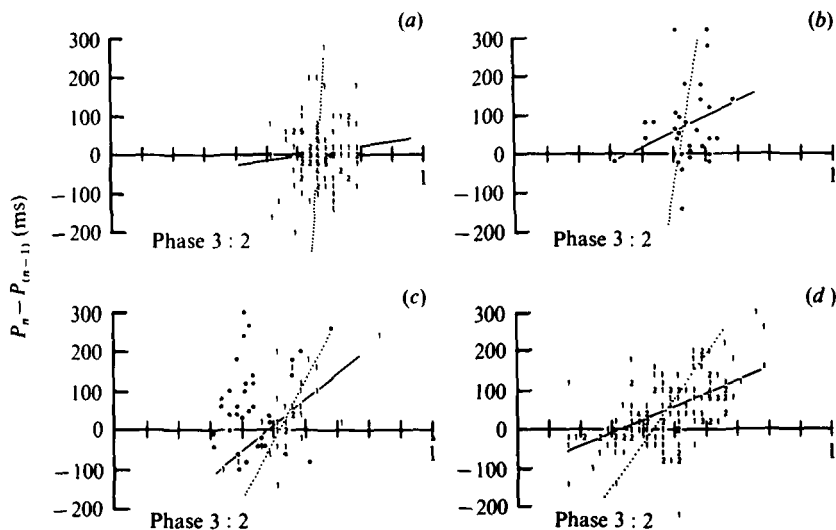


Fig. 3. $P_n - P_{n-1}$ versus phase of leg 3 on leg 2 for an n th step. Full line shows regression for phase as the independent variable. Dotted line shows regression for ΔP as the independent variable. See text and Table 1 for statistical parameters. (a) Complete walk; digits show the number of identical observations; (b) isolated absences; (c) first of a pair of absences (closed circles) and second of a pair (digits). Regression lines are for second of pair only; (d) systematic absences.

Table 1. Statistical parameters for the period difference versus phase plots shown in Fig. 3

Absences	n	Centre of gravity (\pm s.d.)		Correlation coefficient			Fig.
		Phase	$P_n - P_{n-1}$	r_0	$P \leq 5\%$	$P \leq 1\%$	
None	110	0.66 \pm 0.06	7 \pm 60	0.098	0.195	0.254	3(a)
Isolated	32	0.53 \pm 0.07	70 \pm 100	0.284	0.349	0.449	3(b)
First of pair	34	0.44 \pm 0.08	72 \pm 100	0.208	0.339	0.437	3(c)
Second of pair	30	0.55 \pm 0.09	40 \pm 80	0.643	0.361	0.463	3(c)
Systematic	140	0.48 \pm 0.14	48 \pm 80	0.554	0.159	0.208	3(d)

average step pattern shown previously (Fig. 3a and inset (a) in Fig. 4 of Graham, 1977c). There is no significant correlation. Every other step in a series of walks was used in this analysis and there is no indication of any systematic oscillation in middle leg period for a complete walk.

Fig. 3(b) is a similar plot for all the isolated absences preceding an n th step. An isolated absence is defined as one which does not have another absence within one complete step of a rear leg either in front of it or behind it including absences on both sides. The centroid of this distribution lies at $\Delta P = +70$ ms and phase = 0.53, showing that there is now a consistent reduction in the period preceding the n th step and the average phase has moved forward. The correlation coefficient 0.284 is significant for $P < 10\%$. Thus there is a weak relationship between the difference in period and the position of the rear leg protraction in the middle leg cycle.

Fig. 3(c) shows the same plot for a pair of absences (see Fig. 2 for a typical pair of absences). The filled circles are for the first of a pair. The centroid is at $\Delta P = +72$ ms and phase = 0.44 showing an even stronger forward shift in the phase. For the first

of a pair the correlation is less significant than for isolated absences. However, for the second of a pair represented by the digits the centroid is at $\Delta P = +40$ ms with a mean phase of 0.55. The correlation factor is highly significant (Table 1) and produces a relatively small angle between the regression lines for this data.

This shows decisively that for the second absence of a pair, when the phase of leg 3 on leg 2 is large there is a shift in ΔP towards positive values. Thus the period of the leg 2 step containing a protraction of leg 3 is significantly longer than the preceding step. The phase range of the data extends from 0.32 to 0.85.

Now let us look at the systematic absence data of the kind shown in Fig. 1, in which 'relative co-ordination' or drift occurs. Fig. 3(d) shows that the data covers the phase range 0.15–0.80 and the correlation coefficient is 0.58. Reference to Table 1 shows that the larger sample gives a more significant result than for the second absence of a pair but surprisingly the coefficient itself is smaller. There are no data points at each end of the phase range. This is also a little surprising as one might expect that with drift in both directions there would be a continuous distribution of the phase data. Larger zones containing no data points appear in the earlier figures but these are to be expected as the walking patterns from which these absences come were phase locked and showed no relative co-ordination.

In conclusion, it should be noted that a steadily decelerating walk will make ΔP positive. However, the decelerations occurring within the records are insignificant compared to the displacements measured in all the figures except Fig. 3(a), where the small positive vertical displacement of +7 ms corresponds to a deceleration from 3 to 2 steps per second over 30 consecutive steps for 3 separate walks.

A comparison of the experimental findings with various models of insect co-ordination

The invention of a model is a hazardous procedure fraught with all manner of temptations. One tries to steer a course between the 'Scylla' of high specificity and the 'Charibdis' of generality while listening to the 'Sirens' sing of the advantages of distorting the data (with apologies to Homer). In the absence of sufficient evidence the specific model may be presumptuous and misleading, while the more general model is difficult (if not impossible) to test and often can only be compared with data by the formulation of a more specific model.

The statements of a general model, such as the 'Magnet Effekt' of von Holst (1943), should be capable of being reduced to a testable hypothesis. Two features of the magnet effect that might be expected to appear in such a model are: (1) A mutual magnetic kind of interaction producing both action and reaction between the oscillators which is present at all parts of the cycle (syrup concept). (2) Gliding co-ordination, defined as a distribution of phases over the whole range 0–360° when relative co-ordination occurs.

Wendler (1968) describes the major information pathways to be expected between oscillators based on the phase relations of step patterns from intact and middle leg amputee stick insects walking on a wheel. This model appears to use an interaction of the magnet type but no information is given on the nature of the coupling or the model logic. Thus the stability of the simulated step pattern for an intact animal and

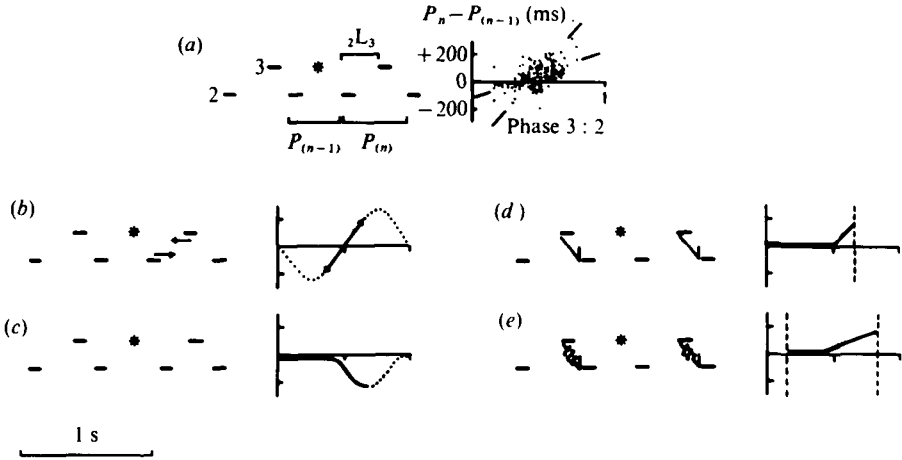


Fig. 4. Representations of step patterns and ΔP versus phase plots for (a) the data of Fig. 3 (d), (b) a 'magnet effect' model, (c) excitatory model of Wilson (1968), (d) inhibitory model of Graham (1972, 1977b) using a rigid barrier of 200 ms duration, and an intrinsic period of 400 ms, (e) combined central and inhibitory delay model using a barrier that is compressible to 50% of its original length. See text. In (d) and (e) vertical dotted lines show the expected limits of the data and define the 'forbidden zone' described in the text.

the ability of the model to show the changing step patterns found in free walking animals cannot be assessed.

In Fig. 4 various model interactions are compared with the data for *N. robustus*. Fig. 4(a) shows the period difference versus phase data and the average step pattern associated with systematic absences. In the following models I have temporarily ignored coupling across the body. This is justified by the appearance of simultaneous protractions in legs of the same segment and I consider only the interactions between rear and middle legs. The effects of interactions across the body are discussed at the end of this section.

In the absence of any specific formulation of the magnet effect for insects, Fig. 4(b) shows the data distribution to be expected from one possible model based on the ideas most often associated with the 'magnet effect'. It is assumed that there is a mutual interaction between the oscillators for legs 2 and 3 which are operating at frequencies f and $\frac{1}{2}f$ respectively. This mutual reaction would influence the protractions to move in the directions shown by the arrows. Thus the low frequency of leg 3 tends to reduce the high frequency of leg 2 and vice versa. These influences would lead to a more symmetrical arrangement of the protractions and would tend to minimize the differences between the successive middle leg step periods. The inclusion of further assumptions might improve the fit but the data for the animal seems to show a more positive distribution of ΔP in the phase range 0-0.5 than the model predicts. The continuation of the model curve to produce a sinusoid emphasizes that in the magnet effect all phases can occur during gliding co-ordination and the distribution of data would be expected to cover the whole phase region with a minimum in the region 0.1-0.2. This does not agree with the *N. robustus* data, which shows a complete absence of data points in the range 0.8-0.1 in the next cycle.

Let us now examine the models of Wilson (1966). He proposed two alternative models, one using excitatory coupling, and the other an inhibitory interaction. In

both models a hierarchy of oscillator frequencies was proposed to provide a metachronal rhythm and fixed delays were used to model the phase relations along the body axis. Right-left coupling was simplified to a strict alternation (phase right on left = 0.5). His later work caused him to favour the excitatory version of the model for intuitive reasons which are not clear from his last two publications (1967, 1968). The nature of the coupling is not precisely stated and there is no special mention of the onset of protraction as the decisive event in the leg cycle but this is implied by the description of the model behaviour.

In the excitatory model the co-ordinated metachronal sequence is produced by an inherent frequency difference between the legs such that the middle leg operates at a lower frequency than the rear leg. Thus the rear leg excites the middle leg into operation at its own higher step frequency. If such a model is constructed for the 'systematic' step pattern then we should expect that in the absence of a rear leg protraction the middle leg period would extend to its natural (or inherent) period and the subsequent step would be shortened due to the excitation provided by the rear leg protraction. The net result is the exact inverse of the oscillation in period found for *N. robustus*. The model gives a step pattern and distribution of the kind shown in Fig. 4(c) and would predict a negative correlation factor. An alternative model in which the excitatory interaction is assumed to act posteriorly from the middle leg to the rear leg would reverse the frequency hierarchy but there would then be no influence of the rear leg on the middle leg. Thus neither version of this model appears to explain the present results.

Wilson's inhibitory model uses an interaction which prevents or delays the protraction of a middle leg for a specific time interval following a rear leg protraction. Co-ordination into a metachronal rhythm is produced by maintaining the rear legs at a lower inherent frequency than those in front. Thus anterior legs are constrained to a lower frequency of operation by the protractions of the posterior legs. An exact version of this model is defined by Graham (1972, 1977*b*). To facilitate the construction of the mathematical model it is assumed that the onset of protraction is a decisive event in the leg cycle (being the time at which the animal may begin to fall over). This onset of protraction determines the time at which a barrier to protraction is imposed on the contralateral leg and the anterior ipsilateral leg. The proposed model differs from the original Wilson model in three respects. (1) The co-ordinating interaction is assumed to be initiated by the onset of protraction. (2) The duration of the barrier to protraction imposed on the anterior ipsilateral leg is dependent upon the step period. This makes it possible to model the frequency or speed dependence of the step pattern for a wide variety of insects ranging from the cockroach to the stick insect (including the grasshopper and locust), see Graham (1977*b*). (3) The interaction between legs of the same segment is the same as that producing the metachronal sequence of protractions in the ipsilateral legs. This simplifying assumption also permits the generation of the asymmetrical step patterns found in intact adult stick insects, first instar amputees and several other insects, see Wilson (1966).

The step pattern produced by this model for an insect walking with systematic absences is shown in Fig. 4(d). To construct the period difference versus phase plot it is assumed that the inherent frequency of the middle leg is 400 ms (derived from Fig. 1), that the barrier to protraction is rigid, and that the barrier length is equal to

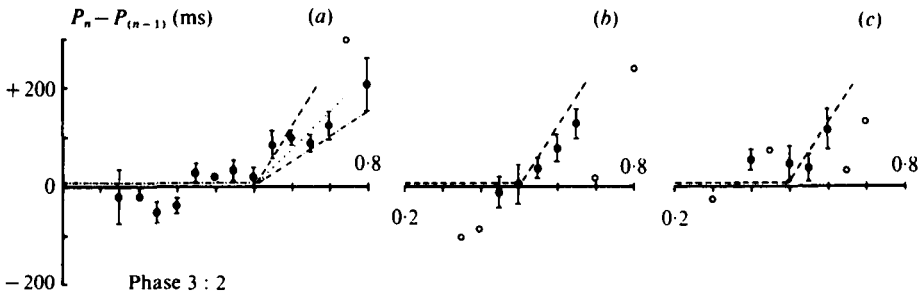


Fig. 5. Replotting of $P_n - P_{n-1}$ versus phase 3:2 with period difference as the dependent variable. (a) Systematic absence data, Fig. 3(d), (b) second of a pair of absences data, Fig. 3(c), (c) isolated absences data, Fig. 3(b). Filled data points are averages, with error bars showing standard error of mean. Open data points are single measurements. Right and left sides of the body are strongly coupled in (b) and (c) but are operating almost independently in (a). The dashed line represents the rigid barrier configuration shown in Fig. 4(d). The dot and dot-dash lines represent barriers that are compressible to 70% and 50% of their length for inherent periods of 500 and 600 ms respectively. The mean duration of the protraction stroke is represented by a phase interval of ~ 0.15 . Thus the early 'forbidden zone' corresponds approximately to the duration of the middle leg protraction stroke.

half the inherent period. Thus in the co-ordinated condition the period of the middle leg lies between 500 and 600 ms and the barrier has a phase length of ~ 0.2 .

The model predicts the observed changes in the period duration of the middle leg in response to the presence or absence of a rear leg protraction, as shown in the previous paper (Fig. 7b of Graham, 1977c), and is consistent with the general distribution of the data in Fig. 4(a). The model gives ΔP equal to zero in the phase range 0-0.5 and increasing positive values in the range 0.5-0.7. It also predicts a 'forbidden' region in the phase space 0.7-1.0 in which no phase values for leg 3 on leg 2 can appear. The existence of this region can easily be understood if one considers what happens as the rear leg protractions occur at larger and larger phase values in the model. When the phase exceeds 0.7 there is a high probability that any further delay in the appearance of the rear leg protraction will permit a new protraction of the middle leg to occur first. This produces a second 'short period' step during the absence. This is shown by the step pattern of *N. robustus* in Fig. 1(c). The phase of 3 on 2 will now occur in the early part of the phase range in the next cycle of the middle leg and the model gives a 'forbidden zone' in the range 0.7-1.0. In an analogous manner if the rear leg protraction occurs at earlier phases there comes a moment when the rear protraction precedes that of the middle leg and forces the middle leg to delay its protraction, giving a phase of ~ 0.7 . This is also shown in the *N. robustus* step pattern in Fig. 1(b). This close qualitative agreement with the model of Graham (1972, 1977b) appears to confirm the basic concept of the inhibitory hierarchy model first defined by Wilson (1966).

To examine the quantitative fit between the model and the data the results were replotted, assuming that phase is indeed the independent variable as suggested in the model.

In Fig. 5 the original data is grouped according to phase and replotted as a mean value for the dependent variable ΔP . Fig. 5(a) shows the systematic absence data of Fig. 3(d) and Fig. 5(b) and (c) show the data for the second of a pair of absences and

isolated absences, respectively. All three data sets can be superimposed and are not statistically distinguishable from one another. It should be noted that only Fig. 5(a) represents a system in which right and left sides are weakly coupled. In Fig. 5(b), (c) there is stronger coupling across the body causing some distortion of the ΔP versus phase relationship.

The rigid barrier version of the model is a close fit to the data for the second absence of a pair (Fig. 5b) and approximates the distribution of the data for isolated absences (Fig. 5c). However, in the weakest coupling condition (Fig. 5a) the fit is inadequate on two counts. Firstly, the forbidden zone it predicts is much greater than that observed and secondly the slope of the model curve is greater than the trend of the data. No variation in rigid barrier parameters can significantly improve the fit. The two other model curves are for compressible barriers and with this assumption a much better fit can be achieved. This concept of a compressible barrier is not unreasonable in view of the weaker coupling that is evident under the systematic absence condition.

There only remains the problem of the 'forbidden zone' which extends into the next cycle in the phase range 0-0.15. The removal of this incongruity is not merely a matter of choosing a new reference point in the leg cycle but implies that either the middle leg protraction can exert an influence on a rear leg if the middle leg steps first or that the points of reference for measuring phase are in fact different for the two legs under consideration. This latter possibility raises a number of difficulties (the least of which is a redefinition of the term phase). It cannot be rejected but as yet there is no indication that this is the best interpretation. The former alternative implies that there is a short range and possibly mutual inhibition between legs corresponding approximately to the duration of the protraction stroke. This interpretation is supported by the deafferentation experiments of Pearson & Iles (1973) on the cockroach. Their experiments showed that when one removes the peripheral afference one also destroys the coupling which gives the normal walking phase relations but a short range mutual inhibitory interaction remains between the meso- and meta-thoracic ganglia. This residual interaction opposes the simultaneous formation of ipsilateral levator motor output (protraction type movements) in middle and rear legs. The phase histogram for these legs, Fig. 4(a) (*ibid.*), shows that the two zones at 0-0.1 and 0.9-1.0 are almost empty of data points. These results suggest that there is a central interaction between the legs which minimizes the overlap of protraction bursts. The inclusion of such a central component in parallel with a compressible barrier version of the Graham (1977b) model would then give good agreement between the combined model shown in Fig. 4(e) and the data for systematic absences in the intact insect.

An interesting feature of the Pearson & Iles histogram is that the peak on the left is considerably larger than that on the right. The frequency of occurrence difference is 3:1 which suggests that the mesothoracic oscillator is inherently faster than that in the metathorax for 75% of the measurements and agrees with the hierarchy proposed in the model of Fig. 4(d), (e). This appears to be the first direct physiological evidence for the proposed frequency hierarchy in insects and is supported by the behavioural evidence presented here in the form of large positive values of ΔP .

Having made a reasonable case for the application of this model to the data it

should now be possible to explain some of the more subtle features of the walks in these animals as described in Graham (1977*c*). For example: 'Why do the oscillations in middle leg period show up more strongly on one side of the animal?' 'Why is this correlated with the asymmetry of the absences?' These questions can be answered in exactly the same manner as another problem, that of the poor correlation in the first absence of a pair (see Fig. 3*c* and Table 1) by considering the influence of coupling across the body.

A reconstruction of the typical complete walk based on the principles of the model will show that the absence of a rear leg protraction on one side does not necessarily permit a relaxation of the middle leg to its natural period if 'across the body' coupling is maintained at full strength (see Fig. 7*d* of Graham, 1977*c*). The relaxation fails to appear because the middle leg on the other side prevents it. Thus ΔP is zero for such an absence. However, if there is any reduction in coupling strength across the body then some relaxation may be permitted. In a pair of absences the opportunity for relaxation is doubled for the second of the pair. As an example, if a reduction in across the body coupling allows the period of the middle leg to decrease by 5% (in response to the absence of the rear leg protraction on that side) for the first of a pair, then this will permit a 10% reduction in the period of the middle leg on the opposite side when the second absence occurs. Thus the first absence provides a more relaxed environment for the second absence giving a more positive value for ΔP . This ensures that the second absence of a pair always shows the highest correlation. This can be clearly seen in Fig. 2 where the single absence gives $\Delta P \sim 0$, while ΔP for the second absence of the pair is considerably greater than that for the first. When across the body coupling is reduced further, right and left middle legs become more independent. In systematic absence walks where relative co-ordination across the body is present the magnitude of the period difference for the middle legs is determined almost exclusively by the relative position in time of the rear and middle legs on the same side. Under this condition the maximum ΔP values on right and left sides can either alternate as in Fig. 1 or adopt any other temporal relationship.

Finally, the lower correlation coefficient for the systematic absence data of Fig. 3(*d*) compared to that for the second of a pair of absences in Fig. 3(*c*) can be simply explained by the non-linearity of the model in the larger phase range for which a measurement of linear correlation was improperly determined.

In *N. robustus* it is only possible to investigate the interactions between a rear and middle leg and it is pertinent to consider whether the interaction shown in Fig. 5 can be generalized across the body and between middle and front legs. The answer is a cautious 'Yes', to the first question for, as I have just shown, an identical interaction can be used to explain the change in magnitude of ΔP across the body when right and left sides are coupled. In the case of the interaction between middle and front legs, Fig. 1 shows that the oscillations in the front leg period are phase locked with those of the middle legs but the amplitude is much smaller. Such a reduction in amplitude is automatically generated by the model if the frequency of the front leg oscillators is maintained at a value only slightly greater than the average frequency of the middle legs. Thus the front legs do appear to take their timing from the posterior legs and the model is able to explain the reduced amplitude of the period difference.

DISCUSSION

Insects do not adopt the balanced bounding kind of locomotion used by most higher animals but in the truest sense walk. Legs are picked up in sequence maintaining at all times a stable array of legs in support. The moment to moment irregularity of forward velocity in stick insects (Graham, 1972) and locust (Burns, 1973) shows clearly that in insects the co-ordination of legs is not used to achieve smooth forward propulsion. Rather, the precise co-ordination of insects seems to be directed towards the one purpose of providing adequate support for the body during the time when legs must be lifted and moved forward in preparation for new propulsion strokes.

In animals where no appendage support is necessary, such as fish or sliding land animals, or those which can dynamically support themselves by complex balancing mechanisms, this precise phase locked co-ordination appears to be unnecessary; gliding co-ordination can occur and occasionally adjacent legs on the same side protract simultaneously (see walking in the dog; von Holst, 1937).

In insects relative co-ordination between adjacent legs on the same side is rare but even when it is present there is a strong tendency to avoid simultaneous protractions. This gives the insect an inherently stable walking system. The locomotory systems of insects and mammals appear to be fundamentally different from each other in this respect. In another respect, however, the two systems may be rather similar, for the treadmill experiments of Kulagin & Shik (1970) and Grillner (1975) suggest that co-ordinative interactions in mammals take place at the turning points of the leg movement as proposed in this study of insect locomotion.

It is regrettable that most of the more recent neuronal models representing co-ordinating influences in insect walking are not sufficiently well defined in the literature to permit the prediction of their behaviour under the conditions of these experiments. The closest parallel can be drawn with the studies of swimmeret motor output in the deafferented crayfish by Stein (1973, 1974) where a similar phase analysis has been performed. However, in this system, where the concept of distributed central oscillators is common to both insects and crustaceans, the deafferented preparations appear to behave quite differently. While Stein has established an ascending excitatory influence which is contingent and therefore for small differences in oscillator frequency requires no intrinsic gradient, the data of Pearson & Iles (1973) on the deafferented cockroach suggest a mutual inhibitory interaction between homologous muscles and are consistent with a hierarchy in which the metathoracic oscillator, on average, has the lowest intrinsic frequency.

In the present study of the intact system a third kind of interaction has been found. Here, the free walking co-ordination is produced by a longer range ascending influence capable of producing delays of several 100 ms rather than the short delays associated with both of the above deafferented systems.

It is important to emphasize this separation between the central component which remains after deafferentation – and is only capable of preventing simultaneous protractions of adjacent legs – and those peripherally mediated influences which appear to be responsible for the normal co-ordination of leg movements in an intact animal which must support its body efficiently on its legs. In the cockroach the differences in co-ordination are large, especially when walking slowly. A similar behavioural

difference has been found in the swimming leech. Kristan & Calabrese (1976) report that a deafferented preparation only shows a constant short intersegmental delay, but in the intact preparation this delay increases uniformly with period so that 'the swimming leech body always takes on the optimal hydrodynamic shape of a single wavelength'.

The step patterns of *N. robustus* suggest that co-ordination in the intact animal is a discrete rather than a continuous process. The protraction movement of the leg is either associated with or produces the 'switching on' of a delaying co-ordinating influence. This appears to be of a different nature to the residual co-ordinating influences which are observed after deafferentation in insects and those found in the crayfish swimmeret system. It is still not possible to say with certainty whether the intact co-ordinating influence comes directly from the periphery or is a copy of the protraction motor output and is therefore central in origin, for this depends on the explanation of the absences. However, it seems very likely that deafferentation of *N. robustus* would produce similar results to those found for the cockroach. This indirect evidence implies that in intact animals co-ordinating information is indeed peripheral in origin. This information does not appear to come from any single sense organ but is a distributed input permitting co-ordinative decisions to be maintained in spite of damage to many individual sense organs of the leg.

Finally, the relationship between phase and period difference, under the weak coupling condition, establishes that the middle leg rhythm is only delayed when a rear leg protraction occurs late in the cycle. When it occurs early there is no statistically significant advance in the timing of the next middle leg protraction. This observation rejects the hypothesis of a magnetic or contingent type of interaction which could maintain a given co-ordination in the absence of a frequency gradient. In *N. robustus* a positive anteriorly directed gradient appears to form an integral part of the co-ordinating mechanism.

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