

The Coordination of Force Oscillations and of Leg Movement in a Walking Insect (*Carausius morosus*)^{*}

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Abstract. As in the preceding paper stick insects walk on a treadmill and different legs are put on platforms fixed relative to the insect's body. The movement of the walking legs is recorded in addition to the force oscillations of the standing legs. The coordination between the different legs depends upon the number and arrangement of the walking legs and the legs standing on platforms. In most experimental situations one finds a coordination which is different from that of a normal walking animal.

Introduction

In the preceding paper qualitative results are reported which are obtained in the following experimental situation. A stick insect *Carausius morosus* was fixed dorsally on a holder and was allowed to walk on a treadmill. Then one leg was placed on a platform fixed relative to the insect's body beside the treadmill. If the position of the platform is far enough forward, this leg remains standing on the platform while the other legs walk and turn the treadmill. When the animal walks the standing legs develop forces which oscillate in the walking rhythm. In this paper the quantitative results concerning the temporal coordination of the force oscillations of the standing legs as well as of the movements of the walking legs are presented.

Methods

The methods of measuring the forces of the standing leg and the movement of one walking leg were described earlier (Cruse and Saxler, 1980). To obtain the coordination of the walking legs, in a separate experimental series the animals were filmed using a Cine Beaulieu S-8 camera (18 frames/s). The temporal

pattern of the retraction (stance phase) and the protraction (swing phase) of the different walking legs was determined by single frame analysis. From these data the phase plots between all pairs of walking legs are calculated with the help of a computer. The phase plots show the frequency of occurrence of the onset of the retraction of the first leg relative to the period (retraction time plus protraction time) of the second (reference) leg. A *period* used here always begins with the *retraction* movement. In the phase plots period is normalised to 360°. The data are distributed over 12 classes of 30° interval. The same method is used for the phase distributions of the force maximum values.

Statistics: As all these phase values are circular variables the mean angle and the circular standard deviations must be calculated by the methods of circular statistics (Batschelet, 1965). The smaller the deviation of a phase plot the better the two legs are coordinated. To obtain a qualitative but short description of the strength of coordination in the following it will be called "good coordination", if the amount of the circular standard deviation is less than 63°, it will be called a "weak coordination", if this value lies between 63° and 72°. It will be called "no detectable coordination" when the amount of the circular standard deviation is higher than 72° (the highest possible value is 81°). If $n=130$ 72° corresponds to a significance level of $p \leq 1\%$ (for a circular normal distribution). Often the force oscillations of two standing legs can qualitatively be described as being "in phase", i.e. the maxima or the minima of both legs occur at the same time. To use a quantitative measure two standing or two walking legs are said to be "in phase" if $|s| \leq 72^\circ$ and the value of the mean angle of the phase plot lies in the range of $\pm 30^\circ$. When coordination exists but the mean angle is different, then both legs will be said to *alternate*. It should be stressed that this definition includes not only a phase difference of 180° but all phases different from "in phase" coordination. Sometimes the phase distribution seems to have two peaks. Then only a qualitative description is used. In these cases the circular standard deviation is no longer a useful parameter. Therefore, in cases where an obvious bimodal distribution seems to exist, the two mode values are given in the tables.

Results

a) The Different Experimental Situations

The experimental situation examined first is the case where both hindlegs stand on force transducers and all the other legs walk on the treadmill (L1L2R1R2). To determine the coordination between different pairs of legs, the mean angle and the circular standard deviation of all the phase distribution measured are given

* Supported by DFG (Cr 58/1)

Table 1. Phase distributions between the movement of walking legs and the force oscillations of standing legs. In a walking leg the onset of retraction movement, in a standing leg the maximum of the force is used as reference point. The first value gives the mean angle, the second in brackets the circular standard deviation. If a bimodal distribution exists, the first two values show the mode values. The third value gives the number *n* of evaluated cycles. If a fourth value occurs this shows the number of "no phases" (see text). **a** Experimental situation L1L2R1R2

	Reference leg					
	L1	L2	L3	R1	R2	R3
L1	X	163° (± 52°) 105 10%		193° (± 49°) 108 5%	349° (± 54°) 108 15%	
L2	225° (± 49°) 109 8%	X		53° (± 61°) 105 13%	204° (± 55°) 108 9%	
L3	188° (± 62°) 645		X			
R1	194° (± 49°) 107 7%	338° (± 62°) 101 14%		X	152° (± 49°) 106 8%	
R2	46° (± 52°) 108 15%	185° (± 54°) 105 9%		232° (± 49°) 106 7%	X	
R3	318° (± 62°) 657		157° (± 53°) 359			X

Table 1b. Experimental situation L2L3R2R3

	Reference leg					
	L1	L2	L3	R1	R2	R3
L1	X	36° (± 60°) 295				
L2		X	164° (± 63°) 153 20%		164° (± 78°) 158 16%	282° (± 79°) 151 22%
L3		209° (± 68°) 138 26%	X		11° (± 77°) 139 20%	185° (± 73°) 139 18%
R1	358° (± 27°) 108	42° (± 60°) 301		X		
R2		202° (± 77°) 146 19%	22° (± 79°) 146 17%		X	167° (± 64°) 139 23%
R3		130° (± 80°) 147 24%	193° (± 74°) 149 16%		205° (± 72°) 145 22%	X

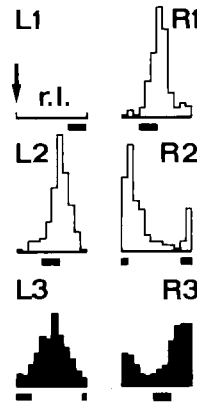


Fig. 1. Experimental situation L1L2R1R2. Phase histograms of walking legs (reference point is onset of retraction, white columns) and of the forces of standing legs (reference point is the maximum value of force, black columns). The reference leg is the left frontleg L1. The black bars show the occurrence of protraction movement expected for free walking animals

in Table 1a. The coordination of the four walking legs agrees well with the coordination in free walking animals. This is more clearly seen in Fig. 1. Here the five phase distributions obtained with L1 as reference leg are shown. The position of the black bars showing the occurrence of protraction is calculated using the data of Wendler (1964). In addition Fig. 1 shows that in the standing legs (L3, R3) the expected protraction occurs at the same time as the force minimum.

Sometimes a walking leg makes no step during the whole period of the reference leg. This will be called "no phase" and the number of such occurrences is given as a percentage of the whole number of steps for the reference leg. These values are also shown in Table 1. For comparison Graham (priv. comm.) showed that in intact free walking animals these values are about 1% for the frontlegs, 0.01% for the middlelegs and 0.4% for the hindlegs.

In the experimental situation L2L3R2R3 both frontlegs stand on force transducers, while the middle- and hindlegs walk on the treadwheel. The results are shown in Table 1b. When looking at the force measurements the most impressive result is the strong "in phase" coupling between L1 and R1. The legs R2 and R3 show no detectable coordination when referred to L2. However, reference to Table 1b shows that R2 and R3 are better coordinated and alternate as is the case for L2 and L3. This means that the coordination between R2 and R3 and between L2 and L3 agrees with the coordination of a free walking animal but not the coordination across the body (i.e. between L2 and R2 and between L3 and R3).

The results of the experimental situation L1L3R1R3, where both middlelegs are standing on the force transducers are shown in Table 1c. Except for the

Table 1c. Experimental situation L1L3R1R3

	Reference leg					
	L1	L2	L3	R1	R2	R3
L1			159° (± 76°) 153 15%	187° (± 61°) 155 10%		286° (± 78°) 151 15%
L2			1° (± 68°) 206			
L3	284° (± 74°) 141 21%			38° (± 79°) 135 24%		58° (± 81°) 135 21%
R1	212° (± 58°) 154 11%		38° (± 79°) 149 14%			186° (± 78°) 146 18%
R2		33° (± 77°) 202	55° (± 73°) 204			
R3 ...	97° (± 78°) 144 20%		164° (± 80°) 146 16%	276° (± 80°) 147 19%		

Table 1d. Experimental situation L1R1

	Reference leg					
	L1	L2	L3	R1	R2	R3
L1				178° (± 73°) 165 18%		
L2	155° (± 71°) 160					
L3	155° (± 71°) 158	6° (± 61°) 155				
R1	209° (± 71°) 157 22%					
R2	151° (± 66°) 154	5° (± 65°) 154	13° (± 58°) 148			
R3	199° (± 72°) 162	13° (± 72°) 156	13° (± 73°) 152		16° (± 59°) 150	

pairs L2, L3 and L1, R1 no coordination can be seen. In this situation only the coordination between the frontlegs agrees with the coordination of a free walking animal, but not the coordination between front- and hindlegs nor between both hindlegs. It should be mentioned that in this experimental situation the coordination of the walking legs was also investigated

Table 1e. Experimental situation L2R2

	Reference leg					
	L1	L2	L3	R1	R2	R3
L1		345° (± 70°) 195				
L2					271° (± 81°) 75 25%	
L3		20° (± 66°) 191				
R1	3° (± 36°) 111	336° (± 78°) 198				
R2		110° (± 78°) 84 14%				
R3		39° (± 77°) 181	260° (± 78°) 166	354° (± 72°) 202		

Table 1f. Experimental situation L3R3

	Reference leg					
	L1	L2	L3	R1	R2	R3
L1			359° (± 72°) 182			
L2	34° (± 46°) 172		36° (± 61°) 163	21° (± 49°) 136		
L3						161° (± 56°) 39 11%
R1	21° (± 42°) 179		345° (± 75°) 187			
R2	21° (± 51°) 120	356° (± 57°) 180	194° (± 78°) 225	22° (± 52°) 180		
R3			189° (± 62°) 51 15%			

by Wendler (1964). In contrast to our results Wendler found an alternating phase relationship between ipsilateral front- and hindlegs. The only detectable difference between both experiments seems to be the different mechanical properties of the treadwheels. The moment of inertia of Wendlers treadwheel seems to be about a factor 10 higher and the friction about a factor 7

Table 1g. Experimental situation L1

	Reference leg					
	L1	L2	L3	R1	R2	R3
L1	✗					
L2	224° (± 60°) 209	✗				
L3	164° (± 63°) 106	6° (± 51°) 93	✗			
R1	195°; 345° 217			✗		
R2	195°; 345° 185	2° (± 23°) 60		1° (± 31°) 73	✗	
R3	203 (± 66°) 189		353° (± 47°) 35	347° (± 53°) 90		✗

Table 1h. Experimental situation L1L2

	Reference leg					
	L1	L2	L3	R1	R2	R3
L1	✗	105° (± 65°) 108 16%				
L2	274° (± 63°) 106 22%	✗				
L3	201° (± 70°) 129		✗			
R1	15°; 195° 188			✗		11° (± 69°) 181
R2	190° (± 61°) 191			353° (± 38°) 159	✗	
R3	75° 225° 177		15°; 105° 122		75°; 255° 242	✗

smaller than in our case. In addition the breadth of Wendlers treadmill was 30 mm in contrast to ours of 9 mm.

In the experimental situation L1R1 both frontlegs walk while the middle- and hindlegs stand on the force transducers. The results are shown in Table 1d. Both walking legs alternate (which is in agreement with the behaviour of the free walking animal) and all the standing legs are "in phase" with one another. When L1 is the reference leg in L2 and L3 however a small second mode seems to exist.

Table 1i. Experimental situation L1L2L3

	Reference leg					
	L1	L2	L3	R1	R2	R3
L1	✗	153° (± 63°) 154 9%	213° (± 77°) 138 23%			
L2	234° (± 54°) 122 28%	✗	111° (± 69°) 113 32%			
L3	168° (± 72°) 149 20%	305° (± 74°) 145 12%	✗			
R1	15° 195° 172			✗		
R2	166° (± 68°) 348			4° (± 53°) 316	✗	
R3	105°; 255° 207			1° (± 73°) 256	15°; 255° 157	✗

Table 1k. Experimental situation L2

	Reference leg					
	L1	L2	L3	R1	R2	R3
L1	✗	278° (± 69°) 104				
L2		✗				
L3		319° (± 72°) 72	✗			
R1	26° (± 47°) 99	233° (± 65°) 102		✗		38° (± 76°) 91
R2		36° (± 74°) 90		2° (± 42°) 80	✗	26° (± 75°) 91
R3		179° (± 66°) 96	206° (± 72°) 69			✗

In the experimental situation L2R2 both middlelegs walk while the front- and hindlegs stand on the force transducers. The results are shown in Table 1e. Between L2 and the legs L1 and L3 there is a detectable coordination while no coordination can be detected between L2 and the legs of the right side of the body. In contrast to this result both middlelegs alternate in free walking animals. However, between L1 and R1 one often finds a rigid "in phase" coupling.

In the experimental situation L3R3 both hindlegs walk, while the front- and middlelegs stand on the

force transducers. The results are shown in Table 1f. All standing legs are "in phase". Both hindlegs alternate in agreement with free walking animals.

In the experimental situation L1 all legs except L1 stand on force transducers. The results are shown in Table 1g. R1 seems to have two modes in the F_{\max} -distribution which are shown in Table 1g, while the F_{\min} -distribution is unimodal with $110^\circ (\pm 68^\circ)$ (mean angle and circular standard deviation). The same is true for R2. Here the corresponding values of the F_{\min} -distribution are $74^\circ (\pm 63^\circ)$. All the standing legs are "in phase".

In the experimental situation L1L2 the left front- and middlelegs are walking while the remaining four legs are standing on force transducers. The results are shown in Table 1h. Except for the pair R2-R3 all standing legs are "in phase". As R3 seems to show a bimodal distribution, when L1 is the reference leg, the coordination between R3 and the other legs is weak. A bimodal distribution also seems to exist for R3 when L3 or R2 are used as a reference leg. The legs L1 and L2 alternate in agreement with free walking animals.

In the experimental situation L1L2L3 all the legs of the left side of the body walk, while those of the right side stand on force transducers. The results are shown in Table 1i. R1 and R3 seem to have two modes, when L1 is the reference leg. However, the standing legs themselves are "in phase". Between R2 and R3 two modes seem to exist. As in the situation L1L2 the walking legs L1 and L2 show the same coordination as in the free walking animal. This is also true for the walking leg L3 although this distribution is relatively broad. The nonsymmetrical values of the "no phases" indicate that the middleleg makes less steps than do front- and hindlegs in this situation.

In the last experimental situation examined (L2) only the leg L2 walks while all other five legs stand on force transducers. The results are shown in Table 1k. Both frontlegs show good "in phase" coordination. As in other experimental situations good "in phase" coordination can be seen between the ipsilateral front- and middleleg (R1-R2). For all other legs coordination is weak or undetectable. The legs L3-R3 alternate.

The period duration measured as mean value of all period values for all walking legs is shown in Table 2 for the different experimental situations. The mean values of the protraction times lie between 145 ms and 189 ms except for those of the experimental situation L2R2 with a mean protraction time of 323 (S.E. ± 13)ms ($n=198$), L3R3 with 376 (S.E. ± 24)ms ($n=78$) and for L2L3R2R3 with 230 (S.E. ± 6)ms ($n=671$). This indicates that the period is smaller when the frontlegs are walking. The mean value of all protraction times is 193 (S.E. ± 4)ms ($n=3181$) which

Table 2. The mean values of the period time (retraction time plus protraction time) and their extreme values obtained in the different experimental situations

	Mean value (ms)	Minimum value (ms)	Maximum value (ms)
<u>L1L2R1R2</u>	735	389	3053
<u>L2L3R2R3</u>	875	278	1887
<u>L1L3R1R3</u>	714	278	3330
<u>L1R1</u>	558	222	1998
<u>L2R2</u>	804	500	2942
<u>L3R3</u>	1915	944	4940
<u>L1</u>	672	325	975
<u>L1L2</u>	732	500	3164
<u>L1L2L3</u>	770	222	1610
<u>L2</u>	672	325	1626

agrees well with the results of Wendler (1964) where the animals walk on a treadwheel.

b) The Different Pairs of Legs

The manner in which the phase relations between the movements of two walking legs or between the forces of two standing legs can be obtained has already been described. But no definition has been given up to now regarding how to describe the phase relations between a walking and a standing leg. One might assume that the force maximum corresponds to a retraction and a force minimum corresponds to a protraction. This assumption is supported by the following results. In the experimental situation L1L2R1R2 in the standing legs L3 and R3 the mean value of the force minimum occurs at that time when in the free walking animal the protraction of each leg would occur (Fig. 1), which agrees with this assumption. This is more clearly indicated by the observation of Bässler (1979) on larvae of *Extatosoma tiaratum*. He found, in similar experiments involving one or both middlelegs standing on a force transducer, that all transitional stages from the usual force minimum to development of anteriorly directed forces, followed by short lifting of the leg and finally real protraction movements were present. We found similar results after re-examining the *Carausius* films used in this study. However, it does not occur so regularly as in *Extatosoma* larvae. Thus, a standing and a walking leg are said to be "in phase", when the mean value of the force maximum appears in the middle of the retraction of the walking leg or the mean value of the force minimum appears during the protraction of the walking leg.

Regarding the pair of legs L1-R1 one finds that both legs alternate when walking but they are "in phase" when both stand. When only one leg of a pair walks (L1, L1L2, L1L2L3), the phase distribution of the standing leg is bimodal.

Considering the pair L2–R2, these legs are “in phase” in the situations L1R1, L3R3 and L1. They alternate in the situations L1L2R1R2, L1L2, and L1L2L3 although the latter two can only be concluded indirectly from Table 1h and i, for only the coordination of both legs relative to L1 has been measured. No detectable coupling appears to exist in the situations L2L3R2R3, L1L3R1R3 and L2R2.

For legs L3–R3, one finds “in phase” coordination in the situation L1, alternating coordination with a phase shift of about 180° in the situations L1L2R1R2, L3R3 and L2, no detectable coordination in L2L3R2R3, L1L3R1R3, L1R1 and L2R2, and a bimodal distribution (where one mode is “in phase” the other is alternating) in the situation L1L2 and probably also in L1L2L3 (only an indirect conclusion in the last case). When legs L3 and R3 are standing, both “in phase” and alternating coordination appears. The “in phase” coordination between L3 and R3 arises when both middlelegs are also standing (L1) and the alternating coordination arises when one or both middlelegs are walking (L1L2R1R2, L2).

Discussion

In the preceding paper two alternatives were described for the neuromuscular subsystems controlling the movement of an individual leg. The subsystem could either consist of (a) an oscillator which itself can be influenced (e.g. stopped) at different cycle positions or, as a second possibility, (b) the oscillator itself is not influenced by the sensory feedback but goes on running although the leg stands. What can be said regarding the connections which act between the subsystems? The experimental results show that only in the situation L1L2R1R2 does a coordination occur which agrees with that of a normal walking animal. In all other situations the coordination is different except for certain individual pairs of legs. This indicates that the connections may be altered in different experimental situations. Under this condition it is impossible to draw any necessary conclusions on the nature and direction of the connection but one can only speculate on these connections for each individual experimental situation. In addition the open question of whether the subsystems are of type (a) or (b) makes further conclusions difficult. It is possible to propose a series of necessary conclusions if one assumes that the subsystems are all of type (a) and that, at least between subsystems of walking legs, the same connections always exist in all the situations investigated; assuming the existence of type (b) subsystems it is much more difficult to draw direct conclusions from the experimental results because each standing subsystem could

itself act as a pacemaker and this greatly increases the number of possible models. Therefore, the main purpose of the experiments was to provide an increased data base for quantitatively testing models of the nature of the subsystems and their connections (see Wendler, 1968, 1978; Graham, 1972, 1977; Bässler, 1977). This seems to be a sensible strategy for the investigation of such a complicated system as the number of possible models is hopefully reduced in proportion to the size of the data pool, particularly if the model is also required to describe the coordination pattern of the free walking animal over the whole speed range. The models describing this data is presented in two subsequent papers (Cruse, 1980a, b).

If it is assumed that the connections between subsystems of walking legs are not changed in the different experimental situations it is possible to exclude several possibilities of connections between the subsystems. The first possibility (I) assumes a connection across the body between both frontlegs and then connections along the body from each frontleg to the ipsilateral middleleg and from there to the ipsilateral hindleg. The second possibility (II) assumes connections across the body between the middlelegs and connections along the body from each middleleg to the ipsilateral frontleg and to the ipsilateral hindleg. The third possibility (III) assumes connections across the body between both hindlegs with the connections along the body running from each hindleg to the ipsilateral middleleg and from that to the ipsilateral frontleg. All these connections have to produce alternating coupling in order to describe the coordination pattern of the free walking animal. In addition these three hypotheses include the assumption that in the normal walking animal the pacemaker is the subsystem of one of those legs which have a cross connection to the contralateral subsystem, i.e. the frontlegs in I, the middlelegs in II or the hindlegs in III.

The possibility III can be excluded as it contradicts the coordination of the walking legs found in the situation L2L3R2R3 and of the hindlegs in the situation L1L3R1R3 as assuming possibility III here both legs should alternate. Also the possibility II can be excluded as it contradicts the coordination of walking legs in the situation L2L3R2R3 and L2R2. According to the coordination of walking legs the results of most of the investigated situations do not contradict possibility I but the alternating coordination of the hindlegs in the situation L3R3 cannot be explained by this hypothesis. However nothing has been said about the influences between subsystems of standing legs which possibly might produce this particular result. Besides possibility II and III one can also reject others with one or two additional intersegmental cross connections in other segments. Generally these considerations

show that with the prepositions stated above the pacemaker cannot in every situation be in either one of the middleleg subsystems or one of the hindleg subsystems.

Acknowledgements. We want to thank Prof. Dr. U. Bässler and Dr. D. Graham for many helpful discussions.

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Received: November 2, 1979

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