

COUPLING MECHANISMS BETWEEN THE CONTRALATERAL LEGS OF A WALKING INSECT (*CARAUSIUS MOROSUS*)

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Summary

Interactions between contralateral legs of stick insects during walking were examined in the absence of mechanical coupling between the legs by studying animals walking on a horizontal plane covered with a thin film of silicone oil. Investigations of undisturbed walks showed that contralateral coupling is weaker than ipsilateral coupling. Two types of influence were found. (i) For each pair of front, middle and rear legs, when one leg started a retraction movement, the probability for the contralateral leg to start a protraction was increased. (ii) For front- and hind-leg pairs, it was found that the probability of starting a protraction in one leg was also increased, the farther the other leg was moved backwards during retraction. Whether such influences exist between middle legs could not be determined. Both 'excitatory' mechanisms very much resemble those influences which have been found to exist between ipsilateral legs. However, in contrast to ipsilateral legs, the interaction between two contralateral legs was found to act in both directions.

Introduction

In a previous paper (Cruse & Schwarze, 1988) interactions between ipsilateral legs of a walking stick insect were explored. Three different mechanisms were established which influence the start of the protraction: two elicit and one inhibits the start of protraction of the other leg. Two other mechanisms are also known. One influences the end of protraction, the so-called 'targeting' mechanism, and the other influences the motor output during retraction. This is called a 'coactivating' influence because it increases the motor output of one leg when the retraction movement of another leg meets an increased resistance to its movement.

Less information is available regarding the interactions between contralateral legs. Coactivating influences across the body have been shown to exist between the front legs and between the middle legs, but have not been found between the hind legs (Cruse & Saxler, 1980; Cruse, 1985). In the passive, non-walking animal,

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Graham & Wendler (1981) found a reflex synchronizing the retractor muscles in both hind legs. No corresponding effect was found in middle legs. It is, however, not known whether this reflex in passive animals corresponds to the coactivating influences found in walking animals.

Coactivating influences do not produce an alternating movement of the legs coupled in this way. Influences which produce alternating coordination between contralateral legs are of greater importance when considering the normal walking pattern, but information is available only from the following three results.

(a) Foth & Graham (1983) described an experiment in which stick insects walked on a double wheel so that the right legs were mechanically uncoupled from the left legs. When the right wheel was under higher friction, the left legs could walk with two or three times the frequency but were still coordinated with the legs on the right. The results clearly show that a coordinating mechanism exists. The retraction of a step is longer for that step during which a protraction of the other leg occurs. They interpreted this result as evidence for an inhibitory influence similar to that found between ipsilateral legs in an anterior direction (Graham, 1978; Dean & Wendler, 1982; Cruse & Epstein, 1982): a leg is inhibited in starting a protraction as long as the posterior leg performs a protraction. However, from the experiments of Foth & Graham it is not known which contralateral leg pairs are involved. Furthermore, another interpretation is also possible, as will be shown in the discussion.

(b) Dean & Wendler (1982) showed a contralateral effect which acts between hind legs but not between middle legs. They found the phase between both hind legs to be delayed when the protraction of one hind leg is prolonged. This might be interpreted as an inhibitory influence as described above. This should then lead to a shift of the posterior extreme position of one leg during the protraction of the other leg, as found in ipsilateral legs. However, for the two hind legs this is not found to be the case (Dean & Wendler, 1982; Cruse & Epstein, 1982). Thus, another interpretation might be required.

(c) Bässler *et al.* (1985) showed that in a preparation in which only the front legs are intact and both middle and hind legs are cut off, the front legs walk in an alternating way. This shows that a coordinating mechanism exists across the body which most probably directly links both front legs, but indirect coupling, e.g. *via* the mesothoracic ganglion, cannot be excluded. There is no information on the underlying mechanism.

The present paper was planned to investigate systematically the coordination of all three contralateral leg pairs in the stick insect, in the absence of mechanical coupling between legs, by studying animals walking on a thin film of silicone oil. The phase relationships between neighbouring legs have been described previously for stick insects walking continuously in an unrestrained fashion (Graham, 1972) or on a treadwheel (Graham, 1981). In these situations the animals walk very regularly and the distributions of phase values are narrow. In contrast, relatively irregular coordination can occur for walking on silicone, producing a broad distribution of phase values. In this case histograms and phase-response curves

(see below) might provide specific information on coupling mechanisms which are not available when considering only perfect coordination.

Materials and methods

All experiments were performed with adult female stick insects *Carausius morosus*. The animal was restrained ventrally on a balsa-wood holder by means of wire clamps. It walked on a horizontal Plexiglas plate covered with silicone oil (viscosity $1.6 \text{ cm}^2 \text{ s}^{-1}$, Merck type 550) to prevent mechanical coupling between the legs (Cruse & Epstein, 1982; Epstein & Graham, 1983). The distance between body and substrate was 8 mm. The movement of the legs was recorded using a video camera (Panasonic Type WV 1460) connected to an Apple II microcomputer. The system was developed by Godden & Graham (1983) and detects the intersection of the femur of each leg by scanning parallel to the longitudinal axis of the body. Two such scans, one for each side of the body, can be adjusted to a selected distance from the body.

For the evaluation of coordination, the recorded movements of all six legs were plotted on paper. A graphic tablet (Apple II) was used to select points on the movement traces of the legs for calculation of time intervals. The time intervals could be determined with an accuracy of ± 20 ms.

The system is well suited to measure the time of occurrence of several events which occur during the step cycle of a leg. The cyclic movement of a walking leg normally consists of a protraction and a retraction. Stick insects walking on a slippery surface often make pauses between the end of the retraction movement (EoR) and the beginning of the protraction movement, and also between the end of the protraction movement and the beginning of the following retraction movement (BoR) (Graham & Cruse, 1981; Epstein & Graham, 1983). These pauses will be called the posterior and anterior pauses, respectively. These pauses also exist in normal walking in locusts (Burns, 1973). Bässler (1972) defined the anterior and posterior extreme positions (AEP, PEP) which are normally used to describe the two sections of a step, namely protraction and retraction. In these experiments, temporal values rather than position are measured: the temporal occurrence of the anterior extreme position is here defined as corresponding to the end of the protraction movement (EoP) and the occurrence of the posterior extreme position as corresponding to the beginning of the protraction movement (BoP). Thus, four different points (BoP, EoP, BoR, EoR) can be distinguished within one step cycle (see Fig. 1).

The usual way of describing the coordination of two legs is to measure the phase of an event, for example the PEP in the cyclic movement of the test leg within the cycle of another (the reference leg). The beginning and end of this reference cycle are defined by the same events in the reference leg. A phase value of 0 or 1 means that both cycles are in phase, a phase value of 0.5 means the two cycles exactly alternate. An event used commonly for this purpose is the occurrence of the PEP, in temporal terms, the BoP. This kind of evaluation is well suited for obtaining

a good estimate of the mean value and the deviation of the phase between two legs and is therefore used throughout the literature. Results of investigations of ipsilateral coupling (Cruse & Schwarze, 1988) have shown that the phase of an event in the test leg other than that which defines the cycle of the reference leg might be even more interesting. Therefore, in the first type of evaluation the phase of the EoP of the test leg was measured in the cycle of the reference leg which runs from BoP to BoP.

More detailed information could be obtained from another type of evaluation. In this second evaluation the basic reference cycle is the same as above: it starts and ends at the BoP (the beginning of the protraction movement). The phase values of the three other points of the reference leg (EoP, BoR, EoR) and of all four values of the test leg are also recorded. This gives a series of 16 phase histograms which can be plotted for each pair of legs investigated. To save space and to allow easier comparison, with one exception (Fig. 7), only those histograms are shown where the reference cycle starts (and ends) with the BoP of the reference leg.

Results

The first evaluation included both ipsilateral and contralateral legs to allow a comparison. For each pair, one leg was used as reference leg. The EoP of the test leg within the period of the reference leg was recorded. The reference point (beginning and end of reference period) was the BoP of the reference leg. Thus any changes of the frequency of the EoP of the measured leg around the BoP of the reference leg could be demonstrated clearly. Fig. 1 shows these distributions for both ipsilateral pairs, namely middle and front leg as well as hind and middle leg. The frequency of EoP of the posterior leg decreased sharply before the beginning of the protraction in the reference leg so that overlapping of protractions of neighbouring legs occurred only rarely. This corresponds to the results shown in fig. 5 of Cruse & Schwarze (1988), where zones free of data points have a duration about twice that of protraction. However, the borders were not as sharp in the continuous walks described here.

The strength of coupling can be measured with the concentration parameter C (Graham, 1977; Clarac & Chasserat, 1983). The durations of protraction and retraction (which includes both pauses) of the reference leg and the concentration parameters are shown in Table 1. For ipsilateral pairs the value of C was higher than 0.55. Consideration of contralateral legs of the same segment (Fig. 2) shows that the coordination was less strong than that of ipsilateral neighbours ($C < 0.55$). This agrees with results of Graham (1977), Dean & Wendler (1982) and Foth & Bässler (1985). But clear differences can also be seen within different contralateral pairs. The concentration of contralateral coupling was good between the two front legs and between the two hind legs ($C > 0.5$) but was much worse between the two middle legs ($C < 0.4$). The latter had about the same deviation values as diagonally neighbouring legs (Fig. 3; Table 1). For comparison, in free-walking stick insect

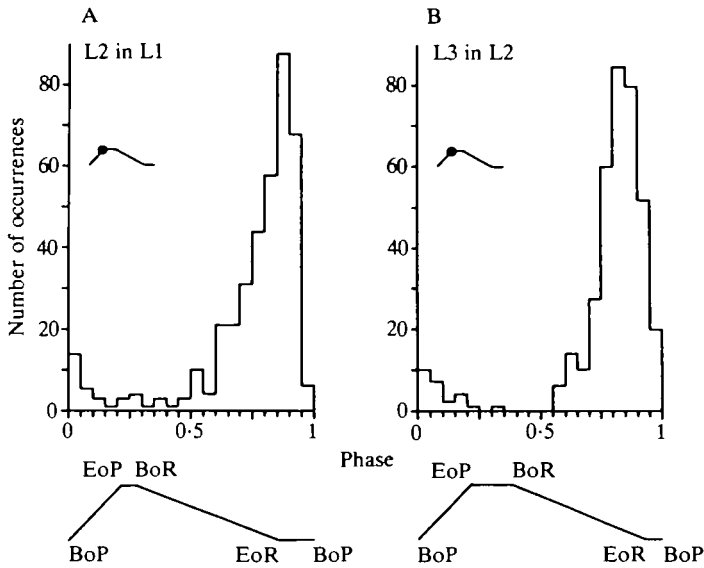


Fig. 1. Coordination between ipsilateral legs. Number of occurrences of the end of the protraction (EoP) of the test leg (see inset) in the cycle of the reference leg which runs from the beginning of the protraction (BoP) to the following BoP, as shown schematically below the abscissa. BoR, beginning of retraction; EoR, end of retraction. (A) Test leg is left middle leg (L2), reference leg is left front leg (L1). (B) Test leg is left hind leg (L3), reference leg is left middle leg (L2).

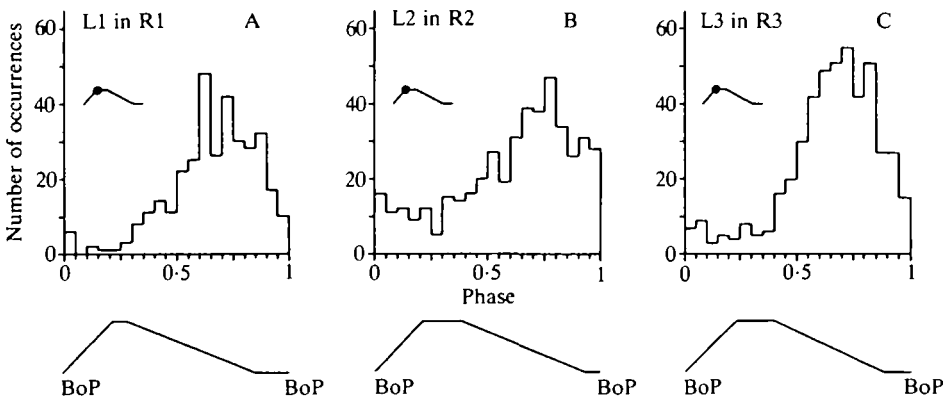


Fig. 2. Coordination between contralateral legs. Number of occurrences of the EoP of the test leg (see inset) in the cycle of the reference leg which runs from the BoP to the following BoP, as shown schematically below the abscissa. (A) Test leg is left front leg (L1), reference leg is right front leg (R1). (B) Test leg is left middle leg (L2), reference leg is right middle leg (R2). (C) Test leg is left hind leg (L3), reference leg is right hind leg (R3).

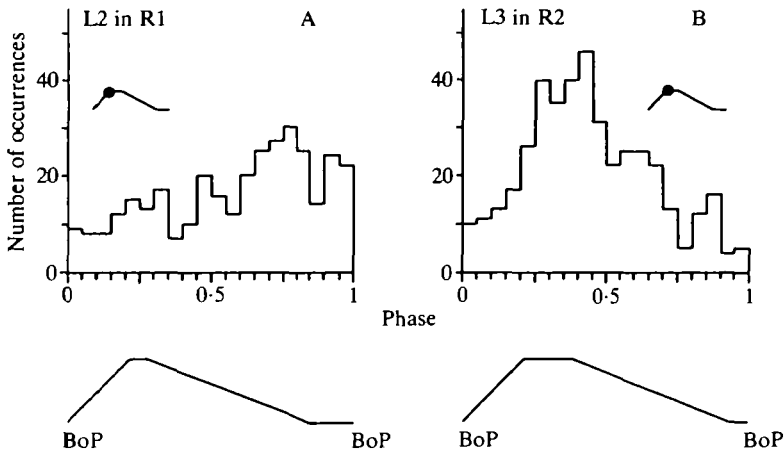


Fig. 3. Coordination between diagonally neighbouring contralateral legs. Number of occurrences of the EoP of the test leg (see inset) in the cycle of the reference leg which runs from the BoP to the following BoP, as shown schematically below the abscissa. (A) Test leg is left middle leg (L2), reference leg is right front leg (R1). (B) Test leg is left hind leg (L3), reference leg is right middle leg (R2).

the concentration parameter C lies between 0.88 and 0.95 for adjacent ipsilateral legs and between 0.88 and 0.83 for contralateral legs (Graham, 1977, 1981).

To concentrate on the coupling between contralateral legs, the second type of evaluation was used, so the occurrence of four different events (BoP, EoP, BoR, EoR, see Materials and methods) was recorded. This evaluation also included additional walks with more irregular steps (producing smaller values of concentration parameters). These walks could include curve walking and 2:1 coordination between right and left legs. In the latter cases legs used as reference were always those which walked with the lower frequency. This was done to obtain a distribution of phase values as broad as possible. The evaluation was restricted to the steps of walks which consisted of at least 10 consecutive steps. Figs 4, 5 and 6 show the results for front, middle and hind legs, respectively. In all cases the reference period runs from BoP to BoP. Part A of each figure presents, in the usual way, the number of occurrences of the BoP of the test leg. Part B presents the number of occurrences of the EoP of the test leg and, thus, corresponds to the presentation of Figs 1, 2 and 3. Part C shows the number of occurrences of the beginning of the retraction (BoR) and part D of the end of the retraction (EoR) of the test leg. Comparison of the concentration parameters again shows that the coordination between middle legs was worse than that between front legs or between hind legs. Qualitative inspection shows that the form of the distributions could be quite different (see e.g. Fig. 4A and 4C). Thus, rather than use the concentration parameter alone as a measure for comparing the histograms, direct comparison of the data is more appropriate. When considering the results in detail, the most obvious difference was found between data shown in Fig. 4C and

Table 1. *The duration of protraction and retraction (including both pauses) of the reference leg (mean \pm s.d.) and the concentration parameters C of the distributions of the beginning of protraction (BoP) and the end of protraction (EoP) of the measured leg*

| Test leg in reference leg | Protraction (ms) | Retraction (ms) | N | | C |
|--|------------------|-----------------|-----|-----|------|
| Ipsilateral leg pairs | | | | | |
| R2 in R1 | 156 \pm 47 | 529 \pm 162 | 438 | BoP | 0.57 |
| | | | | EoP | 0.71 |
| R3 in R2 | 150 \pm 44 | 599 \pm 161 | 561 | BoP | 0.60 |
| | | | | EoP | 0.70 |
| L2 in L1 | 139 \pm 37 | 397 \pm 113 | 389 | BoP | 0.56 |
| | | | | EoP | 0.70 |
| L3 in L2 | 141 \pm 36 | 477 \pm 116 | 379 | BoP | 0.70 |
| | | | | EoP | 0.80 |
| Contralateral leg pairs of the same segment | | | | | |
| L1 in R1 | 138 \pm 40 | 584 \pm 194 | 418 | BoP | 0.52 |
| | | | | EoP | 0.53 |
| L2 in R2 | 134 \pm 39 | 581 \pm 173 | 450 | BoP | 0.31 |
| | | | | EoP | 0.32 |
| L3 in R3 | 153 \pm 47 | 581 \pm 163 | 472 | BoP | 0.53 |
| | | | | EoP | 0.52 |
| Contralateral, diagonally neighbouring leg pairs | | | | | |
| L2 in R1 | 140 \pm 37 | 583 \pm 178 | 334 | BoP | 0.21 |
| | | | | EoP | 0.27 |
| L3 in R2 | 146 \pm 36 | 576 \pm 153 | 418 | BoP | 0.34 |
| | | | | EoP | 0.37 |

Some of the distributions are shown in the Figs 1, 2 and 3.
Data are from four animals.

those in Fig. 6C. For the front legs (Fig. 4C) there was a range of phase values from 0.10 to 0.30 where only a few starts of the retraction of the test leg can be observed. At all other phase values the starts appeared with a higher probability. In contrast, in the hind leg a high probability of protraction starts occurred in a small range from 0.8 to 0.1 (note that because of the cyclic nature of phase data in the figure this interval is divided into two, one from 0.8 to 1.0 and the other from 0.0 to 0.1). All other phase values were possible but occurred with a lower probability. This means that in the hind leg there was a high probability of starting the protraction movement at that time when the other hind leg had just begun a retraction movement. In the front legs the phase range of a highly probable retraction start (BoR) was much broader and could be bimodal (Fig. 4C). Again, there was a peak at phase values of 0 or 1 but there seemed to be another broader

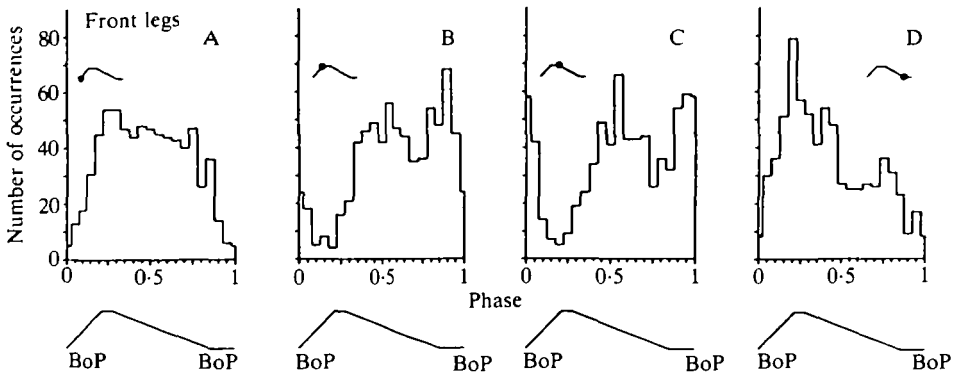


Fig. 4. Coordination between the front legs. Number of occurrences of four different events in the test leg measured in the cycle of the reference leg which runs from the BoP to the following BoP, as shown schematically below the abscissa. These events are (A) the beginning of protraction (BoP), (B) the end of protraction (EoP), (C) the beginning of retraction (BoR) and (D) the end of retraction (EoR). These events are indicated schematically as dots in the inset figures.

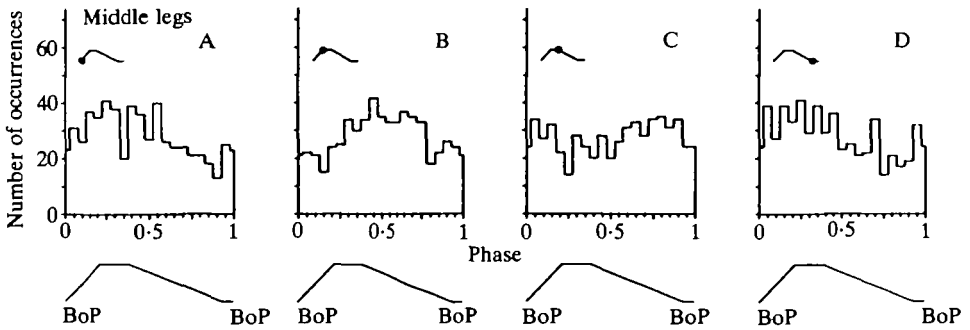


Fig. 5. Coordination between middle legs. Presentation as in Fig. 4.

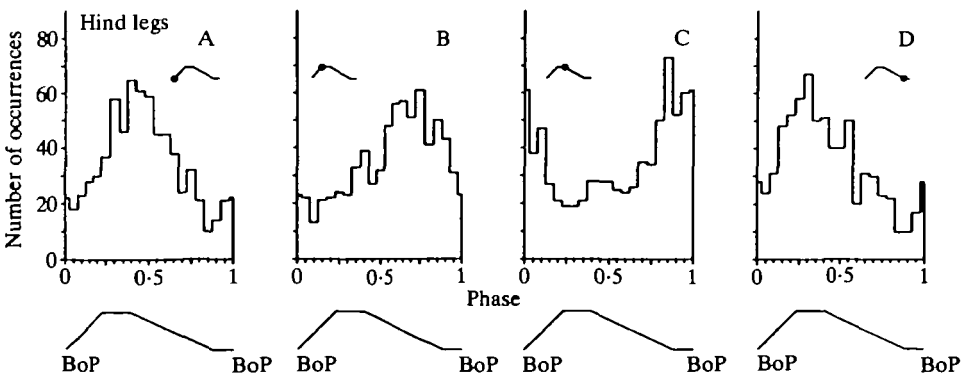


Fig. 6. Coordination between hind legs. Presentation as in Fig. 4.

Table 2. *The duration of the different parts of a step as a percentage of the duration of the whole step*

| | Protraction (%) | Anterior pause (%) | Retraction (%) | Posterior pause (%) |
|------------|-----------------|--------------------|----------------|---------------------|
| Front leg | 21.2 ± 8.5 | 6.5 ± 6.3 | 57.3 ± 17.0 | 15.2 ± 15.0 |
| Middle leg | 21.5 ± 6.7 | 17.0 ± 18.3 | 55.0 ± 18.6 | 6.6 ± 5.5 |
| Hind leg | 23.4 ± 9.8 | 16.6 ± 11.7 | 47.7 ± 19.6 | 12.9 ± 10.9 |

Values are means ± s.d.

maximum at about 0.6. In agreement with the results shown in Fig. 2, only weak coordination was found in middle legs.

To obtain further information, so-called phase-response curves were plotted to find out whether different parts of the step of the test leg showed a dependency on their phase within the step of the reference leg. According to the four different points measured within a step, the step is divided in four different parts and here the durations of each are measured. These parts are the protraction, the retraction and two 'pauses', the anterior pause and the posterior pause. The corresponding mean values are shown in Table 2. In the middle leg no dependency on phase was found in any case. For front and hind legs neither the duration of the pauses nor that of the protractions showed a significant dependency, but the duration of the retractions did. In Fig. 7 phase-response curves are shown for the front, middle and hind legs. In contrast to the abscissae used in Figs 4, 5 and 6, here phase zero corresponds to the beginning of retraction of the reference leg, as indicated below the abscissa. The right ordinate gives the duration of retraction, i.e. the interval between BoR and EoR of the test leg as a fraction of step period. This is plotted at the phase values which correspond to the end of the retraction. The results show that for front and hind legs the retraction duration of the test leg decreased in parallel with the retraction movement of the reference leg. Furthermore, the figures include the corresponding histograms showing the number of occurrences of EoR (left ordinate). It is most obvious for middle legs and less clear for hind legs that the greatest occurrences of EoR were found shortly before the beginning of retraction in the reference leg. This means that for these steps, taking into account the duration of the posterior pause, the beginning of retraction of the reference leg and the beginning of protraction of the test leg occurred at about the same time.

Discussion

Investigating the strength of coupling in weakly coordinated but continuously walking animals should give insight into the coupling mechanisms between different pairs of legs. The results show that ipsilateral coupling is stronger than contralateral coupling (see also Graham, 1977; Dean & Wendler, 1982; Foth & Bässler, 1985). Differences were also observed between different contralateral

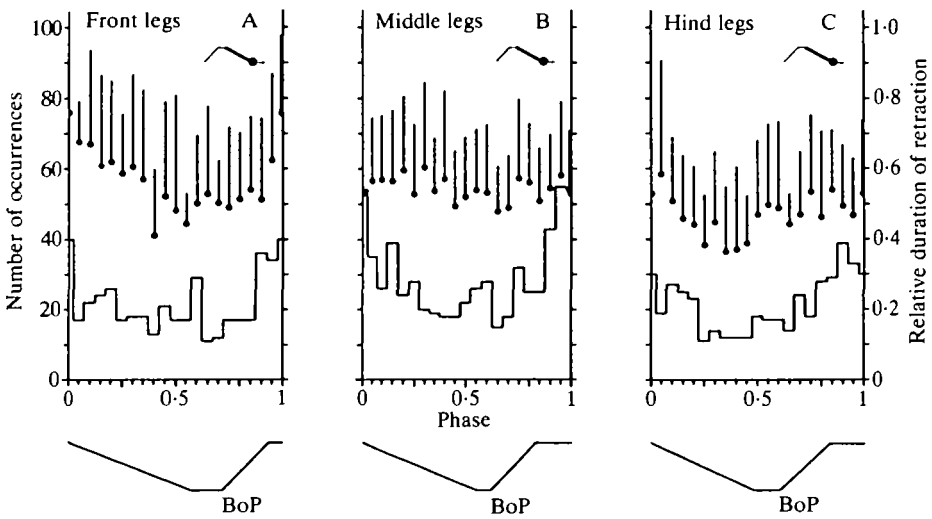


Fig. 7. Coordination between (A) front legs, (B) middle legs and (C) hind legs. The histograms (columns, left ordinates) show the number of occurrences of the end of retraction of the test leg (see inset figures) in the cycle of the reference leg which runs from the beginning of retraction to the beginning of the following retraction, as shown schematically below the abscissa. The phase-response curves (dots, right ordinates) show the duration of retraction of the test leg as a fraction of step period. As for the histograms, the end of the retraction of the test leg is chosen as a reference value. The vertical bars show the standard deviation, which are plotted in only one direction for the sake of clarity.

pairs. Both front legs are about as well coordinated as both hind legs. However, both middle legs are as badly coordinated as diagonally neighbouring legs. The possibility of coupling mechanisms that might exist between the middle legs will be discussed later. The weak coordination found for middle legs, however, simplifies the discussion of the coupling mechanisms between front legs and between hind legs. Coordination between these two pairs cannot result from indirect coupling *via* the middle legs but must result from contralateral mechanisms which exist directly between the two front legs or between the two hind legs.

When interpreting these results in terms of the nature of the coupling mechanisms, two restrictions have to be made. (i) As will be discussed for the example of the middle leg, existing coordinating mechanisms might be masked and not be detected when other interactions, in this case the ipsilateral mechanisms, are relatively strong. Thus only the existence, not the non-existence, of a mechanism can be shown in this way. (ii) As quite irregular walking is investigated here it is possible that coordinating mechanisms appear in this investigation which in a more regular, straight walk might play a minor role but may be important when walking over irregular surfaces or during turning. With these restrictions in mind the results can be interpreted in the following way. Fig. 6C shows that there is a high probability for the hind leg to start a protraction movement directly after

the other hind leg has started a retraction movement. This indicates that an 'excitatory' influence between the hind legs exists which is similar to that described between ipsilateral legs in an anterior direction (see fig. 4 in Cruse & Schwarze, 1988). In the front legs the same maximum can be found and might be explained as a result of a corresponding mechanism acting between front legs. This means that in both front and hind legs the start of the retraction of one leg can elicit the start of protraction in the other leg. This is also supported by the histograms shown in Fig. 7A,C. The EoR of the test leg occurs with higher probability shortly before the BoR of the reference leg. This means that when taking into account the duration of the posterior pause (see sketch below the abscissa and Table 2), the BoP of the test leg occurs directly at or shortly after the BoR of the reference leg. In front legs there is also another, broader maximum in the phase range 0.4–0.7. The existence of this maximum does not require the assumption of another coordinating mechanism, but can be interpreted as resulting from the same mechanism acting in the opposite direction, i.e. by the simple assumption that this mechanism can act mutually between the two front legs. Following this interpretation, the second maximum in Fig. 4C between 0.85 and 1.0 occurs because the BoR of the test leg elicits a BoP in the reference leg. The first, broader maximum might have occurred because the BoR of the reference leg (which appears at a phase value of about 0.28, i.e. the duration of protraction plus anterior pause) elicits a BoP in the test leg. This would lead to a BoR in the test leg at about another 0.28 units later, i.e. around a phase value of 0.56 in Fig. 4C. The same mechanism might exist in the hind leg. Here a corresponding, but very flat, second maximum might be recognized in Fig. 6C. Because of the larger scatter of the duration of protraction and anterior pause in the hind leg the values are more distributed and, therefore, this effect might be seen less clearly.

The results indicate that coupling between the front legs and between the hind legs occurs by means of an excitatory influence such that the start of the retraction in one leg increases the probability of the start of a protraction in the contralateral leg. According to our present knowledge, this excitatory influence corresponds to that found between ipsilateral legs in the anterior direction with the essential difference that the ipsilateral mechanism was not found to act in both directions.

This excitatory influence could not explain the results of Foth & Graham (1983) (see Introduction). By loading the left and the right legs differently, the right legs could be made to walk with double the step frequency compared to the left legs. In this case right leg steps that included a protraction of the left leg were shown to be somewhat longer than those right leg steps which did not include the left leg protraction. We could confirm this result for one animal which walked with 2:1 coordination and could, therefore, be evaluated in this way. This was interpreted by Foth & Graham as resulting from an inhibitory coupling which does not allow one leg, e.g. the right leg, to begin a protraction as long as the other leg is protracting. This mechanism would prolong the step of the right leg until the left leg has finished its protraction (Fig. 8A). However, as an alternative hypothesis, another coupling mechanism might exist which could produce a corresponding

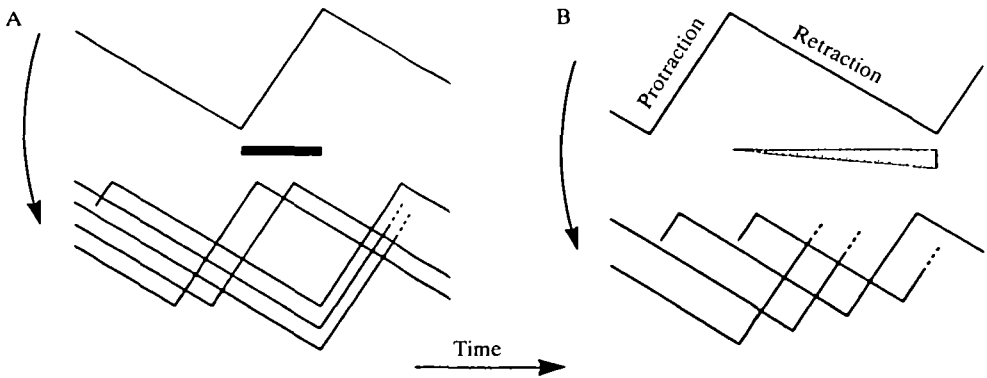


Fig. 8. Diagram showing the effect of two different coordinating mechanisms on the duration of the retraction of the influenced leg. (A) The start of protraction of the influenced leg (lower trace) is inhibited when the influencing leg (upper trace) performs a protraction (black bar). (B) The start of protraction of the influenced leg is more excited, the farther the influencing leg has moved backwards during its retraction (wedge).

effect. This mechanism is most similar to that found to act between a leg and its ipsilateral posterior neighbour. For ipsilateral legs it was shown (Fig. 8B) that the farther the position of a leg has moved backwards during the retraction, the earlier the posterior leg is excited to start a protraction (Dean & Wendler, 1983; Cruse & Schwarze, 1988). When the same mechanism exists between contralateral legs which walk with a 2:1 coordination then, assuming that the right leg steps faster, this mechanism would produce the following result. The right leg step not including the left leg protraction occurs late within the retraction of the left leg. Therefore this hypothetical excitatory influence would be strong and produce a relatively early stop of this right leg retraction. The right leg step including the left leg protraction has its BoP quite early in the left leg retraction. In this case the excitatory influence from the left leg would be weak and this would produce a longer duration of this right leg step. Thus the coupling mechanism described here could also describe the effects found by Foth & Graham. How is it possible to distinguish between these hypotheses? According to the hypothesis of an inhibitory mechanism, the duration of the retraction of the test leg should be constant for all phase values except for those retractions that are finished directly after the end of protraction of the reference leg (Fig. 8A). Following the hypothesis of the excitatory mechanism, the retraction duration of the test leg should be long when ending at the beginning of the retraction but should become shorter the farther the reference leg has moved backwards during retraction (Fig. 8B). As can be seen in the phase-response curves of Fig. 7 for the front legs (less obvious for hind legs), the results agree better with the hypothesis of an excitatory mechanism. Thus, the data show that the excitatory mechanism exists but so far they do not exclude the possibility that the inhibitory mechanism exists in addition. The latter assumption is not in agreement with the results of Cruse &

Epstein (1982). Effects of such inhibitory mechanisms between ipsilateral legs have been found in the experiments of Cruse & Epstein (1982) but the same experiments with contralateral legs did not show corresponding effects. This agrees with the result of Dean & Wendler (1982). As mentioned in the Introduction, the experimental prolongation of the protraction of one hind leg produced a phase delay in the other hind leg but did not show a shift in the posterior extreme position. The latter should have been produced if an inhibitory coupling existed. However, the results can be explained by the assumption of the excitatory mechanism discussed earlier, namely that the start of retraction increases the probability of the other leg starting protraction. Thus, all the results are in agreement with the interpretation that coupling between front and between hind legs occurs in two ways. (a) When one leg starts retraction, this can elicit the start of a protraction in the contralateral neighbour. (b) The protraction can be started by an excitatory influence produced during the retraction of the neighbouring leg. This influence increases its strength when the leg moves backwards.

On the basis of the results shown in the histograms of Figs 2 and 5, two interpretations are possible considering direct coupling influences between middle legs. There might be no (or very weak) direct coupling between the two middle legs. In this case the coordination found is based on indirect coupling involving ipsilateral mechanisms and the pathways connecting the front legs or the hind legs. Alternatively, the middle legs might be coupled in a similar way to the front or the hind legs. Because of the relatively strong ipsilateral influences, a middle leg in a weakly coordinated walk might obtain contradictory influences from its ipsilateral front and hind leg. Therefore, coordination between both middle legs might be disrupted by means of the influence from front and hind legs. The histograms of Fig. 7 show obvious high frequencies at phase values between about 0.9 and 1.0 for all three leg pairs. This agrees well with the excitatory influence discussed above for front and hind legs, because the start of retraction in one leg, here the reference leg, elicits the start of protraction in the other leg, thereby interrupting a retraction at this point. This effect becomes more obvious when the reference cycle is chosen to start with the beginning of retraction, as shown in Fig. 7. As the same result is found in middle legs, this shows the existence of a corresponding direct influence between middle legs.

The coordinating mechanism which at the start of retraction elicits a protraction in the other leg caused the maximum in Fig. 4C at phase values between 0.85 and 1.0. The second maximum occurring between phase values of 0.4 and 0.7 was assumed earlier to be produced by the same effect acting between the two legs in the opposite direction. This mutual coupling was also shown by the evaluations mentioned earlier using other reference periods than those shown in Figs 1–6. As in a leg the start of the protraction is not in exact antiphase with the start of retraction, this mutual effect between neighbouring legs cannot produce a stable symmetrical pattern of coordination between these legs. Rather, one can assume that either one or the other leg plays a dominant role. It was shown by Foth & Graham (1983) that such a dominance exists and can be influenced experimentally

by allowing the left and right legs to walk under different friction. Those legs which were less loaded and, therefore, walked faster appeared to be the dominating ones.

Coordination between diagonally neighbouring legs is of the same order of magnitude as the coordination between middle legs (Table 1). Thus, as discussed above for the middle legs, a direct coupling between diagonally neighbouring legs does not seem to play a significant role. This is in contrast to the assumption proposed in a model calculation by Cruse (1980) for a simulation of the tetrapod gait (Graham, 1972). Direct diagonal coupling might also have been implicitly assumed as an explanation for the coordination of the tripod gait.

As mentioned in the Results, the pauses show no dependence on the phase. The mean durations differ for anterior and posterior pauses and for the different legs (Table 2). One reason for this difference might be the following. Because the front, middle and hind legs attach to the body at different angles, the velocity of the femur point measured by the video system (see Materials and methods) changes during the retraction, even for a constant angular velocity of the leg. In addition, the limited resolution of the recording system may make a pause appear longer if the retraction near the pause is slow. Therefore, the measured pause durations might be biased in different ways for each leg.

Taken together, apart from the coactivating influences mentioned in the Introduction, two types of excitatory influences are found to coordinate contralateral legs. In all legs the protraction of a leg can be elicited at the beginning of the retraction of the contralateral neighbouring leg. Furthermore, in front and hind legs the protraction can be elicited during the retraction of the contralateral leg and the effect is stronger the farther the leg has retracted. Such a mechanism might also exist between middle legs but could not be shown here. However, as is particularly obvious for the middle legs, the effects of these coupling mechanisms are masked by the effects of ipsilateral coupling mechanisms which are shown to be stronger. We assume that these coupling mechanisms should not be considered to work in the sense of a switch-like on-or-off manner but rather in such a way as to increase or decrease the probability of occurrence of an event, for example the start of a protraction.

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