The contralateral coordination of walking legs in the crayfish Astacus leptodactylus

I. Experimental results

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

Introduction

The legs of a walking animal have to move in a coordinated way in order to prevent it from falling, in particular when it walks on uneven ground. The coordinating mechanisms have to be highly adaptive because the whole system has to cope with very different disturbances. The aim of this paper is to contribute to the elucidation of the nature of these mechanisms.

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

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

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

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

Results

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