

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

I. GENERAL FEATURES OF THE STEP PATTERNS

By D. GRAHAM

*Department of Zoology, Glasgow University, Scotland**

(Received 4 July 1977)

SUMMARY

The free walking step patterns of the tettigoniid *Neoconocephalus robustus* are described and compared with the predictions of a model for walking co-ordination developed for the stick insect. Regular absences of rear leg protractions are found when the animal has walked for some minutes. The relative phasing of leg protractions before and after isolated absences suggests that an absence is created by a failure to meet all the conditions required for a protraction and that a 'central oscillator' maintains its intrinsic rhythm during such an absence.

INTRODUCTION

Among the many different kinds of step pattern that occur in insects one of the most remarkable is that shown by the long legged grasshopper (tettigoniid) *Neoconocephalus robustus*. The rear legs in this animal are twice as long as the front or middle legs (Fig. 1) and are capable of much greater strides; it is possible for an anterior leg to make as many as three steps during one cycle of a rear leg. A preliminary examination showed that the rear legs often stepped at half the frequency of the anterior legs and were co-ordinated with them. Similar observations have been made for *Locusta viridissima* (von Holst, 1943). The preliminary study confirmed two of the assumptions of a model of stick insect co-ordination (Graham, 1972), but raised questions about the stability of the step patterns in *N. robustus*. In this paper I shall describe the step patterns and the unusual absences of rear leg protractions that appear in them. In a second paper a statistical analysis of these results is used as a behavioural test of some of the leg interactions that have been proposed to explain co-ordination in insects.

METHOD

N. robustus were kindly collected by Professor R. K. Josephson at Woods Hole and shipped air freight to Glasgow. They were fed on lettuce and local grass, and the eight animals used for the behavioural experiments lived for at least 12 days after the last sequence of filming, which was completed within 5 days of their arrival.

The walks were recorded using a Shibaden video-tape machine (under normal

* Present address: FB Biologie, der Universität D-675 Kaiserslautern, F.R.G.

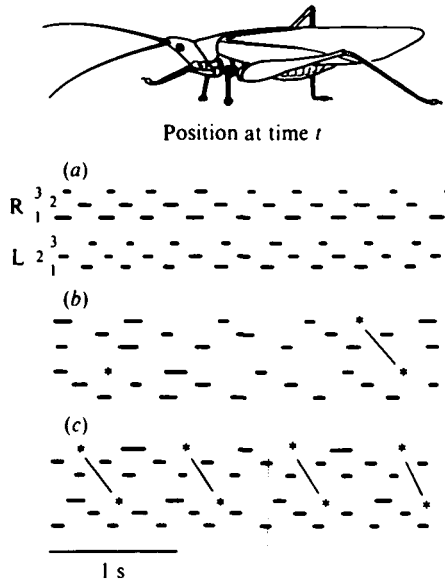


Fig. 1. Side elevation of *N. robustus* walking in the systematic absence mode at the moment shown by \cdots in step pattern (c). (a) Step pattern of 'complete' walk (no absences). Black bar denotes the duration of the protraction movement in which the leg is lifted and moves forward. (b) Same animal some minutes later shows occasional 'isolated' and 'paired' absences marked by asterisks. (c) Fully co-ordinated systematic absence walk. Note asymmetry of rear leg protractions. R denotes right legs and the legs are numbered from 1 to 3 from the front of the animal.

indoor artificial light) as the animals walked over a horizontal graph paper surface passed by hand beneath the camera lens. The animals did not slip on this surface and were entirely unrestrained. Long, uninterrupted walks were recorded by rapidly turning the walking surface under the visually fixated animal so that it traversed the same surface several times.

The video tapes were examined frame by frame (interval 20 ms) to determine the timing of the leg movements. Time interval and phase information were evaluated using the Fortran programs of Delcomyn (1971).

RESULTS

Fig. 1 shows typical step patterns of *N. robustus*. Pattern 1(a) is from the first walk of a rested animal and shows a normal symmetrical metachronal step sequence. As the walk continued the average step frequency decreased a little and the step pattern 1(b) was recorded. This shows occasional 'absences' in the protractions of the rear legs. These gaps in the step pattern are called 'absences' because they can be described as an error in the regular metachronal sequence where a rear leg protraction is absent from the normal pattern. An alternative description might be that occasionally the rear leg steps at approximately half its normal frequency. The word 'absence' will be used only as a convenient descriptive word and is not meant as an assumption of the underlying mechanism responsible for the phenomenon. As the walk is continued these 'absences' aggregate into pairs occurring successively on alternate sides until

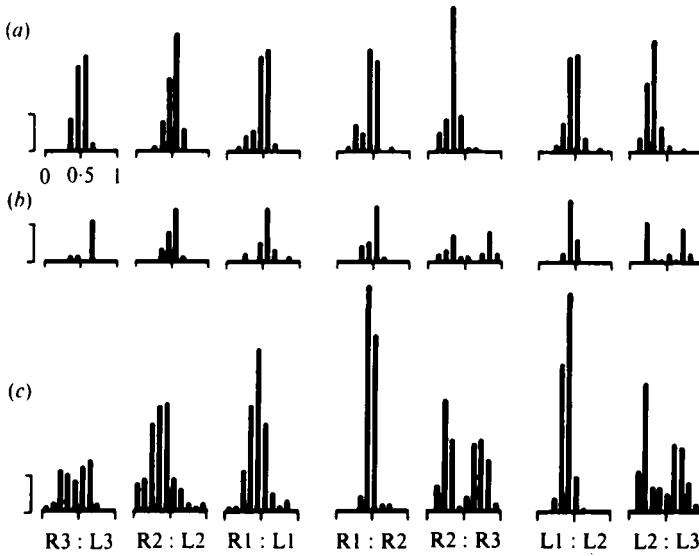


Fig. 2. Phase relations between various legs. Vertical bar denotes ten events. Phase 0-1 is equivalent to 0-360°. (a) Animal using complete walk (no absences). (b) Same animal walking with a systematic absence pattern. (c) Another animal walking with a systematic absence pattern in which relative co-ordination occurs. Statistical data for these walks are given in Table 1.

Table 1. *Statistical parameters for the data shown in Fig. 2*

	R3:L3	R2:L2	R1:L1	R1:R2	R2:R3	L1:L2	L2:L3
				Fig. 2(a)			
<i>n</i>	62	68	67	67	*	68	67
θ	0.49	0.51	0.48	0.47	0.35	0.49	0.33
<i>r</i>	0.840	0.849	0.835	0.807	0.811	0.829	0.761
				Fig. 2(b)			
<i>n</i>	13	26	25	25	13	25	12
θ_1	0.62	0.50	0.53	0.50	0.31	0.47	0.26
r_1	0.859	0.895	0.786	0.879	0.868	0.944	0.946
<i>n</i>	—	—	—	—	13	—	12
θ_2	—	—	—	—	0.84	—	0.75
r_2	—	—	—	—	0.844	—	0.911
				Fig. 2(c)			
<i>n</i>	60	119	120	120	60	117	61
θ_1	0.47	0.35	0.44	0.49	0.28	0.42	0.26
r_1	0.528	0.589	0.744	0.918	0.905	0.905	0.867
<i>n</i>	—	—	—	—	59	—	52
θ_2	—	—	—	—	0.73	—	0.72
r_2	—	—	—	—	0.826	—	0.828

θ is a measure of the mean phase, r is a concentration parameter and n is the number of measurements. θ_1 and θ_2 denote the two modes of a bimodal distribution separated at a phase value of 0.5. Significant differences relevant to the text are marked by an asterisk. For further information on circular statistics see Batschelet (1965).

$$\theta = \text{tangent}^{-1} \frac{\sum_0^n \sin \alpha}{\sum_0^n \cos \alpha} \quad \text{and} \quad r = \frac{[\sum_0^n \sin \alpha + \sum_0^n \cos \alpha]^{\frac{1}{2}}}{n}$$

where α = phase angle and n = vector number.

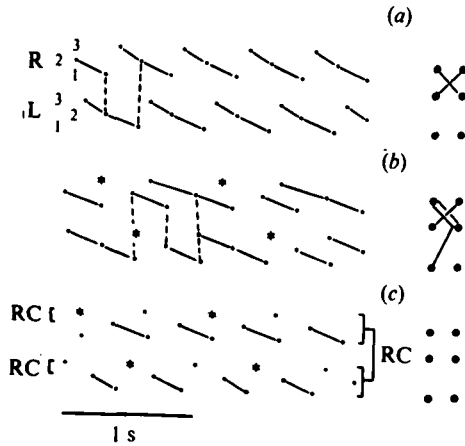


Fig. 3. Average step patterns derived from Table 1 (Fig. 2). Dots represent the onset of the protraction movement and are joined by lines to emphasize the metachronal rhythm except where relative co-ordination is occurring. Dashed lines join protractions whose onsets are within 20 ms of each other and can be considered simultaneous. Legs protracting simultaneously are shown in plan view on the right, head uppermost. Asterisks mark the approximate position of absences. (a) Complete step pattern. (b) A phase-locked systematic absence pattern. (c) A systematic absence pattern in which relative co-ordination is occurring between right and left sides and between rear and middle legs on both sides.

finally the pattern shown in 1(c) appears and an 'absence' in the rear leg step pattern occurs after every protraction. The pattern of 1(a) will be referred to as a 'complete' pattern, that of 1(c) a 'systematic absence' pattern and a pattern of type 1(b) will be termed an 'intermediate absence' pattern. Normally, in the systematic absence pattern, two protractions of a middle leg occur for each protraction of a rear leg, but occasionally, three protractions of a middle leg appear during one cycle of a rear leg. This would correspond to two successive absences on the same side. No absences appeared in the walking pattern of middle or front legs.

Five of the eight animals were females and as there appear to be no sex differences between step patterns data from both sexes are pooled. Three of the eight animals showed the complete range of step patterns given in Fig. 1. Three produced only patterns of type 1(a) and (b) and two produced only walks of type 1(c). In some animals the frequency of occurrence of absences appeared to be related to the time elapsed in a given series of walks, for absences became more frequent towards the end of a prolonged period of walking (5–10 min).

The relative timing of protractions of different legs are shown in the histograms of Fig. 2, and the statistical parameters are given in Table 1. In Fig. 2(a) the phase relations are strongly concentrated and similar in most respects to those found in other insects. In Fig. 2(b) the absences are systematic. The right and left sides are phase locked in this example and only one of the two possible asymmetries in the rear leg phase relationship is favoured. In Fig. 2(c) coupling across the body is relatively weak. Both asymmetrical possibilities for the rear leg protractions are equally represented and there is no strong minimum between them. Relative co-ordination is present both across the body and between middle and rear legs. This is indicated by the more distributed data for the phase histograms of leg 2 on leg 3 and right on left. Compare these distributions with those of leg 1 on leg 2 which are still phase locked.

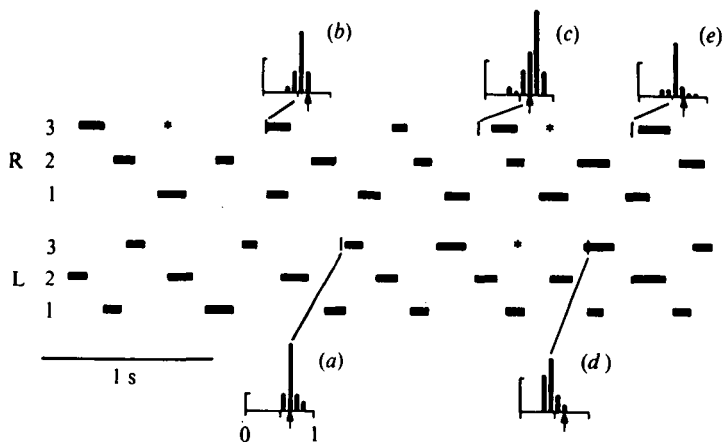


Fig. 4. Typical step pattern showing isolated and paired absences. Phase histograms show the phase distribution for leg 3 on leg 2 at various positions in the step pattern. The position of the mode is shown by a vertical bar in the step pattern associated with each histogram. Vertical arrow shows the mean phase of 3:2 = 0.65 for a 'complete' walk determined from Fig. 3*a*. (*a*) Phase histogram for a rear leg protraction occurring one step cycle before an absence; (*b*) following an isolated absence; (*c*) preceding the second of a pair of absences; (*d*) following the first of a pair of absences; (*e*) following the second of a pair.

The average step patterns determined from the mean values of phase, given in Table 1, for these three different kinds of walk are shown in Fig. 3. The symmetrical stepping of the rear legs ($R_3:L_3 \approx 0.5$) in 3(*a*) becomes asymmetrical in 3(*b*) ($R_3:L_3 \approx 0.6$), and 3(*c*) shows one of the asymmetrical modes ($R_3:L_3 \approx 0.6$) from the phase data of 2(*c*). The animals using only the systematic absence pattern slowly drift through the alternative asymmetrical modes ($R_3:L_3 \approx 0.6$ and $R_3:L_3 \approx 0.4$) producing about 10–15 middle leg steps in each mode.

Measurement of the time intervals between successive protractions of the same leg in the average patterns of Fig. 3(*b*) and 3(*c*) shows that for front legs there is no marked change from step to step. For a middle leg on the left side the step period occurring during the absence is slightly shorter than that following it in 3(*b*) and is much shorter on the left in 3(*c*). The average pattern of Fig. 3(*c*) shows that there is a relationship between the asymmetry (phase of right on left $\neq 0.5$) in the systematic absence step patterns and the magnitude of the difference between successive middle leg periods. Thus the difference is slightly larger on the left when $R_3:L_3 \approx 0.6$. This is also found in paired absences where the greatest difference occurs for the second of a pair which is consistent with the above relationship and can be seen in Fig. 4.

Further examination of the average step pattern of Fig. 3(*a*) shows that unlike the stick insect and cockroach, where the time intervals or lags between the protractions of neighbouring ipsilateral legs are approximately equal (${}_3L_2 \approx {}_2L_1$), in this animal ${}_3L_2$ is only 80% of ${}_2L_1$. This difference in interval measured as an average phase difference is 0.12 and 0.16 for the right and left sides respectively. For a concentration parameter of 0.8 and a sample size of 70 this is significant at $P < 0.01$ (see appendix, Graham, 1977*a*, for circular statistical approximations). When absences occur frequently, as in 3(*b*) and 3(*c*), these intervals become approximately equal.

The relative timing of rear leg protractions which occur just before or just after

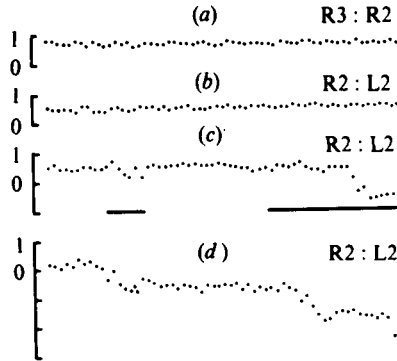


Fig. 5. The phase of successive protractions is shown for ipsilateral and contralateral legs in an animal using a complete step pattern (a) and (b). (c) Shows that relative co-ordination sometimes occurs when an animal begins to show absences (regions underlined). (d) Shows relative co-ordination occurring in a systematic absence pattern.

absences are summarized by the inset histograms in Fig. 4. This pattern is typical of the 'intermediate' absence type of walk and shows a single isolated absence in the right rear leg; followed by some 'complete' walk; followed by a pair of absences, where the first of the pair occurs on the left and the second occurs on the right. Inset (a) shows the typical co-ordination for leg 3 on leg 2 of 0.65 (compare with Fig. 3a). The remaining histograms show the changes in mean phase that occur for rear leg protractions at various positions relative to the absences. The changes compared to the 'complete' phase value are all significant at the 1% level.

The incidence of relative co-ordination is shown in Fig. 5. It is never present in walks of type 1 (a). In 'intermediate' walks it sometimes appears briefly when absences are present, as can be seen in Fig. 5(c). In the systematic absence pattern relative coordination occurs frequently and an example is shown in Fig. 5(d).

The term 'relative co-ordination' as used by von Holst (1943) describes the behaviour of two weakly coupled oscillators having slightly different inherent frequencies. A preferred phase relationship is maintained only temporarily and at intervals one oscillator slips forward or backward in time until it reaches a metastable position again, having gained or lost one cycle compared to the reference oscillator. In this paper the above term is used in preference to 'gliding co-ordination' to avoid the implication that there are no discontinuities in phase. The 'forbidden zones' which may appear during 'relative co-ordination' are a logical property of certain kinds of coupling between oscillators.

To examine the manner in which the step pattern changes with step frequency, the time interval between the onset of a protraction in a rear leg and the following metachronal protraction of the front leg on the same side may be compared with the step period of the rear leg. This interval is equivalent to the sum of the lags between adjacent leg protractions ${}_3L_2$ and ${}_2L_1$. A straight line plot of unit slope would imply that the front and rear legs protract simultaneously at all step frequencies and this indicates the presence of the tripod gait, assuming that the appropriate coupling across the body is present.

The lag (${}_3L_2 + {}_2L_1$) versus step period relationship for these animals, using only the step patterns without absences, is shown in Fig. 6. The gait (frequency dependence

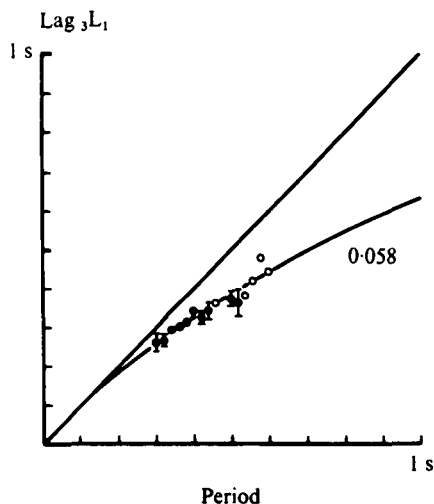


Fig. 6. Lag ${}_3L_1$ (${}_3L_2 + {}_2L_1$) versus period plot for *N. robustus* derived from complete walk data. Open circles represent individual data points, closed circles are averages. The standard error of the mean is shown by an error bar where this is greater than the point size. For a detailed explanation of the parameter $E_0 = 0.058$ used in fitting this data see Graham (1977b).

of the step pattern) resembles that of the first instar stick insect using gait II (Graham, 1972), but right and left sides are coupled rigidly into alternation ($R_3:L_3 \approx 0.5$) and it must be remembered that in *N. robustus* the lag ${}_3L_1$ is the sum of two unequal contributions (${}_3L_2 \neq {}_2L_1$).

For middle legs 83% of the data on step period falls within the range 300–500 ms and no significant change in protraction duration with period can be detected. Front and rear legs have a similar mean protraction duration to that for the middle legs (92 ± 16 ms). When systematic absences are present the average protraction duration for rear legs increases to 132 ± 29 ms but front and middle leg durations do not change significantly.

The speed range of these animals is rather restricted compared to the cockroach, but is similar to that of *Locusta*, *Carausius* and *Schistocerca* which use a relatively constant step frequency in the range of 2–3 steps per second. *Schistocerca* shows similar absent protractions of the rear legs but they are more rare. *Romalea*, at the other extreme, frequently walks with rear legs held aloft for long periods of time. These are cursory observations of my own, and Wilson (1966) describes similar effects for both *Romalea* and *Locusta*.

DISCUSSION

The measurements on 'complete' walks of this insect show that in most respects the walking behaviour resembles insects such as the locust or stick insect. However, there is a significant difference in the lag between front and middle legs when compared with that between middle and rear legs on the same side. This is unique, as the intact stick insect (Graham, 1972), locust (Burns, 1973) and cockroach (Delcomyn, 1971) all show an approximate equality in these lags.

The general similarities between the step patterns of *N. robustus* and the stick

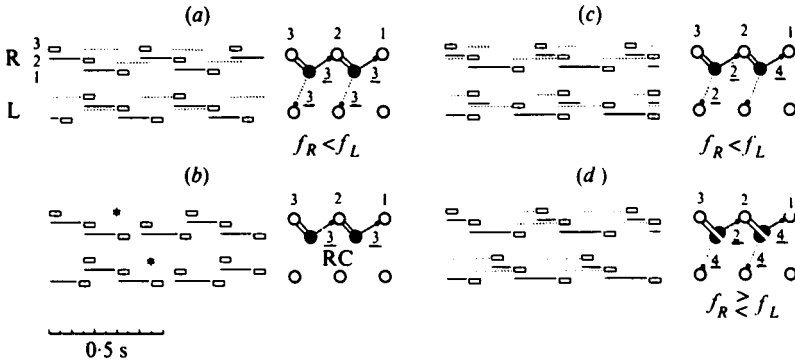


Fig. 7. Model and step pattern simulation. The model shows the leg oscillators (open circles) and interacting delays (closed circles) for one side only. The pathway between ipsilateral legs is shown as a solid line while those across the body are shown broken with delay duration in units of 50 ms underlined. A similar symbolism is used to show the corresponding barriers to protraction which produce the model step pattern. The step pattern uses a constant protraction duration of 50 ms to make the steps clear. (a) Intact stick insect model. Period hierarchy: leg 3 = 400 ms, leg 2 = 375 ms, leg 1 = 375 ms. Across the body the L_3 period is a few percent less than R_3 , thus $f_R < f_L$. Notice all legs have a step period of 400 ms in the co-ordinated pattern and the right side determines the timing of the left side. (b) Intact stick insect model used to show effect of rear leg absences on the timing of middle legs. Notice no coupling across the body and right and left sides free to show relative co-ordination. Period hierarchy: leg 3 = 600 ms, leg 2 = 250 ms, leg 1 = 275 ms. Difference in period between middle leg step during absence and that following is 100 ms. (c) Attempt to fit an exaggerated form of 'complete' *N. robustus* step pattern using simple stick insect model. Period hierarchy is: leg 3 = 400 ms, leg 2 = 350 ms, leg 1 = 350 ms. Here ${}_3L_2$ is 50% of ${}_2L_1$ rather than 80% observed in reality but the difference has been exaggerated to emphasize the co-ordination problem in the rear legs. The simulation shows one mode $R_3:L_3 = 0.75$. An increase in the step frequency on the right such that $f_R > f_L$ would give $R_3:L_3 = 0.25$. Notice different patterns of stepping on right and left sides. (d) General model separating the delays along and across the body. This exaggerated simulation describes the 'complete' step pattern of *N. robustus* and is stable for small inequalities in frequency between right and left sides.

insect suggest that the co-ordination model of Graham (1972, 1977b) for the stick insect should provide an acceptable fit to the data. This model proposes that when a leg protracts it prevents the leg immediately in front of it and that on the opposite side from protracting for a time interval dependent upon the step period. To produce a metachronal sequence in the model a hierarchy is assumed in which the natural frequency of a leg oscillator increases from the rear legs to the front legs. The anterior legs are constrained by the protraction of the more posterior legs so that all legs exhibit the same step frequency. An identical interaction across the body controls the timing of right and left legs. Thus, for an imbalance of oscillator input across the body, the side with the lowest stepping frequency determines the timing of the other. A simulation, using the most simple version of the model for the intact stick insect, is shown in Fig. 7(a).

Use of the parameters defined for the stick insect in such a model, with equal lags along and across the body, gives an approximate description of the grasshopper walk and shows the oscillations of middle leg period that appear when the rear leg absences occur, see Fig. 7(b). Unfortunately, while a quantitative fit is possible for the systematic absence pattern where ${}_3L_2$ and ${}_2L_1$ are approximately equal, an exact quantitative fit is not possible for the 'complete' walk. This is caused by a problem in cross body coupling. Although suitable changes in the delay or lag parameters make it

possible to simulate the difference in the lag of adjacent legs on the same side the model then gives two alternative phase values for the rear legs.

In the model the timing of right and left sides is determined by the interactions having the longest durations, so the middle legs produce a phase relation across the body of 0.5. However, the rear legs must then adopt an asymmetrical phase of either 0.4 or 0.6. An exaggerated simulation of the latter mode is shown in Fig. 7(c). The experimental observation of 0.5 in Fig. 2(a) for R2 on L2 shows that the middle legs are correctly modelled but peaks should appear at 0.4 or 0.6 for R3 or L3 indicating asymmetrical stepping of the rear legs. There is no evidence of this in the histogram for the complete walks of the animal.

The model can only be fitted exactly to the complete walk data by permitting slightly different durations for lags along and across the body. This is achieved by dividing each delay oscillator into two separate parts. A similar hypothesis is advanced for the first instar stick insect model (Graham, 1977a) to explain certain bilateral amputee step patterns which must be made symmetrical in order to prevent the occurrence of simultaneous protractions between pairs of the remaining four legs.

An exaggerated simulation of the complete walk using the more general model is shown in Fig. 7(d). The different durations of the delays across the body give a symmetrical step pattern and all legs are phase locked.

When relative co-ordination occurs the delays along the body between middle and front legs become equal to those found between middle and rear legs. This would suggest that the simple rectangular barrier produced by an increase in threshold of the model oscillator is an over-simplification and that a graded or compressible barrier could show the short lag under the strong interaction condition of the complete walk and a longer one under the weaker interaction condition of systematic absences.

The quantitative description of the systematic absence patterns using the original model is quite straightforward for either the phase locked pattern of Fig. 3(b) or the changing pattern of 3(c) (see the succeeding paper, Graham, 1977c). This model derives the step pattern from the relative temporal positions of the protractions and thus if no rear leg protraction occurs during a middle leg step then no influence is brought to bear on the middle leg and this leg reverts to its natural higher step frequency for one cycle (hierarchy requirement). The appearance of a protraction of a rear leg during the next cycle of the middle leg will cause this middle leg step period to be prolonged if the rear leg protraction occurs relatively late in the middle leg retraction stroke. The model also predicts the two alternative asymmetries that occur in this step pattern.

So far I have shown that in principle one can model the co-ordination changes produced by the absences but the reason for their occurrence remains unknown. They appear to be correlated with the presence of relative co-ordination which in turn appears to be related to the length of the walk, and possibly the age or condition of the animals. Von Holst (1943) found that absences occurred most often in *Locusta veridissima* when the animals climbed vertically. This suggests that the probability of the occurrence of absences may be entirely a function of the condition of the rear leg muscles relative to the locomotory task on which they are engaged.

To try to establish the most probable cause of an absence, I shall now compare two possible hypotheses with the experimental data.

The first possibility is that the rear leg very rapidly reduces its step frequency at intervals, creating an absence. This seems unlikely in view of the relatively slow deceleration rates in insects other than when stopping walking activity completely, see Graham (1977*b*). It is more likely that such changes would occur relatively slowly over several cycles of leg movement and one might expect to see gradual changes in the relative phase of rear and middle legs before or after the appearance of a low frequency cycle.

A second possibility is that the oscillatory behaviour that we see in the external movements of a leg is only a partial representation of the underlying nervous process. As a leg approaches the end of its retraction stroke one suspects that the decision to protract involves a complex summation of many influences: some relate to leg position (Bässler, 1977); some are associated with stress in the leg cuticle (Pearson & Iles, 1973); others are of an oscillatory nature (Pearson & Iles, 1973); and, finally, there are co-ordinating signals related to the movement of other legs, Graham (1977*b*). If such is the case then it is conceivable that a leg may fail to protract, particularly in view of the oscillatory central component. For if the leg misses an opportunity to protract, and the central component is an important one, then it must continue to retract (either actively or passively) until the next cycle of the central component permits a protraction. Clearly, if dragging of the leg is to be avoided this could only take place in normal intact animals where the legs concerned are capable of taking very long strides and the demand for a protraction in response to extension of the leg is not severe. This condition is present in orthopterans such as *N. robustus*.

In this work five separate behavioural observations tend to support the second hypothesis.

1. The random occurrence but progressive increase in the number of isolated absences followed by the formation of pairs and then systematic absences suggests a probabilistic mechanism rather than slow frequency changes in the rear legs.

2. The phase of rear leg steps on middle leg steps before and after an absence does not change significantly as a function of the proximity of the absence, until the absence actually occurs. See Fig. 4(*a*) and compare with the complete walk phase value of 0.65. Steadily increasing differences might be expected two or three steps before and after an absence if the rear leg frequency changed slowly.

3. Protractions in rear legs occur either with the same period as middle legs or at approximately $2 \times$ the period, although protractions might be expected anywhere between these extreme values. Notice in Fig. 4 that no data appears in the phase range 0–0.4 for any of the insets (*b*), (*d*) or (*e*). This strongly suggests a discontinuous change in the step period of the rear leg.

4. The modal values of the phase for rear legs on middle legs during a single absence, and the first and second of a pair of absences, all show a significant shift forward in phase when compared with the complete walk phase relation of 0.65. See Fig. 4(*b*), (*d*) and (*e*). Such a shift might be expected if the leg, having missed a potential protraction zone, anticipates, by a reduction in threshold, the next opportunity to do so.

5. One indication that might appear to support the 'low frequency step' hypothesis is the longer rear leg protractions associated with systematic absences. These can take a wide range of values but are approximately $2 \times$ the protraction duration for front

and middle legs. However, it would seem that the most probable explanation of these prolonged protractions is that the rate of protraction remains constant while the leg has to move forward through $2 \times$ the normal distance. The longer protraction duration is therefore entirely consistent with the 'failure of protraction' hypothesis and cannot be used to support the 'low frequency step' hypothesis.

An essential feature of the proposed model is that it is the decision to make a protraction stroke or its subsequent performance which establishes the coupling with other legs. Furthermore, if the interaction is assumed to occur exclusively between central components, and the 'failure of protraction' hypothesis were correct, then the short middle leg period during the absence would not appear because the step cycle duration could not be influenced by the subsequent presence or absence of the protraction stroke. One cannot conclude that co-ordination is a peripheral phenomenon but it would seem that it can only arise after the decision to protract has been taken, and that the precise co-ordination of other legs depends upon the exact timing of this decision.

In conclusion, the main features of the walk of *N. robustus* can be described quantitatively by the model proposed for stick insects (Graham, 1972). In its general form the model appears to provide a quantitative description of all the insect step patterns so far reported in the literature.

REFERENCES

- BÄSSLER, U. (1977). Sensory control of leg movement in the stick insect *Carausius morosus*. *Biol. Cybernetics* **25**, 61-72.
- BATSCHLET, E. (1965). *Statistical Methods for the Analysis of Problems in Animal Orientation and Biological Rhythms*. A.I.B.S. monograph.
- BURNS, M. D. (1973). Control of walking in orthoptera. *J. exp. Biol.* **58**, 45-58.
- DELCOMYN, F. (1971). The locomotion of the cockroach *Periplaneta americana*. *J. exp. Biol.* **54**, 443-452.
- GRAHAM, D. (1972). An analysis of walking movements in the first instar and adult stick insect. *J. comp. Physiol.* **81**, 23-52.
- GRAHAM, D. (1977a). The effect of amputation and leg restraint on the free walking co-ordination of the stick insect *Carausius morosus*. *J. comp. Physiol.* **116**, 91-116.
- GRAHAM, D. (1977b). A model for the control of coordinated leg movements in free walking insects. *Biol. Cybernetics* **26**, 187-198.
- GRAHAM, D. (1977c). 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. *J. exp. Biol.* **73**, 159-172.
- HOLST, E. VON (1943). Über relative Koordination bei Arthropoden. *Pflügers Archiv.* **246**, 847-865.
- PEARSON, K. F. & ILES, T. F. (1973). Nervous mechanisms of intersegmental co-ordination. *J. exp. Biol.* **58**, 725-744.
- WILSON, D. M. (1966). Insect walking. *Ann. Rev. Entom.* **11**, 103-122.

