The contralateral coordination of walking legs in the crayfish *Astacus leptodactylus*

I. Experimental results

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Abstract. The coupling mechanisms which coordinate the movement of ipsilateral walking legs in the crayfish have been described in earlier investigations. Concerning the coupling between contralateral legs it was only known that these influences are weaker than those acting between ipsilateral legs. The nature of these coupling mechanisms between contralateral legs of the crayfish are investigated here by running left and right legs on separate walking belts at different speeds. The results show that coordination is performed by a phase-dependent shift of the anterior extreme position of the influenced leg. This backward shift leads to a shortening of both the return stroke and the following power stroke. As the coupling influence is only weak, several steps might be necessary to retain normal coordination after a disturbance. This corresponds to v. Holst's *relative coordination*. The influences act in both directions, from left to right and vice versa. However, one side may be more or less dominant. A gradient was found in the way that anterior leg pairs show less strong coordination than posterior legs. In some cases the coupling between diagonally neighbouring legs was found to be stronger than between contralateral legs of the same segment. The interpretation of this result is still open.

Introduction

The legs of a walking animal have to move in a coordinated way in order to prevent it from falling, in particular when it walks on uneven ground. The coordinating mechanisms have to be highly adaptive because the whole system has to cope with very different disturbances. The aim of this paper is to contribute to the elucidation of the nature of these mechanisms.
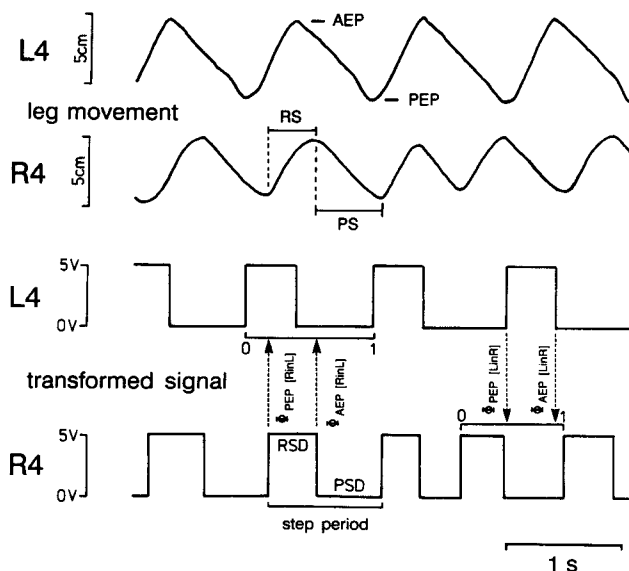
It has long been accepted that the movement of each leg is controlled by its own neuro-muscular sub-system, and that coordination is implemented in such a way that these subsystems are coupled by some neuronal mechanisms (for reviews see Graham 1985; Bässler 1987; Cruse 1990). In the crayfish the coupling mechanisms acting between ipsilateral legs have been investigated in detail (Cruse and Müller 1986). In this earlier work the analysis of the mechanisms which couple contralateral legs was postponed because the latter are apparently much weaker than the former, a property found in several arthropods (for reviews see Clarac 1982; Clarac and Barnes 1985). This is an advantage when investigating the ipsilateral coupling mechanisms because coupling influences from contralateral legs, which may disturb the effects produced by the ipsilateral coupling mechanisms, are weak and can thus be neglected at a first approximation. However, when we want to study the nature of the contralateral coupling mechanisms, the same property can pose enormous problems.

Coordinating mechanisms are often investigated by way of an experimental disturbance of the system (Stein 1976). Then the reaction of the system to these disturbances is observed. This was done earlier (Cruse and Müller 1986) by interrupting the power stroke of a single leg and observing how the legs retain their normal coordination. It was found that all but one leg remained undisturbed in these experiments. In the experiments presented here, the problem caused by the weak contralateral influences is partly overcome by applying the same disturbance to all legs of one side of the body so that ipsilateral influences play a minor role. This is done in the following way: the crayfish walks on two parallel motor-driven belts each of which drives the legs on one side of the body (Clarac and Chasserat 1983; Clarac and Chasserat 1986). When both belts are driven at slightly different speeds, the animal still tries to coordinate its legs. By means of this continuous disturbance it can be investigated how the legs manage to retain proper coordination.

Methods

Thirty-seven adult animals (*Astacus leptodactylus*) of both sexes weighting about 60 g each were used in the experiments. The animals walked on a split treadmill placed inside an aquarium. They were fixed dorsally by the carapace, using dental cement (Scutan) and a holder. The holder was counterbalanced, so that the animals were able to carry their own weight. A cardan suspension allowed the animals slight scope for movement in all three spatial dimensions, but prevented rotations around the vertical body axis. Only forward walking in the range between 6 and 12 cms^{-1} was investigated. The aquarium was coated with transparent paper, to prevent optical orientation of the animals. The position of the pereiopods of all eight walking legs (2–5) of the left (L) and right (R) side were continuously recorded, using specific transducers developed by Cruse and Müller (1984) with which the position of the dactylopodite of each leg can be measured parallel to the longitudinal body axis. The position signals were monitored using an eight-channel digital scope (Natic) and stored on tape for further analysis. Figure 1a shows a registration of two selected walking legs. The abscissa is time. An upward deflection of a single trace indicates a return stroke. This is the time interval when the leg in question is lifted away from the substrate and produces an anteriorly directed movement. A downward deflec-
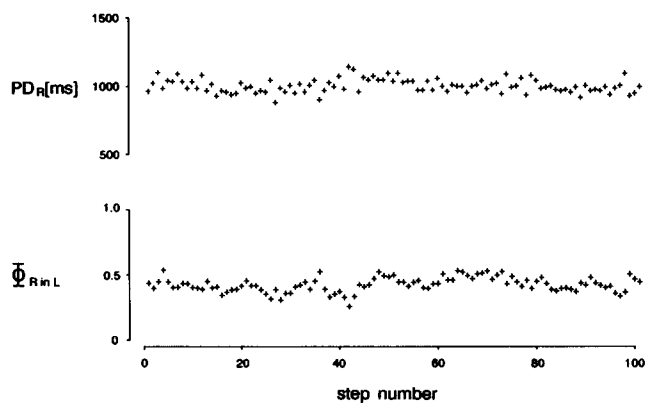
tion indicates a power stroke. Here the leg has ground contact and supports the body. The position at the transition from the return to the power stroke is called the anterior extreme position (AEP). Correspondingly, the transition from power to return stroke occurs at the posterior extreme position (PEP).

A special device was constructed, which permitted a first analysis of a walk during the running experiment. For this purpose the position signals of two chosen legs were differentiated, serving as the input of a Schmitt-Trigger, whose output is shown in Fig. 1b. The positive and negative flanks of the rectangular signal corresponded to the occurrences of the PEP and the AEP of the test leg and were used to trigger TTL pulses. The TTL pulses were fed through an external hardware supplement into a microcomputer. The time durations of return and power stroke (RSD, PSD), the period (measured between one PEP and the following PEP), as well as the phase of the occurrence of PEP and AEP (ΦPEP, ΦAEP) were calculated and could be displayed graphically. The expression of the form "L4inR4" is used to mark the test leg (in this example leg L4) and the reference leg (in this example leg R4). Mean phase and concentration parameters were calculated using circular statistics (Batschelet 1983).

Results

When the belts on both sides move at the same speed, a proper coordination between the legs of both sides can be observed. This is shown below in the sequence of steps of R4 in Fig. 2, where the step duration of R4 and the phase of R4inL4 are fairly constant. When the two belts are driven at different speeds, this would for a given stride length lead to different frequencies for the legs of both sides. The animal nevertheless walks while trying to move both legs at the same frequency. However, under these circumstances this is only partly possible, and therefore the coordination between both legs is less strong. One example of such an experiment is shown in Fig. 3a, part I, where the left belt moves

Fig. 1.a Stepping pattern of the legs 4 of the left (L4) and right (R4) side of a crayfish. The relative position of the dactyl is measured parallel to the body's longitudinal axis. An upward deflection indicates a return, a downward deflection indicates a power stroke. b peak discriminator: the two traces show the transformed signals of a. The positive and negative flanks of the rectangular signals were correlated with the occurrence of PEP and AEP. The period was measured between the occurrence of one posterior extreme position (PEP, lower turning point) and the next following one. The phase was defined either as the occurrence of PEP of a chosen test leg (ΦPEP$_{[RinL]}$) or as the occurrence of AEP (ΦAEP$_{[RinL]}$) within the period of a given reference leg. In a second evaluation reference and test legs were changed and the same parameters measured again (see right part of b)

Fig. 2. Period durations of the leg R4 (upper trace) and phase relations of the leg R4, the reference leg being L4 (lower trace). The sequence shows 100 single steps of R4 at identical belt speeds
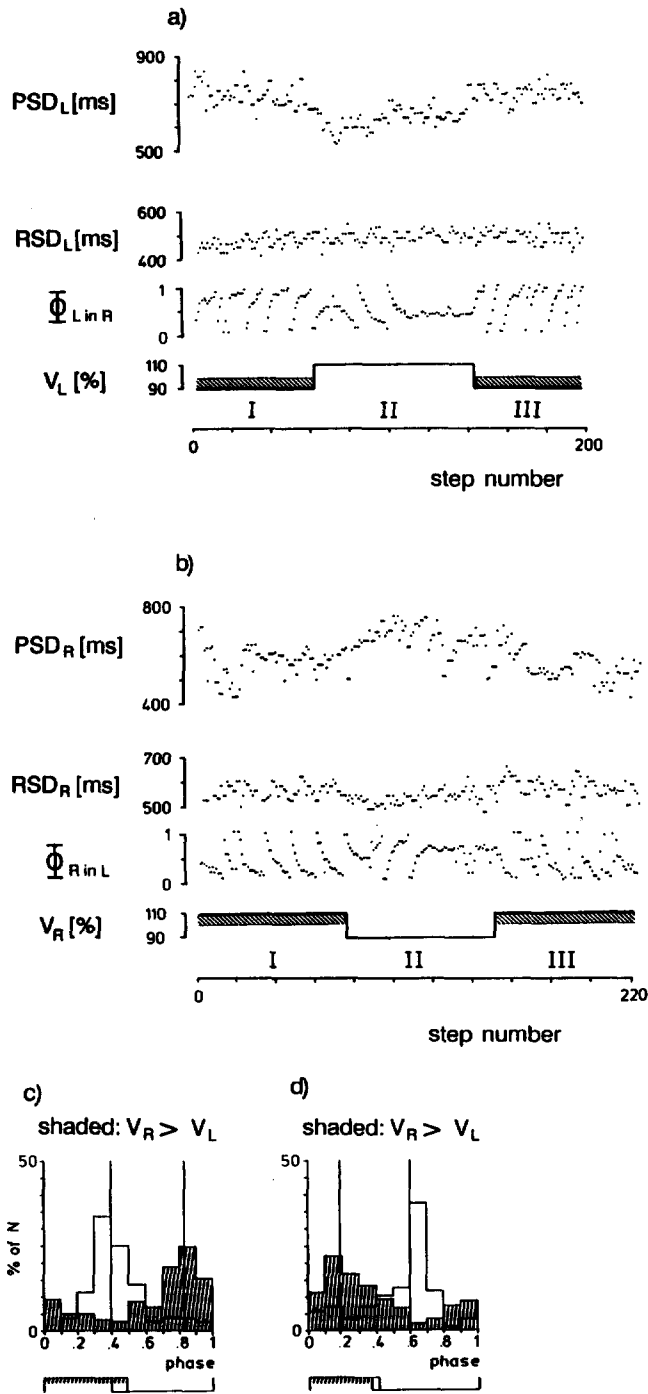
Fig. 3. a–d. Responses of the fourth contralateral leg pair L4-R4 during an exchange of the belt speed ratio between both sides. **a** Test leg is L4, reference leg is R4. **b** Test leg is R4, reference leg is L4. The abscissa in both cases is the same as in Fig. 2. The left ordinate from top to bottom shows the time durations of power and return stroke, the measured phase relation of the occurrence of PEP (within the reference leg), and the ratio of belt speeds (in **a**: V[L/R]; in **b** V[R/L]). The phase is also shown in the histograms in **c** and **d**. Here, the hatched histograms show the situation of part I and III. The open ones show the situation of part II, when the speed ratio was inverted. Mean phases (MP, indicated by the vertical lines in the histograms) and concentration parameter (CP) in **c**, hatched: MP = 0.82, CP = 0.34; open: MP = 0.4, CP = 0.62. In **d**, hatched: MP = 0.2, CP = 0.39; open: MP = 0.6, CP = 0.48. The edged marks below the histograms correspond to the ratio of return and power stroke within the step period

slower, and part II where the speed ratio between both belts is reversed. In the upper two traces the duration of power and return stroke are represented separately. Part III repeats the situation of part I. A comparison with Fig. 2 shows that the scatter is much higher, particularly for the phase values. As can also be seen in the corresponding phase histograms (Fig. 3c, shaded), most of the steps maintain a given phase value, but other values occur as well. As shown in Fig. 3a, the phase values stay near a given level for several steps and then shift step by step until they are again "caught" at a fixed value. This phenomenon was called gliding or relative coordination by v. Holst (1939). According to v. Holst this occurred when both leg oscillators had different intrinsic frequencies and the oscillators were only weakly coupled.

A comparison of the results of both experiments (parts I and II) shows that, although the experimental situation is exactly inverted, the mean values are not. The mean phase value in Fig. 3c is 0.82 for the left belt when it is slower (shaded histogram), and is 0.4 when the right belt is slower (open histogram), but a value of 0.18 should be expected if the situation was exactly symmetrical. In both cases R4 was used as reference. The difference became more obvious when for part II L4 was used as reference (Fig. 3d, open histogram) because in this situation the phase distributions could be directly compared. Here the mean value is 0.6, which is significantly different from the value of 0.82 in Fig. 3c (chi-square test, $p < 0.001$). Moreover, the measured concentration parameters increased from 0.34 (c, shaded) and 0.39 (d, shaded) in part I to 0.62 (c, open histogram) and 0.48 (d, open histogram). These findings show that, although the experimental situations are symmetrical, behaviour is asymmetrical, which suggests that there is some a priori or endogenous asymmetry between the right and left sides of the animal.

This assumption is supported by the result that, when the left leg walks slower, the period of the right leg shows a higher standard deviation than the period of the left leg, but no significant difference is found when the right side is slower. When two oscillators with different intrinsic frequencies are coupled, the period of the dominant oscillator, i.e. the one that influences its companion more strongly, is more stable, showing a smaller standard deviation. Thus, when the left leg walks slower some sort of dominance of the left leg becomes obvious because the period of the left leg is influenced less than the period of the right leg. On the other hand, no dominance can be found on the basis of period changes in the example shown in Fig. 3, when the right side walks slower. We investigated 27 walks altogether, varying the speed differences between right and left belt. Of these walks only those were further evaluated that (a) consisted of at least 100 steps without interruption and (b) showed no obvious change of dominance. According to these criteria 13 walks (containing between 119 and 338 steps) were selected. In these walks (9 animals) an endogeneous dominance, as described above, was found in 8 cases to be on the left and in 5 cases on the right side. The coupling
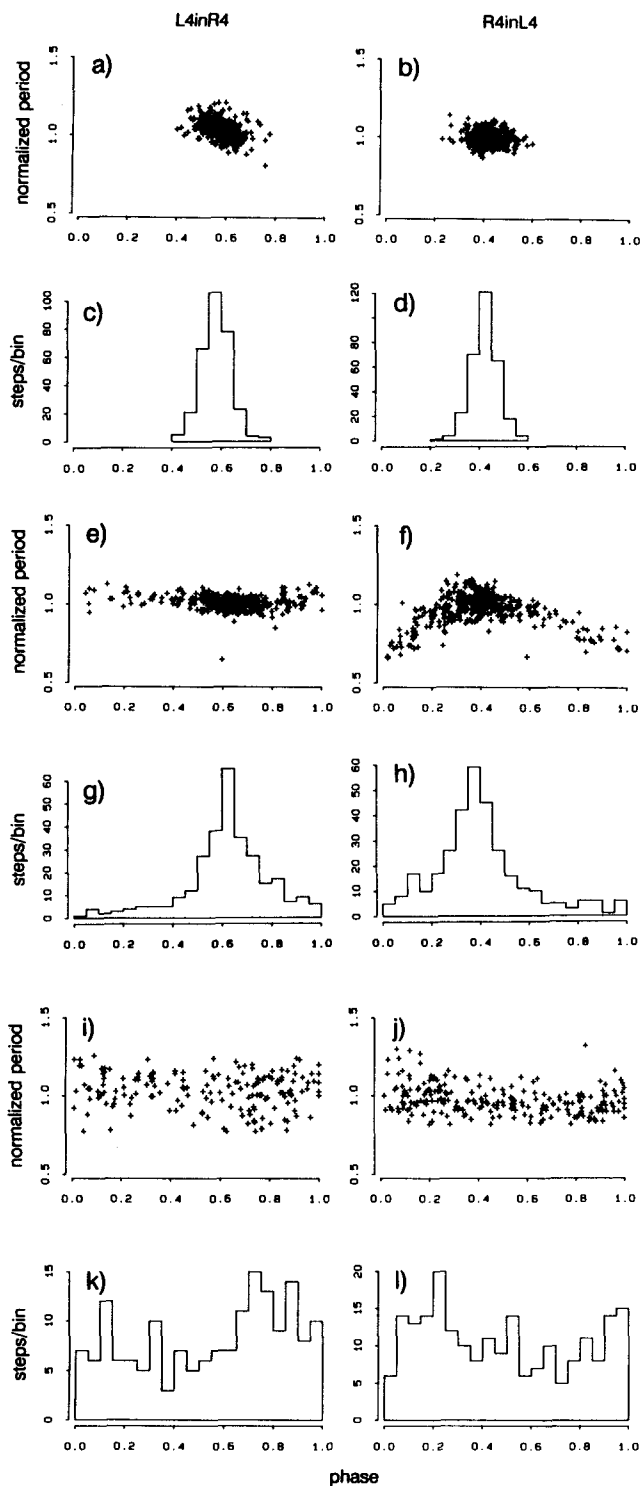
Fig. 4. Phase response curves (a, b, e, f, i, j) and phase histograms (c, d, g, h, k, l) of the contralateral leg pair L4–R4 for three different ratios of belt speeds (see Table 1). In all cases the abscissa is the phase of the PEP of the test leg, within the actual period of the reference leg. The ordinate in the phase response curves is the normalized period (period of the measured step/mean uninfluenced period; see text for further details). The ordinate in the histograms is the number of occurrences of measured phase relations within an interval of 0.05 phase units. This corresponds to the density of the dots in the phase response curves. Refer to Table 1 for mean phases and concentration parameters

mechanisms can be studied over the whole phase range only when all phase values occur. Therefore, after a preliminary test covering all walks a speed difference was chosen by which the dominant leg walked slower because only in this situation do all phase values occur. To simplify the matters the following results are shown and discussed as if the left side was always dominant and therefore was forced to walk slower.

To investigate this behaviour in more detail the method of evaluating the phase response curves was applied (Pavlidis 1973). The period of the test leg was normalized by the mean period of those steps that were not influenced and normally coordinated with the contralateral legs. These steps were selected in the following way: in considering the phase histograms we selected only those steps whose phase values did not differ more than 0.05 units from the average mean phase. Due to this normalization an ordinate value smaller than 1 means a shortening of period and therefore an increase in step frequency. Figure 4 shows a series of three successive experiments with increasing speed differences between right and left side. The resulting mean phase values and concentration parameters are summarized in Table 1. In Fig. 4a, b both sides walk at the same speed, and the animal displays absolute coordination. This is shown by the narrow distribution of the phase histograms (Fig. 4c, d). The situation does not change when the speed of the right leg is decreased slightly (not shown). When the speed of the left leg is decreased (Fig. 4e, f), a relative coordination results, shown by the broader distribution of the phase values (Fig. 4g, h). The period duration of the left leg shows hardly any dependence on the phase of the right, i.e. the reference leg, whereas an obvious influence is found on the duration of the right leg. The period of the right leg is shortened in most of the phase ranges. This means that according to the above definitions the left leg is dominant. When the speed difference is further increased (Fig. 4i, j) coordination is lost, resulting in a more or less equal distribution of phase values (Fig. 4k, l).

This shows that the a priori dominance (assumed to be based on an endogenous factor) becomes obvious when the speed of the dominant leg is decreased. In this case we find relative coordination. When, on the other hand, the speed of the dominant leg is increased, absolute coordination is observed.

Figure 4 shows an extreme case where one leg is clearly dominant. However, intermediate situations can also be found. Figure 5 shows in another animal the situation where no clear endogenous dominance can be found. In this situation both legs seem to influence each other to about the same extent.

In Figs. 4 and 5 the coordinating effects were only considered with respect to their influence on the duration of the whole period. The period consists of power stroke and return stroke, and, as could be seen in the example of Fig. 3, both the duration of power and return stroke seem to be influenced by coordination. To investigate this in more detail, the phase response curves (together with their phase histograms) in Fig. 6
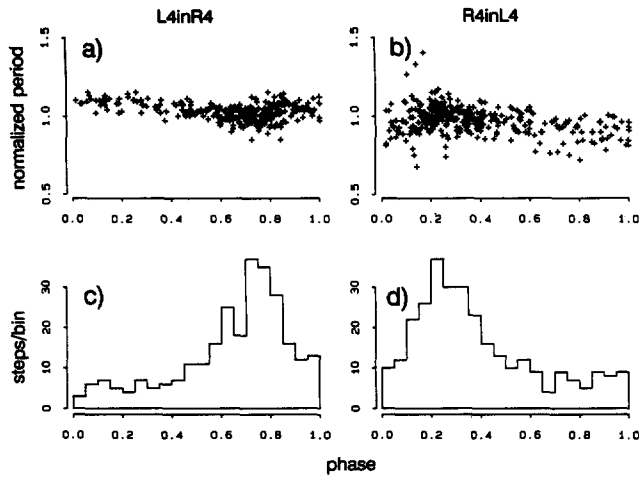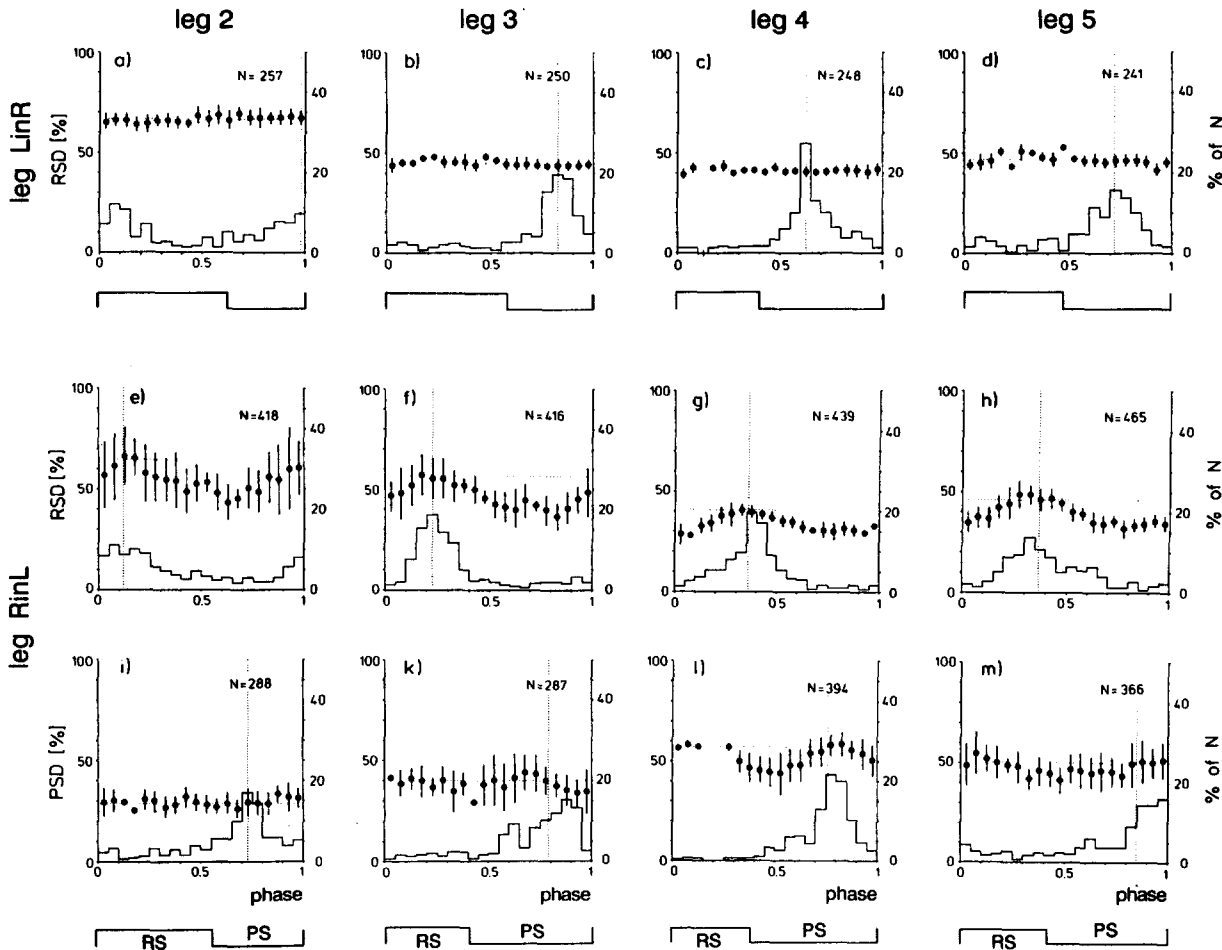
Fig. 5. Phase response curves (a, b) and phase histograms (c, d) of the contralateral leg pair L4–R4 for a belt speed ratio of 1.11. All other parameters are the same as in Fig. 4

**Table 1.** Mean phases (MP) and concentration parameters (CP) of the experiments shown in Figs. 5 and 6

Exp. no.	v%	MP(LinR)	MP(RinL)	CP(LinR)	CP(RinL)
Fig. 4a–d	1.00	0.58	0.42	0.93	0.94
Fig. 4e–h	1.10	0.64	0.36	0.60	0.55
Fig. 4i–1	1.29	0.83	0.17	0.19	0.14
Fig. 5a–d	1.11	0.74	0.26	0.45	0.39

are shown separately for PSD and for RSD. As a control in Fig. 6 the phase response curve of the RSD of the dominant, slower, left legs were also presented. Because of their dominance, these curves should form a horizontal line. The results show that both the RSD and the PSD of the subdominant legs are shortened in a phase-dependent manner. In order to investigate how these temporal values correlate with geometrical ones,

Fig. 6. a–m. Phase response curves and phase histograms for all tested contralateral leg pairs 2–5. The abscissa corresponds to that in Figs. 4 and 5. The columns show (from left to right) the reactions of legs 2–5. The return stroke durations of the legs of the left body side (as a percentage of the whole step period) are measured on the left ordinate of the upper row. The horizontal line indicates the value of the uninfluenced mean return stroke. The right ordinate shows the frequency of occurrence of PEP (which corresponds to the beginning

of the return stroke) within phase intervals of 0.05 units. The second row shows the same parameters, but for the legs of the right side, which were measured using the legs of the left side as reference. In the third row, again, the legs of the right side were measured. Here the left ordinate shows the power stroke durations, while the right shows the frequency of occurrences of AEP (which corresponds to the beginning of the power stroke)
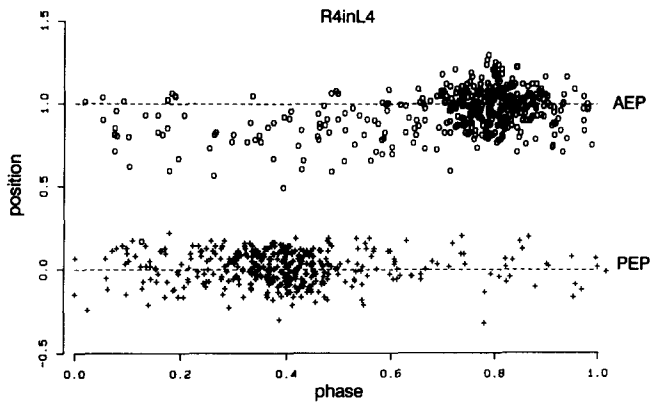
Fig. 7. Dependence of AEP (circles) and PEP (crosses) of the test leg R4 on the phase, within the reference leg L4. The analysed steps, as well as the abscissa are the same as used for Fig. 4e, f. The positions of AEP and PEP were plotted on the ordinate (measured in relative units of a body-fixed coordinate system). The values were normalized in such a way that the mean, uninfluenced PEP was given the value of 0, and the corresponding mean AEP the value of 1 (dashed lines). Circles with values below 1 show that during these steps AEP was shifted backward

Fig. 7 shows the values of the AEP (circles) and of the PEP (crosses), related to the phase of the reference leg, when both extreme positions are measured in a laboratory-fixed coordinate system. The results indicate that no dependence is obvious when considering the PEP. By contrast, the AEP shows obvious shifts which parallel the shortening of return and of power stroke duration (see Fig. 6g, 1).

Figure 6 shows the results of one walk of one animal. In the 13 walks evaluated in detail, different ratios between right and left belt speed were used. When comparing the concentration parameters obtained for all leg pairs and all walks, two qualitative results are obtained. First, there is an obvious gradient such that, in general, the two leg pairs of the anterior segments 2 and 3 are less strongly coupled than those of the two posterior segments 4 and 5. Second, the larger is the speed difference the weaker becomes coordination between the contralateral legs. Furthermore, the mean phases depend on the speed difference. The quantitative results are presented in Fig. 13 of the companion paper Müller and Cruse (1991) where they will be compared with the results of a computer simulation.

Up to now only the concentration parameters between intrasegmentally neighbouring legs have been studied. However, contralateral coupling mechanisms may also exist between diagonally neighbouring legs. For the purpose of comparison, the concentration parameters between diagonally neighbouring legs were calculated. For each pair of legs two concentration parameters were calculated, using either one or the other leg as reference. A general result was that the concentration parameter, for whose calculation reference was made to the dominant leg, was always about 5% larger than its companion. Here the larger of both concentration parameters is given throughout. Only the relation between the legs of the fourth and the fifth
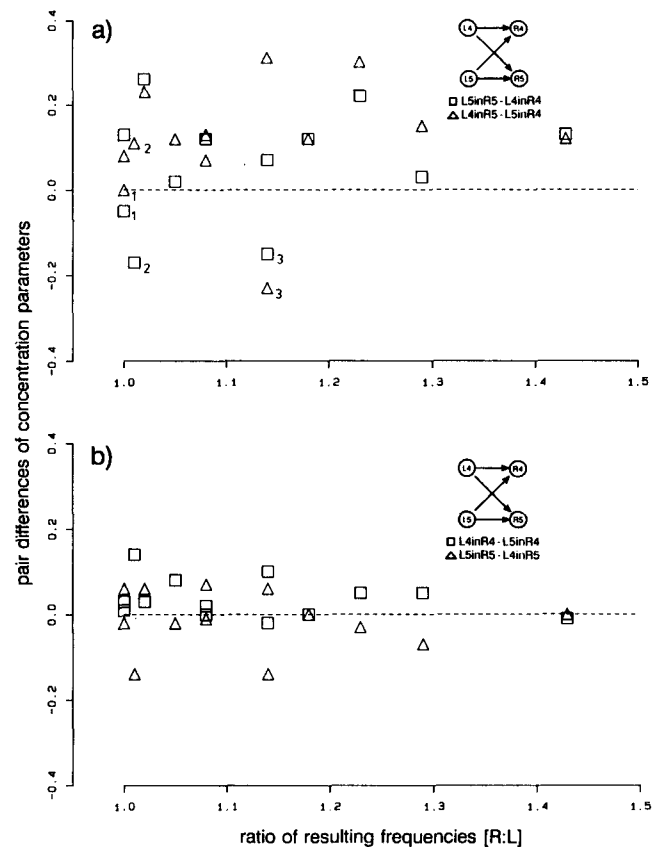
Fig. 8. a, b. Pair differences of the intrasegmental and diagonal concentration parameters for legs 4 and 5. Data from 13 different experiments with an increasing ratio of stepping frequencies between the legs of the left and right side (shown on the abscissa). The ordinate shows the pair differences of the opposed concentration parameters. In **a**, squares: intrasegmental pair differences (L5inR5-L4inR4), triangles: diagonal pair differences (L4inR5-L5inR4). In **b**, squares: (L4inR4-L5inR4), triangles: (L5inR5-L4inR5)

thoracic segment will be examined in detail because the coordination between the anterior legs is weak, which, due to the high scatter, allows only weak inferences. In agreement with the above results, in 10 out of 13 cases the coordination between legs L5 and R5 was stronger than between L4 and R4 (Fig. 8a, squares). Comparison of the two diagonal concentration parameters shows that in all 10 cases the concentration parameter L4inR5 is higher than L5inR4 (Fig. 8a, triangles). No clear tendency can be established when comparing L4inR4 with L5inR4 (Fig. 8b, squares) and L5inR5 with L4inR5 (Fig. 8b, triangles). In all cases the concentration parameters between ipsilateral legs on the dominant side were distinct higher (> 0.8 for L5inL4) than between contralateral legs. The ipsilateral concentration parameters of the subdominant side were also higher than the measured contralateral ones (> 0.5 for R5inR4), but with a smaller difference (not shown here).

The following, unexpected results should be stressed in particular: in some cases (the negative values in Fig. 8b) the concentration parameter for segmentally neighbouring legs L5inR5 is smaller than for diagonally

neighbouring legs L4inR5. This raises the question of whether or not these high diagonal values express the existence of direct neuronal coupling between diagonally neighbouring legs.

Discussion

The results show that the movement of a walking leg can be influenced by legs of the contralateral side. For the moment we will postpone the question of whether this influence is based on a direct neuronal connection between the neuronal systems, controlling the movement of both legs, or whether it acts via indirect connections, passing the control systems of other legs. Instead, we will first concentrate on the question in which way these coordinating mechanisms influence leg movement.

A situation as was shown in Fig. 5 is not appropriate to answer this question, for two reasons: first, the absolute effects – for example, the changes of period duration – are small, and second, the results show high scatter in this case because for each phase response curve the reference period itself is not fixed but always subject to influences from the other leg. Therefore, for the present only those walks will be considered in which one leg shows a clear dominance. The phase response curves shown in Fig. 6 indicate that the duration of the power stroke as well as of the return stroke is influenced by coordinating mechanisms (the latter is less obvious for legs 2 and 3 and will be discussed below). This is apparently caused by caudally shifting the AEP of the influenced leg in a phase-dependent manner (Fig. 7). Thus both phase response curves, i.e. for the return and for the power stroke duration (Fig. 6g, 1), could be simply added to produce the phase response curve of the period duration. This is shown schematically in Fig. 9. In this figure a dominance is assumed such that the coordinating effect operates only in one direction, i.e., from the leg shown in the upper trace to the leg shown in the lower trace. The phase response curve is taken

from Fig. 6 but is shifted to the right by the duration of the corresponding return stroke. This had to be done because in Fig. 6 the beginning of the return stroke was used as phase value, whereas, the experiments showed, that the coordinating influences affect the leg at the end of the return stroke. As can be seen in Fig. 9, the threshold for the position where the return stroke is finished and the next power stroke is started has shifted caudally for nearly the whole phase range. This shortens both the return stroke and the following power stroke. The examples in Fig. 9 show that in this way steps which could start at very different phase values are concentrated in a smaller phase range in the next step. However, the coordinating effect is weaker compared to ipsilateral coupling (Cruse and Müller 1986), which means that several steps may be necessary to retain normal coordination. In principle, the coupling mechanism seems to be similar to the mechanism that was found to operate caudally between ipsilateral legs. However, although this influence covers the whole phase range in the contralateral case, the overall effect is weaker. It should be stressed that the general effect of this influence is an increase in the stepping frequency of the influenced leg.

The results relating to the anterior leg pairs are less clear. Besides the higher scatter resulting from weaker coupling, there is an additional reason: during the return stroke their movements have a different form compared to the posterior legs. In the anterior legs, particularly legs 2, the velocities of the movements are low during the last part of return stoke and at the level of AEP, the effect being that the change in period duration is mainly due to the change in the return stroke duration. Therefore, only the four legs of the posterior segments 4 and 5 (Fig. 8) have been considered in the comparison of the strength of the influences which act between different leg pairs. The results can be summarized as follows: three of the four legs are connected by higher concentration parameters and form a "stable triangle". This means that the two ipsilateral legs of the dominant side (i.e. the one that walks slower) have strong connections to one of the two legs of the other side, namely the one that shows the higher intrasegmental concentration parameter. This rule holds for 11 out of the 13 experiments considered. One example of such a "stable triangle" is shown in Fig. 10. The values of the concentration parameters are visualized by the thickness of the lines connecting the legs. In one of these 11 experiments (see Fig. 8, Nr. 13) the concentration parameter L4inR4 was higher than that of L5inR5. According to the rule, in this case too the concentration parameter between the diagonally neighbouring legs L5inR4 was higher than between L4inR5. Two experiments (No. 1 and No. 2) of Fig. 8 do not follow this rule. How are we to interpret these exceptions? In experiment No. 1 the differences between the measured concentration parameters are small. This indicates a nearly symmetrical situation concerning the endogenous dominance, similar to the results shown in Fig. 5. Thus, according to the above rule, no effects should be expected in experiment No. 1.
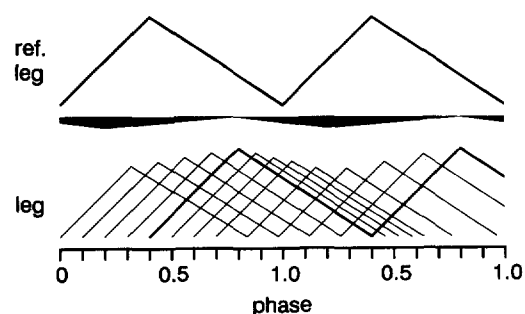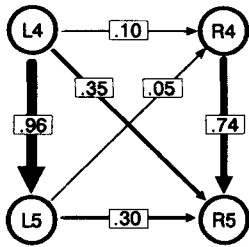

Fig. 9. Hypothetical scheme of the contralateral coordination. Abscissa: phase, related to the reference leg. Upper trace: position of the reference leg. Lower trace: position of the test leg. The phase response curve shown in Fig. 6g was shifted to the right for the duration of the return stroke (see text for further explanation); it serves as a limitation for the AEP of the test leg (see lower margin of the mark between the two traces). This mark indicates the approximated influence of the reference on the test leg

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velocity ratio R:L = 1.23

Fig. 10. Concentration parameters between the four posterior legs 4 and 5, for a single experiment. The speed ratio between right and left legs (V[R:L]) amounts to 1.23. The thickness of the lines corresponds roughly to the values of the measured concentration parameters. The dominant triangle includes legs L4, L5 and R5

However, this is not the case for experiment No. 2, whose data have already been shown in Fig. 4a, b. As was the case for experiment No. 1, no differences in the period durations between right and left legs were found because the belt speeds were adjusted equally. Thus, a decision about the endogenous dominance of the animal is very difficult in this situation. In Fig. 4a, b the left leg shows a higher variation in the period duration than the right leg, indicating that the right leg is dominant, whereas in the experiment of Fig. 4e, f, with the same animal the left leg is clearly dominant. Furthermore, all concentration parameters were exceptionally high in this walk. One possible explanation may be that the effect observed in experiment No. 2 results from the caudally directed ipsilateral coupling influence discussed in Cruse and Müller (1986).

Although the coordination between contralateral legs can be easily understood when the dominance relation, which exists between two legs, is made obvious by the experimental arrangement, several questions remain. Figure 5 shows that occasionally less clear situations occur. Can they also be explained by the same coordinating mechanisms acting in both directions? Furthermore, considering the endogenous dominance the following questions arise: (*I*) how does the variance of dominance strength and (*II*) why and how does the speed difference between both belts, influence coordination? (*III*) in which way do both phenomena act together? Another question raised by the finding of high diagonal concentration parameters is (*IV*) whether assuming intrasegmental neuronal connections only is sufficient to explain the results, or whether direct neuronal connections between diagonally neighbouring legs have to be assumed instead. As these questions cannot be answered on the basis of our experimental data alone, a model calculation will be presented in the companion paper Müller and Cruse (1991). In this model the different parameters not accessible in the

biological experiment can be varied systematically and the resulting effects can be observed. This will permit an answer to at least some aspects of the above questions. The results of the model calculation will show, first, that the existence of direct diagonal connections is not necessary and, second, that the results found here can be completely explained when it is assumed that an asymmetry in the coupling factors between two legs corresponds to an endogenous dominance which is independent of the speed differences of both belts.

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