

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

II. Model calculations

U. Müller and H. Cruse

Fakultät für Biologie, Abteilung für Biologische Kybernetik, Postfach 8640, Universität Bielefeld, W-4800 Bielefeld 1, Federal Republic of Germany

Received September 11, 1990/Accepted in revised form November 28, 1990

Abstract. In an earlier investigation of those mechanisms which synchronize the leg movements of a multi-legged animal during walking (Müller and Cruse 1991) several questions remained open. The movement of an individual leg can be described in analogy to the behaviour of a relaxation oscillator. Following this analogy the interactions between the legs can be compared with the interactions between coupled relaxation oscillators. To understand the behaviour of a system of such coupled oscillators, model calculations were performed by systematically varying the relation of the intrinsic frequencies and the character as well as the strength of the coupling influences to which each oscillator was exposed. The behaviour of several three- and four-oscillator systems was investigated. We found that prediction of the behaviour is often difficult and in some cases even counter-intuitive. It could be shown that in a four-oscillator system (which corresponds to two legs on the left and two legs on the right side of the body) diagonal neighbours can sometimes be more strongly coordinated than direct segmental neighbours, although no coupling was implemented between the diagonally neighbouring oscillators. Necessary conditions for the occurrence of this effect are described. These conditions were fulfilled in the biological experiments described in Part I. A four-oscillator model whose properties are adapted to those found in the above experiments can sufficiently describe the animal's behaviour.

Introduction

In investigating the organisation of leg movement of a multi-legged animal, one important problem to be looked at is the coordination between the different legs (for review see Clarac 1982; Clarac and Barnes 1985; Cruse and Müller 1986; Cruse 1990). It is generally agreed that the movement of each walking leg of an

arthropod is controlled by a separate neuro-muscular subsystem (for review see Delcomy 1985; Graham 1985). This can be regarded as a relaxation oscillator because during walking the legs move cyclically forward and backward. When investigating the question of how the legs are coordinated, a system is studied, which consists of several such oscillators, coupled together in an unknown way (Pavlidis 1973). For the solution of this problem two questions have to be addressed. First, what is the nature of the coupling mechanisms (for review see Stein 1976) and, second, between which oscillators do these mechanisms act. Particularly the second question may be difficult to answer because the fact that, for example, two out of eight oscillators are coordinated does, of course, not permit the conclusion that a coupling mechanism exists which directly connects both oscillators. Indirect coupling is also possible.

In two earlier papers the question concerning the nature of the coupling mechanisms between the legs of a crayfish could be answered on the basis of experimental investigations. Cruse and Müller (1986) demonstrated that two coupling mechanisms act between ipsilateral legs, i.e. legs of the same side of the body. Müller and Cruse (1991) showed a mechanism which acts between contralateral legs. As the ipsilateral mechanisms are much stronger than the contralateral ones, the investigation of the first was possible by simply neglecting the latter. By contrast, the investigation of the latter is more complicated. However, we were able to set up an experimental situation in which the nature of the contralateral influence could be demonstrated. This was possible by experimentally changing the step period of the right and left legs differentially. The animal walked on two motor-driven belts, the speeds of which could be controlled independently. This can result in a so-called *relative coordination* (v. Holst 1939) which means that the cyclic movements of two legs are not phase-locked, as is the case in the so-called *absolute coordination*, but that any phase value can occur. In

contrast to the uncoordinated situation, however, a particular phase value occurs more often than do others.

The nature of the coupling mechanisms can be made obvious by plotting the so-called phase response curve (Pavlidis 1976). Here, a measure of the steps of the test leg, e.g. the duration of the step period, is plotted versus its phase in the other, the reference leg. By using this method we could show that the step period of the influenced leg can be shortened, thus increasing the step frequency. This is done in the following way: a step consists of two parts, the power stroke and the return stroke. During the power stroke the leg is on the ground, supports the body and moves backwards until it reaches the so-called posterior extreme position (PEP). Here the leg is lifted off the ground to start the return stroke. This means that the leg is moved forward until it reaches the anterior extreme position (AEP), where again it switches to the power stroke state. The coordinating influence found was interpreted as shifting the AEP in a more posterior direction, thus shortening the ongoing return stroke and, as the PEP is not influenced, the following power stroke as well. In this way, the actual frequency of the oscillator becomes higher than its intrinsic frequency. This is the frequency assumed by the oscillator when it is not influenced by coupling effects resulting from other oscillators.

Apart from this clear result several open questions remain. In studying two contralateral legs of the same segment (i.e. two directly neighbouring legs of opposite sides of the body), the following results were obtained: there was an a priori dominance in that one leg was more dependent on the other leg than was the latter on the former. This could be shown using the following method: variation of the belt speed ratio had a direct influence on the speed of the power stroke and, for a given AEP and PEP, its duration and thus the duration of the whole period. Thus, by varying the speed ratio of the belts of the left and right side, the mean frequency ratio of the oscillators of the left and right side was changed. When the intrinsic frequency of the left legs was increased, coordination was found to be different to when that of the right legs was increased by the same amount. Not only was the mean phase value different, but also the type of coordination. In one case absolute coordination, in the other relative coordination, was found. Thus, several questions remained, which could not be answered on the basis of the experimental investigation: first, how does the variance of the strength of the dominance and second, how does the speed difference between both belts influence coordination, and, third, how do these two phenomena act together?

A fourth question which could not be answered on the basis of the experimental result was this: in some cases coordination between diagonally neighbouring legs was stronger than between directly neighbouring legs. Two explanations of this effect are possible: first, it could be that in these cases direct neuronal coupling connections exist between diagonally neighbouring legs and that they do not exist in the cases when segmental coordination was stronger. Secondly, is it possible under certain circumstances (and if so, which) that such

strong diagonal coordination can occur, though only contralateral coupling between legs of the same segment of the body exists? As we are not aware of any analytic mathematical solution to these problems, we have tried to solve them by means of numerical model calculations. The problems in question will be investigated by testing the behaviour of three or four oscillators whose coupling parameters are varied systematically.

The model

Each oscillator works as a simple relaxation oscillator (see Cruse and Graham (1985); Bässler (1986) for a detailed description). Its output value corresponds to the position of the leg tip. This position moves forward during the return stroke, and backward during the power stroke, between two extreme positions called AEP (anterior extreme position) and PEP (posterior extreme position). The PEP corresponds to 0, the AEP, if uninfluenced, to 1.

The speed during the return stroke is always constant. The speed during the power stroke is fixed during a model walk, but variable from experiment to experiment, representing the differential belt speeds. The PEP is always fixed, whereas the AEP is subject to coordinating influences. The AEP of the influenced oscillator (AEP_i) is changed simply proportionally to the position of the influencing oscillator (x_j). The position value, after multiplication with the coupling factor (CF), is subtracted from the default value of the upper switchpoint: $AEP_i = 1 - x_j * CF_{ij}$. This represents a simplified version of the mechanism found to act between contralateral legs, as is summarized in Fig. 9 of Part I.

Results

The coordination between two oscillators is measured by means of the concentration parameter (CP). This is obtained by measuring the phase value of a given event in the cycle of the test oscillator (here the PEP) in the period of the reference oscillator. For a given number of steps ($N = 250$) the circular mean and, as a measure for the circular standard deviation, the concentration parameter is calculated (Batschelet 1983). This is 0 when both oscillators are completely uncoupled and 1 in the case of strict coordination.

The strength of coordination between two oscillators, i.e. their concentration parameters, depends on the ratio of the intrinsic frequencies, on the number and arrangement of the coupling connections, and on the value of the coupling factors. These dependencies will be investigated below. To simplify the presentation of results the concentration parameter is not given twice, for each oscillator as a reference. By contrast, the subdominant oscillator, i.e., that with the smaller coupling influence, is always used as a reference. Preliminary results showed that the concentration parameter measured in this way was always about 4–6% higher, compared to the concentration parameter obtained

when the dominant oscillator was used for reference. Similar results were obtained in biological experiments (Müller and Cruse 1991). The following section will consider, first, the coupling of two oscillators, then of three oscillators, and finally of four oscillators. In the final section the coupling mechanisms introduced in the model will be modified to fit those found in the biological experiments. In the first three sections, coupling mechanisms are studied that qualitatively, but not quantitatively, agree with those found in the biological experiments. Therefore only the concentration parameters are presented, but not the mean phase values.

Coordination between two oscillators

First, two oscillators OL and OR (L for left and R for right) will be considered, which have a fixed relation of intrinsic frequencies of 1.05. This means that the intrinsic frequency of OR is 5% higher than that of OL. The value of the intrinsic frequency is determined by the speed of the power stroke. In the experiment this was achieved by adjusting the speed of the right and left belt accordingly. The coupling influence is assumed to act only from OL on OR, but not in the opposite direction. Thus, the left, slower oscillator is dominant. When the coupling factor is increased, the concentration parameter of OL measured within the period of OR (defined as "OLinOR") increases as well. This dependence is shown in Fig. 1 and can be approximated by a square root function. Figure 2 shows the values of the concentration parameters of OLinOR, when the coordinating influence acts in both directions between the two oscillators. The coupling factors are varied between 0 and 0.25. In the left half of Fig. 2 the slower oscillator is dominant, which means that it influences the other oscillator by a higher coupling factor. In the right half the faster oscillator is dominant. Here, absolute coordination occurs over nearly the whole range, whereas in the left half coordination is weak. The left lower margin

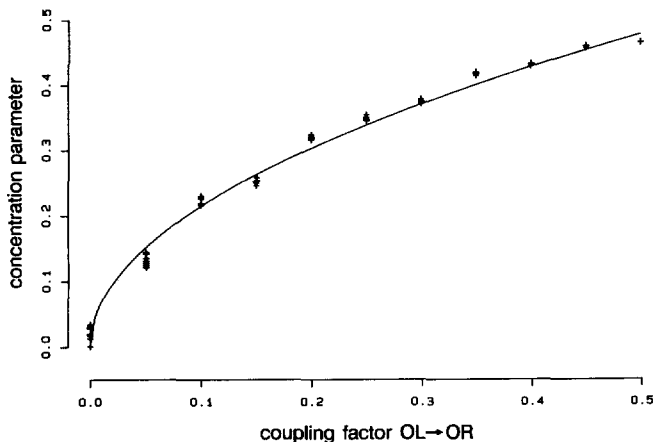


Fig. 1. Dependence of the concentration parameter on the coupling factor for a unilaterally coupled two-oscillator system. The dependence can be approximated by a square root function. The ratio of the intrinsic frequencies OR:OL was adjusted to 1.05

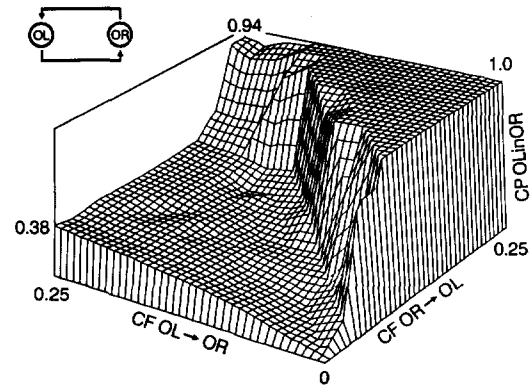


Fig. 2. Dependence of the concentration parameter on the coupling factor in a mutually coupled two-oscillator system (see inset). Left abscissa: coupling factor OL on OR. Right abscissa: coupling factor OR on OL. Ordinate: resulting concentration parameter OL, measured in OR (defined as "OLinOR"). The ratio of the intrinsic frequencies OR:OL was adjusted to 1.05

of Fig. 2 ($CF\ OR \rightarrow OL = 0$) corresponds to Fig. 1. The result can be explained as follows: with the coupling influence, as used here, the frequency of the influenced leg can only be increased, not decreased. Hence the faster, right oscillator has the possibility of increasing the slower, left one such that both oscillators have the same frequency and show absolute coordination. On the other hand, the slower oscillator can never influence the faster oscillator to adopt the same frequency. It can only make the faster one even faster for some steps until both oscillators have the proper phase value. However, as the slower oscillator cannot slow down the faster one, the phase value will shift again, and will therefore again be subject to the coordinating influence. As a result relative coordination occurs.

This agrees with the results found in the biological experiments. Assume that the faster oscillator is dominant. This means considering the right part of Fig. 2. When the right leg is faster, as is assumed for the calculation of the values shown in Fig. 2, absolute coordination occurs. When the ratio of the intrinsic frequencies is reversed, meaning that the slower leg is dominant, the situation corresponds to the left part of Fig. 2. Here only relative coordination can occur. This was in general also true when other ratios of intrinsic frequencies were used, as shown in Fig. 3. Here the left leg is dominant, and four different coupling factors are considered. The coupling factor from the right to the left oscillator is adjusted to 0. The concentration parameters are shown for different ratios of intrinsic frequencies. With the exception of high coupling factors ($CF = 0.4$), the concentration parameters decrease when the frequency ratio increases. The exceptions can be explained as follows: some period ratios produce integer relations so that, for example, the ratio 1.5 corresponds to 2:1 coordination, ratio 1.33 to 4:3 coordination, and ratio 1.25 to 5:4 coordination. For these special cases higher concentration parameters occur. This is particularly prominent in the case of 2:1 coordination for the highest coupling factor investigated.

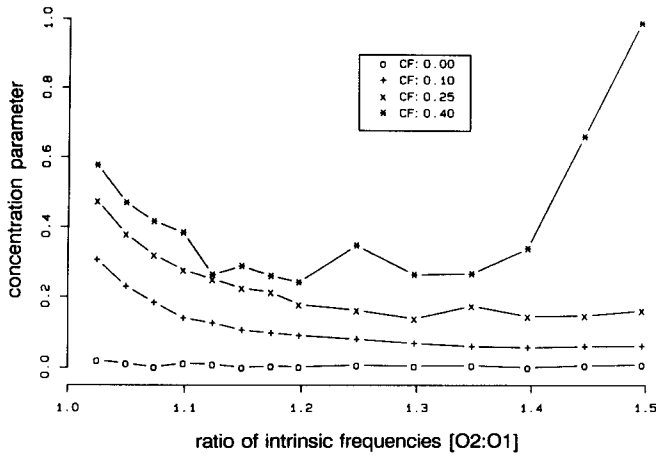


Fig. 3. Dependence of the concentration parameter on the intrinsic frequency ratio for a unilaterally coupled two-oscillator system. Four different coupling factors were tested (see inset)

Three oscillators in series

In the following examples three oscillators, O1, O2, and O3 are connected in series. O1 influences O2, and this in turn influences O3. No influences in the opposite direction are implemented. For the sake of simplicity the ratio of intrinsic frequencies O1 : O2 as well as O2 : O3 has been adjusted to 1.05. This means that the influencing oscillator is always the slower one. The concentration parameters that arise, when the coupling factors between both pairs of oscillators are varied between 0 and 0.5, are shown in Fig. 4a, b. The concentration parameter O1inO2 depends, of course, only on the coupling factor between O1 and O2 (Fig. 4a). This result corresponds to that shown in Fig. 1, but is here represented in another coordinate system to allow comparison with the following results: the concentration parameter O2inO3 does not only depend on the coupling factor between O2 and O3, but also on that between O1 and O2 (Fig. 4b). This happens because for high coupling factors between O1 and O2 the mean frequency of O2 is increased such that it is higher than that of O3. Thus, the situation between O2 and O3 becomes similar to that shown in the right part of Fig. 2. As was tested above for the first two oscillators O1 and O2 (Fig. 3) the concentration parameter O2inO3 generally decreases, when the relation between the intrinsic frequencies of both oscillators increases (Fig. 5). As shown, exceptions occur for values which produce integer ratios, as is the case with a frequency period of 1.33 or 1.5 (CF = 0.4).

Looking at the coordination between O1 and O3 which have no direct coupling connections, the concentration parameter is in general below those measured for direct connections between O1–O2 and O2–O3, as shown in Fig. 6. No simple formula can be approximated to calculate the concentration parameter of O1inO3 as a result of the other two concentration parameters. The surface of the resulting function can only roughly be approximated as a multiplicative superposition of the two concentration parameters measured

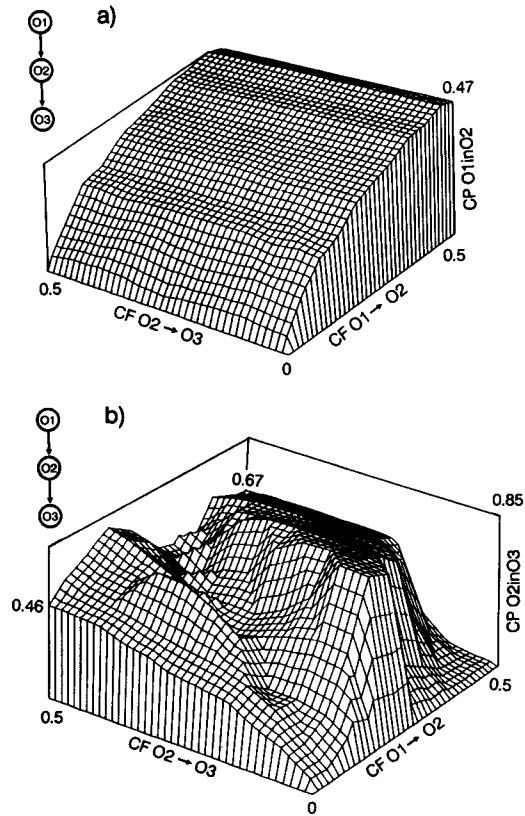


Fig. 4a, b. Dependence of the concentration parameter on the coupling factor for a unilaterally coupled three-oscillator system (see inset). Right abscissa: coupling factor O1 on O2. Left abscissa: coupling factor O2 on O3. Ordinate in a resulting concentration parameter O1inO2. Ordinate in b resulting concentration parameter O2inO3. The ratio of the intrinsic frequencies O2:O1 and O3:O2 was adjusted to 1.05

between the direct coupled oscillators (Fig. 4a, b). The strong coupling between O2 and O3 for coupling values above 0.25 also influences the concentration parameter O1inO3, as shown by a slight elevation of the surface in this area.

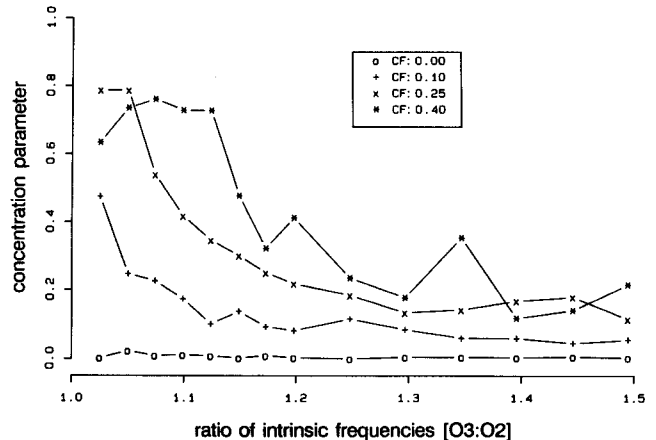


Fig. 5. Dependence of the concentration parameter on the intrinsic frequency ratio for the two coupled oscillators O2 and O3, when O2 was additionally influenced by O1 (as shown in Fig. 3). Four different coupling factors were tested (see inset)

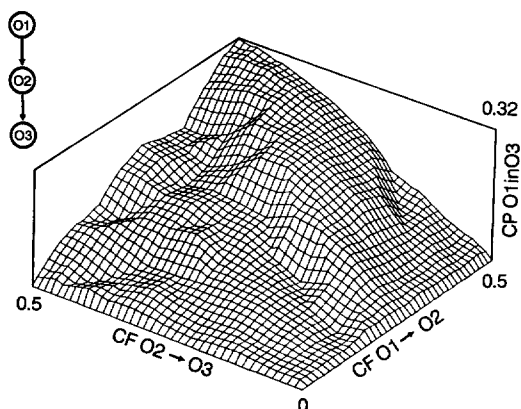


Fig. 6. Dependence of the indirect concentration parameter $O1inO3$ on the coupling factor for a unilaterally coupled three-oscillator system (see inset). Same parameters as described for Fig. 4

Three oscillators arranged in a triangle

The biological situation consists of two legs on the right and two legs on the left side of the body. This corresponds to four oscillators arranged in a square. In the following, subsystems consisting of three of these oscillators will be investigated. Accordingly the oscillators are called OL1 and OL2, corresponding to a left anterior and left posterior leg and, in the same way, OR1 and OR2 for legs on the right side of the body. The relation between any left and any right oscillator will be called "contralateral". This will be specified as "segmental" referring to relations within the first (L1-R1) or the second (L2-R2) segment, or as "diagonal", which includes the relations L1-R2 and L2-R1. A similarity with the situation of our biological experiments is also provided because the intrinsic frequencies of both legs of one side are the same, but are different for the two sides. The ratio $OR:OL$ is 1.05, meaning that the oscillators of the right side have a higher intrinsic frequency. In contrast to the biological situation, and for the sake of simplicity, the "ipsilateral" coupling mechanisms are chosen to be of the same nature and the same strength as the contralateral ones. This simplification will be abandoned later on.

In this part of the investigation the coupling parameters and the period durations were not changed, as was done in the other calculations. Instead, the arrangement of the coupling connections was varied, and the concentration parameters for only one case were calculated. In all cases where the coupling acts only in one direction, the coupling factor was set at 0.25. These influences are shown in the inset figures by straight arrows. In those cases where, in addition, an influence in the opposite direction ("recurrent influence") was introduced, the coupling factor was set at 0.05. The latter influences are shown by double-edged arrows in the insets. Thus, in these simulations the slower side dominates the faster one, which in the earlier simulation (Fig. 2, left side) and in the biological experiments was found to be the more interesting case

compared to the reverse situation, where absolute coordination was found.

At this stage the comparison between the concentration parameters of segmentally neighbouring oscillators (i.e. those which have direct coupling connections) and diagonally neighbouring oscillators (i.e. those which don't have direct coupling connections) is of special interest. First, two different situations will be considered, where three oscillators are connected in series. In contrast to the situation described above, the ratio of intrinsic frequencies of the two pairs of oscillators is now no longer the same.

In the first system, the first two oscillators (OL1 and OL2) have the same intrinsic frequency, whereas the second pair (OL2 and OR2) has different intrinsic frequencies, the right side being 5% faster. In principle the results described in Fig. 7 correspond to those obtained earlier (Figs. 4–6). The diagonal concentration parameter is smaller than the segmental one and roughly corresponds to the product of both concentration parameters of the directly coupled oscillators. When we introduce weak recurrent influences, the concentration parameter $OL1inOL2$ decreases, whereas that of $OL2inOR2$ increases. The diagonal concentration parameter is again something resembling the product. This increase in the concentration parameter of $OL2inOR2$ is to be expected because through the recurrent influence the coupling becomes tighter, leading to a higher concentration parameter. However, this argument does not seem to hold for the coordination between OL1 and OL2. This can be explained in the following way: although the coupling between OL1 and OL2 becomes tighter, the coordination becomes weaker because now the influence from OR2 on OL2 to some extent disturbs the coordination between OL1 and OL2.

Regarding the second system, where OL1 influences OR1, which in turn influences OR2 (Fig. 7c), the result again qualitatively follows the result obtained for the case of equal ratios of intrinsic frequencies (Figs. 4–6). The coordination between OR1 and OR2 is weaker than between OL1 and OL2 in Fig. 7a. This is caused by the "disturbing" influence from OL1 on OR1. Introduction of weak recurrent influences (Fig. 7d) decreases all concentration parameters. The decrease in coordination between OR1 and OR2 can be explained in such a way that the disturbing influence from OL1 is now stronger, although the coordination between OL1 and OR1 is weaker. This can be understood as being the result of the stronger influence of OR2.

As a third system the relatively simple situation of one oscillator, OL1, influencing two others, namely OR1 and OL2 simultaneously is shown. The results (Fig. 7e) are identical with parts of the couplings shown in the former two systems. The diagonal concentration parameter $OL2inOR1$ is weaker than the segmental one ($OL1inOR1$) which is to be expected. When introducing the recurrent influences (Fig. 7f), the coordination between both pairs increases, as does the diagonal concentration parameter. However, it is no longer larger than the segmental one. This result was unexpected and we

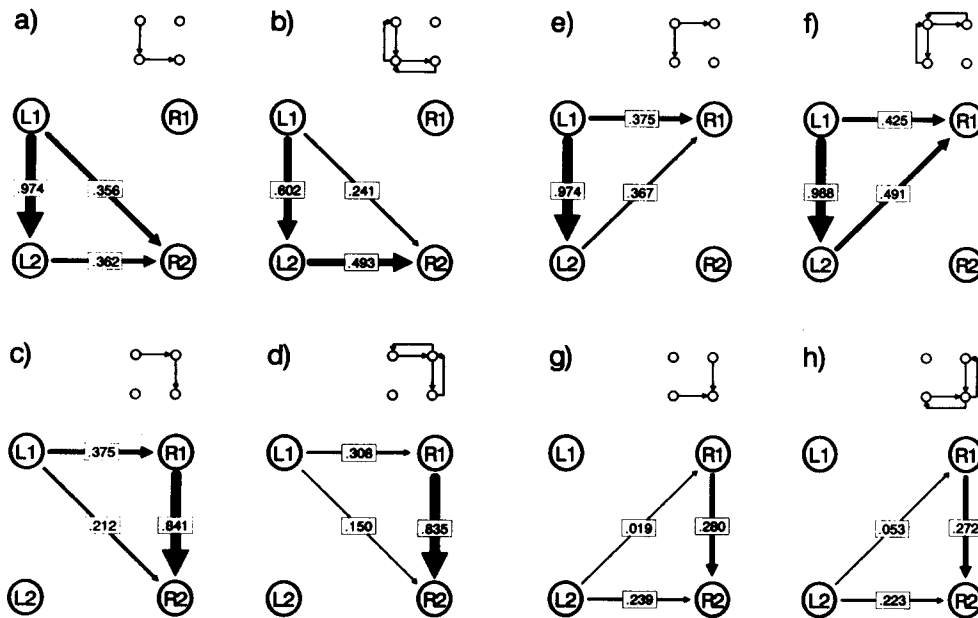


Fig. 7a–h. Concentration parameters of four different three-oscillator systems. In each case the ratio of the intrinsic frequencies between the oscillators of the right and the left side R:L was adjusted to 1.05. The oscillators in (a, c, e, g) were unilaterally coupled systems with coupling factors of 0.25. In (b, d, f, h) additionally, weak recurrent influences with coupling factors of 0.05 were implemented (see insets). The thickness of the lines corresponds roughly to the values of the resulting concentration parameters

have no complete explanation. A comparison of the standard deviations shows that in this situation the mean frequency of OL1 is more modulated than that of OL2. This is based on the fact that OL1 and OL2 (because of their identical intrinsic frequencies) were completely synchronized after a few cycles. Therefore, the coupling factor of OL1 on OL2 (which is five times higher than that of OL1 on OR1) exercises only weak influences. By contrast, based on their different intrinsic frequencies, OL1 and OR1 were subject to sustained recurrent influences, which decreases the segmental concentration parameter of OL1inOR1 more than the corresponding diagonal one of OL2inOR1. It should be mentioned that this difference is significant and has been found in several runs of the simulation, over a broad spectrum of frequency ratios.

In the final, fourth system of three-coupled-oscillators again a situation is encountered where the introduction of recurrent influences decreases coordination. When the two oscillators OL2 and OR1 influence the third oscillator (OR2), all concentration parameters are weak (Fig. 7g), which is to be expected in this situation. With additional recurrent influences the diagonal concentration parameter increases, whereas both other concentration parameters decrease (Fig. 7h). The latter fact can be understood in such a way that the tighter coupling increases the disturbing effect of each of the oscillators on the pair of the other two oscillators. The diagonal concentration parameter in Fig. 7h increases because in the situation shown in Fig. 7g both oscillators OL2 and OR1 are not influenced but subject to some, however weak, indirect coupling.

Four oscillators arranged in a square

In the following, the same arrangement is used, but all four oscillators are now connected in different ways.

Figure 8a shows a system of four coupled oscillators. The coordination between the oscillators OL1, OL2, and OR1 corresponds exactly to the situation presented in Fig. 7e. The addition of oscillator OR2 produces results that correspond to those shown in Fig. 7c. After introduction of the recurrent influences in Fig. 8b, the situation again corresponds to the combination of the two systems shown in Fig. 7f and 7d. Fig. 8b shows a diagonal concentration parameter of OL2inOR1 which is higher than all other contralateral concentration parameters, although there is no corresponding connection between these two oscillators. When the system is completed by a connection from OL2 to OR2, as shown in Fig. 8d, the results change in some respect. The concentration parameter of OL2inOR2 increases as expected. This leads to a decrease in the concentration parameter of OR1inOR2. The diagonal concentration parameters are smaller than both concentration parameters between segmental neighbours. This system is apparently quite stable since an introduction of recurrent influences produces only minor changes.

Up to now the coupling factors between ipsilateral and contralateral oscillators were assumed to have the same values, which however, is in strong contrast to the situation encountered in the biological experiments. For a better approximation of the biological situation, the coupling factors between ipsilateral oscillators are increased from 0.25 to 0.4, whereas the contralateral ones are kept at 0.25. All recurrent influences are also kept at the level of 0.05. Here again, only minor changes were found, but the diagonal concentration parameter of OL2inOR1 again shows the highest value of all contralateral parameters (Fig. 8e, f).

As this case is of special interest here (see Introduction), it will be investigated in more detail. Figure 9 shows the four contralateral concentration parameters when the ratio between the intrinsic frequencies of left and right oscillators (which has been 1.05 up to now) is

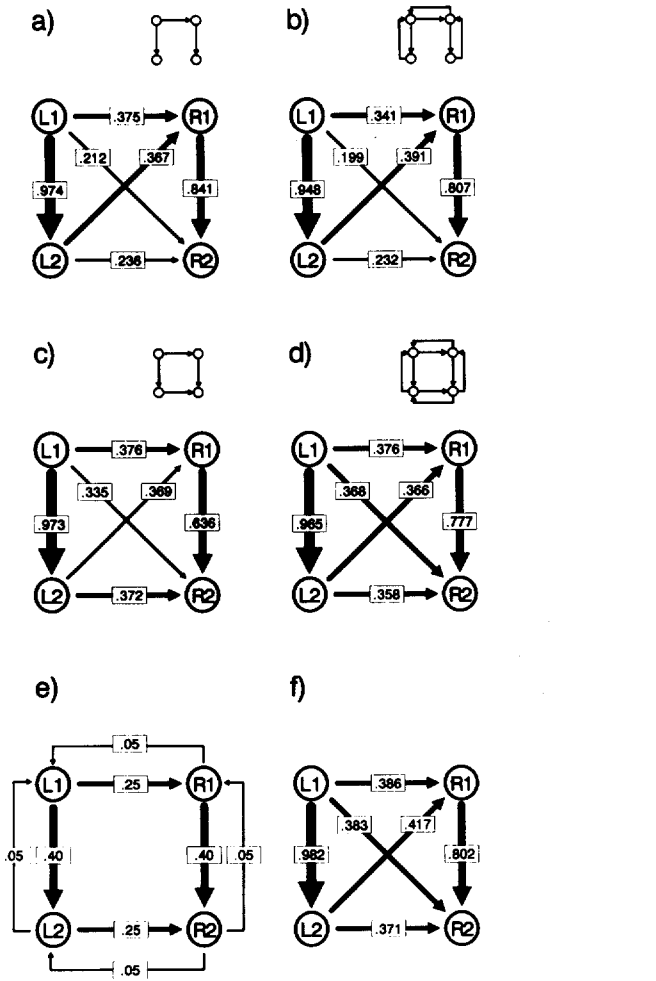


Fig. 8a-f. Concentration parameters for three different four-oscillator systems. e shows the implemented connections of f. Those of a-d are shown in the insets. All other parameters correspond to those in Fig. 7

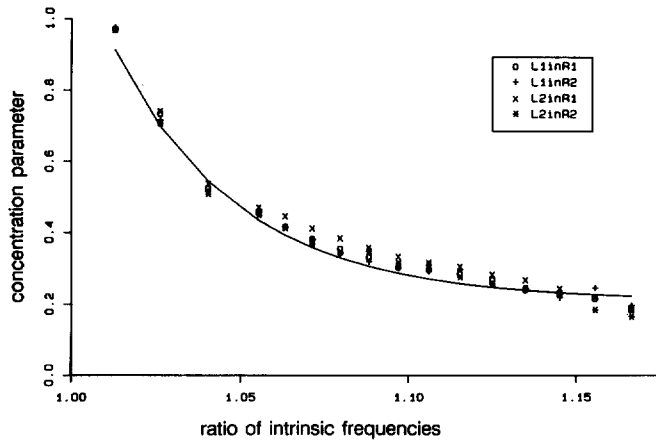


Fig. 9. Dependence of the concentration parameter on the intrinsic frequency ratio for the four-oscillator network shown in Fig. 8e. The abscissa shows the intrinsic frequency ratio between the oscillators of the right and left side. The fitted curve shows the approximated power function $f(x) = k_1 + 1/k_2x$

changed. All four concentration parameters decrease with increasing difference between right and left intrinsic frequencies. In all but two cases the diagonal concentration parameter of OL2inOR1 reaches the highest value. In the remaining two cases the diagonal concentration parameter of OL1inOR2 shows the highest value.

The experiments of Part I (Müller and Cruse 1991) suggested that the diagonal concentration parameter depends on the value of the direct concentration parameters in the following sense: the larger diagonal concentration parameter is that one which connects the ipsilateral legs of the dominant side with the intrasegmental legs pair that has the larger intrasegmental concentration parameter. Therefore, and first for a fixed period ratio, the contralateral concentration parameters were calculated by varying the coupling factor between OL1 and OR1. Figure 10 shows that with decreasing coupling factors between OL1 and OR1 the corresponding diagonal concentration parameter actually increases relatively to the other contralateral concentration parameters. Two cases, (I) where the diagonal concentration parameter of OL1inOR2 is smaller and (II) where it is higher than the posterior segmental concentration parameter of OL2inOR2, will be investigated as to their dependence on the ratio of intrinsic frequencies between right and left side.

Figure 11a shows that for a coupling factor OL1 on OR1 of 0.12 (see (I) in Fig. 10) only for low and high intrinsic frequency ratios the diagonal concentration parameter is higher, whereas for a coupling factor of 0.05 in Fig. 11b (see (II) in Fig. 10) in nearly all cases the diagonal concentration parameter is higher than all other contralateral ones. This illustrates that, under certain conditions, the diagonal concentration parameter may in fact be higher than the other concentration parameters between segmental oscillators, although no direct connection between these diagonally neighbouring oscillators was implemented.

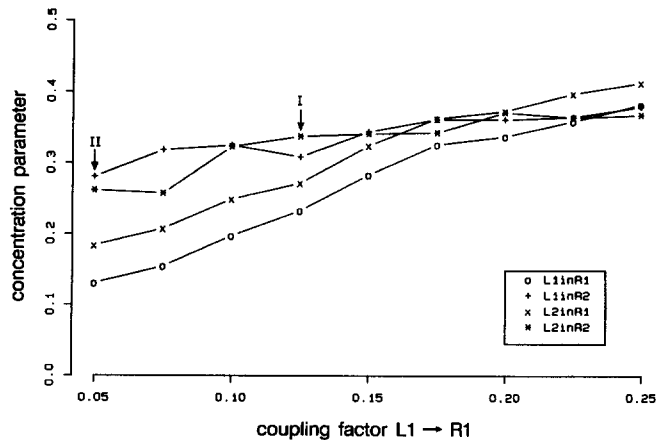


Fig. 10. Dependence of the concentration parameter of a four-oscillator system on the variation of the coupling factor OL1 on OR1 (shown on the ordinate). All other parameters correspond to the network shown in Fig. 8e

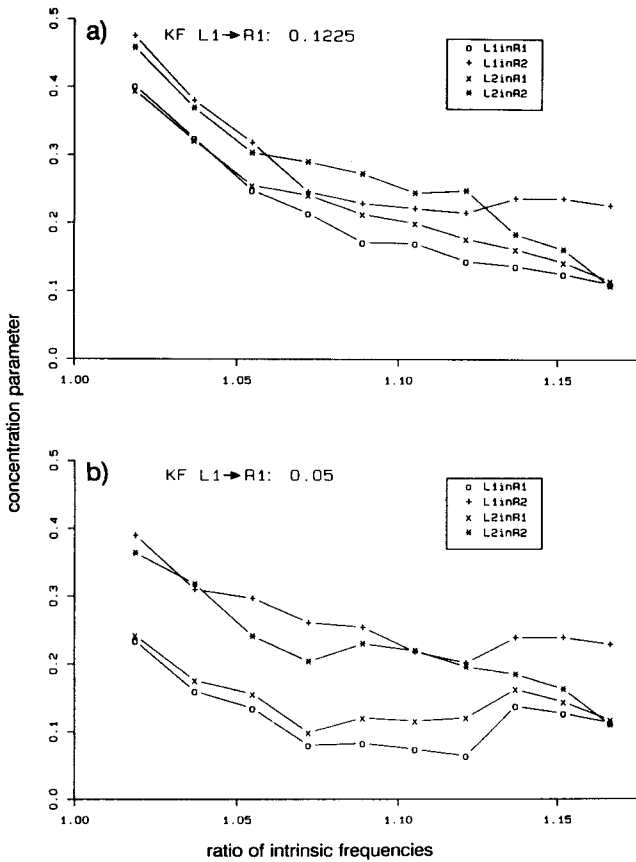


Fig. 11a, b. Dependence of the concentration parameter of a four-oscillator system on the intrinsic frequency ratio. The coupling factor OL1 on OR1 amounts to 0.1225 in **a** and 0.05 in **b**. All other parameters are the same as in Fig. 9

A more realistic model

The results presented up to now were obtained by using a model which is somewhat simplified compared to the actual biological situation. A major difference is the fact that the coordinating mechanisms between the ipsilateral legs are of a different nature than those between the contralateral legs. However, the activity of the former was only approximated by the latter mechanisms using higher coupling factors. For the sake of completeness, the four-oscillator model was now changed in such a way that the actual modes of operation of ipsilateral coupling mechanisms were implemented. Furthermore the form of the contralateral influence, which has been a linear function of the position, was shifted in phase, until it corresponded to the actually observed influence as shown in Fig. 9 of the previous paper (Müller and Cruse 1991). In addition, the thresholds were subjected to a small random variation to simulate the scatter found in the biological experiment. With this adapted model the following results were obtained. Figure 12 shows the phase response curve between OL1 and OR1 when the intrinsic frequency ratio OR1:OL1 is 1.05. The phase response

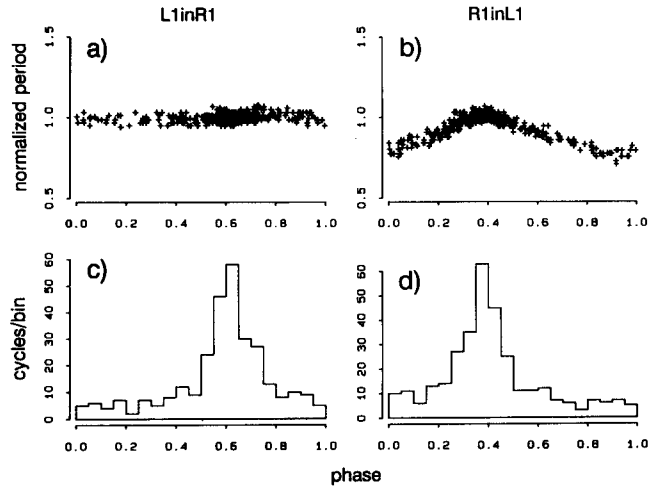


Fig. 12. Phase response curves (**a, b**) and phase histograms (**c, d**) of a four oscillator system. Shown are the two intrasegmental oscillators OL1 and OR1. The abscissa is the phase of the lower switchpoint of the test oscillator, within the actual period of the reference oscillator. The ordinate in the phase response curves is the normalized period (period of the measured cycle/mean uninfluenced period). 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. This figure should be compared with Fig. 4e-h of the previous paper

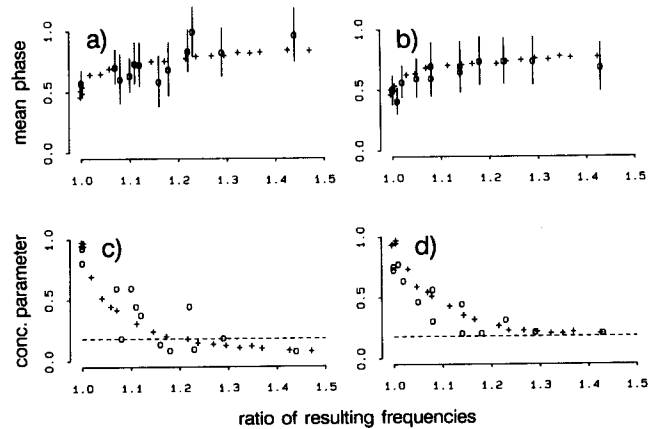


Fig. 13. Dependence of the mean phases **a, b** and concentration parameters **c, d** on the resulting frequency ratio when the ratio of the belt speeds in the experiments and the ratio of the intrinsic frequencies in the model calculations were adjusted correspondingly. **a, c** shows L4inR4; **b, d** shows L5inR5. Comparison between 13 experiments (circles) and a corresponding model calculation (crosses). The vertical lines in **a** and **b** indicate the standard phase deviation. The horizontal lines in **c, d** indicate the significance level of the measurements: mean phases with a concentration parameter below this level were not distinguishable from a random distribution (Rayleigh test). Each measurement of the experiments represents the mean value of between 125 and 345 steps. The model calculation encloses 250 cycles

curves and the corresponding phase histograms have to be compared with Fig. 4e, f of Part I.

For fixed coupling factors the mean phase values and the concentration parameters were calculated when the frequency ratio between the right and left oscillators was systematically varied between 1.0 and 1.5, as was the case for the stepping frequency ratio in the biological

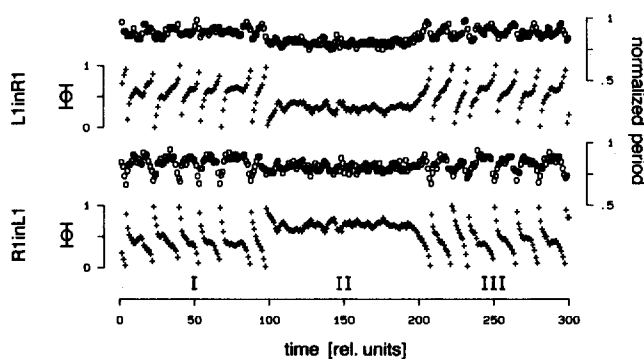


Fig. 14. Simulation of the experiment shown in Fig. 3 of Part I. The abscissa shows time in relative units. The four traces on the ordinate from top to bottom show: (1) the period duration (in relative units) of OL, (2) the phase of OLinOR, (3) the period duration of OR, and (4) the phase of ORinOL. The intrinsic frequency ratio OR:OL was adjusted to 1.05

experiments. The results of the model calculation and of the biological experiments are compared in Fig. 13. Finally, a simulation of the experiment shown in Fig. 3 of the previous paper should be demonstrated: the chosen model system corresponds to that described in Fig. 13, with the exception that now the coupling influences acting from right to left amount to 0.15 and those acting from left to right to 0.25. This means that the left side is slightly dominant. Figure 14 shows the behaviour of the two front oscillators OL1 and OR1. The abscissae in both cases represent time, the four traces of each ordinate show (from top to bottom) the period of OL, the phase of OLinOR, the period of OR, and the phase of ORinOL. At the beginning (I) and at the end of the simulation (III) the intrinsic frequency of the right oscillators is about 5% higher than that of the left ones. In the middle (II) the frequency ratio was reversed. As long as the oscillators of the left side (which have a slightly stronger influence on the right ones reversely) possessed the slower intrinsic frequency, relative coordination could be observed. As soon as the frequency ratio was reversed (II), absolute coordination occurred. Similar to the experimental results a shift of mean phases, as well as an increase in concentration parameters could be measured. Thus, as in the biological experiments, the intrinsic frequency ratio between both sides was exactly reversed, but the resulting parameters were not.

Discussion

The investigation provides general results concerning the question of in which way the strength of coordination, measured using the concentration parameter, depends on the coupling factor. As coupling influence a mechanism was studied which, in agreement with results of the biological experiments, can only shorten the period of the influenced oscillator. For two oscillators with unidirectional coupling, the concentration parameter was found to show a square root dependence on the

coupling factor. No such easy relationship was found for the second pair of three oscillators. Moreover, for cases of a somewhat more complicated arrangement of connections, a prediction was shown to be very difficult and occasionally contrainuitive. Besides these more basic outcomes two specific results are interesting in view of the interpretation of the experimental results presented in Part I. Regarding the coordination between a left and its segmental right neighbouring leg, it was found, that there was some sort of a priori dominance, i.e., the period of the dominant leg was less influenced than the period of the subdominant leg. The type of coordination could be influenced experimentally by driving the legs at different speeds during the power stroke. When increasing the speed of the dominant leg, absolute coordination was observed. When decreasing the speed of the dominant leg, coordination was relative. A question arose therefore, as to the kind of systems underlying these results. Modelling a two- as well as a four-oscillator system with mutual influences of various strengths produced exactly corresponding results. Thus, the experimental results could be interpreted with the aid of the following, simple hypothesis: dominance results from an endogenously given difference between mutual coupling factors. Changing the intrinsic frequencies in such a given system produces absolute coordination when the dominating oscillator is faster, but weak and relative coordination when the dominating oscillator is slower. This could be applied to a situation where the animal walks in curves as follows: assuming that the legs which walk at the outside of the curve and therefore have to walk faster are made to be endogenously dominant by means of a central influence, absolute coordination would always occur during curve walking. Relative coordination would only occur when an animal which intends to turn to one side, but is forced to turn to the other side by an external influence, e.g. a water stream.

The second question which had remained unanswered by the experimental results was the following: how can one infer the existence of actual neuronal connections between both legs under review from the existence of strong concentration parameters? It is immediately clear and has also been shown in the model calculation, that oscillators are coordinated to some extent, even when there is no direct coupling connection between them and they are coupled only indirectly via other oscillators. Therefore, one would expect that a direct connection would lead to high concentration parameters, and indirect connections could be identified by low ones. Since in the experiment, diagonally neighbouring legs eventually showed the highest contralateral concentration parameters, this hypothesis would have led to the conclusion that direct neuronal connections exist between diagonally neighbouring legs, in contrast to direct neighbouring legs of the same segment. Or, at least that the diagonal connections are stronger than the direct segmental ones. However, the model calculations have clearly shown that under particular conditions diagonal concentration parameters can be higher than direct segmental concentration parameters,

although no diagonal connections exist. These conditions are as follows:

* There have to exist mutual influences with different strengths between the segmental pairs of contralateral legs. This means that one side (e.g. the left) has to be dominant.

* Moreover, the strengths of the coupling influences between two neighbouring segmental leg pairs (e.g. pairs L4-R4 and L5-R5) have to be different.

If both conditions were fulfilled, high diagonal concentration parameters with values above the corresponding segmental ones resulted, although no direct diagonal connections were implemented in the model. As could be demonstrated, these conditions have been fulfilled in those experiments which showed a high diagonal concentration parameter. Therefore the most probable interpretation is that no diagonal, but only segmental connections exist between contralateral legs.

Acknowledgements. This study was supported by DFG (CR 58/2).

References

- Bässler U (1986) On the definition of central pattern generator and its sensory control. *Biol Cybern* 54:65–69
- Batschelet E (1983) Circular statistics in biology. Academic Press, London New York
- Clarac F (1982) Decapod crustacean leg coordination during walking. In: Herreid CF II, Fourtner C (eds) Locomotion and energetics in arthropods. Plenum Press, New York London, pp 31–71
- Clarac F, Barnes WJP (1985) Peripheral influences on the coordination of the legs during walking in decapod crustaceans. In: Bush BMH, Clarac F (eds) Coordination of motor behaviour. University Press, Cambridge, pp 249–269
- Cruse H (1990) What mechanisms coordinate leg movements in walking arthropods? *TINS* 13:15–21
- Cruse H, Graham D (1985) Models for the analysis of walking in arthropods. In: Bush BMH, Clarac F (eds) Coordination of motor behaviour. University Press, Cambridge, pp 281–301
- Cruse H, Müller U (1986) Two coupling mechanisms which determine the coordination of ipsilateral legs in the walking crayfish. *J Exp Biol* 121:349–369
- Delcomyn F (1985) Factors regulating insect walking. *Ann Rev Entomol* 30:239–256
- Graham D (1985) Pattern and control of walking in insects. In: Advances in insect physiology, vol 18. Academic Press, London, pp 31–140
- Holst E von (1939/1973) Relative coordination as a phenomenon and as a method of analysis of central nervous function. Reprinted in: The collected papers of Erich von Holst, University of Miami Press, Coral Gables, Fla
- Müller U, Cruse H (1991) The contralateral coordination of walking legs in the crayfish *Astacus leptodactylus*. I. Experimental results. *Biol Cybern* 64:429–436
- Pavlidis T (1973) Biological oscillators: their mathematical analysis. Academic Press, London New York
- Stein PSG (1976) Mechanisms of interlimb phase control. In: Hermann RM, Grillner S, Stein PSG, Stuard DG (eds) Neural control of locomotion. Plenum Press, New York London, pp 465–487

Prof. Dr. Holk Cruse
Fakultät für Biologie
Universität Bielefeld
Postfach 8640
W-4800 Bielefeld 1
Federal Republic of Germany