

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

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Summary

The mechanisms by which the legs of a stick insect influence one another during walking were investigated by running the animals on a horizontal plane covered with a thin film of silicone oil to prevent mechanical coupling between the legs. Coupling between ipsilateral legs was investigated by interrupting the retraction (power stroke) of a leg for a short time and observing how the legs return to normal coordination following this disturbance.

The results show that three ipsilateral coupling mechanisms exist: (a) a forward-directed influence that inhibits the start of a protraction of the leg as long as the posterior leg is performing a protraction; (b) a forward-directed influence that excites the start of a protraction of the leg when the posterior leg starts a retraction movement; (c) a backward-directed influence that excites the start of a protraction, the influence being stronger the further the anterior leg has moved backwards during its retraction. The latter influence depends on the position but not the phase of the anterior leg.

Introduction

The legs of a walking animal have to be properly coordinated to produce a gait which moves the animal forward and prevents it from falling. In this work we examined the nature of those mechanisms which provide the coordination between ipsilateral walking legs. Probably the most investigated animal in this respect is the stick insect and several coordinating mechanisms have been proposed.

During forward walking, the rhythmic movement of each leg consists of a sequence of leg retraction during the power stroke (or stance phase) followed by leg protraction during the return stroke (or swing phase). Most of the coordinating mechanisms are assumed to act on the beginning of the protraction. A rostrally directed influence which inhibits the beginning of the protraction of a leg as long as the next posterior leg is performing protraction was first established experimentally for the grasshopper *Neoconocephalus* (Graham, 1978). It was later shown to exist between hind and middle legs and between middle and front legs in the stick

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insect *Carausius morosus* (Dean & Wendler, 1982; Cruse & Epstein, 1982; Foth & Bässler, 1985*b*). The demonstration of the existence of caudally directed influences follows indirectly from the experimental results of Cruse & Saxler (1980*b*). Dean & Wendler (1983) showed that the position of a fixed middle leg influences the movement of the walking hind leg. Caudally directed influences in animals walking with all legs have been shown to exist (Bässler & Wegner, 1983; Foth & Bässler, 1985*a*); they are implied in the results of Foth & Bässler (1985*b*). Other mechanisms influence the position at the end of protraction (Cruse, 1979*a*; Dean & Wendler, 1983), depending on the position of the next anterior leg ('targeting'), or act during the retraction to increase the motor output when a leg is under load (Pearson, 1972, for the cockroach; Bässler, 1979; Cruse & Saxler, 1980*a*; Cruse, 1985*a*, for the stick insect). The latter were called 'coactivating' influences.

Although a number of coordinating mechanisms are known, further investigation of this system is necessary because (i) the nature of these mechanisms is not known in detail and (ii) it is possible that additional influences exist. A fruitful method for investigating the coupling mechanisms between rhythmically oscillating systems is to move the oscillators out of their normal phase relationship and then observe how normal coordination is re-established. This method, applied by Cruse & Müller (1986) to the crayfish, is adapted here to investigate the coupling mechanisms between the ipsilateral legs of stick insects. The former results were confirmed, some mechanisms are described in more detail and a new mechanism is presented. The variability in the step data is increased compared with the results of Graham (1972, 1977, 1981) and Foth & Bässler (1985*a*), and nearly all possible phase values can be experimentally produced. Thus coupling effects which might not be recognizable when considering only 'normal' phase values may be uncovered by this method.

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. The distance between body and walking surface was 8 mm. The animal walked on a horizontal Plexiglas plate covered with silicone oil (viscosity 1.6 St (=cm² s⁻¹), Merck type 550) to prevent mechanical coupling between the legs (Cruse & Epstein, 1982; Epstein & Graham, 1983). The movement of the legs was recorded using a video camera (Panasonic type WV 1460) connected to an Apple II microcomputer. The system has been described by Godden & Graham (1983) and detects the intersection of the femur of each leg with a line parallel to the longitudinal axis of the body. Two such lines, one for each side of the body, can be adjusted at a suitable distance to the body. The sampling line for measuring the position of the right legs is represented by a vertical dashed line in Fig. 1. This recording system does not measure the absolute position of the tarsus or the exact value of the angle between body and femur. It provides a value for the position of the leg which we call femur position. This is measured in length units (femur

position units, FPU) relative to an arbitrary but fixed point which, in the presentation of Fig. 1, would correspond to a horizontal baseline. The system is well suited to measure the time of occurrence of several events which occur during the step of a leg, such as the anterior extreme position (AEP), which corresponds to the end of the protraction movement, and the posterior extreme position (PEP), which corresponds to the start of the protraction movement. AEP and PEP are defined by Bässler (1972) as tarsus position. To avoid confusion, it should be stressed that with our method the time, but not the exact position, of the AEP or PEP can be measured.

Leg movements were interrupted by inserting a vertically oriented wire behind the femur of a leg and so preventing it from continuing a normal rearward movement. The wire was fixed in a holder to allow reproducible interruptions at constant positions. The leg was stopped for varying intervals (100–2000 ms). Then the wire was removed upwards so that the leg could continue its step. Before the next stimulus was applied the animal had to walk at least 10 normal steps.

For the evaluation of how the legs again reached normal coordination, the recorded movements of either all six legs or the three ipsilateral legs were plotted (Fig. 1). A graphic tablet (Apple II) was used to record selected points of the movement traces of the legs and calculate the relevant time intervals and position values. Time intervals could be determined within ± 20 ms.

Measurements of time intervals are given in absolute values (ms) in one case (Fig. 5) and in relative units (RU) for all other cases. The latter are obtained by dividing the measured interval by the value of the step period of the first step of the middle leg. This allows us to present the data independently of the actual period length (i.e. the walking speed), which differed considerably. The mean value (\pm s.d.) of the duration of this step was 958 ± 208 ms (minimum 520 ms, maximum 1580 ms).

The results show that during the interruption of a leg movement the neighbouring leg acted in two ways: it either performed the same total number of steps as the hindered leg, i.e. it performed only one step when the hindered leg made one step (this is called a single step) or, sometimes, the free leg performed two steps when the hindered leg made one step (this is called a double step). The durations of different steps or parts of a step were measured and compared. For simplicity, the steps were numbered as follows. In the example of Fig. 1 the retraction of the middle leg is interrupted. The front leg makes a double step and the hind leg a single step during the interrupted step of the middle leg. A step is defined here as beginning with a protraction. The step of each leg before the interruption is called step 1. Due to the non-zero phase between neighbouring legs step 1 of the front leg starts some time after that of the middle leg and this follows that of the hind leg. The step in which one leg, either the hind or the middle leg in our experiments, is interrupted is called step 2. If a double step occurs in a neighbouring leg, the first is called 2a, the second 2b. As mentioned, such a double step can occur in any of the neighbouring legs, not only in the front leg as shown in the scheme of Fig. 1. Finally, the step following the interrupted step is called step 3 in all ipsilateral legs.

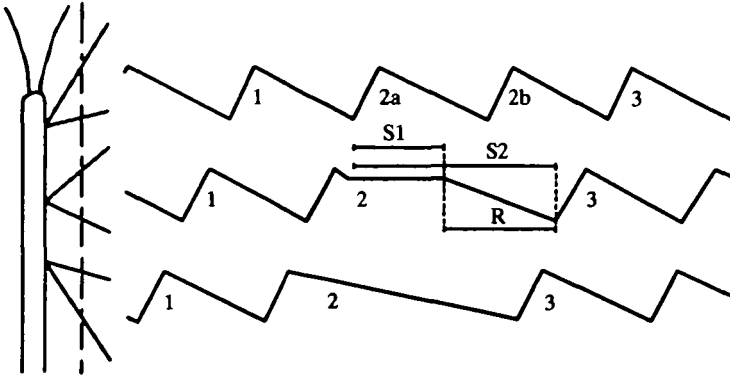


Fig. 1. Schematic drawing of a step pattern. The left-hand side shows a stick insect seen from above. The interrupted line represents the sampling line of the system measuring the femur position. The right-hand side shows some steps measured by this system. In this example the retraction of a middle leg (step 2) is interrupted. If a double step occurs in a neighbouring leg, as shown here for the front leg, these two steps are called step 2a and step 2b. Furthermore, the parameters S1, S2 and R are presented. For further explanations see the text.

Two measurements, S1 and S2, are used to represent the duration of the interruption. Both start at the occurrence of the PEP of the leg in front of the interrupted leg. S1 ends when the interrupted leg starts its retraction movement again. S2 ends when this retraction movement is finished, i.e. at the PEP of the interrupted retraction. The duration of this retraction part is called R, so $S2 = S1 + R$ (Fig. 1). S1 is better suited to describe events associated with the end of the interruption, whereas S2 is better suited to describe events associated with the end of the retraction. When walking on a slippery surface the legs often pause at the AEP and the PEP. When this occurs the beginning and the end of the protraction movement are always used as the reference points. This means that both pauses are considered as part of the retraction.

Of 453 step interruptions, 30 steps were excluded because three steps were performed during one step of the interrupted leg or because of unusual lag values either before or after the interruption. Most experiments were performed on left legs. In a few cases experiments were performed with right legs and, as no differences were found between right and left legs, all data were pooled.

Results

Interruption of the retraction movement of middle and hind legs

The retraction of a middle or a hind leg was interrupted for various durations (100–2000 ms). The coordination between the ipsilateral legs was examined during and after this interruption. During the interrupted step of one leg the other legs could either perform a single step (step 2) or a double step (step 2a + 2b) and the cases were treated separately.

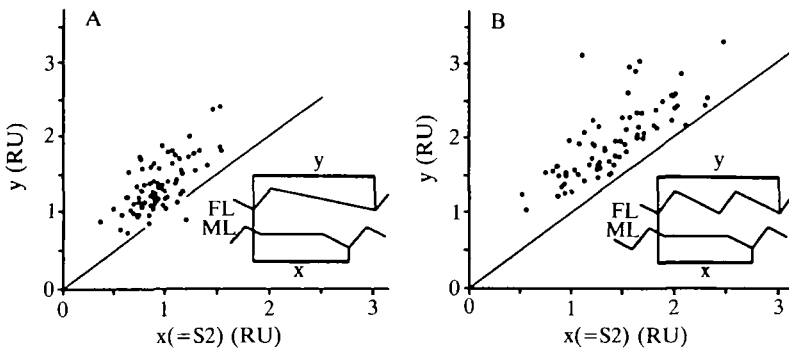


Fig. 2. Interruption of a middle leg (ML) retraction. The dependency of the duration of step 2 ($N = 79$) (A) or of step 2a + 2b ($N = 74$) (B) of the front leg (FL) upon the duration of the interruption, measured as S2. Data from 10 animals. The correlation coefficients are 0.69 (A) and 0.78 (B).

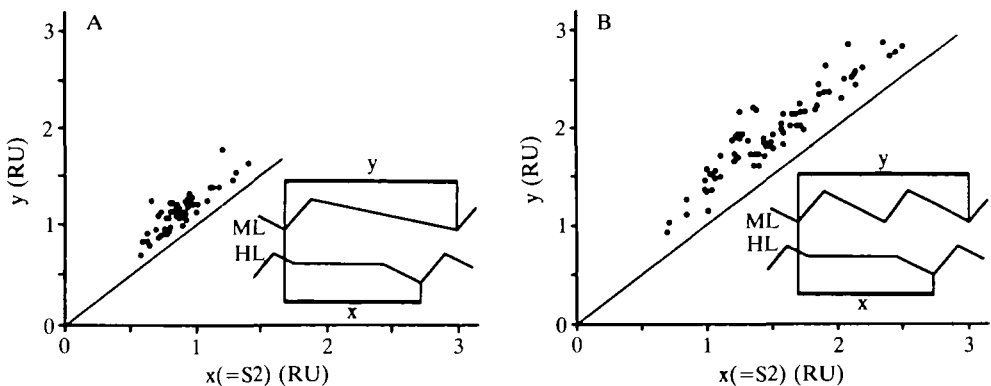


Fig. 3. Interruption of a hind leg (HL) retraction. The dependency of the duration of step 2 ($N = 52$) (A) or of step 2a + 2b ($N = 73$) (B) of the middle leg (ML) on the duration of the interruption, measured as S2. Data from four animals. The correlation coefficients are 0.87 (A) and 0.94 (B).

The influences acting between the interrupted leg and the next anterior leg are described first. Normal coordination between the interrupted leg and the next anterior leg was almost re-established by the beginning of step 3. This is shown for the interruption of the middle leg in Fig. 2A for single steps and in Fig. 2B for double steps. The corresponding results for the interruption of the hind leg are to be seen in Fig. 3A for single steps and Fig. 3B for double steps. The vertical distance between each point and the plotted line gives the time interval between the occurrence of the PEP of a leg and the PEP of the leg in front, which was called lag by Graham (1972). The coordination between middle and front leg seems to be somewhat worse than between hind and middle leg. This is supported by the values of the correlation coefficients (see figure legends). For the single step cases

(Figs 2A, 3A) the duration of the step in the anterior leg is most often prolonged (ordinate value > 1). For double steps (Figs 2B, 3B) many steps occur which are shorter than the normal step duration (ordinate values < 2).

Considering double steps of the middle leg after interruption of the hind leg, the results show that step 2b of the middle leg starts its protraction at approximately the same time as the beginning of the retraction of the hind leg. This can clearly be seen in Fig. 4, in which the occurrence of a middle leg PEP is plotted *versus* this time interval. There is an obvious accumulation of data points between abscissa values of -0.13 and 0.25 RU. This result shows a temporal coincidence between the start of hind leg retraction and the start of middle leg protraction. Because middle leg protraction usually follows the start of hind leg retraction, the latter might be considered as the cause of the former. The occurrence of negative values could be explained as an artefact of the measuring system: owing to the limited accuracy of the position measurement, the start of movement from a fixed position (in this case retraction of the hind leg) is generally registered later than the change in direction of movement (in this case the middle leg). Results corresponding to those in Fig. 4 were less clear for middle and front legs (not shown).

The results found for middle and hind legs are supported by other experiments, where retraction of the middle leg was interrupted and the coordination between it and the posterior leg (i.e. the hind leg) is considered. In this case the time interval between the start of hind leg retraction (i.e. the occurrence of the AEP) and the start of middle leg protraction (the occurrence of the PEP) was measured. The

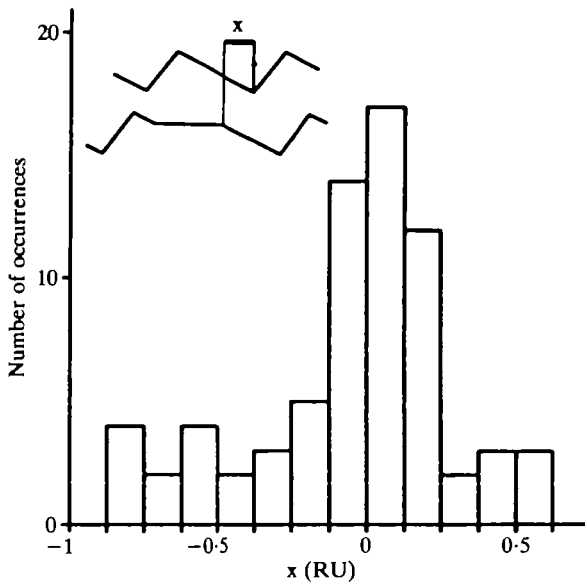


Fig. 4. The number of occurrences of the beginning of step 2b of a middle leg protraction when the hind leg retraction was interrupted. The abscissa shows the time between the removal of the obstruction of the hind leg and the beginning of step 2b of the middle leg. Data from four animals, $N = 73$.

results show that when the hind leg started its retraction during the interruption of the middle leg, this interval assumed very variable values, showing weak coupling between middle leg and hind leg. However, when the start of hind leg retraction occurred during retraction of the middle leg, only a small range of values (between 0.05 and 0.3 RU) of this interval were found.

The end of a hind leg retraction does not occur randomly within the cyclic movement of the middle leg. This is shown in Fig. 5A for steps where the movement of the middle leg was interrupted. The abscissa shows the absolute time interval between the middle leg PEP (end of step 2) and the hind leg PEP at the beginning and end of step 3. The ordinate shows the time interval between these hind leg PEPs and the AEP of the middle leg step 3. Using the inset figure as an illustration, this value shows how near the middle leg protraction can approach the hind leg protraction. There is an obvious empty zone between -160 and 220 ms on the abscissa and between -400 and 10 ms on the ordinate. The corresponding effect between middle and hind legs was found when retraction of the hind leg rather than the middle leg was interrupted (not shown). A similar gap can be seen when considering the same relationship between middle and front leg (Fig. 5B). The abscissa again shows the absolute time interval between the PEP of the middle leg (end of step 2) and the PEP of the front leg (at the beginning and end of step 2 or step 2a). The ordinate shows the absolute time interval between these PEP values of the front leg and the AEP of the middle leg step 3. Using the inset figure as an illustration, the ordinate shows how near the middle leg protraction can approach the front leg protraction. The empty zone appears between -160 and 120 ms on the abscissa and between -20 and 280 ms on the ordinate.

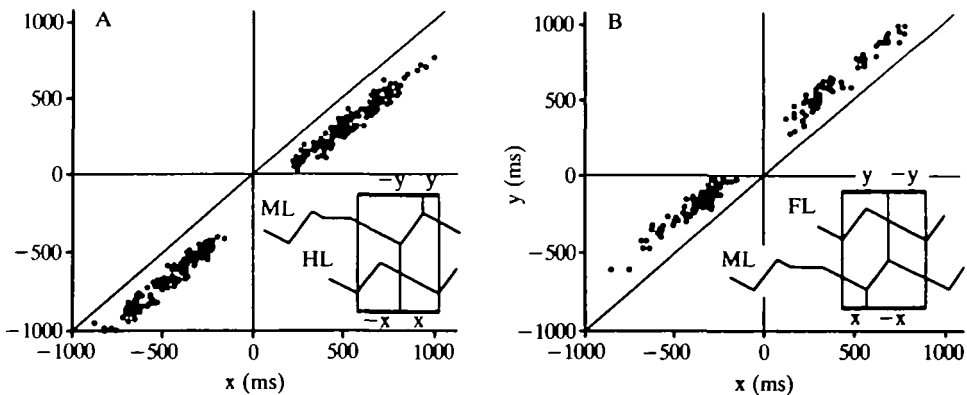


Fig. 5. Interruption of middle leg (ML) retraction. The abscissae show the absolute time interval between the occurrence of a PEP of the hind leg (HL) and that of the middle leg (A) and the same interval between middle and front leg (FL) (B). Negative values mean that the PEP of the posterior leg occurs before that of the anterior leg. In A the ordinate shows the absolute interval between the AEP of the middle leg and the PEP of the hind leg. Data from 11 animals, $N = 253$. In B the ordinate shows the absolute interval between the AEP of the middle leg and the PEP of the front leg. Data from 11 animals, $N = 147$.

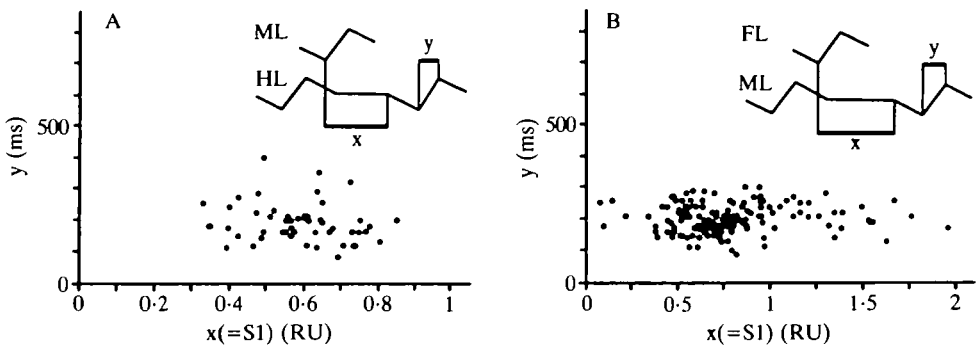


Fig. 6. The relationship between the absolute value of protraction duration upon the duration of the interruption. (A) The duration of hind leg (HL) protraction of step 3 following the interruption of the hind leg. Data from three animals, $N = 52$. (B) The duration of the middle leg (ML) protraction of step 3 following the interruption of the middle leg. Data from 11 animals, $N = 138$. FL, front leg.

The fact that the empty zones appear for both positive and negative abscissa values shows not only that no protraction of the middle leg starts during a protraction of the hind leg but also that no hind leg protraction starts during a protraction of the middle leg. The empty zones have a breadth of approximately twice the normal protraction duration. For the middle leg this value can be obtained from Fig. 5 by measuring the vertical distance between the regression line and the line through the origin with a slope of 1, which amounts to 204 ms. Another evaluation (see H. Cruse & A. Knauth, in preparation) has provided values for the duration of the protraction of the order of 150 ms. A delay of at least 20 ms occurs between the end of middle leg protraction and the beginning of the following front leg protraction (Fig. 5B). This value corresponds to those found by Foth & Bässler (1985*b*) for middle and hind legs.

Finally, those effects which act on the movement of the interrupted leg itself should be considered. The duration of the protractions is not dependent on the duration of the stop. Fig. 6 shows this for the interruption of the hind leg and the subsequent protraction of step 3 of the hind leg (Fig. 6A) and for the interruption of the middle leg and the subsequent protraction of the middle leg (Fig. 6B).

The duration, R , of hind leg retraction following the interruption decreases with increasing duration of the interruption ($r = -0.47$, $P < 0.001$). The shortening of R might result from an increase in the speed of the retraction movement or from a shift of the hind leg PEP in the anterior direction, i.e. a shortening of the step amplitude. Fig. 7 shows on the ordinate the measurement of the amplitude of this part of the step. As mentioned in Materials and methods, the amplitudes are measured as femur position. They are given in relative femur position units (FPU). The amplitude of a normal step of the hind leg is about 4.4 FPU. The results show that the retraction movement is more reduced in amplitude, the later it occurs in the step of the middle leg ($r = -0.46$, $P < 0.001$). A decrease in the

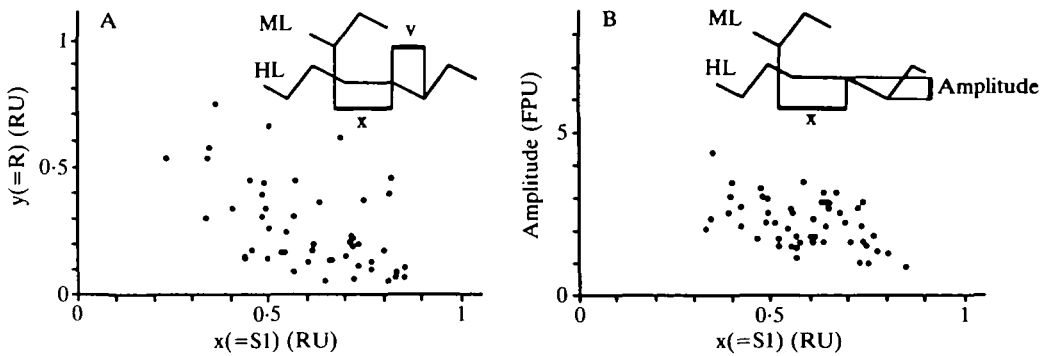


Fig. 7. Interruption of hind leg (HL) retraction. Dependency of the duration of the hind leg retraction R following the interruption (A) and the amplitude of this retraction (B) on the duration of the interruption measured as S_1 . The amplitude is measured in femur position units (FPU). The amplitude of a normal hind leg step amounts to about 4.4 FPU. Data from three animals, A, $N=50$; B, $N=52$. ML, middle leg.

duration of hind leg retraction was also found when middle leg retraction was interrupted. The longer step 2 of the middle leg is delayed, the longer is the retraction of the hind leg (not shown). In both cases the effect is relatively small (in the latter case the slope of the regression line is -0.21 , when using absolute time as coordinates).

Continuously walking animals

The correlation between the middle leg step parameters and the elicitation of the hind leg protraction was shown in another series of experiments. In these experiments continuously walking animals were investigated.

When walking on the oiled plate, irregular walking patterns were often observed. Several animals even made two hind leg steps when the middle leg only made one step (2:1 coordination *versus* 1:1 coordination). In the two-step cases, the PEP of that hind leg step which occurred later within the retraction of the middle leg was shifted in the anterior direction. This corresponds to the results of Foth & Bässler (1985b) who found the duration of the second step to be reduced. This either depends on the relative time (phase) value of the occurrence of the hind leg PEP within the retraction of the middle leg or on the position of the middle leg. The quantitative evaluation is shown in Fig. 8. The ordinates in all diagrams of Fig. 8 show the femur position (FPU) of the hind leg PEP measured relative to an arbitrary fixed baseline. The abscissae of Fig. 8A,B show the relative time or phase of occurrence of the hind leg PEP as a percentage of the duration of the middle leg retraction. Thus, 0% represents the beginning of the middle leg retraction and 100% its end. This was done to obtain better resolution than that obtained when using the whole step period as reference. The abscissae of

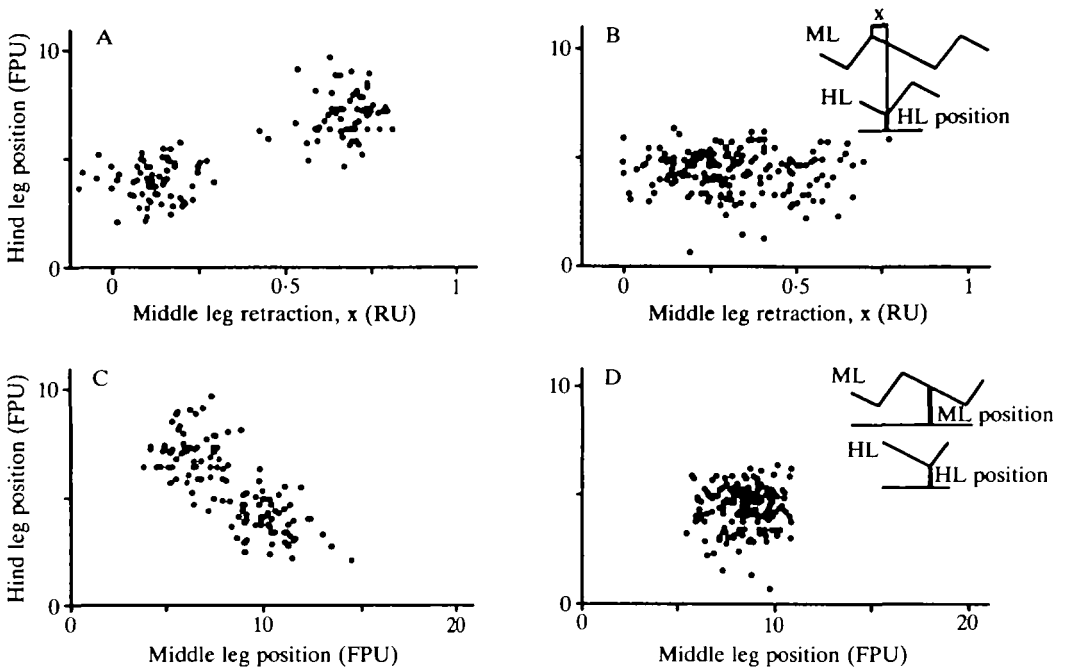


Fig. 8. Dependency of the value of the posterior extreme position (PEP) of the hind leg upon the relative time as a percentage of the duration of the retraction of the middle leg (ML) (A,B) and upon the actual position of the middle leg (C,D) (see also the corresponding inset figures). A value of 0% corresponds to the beginning and a value of 100% to the end of the retraction of the middle leg. Position values are given in femur position units (FPU) measured with respect to arbitrary, but fixed, baselines which are schematically indicated in the inset figures. The amplitudes of the normal middle leg steps and the normal hind leg (HL) steps are 6.0 and 4.4 FPU, respectively. (A,C) 2:1 coordination between hind and middle legs, (B,D) 1:1 coordination. All values are from one animal, A,C, $N = 130$; B,D, $N = 175$.

Fig. 8C,D show the actual position of the middle leg femur relative to an arbitrary but fixed baseline and measured at the time when the hind leg arrived at its PEP. As the results for the 2:1 coordination (Fig. 8A,C) show, a clear correlation was found between the hind leg PEP and both time (Fig. 8A) and the actual middle leg position (Fig. 8C). For the 1:1 coordination, no correlation was found for the time parameter (Fig. 8B), although the value range is about the same as for the 2:1 coordination. Thus, relative time cannot be the critical parameter. In spite of the broad range, the values of the actual middle leg positions of the same steps were much more concentrated. This means that the reason for the PEP shift in the 2:1 coordination is not the temporal parameter 'phase', but the geometrical parameter 'position of the middle leg'. The data shown in Fig. 8 are from one animal. Other animals showed qualitatively the same results but are not shown because normalization of the data was difficult.

Discussion

The investigation of walking with interrupted steps provides a new insight into the coupling mechanisms. No effect on the duration of protraction was found (Fig. 6). This shows that most, if not all, coordinating effects influence the duration of the retraction movement. Coordinating effects on the amplitude of protraction are known (Cruse, 1979*a*; Dean & Wendler, 1983) but as protraction is very fast these apparently do not influence the duration significantly.

The results show that coordination influences are sufficiently strong to regain normal coordination in the step directly following the interrupted step. In single-step examples the step of the neighbouring leg was prolonged by a similar amount to that of the interrupted leg (Figs 2A, 3A). The same is true for the duration of both steps together in the double-step cases (Figs 2B, 3B). A possible reason for this prolongation might be that during the interruption all legs move more slowly. This contradicts earlier findings. Stopping the retraction of a leg leads to the development of stronger forces in that leg. This, in turn, increases the forces in neighbouring legs (Bässler, 1979; Cruse, 1985*a*). Thus the neighbouring leg should try to move faster than normal. This could provide an explanation for the occurrence of double steps. In all cases a protraction of the anterior leg followed directly upon the protraction of the posterior leg. These prolongations can therefore be explained by the coordinating mechanism described earlier (Graham, 1978; Dean & Wendler, 1982; Cruse & Epstein, 1982; Foth & Bässler, 1985*b*). During the protraction of a leg the next anterior leg is inhibited from starting a protraction. At least one form this inhibition takes is a posterior shift in the position threshold for starting the protraction as long as the posterior leg is performing its protraction (Cruse, 1985*b*).

The data in Fig. 4 show that the start of a protraction in the middle leg can occur at any time with reference to the end of the hind leg retraction. However, there is an increased probability of the middle leg starting the protraction directly after the new retraction of the hind leg has begun. This shows that there exists an 'excitatory' influence from hind leg to middle leg. Pearson & Iles (1973) speculated about such an excitatory influence. They described it hypothetically as a negative rebound following the inhibitory influence during the protraction. However, our results indicate that this excitatory influence is not coupled to the end of the protraction but to the beginning of the retraction. Between middle and front legs no correspondingly clear results have been found. However, this does not necessarily mean that a corresponding effect does not exist. Because of the stronger contralateral coordination between front legs than between middle legs (see H. Cruse & A. Knauth, in preparation) it is probable that the effect between middle and front legs is masked by contralateral coupling.

Several results show that excitatory influences (i.e. the eliciting of a protraction movement) exist which act in a posterior direction. When the step of a hind leg is prolonged by means of an interruption, the end of the step of the hind leg is delayed. The later within the step of the middle leg is the interruption, the longer is the delay. In these cases the results showed a shortening of the retraction by

shifting the PEP of the hind leg forward when the hind leg (Fig. 7) or the middle leg (not shown) was delayed experimentally. This shows an excitatory influence on the hind leg, probably arising from the ipsilateral middle leg. However, the possibility that it might arise from the contralateral hind leg cannot be excluded. It is considered to be improbable because of the following experiment. In continuously walking animals the PEP of the hind leg shifts in the anterior direction as the posterior position of the middle leg is increased (Fig. 8C). This effect is not associated with phase but depends on the position of the middle leg. These results also show that the strength of this effect gradually increases with the rearward position of the middle leg.

Other authors have described effects of coordinating influences in the posterior direction which might be caused by the same mechanism. Dean & Wendler (1983) described the PEP of the hind leg shifting correspondingly when the middle leg was held fixed in various rostral-caudal positions. Our results agree with these findings and show that fixation of the middle leg seems not to disturb significantly the coordinating mechanisms. Stimulation of the campaniform sensillae of the middle leg elicited a rhythmic output in the middle leg with a phase opposite to that of the ipsilateral hind leg (Bässler & Wegner, 1983, fig. 15). When the animal walked on a wheel with one hind leg walking on a separate motor-driven belt, the belt speed could be chosen so that the hind leg made only one step while the other legs made more than one step. Extracellular recordings from retractor and protractor nerves showed that the retractor burst of a hind leg was interrupted in the same rhythm as the middle leg retractor burst (Foth & Bässler, 1985a). As no quantitative evaluations have been made and contralateral influences cannot be entirely excluded, a direct comparison with our results is not possible. Qualitative inspection, however, suggests that both effects result from the same mechanism. Measurements of the step duration of a hind leg when it is stepping with twice the frequency of the other legs can be interpreted to suggest that signals from the middle leg retraction elicit protraction in the hind leg (Foth & Bässler, 1985b). As they showed, this coordinating mechanism is less dependent on absolute time than on phase. Assuming that it is the same mechanism as that described here we could, in addition, show that it is even more dependent on position than on phase. Other indirect support for the existence of such mechanisms is given by the results of Cruse & Saxler (1980b).

The results presented in Fig. 5 show that some of the possible temporal relationships between neighbouring legs do not occur. This might indicate a 'forbidden' zone (Graham, 1978). The question arises whether this empty zone can be explained by the coordinating mechanisms described above or whether additional mechanisms must be assumed to explain these results. The forward-directed inhibitory influence which prevents the start of the protraction of the anterior leg could cause that part of the empty zone which lies between -160 and 0 ms on the abscissae of Fig. 5A,B. However, the empty zone found for positive values on the abscissae cannot be explained by this mechanism. The existence of this zone means that protraction of the hind leg does not begin before the middle

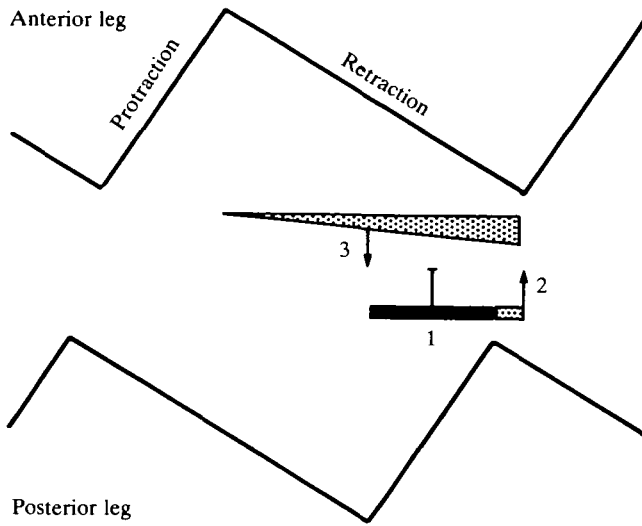


Fig. 9. Schematic summary showing three ipsilateral coordinating influences. Anterior leg is above. The black bar and \rightarrow symbolize influences that inhibit the start of a protraction in the anterior leg. The stippled areas and the arrow symbolize influences which excite the start of a protraction. The thickness of the wedge indicates qualitatively the intensity of the influence which increases towards the rear.

leg protraction has finished (Fig. 5A, and the corresponding result for middle and front legs, Fig. 5B).

Three different hypotheses might explain this effect. First, the most obvious hypothesis is that a mirror-image-like inhibitory influence acts from middle to hind leg, as assumed by Pearson & Iles (1973) for the cockroach. This, however, clearly contradicts the results of Dean & Wendler (1982) and Cruse & Epstein (1982). Second, the empty zone for positive values could be explained by the assumption that the inhibitory influence from hind to middle leg (and from middle to front leg, correspondingly) acts not only during the protraction but also during the last part of the retraction of the hind leg. This is improbable, as such a mechanism should have led to posterior shifts of the middle leg PEP in those experiments of Cruse & Epstein (1982) where the hind leg retraction was prolonged. Third, as discussed above, an excitatory influence might exist which elicits the start of protraction in the hind leg when the middle leg has reached a given position during retraction.

This last mechanism would explain the positive part of the empty zone in the following manner. Protractions in this empty zone would occur any time the retraction of the hind leg is late in the cycle of the middle leg. However, as our results show, this timing does not occur because the excitatory influence from the middle leg elicits an earlier start of the hind leg protraction. After the start of the subsequent retraction the hind leg needs a minimum time before it can arrive at a position where a new protraction could be started. This leads to an empty zone for positive values on the abscissa of Fig. 5. According to our results this time is about

220 ms for the hind leg and 120 ms for the middle leg. Using this explanation the positive range of the empty zone is not forbidden, but is the consequence of the earlier action of an excitatory influence. Thus no additional mechanisms have to be assumed to explain these results.

The results presented by H. Cruse & A. Knauth (in preparation) show that ipsilateral coupling is stronger than contralateral coupling. Thus contralateral influences might mask the effects of ipsilateral influences but the effects described in this paper cannot be explained by contralateral coupling.

Three different ipsilateral coordinating mechanisms are described (Fig. 9). All influences act in an excitatory or an inhibitory way on the start of the protraction of a neighbouring leg. There is (1) the well-known forward-directed inhibitory influence which delays the start of a protraction by shifting the PEP of the leg to the rear as long as the next posterior leg is performing a protraction; (2) a forward-directed excitatory influence which elicits a protraction when the posterior leg starts a retraction; and (3) a rearward-directed excitatory influence which elicits protraction depending on the position of the retracting anterior leg. The strength of this last influence increases gradually with the rearward position and probably depends on the walking speed (Cruse, 1979*b*). All three mechanisms tend to produce the same result. For reasons of completeness it should be mentioned that two other coupling mechanisms mentioned earlier are not shown in the figure: the coactivating influence (Bässler, 1979; Cruse, 1985*a*) and the targeting movement (Cruse, 1979*a*; Dean & Wendler, 1983). In contrast to the findings in the crayfish (Cruse & Müller, 1986) no influences were found in the stick insect which excite or inhibit the start of the retraction movement. This shows obvious differences in the coupling of these species, possibly reflecting differences between decapods and insects.

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