THE CONTROL OF WALKING IN ORTHOPTERA

I. LEG MOVEMENTS IN NORMAL WALKING

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INTRODUCTION

Most of the information available on the control and co-ordination of leg movements during walking in insects has been obtained from the cockroach (Hughes, 1952, 1957; Wilson, 1965, 1966; Delcomyn, 1971 *a*, *b*) and the stick insect (Wendler, 1965; Graham, 1972). However, much of the work done so far on the neural control of posture and of the movements of single legs in walking has concentrated on the locust and grasshopper (Hoyle, 1964; Runion & Usherwood, 1968; Usherwood, Runion & Campbell, 1968; Usherwood & Runion, 1970). In view of this and the wealth of information available on the structure and physiology of the nerves and muscular systems in locusts and grasshoppers, they were chosen as the subjects of the present investigation, which is intended to extend walking and posture studies to the neural control of all six legs. As a preliminary, a quantitative analysis of leg movements during normal walking in the locust, *Schistocerca gregaria*, and a grasshopper, *Romalea microptera*, has been made and the results of this study are made the subject of this paper. This behavioural information was necessary as a basis for an investigation of the neural control of some of the leg muscles during walking (Burns & Usherwood, 1973) and of the effects of motor and sensory perturbations on the motor commands to these muscles and the leg movements (Burns, 1973).

Since the metathoracic legs of the locust and grasshopper are specialized and are used for jumping as well as walking, differences between the walking behaviour of these insects and that of the cockroach and stick insect might be expected. In fact the main conclusion from the data presented in this paper is that, although the locust is like the other two species in that it walks with an alternating tripod gait, it differs from them in showing a remarkably high level of variability in the stepping movement of its legs.

MATERIALS AND METHODS

The locusts used in these studies were adult male *Schistocerca gregaria*, usually selected less than a week after ecdysis to minimize fat accumulation. Some experiments were also carried out on the grasshopper *Romalea microptera*.

Recordings from nerves of free-walking preparations were made by a method similar to that described by Runion & Usherwood (1966). A harness of 36-gauge wire was fixed around the thorax of the insect just anterior to the metathoracic coxae and secured with a saddle of model plastic placed over the wings. This prevented the wings from moving and served as an attachment point for a flexible cable formed by twisting up to six pairs of enamelled copper wire electrodes, each of $25\,\mu$m diameter,
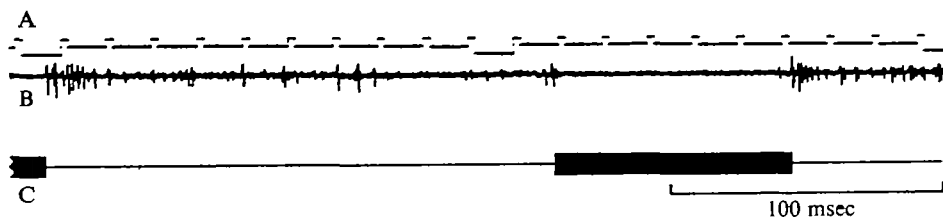
M. D. BURNS

Fig. 1. Sensory activity recorded from a prothoracic tarsus of a free-walking locust (B). Also shown are (A) the frame times of the cine camera photographing the animal and (C) the corresponding step bar plot (conventions as for Fig. 3).

around a nylon monofilament. Each pair of wires was then glued with Eastman 910 adhesive to simple frames of 40 μm diameter wire fixed around the femoral and tibial segments of one of the legs. The cleaned ends of the electrodes were inserted into the tibia of the metathoracic legs and into the most proximal segments of the tarsi of the prothoracic and mesothoracic legs. The positions of the electrode tips were adjusted to obtain clear records from the ventral nerve in the tibiae and both dorsal and ventral nerves in the tarsi. Since the tarsi contain no muscles it is assumed that all activity monitored in this way originates from sensory fibres. The electrical signals recorded by these electrodes were amplified by Isleworth A 101 pre-amplifiers, displayed on a Tektronix 565 oscilloscope and photographed with a Grass C 4 camera. Details of leg movements during walking, of forward velocity, and of posture were obtained by photographing the preparation with a 16 mm cine camera operating at 64 frames/sec. The frame times of the cine camera were indicated on the oscilloscope record.

An example of the nerve records obtained from these preparations is shown in Fig. 1. When the tarsus is in contact with the ground the small axons in the sensory nerves from the tarsi are continuously active. These axons probably originate in the trichoid sensilla (Runion & Usherwood, 1968) and campaniform sensilla (Kendall, 1970) on the ventral pads of the tarsus. The larger spikes which are usually observed when the tarsus is flexing or extending probably result from stimulation of the chordotonal organs in the tarsus (Kendall, 1970), as suggested by Runion & Usherwood (1968). Since the tarsal sensory receptors are most active when the tarsus is in contact with the ground, records from the tarsal afferents obtained during walking clearly indicate when the leg is lifted off the ground and when it is replaced. This information, verified with the cine film records, has been the basis for the analysis of leg movements during walking. Owing to the difficulties of measurement, angles between leg segments were not normally monitored.

Analyses of leg movements were restricted to records of animals walking in a straight line at a relatively constant speed. The platform used was long enough to allow a locust to take about 15 steps. Walking was usually initiated by touching the abdomen of the animal which, in the case of the locust, resulted in walking speeds of 2–9 steps/sec. Walking speeds below 2 steps/sec rarely occurred, presumably because of the effect of the bright illumination which was required for photographing the preparation. Attempts to overcome this limitation by covering the eyes and ocelli with opaque paint were unsuccessful since the treatment induced walking in circles. Although there was some variation between locusts in general walking behaviour, the differences were mainly restricted to the jerkiness of their movements and the height at which their

bodies were held above the platform. An additional effect of the high level of illumination used was to cause most animals to maintain a low posture that resulted in the tips of their abdomens dragging along the platform. However, this did not visibly affect the pattern of leg movements during walking.

For analytical purposes each step of a leg has been divided into the following two phases (Delcomyn, 1971 *a*): *protraction*, during which the leg moves forward relative to the body and the ground, and *retraction*, during which the leg moves backwards relative to the body, but not to the ground.

Most of the analyses were accomplished with the assistance of digital computers. Correlation analysis was used to test for relationships between variables, and the equations of any lines fitted to plots of these variables were calculated as the principal axes of the relevant correlation ellipses.

<center>RESULTS</center>

<center>*Locust*</center>

Leg movements during walking

The ranges of angles moved through by the tibial and femoral segments of each leg of the locust during normal straight-line walking are shown in Fig. 2. In the prothoracic and mesothoracic legs the coxae produce most of the movements of protraction and retraction by swinging the femoral segments horizontally through 40–50° and by rotating them about their long axes. The movements of the coxae also result in lifting of the legs at the beginning of protraction. Movements of the tibio-femoral joints also contribute to protraction and retraction, each tibia moving through an arc of 50–60°. The small angles reached (60°) by the prothoracic legs at the end of their retraction strokes are partly caused by yawing movements of the body. Such movements are common to most walking insects (Hughes, 1952) and are oscillatory, in this case with an amplitude of about 5°, in phase with the movements of the metathoracic legs.

In the metathoracic legs, since the femoral segments are held almost parallel to the body when the locust is walking, protraction and retraction movements consist exclusively of flexion and extension of the tibia. The coxae are still used to lift the metathoracic legs off the ground during protraction, but movements of the coxal segments and tibial segments are often not exactly in phase, with the result that flexion of the tibia precedes levation of the leg and the tarsus is dragged along the ground during the first part of protraction. It was, therefore, not possible in the metathoracic legs to use the change in output from the tarsal sensory receptors to identify the start of protraction as in the other legs. This information had to be obtained from the cine films alone, which led to an inevitable slight loss in accuracy (± 8 msec).

The protraction and retraction times of all six legs of a locust during normal walking at about 4 steps/sec are illustrated diagrammatically in Fig. 3. The duration of each protraction is about one half that of the following retraction, and the gait used approximates to an alternating tripod. This means that the prothoracic and metathoracic legs on one side of the insect and the mesothoracic leg on the other move together so that the animal is always supported by at least one tripod of legs enclosing the insect's centre of gravity. This results in a rather jerky forward motion with rapid
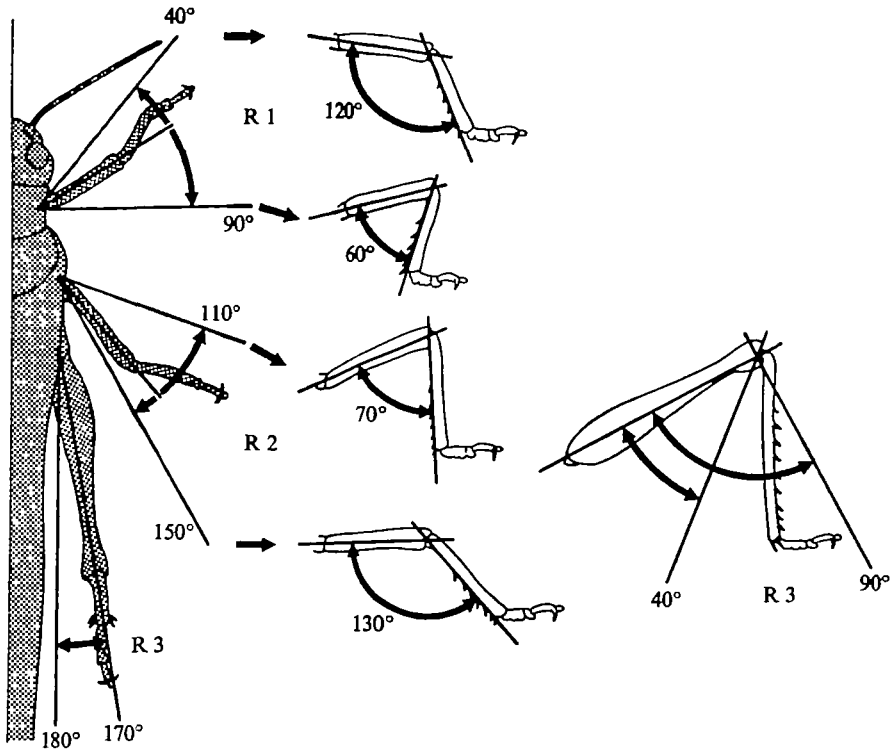
Fig. 2. Locust. Limiting values of the femur–thorax and tibia–femur angles during normal walking. The femur–thorax angles were measured horizontally between the anterior end of the body axis and the mid line of each femur. The limiting tibia–femur angles corresponding to each of the femur–coxa angles are shown for the prothoracic and mesothoracic legs. Change of the femur–coxa angle of the metathoracic leg is related to body yaw and not directly to the movements of its own leg.
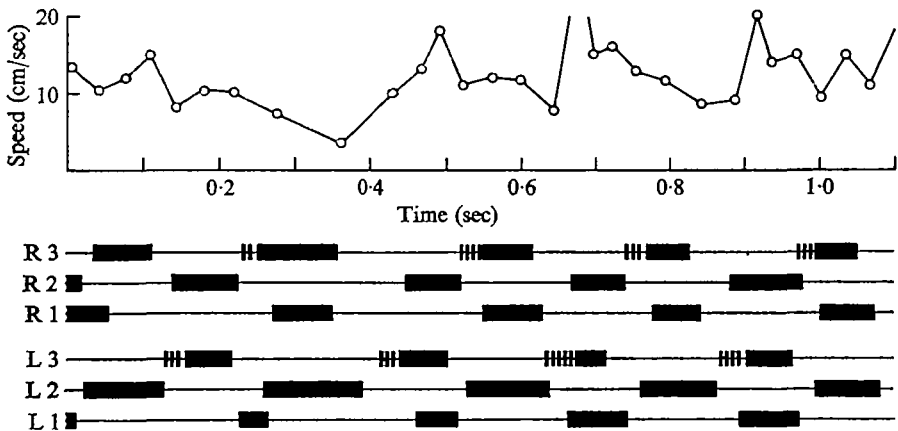

Fig. 3. Locust. Stepping patterns of a locust walking at an average of 4·4 steps/sec. The step bar plot is based on the conventions set by Wilson (1966). Each row shows the movements of one leg, the solid bars representing protractions, the spaces between, retractions. Broken bars indicate parts of protractions where the tarsus was not lifted clear of the surface. The alternating tripod pattern can be seen as the protraction of legs in two groups: L 1, R 2, L 3 and R 1, L 2, R 3. The forward speed of the locust, measured for every 0·5 cm travelled, is shown in graph at top. Note the very rapid fluctuations in speed.
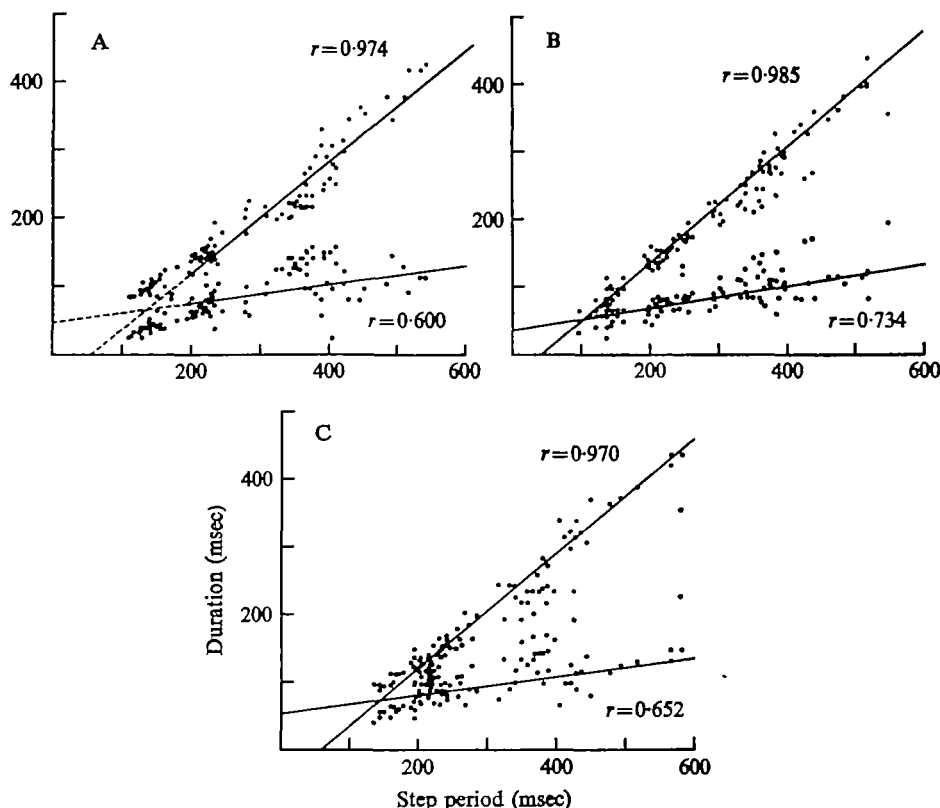
Fig. 4. Locust. Plot of duration of protraction (open circles) and retraction (closed circles) against step period. (A) Prothoracic, (B) mesothoracic and (C) metathoracic legs. The straight lines fitted to the data points are drawn for each parameter and the correlation coefficients (*r*) are shown. The correlations in (A) were calculated only for periods $\geq$ 200 msec, since below this value the data do not fit a straight line. Data from 4–6 animals.

accelerations that usually coincide with the protraction of a tripod alternating with brief periods of deceleration (see speed graph, Fig. 3).

The movement patterns of individual legs have been analysed in greater detail by plotting protraction time (*P*) and retraction time (*R*) against step duration for the different legs (Fig. 4) and by plotting the ratio *P/R* for each leg against step frequency (Fig. 5). It is evident from Fig. 2 that there is greater variability in the movements of the prothoracic legs than in the movements of the other legs. Although straight lines could be reasonably fitted to plots of *P* and *R* against step period for step periods greater than 200 msec, this was not possible for steps of shorter duration (Fig. 4A). At these low step periods the *P* and *R* data points seem to be best represented by curves that are convex in opposite directions and never cross. As a result the *P/R* ratio for the prothoracic legs is rarely unity and shows no correlation with step frequency (*r* = 0·01).

In the mesothoracic legs *P* and *R* increase linearly with step duration and the rate of increase of *P* is greater than that of *R* (Fig. 4B). As a result the plot of *P/R* ratio against step frequency for the mesothoracic legs extends to values greater than one, and a significant line can be fitted to the points (Fig. 5B). Delcomyn (*1971a*) obtained
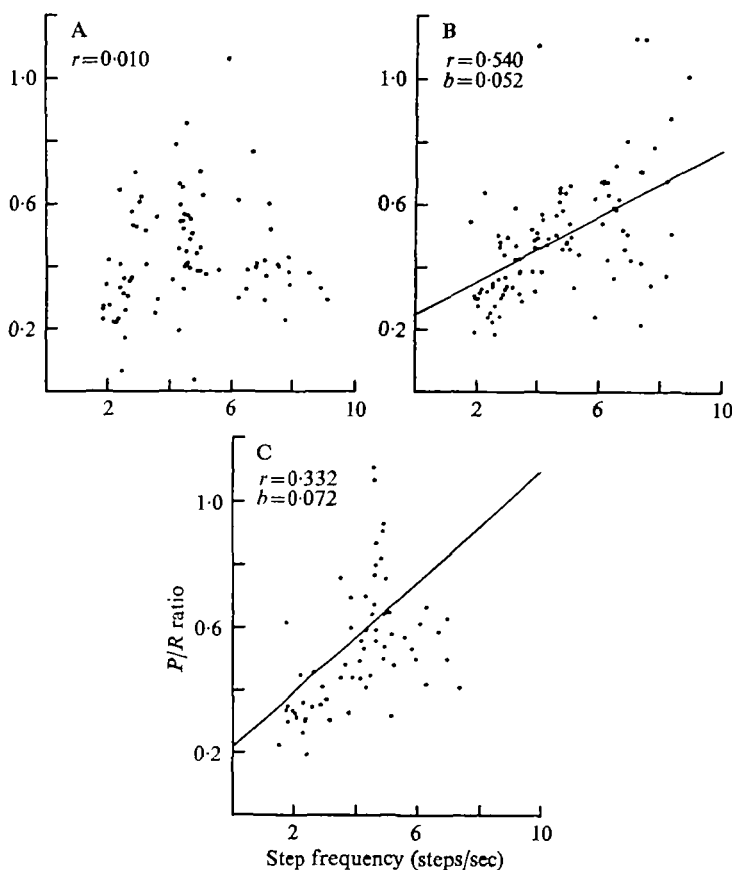
Fig. 5. Locust. Plot of P/R ratio against stepping frequency. (A) Prothoracic, (B) mesothoracic and (C) metathoracic legs. The fitted lines are drawn for (B) and (C) and the values of the correlation coefficients (r) and slopes (b) are indicated. In (A) there is no correlation between the two parameters. Data from 4–6 animals.

similar results for the mesothoracic legs of the cockroach *Periplaneta americana*, although the fitted line for P/R against step frequency is about one half as steep as that of the locust.

The stepping patterns of the metathoracic legs of the locust are somewhat similar to those of the mesothoracic legs. Although significant lines could be fitted to plots of P and R against step duration for all the data obtained, at short step durations there is an increase in variability and a tendency for P and R points to diverge in a similar but less marked fashion to those of the prothoracic legs. As a result the plot of P/R ratio against step frequency contains highly scattered points at higher step frequencies and in the animals so far studied the ratio has rarely reached unity (Fig. 5 C).

There are no significant differences between legs in the slopes of the lines for P and R against step period or P/R ratio against step frequency, nor in the absolute values of P and R for any given step duration. However, the P/R ratio for the mesothoracic legs was, for any given step frequency, slightly higher than that of the other legs. Thus the mesothoracic legs are off the ground for slightly longer than the other legs, in contrast to the cockroach where the converse is true (Delcomyn, 1971 a). The curva-
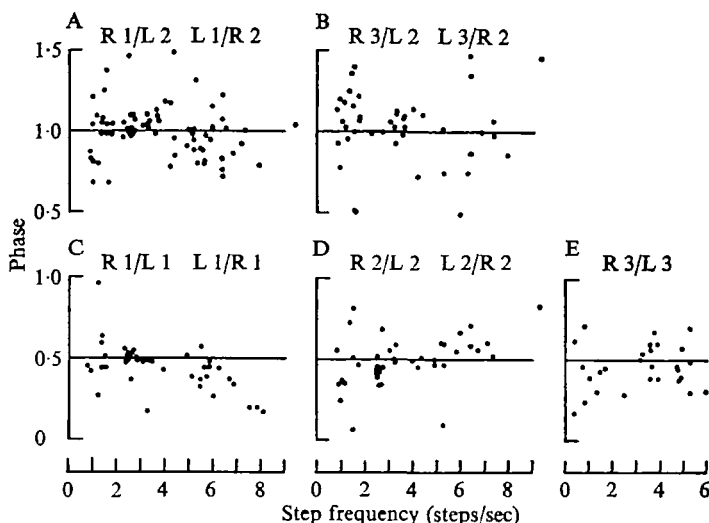
Fig. 6. Locust. Plot of inter-leg phases against stepping frequency. Leg pairs are indicated; for example, L 1/R 2 is the phase of L 1 protractions on R 2 steps. The centre line of each plot is a reference line only. There is a very high level of variability, but the only trend apparent is in (C) and this is due to one animal. Data from four animals.

ture of the plots of P against step duration for the prothoracic (Fig. 4A) and meta-thoracic legs (Fig. 4C) indicates that the locust also differs from the cockroach in that it achieves its highest step frequencies chiefly by reduction of the duration of the pro-traction phase. In all the legs the duration of this phase is more variable than the duration of retraction (Fig. 4), though the variation in both is high.

Relationships between legs

An alternating tripod gait implies that the three legs comprising each tripod should all move simultaneously so that the phase of any pair of legs in a tripod must be zero (the phase of two legs is defined as the difference between the times at which protrac-tion commences in each leg divided by the step duration of the leg which moved first (Delcomyn, 1971 a)). Fig. 6 shows the relation between phase and step frequency for a number of different leg pairs. A mesothoracic leg has been used as the reference leg in each intersegmental pair in view of the fact that the movements of the meso-thoracic legs in walking are less variable than those of the other legs. It is evident that although there is considerable variation in the phase value for intersegmental leg pairs that form part of a tripod, it does not deviate in any systematic way from the expected value of 1·0 with changing step frequency. Similarly the phase value for intrasegmental leg pairs approximates to 0·5 at all step frequencies, with less variation (Fig. 6) and a similar lack of dependence on step frequency.

Much of the variation in Fig. 6 is due to combining data measured from different records, for each pair of legs showed short-term drifts of phase away from the value expected for an alternating tripod gait. Such phase drifts are frequently observed and should be borne in mind in any consideration of the neural mechanisms con-trolling walking behaviour in the locust. Table 1 gives the average phases for a number of pairs of legs, and it is apparent from these and Fig. 6 that the locust uses an

Table 1. *Locust: average phase values and phase variation*

(i) Intrasegment

	L 1/R 1	R 1/L 1	L 2/R 2	R 2/L 2	L 3/R 3	R 3/L 3	Average
Phase	0·56	0·44	0·50	0·51	0·54	0·46	
Standard deviation	0·10	0·10	0·12	0·14	0·11	0·12	0·12
	(0·02–	(0·02–	(0·05–	(0·05–	(0·08–	(0·06–	
	0·18)	0·19)	0·21)	0·27)	0·15)	0·17)	

(ii) Intersegment

	Prothoracic/ mesothoracic	Metathoracic/ mesothoracic	Average
Phase	1·02	1·06	1·04
Standard deviation	0·10	0·16	0·13
	(0·03–0·22)	(0·04–0·27)	

Phase values are averages from four animals, five records of 8–10 steps each. Standard deviations quoted are used as a measure of variation, and are averages of the standard deviations for individual records.

Table 2. *Locust: correlation coefficients (r) between protraction or retraction durations (P and R) and the preceding phase*

	P		R		With phase
Leg	r	t	r	t	on leg:
L 1	−0·553	4·9	0·027	0·2	R 1
	−0·3985	3·0	−0·2360	1·7	R 2
R 2	−0·031	0·2	0·104	0·7	L 2
	−0·116	0·8	−0·064	0·4	L 1
	0·066	0·5	−0·003	0·0	L 3
L 3	−0·334	2·7	−0·191	1·5	R 3
	−0·016	0·1	0·063	0·4	R 2

The significance of each r is indicated by the t value ($n \geqslant 50$).

approximately alternating tripod gait at all step frequencies. The standard deviations of phase in Table 1 and the plots in Fig. 6 give an estimate of the variability of leg phases, and this is slightly higher for intersegmental phases than for phases across one segment. This suggests that there is a more rigid relationship between legs of the same segment than between legs of different segments. In this respect the locust resembles the cockroach (Delcomyn, 1971 a).

The considerable variation visible in Fig. 6 suggests that there may be regulating mechanisms present in the locust to correct for drifts of phase away from the preferred value for each pair of legs. Such corrections would take the form of adjustments to the durations of protraction or retraction and would cause these parameters to be correlated with phase. The values of the correlation coefficients for duration against phase are shown in Table 2. There are significant negative correlations between the durations of protraction and intrasegmental phase in the prothoracic and metathoracic legs implying that if one of these legs slips behind the preferred time relation with the opposite leg of the same segment its next protraction is shortened to compensate. For intersegmental phases this effect is only seen in the prothoracic legs, where a significant negative correlation exists with the phase on the mesothoracic member of the same tripod. Individual records sometimes produce similar correlations for the mesothoracic legs and for retraction durations but they are rarely significant and are not consistent between animals.
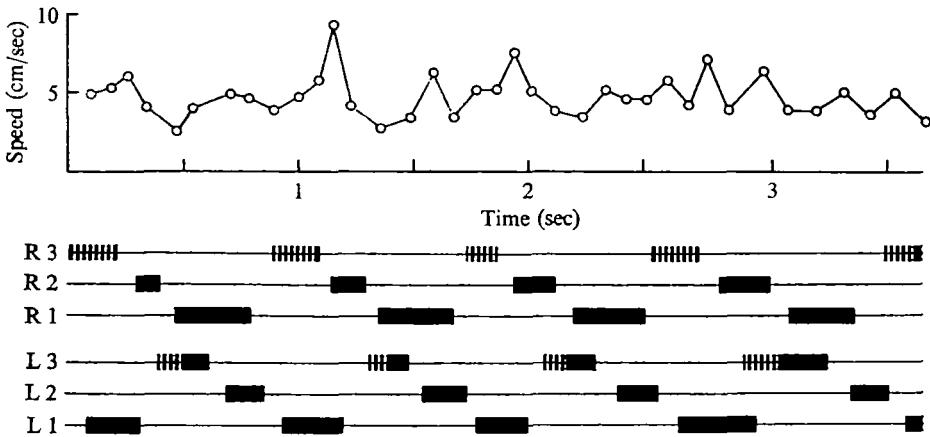
Fig. 7. Grasshopper. Stepping pattern of *Romalea* walking at an average step frequency of 1·3/sec. Conventions as for Fig. 3. The pattern used is not alternating tripod. The forward speed of the insect, shown above the step plot, varies less than that of the locust.

Grasshopper

Leg movements during walking

Romalea microptera is about twice the size of *Schistocerca gregaria* and has very much longer legs and antennae. At 22 °C, the normal temperature for free-walking experiments, the walking movements of the grasshopper were slower than those of the locust. The maximum step frequency observed was about 2 steps/sec and this was not significantly increased by raising the temperature. The limiting values of the angles between the various leg segments during walking in the grasshopper are similar to those of the locust.

The step durations and the relative timing of the legs of one animal during normal walking are shown in Fig. 7. The gait used differs from an alternating tripod in that there is a noticeable delay between the protraction of the left prothoracic leg (L 1) and the right mesothoracic leg (R 2) and another between the protraction of R 2 and the left metathoracic leg (L 3). These delays are long enough to produce an overlap between the protractions of the metathoracic and prothoracic members of different tripods. Thus the right metathoracic leg (R 3) is protracted almost simultaneously with L 1 instead of stepping alternately as in an alternating tripod gait, and the sequence of protractions is:

$$R 3 \quad R 2 \quad R 1 \qquad R 3...$$
$$...L 1 \qquad L 3 \quad L 2 \quad L 1$$

(L 2 = left mesothoracic leg, R 1 = right prothoracic leg). It seems likely that this stepping pattern is responsible for the more constant forward velocity of the grasshopper (Fig. 7) compared with the locust (Fig. 3) although the greater inertia of the larger animal may also contribute.

The relationship between protraction time (P), retraction time (R) and step duration for the different legs of the grasshopper are illustrated in Fig. 8. The slopes of the lines fitted to the data points are not significantly different ($P > 0.9$) from those for the locust (also on Fig. 8) and they could almost be considered as extensions of the locust lines. However, in the prothoracic and to a lesser extent in the mesothoracic
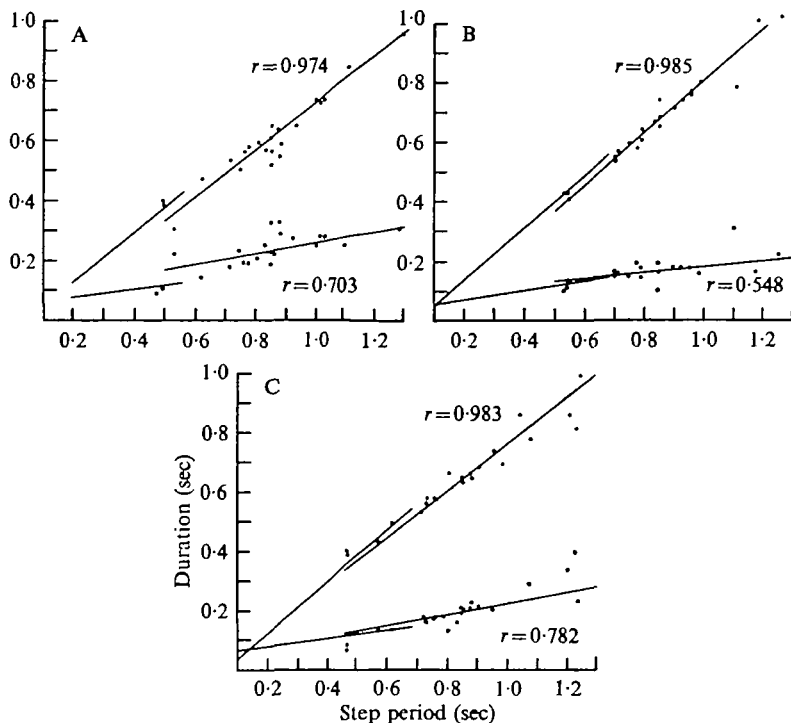
M. D. BURNS

Fig. 8. Grasshopper. Plot of durations of protractions (open circles) and retractions (closed circles) against step period. (A) Prothoracic, (B) mesothoracic and (C) metathoracic legs. The lines fitted for each parameter are drawn and the correlation coefficients (r) are shown for each line. The left-hand pair of lines on each plot are the corresponding ones for the locust, taken from Fig. 4 and included for comparison. Data from two animals.

and metathoracic legs there appears to be a tendency for R to be shorter and P correspondingly longer for any given step duration, although more data is required before this can be statistically tested. With the small number of measurements available the P/R ratios show no relationship with step frequency, but the values obtained are compatible with the low frequency end of the lines fitted to the appropriate plots of P/R ratio against step frequency for the locust.

Relationships between legs

Analyses of the relationships between leg phases and step duration were not attempted for the grasshopper but the average phases for two animals were calculated and are shown in Table 3. The average phases for contralateral pairs of legs indicate that each pair approximately alternates in one animal (A), whereas in another animal (B) only the prothoracic legs do so, the remaining segments showing phases of less than 0·5 so that the left legs lead the right. The intersegmental phases differ from the values expected for a tripod gait so that L 1 and R 1 lead R 2 and L 2 respectively, and L 3 and R 3 lag behind R 2 and L 2. The fact that the average phase values for L 1/R 3 and R 1/L 3 are greater than 1·0 substantiates the observation that the two tripods overlap. These pairs of legs represent the first and the last legs to protract in each tripod, and for an ideal alternating tripod gait should maintain a relative phase of

Table 3. *Grasshopper: average phase values and phase variation for two animals*

	Phase	Standard deviation	Phase	Standard deviation	Phase	Standard deviation	No. steps
			(i) Intrasegment				
Animal	L 1/R 1		L 2/R 2		L 3/R 3		
A	0·45	0·02	0·46	0·02	0·48	0·03	5
B	0·47	0·04	0·38	0·07	0·34	0·05	7
			(ii) Intersegment				
Animal	L 1/R 2 R 1/L 2		L 3/R 2 R 3/L 2		L 1/R 3 R 1/L 3		
A	0·75	0·05	1·04	0·15	1·08	0·04	5
B	0·89	0·09	1·17	0·04	1·31	0·11	7
Expected for tripod gait	(1·0)		(1·0)		(0·5)		

0·5. It must be emphasized that the grasshopper data have been obtained from only two animals and take no account of the possibility that the gait might alter with changes in step frequency.

It was observed that the grasshopper occasionally used a walking pattern, different from that described above, in which the step frequency of the metathoracic legs was exactly half that of the other legs. Although this pattern of behaviour was not analysed, it is nevertheless of considerable interest in considerations of the neural control of walking. A similar pattern is seen in katydids (D. Graham, personal communication).

DISCUSSION

One of the most interesting features of insect walking is the great flexibility of the system for control of leg movements. This is reflected in the high level of variability seen in the movements of individual legs and the relationships between legs, and in fact appears in all measurements made on walking. In previous papers on insect walking the regular features of the stepping patterns have been presented but the variability of leg movements has not been emphasized. In the locust, although a gait approximating to an alternating tripod is used during walking, there is a remarkably large variation in the leg movements. Thus all leg phases show a standard deviation of 0·1–0·15 (see Table 1), which is considerably higher than the values of 0·05 observed by Delcomyn (1971 a) for the cockroach and 0·07 for ipsilateral phases in the adult stick insect (D. Graham, personal communication). The standard deviation for contralateral leg phases in the adult stick insect is comparable to that in the locust, but only because the movements of the legs on the two sides of the animal are loosely coupled and continuous drifts in the relative phases of contralateral pairs of legs often occur (Graham, 1972).

In view of the variability in leg phases in the locust it is perhaps not surprising that the existence of stabilising mechanisms can be demonstrated. It is interesting, however, that they operate by adjusting the duration of protraction, leaving retraction unaffected. It suggests that protraction may be the more flexible part of each step, an idea which is supported by the fact that the duration of protraction is more variable

than that of retraction (see Fig. 4) and that it is disproportionately shortened at high walking speeds. Similarly the fact that these stabilizing mechanisms are least evident in the mesothoracic legs and most obvious in the prothoracic suggests that these are respectively the least and the most flexible leg pairs. It should be noted that, although a tripod gait can be maintained by adjustments to only prothoracic and mesothoracic legs, corrections to both parts of the step in all the legs sometimes occur. Such corrections may correspond to extreme phase errors.

Leg specialization

Unlike the species previously used in studies of insect walking behaviour, the locust and grasshopper do not have legs that are all alike in structure and function. The metathoracic legs are very large and are specialized for jumping and there are also small functional differences between the other two pairs of legs. The jumping reflex for which the metathoracic legs are specialized may account for the variability seen in the patterns of movement of all the legs during walking. Any stimulus that is sufficiently alarming to trigger the escape reflex in a walking locust will cause the animal to slow down and to flex its metathoracic legs in preparation for a jump, whereas a similar stimulus delivered to a running cockroach merely induces it to accelerate. Many of the stimuli received by a walking locust may be to some extent alarming and may thus initiate a response that is antagonistic to walking. Even if the jumping reflex is suppressed centrally or if only parts of it are triggered or are perhaps continuously active, the interaction between the central activity associated with it and the control system for walking may give rise to the observed variability in leg movements.

The prothoracic and mesothoracic legs of the locust are not so obviously specialized but they exhibit certain important functional adaptations. For example, one result of the approximately alternating tripod gait used by the locust is that for much of the time the animal is supported by only three legs, and as a result the mesothoracic member of the three must carry more than one-third of the body weight. It seems probable therefore that this is the major function of the mesothoracic legs, and their postural role is reflected in their size and in the properties of some of their muscles (Burns & Usherwood, 1973).

Unlike the cockroach, the locust shows pronounced differences between the behaviour of the prothoracic and mesothoracic legs. Although the phase relationships of each prothoracic leg are normal, the P/R ratios seem to be governed by some speed-independent factor. A possible explanation for this can be based on the differences between the antennae of the two species. The locust has comparatively short antennae that are used in flight (Gewecke, 1970), but do not appear to function as tactile receptors during walking. Thus the exploratory function that they fulfil in the cockroach (Hullo, 1948) may have been partly taken over by the prothoracic legs. There is insufficient data on the grasshopper to allow a comparison, but since this animal has much longer antennae and does use them for exploration while walking it would not require to use its prothoracic legs in a similar fashion.

Leg movements

The highest stepping frequency observed in the locust in this investigation was 8 steps/sec, but this is probably not the maximum possible. An estimate of the

heoretical maximum may be made from the regression line for P/R ratio against step frequency in Fig. 4B. Both Wilson (1965) and Delcomyn (1971*a*) give the maximum stepping frequency of the cockroach as about 20 steps/sec and at this speed the P/R ratio for the mesothoracic legs is about 1·2. The same ratio would occur in the locust at 15 steps/sec, although from the sample of locusts studied it seems unlikely that this speed is ever actually achieved.

Delcomyn (1971*a*) showed that the alternating tripod gait of the cockroach breaks down below 4 steps/sec, but is constant for all speeds above. This investigation shows that the locust uses the same gait for all the speeds examined. However, if it is assumed that the tripod gait breaks down at the same speed relative to the maximum as in the cockroach then it would do so at 1·7–2·6 steps/sec for maximum speeds of 10–15 steps/sec. As no phase shifts were observed at speeds near 2 steps/sec, it is possible that there is no gait change at low speeds but merely an increase in variability.

The constancy of gait in the locust is not compatible with Wilson's (1966) model, which proposes speed-dependent gait changes. However, the gait used by the grasshopper is identical with one of the slower speed patterns in his range of hypothetical gaits that also includes the alternating tripod for high speeds. If the locust does in fact use a speed-dependent pattern at very low stepping frequencies then the grasshopper may perhaps be regarded as a 'slow-walking locust'. This idea is supported by the remarkable similarity between the behaviour of single legs in the grasshopper and in the locust (see Fig. 8), which suggests that they use similar control systems for individual legs and so may also have similar systems for determining inter-leg phases. The gaits of both animals can be fitted into the model proposed by Graham (1972) although, like all models based on metachronal rhythms, the master oscillator is placed in the metathoracic ganglion. This does not seem likely in view of the ease with which movements of the metathoracic legs of the locust, grasshopper and katydid (D. Graham, personal communication) can be uncoupled from those of the other legs during walking. In these insects the master oscillator might be located in the mesothoracic ganglion, which has already been shown to contain the flight oscillator (Wilson, 1968), or the mesothoracic oscillator may simply be able to replace the metathoracic one when necessary.

The information obtained in this investigation is not sufficiently comprehensive to justify construction of a theoretical model of the control system involved in walking in the locust and grasshopper since it would be necessary to study behaviour other than normal walking in a straight line such as turning behaviour and the step patterns adopted after leg amputations. It does, however, provide a behavioural description upon which to base an investigation of the neural control of walking in Orthoptera and gives the following important characteristics that any model intended to cover the locust and grasshopper must be able to reproduce:

(*a*) an approximately alternating tripod gait for at least all speeds above 2 steps/sec,

(*b*) the ability to uncouple the metathoracic legs,

(*c*) a high level of variability, and

(*d*) a degree of autonomy in the movements of the prothoracic legs, presumably in response to sensory input.

SUMMARY

1. The patterns of leg movements during normal straight-line walking of the locust *Schistocerca gregaria* and the grasshopper *Romalea microptera* were recorded and analysed.

2. The ratio of protraction to retraction increased with walking speed except in the prothoracic legs. At any one speed both protraction and retraction durations were variable but the variation was greatest for protraction.

3. The locust employed an alternating tripod gait at all walking speeds recorded (2–8 steps/sec.) It displayed a high level of variability in its leg movements which appeared to be held in check by stabilising mechanisms operating on the first and last leg pairs.

4. The movements of individual legs of the grasshopper were very similar to those of the locust but the gait used was not alternating tripod.

5. Comparisons were made with other insects and it was suggested that the specialization of the metathoracic legs in the locust gave rise to most of the variability in leg movements and that the relative independence of the prothoracic legs reflects an exploratory role in walking.

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