

## What Mechanisms Coordinate Leg Movement in Walking Arthropods?

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As mentioned in the contribution of U. Bässler, the system controlling the movement of a walking leg can be considered as a relaxation oscillator. The timing influences are provided by the modalities position and load. The strength of the motor output can be influenced by direct feedback (e.g. velocity control). Timing and shaping can also occur via central influences. The latter can be divided into more general influences as for example those which determine the walking speed of all legs and more specific ones which influence the individual leg in order to produce a coordinated walk. This article will concentrate on the latter. To allow a comparison, the coupling mechanisms for two species, the crayfish *Astacus leptodactylus* and the stick insect *Carausius morosus* will be described.

In the stick insect three different coordinating mechanisms influence the transition from power stroke to return stroke. Two influences are rostrally-directed. One (a) hinders a leg from starting a return stroke as long as the posterior leg performs its return stroke and may continue for about another 100 ms. This influence can prolong the power stroke. In contrast to this "inhibitory" influence the following two have an "excitatory" effect. The second rostrally-directed influence (b) can elicit a return stroke in a leg when the posterior leg starts a power stroke. This influence shortens the duration of the power stroke. A third influence is caudally-directed (c): the start of a return stroke of a leg is more strongly excited, i.e. occurs earlier, the farther the anterior leg is moved rearward during its power stroke. This has the effect that the posterior leg performs a return stroke before the anterior leg begins its return stroke. In addition two other, less important coordinating mechanisms are found in the stick insect which will not be mentioned in detail.

As was found for other arthropods, coupling between contralateral legs is weaker than that between ipsilateral legs. However, two of the three mechanisms found for ipsilateral legs also act between contralateral legs of the same segment. These are the two "excitatory" mechanisms shown for ipsilateral legs; both elicit the start of a return stroke in the other leg. These contralateral influences, unlike the ipsilateral coupling, seem to act in both directions between the two legs of one segment.

In the crayfish, two coordinating mechanisms are found acting between neighbouring ipsilateral legs. One coordinating mechanism is only rostrally-directed: as long as the posterior leg performs a power stroke, the anterior leg has to perform or continue a return stroke. Thus the return stroke can be prolonged so that normal coordination is regained in the next step. The second influence is caudally-directed: when the anterior leg is near the end of its power stroke or at the beginning of its return stroke, an influence with increasing intensity has the effect of ending the return stroke and beginning the power stroke of the posterior leg, thus shortening the return stroke of this leg. Both coordinating mechanisms influence the transition from return stroke to power stroke.

To couple contralaterally neighbouring legs, i.e. legs of the same segment, the crayfish uses a mechanism which very much resembles the ipsilateral, caudally-directed influence (U. Müller, in prep). In contrast to the ipsilateral mechanism where the influence is only active during a small fraction of the whole step cycle, the contralateral influence continues during most of the cycle. With the exception of a small phase range the return stroke of the other leg is always shortened. The effect is much weaker than ipsilateral influences. While in ipsilateral legs the effect of a disturbance is compensated within the following step, because of the weaker coupling in contralateral legs a disturbance results in a so called gliding coordination (the relative coordination of v. Holst). This contralateral influence acts in the same way in both directions but one leg might be somewhat more dominant.

The results show that each walking leg can be considered as an oscillating unit with the properties of a relaxation oscillator. While the internal organisation of this oscillator seem to reflect a hierarchical structure, the coupling between the different oscillators is organized in a non-hierarchical manner. The coupling between two such oscillators is not continuous as is the case in many mathematical descriptions of coupled oscillators. In contrast, the coupling between walking legs seems to be active only within selected phase ranges and "switched off" at other times. Ipsilateral influences are asymmetric in the sense that rostrally-directed influences are in general qualitatively different to caudally-directed ones. Contralateral mechanisms seem to be symmetric although quantitative differences can be found such that one side is able to dominate the other to some extent. There is a redundancy in the sense that different mechanisms produce basically the same result, namely a proper coordination between legs. The existence of several different mechanisms provides the possibility of a faster recovery of normal coordination after a disturbance. It also achieves a higher stability of the whole system.

The mechanisms seem to be quite different in different animals. A general difference between both species investigated here seems to be that in the crayfish in general the oscillator is influenced at the return stroke / power stroke transition, whereas in the stick insect the coupling mechanism influences the power stroke / return stroke transition. What might be the reason for the different strategies used for the coordination of legs in crayfish and in the stick insect? A basic difference is that maintaining the stability of the body position is much less a problem for the crayfish walking under water and using eight legs than for the stick insect walking on land with only six legs and climbing on branches. Therefore the stick insect is under much more constraint to keep as many legs on the ground as possible at each moment. Thus one might speculate that in stick insects coordination has to be obtained by a shorter or longer prolongation of the power stroke whereas the crayfish can afford to solve the coordination problem by maintaining legs for a longer time in the return stroke. The latter might be the simpler task from the viewpoint of computation because (a) stability problems arising when changing the end of the return stroke might generally be less critical than those when changing the end of the power stroke and because (b) the control of the leg movement is easier during the return stroke when the movement of the leg is not mechanically coupled to the other legs.