

PERIPHERAL INFLUENCES ON THE
MOVEMENT OF THE LEGS IN A WALKING INSECT
CARAUSIUS MOROSUS

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SUMMARY

Anterior extreme position (AEP) and posterior extreme position (PEP) of the legs of stick insects were measured during walking on a treadwheel or on a slippery glass plate. In several experiments, either protraction or retraction of a middle or hind leg was interrupted. The AEP of other legs was independent of a protraction interruption but PEP was displaced backward in the leg anterior to the interrupted leg. When a leg was standing on a fixed platform (interruption of retraction) no changes were found in AEP and PEP for the other legs but if the platform was slowly moved, PEP of leg on the platform was moved forward. These results disagree with several published hypotheses. The results suggest the hypothesis of a position-dependent threshold value for protraction which is modulated by co-ordinating influences from other legs.

INTRODUCTION

A walking stick insect can move its legs in a clearly co-ordinated pattern when walking free (Buddenbroock, 1921; Graham, 1972) or on a treadwheel (Wendler, 1964; Graham, 1981). This pattern is also produced when no mechanical connexions are present between the legs (Graham & Cruse, 1981). Therefore neuronal connexions must exist which can influence the temporal relationship between the cyclic movement of different legs. This cyclic movement of a forward-walking leg can be divided up into two phases, protraction or swing phase (when the leg is not touching the ground) and retraction or stance phase (when the leg is on the ground). The question arises, by what mechanism might a leg be influenced to maintain its phase relative to another leg. Different hypotheses are proposed in the literature (Wilson, 1967; Wendler, 1968, 1978; Graham, 1972, 1977; Pearson & Iles, 1973; Cruse, 1979*b*, 1980*a, b*). In this paper a series of new experiments is presented which can be used to test these hypotheses.

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METHODS

Adult female stick insects (*Carausius morosus*) were used. In one series of experiments the animal was fixed dorsally to a holder and walked on a treadwheel at a fixed distance beneath the body. The treadwheel had a diameter of 38.5 cm, a breadth of 9 mm, a moment of inertia of 720 g cm² and a friction 0.8 mN at the outer margin (for details see Cruse & Saxler, 1980). The anterior extreme position (AEP) is the point where the leg touches the ground to begin retraction, the posterior extreme position (PEP) is the point where the leg is lifted from the ground to start protraction. The distal end of the tibia was used as a reference point. Following Bässler (1972), AEP and PEP were measured as projections onto the longitudinal axis of the body, with the tip of the head as origin. Positions anterior to the head are positive. AEP and PEP were measured by eye, using a millimetre scale parallel to the body and a mirror system to avoid parallax errors. The values were read by the experimenter and recorded on magnetic tape. In some experiments the animals were filmed from above with a Super 8 cine Beaulieu movie camera in order to describe the movement of the legs during interruption of the protraction stroke (see below). Legs are named L for left side and R for right side followed by 1, 2 or 3 for front, middle and hind leg, respectively.

Two types of experiments were performed.

(a) *Interruption of protraction.* The protraction of a leg can be interrupted for any desired duration by holding a stick vertically in front of the femur of this leg (Cruse & Saxler, 1980; Dean & Wendler, in press). For details see Results.

(b) *Interruption of retraction.* Following Wendler (1964), a leg can be placed on a fixed platform beside the treadwheel. If the position of the platform is far enough in the anterior range of the normal movement of the leg, it does not start a protraction although the other five legs continue walking. The leg develops a strong force in the posterior direction (Cruse & Saxler, 1980).

In the first series of experiments the AEP or PEP of a leg was measured during an undisturbed walk as a control, then in the same leg during interruption of protraction or retraction in one of the other legs, and finally, as a second control, during another undisturbed walk. Only those experimental values were used for further evaluation for which no differences were found between pre- and post-interruption controls. This procedure served to eliminate data in which changes in extreme positions were produced by 'spontaneous' changes in the internal state of the animal, as e.g. changes in the turning tendency.

Data for each experimental condition were obtained from at least three animals. As the animals varied in body length, the values of the extreme positions for control walks were normalized to the corresponding mean for all animals. The values obtained in the experiment were then normalized for each individual animal to this mean value for all control walks. Mean values are given with their standard deviations. As a rough criterion of significance, two mean values are considered significantly different when they are separated by more than the larger of their standard deviations (n between 80 and 521).

In the second series of experiments the animal was ventrally fixed on a holder

Table 1. *AEP and PEP of left legs of the intact animal and the differences in AEP and PEP when protraction of a leg is interrupted*

(Values are given in mm. Anterior direction is positive. Mean values are shown with their standard deviation and sample size. Significant differences to control are labelled by (x).)

	Control	Interrupted leg					
		L1	L2	L3	R1	R2	R3
L1							
AEP	15.5 ± 1.6 568	—	-1.7 ± 3.0 132	-0.9 ± 1.7 167	-0.3 ± 1.1 80	-0.6 ± 1.5 107	0.3 ± 1.6 195
PEP	-4.2 ± 2.8 911	—	-7.9 ± 3.3 (x) 231	-0.7 ± 2.2 249	-1.3 ± 1.9 185	-1.2 ± 3.3 99	0.1 ± 2.9 119
L2							
AEP	-11.7 ± 1.1 1099	-2.0 ± 2.7 419	—	-0.5 ± 1.1 138	-0.2 ± 1.4 269	-0.3 ± 1.0 134	-0.3 ± 1.1 147
PEP	-28.6 ± 2.5 1317	-0.4 ± 2.9 417	—	-5.0 ± 2.0 (x) 192	-0.7 ± 2.6 329	-1.1 ± 2.3 200	-1.0 ± 1.5 374
L3							
AEP	-33.1 ± 2.3 992	-1.9 ± 3.1 132	-0.5 ± 2.7 114	—	-0.1 ± 1.9 203	0.1 ± 2.1 426	-0.6 ± 2.4 291
PEP	-52.0 ± 2.3 1346	-0.6 ± 2.9 148	-0.6 ± 2.9 290	—	-0.5 ± 3.0 154	-0.6 ± 2.8 521	-0.5 ± 2.7 203

(S. Epstein and D. Graham, in preparation). The animal walked on a horizontal glass plane covered with silicone oil. As on a mercury surface (Graham & Cruse, 1981), the animal can walk with perfect co-ordination on this slippery surface. As no mechanical connexions exist between the legs, this experimental arrangement reveals the central nervous coupling of the individual legs. The animals were filmed from above. The movement of the tip of the tibia was measured by single frame analysis for each leg.

RESULTS

Interruption of protraction

The protraction of a leg of an animal walking on a treadmill was interrupted by holding a stick vertically in front of the femur (see Methods). If the stick was held so that the leg could not reach the anterior half of the normal range of movement, it did not finish its forward movement, i.e. the leg was not depressed and then retracted in the normal pattern of transition to stance phase. Instead the leg performed oscillating movements whereby the femur moved backward and upward and then forward until it touched the stick, then backward and upward again, and so forth. As determined from single frame evaluation of cine films, these movements were repeated with a frequency between 3 and 4 Hz and had an amplitude of about 20°–40°.

This behaviour is very similar to that of a leg with 'crossed receptor apodeme' (Graham & Bässler, 1981). After an operation to change the point of attachment of the receptor apodeme of the femoral chordotonal organ, the leg is often held upwards whilst the animal is walking. The operated leg performs movements about an angle of 30°–50° and with a frequency of about 4 Hz.

In our experiments a protraction was most often accompanied by a flexion in the

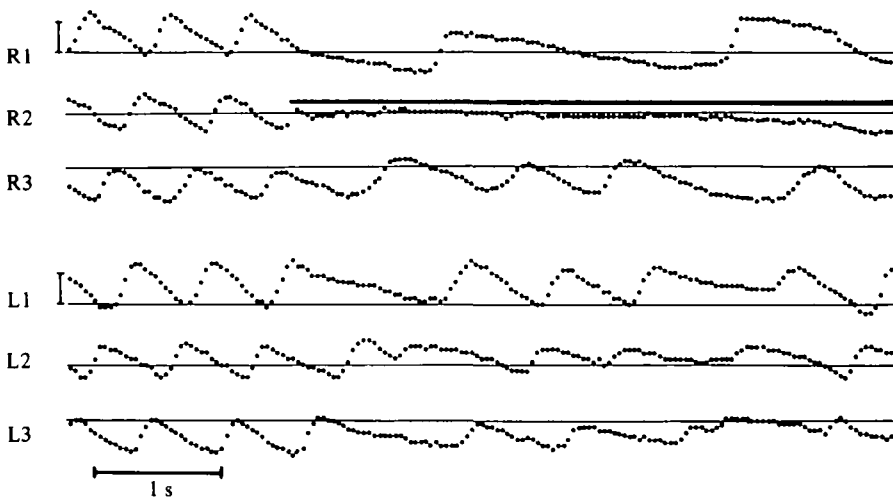


Fig. 1. Movement of the legs of an animal walking on a glass plate covered with silicon oil. The bar shows interruption of protraction of right middle leg. Position values are given for each leg separately and are related to position of the corresponding coxa (horizontal line). Vertical bar represents 20 mm. Upward deflection corresponds to protraction movement.

femur-tibia joint, but not by any obvious depression of the femur. Directly after the beginning of such an interruption of protraction the animal sometimes stopped walking and had to be stimulated by touching the abdomen in order to continue walking.

How does the interruption of protraction of one leg influence the AEP and PEP of the other legs? In six experimental series the extreme positions of each of the left legs were measured while protraction was interrupted in one of the five remaining legs, (Table 1). According to the criterion stated earlier (Methods), in only two cases could significant changes be seen. The PEP of L1 was shifted in the posterior direction when the protraction of L2 was interrupted and the same was true for L2 when the protraction of L3 was interrupted. No effects were found across the body when legs of the right side were interrupted. Also, no effects were found for the extreme positions of R2 when interrupting the protractions of L1 or the extreme position of R3 when interrupting L2. In most experiments with no significant difference one finds a very small, though consistent shift of both extreme positions in the posterior direction (mean value \pm S.D.: 0.7 ± 2.4 mm, $n = 6242$). This seems to be a general effect, possibly produced by the stronger stimulation of the animals during the experiment (see Methods).

When these experiments were performed with the animal walking on the glass plate, qualitatively similar results were obtained. This showed that the PEP of the leg was reached by active movement of the leg, not merely by passive traction produced by the other legs. However, as in this situation the legs were mechanically uncoupled, another effect was found here which could not be seen on the treadmill. As shown in Fig. 1, when the protraction of a middle leg was interrupted, the speed of the retraction movement of the ipsilateral front leg was strongly decreased. Stepping frequency was also reduced in the ipsilateral hind leg although not to the same extent. Qualitative observations of the phase relations between the legs showed that co-ordination of the

Table 2. Changes of AEP and PEP when (a) leg L₂ and L₃ and (b) L₃ is standing on a fixed platform

(Values are given in mm. Anterior direction is positive.)

	(a) L ₂ , L ₃	(b) L ₃
L ₁		
AEP	0.1 ± 1.1	0.0 ± 1.0
	149	178
PEP	-0.1 ± 3.4	-0.6 ± 2.7
	276	253
L ₂		
AEP	—	-0.4 ± 1.4
	—	295
PEP	—	-0.1 ± 3.0
	—	392

legs contralateral to the interrupted leg remained the same, though more irregularities occurred. No obvious co-ordination was found between the two front legs when protraction of a middle leg was interrupted. In one experiment in which a middle leg was amputated, interruption of protraction of the hind leg was accompanied by a rearward shift of PEP in the front leg.

Legs on a fixed platform

Similar experiments were carried out by interrupting the *retraction* of a leg. Such experiments could not, unfortunately, be performed with only a middle leg standing on the platform, since during the first few steps the hind leg also grasped the platform. Moreover, when the front leg stood on the platform the middle leg did not show normal walking behaviour, but instead performed searching movements in the direction of the platform. Therefore the experiments were performed with (a) both L₂ and L₃ and (b) L₃ alone on the platform. No changes of the extreme positions were found (Table 2).

Variation of the position of the platform relative to the body had no detectable influence.

Legs on a platform moved slowly backwards

One might argue that a leg standing on a fixed platform during a series of steps of the other legs cannot be considered as being in continuous 'retraction movement', but might be in some mode other than walking. Results of Cruse & Schmitz (1983) suggest that the leg standing on the fixed platform can be considered as being in walking mode. Nevertheless, to make the situation more natural, the platform was moved slowly in the posterior direction. This was done in the following experiments with each leg of the left side of the body. The leg was placed on a platform fixed to a micromanipulator which was moved backwards by hand, with a speed 5–10 times slower than the normal retraction speed of the leg. This was done while the other legs walked freely. No change occurred in the AEP of the manipulated legs (Table 3). The PEP, however, was shifted strongly in the anterior direction in front and middle legs. As the effect is less obvious in hind legs and as the values show considerable scatter, the distributions of the measured PEP values are shown and compared with those obtained from undisturbed animals (Fig. 2). The results show that

Table 3. *Change of AEP and PEP when the leg stands on a platform slowly moved backwards*

(Values are given in mm. Anterior direction is positive.)

	L1	L2	L3
AEP	-0.9 ± 1.4	0.2 ± 1.3	-2.4 ± 2.5
	100	101	101
PEP	6.4 ± 4.6	6.9 ± 4.5	3.3 ± 5.2
	98	102	152

the hind leg behaved differently from the others because it usually lifted off at the normal PEP. However, in a significant number of cases the hind leg also began protraction at a point well anterior to the control PEP, which rarely occurs in the freely walking hind leg. It should be mentioned that the average AEP in all legs was constant, therefore the amplitude of the protraction movement could be very small as a consequence of the large anterior displacement of the PEP.

Qualitative observations showed that the beginning of protraction occurred in approximately normal temporal coordination with other walking legs. This agrees with similar observations in *Extatosoma* larvae (Bässler, 1979). The experiment was repeated for the front leg but with the middle and hind legs standing on a fixed platform. Again the PEP of the front leg was shifted forward by 9.1 mm (s.d.: ± 6.5 mm, $n = 96$; 3 animals).

DISCUSSION

The results show that an interruption of the protraction of a leg produces a rearward shift of the PEP of the next anterior leg. Interruption during retraction has no effect on extreme positions of the other legs. When the retraction movement of a leg is slowed down no changes of its AEP are found but its PEP is shifted forward.

In free walking animals Bässler (1977) also found a backward shift of the PEP of the front leg when the middle leg was operated on so that it was continuously held upwards ('crossed receptor apodeme of femoral chordotonal organ'). Bässler (1972) in stick insects and Hughes (1957) in cockroaches found a backwards shift of PEP of front legs and also of middle legs when the corresponding posterior leg was amputated. Since in these earlier experiments the animals walked freely on a horizontal plane, one cannot exclude the possibility that these effects were produced by changes in the vertical load on the remaining walking legs. For the experiments presented here this interpretation is not possible, as the body of the animals is supported over a fixed treadmill or a glass plate. Changes in horizontal loading produced by walking with only five instead of six legs on the treadmill can also be excluded as the reason for the shift of the extreme positions, since the observed shifts are specific to the leg immediately anterior to the disturbed leg, while the loading effects are transmitted nonspecifically to all walking legs through the treadmill. The irrelevance of horizontal loading is even more obvious in the experiments on the glass plate, as here there was no mechanical coupling between the legs via the substrate.

We may conclude that the results found here are due to influences transmitted by central nervous connexions. As the results of Bässler (1972, 1977) mentioned above

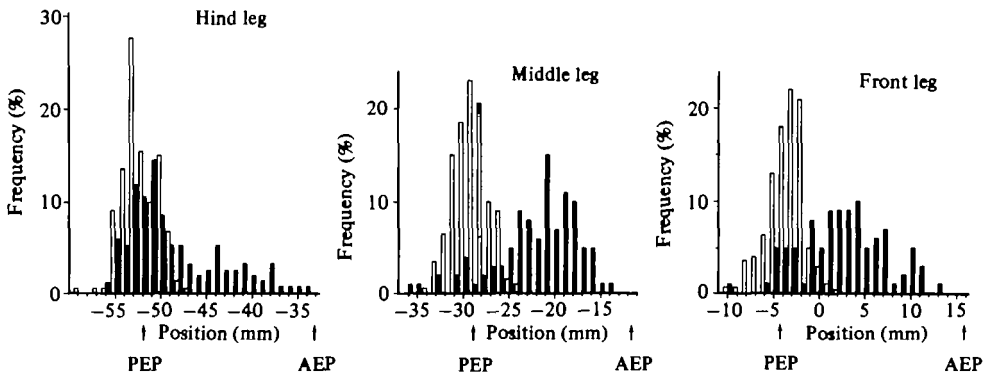


Fig. 2. Distribution of position of PEP when the leg is standing on the slowly moved platform (black columns) and of control (white columns). Mean values of PEP and AEP of the control are shown by arrows. Sample sizes: front leg 98 (control 297), middle leg 102 (control 200), hind leg 152 (control 220).

are similar to our results, it is quite possible that they are at least in part produced by the same influences. This agreement is particularly noteworthy for the crossed receptor apodeme experiment (Graham & Bässler, 1981), as in that case the leg is interpreted as being in continuous protraction.

The changes in ipsilateral leg stepping obtained by interrupting protraction are consistent with the findings of Dean & Wendler (1982) despite differences in experimental conditions and measurements. Dean & Wendler studied shorter protraction interruptions evoked by placing a fixed barrier in anterior parts of a leg's normal step range. Under these conditions, the blocked leg continued to make retractions in 1:1 co-ordination with the other legs. Nevertheless, these results show a small posterior shift in PEP of the anterior leg in parallel with the position of the barrier. We have found larger changes which may simply reflect the continuous interruption of protraction and the more posterior position of the blocked leg in our experiments. Differences in measurement technique – Dean and Wendler measured femur position instead of tarsus position – and in wheel geometry may also contribute to this magnitude difference.

Most of Dean and Wendler's analysis concerned timing changes contingent upon the interrupted protraction. They found that the start of protraction by an anterior ipsilateral leg is prolonged.

In our experiments the protraction of a leg elicited no changes in the AEP or PEP of the contralateral legs. Dean and Wendler did find evidence of a contralateral influence between the two rear legs affecting the timing of protraction. Our data did not include time as a parameter. In particular, we imposed a continuous interruption of protraction, so it is not meaningful to investigate contralateral phase relations.

What kind of nervous coupling might produce these effects? It is very difficult to obtain conclusions about a system consisting of six subsystems which could be coupled together in very different ways. The best we can do is to test certain hypotheses that have been proposed.

Wilson (1967) and Pearson & Iles (1973) published models postulating neural

connexions between two adjacent ipsilateral legs in cockroaches. Both models are based on the assumption that protraction of one leg prevents protraction of the neighbouring leg by means of symmetrical mutual inhibition. With this hypothesis one would expect the same influence upon all neighbouring ipsilateral legs when the protraction of a leg is interrupted. As this is not the case, these models cannot describe the results obtained for stick insects. However, the results agree with the asymmetric influences postulated in the model of Graham (1972, 1977), who assumes an influence inhibiting the beginning of protraction during a definite time after the posterior leg has started protracting. Such anteriorly directed inhibitory influences have also been demonstrated between hind and middle legs of the grasshopper *Neoconocephalus* (Graham, 1978).

Graham's hypothesis (1972, 1977) proposes an oscillator for each leg which starts protraction as soon as it has reached an internal (central oscillator model-COM) or position threshold value (peripheral oscillator model-POM). Ipsilateral co-ordinating influences are constructed so that the onset of protraction in a posterior leg starts a single-cycle 'delay oscillator' the output of which increases the threshold of the anterior leg (and so inhibits the start of protraction of this leg). In a well co-ordinated walk the PEP of the anterior leg corresponds to the position of the threshold value or possibly a value shifted slightly to the rear due to the effect of the delay oscillator. When in our experiments the protraction of the anterior leg is interrupted, the delay oscillator would be started only during the first step, but not in all following steps of the anterior leg. Graham proposes two alternative mechanisms for turning off the delay oscillator. In the COM configuration it is turned off after a fixed time interval. Therefore, according to this model, if the anterior leg does not change its retraction speed, it will begin each protraction after a time interval corresponding to the normal PEP or to a PEP which is shifted slightly forward. This is not in agreement with our results. In Graham's POM version the subsequent rearward movement of the posterior leg in the stance phase is assumed to turn off the delay oscillator by a position input similar to that proposed for initiating protraction. Our results are consistent with this latter hypothesis as in our experiments the delay would be in effect indefinitely, causing the PEP of the leg in front to move to the rear by an amount proportional to the magnitude of the change of threshold created by the delay oscillator. Taken together, the results of the protraction interruption experiments and the moving platform experiments demonstrate that the spatial position of the leg at which protraction is initiated can be greatly altered by peripheral factors while the phase of protraction relative to the other legs remains relatively constant. It is as if the PEP were dynamically changed so as to bring the leg into proper temporal co-ordination. This is consistent with the finding that the standard deviation of the AEP is significantly smaller than that of the PEP in front legs of free walking animals (Bässler, 1972), in front and middle legs of animals walking on a mercury surface (Graham & Cruse, 1981) and on the treadmill (Table 1). The results do not support the model of Wendler (1968, 1978), which assumes that in the unoperated animal the AEP and PEP of all legs are constant and co-ordination is achieved by changing the retraction speed of the legs individually.

The results obtained here are consistent with the hypothesis that the PEP is

Determined by a position-dependent threshold for protraction initiation. The threshold value could be increased (Table 1) or decreased (Table 3) by signals from other legs, as in the model of Cruse (1980*a, b*). However, a completely different interpretation is also possible. The results are consistent with the hypothesis that a command to start protraction is produced by a purely central system independent of the actual position of the leg. In view of the fact that a leg on a platform does not start protraction in the anterior range of movement, this hypothesis has to be expanded to include the assumption that the protraction command has no effect as long as the leg is in this anterior range. Forward shifting of the PEP (Table 3) would then occur because the leg is moved slowly on the platform and therefore the central command comes at a more anterior position. Backwards shifting of the PEP (Table 1) by interruption of protraction of the next posterior leg would be interpreted as resulting from a delay of several hundred milliseconds in the central command, induced by co-ordinating signals from the interrupted leg. According to this hypothesis, in a compound experiment in which the front leg rests on the slowly moved platform and, additionally the protraction of the ipsilateral middle leg is interrupted, the PEP of the front leg should remain in front of the PEP of the intact animal. This should be the case since, because of the very slow movement of the platform, during a time delay of some 100 ms the position of the leg is changed only by a small amount. The actual result of this experiment, however, was that the PEP lies behind even that of the intact animal (the difference amounts to $-6.3 (\pm 5.7)$ mm, $n = 100$, 5 animals). This contradicts the assumption that the change of the PEP produced by interrupted protraction of the posterior leg is produced by the delay of a centrally timed protraction command. However, it does not exclude the possibility of a centrally timed command as such. A temporal command might exist, but be suppressed by the influence of the interrupted protraction of the more posterior leg. The protraction of the leg would then occur when it had reached a geometrical position where it would automatically start protraction by itself, i.e. without co-ordinating signals from other legs.

We conclude that changing the PEP of a leg appears to be an important way to bring a leg in co-ordination with other legs. The results showed no significant influences on the AEP, in agreement with the earlier finding (Cruse 1979*a*) that the AEP is determined geometrically; i.e. that during protraction the tarsus of a leg moves to the position of the tarsus of the next anterior leg. Besides changing the extreme positions there are two other possible ways in which the phase of a leg could be influenced, namely, by changing the speed of protraction or of retraction. However, our results do not allow us to distinguish between these possibilities.

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