BEHAVIOUR AND MOTOR OUTPUT OF STICK INSECTS WALKING ON A SLIPPERY SURFACE

I. FORWARD WALKING

By S. EPSTEIN and D. GRAHAM

Department of Computer and Information Science, University of Massachusetts, Amherst, MA 01003, U.S.A. and Fb. Biologie, Universitaet Kaiserslautern, D-6750, F.R.G.

SUMMARY

The walking coordination and motor output of intact adult stick insects was examined when they were supported above an oiled glass surface. The viscosity of the silicone oil was adjusted so that the animal walked with either tripod or slow-walk coordination. In the absence of mechanical coupling through the substrate, the legs typically moved at different speeds in retraction. If these differences were not too large the walks were well-coordinated in the transitions from stance to swing phase. Motor output was variable and sometimes showed periods of very weak activity in depressors and retractors. Under these conditions an individual leg moved much more slowly than its neighbours, producing 2:1 coordination patterns.

INTRODUCTION

A fundamental problem in the analysis of walking behaviour is the complex mechanical interaction of each leg with all the others, because they are coupled through the substrate on which they walk. This problem has received little systematic attention in the literature, with the notable exception of a study on spider turning by Land (1972) and the recent work by Franklin, Bell & Jander (1981) which examines the turning behaviour of the cockroach, taking into account the distortion of leg movement relative to the body as the animal rotates above the surface. Similar but less obvious problems arise in the interpretation of straight-walking motor output if one leg is passively moved or actively opposes the movement of the body generated by the other legs in contact with the ground (Cruse, 1976; Graham & Wendler, 1981; Graham, 1983).

The first attempt to study interactions through the substrate was made by dividing a treadwheel into two halves, providing a separate walking surface for the right and left sides of the body (Graham, 1981). Observations of high-speed, free-walking coordination and turning behaviour have established the interdependence of right and left sides of the body and shown that coordination of gait across the body is mediated by the central nervous system and does not require a mechanical interaction. When

friction is applied to the wheels, providing the walking animal with a load to wo[k]
against, the free-walking, low-speed coordination is observed and asymmetrical step
patterns appear. The phase asymmetry of these patterns can be controlled by differen-
tial loading of the two wheels (Foth & Graham, 1983).

The mechanical uncoupling of the system has been extended to individual legs by
studying animals walking on a mercury surface (Graham & Cruse, 1981). The body
of the insect was supported above the liquid surface such that each leg was mechanic-
ally independent of the loading and movement of the other legs. The upthrust of the
mercury surface provided an adequate tarsal contact or support for the leg to act
against. This appears to be essential for the expression of coordinated walking activity
(R. Jander, private communication). Normal fast-walking coordination was present
in 48 % of the filmed behaviour and the balance included turning behaviour (different
step frequency on right and left sides) and unusual coordination patterns similar to
those observed in long-legged grasshoppers (Graham, 1978), where one leg steps
more slowly than the others at integral multiples of their step period (different step
frequency of one leg).

Two disadvantages of the mercury system are the toxicity of the liquid and its low
viscosity. The former is an operational hazard and the latter restricts the behaviour
to high-speed walking and simple tripod coordination. This paper describes a new
walking substrate, which allows completely independent action of the legs and per-
mits the propulsive loading of the legs to be varied. In these experiments the animal
is supported above a glass plate covered with a thin film of silicone oil and the walking
load may be varied by changing the viscosity of the oil. Leg coordination and leg
trajectories are described and the motor output of four muscles is examined during
walking behaviour.

METHODS

Adult female *Carausius morosus* were used in all experiments. The animal was
attached to a balsa holder by soft wire clips around the mesothorax, metathorax and
abdomen. The holder was clamped in a manipulator to allow adjustment of the height
of the body above the surface. The body axis was approximately parallel to the glass
surface and was adjusted to a height (in the range 8–15 mm) at which walking could
be readily elicited. Two projection lamps equipped with fibre-optic light guides were
used to introduce light into the edges of a 3 mm thick glass plate, 20 cm long by 10 cm
wide (see Fig. 1).

The glass surface was smeared with silicone oil of viscosity ranging from 10^{-3} to
$10^{-4} \, m^2 \, s^{-1}$. When a leg touched the surface, light was scattered from the plate at the
interface, producing a bright halo of light around each tarsus. This clearly identified
the stance phase. A black card under the block enhanced the contrast and diffuse
lighting from above illuminated the body and legs. The distal ends of the femur and
tibia were usually marked with fluorescent acrylic paint to simplify identification of
the leg position during film analysis. Walking sequences were filmed using a Super
8 Cine Beaulieu camera running at 50 frames s^{-1} with 160 ASA Ektachrome. The film
was projected onto a Houston Instruments Hipad digitizer coupled to a Plessey PDP-
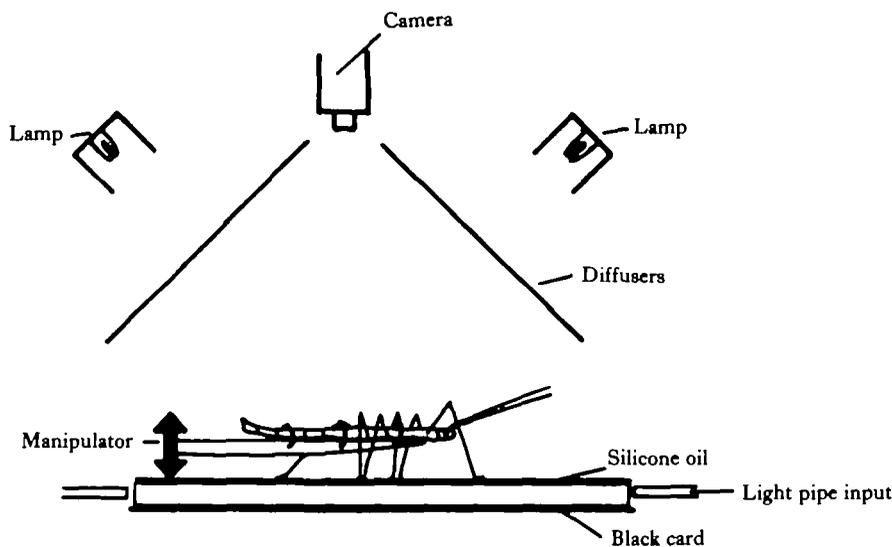11 computer. The position of the coxal articulation, femur-tibia joint and tarsus w[ere]

Fig. 1. Stick insect preparation for walks on a slippery glass surface using silicone oil as a surface lubricant.

recorded for each leg in the horizontal (x–y) plane (x axis parallel to the body long axis).

Motor output to elevators and depressors of the trochanter (femur and trochanter are fused in the stick insect) and protractor and retractor of the coxa were recorded using a single 50 μm insulated copper wire inserted into the muscle bundles and a 1 mm diameter wire inserted forward between two segments of the abdomen close to the metathorax. Motor records were amplified differentially and stored on a seven-channel Phillips tape recorder. A 3 V pulse, 100 ms long, with a period of 200 ms was also recorded and used to drive an LED in the camera viewing field. Superimposed on this driving voltage was a 0·2 V signal derived from the camera shutter.

Walking was studied at an ambient temperature of $23 \pm 2\,^{\circ}\mathrm{C}$. The standard definitions of legs are used, R for right, L for left, and numbered 1 to 3 from front to rear. After Wilson (1966), insect physiologists have tended to use the Gantt bar chart to show the times for which legs are lifted in the swing phase with a leg order, from top to bottom, of R3 R2 R1 L3 L2 L1. This representation differs from that used by workers on other arthropods, who usually show the legs in descending order from the front. When actual leg displacement is shown, the Wilson convention gives an inverted relative displacement. We shall adopt the order R1 R2 R3 L1 L2 L3, which places the legs in their correct relative positions (see Fig. 2). The coxa positions are shown in Figs 2, 5 and 7, separated by unequal intervals to represent the difference in separation between legs 1–2 and 2–3. However, this separation is exaggerated for legs 2 and 3 to avoid overlapping of the traces.

Each step comprises two phases: the power stroke or stance phase, during which the leg is in contact with the substrate, and the return stroke or swing phase, during which it is raised above the substrate and is moved towards the position from which the next step cycle will begin. If the animal walks forward, the horizontal component of the stance phase movement is a retraction and that of the swing phase is a protrac-tion (for backward walks these movements are reversed).

The onset times of swing and stance phases are used as convenient markers for the measurement of step period (onset of swing to onset of next swing), swing duration, stance duration and the lag between the swings of different legs. Lag on one side of the body is represented by 3.L.1 which denotes the interval of time between onset of swing in leg 3 and onset of swing in leg 1. Phase is defined as the ratio 3.L.1/period 3. This denotes the temporal phase of the leg 1 swing onset during the step cycle of leg 3 and is written 1:3, where 3 is the reference leg.

The position and velocity of the distal end of the femur and tibia were measured for each film frame. The extreme positions of the leg movement are denoted by AEP for anterior extreme position and by PEP for posterior extreme position. Positions in the x direction are relative to the coxal articulation of each leg. Position in the y direction is relative to the longitudinal axis of the body projected vertically onto the substrate.

RESULTS

Leg movement and coordination

When positioned at a suitable height above the oiled glass plate, the animals walked
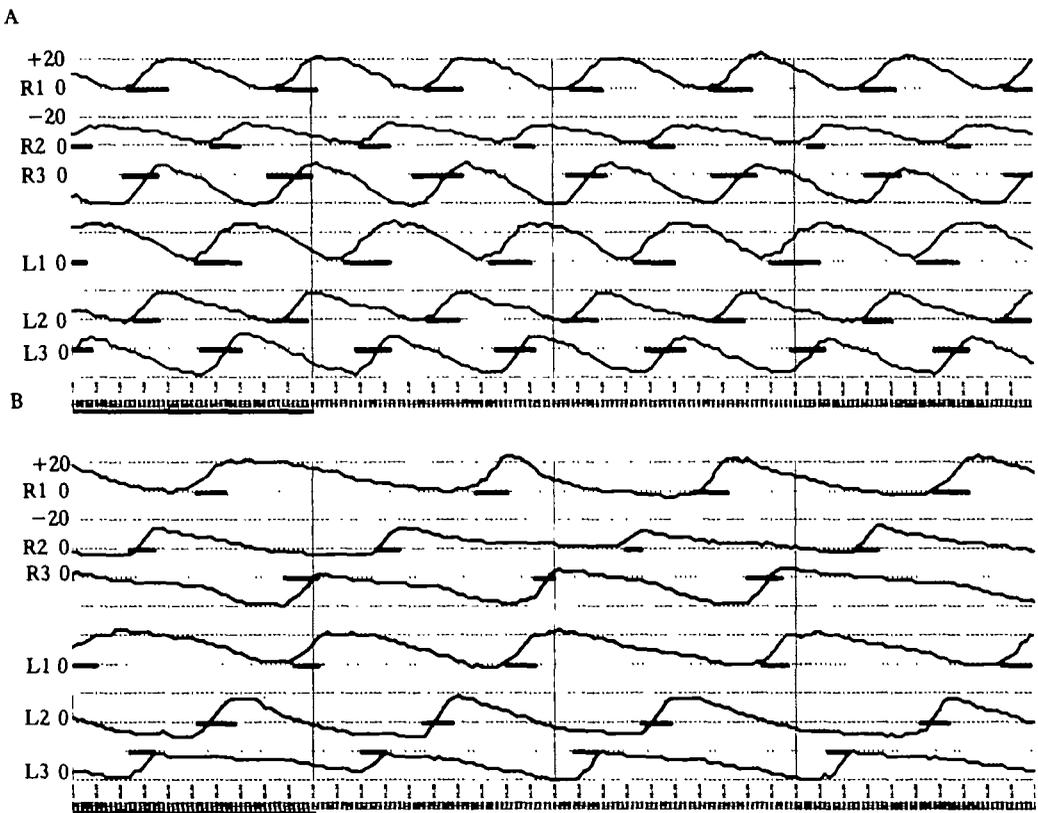

Fig. 2. Forward walks of animal 'Anna' using (A) low viscosity (10^{-4} m^2 s^{-1}) oil and (B) high viscosity (10^{-3} m^2 s^{-1}) oil. The displacement of the tarsus in the x direction (mm) relative to the subcoxal joint is projected onto the body axis. Bars superimposed on each trace indicate swing phase. Time bar is 1 s.

adily with excellent coordination (Fig. 2). If the body position was too high or too low, the legs tended to move sideways and/or show a strong turning tendency. After careful adjustment, long walks of over 100s were recorded without any form of stimulation. The animals appeared to find this substrate more satisfactory than mercury, as approximately 70 % of the filmed walks show well-coordinated behaviour.

Early attempts to use soap films or cooking oil (Sherman, Novotny & Camhi, 1977) were unsatisfactory. The viscosity of the latter could not be satisfactorily controlled, and the former was obnoxious to stick insects, encouraging them to clean their tarsi, normally a very rare behaviour. The introduction of soap solution to the mouthparts made the situation worse; the insects seemed to find the taste of soap most unpleasant and lost all further interest in normal walking. The animals did not, however, appear to be disturbed by silicone oil and rarely groomed unless the antennae became contaminated with it.
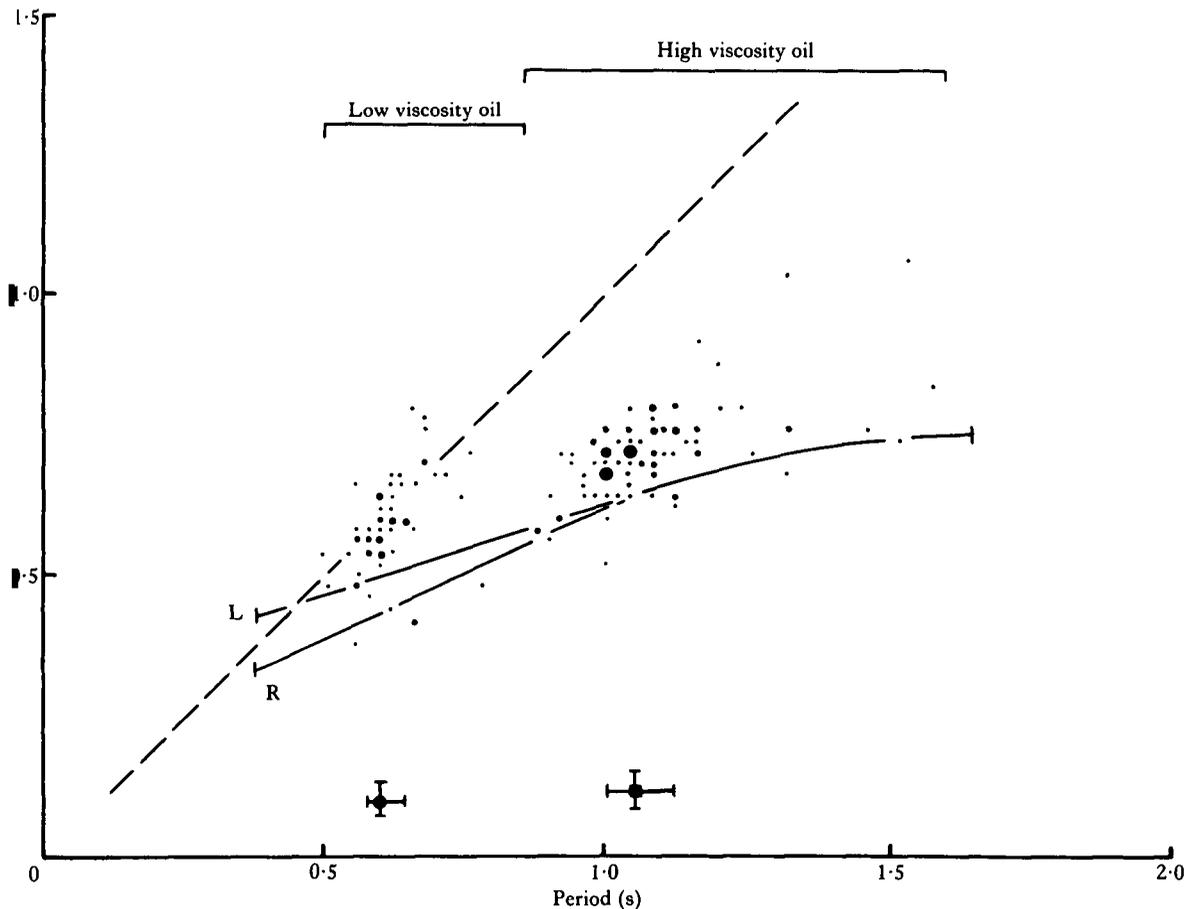

Fig. 3. Lag 3.L.1 *versus* period data for the walks of Fig. 2. The broken curve shows the relationship for first instar nymphs walking free and the continuous curves show the results for the right and left legs of free-walking adults (Graham, 1972). No significant difference between the data for right and left legs was found in the present work. The mean values for the protraction duration and period are shown for the two walks by the filled circle and square symbols respectively, with their standard deviations.
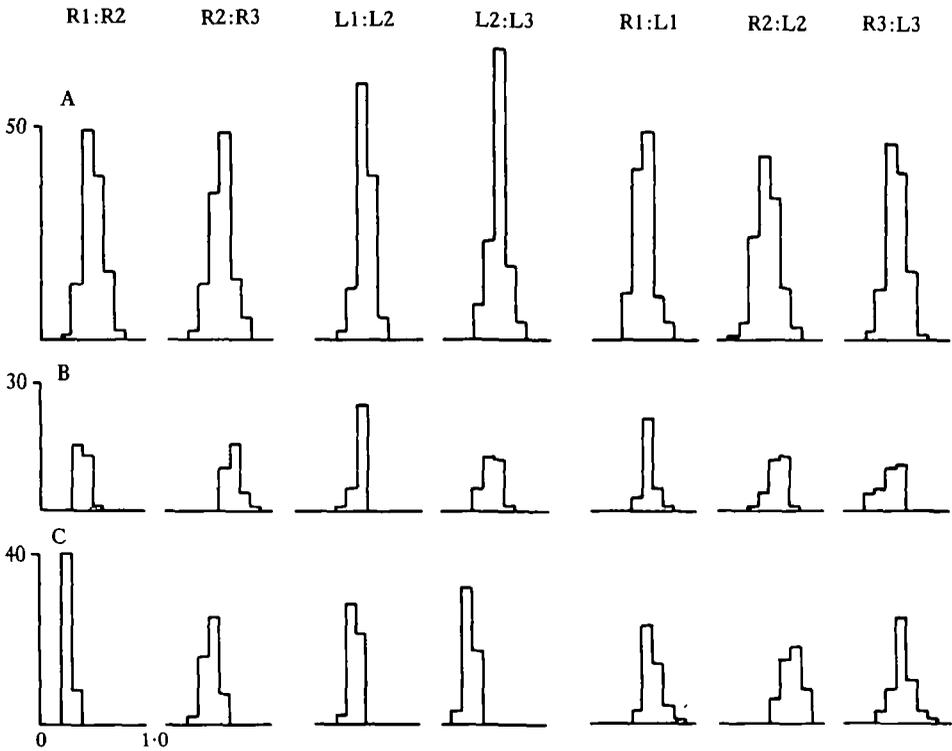
Fig. 4. Histograms of the phase relations between various leg pairs for walking on (A) a light double wheel, (B) low viscosity oil ($10^{-4}\,m^2\,s^{-1}$) and (C) high viscosity oil ($10^{-3}\,m^2\,s^{-1}$).

When the viscosity of the oil was increased, the insects walked more slowly, although they could be stimulated to walk faster by touching the abdomen. When the viscosity approached that of treacle ($10^{-2}\,m^2\,s^{-1}$) regular walks became infrequent. Fig. 2 represents walks on (A) $10^{-4}\,m^2\,s^{-1}$ oil and (B) $10^{-3}\,m^2\,s^{-1}$ oil. The swing duration and inter-leg stepping intervals (3.L.1) for right and left sides are shown as a function of step period for these walks in Fig. 3. Fig. 4 and Table 1 give the histograms, mean values and concentration parameters [s.D. $\sim (1 - C) \div 2$ for a concentration parameter >0.8] for the inter-leg phase relationships and the corresponding values for wheel walking (Graham, 1981). The phase relationships for walks on glass were strongly concentrated, with the highest concentration parameter values ever reported for walking insects. Because these walks were spontaneous and unstimulated, the step period was also relatively constant for a particular oil viscosity. In Fig. 5 the displacements of the distal tip of the femur in the x and y directions and the corresponding velocities are shown for the fast walk of Fig. 2A.

Fig. 6A shows the trajectory of the tarsi in the horizontal (x–y) plane for each leg. The shapes of the trajectories for pro-, meso- and metathoracic legs can be seen to differ. There was no strong turning tendency and tracks were usually symmetrical about the body axis. Front legs initially moved away from the midline as the legs were set down and then pulled in towards the body. Hind legs were pulled inward at first and then thrust diagonally out towards the rear. Middle legs were similar to hind legs

Table 1. *Phase values for adults walking on light wheels and silicone oil*

	R1:R2	R2:R3	L1:L2	L2:L3	R1:L1	R2:L2	R3:L3
Light double wheel walk (friction < 20 mg at rim)	0·50,0·84,119*	0·51,0·81,116	0·48,0·89,117	0·54,0·87,120	0·51,0·85,114	0·48,0·78,120	0·50,0·84,116
Walk on oil (viscosity, $10^{-4}\,m^2\,s^{-1}$)	0·40,0·94,30	0·63,0·92,31	0·43,0·96,31	0·47,0·91,31	0·56,0·94,31	0·58,0·87,31	0·45,0·81,30
Walk on oil (viscosity, $10^{-3}\,m^2\,s^{-1}$)	0·26,0·97,48	0·42,0·91,50	0·31,0·94,51	0·28,0·94,52	0·60,0·87,45	0·71,0·84,47	0·56,0·82,50

*Mean phase, concentration parameter [s.D. ~ $(1 - C) \div 2$ for a concentration parameter > 0·8], (Batschelet, 1965) and sample size.
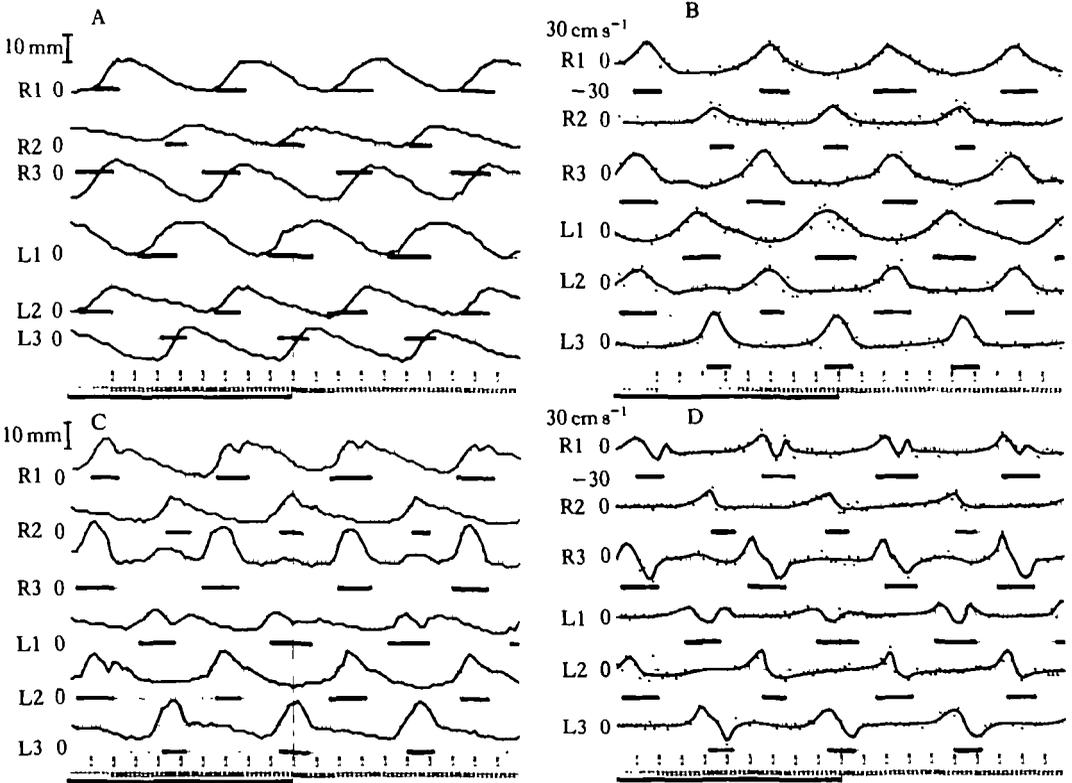
Fig. 5. Displacements of the femur tip in both the x and y directions relative to the subcoxal joint are given in (A) and (C). The corresponding velocities of movement are given in (B) and (D). These data are derived from the walk of Fig. 2A. Time bar is 1 s.

and were pulled inward at touch-down and produced an inward curve followed by an outward push. Fig. 6B compares the trajectories of the distal ends of the tibia and femur tips for the three body segments. The range of femur movement was considerably less than that of the tarsus, and as the angle between femur and tibia remained relatively constant at about 105°, the leg must have rotated appreciably about the long axis of the femur during a step. Thus femur position does not always reflect a corresponding change in the tarsus position.

Fig. 5 shows that the velocity of tarsal movement in the x direction was close to zero at lift-off and touch-down, as might be expected, and that during the first half of the swing phase the tarsus accelerated rapidly to a maximum velocity and then rapidly decelerated at approximately the same rate during the second half. Examination of the y velocity record shows that the leg was moving outward at touch-down of front legs

Fig. 6. The trajectory of the tarsus in the horizontal (x–y) plane is shown for front, middle and hind legs in (A). Stance positions are shown by the filled circles and swing positions by open circles. Numbers denote that the leg is stationary for several film frames. Arrows show the sequence of position changes. Plots on right and left sides of the x axis merely show examples of two different steps. In (B) a comparison of the femur tip (x mm) and tarsus position (y mm) is shown. Stance positions are shown by crosses and swing positions by closed circles. This Figure illustrates the smaller range of movement at the femur tip caused by rotation about the long axis of the femur.
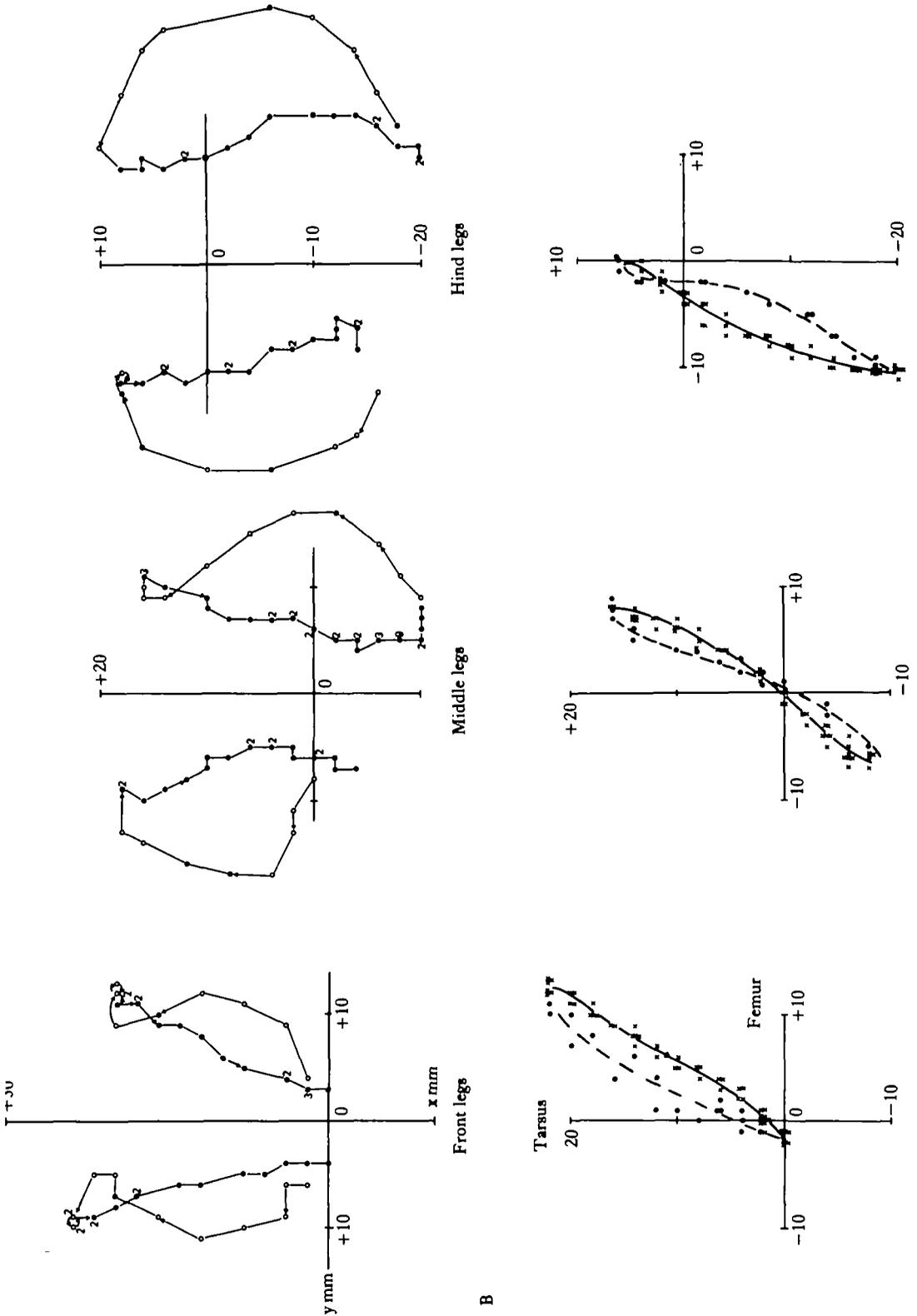
and inward for middle and hind legs. Presumably this ensures that the tarsal hooks
grip to the surface and do not become twisted under the tip of the tibia. In the stance
phase the velocities in the x direction were similar to those found in free-walking
animals and were relatively constant throughout the stroke. Walking behaviour was
examined in a total of six animals, and all results were similar.

The most notable feature of the leg movements as a function of time is that the tarsi
of different legs can move at markedly different velocities; there is no neural mechan-
ism which compels them to move at a common speed (see Figs 2 and 5). In free
walking the substrate serves to integrate the propulsive forces of the legs. When
coupling through the substrate is absent, as in the present experiments, a number of
unusual step patterns can appear. (Fig. 7A–D). The first pattern occurred in most
animals several times and merely demonstrates an extra protraction which resets the
rhythm of the leg concerned. This kind of anomaly occurred with a frequency similar
to that reported for free-walking animals (Graham, 1972). The second pattern is an
example of a failure to protract in a middle leg, which occurred very regularly at
intervals of 15 paces in one well-coordinated walk. The right middle leg failed each
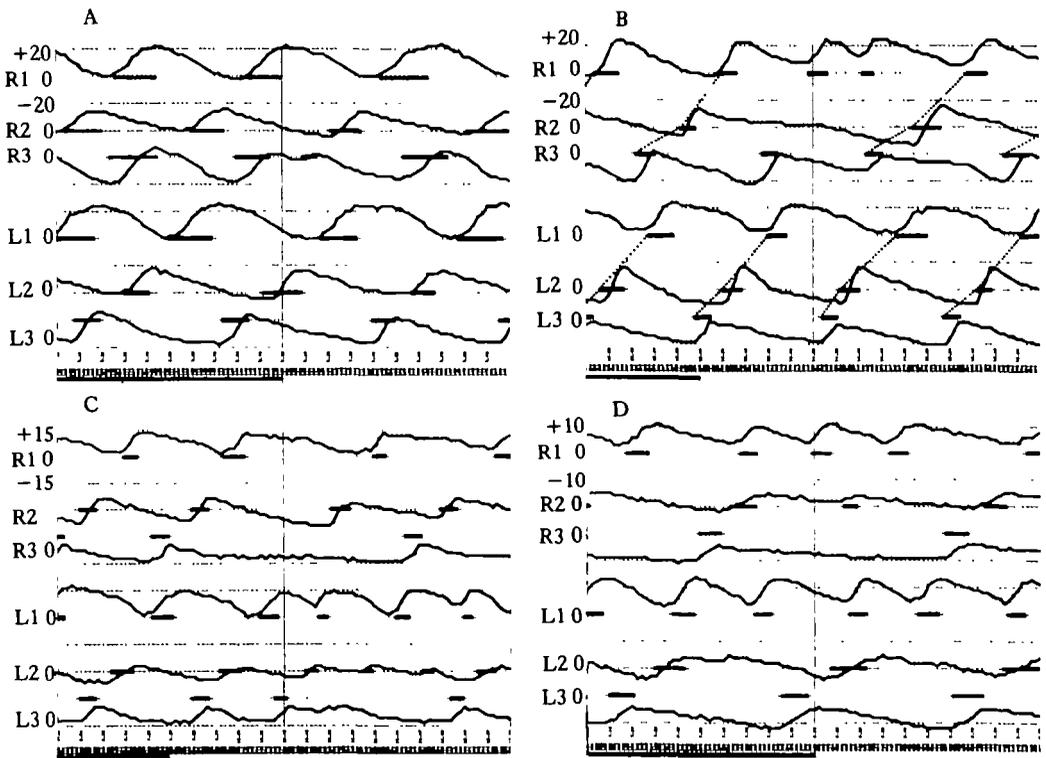

Fig. 7. Step patterns of tarsus position in the x direction showing various types of partially-
coordinated behaviour. (A) Example of extra protraction resetting the rhythm of leg R3. (B) Absence
of a protraction in R2 at regular intervals (15 steps) producing a consistent change in the timing of
R1 and to a lesser extent in L2 compared to the hind leg steps. (C) Turning behaviour towards the
right in which each leg is stepping with a different period. (D) Weak right turn with pronounced 2:1
stepping of front legs on both sides compared to the regular coordinated slow walk of the middle and
hind legs. Time bar is 1 s.

time to swing at the expected time and produced a single step of twice the normal amplitude with interesting effects on the leg in front on the same side and the middle leg (L2) on the opposite side. The contralateral leg advanced slightly in phase compared with L1 and L3 (see dotted lines marking the metachronal sequences). On the same side the failure of leg 2 to swing at the appropriate time allowed the next swing of the front leg (R1) to occur much earlier than usual and this leg stepped again with a very short period, showing clearly that protraction duration is directly related to the distance required to reach the relatively constant AEP position, and indicates a higher inherent frequency in this leg when no control is imposed on it by the posterior middle leg swing.

During turning behaviour to the right (Fig. 7C, D), simultaneous stepping of legs in the same segment was much rarer than would be expected if no coupling were present, indicating that this is in fact rapid gliding coordination. The example of Fig. 7C is particularly interesting because each leg had a different step frequency and yet ipsilateral pairs were quite well coordinated and simultaneous protractions were rare even across the body.

In Fig. 7D, the front legs stepped with a high frequency compared to the middle and hind legs, which were ipsilaterally phase-locked, while the leg pairs on right and left sides had a different step period. In these instances the normal coordinating pathways appear to be active, but the typical coordination has been modified by the large differences in step period that become possible when the legs are no longer coupled through the substrate.

In general these episodes show phase-locked coordination between pairs of ipsilateral legs with step frequencies in integral ratio to the faster stepping legs. Front, middle or hind legs can 'go slow' but the effect is most common in middle and hind legs.

Motor output

The motor activity in two thoraxic and two coxal muscles is shown in Fig. 8 for the left middle leg of three different animals during walks on oil. The records from the levator and depressor of the trochanter show negligible cross-talk, although the muscles are close together in the coxa. For the protractor and retractor of the coxa there is sometimes slight cross-talk, as these muscles lie parallel to each other and electrode position is critical in avoiding mutual recording.

The start of the swing phase is shown by the movement artifact in the retractor record. This appears clearly in each record as a rapid downward excursion of the retractor record and sometimes protractor cross-talk is visible at this time (see 6th step of animal DSF for example). The records show strong levator and protractor activity for each animal. Levator activity led the onset of swing by 50 ms. This was followed by a burst of protractor activity with a duration of 50–80 ms. Immediately following the protractor burst there was strong activity in the depressor. This was sometimes followed by a pause of 20 ms before the depressor activity continued and facilitated rapidly during the stance phase. The depressor activity was quite variable during the stance phase. The records for animals DSD and DSF show that for some steps the depressor activity could become extremely weak with only seven spikes compared to 20 or more normally associated with the stance phase. Retractor activity was

DSF   Forward walk on glass
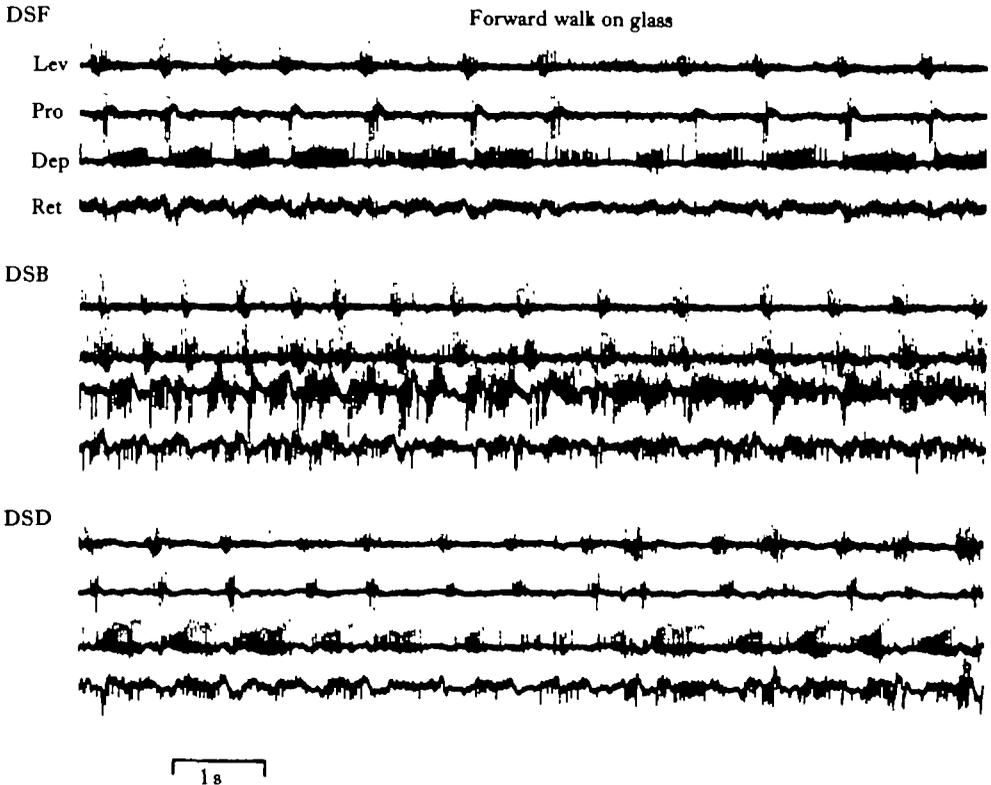
Lev

Pro

Dep

Ret

DSB

DSD

|‾ 1 s ‾|

Fig. 8. Myograms of the activity in the levator trochanteris (Lev), protractor coxae (Pro), depressor trochanteris (Dep) and retractor coxae (Ret), for three different animals labelled DSB, DSD and DSF walking on the same low viscosity oil.

mainly of the semi-fast type (Graham & Wendler, 1981). On rare occasions a burst of fast activity could be seen at the end of the stance phase (end of DSD record). In some steps of animals DSD and DSF even semi-fast units were hardly active and in these instances slow unit activity was apparently sufficient to move the leg slowly to the rear (3rd, 5th and 6th retractions of animal DSD).

Notice that there is no indication of protractor activity extending into the stance phase as observed in walks on a high inertia wheel (Graham & Wendler, 1981). In all other respects the motor activity is similar to that reported for walking on light wheels (Graham & Baessler, 1981; Graham & Godden, 1983).

DISCUSSION

The results show that animals can walk with the simple tripod gait when oil viscosity is low or with the tetrapod gait when oil viscosity is high. The animals walk steadily for long periods without stimulation and exhibit a rather narrow range of step period which is determined by the oil viscosity. The normal substrate appears to be important in the integration of force output from the propelling legs. When individual legs are not coupled mechanically through the surface they are capable of operating w

significantly different step periods, as evidenced by the 'go slow' behaviour of some legs. Reference to the step profiles of well-coordinated walks shows that even at these times individual legs may move at significantly different velocities over the surface and there is no apparent control mechanism to keep all legs retracting at the same rate. Thus legs may often change their motor output, but these variations would normally be integrated by the substrate, compensating to some extent for local differences in propulsive force. On the slippery substrate a leg will often operate with reduced power output for long periods and it may be that in normal walking irregular changes in load stimulate the retractor musculature in a manner that is not observed here. Alternatively, careful examination of motor output during slow walks on a normal substrate may show similar variations which are not easily detected in the integrated movement.

During the recovery or swing stroke the tarsi accelerate to a maximum speed at mid-stroke and then decelerate uniformly as they approach touch-down, such that the velocity in the x direction is close to zero at contact. The tarsus, however, is moving slowly laterally (y direction). In general, front legs move away from the body at touch-down while middle and hind legs tend to move inwards but this is not always the case. The power stroke moves inwards towards the body in front legs and away from it in the hind legs with the middle legs showing both an inward pull at the start and an outward push if the leg moves strongly to the rear of the mean position perpendicular to the body. These movements are similar to those reported in the free walk observations of Cruse (1976) and suggest that the body oscillates appreciably about a vertical axis during a forward walk because of these rather stereotyped actions of the different legs. The precise kinetics of the body are complex and no attempt appears to be made to maintain the tarsus track parallel to the body axis. The legs appear to move in such a way as to take advantage of the muscular specializations characteristic of each of the three pairs of legs. The flexor and extensor muscles of the front and hind legs, respectively, generate propulsive power while the middle legs can operate either forward of the perpendicular position, using the flexors for propulsion, or move behind the perpendicular position, using the extensors. The most usual range is between the two, where this leg appears to depend heavily upon the coxal retractors for propulsion. It should be remembered that in the tripod gait this leg is alone responsible for all the force generated on one side during its stance phase.

The role of the coxal retractors in the front and hind legs may be primarily to stabilize the body against excessive rotation, although they must be important in propulsion at those times when the leg is almost perpendicular to the body, i.e. at the end of the front leg power stroke and beginning of the hind leg power stroke. Motor output to the middle leg shows variations both in the units active and the frequencies of active units. At times depressor activity can become weak and the semi-fast and fast units of the retractor muscle may drop out, leaving only slow unit activity to move the leg to the rear more slowly than the other legs. These results all indicate that individual retraction movements on the glass are quite variable.

Strong activity in the protractor muscle is never observed at the beginning of the stance phase, as has been found in both counter-balanced light wheel walking (Godden & Graham, 1983) and in animals walking on high inertia wheels (Graham & Wendler, 1981). This supports the suggestion that such motor output is produced by a resistance reflex opposing passive movement of the newly landed leg by forces

originating from the other retracting tripod of legs and transmitted *via* the substrate. On the slippery glass no forces can be exerted on the 'landing' leg by other legs and no reflex would be activated. This view is also supported by the observation in the glass-walking records that the leg usually pauses for between 50 and 200 ms at each end of the stance phase (see Figs 2, 5 and 7).

Another interesting feature of the walks is that there is no slipping response. Absence of tarsal hooks in a free-walking animal can cause slippage in the damaged leg. Such behaviour leads to secondary protractions, see Graham (1972). In intact, free-walking animals such extra protractions are relatively rare (1 in 200 steps). There is a similar incidence in the slippery glass studies. This suggests that mere relative movement between tarsus and substrate is not an adequate stimulus for the slipping response.

That the nervous system receives information on the position of a middle tarsus is clear from the targetting phenomenon described by Cruse (1979), but it does not appear to use such information to coordinate exactly or synchronize motor output during retraction in order to control the relative positions of the tarsi. It would seem that the neural 'programme' for walking relies in part on the mechanical coupling between the legs that is provided by most natural substrates to ensure adequate coordination of their relative retraction velocities.

The more frequent appearance of a high step frequency in front legs compared to middle and hind legs supports the view that there is an inherent frequency hierarchy along the body with greatest activity at the front. Such a system is readily controlled by a forward-directed inhibition of the kind proposed in the models of Wilson (1966) and Graham (1977, 1978).

REFERENCES

BATSCHELET, E. (1965). *Statistical Methods for the Analysis of Problems in Animal Orientation and Biological Rhythms*. A.I.B.S. monograph.

CRUSE, H. (1976). The function of the legs in the free walking stick insect *Carausius morosus. J. comp. Physiol.* **15**, 235–262.

CRUSE, H. (1979). The control of the anterior extreme position of the hindleg of a walking insect, *Carausius morosus. J. Physiol. Entomol.* **4**, 121–124.

FOTH, E. & GRAHAM, D. (1983). Influence of loading parallel to the body axis on the walking coordination of an insect. I. Ipsilateral effects. II. Contralateral effects. *Biol. Cybernetics* (in press).

FRANKLIN, R., BELL, W. J. & JANDER, R. (1981). Rotational locomotion by the cockroach *Blattella germanica. J. Insect Physiol.* **27**,4, 249–255.

GRAHAM, D. (1972). An analysis of walking in the first instar and adult stick insect *Carausius morosus. J. comp. Physiol.* **81**, 23–52.

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

GRAHAM, D. (1978). Unusual step patterns in the free walking grasshopper *Neoconocephalus robustus*. I. General features of the step pattern. *J. exp. Biol.* **73**, 147–157.

GRAHAM, D. (1978). Unusual step patterns in the free walking grasshopper *Neoconocephalus robustus*. II. A critical test of the leg interactions underlying different models of hexapod coordination. *J. exp. Biol.* **73**, 159–172.

GRAHAM, D. (1981). Walking kinetics of the stick insect using a low inertia, counter-balanced, pair of independent treadwheels. *Biol. Cybernetics* **40**, 49–58.

GRAHAM, D. (1983). Insects are both impeded and propelled by their legs during walking. *J. exp. Biol.* (in press).

GRAHAM, D. & BAESSLER, U. (1981). Effects of afference sign reversal on motor activity in walking stick insects (*Carausius morosus*). *J. exp. Biol.* **91**, 179–193.

GRAHAM, D. & CRUSE, H. H. (1981). Coordinated walking of stick insects on a mercury surface. *J. exp. Biol.* **92**, 229–241.

GRAHAM, D. & GODDEN, D. H. (1983). A preparation of the stick insect *Carausius morosus* for recording from identified neurones during walking. *J. Physiol. Entomol.* (in press).

GRAHAM, D. & WENDLER, G. (1981). Motor output to the protractor and retractor coxae muscles in stick insects walking on a treadwheel. *J. Physiol. Entomol.* **6**, 161–174.

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

SHERMAN, E., NOVOTNY, M. & CAMHI, J. M. (1977). A modified walking rhythm employed during righting behaviour in the cockroach, *Gromphadorhina portentosa*. *J. comp. Physiol.* **113**, 303–316.

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

.