

## COACTIVATING INFLUENCES BETWEEN NEIGHBOURING LEGS IN WALKING INSECTS

By H. CRUSE

*Faculty of Biology, University of Bielefeld, Postfach 8640, D-4800 Bielefeld, F.R.G.*

*Accepted 7 August 1984*

### SUMMARY

When the movement of one leg of a walking stick insect is interrupted during the power stroke, the force developed by other legs is increased. This effect is shown to occur between all orthogonal nearest-neighbour legs except for the two hind legs. Such effects do not occur between diagonal or next nearest-neighbour pairs. The possible function of these 'coactivating' influences is assumed to be to enable the animal to increase the total force propelling the body.

### INTRODUCTION

Mechanisms which control the movement of a walking leg can be divided into two types. In one type, the controlling influences arise from the leg's own sense organs and there is considerable experimental evidence for this type of mechanism (Wendler, 1964; Runion & Usherwood, 1968; Pearson, 1972; Wong & Pearson, 1976; Bässler, 1977; Cruse & Pfüger, 1981). Influences of the second type arise from the sensory-neural control system of other legs, and some of these influences produce appropriate coordination between the legs. Only a few experimental results are known for the latter influences. For walking insects, one influence acting in the anterior direction is known. It hinders the start of the return stroke movement (swing phase) of a leg as long as the ipsilateral posterior leg is engaged in a return stroke (Bässler, 1977; Graham, 1978; Dean & Wendler, 1982; Cruse & Epstein, 1982). A second influence known to act in the posterior direction affects the position of the endpoint of the return stroke movement (Cruse, 1979; Dean & Wendler, 1983). Another influence seems to increase the probability of the posterior leg starting its return stroke. The existence of such an influence acting in the posterior direction has only been described qualitatively (Graham & Bässler, 1981; Bässler, 1983, Fig. 4.21; Bässler & Wegner, 1983).

This paper focuses upon another kind of inter-leg influence that was first described by Bässler (1979). When a tethered stick insect walks on a treadwheel, it is possible to place one of its legs on a stationary platform beside the wheel. This one leg remains standing on the platform while the others keep on walking (Wendler, 1964). Measuring the forces by which the leg acts on the platform, Bässler found the following effect. If, during walking, the wheel was suddenly

Key words: Stick insects, walking, coordination, load.

stopped by hand, the force developed by the leg on the platform increased. As the sense organs of this leg receive no information about the movement of the treadmill, Bässler concluded that the platform leg must receive information from the sense organs of the other legs.

In the experiment mentioned, the other five legs were usually stopped simultaneously. Thus, it was not clear whether this influence arose from all the other legs or only from selected ones. Therefore, in the experiment reported below I used the same method but tried to stop the movement of selected legs only. This made it possible to isolate and describe the influence between individual pairs of legs.

#### METHODS

The tethered stick insects (*Carausius morosus*) walked on a light-weight double wheel (for details see Graham, 1981), with one leg positioned on a platform mounted on a force transducer (strain gauge BLH type SPB 3-18-100). The experimental design called for one selected leg to walk on one wheel whilst the remaining four legs walked on the other wheel. This is most easily possible by shifting the body of the animal away from the midline between the two wheels. However, this was not possible for all combinations; in such cases one or two of these remaining four legs were placed on an auxiliary platform but without force transducers (see also Discussion). After the insect had walked several steps, the wheel with the individual leg was stopped by hand. The force of the leg standing on the force transducer was then measured and recorded on a pen recorder. As the forces developed by the latter leg oscillate considerably (Cruse & Saxler, 1980), the results were evaluated as follows. The maximum force value in the second before the stop and the maximum force value in the two seconds after the stop were measured (Fig. 1, arrows), after which the difference between the two values was calculated.

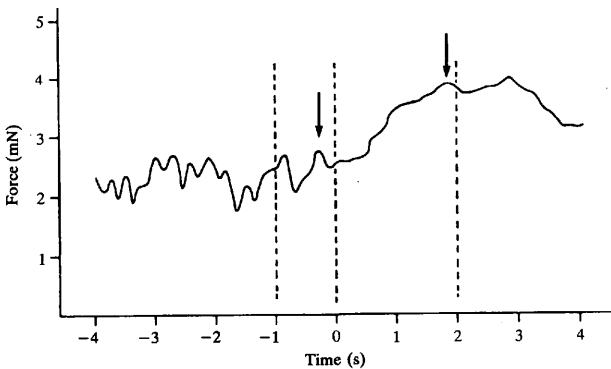


Fig. 1. An example of forces developed by a middle leg when the front leg walking on the wheel was stopped at time 0. The maximum force value was measured during the second before the stop and again in the two seconds following the stop (arrows). Positive forces act in a backward direction.

## RESULTS

The study investigated the effects on each of the three legs on the right side of the body that occurred when either one leg of the same side, or one leg of the opposite side or, in one case, all three legs of the opposite side were stopped. Mean values of the differences between the force value before and after the stop are shown in Table 1 and Fig. 2. Significant effects (paired *t*-test,  $P < 0.2\%$ ) were found only in the case of nearest-neighbour legs (Fig. 2B), except for the hind legs, where the response is similar to that found for more distant legs and is not significant (Fig. 2A). Contralateral influences upon the right hind leg were investigated by stopping all three left legs simultaneously, but again no significant effects were found. Only effects upon legs on the right side of the body were investigated, but one can assume that corresponding effects would be found if the left side were studied.

The results show that the effects are larger between front and middle legs and smaller between middle and hind legs. However, within a given pair of legs the magnitude of the effect is about the same in both directions (Fig. 2B).

In Table 1 the absolute values of force changes are given. To allow calculation of the relative values, Table 2 gives the mean values of the forces measured before the wheel was stopped. The forces developed by the hind leg are about half of those found for front and middle legs. Nevertheless, as Fig. 2 shows, the absolute effects arising from middle and hind legs are very similar.

Fig. 1 illustrates an example in which the force values increase relatively slowly. Averaging 20 such records produced the typical time course shown in Fig. 3. Immediately after stopping the front leg on the wheel, the force produced by the middle leg increased and reached its maximum value after about half a second.

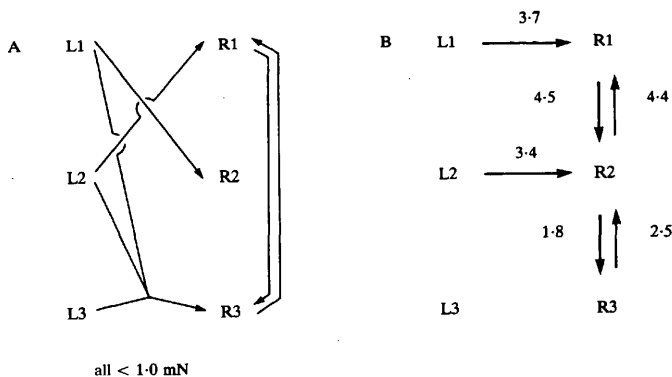


Fig. 2. Influences between legs. (A) Pairs of legs which were investigated but between which no significant ( $P > 10\%$ ) influences were found. (B) Pairs of legs between which significant ( $P < 0.2\%$  or less) influences were found. Numbers indicate the change of force value in mN. Note that only forces of right legs were measured. Legs are named as usual: L for left, R for right and 1,2,3 for front, middle and hind leg, respectively.

Table 1. *Influences between legs*

R1	R2	R3
4.4 ± 4.5 (R2) N = 21, An = 3 P < 0.1 %	4.5 ± 5.4 (R1) N = 20, An = 4 P < 0.2 %	1.0 ± 2.6 (R1) N = 20, An = 5 P > 10 %
0.8 ± 4.2 (R3) N = 20, An = 3 P > 20 %	2.5 ± 3.2 (R3) N = 21, An = 3 P < 0.2 %	1.8 ± 1.8 (R2) N = 20, An = 5 P < 0.1 %
3.7 ± 3.4 (L1) N = 22, An = 4 P < 0.01 %	0.4 ± 2.6 (L1) N = 28, An = 3 P > 20 %	0.3 ± 1.0 (L1-3) N = 30, An = 3 P > 10 %
-0.2 ± 2.1 (L2) N = 20, An = 2 P > 20 %	3.4 ± 7.5 (L2) N = 58, An = 4 P < 0.2 %	

Differences in the forces values for a leg before and after the power stroke movement of another leg (shown in brackets) was stopped experimentally.  
Shown are mean values (in mN),  $\pm$ s.d., sample size (N) number of animals (An) and significance level.

Table 2. *Mean values and standard deviations of forces (in mN) developed by the leg standing on the platform before the wheel was stopped*

R1	R2	R3
21.3 ± 8.8 (R2)	23.0 ± 8.5 (R1)	11.0 ± 7.3 (R1)
27.1 ± 3.5 (R3)	19.5 ± 8.7 (R3)	9.2 ± 7.0 (R2)
23.4 ± 8.3 (L1)	20.5 ± 6.6 (L1)	7.5 ± 4.5 (L1-3)
19.7 ± 3.7 (L2)	26.1 ± 7.7 (L2)	

The symbols in brackets identify the leg walking on the wheel that was later stopped in the running experiment.

For sample size and number of animals, see Table 1.

#### DISCUSSION

A leg on a wheel increases its motor output when the wheel is suddenly stopped (D. Graham, personal communication; Cruse, 1985). This may result from the increased stimulation of load sense organs and/or from an increased error signal of a servomechanism (deviation between actual output value, e.g. leg position or velocity, and the corresponding reference signal of the servomechanism). As Bässler (1979) has shown, corresponding signals of either origin are transferred to the neural control system of the other legs. The results presented here demonstrate the existence of connections transferring such signals between all directly neighbouring legs. However, such connections could not be shown to exist between the two hind legs. These connections may be labelled 'coactivating influences', since an increase of motor output in one leg leads to an increase of motor output in the neighbouring leg.

Some effects of coactivating influences between front legs have been described by Cruse & Saxler (1980). A coactivating influence from middle to ipsilateral hind leg

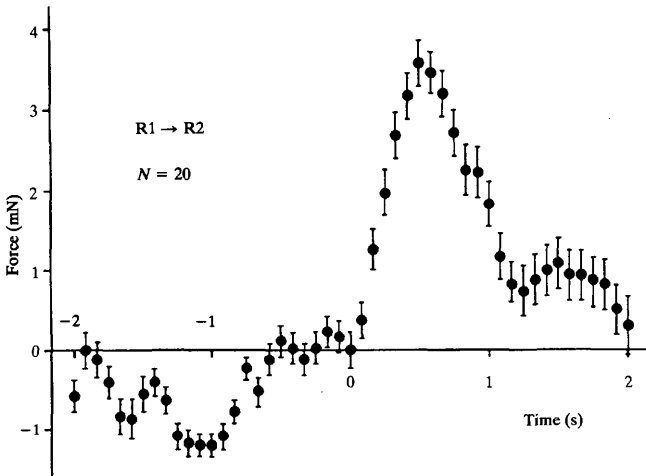


Fig. 3. Time course of the force developed by a middle leg when the front leg walking on the wheel was stopped at time 0. Mean values and standard deviations from 20 experiments. Positive force acts in a backward direction.

was also described by Bässler & Wegner (1983). In the latter case, when the campaniform sensillae of the middle leg were stimulated an increase of motor output in the hind leg was produced. The step frequency of the left legs was increased when the load parallel to the body axis was increased for the right legs (Foth & Graham, 1983). Such coactivating influences may be responsible for in-phase coupling between front legs and the stumps of amputated middle legs (Wendler, 1964), and for similar effects found in the rock lobster (Clarac & Chasserat, 1979). What is the function of these coactivating influences? They may increase the propulsive force of the whole animal in situations when it walks under an increased load. Such simultaneous increase of motor output of all legs has indeed been found in the case of stationary animals starting to walk (Cruse & Saxler, 1980).

One might assume that during normal walking such coactivating influences between neighbouring legs could not occur, as they would interfere with normal coordination. However, a recent model calculation showed that normal coordination is quite possible even when coactivating influences are active (Cruse, 1983). Although this model calculation demonstrates that the activity of such influences during walking does not prevent normal coordination, it is an open question whether these coactivating influences can change the timing of the legs during walking. Fig. 3 shows that these influences are sufficiently fast to be effective during the on-going step. However, as in the experiments described here, strong effects are found only when the animals walk under an increased load, and it can be assumed that coordination is not affected by this mechanism when the animal walks

on a flat horizontal surface. However, under increased load conditions – e.g. when an insect walks vertically upwards – these coactivating influences may play a role. For example, they may be responsible for the kind of coordination that occurs when neighbouring legs protract nearly simultaneously, an event often observed under such conditions.

In an earlier model calculation, the existence of in-phase influences very similar to those described here was postulated (Cruse, 1980; connection type 4). The experimental results support this assumption. However, more connections exist than was earlier assumed: all the connections between two legs, found here, act in both directions. This was not assumed for all cases in the model calculation. In this model calculation another type of in-phase coupling influence was postulated to exist between legs L1 and R2, and between legs L2 and R3 (called type 2); however, this second type was not found in the present experiments.

One could argue that the effects found here were not in all cases the result of direct connections between the two legs under view. In the cases in which one or two additional legs had to be placed on auxiliary platforms (see Methods), the increase of force in the leg on the force transducer may have been caused by indirect connections in the following way. Stopping only one leg could by direct influence have increased only the force of a leg on the auxiliary platform but not the force of the leg on the force transducer. In that case, there would have to be a second direct connection between the leg on the auxiliary platform and the leg on the force transducer. As the load on the leg on the auxiliary platform is increased, this connection would then in turn lead to an increase of force in the leg on the force transducer. Thus, the force increase measured may have been caused by indirect connections running through a third leg. However, this possibility can be excluded for all six cases shown in Fig. 2B. In the four cases in which connections between two ipsilateral legs were found, the third ipsilateral leg (either R1 or R3) stood on an auxiliary platform. If we assume the existence of an indirect influence, as discussed above, then in all four cases a direct connection between front and hind leg has to exist. However, such influences were shown to be non-significant (Fig. 2A). In two experiments in which influences across the body were found (Fig. 2B), either L1 or L2 walked on the wheel and the two remaining left legs stood on auxiliary platforms. If we assume indirect influences to exist, then diagonal direct connections across the body would have to occur as well – but again these were not found to be significant. Of course, one cannot exclude the possibility that a definite connection was 'switched off' in one experimental situation but not in the other. If this did in fact occur, then it is possible that such indirect connections do exist.

I want to express my thanks to Dr D. Forsythe for checking the English of the manuscript. Supported by DFG (Cr 58-3).

#### REFERENCES

- BÄSSLER, U. (1977). Sensory control of leg movement in the stick insect *Carausius morosus*. *Biol. Cybern.* **25**, 61–72.  
BÄSSLER, U. (1979). Interactions of central and peripheral mechanisms during walking in first instar stick insects, *Extatosoma tatarum*. *Physiol. Entomol.* **4**, 193–199.

- BÄSSLER, U. (1983). *Neural Basis of Elementary Behavior in Stick Insects*. Berlin, Heidelberg, New York: Springer-Verlag.
- BÄSSLER, U. & WEGNER, U. (1983). Motor output of the denervated thoracic ventral nerve cord in the stick insect *Carausius morosus*. *J. exp. Biol.* **105**, 127–145.
- CLARAC, F. & CHASSERAT, C. (1979). Experimental modification of interlimb coordination during locomotion of a crustacean. *Neurosci. Letters* **12**, 271–276.
- CRUSE, H. (1979). The control of the anterior extreme position of the hindleg of a walking insect. *Physiol. Entomol.* **4**, 121–124.
- CRUSE, H. (1980). A quantitative model of walking incorporating central and peripheral influences. I. The control of the individual leg. *Biol. Cybernetics* **37**, 131–136.
- CRUSE, H. (1983). The influence of load and leg amputation upon coordination in walking Crustacea: a model calculation. *Biol. Cybernetics* **49**, 119–125.
- CRUSE, H. (1985). Which parameters control the leg movement of a walking insect. I. Velocity control during the stance phase. *J. exp. Biol.* (in press).
- CRUSE, H. & EPSTEIN, S. (1982). Peripheral influences on the movement of the legs in a walking insect *Carausius morosus*. *J. exp. Biol.* **101**, 161–170.
- CRUSE, H. & PFLÜGER, H.-J. (1981). Is the position of the femur-tibia joint under feedback control in the walking stick insect? II. Electrophysiological recordings. *J. exp. Biol.* **92**, 97–107.
- CRUSE, H. & SAXLER, G. (1980). Oscillations of force in the standing legs of a walking insect (*Carausius morosus*). *Biol. Cybernetics* **36**, 159–163.
- DEAN, J. & WENDLER, G. (1982). Stick insects walking on a wheel: perturbations induced by obstruction of leg protraction. *J. comp. Physiol.* **148**, 195–207.
- DEAN, J. & WENDLER, G. (1983). Stick insect locomotion on a walking wheel: interleg coordination of leg position. *J. exp. Biol.* **103**, 75–94.
- FOTH, E. & GRAHAM, D. (1983). The influence of loading parallel to the body axis on the walking coordination of an insect. II. Contralateral changes. *Biol. Cybernetics* **48**, 149–157.
- GRAHAM, D. (1978). Unusual step patterns in the free walking grasshopper, *Neoconocephalus robustus*. I. General features of the step patterns. *J. exp. Biol.* **73**, 147–157.
- GRAHAM, D. (1981). Walking kinetics of the stick insect using a low-inertia counter-balanced, pair of independent treadwheels. *Biol. Cybernetics* **40**, 49–57.
- GRAHAM, D. & BÄSSLER, U. (1981). Effects of afference sign reversal on motor activity in walking stick insects (*Carausius morosus*). *J. exp. Biol.* **91**, 179–193.
- PEARSON, K. G. (1972). Central programming and reflex control of walking in the cockroach. *J. exp. Biol.* **56**, 173–193.
- RUNION, H. J. & USHERWOOD, P. N. R. (1968). Tarsal receptors and leg reflexes in the locust and grasshopper. *J. exp. Biol.* **49**, 421–436.
- WENDLER, G. (1964). Laufen und Stehen der Stabheuschrecke: Sinnesborsten in den Beingelenken als Glieder von Regelkreisen. *Z. vergl. Physiol.* **48**, 198–250.
- WONG, R. & PEARSON, K. G. (1976). Properties of the trochanteral hair plate and its function in the control of walking in the cockroach. *J. exp. Biol.* **64**, 233–249.