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The control of the anterior extreme position of the hindleg of a walking insect, *Carausius morosus*

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ABSTRACT. It is shown that the anterior extreme position of the hindleg of a walking insect is not fixed relative to the body but is determined by the position of the ipsilateral middleleg. This mechanism presumably helps the animal to find support for the hindleg when climbing on branches.

Introduction

In a walking insect it is not clear how the position of a leg is controlled relative to the body when the protraction (swing phase) stops and the retraction (stance phase) begins. Hitherto this has been examined only qualitatively and sense organs appear to play an important role in the control of the anterior extreme position. Wong & Pearson (1976) showed in cockroaches that removal of the trochanteral hair sensillae causes forward displacement of the anterior extreme position of the treated leg. In stick insects, Bässler (1972) found that the anterior extreme position can be changed when other legs are amputated, though this is possibly an effect of the changed load situation. However, the question is still open as to whether in intact animals the anterior extreme position is fixed relative to the body or whether it varies with the position of the other legs.

Methods

In the experiments described first the insects (adult female *Carausius morosus*) walked freely on a horizontal plane made from styrofoam. Perpendicular to the direction of walking a 15 mm wide ditch was made. In comparison, the mean step amplitude of these animals is 18 (SD ± 7.1) mm. Further detailed geometrical measurements on these animals are given by Cruse (1976). The number of animals used was seventeen.

In the second experiment the animal was fixed dorsally to a holder with the longitudinal axis of the body horizontal. The insect could move a styrofoam tread-wheel with the following properties: diameter 38.5 cm, breadth 9 mm, moment of inertia 720 g cm^2, friction 80 mg. The distance between the insect's body and the wheel was fixed. The number of animals used for this experiment was eight.

Results and Discussion

Earlier experiments in free walking animals (Cruse, 1976) showed that the mean distance between the posterior extreme position (PEP) of the front leg and the anterior extreme position (AEP) of the ipsilateral middleleg is 10 (SD ± 6.3) mm, and that the mean distance between the PEP of the middleleg and the AEP of the ipsilateral hindleg is 5 (± 7.1) mm. These measurements are averages, however, and one does not know what happens from step to step. As the anterior leg releases the ground and starts its protraction after the posterior leg has finished its protraction and found tarsal contact, the above observation led to the hypothesis that at least between middle- and hindlegs the following mechanism existed. (a) When finishing its protraction, the tarsus of the hindleg is put a few millimetres

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behind and outside the tarsus of the ipsilateral middleleg. (b) This could depend upon the actual position of the middleleg relative to the body, which would imply that the neuronal system controlling the movement of the hindleg obtains information upon the actual position of the middleleg tarsus. This mechanism would be sensible for an animal climbing in branches because without it the probability of stepping on to solid support would be much reduced (when walking on a flat plane no such problem would arise, of course). The first experiments to test the hypothesis were the following.

The stick insects were made to walk across a ditch 15 mm wide and so deep that the insects could not reach the ground with their legs. For each walk observed, whether a frontleg, middleleg or hindleg stepped into the ditch while trying to find tarsal contact was recorded. Qualitative observation showed that each leg which stepped into the ditch and therefore found no support made 'searching' movements until it found tarsal contact either at the front or the hind margin of the ditch. As the animal moves forward during the searching movements, most often the front margin was reached. The results showed that in the 455 walks investigated, the probability of stepping into the ditch decreased from front- to hindleg (per cent stepping in ditch—means ± SD): frontleg, 65.2 ± 2.2; middleleg, 47.7 ± 2.3; hindleg, 24.8 ± 2.0; no legs, 10.9 ± 1.5. Control experiments on a flat plane showed that all three legs stepped with about equal probability on to a defined 15 mm wide band on the plane: frontleg, 60.0 ± 3.3; middleleg, 56.0 ± 3.3; hindleg, 56.0 ± 3.3; n = 225 walks. Different optical marking of this band (black band on white plane or white band on black plane) showed no significant difference.

These results show that the frontleg steps into the ditch with the frequency to be expected from the control experiments. The middlelegs and, even more so, the hindlegs step significantly less often into the ditch. This result agrees with the hypothesis stated above that the hindleg moves forward to a point where the middleleg tarsus has found support. It also does not contradict the hypothesis that a corresponding mechanism exists between middle- and frontleg, as the difference between the values of frontleg and middleleg is smaller but still significant. The higher values obtained for the middlelegs could be explained by the result mentioned above (Cruse, 1976) that the difference between the setting points of front- and middleleg is larger and that therefore the middleleg is expected to step sometimes into the ditch although the frontleg has found the front margin of the ditch.

However, these results do not test the hypothesis that the neuronal system which controls the movement of the posterior leg obtains information upon the actual position of the tarsus of the anterior leg. It is possible, for example, that when walking over the ditch, although the anterior leg had to change its position in the beginning of the retraction phase because of the necessary searching movements, during the retraction this change is compensated in order to bring the PEP of the anterior leg to a position that is always constant relative to the body. With this mechanism the neuronal system of the posterior leg would not need any actual information upon the position of the tarsus of the anterior leg. However, such a mechanism is improbable as observation of free walking stick insects often indicates a considerable change of the PEP from step to step in all legs. The following experiment was therefore performed to test whether the neuronal system of the hindleg can obtain information on the position of the middleleg tarsus.

In these experiments, the stick insects were tested on the tread-wheel (Methods). An animal was fixed dorsally at the thorax with five legs free to move on the wheel, but with its right middleleg standing on a rigid horizontal platform placed beside the wheel so that the femur was held horizontal and perpendicular to the longitudinal body axis while the tibia was directed vertically downwards. The animal was then excited by gently touching the abdomen to start it walking. During the next protraction phase of the ipsilateral hindleg the animal put the tarsus of this hindleg on the platform beside the tarsus of the middleleg. The distance between the distal end of the tibia (which is geometrically better defined than the tarsus) of both legs was measured in the direction perpendicular (x) and parallel (y) to the longitudinal axis of the body. The values of x and y are defined as positive when the tarsus of the hindleg is distal and posterior to the tarsus of the middleleg. The mean values were $x = 2.5$ (SD ± 1.2) mm and $y = 3.2$ (±1.4) mm ($n = 245$).

This experiment was repeated for various positions of the middleleg relative to the body with the tarsus of the middleleg always remaining in the same horizontal plane. The position described in the above paragraph is defined as position 1, and the new positions are defined with reference to it as follows: position 2, with the distal end of the tibia moved 10 mm in the anterior direction from position 1; position 3, 10 mm posteriorly; position 4, 5 mm laterally; position 5, 5 mm medially. In Fig. 1 these positions are shown as closed circles in a coordinate system fixed relative to the body (viewed from above). The mean values of the points where the tarsus (distal end of the tibia) of the hindleg reached the platform are shown by crosses for the different positions. Table 1 gives the mean values of the differences (Δx and Δy) between the placing of the hindleg for test positions 2–5 and position 1. These values indicate that the position of the hindleg tarsus relative to the middleleg tarsus remained essentially constant even though the position of the middleleg relative to the body changed considerably. This is particularly apparent when one bears in mind that the measurements could only be made to about the nearest millimetre.

TABLE 1. Placing of the hindleg tarsus of a walking stick insect relative to the middleleg tarsus, for different placings of the latter (see text) (means ± SD)

Middleleg position	Difference from mean values of position 1 (mm)		
	Δx	Δy	n
2	0.9 ± 3.1	0.6 ± 1.7	80
3	−0.6 ± 1.8	0.6 ± 4.3	80
4	1.0 ± 2.9	−1.0 ± 2.4	147
5	−1.9 ± 1.7	0.3 ± 2.9	149

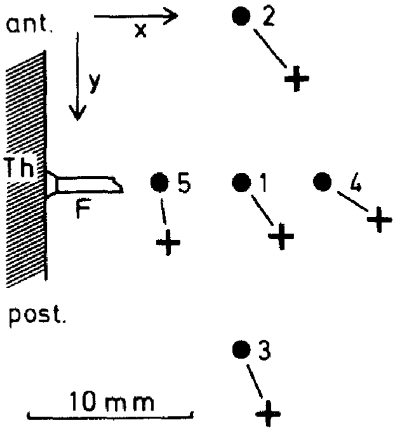

FIG. 1. The five test positions of the middleleg tarsus (circles) relative to the insect's thorax (Th) and the mean points, for each of these test positions, where the hindleg tarsus reached the platform (crosses), viewed from above. The proximal part of the femur of the middleleg is shown schematically (F). For further explanations see text.

This implies that the anterior extreme position of the hindleg is not fixed within a coordinate system relative to the body but is controlled by the position of the ipsilateral middleleg. Therefore the neuronal system controlling the movement of the hindleg must obtain information on the spatial position of the middleleg. As these results are not from free walking animals but from animals which are walking with five legs while one leg is standing still, this does not prove that this mechanism is also used in the free walking insect. However, because of the irregularity of the posterior extreme positions of the legs mentioned earlier, it is very probable that the animal also uses this mechanism when walking. In addition, Graham & Bässler (1979) have performed an experiment in which they operated on the apodeme of the femoral chordotonal organ of the middleleg in such a way that the CNS is informed that the femur–tibia joint is extended when it is flexed and vice versa. When such operated animals walk on a wheel the hindleg performs 'searching' movements in the direction where the middleleg tarsus would be found if the femoral chordotonal organ were reporting the correct information. This indicates that the mechanism investigated here is also present in the free-walking animal. It additionally shows that one sense organ from which the hindleg obtains information on the position of the middleleg tarsus is the femoral chordotonal organ of the middleleg. Finally, Graham (1979) has reported that in free walking, decerebrate stick insects, and in slow-stepping intact stick insects there is a tactile inter-segmental reflex which causes a posterior leg to make a short step to the rear if the upper surface of the leg in front is touched either by the posterior leg or by the experimenter. Such a reflex would be most appropriate for correcting errors in the 'close' placement of the posterior leg suggested in the present study.

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