

BEHAVIOUR AND MOTOR OUTPUT FOR AN INSECT WALKING ON A SLIPPERY SURFACE

II. BACKWARD WALKING

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Accepted 20 March 1985

SUMMARY

Coordination of the legs and the motor activity of four muscles in a middle leg were recorded in adult stick insects walking on a slippery glass surface. Backward walking was not achieved by a simple phase shift of levators and depressors. In all muscles examined, there was a considerable disturbance of motor activity during backward walking when compared with that found in forward walking. In backward walking, recovery was performed, in the middle leg, by strong fast unit activity in the retractor muscle and all muscles showed weak activity at inappropriate times. Fast motor output appeared to be superimposed on the forward walking motor pattern to produce the movements required for backward walking in this insect.

INTRODUCTION

It is easy to persuade stick insects to walk backwards by gently pulling their antennae (F. Krieger, unpublished observations, see Dedication). Spontaneous backward walking of these insects has only been observed during rapid turning behaviour when legs on the inside of the turn may briefly step to the rear (H. Cruse, personal communication). Franklin, Bell & Jander (1981) have also observed backward walking on the inside of tight turns during courtship in the cockroach. The authors are not aware of any reports of insects spontaneously performing continuous backward walking on both sides. In hunting spiders backward walking frequently occurs, on one side of the body, during rapid turning movements (Land, 1972). The backward stepping is well coordinated, with adjacent legs on the same side lifting in antiphase. The timing appears to be identical to that used in forward walks. Backward stepping on both sides at the same time has not been reported.

In scorpions, the normal order of leg recovery in forward walks takes the form of a metachronal wave in which protractions appear to run from front to rear

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Key words: Backward walking, motor output, behaviour.

(assuming that the shorter lag between adjacent legs on the same side defines the metachronal wave) (Bowerman, 1981). This differs from that observed in slow walking insects where a wave of protractions passes forwards along the body (Wilson, 1966). Scorpions often walk backwards on both sides and show a similar coordination pattern to that found in their forward walks.

In crustaceans lateral, diagonal and full backward walking are common. The lobster appears to be the most active backward walker of the crustaceans that have been studied (see review by Clarac, 1982). In rock lobsters walking forward, the relative phase of a more posterior leg on the adjacent ipsilateral leg lies in the range 0.9–0.6 compared to the value of 0.3–0.4 which is typical of a slow walking insect (Hughes 1952; Wendler, 1966; Graham, 1972). This crustacean, therefore, exhibits rearward directed waves of protraction, similar to those in scorpions. In backward walks the rock lobster shows a reversal of this behaviour in the leg 2 to leg 3 phase and a phase of 0.5 for the more posterior legs. In addition, the ipsilateral phase is much more distributed in all legs suggesting weaker leg coordination in this mode of behaviour. Within one leg the motor activity of the remotor or powerstroke muscle occurs in well-defined bursts with similar units active in both directions of walking. The timing and burst parameters for the motor output to several muscles, except the levators, of one leg have been shown to differ significantly between forward and backward walking (Ayers & Davis, 1977). The levator units show a constancy of behaviour which suggests that they may have a close association with those elements which generate the stepping movement in the lobster.

METHODS

The preparation and recording techniques were identical to those described by Epstein & Graham (1983). The animals walked on oil of 1 stoke viscosity ($1 \text{ St} = 10^{-4} \text{ m}^2 \text{ s}^{-1}$) spread thinly over a glass block. The same experimental animals were persuaded to walk backwards by holding the antennae with the fingertips and applying slight tension in the forward direction. They immediately attempted to escape to the rear and walked backwards for 5–30 s. Backward walks were first achieved with free-walking animals (see Dedication) and have also been successfully demonstrated on the wheel system of Graham (1981).

RESULTS

Backward walks are easily elicited by the method described above. This appears to be a more effective stimulus for backward walking than the abdomen stroking used to stimulate forward walking. Antenna tension is often used to stimulate a brief backward walk in preparation for the study of forward walking in animals that show reluctance to start a forward walk in response to abdominal stimulation.

The backward walks appeared to be relatively straight when both antennae could be held, but tension on only one antenna produced a strong turning component. When one antenna is pulled the animal walks backwards most

vigorously on that side. Interleg coordination in backward walking is irregular compared to that found typically in forward walking, as shown in Figs 1 and 2.

Patterns of backward walking

The most common types of backward walking are shown in Fig. 1. In one type most of the legs are well coordinated with 3,2,1 sequences on both sides and movements of legs of the same segment alternating with varying phase (Fig. 1A). The range of movement is also approximately equal for all the legs. Another typical sequence is shown in Fig. 1B, where the middle and hind legs step in the order observed in forward walking but the front legs step more slowly and show a larger range of movement. In this record there are three examples of the sequence 1,2,3 for legs on the same side. Such sequences are extremely rare in forward walking and have only been observed in some start sequences (Graham, 1972).

In most backward walks the range of leg movement is biased towards the rear of the animal (the legs reach well to the rear during swing phase). This is best shown

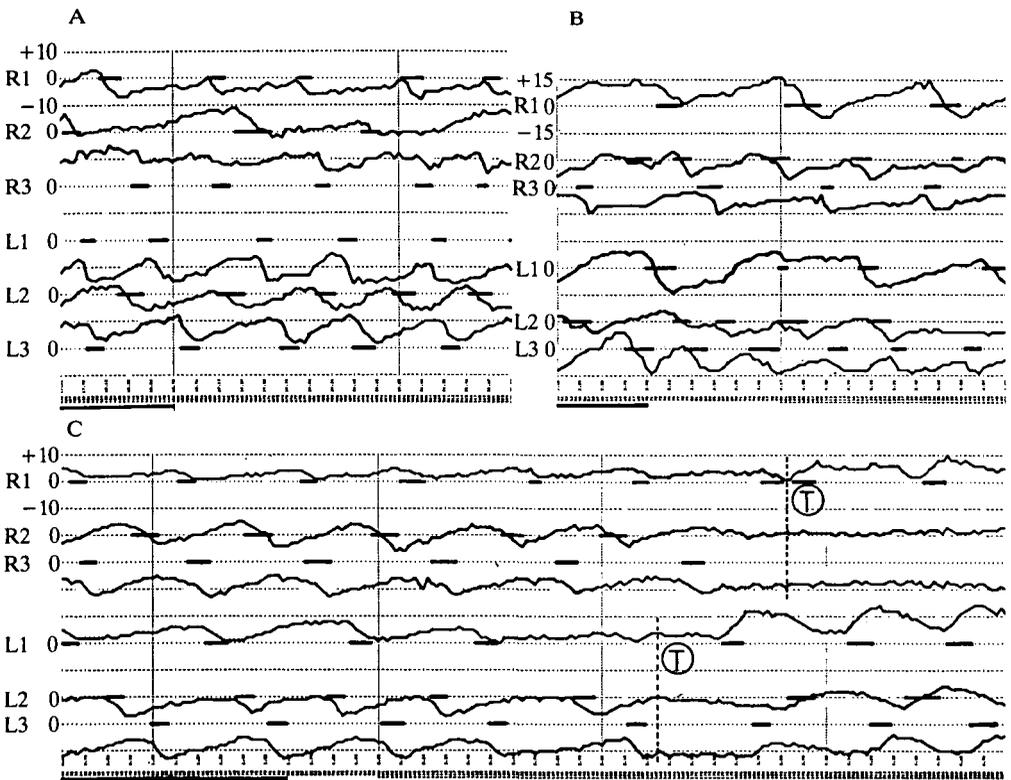


Fig. 1. The position of the distal tip of the femur is projected onto the body axis and is shown (in mm) relative to the coxa-thorax articulation for each leg. Black bars show when the leg is lifted in swing phase. In (A) and (B) the animal walks steadily backwards. In (C) the animal walks backwards for a few seconds and then walks forward as soon as the left and then the right antenna is released at T. Time bar is 1 s and vertical dimension is in mm. Forward movement is up.

in the transition sequence of Fig. 1C. In this record the middle leg on the left (L2) only moves, forwards to the level of the subcoxal joint in stance phase, when walking backwards (first part of record). After the transition to forward walking (T) the middle leg adopts its normal range of movement. At the start of the record for the left side the step order is 1,2,3. The smaller amplitude of femur tip movement when walking backwards is probably caused by rearward biasing of the leg movement which means that the extension of the tibia contributes more to the body displacement than does the retraction of the femur.

The transition from backward to forward walking on each side is separated by an interval of almost 1 s and shows that each side can temporarily move in opposite directions. Notice, that in the front leg (R1) two separate protractions occur immediately before and after the transition. Identical behaviour has been reported for walk reversals in jumping spiders (Land, 1972), which indicates that the mechanism for generating protractions reverses itself at this time rather than running continuously with a constant periodicity as would be expected if the

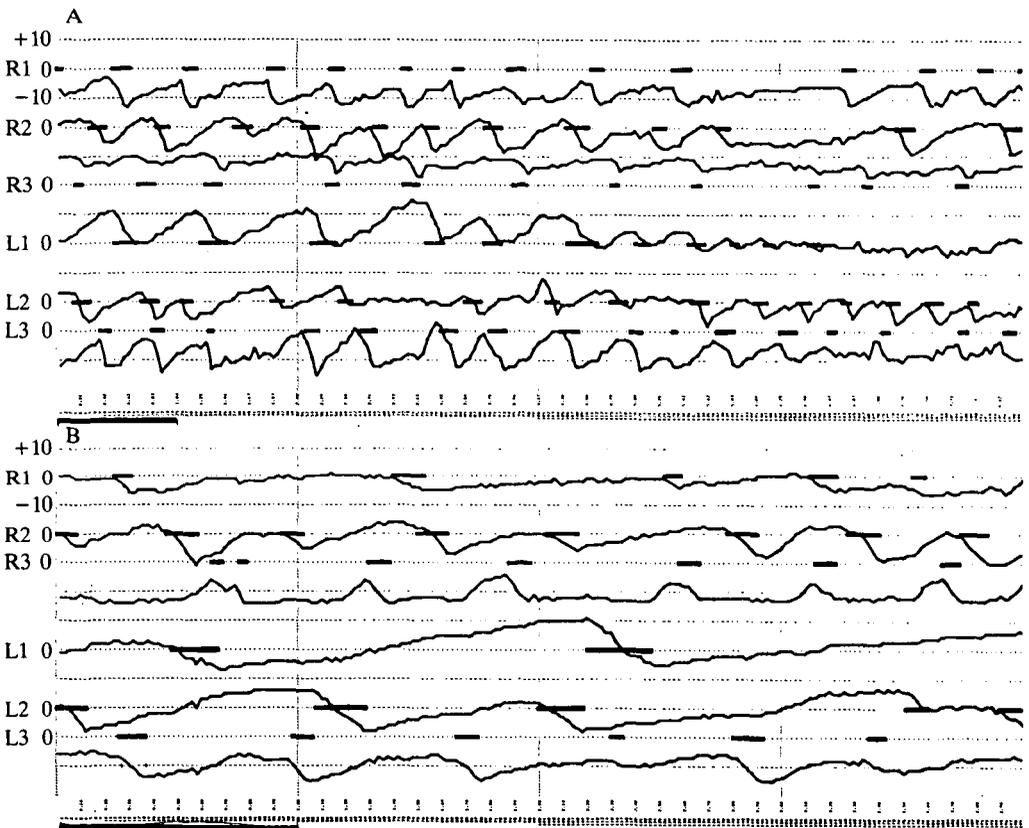


Fig. 2. Similar measurements to those of Fig. 1 showing backward walking (A) in which there is considerable variability in the sequence of protractions and (B) slow stepping of the front legs compared to the behaviour of the middle and hind legs. Time bar is 1 s and vertical dimension is in mm. Forward movement is up.

reversal of walking merely involved switching the role of the muscles in a centrally generated pattern. This suggests that the whole programme for stepping reverses itself at the transition point, and that the leg itself and its position are important components of the oscillating system.

Another sequence of steps with gliding coordination and some 1,2,3 sequences is shown in Fig. 2A. In general, the step order is 3,2,1 and the order 1,2,3 is seldom observed for a series of steps. This suggests that such sequences are the result of relative coordination caused by variability in the step frequency of all the legs, and is consistent with a hierarchical inhibitory-coupling model of the Wilson (1966) kind, in which strict ordering of the inherent frequency of the ipsilateral legs is not maintained.

An example of the front legs on both sides operating at approximately half the step frequency of the middle and hind legs is shown in Fig. 2B. Such sequences are analogous to those reported in the forward walks of katydids (Graham, 1978) where hind legs step with half the frequency of the middle and front legs on the same side. In both cases the slower-stepping legs have larger amplitudes of movement than the other legs and it is the rearmost legs (relative to the direction of body movement) which exhibit this slow stepping behaviour.

Most of these experimental runs were accompanied by blocking interruptions (described in S. Epstein & D. Graham, in preparation). The coordination of the walks was often disturbed, so that the regularity of the coordination or preferences for particular phase relationships could not be assessed. However, the incidence of well coordinated walking was much lower than that of similarly disturbed forward walks.

Motor patterns during backward walking

Myograms of the motor output to four muscles in a middle leg during backward and forward walking are shown in Fig. 3. Comparison with the forward walk examples (Epstein & Graham, 1983 and Fig. 4) shows that there is more overlap in antagonist muscles and a general irregularity in motor output during backward walks. In a forward walk the levators are active in brief bursts at the onset of protraction and sometimes show a few potentials at the end of the recovery stroke. A strong burst in the protractors produces the recovery stroke. During the early part of recovery, when the levators are active, the depressors are normally silent. Retractor activity is approximately synchronized with the depressors but rarely appears during the recovery stroke. It is usually concentrated towards the end of the stance phase.

In backward walking, levators are sometimes continuously active but the strongest activity usually precedes, and sometimes immediately follows, the recovery stroke. During leg recovery a large unit of the retractor muscle is strongly active, swinging the levated leg rapidly towards the rear. For walks on glass or on light wheels this large unit is rarely active in forward walks except for the occasional spike near the end of the stance phase. This may be seen in Fig. 4, where the animals DSD and DSF are walking forwards with the same recording

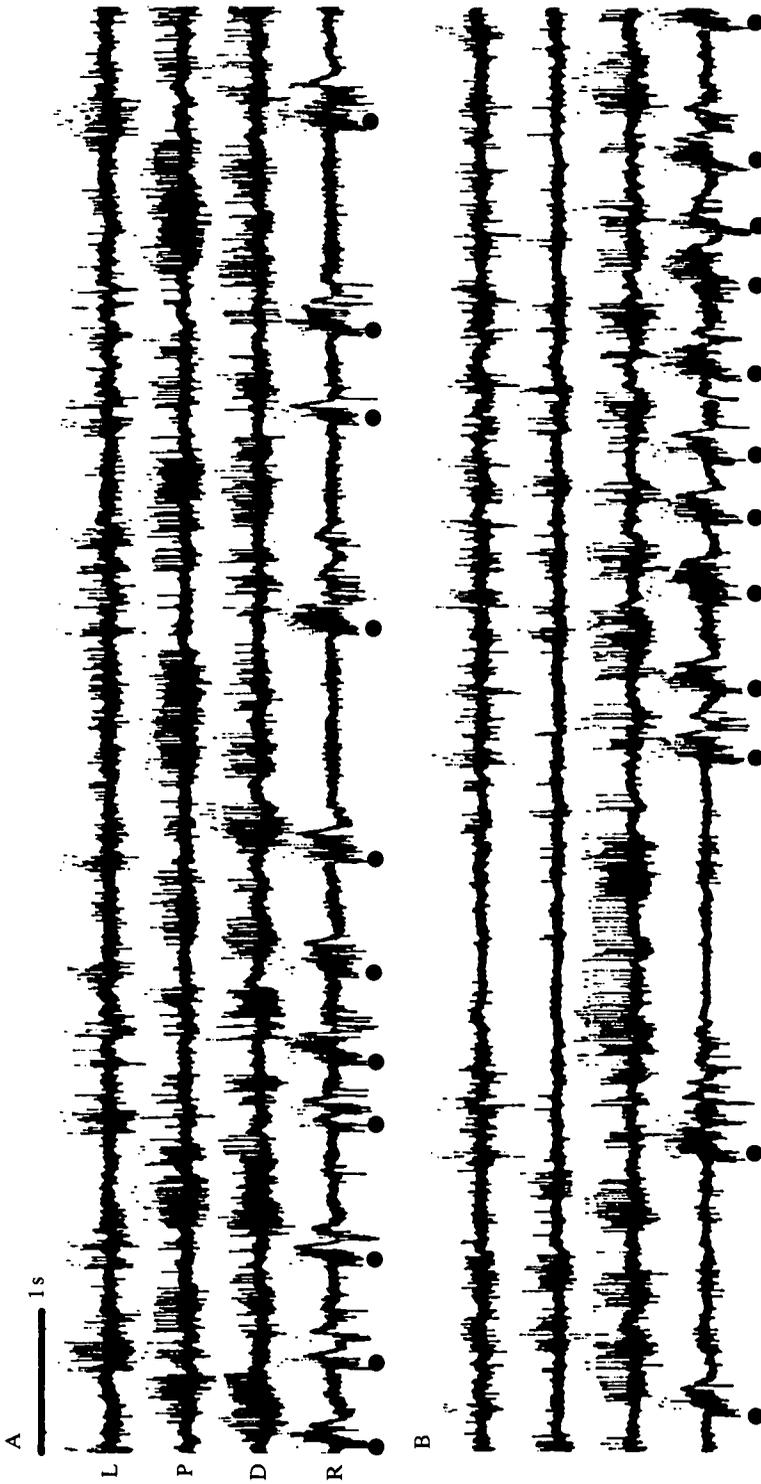


Fig. 3. Electrical activity in the levator trochanteris (L), promotor (promotor) coxae (P), depressor trochanteris (D) and retractor (retractor) coxae (R) for the left middle leg of a stick insect walking on silicon oil of viscosity $10^{-4} \text{ m}^2 \text{ s}^{-1}$. Records (A) and (B) run consecutively for animal DSD. The onset of the swing or recovery stroke is shown by a dot under the muscle record responsible for the recovery movement (protractor during forward walk and retractor during backward walk). This marker was derived from a synchronized film record. Time bar, 1 s.

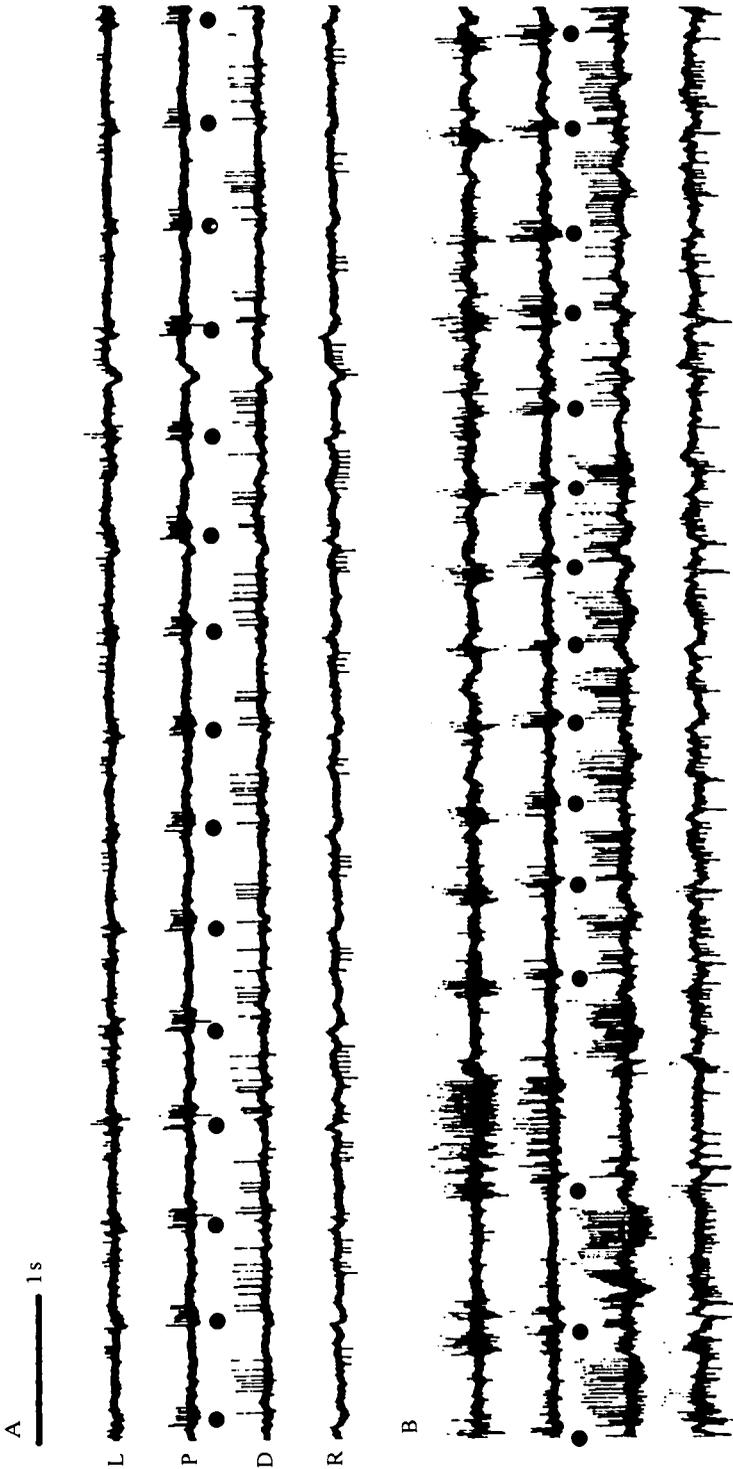


Fig. 4. Myograms of the same animals (DSD and DSF) walking forward on oil of the same viscosity as in Fig. 3. See Epstein & Graham, (1983) for further details. The motor records are directly comparable with Fig. 3 and were recorded at the same gain. Notice the much lower levels of activity in all records when walking forward. Time bar, 1 s.

electrodes as in Fig. 3. Careful examination of the backward walking records show that each large muscle potential is preceded by its nerve potential. This identifying feature is often observed in recordings from the retractor-coxae muscle. The smaller potentials in this muscle appear to be continuously active throughout the stance phase in backward walking, although the protractor muscle is the powerstroke muscle at this time. The large and small potentials correspond to the fast and semi-fast units identified in the nerve recordings of the retractor muscles (Graham & Wendler, 1981). The peaks in the activity of the small units appear to be associated with those times when the depressors are most strongly active and it is clear from the individual potentials that this is not crosstalk from the depressor muscle. Depressor activity is mainly confined to the stance phase during backward walking but again there are sometimes strong bursts during the swing phase (steps 7 and 10 in Fig. 3A, and 1 and 2 in Fig. 3B). In most steps the depressors are strongly active throughout the stance phase but in some walks the burst only appears at the beginning of the stance phase or, as in 3B, is broken up into two or three short bursts.

The protractor muscles rarely show any activity during the recovery stroke in backward walks but usually produce strong activity during the stance phase and move the leg towards the front in the powerstroke. Sometimes, these bursts show an intermittent firing pattern similar to that of the depressors, or very weak activity with a tendency to fire only briefly at the beginning of the stance phase.

DISCUSSION

Antennal stimulation appears to cause the activation of rearward walking on the stimulated side. This is assumed to be an excitatory process for backward walking, because the work of Roeder (1937) in mantids and Graham (1978) in stick insects suggests that forward walking is a spontaneous property of the combined sub-oesophageal and thoracic ganglia. Antennal stimulation appears to override this system and replace it by direct commands.

The major motor activity is consistent with the observed movement of the leg during backward walking. The motor output required for this kind of behaviour appears to have been achieved in broad outline but the detailed coordination and economy of activity that is clearly displayed in the forward walk is no longer present. It may be that the animal is more disturbed in the backward walks and this involves a reduction in the precision of control. This seems an unlikely explanation as strong stimulation in forward walking does not disorganize the behaviour, instead it tends to channel the system into a more precisely controlled behaviour accurately tuned to the walk rhythm. One possible interpretation would be that the reflexes and interactive pathways between the legs have primarily evolved for forward walking and that under the stress of enforced backward walking, the inappropriate responses of the slow units which are used in forward walking cannot be adequately suppressed, although suitable responses in fast units can be activated.

A direct comparison of motor output in forward and backward walking in the same animal does not suggest a simple switching process in which the actions of the muscles are inverted for reversal of locomotion. In other arthropods which often walk backwards, such as lobsters, hunting spiders and scorpions, the regular coordination patterns suggest that a well-defined motor output is achieved and simple switching is possible.

The disturbance of the levators and depressors by the reversal of movement is surprising because these muscle groups could use similar motor output patterns, with an appropriate phase shift, for both forward and backward walks. Had these motor patterns remained undisturbed the results would have indicated a similar mechanism to that advanced for the crustaceans (Ayers & Davis, 1977). In this system it is the protractors and retractors that at first sight appear to have the least difficulty in reversing their roles. Certainly, the major bursts are confined to the appropriate parts of the walking cycle, but the activity of the smaller units during the stance phase in the retractor muscles suggests that it is only the large units which can be programmed for the backward walk. The smaller units always appear to be closely coupled to the depressor motor neurones.

Examples of both posteriorly and anteriorly directed metachronal coordination between legs have been observed, indicating that pre-motor inputs to the leg motor neurones are not simply switched over to produce backward walks. The posterior ipsilateral leg pairs (2 and 3) show good phase-locked coordination most of the time with the short latency coupling going forward. However, posteriorly directed sequences are also present in some walks for several steps (see later part of Fig. 2A), which implies that the inhibitory coupling proposed in several models of walking may be both anteriorly and posteriorly directed, producing metachronal sequences in either direction depending upon the relative step frequencies of the segments (Cruse & Graham, 1985). The front legs, in backward walks, often step with large amplitude at a correspondingly lower frequency than the middle and hind legs and are usually phase locked to the other legs. Similar behaviour has been described in forward walking grasshoppers (Graham, 1978). In this case the rather long hind legs step at half the frequency of the legs in front, taking strides of twice the amplitude of the shorter front legs. In the stick insect the front legs are the longest legs but the difference is not large. However, long steps of the front legs sometimes appear in forward walks under certain conditions (Graham, 1972).

During backward walking the motor output patterns are much less regular. Often bursts of activity appear in the antagonist of the observed movement but these are brief and even here the activity of the synergist tends to be diminished. Thus there appear to be neural connections which inhibit the simultaneous contraction of certain muscles during walking behaviour. These connections do not exist directly between the motor neurones (Burrows & Siegler, 1978) and presumably interneurones provide this selective inhibition between antagonists (Burrows, 1980).

Backward walking appears to be a disorganized type of behaviour compared to forward walking in this insect and may be achieved by overriding the normal

connectivity between the units which are responsible for forward walking. In insects, there does not appear to be any strong indication of a special role for the levators as the organizing elements of the motor output.

DEDICATION

This work is dedicated to the memory of Franz Krieger, a young scientist at this laboratory, who died of leukaemia at the age of 23 years on April 22, 1980. His first efforts in research were directed towards the study of stick insect movement over irregular terrain, during which he discovered the simple technique for eliciting the backward movement described in this report. His premature death and also that of Cornelia Peschke in a tragic road accident is deeply regretted by all members of this department.

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