

THE CUTICULAR STRESS DETECTOR (CSD2) OF THE CRAYFISH

II. ACTIVITY DURING WALKING AND INFLUENCES ON LEG COORDINATION

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SUMMARY

1. When a crayfish walks forward, its legs are not loaded equally. The third pair is the one exerting the largest vertically directed force, and the fourth legs produce the major part of the propulsive force.

2. Chronic recordings from a CSD2 nerve were made in crayfish walking on a treadmill. The activity of CSD2 rises during the stance phase. The activity peak at the beginning of the power stroke is especially pronounced in leg 4, which was studied in detail. The average spike frequency of CSD2 recordings during the first part of the power stroke is positively correlated with the initial increase in force produced by the leg. This suggests that CSD2 responds especially well to rapid load changes.

3. When a wire was fixed around a fourth leg such that it depressed the patch of compliant cuticle associated with CSD2, the activity of the sense organ was elevated throughout the entire step cycle, and the time between leg 4 touching the ground and leg 3 lifting off was more variable than in normal walking. Thus, CSD2 seems to be involved in the coordination of the walking legs.

4. Depressing the compliant cuticle of CSD2 elicits reflexes in the flexor muscle and the anterior levator in tethered crayfish. Interleg reflexes were not found.

INTRODUCTION

Cuticular stress detectors (CSDs) are chordotonal organs in the legs of decapod crustaceans. They are coupled to patches of relatively compliant cuticle in the basi- or ischiopodite (Fig. 1A) (Wales, Clarac & Laverack, 1971). Deforming this patch or nearby cuticle stimulates and excites sensory units of the CSD (Clarac, Wales & Laverack, 1971; Klärner & Barth, 1986). Thus, any stress in the leg which deforms the compliant cuticle is likely to stimulate the sense organ. Such stresses may be produced by loading the legs during locomotion.

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The role of CSD1 in autotomy of crab legs has been studied in detail (Clarac, 1976; Findlay, 1978). But little is known about other behavioural functions of CSDs. Other mechanoreceptors in the exoskeleton of arthropods have been shown to affect locomotion. For example, in cockroaches (Pearson & Iles, 1973) and stick insects (Bässler, 1977; Bässler & Wegner, 1983) input from the campaniform sensilla of the trochanter influences the timing of motor neurone activity. Proprioceptive feedback from unidentified receptors is also known to be important for the coordination of legs in decapod crustaceans (Clarac, 1982), and it was proposed that CSDs play a role in postural adjustment and locomotion of rock lobsters (Clarac, 1976; Vedel & Clarac, 1979). The physiology of CSDs (see Klärner & Barth, 1986) makes it likely that they are the sense organs involved.

The following hypothesis was tested. When a leg hits the ground during the power stroke, the resulting deformation of the cuticle excites the CSDs. This information about leg loading is then used for coordinating the steps.

In crayfish, the nerve of CSD1 is much shorter than that of CSD2, so satisfactory chronic recordings were only possible in CSD2. Consequently, this study had to be limited to CSD2. Myograms of the largest muscles moving the mero–carpopodite and coxo–basipodite joints (Fig. 1B,C) were recorded synchronously with CSD2 recordings, as these muscles are mainly responsible for levation/depression movements and pressing the leg against the ground. The reflex responses of these muscles to stimulation of CSD2 were studied in tethered crayfish.

As expected, CSD2 turns out to be mainly active during the stance phase of walking. It is during this part of the step cycle that a leg produces force to counteract gravity and to move the animal relative to the ground. Therefore, the magnitude and temporal distribution of these forces and their correlation with the activity of CSD2 were measured.

MATERIALS AND METHODS

Male *Astacus leptodactylus* (weight, 92 ± 13 g) purchased from a commercial supplier (Langbein, Hamburg) were kept in running fresh water at about 13°C.

Force platform experiments

Using a simple force platform it was possible to measure the force components exerted by a crayfish leg in three different directions. The animals walked in water on a 100×35 cm runway made of Perspex. Its floor was covered with expanded acrylic foam (Rohacell) to keep the legs from slipping. A force platform (Fig. 2C) was positioned in the middle of this runway. The strain gauges (Tinsley Telcon, type 2/120/ECII) for this platform were fixed to strips of 0.8 mm Perspex. They formed half bridges and measured the vertical ($7.8 \text{ mV N}^{-1} \text{ V}^{-1}$ source voltage) and the lateral–medial or anterior–posterior force component ($10.8 \text{ mV N}^{-1} \text{ V}^{-1}$ source voltage) depending on how the platform was fixed in the runway. Since leg placement in the platform area (2.2 cm^2) varied somewhat, errors of maximally $\pm 8\%$

for horizontal and $\pm 11\%$ for vertical forces resulted. Maximal mechanical crosstalk between the strain gauges measuring vertical and horizontal force was 5%.

A method developed by Clarac & Cruse (1982) was used to measure the force exerted vertically by a leg of a crayfish walking on the treadmill. A strain gauge (Tinsley Telcon, type 2/120/ECII) was mounted with cyanoacrylate glue (Permabond C3) onto a strip of 0.05 mm spring steel foil (Fig. 2B). The steel foil replaced the amputated dactylopodite of a fourth leg. A tiny bit of foam rubber at the tip of the foil provided leg friction on the treadmill. The angle between propodite and ground changed during the power stroke. The strain gauge ($2 \text{ mV N}^{-1} \text{ V}^{-1}$ source voltage) therefore mainly measured vertical force at the beginning and a high proportion of horizontal force at the end of the stance phase (see Results).

Treadmill experiments

In some of the experiments, the crayfish walked on a treadmill in a tank of aerated fresh water (13°C). The treadmill wheel was 38 cm in diameter and 14 cm wide (Barnes & Kidd, 1977), and was free to turn under the animal as it walked. The crayfish was attached at its carapace to a glass rod with dental cement. This in turn was attached to a counterbalanced lever, adjusted so that under water the animal was at its normal weight. A coiled spring between the rod and the lever allowed some turning and sideways movement.

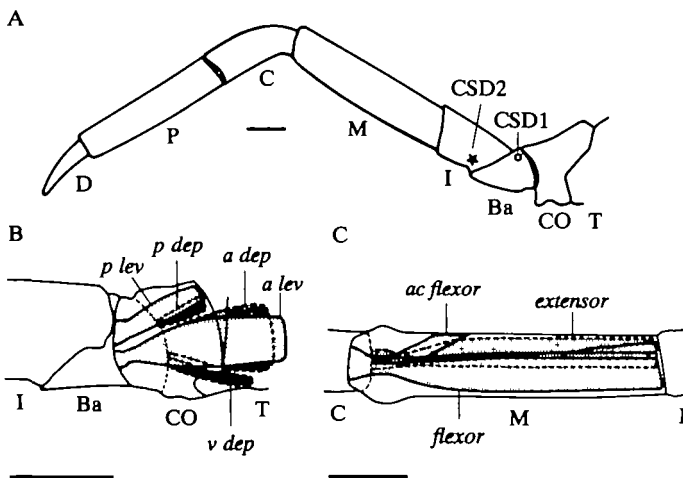


Fig. 1. Fourth leg of *Astacus leptodactylus*. (A) Position of CSD1 (dorso-anterior) and CSD2 (ventro-posterior). Ba, basipodite; C, carpopodite; CO, coxopodite; D, dactylopodite; I, ischiopodite; M, meropodite; P, propodite; T, thorax. (B) Dorsal view of the muscles moving the coxo-basipodite joint: posterior levator (*p lev*) and posterior depressor (*p dep*) insert in the coxopodite; anterior depressor (*a dep*), anterior levator (*a lev*) and ventral depressor (*v dep*) insert in the thorax. (C) Ventral view of the muscles moving the mero-carpopodite joint: extensor, flexor and accessory (*ac*) flexor. Scale bars, 5 mm.

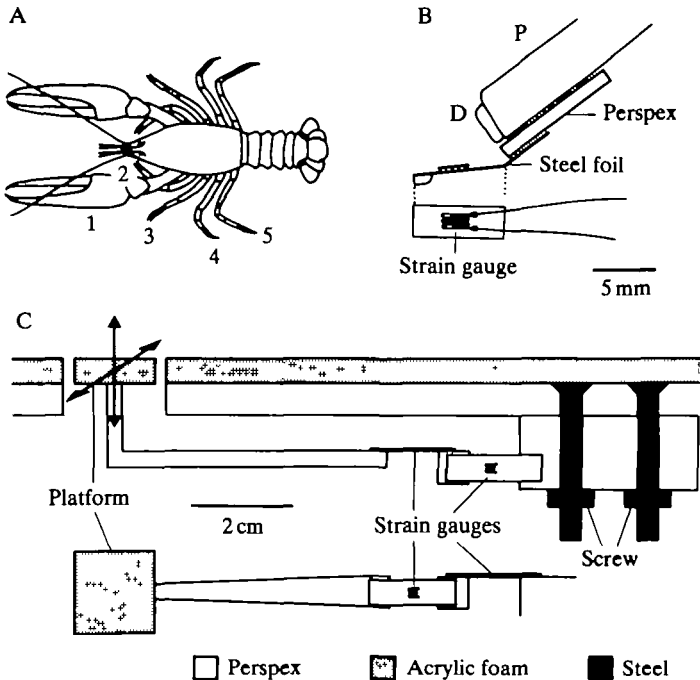


Fig. 2. (A) Dorsal view of a crayfish. (B) A piece of steel foil with a strain gauge glued onto it (shown from the side and from above, insulation with silicone rubber) replaces the amputated tip of a dactylopodite (D) in a crayfish leg. A bit of foam rubber at the tip of the steel foil prevents slipping of the leg on the treadmill when the forces produced during the powerstroke are measured. P, propodite. (C) The force platform is made of Perspex and expanded acrylic foam (Rohacell), which prevents slipping of the crayfish legs. It is shown from the side (top) and from above (bottom). The strain gauges (insulation with Vaseline) are oriented perpendicular to each other so that vertical and horizontal force components can be measured simultaneously and separately. Arrows indicate the directions of the force components measured.

Electrical recordings

Recordings of CSD2 activity were made by placing a pair of insulated copper wires (diameter, 0.1 mm) through small holes in the cuticle close to the CSD2 nerve. Strong activity of the nerve in response to slight depression of the compliant cuticle of CSD2 (accompanied by either very weak or no response induced by slightly depressing nearby parts of the cuticle or moving the joints) indicated that the recordings were in fact from the CSD2 nerve. Myograms were obtained by inserting pairs of insulated copper wires (diameter, 0.05 or 0.1 mm) through the apodeme (anterior levator) or into the cuticle at the proximal insertion points of the muscles (anterior depressor, flexor, extensor). Myograms were tested for crosstalk between muscles by moving the joints to elicit resistance reflexes in the antagonists.

After satisfactory recordings had been obtained, all wires were fixed with cyanoacrylate glue (Permabond C3). Activity of the CSD2 nerve and myograms were recorded on magnetic tape. In some experiments, ciné films of the walking crayfish were taken simultaneously (Bolex H16 Reflex, 25 frames s^{-1}). Single frames of the ciné film were correlated with the electrophysiological data by monitoring the

revolution of the camera motor with a photocell (Barnes & Kidd, 1977) and storing this signal on magnetic tape.

Reflex experiments

To analyse muscle reflexes, the crayfish were fixed, ventral side up, with rubber rings to a Perspex platform and kept under aerated fresh water (13°C). After the leg had been fixed at the ischio-meropodite joint, a vibrator (Advance E1., type VI) driven by a function generator (Levell E1.) was lowered perpendicular to and far enough against the compliant cuticle of CSD2 that the fine rounded glass tip (diameter 0.28 mm) fixed to the vibrator did not lift off the cuticle during stimulation.

Data analysis

The signals of the strain gauges were stored on magnetic tape, displayed using a pen recorder (Watanabe WTB 281) and analysed with a graphic tableau (Kontron, MOP). Stepping parameters were calculated on a MINC computer using FORTRAN programs. Dr V. Moss, Institute of Physiology, Glasgow University, kindly provided a program for digitizing electrophysiological data. For the peri-stimulus-time (PST) histograms and the statistics of the reflex experiments a TUSCAN computer with a program developed by Dr M. Burns, Department of Zoology, University of Glasgow was used.

The circular mean and its standard deviation were calculated for the analysis of the CSD2 activity during the step cycle (Batschelet, 1965). For normal distributions, mean and standard deviation are given; N is the number of animals, n the number of experiments.

RESULTS

Forces exerted by the walking legs

Forces produced by legs 2-5

When crayfish stepped on a force platform during free forward walking, both the vertically and either the anterior-posteriorly or the lateral-medially directed force components were monitored. Fig. 3 shows each component for a representative step taken from animals walking in a straight line and at a constant speed of $10 \pm 1 \text{ cm s}^{-1}$ on the runway.

Means of the peak forces and the phase at which these peaks occurred in the power stroke are shown in Fig. 4. The integral of the force produced during the power stroke over its duration, i.e. the area under the force curve, is also given because the peak force can be exerted for either a long or a short time. The average duration of the power stroke of the legs was $0.47 \pm 0.11 \text{ s}$ (leg 2), $0.61 \pm 0.09 \text{ s}$ (leg 3), $0.59 \pm 0.10 \text{ s}$ (leg 4) and $0.43 \pm 0.10 \text{ s}$ (leg 5). Vertical and anterior-posterior force components were measured in two groups of four crayfish which differed by their mass (means 83 g and 95 g). The results were essentially the same for both groups,

except that, as one would expect, the heavier animals usually produced more force (Fig. 4). Lateral–medial force components were measured in two animals.

Vertical component. The weight of crayfish in water is 91.4% less than in air ($N = 12$); so a 90-g crayfish like the ones used in the experiments has to compensate for only about 8.6 g (85 mN) by exerting vertically directed force. Most force is produced by leg 3, whereas leg 5 exerts only about half as much force as the other legs.

Anterior–posterior component. Force components are generally smaller in the horizontal than in the vertical plane. The posteriorly directed force moves the crayfish forwards; even when the animal is not accelerating it has to compensate for the drag. Propulsive force is mainly produced by the fourth leg, less is exerted by the third, and still less by the second and fifth legs. Anteriorly directed forces are braking forces and are restricted to the beginning of the power stroke. This component decreases from the second to the fifth leg. It is particularly small in the fifth leg, which usually decelerates considerably before its stance phase begins.

Lateral–medial component. The surface to volume ratio decreases with increasing animal size. Smaller animals, such as arthropods, are therefore relatively more affected by wind or water currents. Their legs are spread out, lowering the centre of mass and producing a laterally directed force component, which counteracts any tendency of the body to turn round the roll axis (Alexander, 1971). In crayfish, the third leg produces most of the lateral force, the fourth leg less and the second and fifth legs least of all. All legs exert little medially directed force. This component was only found in about half of the steps.

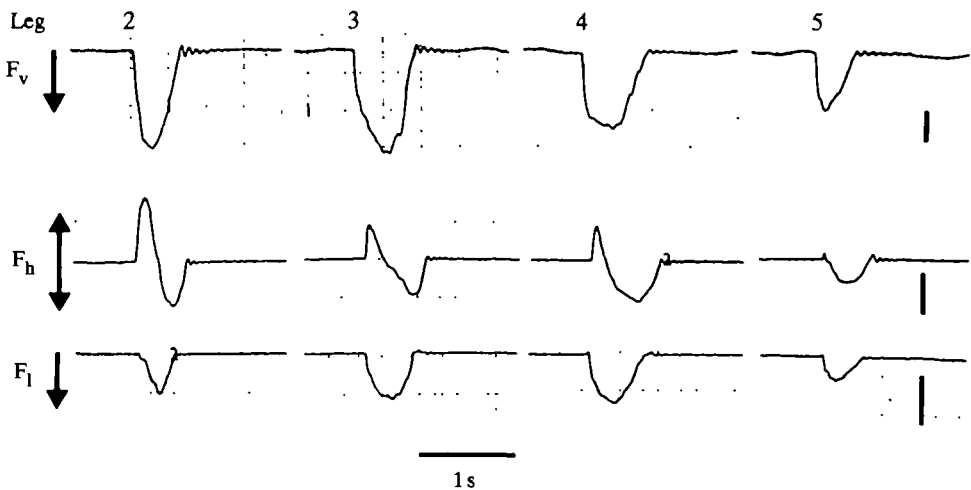


Fig. 3. Representative steps of crayfish walking forwards over a force platform. Vertical, anterior–posterior and lateral force components, each measured in different recordings, are shown for legs 2, 3, 4 and 5. F_v downwards, leg pushing perpendicularly against the force platform; F_h upwards, leg pushing forwards; F_h downwards, leg pushing backwards; F_l downwards, leg pushing laterad. Force scales, 20 mN.

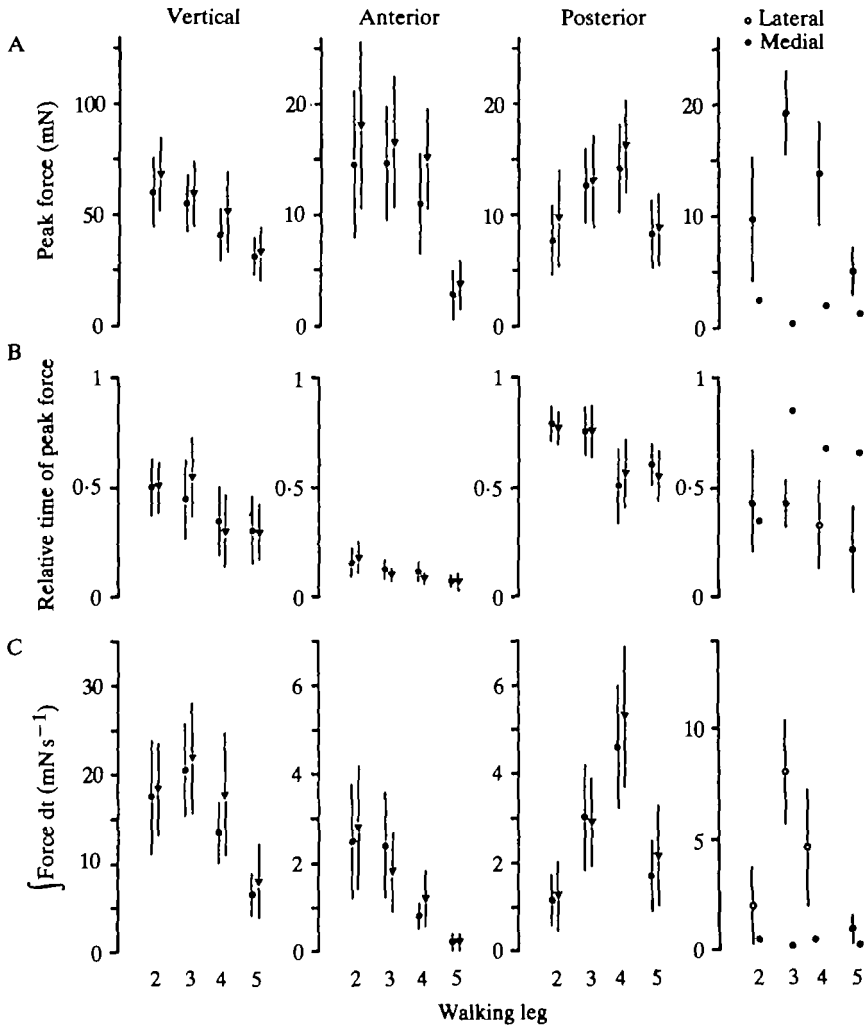


Fig. 4. Forces produced by legs 2, 3, 4 and 5 in crayfish walking forwards over a force platform. When antero-posteriorly and vertically directed forces were measured, the mean weight of the experimental animals was 83 g (●) or 95 g (▼); when laterally and medially directed forces were measured it was 91 g. For medially directed forces the mean alone is given because this component was only found in about half of the steps. For the other components the standard deviation is given as well, $n = 18-58$. Note different scales. (A) Peak force in the force curve of the steps. (B) Relative phase of the force peak during the power stroke; 0, beginning; 1, end of the power stroke. (C) Integral of the force over the power stroke duration, i.e. the area under the force curve.

Forces produced during CSD2 activity

As the crayfish had to be fixed in space to allow chronic recordings of CSD2, the following experiments were made with animals walking on a treadmill. A strain gauge glued onto a piece of steel foil was fixed to the propodite of a fourth leg at an angle of about 30° to its long axis (Fig. 2B). The angle between the propodite and the ground increases during the power stroke. The angular change was measured for 35

steps ($N = 7$). The long axis of the propodite forms an angle of $47 \pm 7^\circ$ with the ground at the beginning of the stance phase and moves through an arc of $59 \pm 15^\circ$ to an angle of $106 \pm 13^\circ$ at the end of the stance phase.

The strain gauge measured mainly vertical force (F_v) at the beginning of the power stroke but an increasing proportion of horizontal force in the anterior–posterior direction (F_h) as the power stroke progressed. The force measured with the strain gauge $F = F_v \cos \varphi + F_h \sin \varphi$ (where φ is the angle between the steel foil and the ground). During the first half of the power stroke, F consists of about 85% vertical force component because F_v is about three times F_h .

Three animals (Fig. 6, A15, A16, A23) walked readily on the treadmill though their stepping frequencies were low (means, 0.48, 0.46, 0.37 Hz). Therefore the previous amputation of the dactylopodite with the concomitant ablation of the funnel canal organs (Schmidt & Gnatzy, 1984) was assumed not severely to disturb walking. Details of the walking pattern may nevertheless have changed. For a more detailed picture of the force pattern exerted, the experiments with intact animals walking over a force platform should be consulted. The CSD2 burst began exactly when the leg started to produce force and the activity of the sense organ remained high while the force increased in the first part of the power stroke (Fig. 5). The average spike

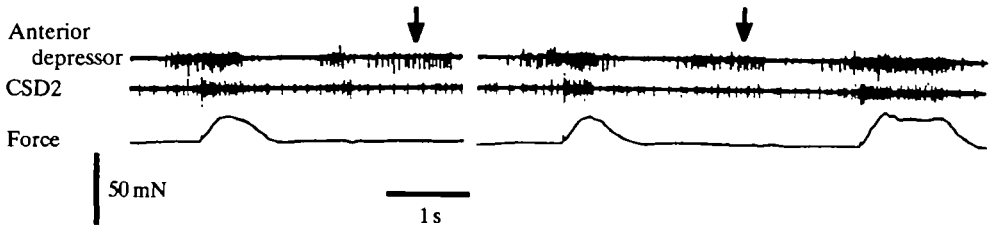


Fig. 5. The force produced by a fourth leg during forwards walking on a treadmill (mainly vertical component) was measured with a strain gauge on a steel foil replacing the dactylopodite. The CSD2 burst begins when the leg touches the ground and exerts force. If a leg produces hardly any force during the stance phase, CSD2 activity increases only moderately, if at all (\downarrow).

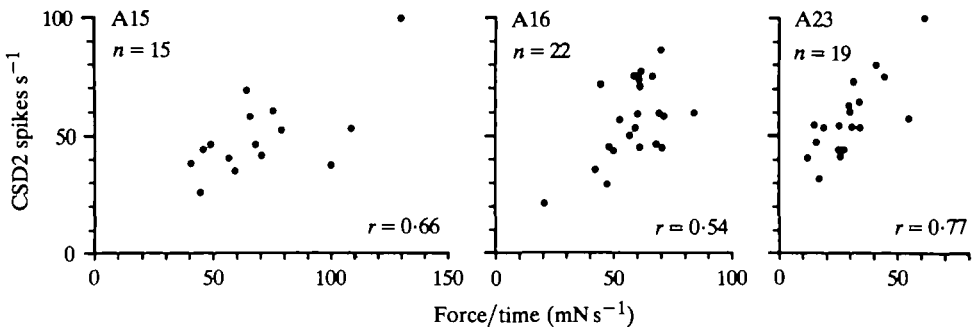


Fig. 6. There is a positive correlation between the average positive slope of the force produced by a leg and the average spike frequency of the CSD2 recordings during this time. The correlation coefficients of all three examples (three animals) are significant ($P < 0.02$).

frequency during this time is positively correlated with the average positive slope of the force curve (Fig. 6).

Sensory control of walking

Activity of CSD2 during walking

To examine the timing of CSD2 activity during locomotion, chronic recordings from the CSD2 nerve were made in legs of crayfish walking on a treadmill. During forward walking a burst of spikes occurs during the power stroke of the leg. In all recordings from the fourth leg ($N = 10$), which was studied in detail, the main activity in the CSD2 nerve occurs when the leg contacts the ground at the beginning of the stance phase (Fig. 7). The shapes of the histograms vary and are likely to depend on which of the 60 or so units of CSD2 (Clarac, 1976) happened to be recorded from.

The CSD2 burst begins shortly after the anterior depressor burst has started ($N = 7$) and shortly before or after the burst of the flexor muscle has begun ($N = 4$) (Fig. 8). CSD2 shows little activity during the swing phase. Therefore its burst is roughly in antiphase to the activity of the anterior levator ($N = 4$) and the burst of the extensor muscle ($N = 4$). The latter can be biphasic as in the example shown in Fig. 8. The phase relationship of muscle activity with respect to the step cycle is in agreement with earlier findings by Barnes (1977) in the same crayfish species.

Influence of CSD2 on the gait

The ipsilateral legs of a crayfish move in a metachronal pattern during forward walking. If CSD2 is a proprioceptor that influences the coordination of leg movement, modifying its output might change the gait. By twisting a copper wire (diameter, 0.19 mm) round a leg the compliant cuticle of CSD2 was constantly depressed. The resulting tonic stimulation of CSD2 had the following effects.

(i) When the animals walked on the treadmill after application of the wire, the average spike frequency of CSD2 during the return stroke was higher than before, while the activity peak at the beginning of the power stroke was much reduced ($N = 4$, Fig. 8). The resulting histogram was much flatter than that for normal walking in the same animal (Fig. 7). The activity of CSD2 during the power stroke was reduced for at least an hour.

(ii) After twisting a wire round a leg, an effect on the walking behaviour of the animal was often noticed when it was first put back on the treadmill. Ten crayfish that resumed walking immediately walked forwards but held up the leg with the wire fixed round it for about half a minute. One walked backwards holding the treated leg down for a short time without it touching the ground.

(iii) When the treated animals seemed to resume normal walking after 1 min, the timing of the stepping pattern of leg 3 was less precise than in untreated animals. The gait of ten animals was analysed by comparing walking sequences (9–15 steps) before fixing the wire and after taking it off (normal walking) with sequences where it depressed the compliant cuticle of CSD2. The circular standard deviation of the

phase difference between leg 3 and leg 4 was significantly larger when a wire was fixed round leg 4 (Wilcoxon signed rank test, one tailed, $P < 0.02$); the mean of the phase difference was not significantly different from that of normal animals.

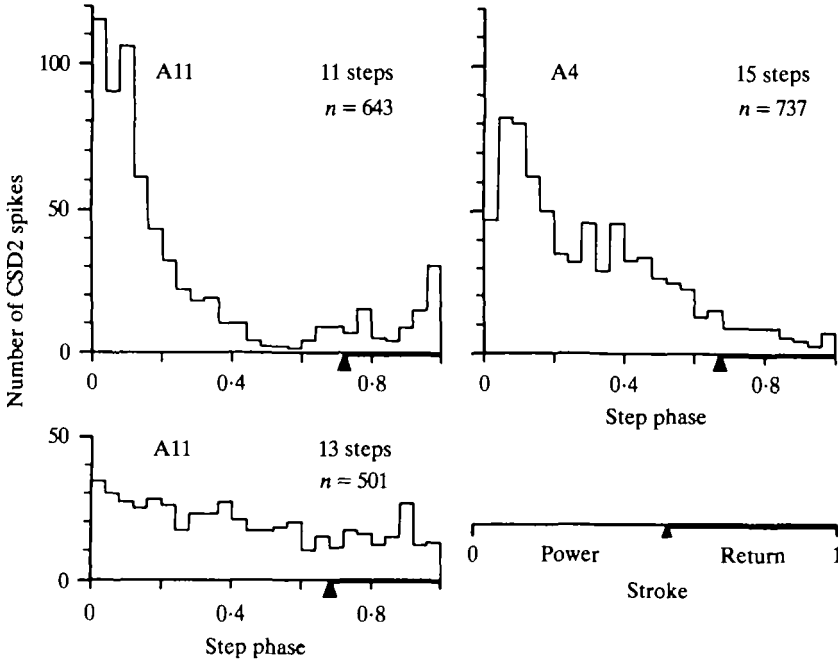


Fig. 7. CSD2 activity in the fourth leg during forward locomotion. Top: in some preparations (A11) the activity decreases rapidly after a peak at the beginning of the stance phase. In others (A4) it remains above the return stroke level until the end of the stance phase. Bottom: activity of CSD2 with a wire depressing its patch of compliant cuticle.

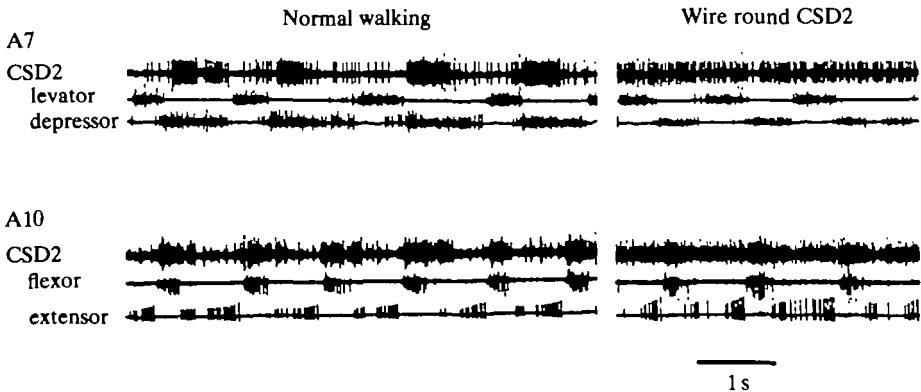


Fig. 8. Two examples (A7 and A10) of CSD2 activity recorded simultaneously with the myograms of anterior levator, anterior depressor, flexor and extensor (see Fig. 1B,C) in the fourth leg during forwards walking. When a wire depresses the compliant cuticle, CSD2 activity is higher in the swing phase (indicated by the activity of levator and extensor) and bursts during the stance phase (indicated by the activity of depressor and flexor) are not visible (A7) or less well defined than before (A10).

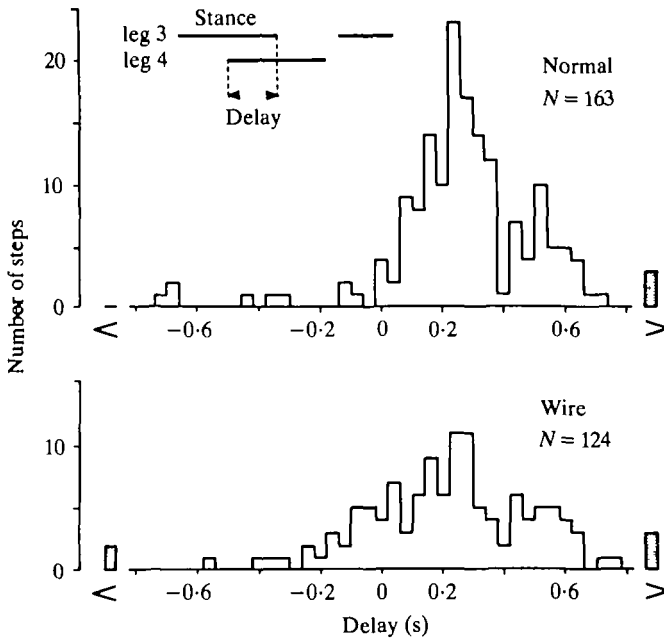


Fig. 9. Time intervals between the beginning of the stance phase in leg 4 and of the swing phase in leg 3. Top: normal walking, leg 3 is rarely lifted off the ground before the stance phase of leg 4 begins (negative values). Bottom: when a wire depresses the compliant cuticle of the CSD2 in leg 4, the time interval varies significantly more.

Usually a leg is not protracted until the leg behind is placed in a supporting position (Clarac & Barnes, 1985). With a wire depressing the CSD2 of leg 4 the mean of the delay between leg 4 touching the ground and leg 3 being lifted off was not significantly different from that of normal animals. The standard deviation of this delay, however, was significantly larger with a wire depressing the CSD2 of leg 4 ($P < 0.005$), and leg 3 was more often lifted before leg 4 had been placed in a supporting position ($P < 0.02$). The pooled data of all animals are shown in Fig. 9.

For legs 4 and 5 these stepping parameters were not significantly different from those of normal animals.

Reflexes elicited by CSD2 activity

In tethered crayfish, four muscles of the coxo-basipodite joint and the mero-carpopodite joint (Fig. 1B,C) were checked for intraleg and interleg reflexes elicited by CSD2 stimulation (1 Hz sine wave, peak-to-peak force 20 mN). The occurrence of a reflex was defined by a significant difference ($P < 0.01$, Rayleigh test) of the PST histograms of 50 stimulus cycles from a uniform distribution. No such reflexes occurred in the extensor and the anterior depressor muscles, which showed little spontaneous activity. In the flexor, however, they were frequently found (in eight out of nine preparations). The activity peak of the flexor muscle occurred during the depression of the compliant cuticle which is in agreement with previous findings by Angaut-Petit & Clarac (1976). If 0° is defined as the phase of the force

maximum, the mean of the PST histograms is at $300^\circ \pm 46^\circ$. Reflexes during depression of the CSD2 cuticle were also common in the anterior levator muscle (in 8 out of 11 preparations, mean of histograms at $280^\circ \pm 40^\circ$). In both cases, stimulation of CSD2 modulated the spontaneous activity of the muscles rather than eliciting more muscle spikes. These reflexes did not habituate quickly but could be observed for several minutes with continuous stimulation.

DISCUSSION

Force produced by crayfish legs

Variability of steps

When the force a crayfish leg exerts on the substrate was measured during walking, its magnitude and distribution in time were found to vary considerably. Similar variability between steps occurs in stick insects (Cruse, 1976), crickets (Harris & Ghiradella, 1980), rock lobsters (Clarac & Cruse, 1982) and land crabs (W. J. P. Barnes & S. J. Lindsay, in preparation). Evidently slowly walking animals are flexible in how they distribute load between the legs.

Differences between legs

In spite of this variability, there were consistent differences between the forces produced by different legs. The chelipeds are held in front of the crayfish and usually do not touch the ground (Fig. 2A). The vertical force component of the second pair is fairly large, while the horizontal forces are small. So these legs support the anterior part of the body with the heavy chelipeds. The third pair of legs exerts the highest amount of laterally and vertically directed forces. This pair produces lift and stabilizes the body in the roll plane (Cruse, 1976). The fourth legs share these functions. In addition they produce the major part of the propulsive force. The fifth legs exert the smallest amount of force of all legs. This may be due to the activity of the pleopods. While crayfish are walking, their abdomen is extended and the pleopods beat forwards and backwards rhythmically (preliminary observations) thereby probably producing some lift which relieves the fifth pair of walking legs of the need to bear much of the weight of the abdomen.

In crayfish, as in all arthropods so far examined, each pair of legs has a different function during walking. How the forces are distributed among the legs depends on the position of the centre of gravity in the animal. Bird spiders produce lift mainly with their third legs followed by the fourth and the second legs. This fits in with the position of the centre of gravity in these animals which lies between the coxae of the third and fourth leg (A. Brüssel, in preparation). In crickets, the peak vertical force increases from pro- to metathoracic legs, which are in the best position to support the abdomen (Harris & Ghiradella, 1980). Cruse (1976) showed in stick insects that the hind legs, which have to bear the weight of the abdomen, produce the largest vertical, lateral and posterior force components.

*Probable function of CSD2**Measuring force*

During the first part of the power stroke, the mean spike frequency in recordings of CSD2 units is high and positively correlated with the mean slope of the force produced by the leg. Thus loading, and especially the change of loading, seems to be a natural stimulus for the sense organ. CSD2 probably monitors the forces acting on the cuticle of a leg in even more detail than is apparent from the recordings of the sensory nerve. As Klärner & Barth (1986) have shown, the units of CSD2 differ considerably in threshold and in phase relationship between the stimulus and their response. Both are also dependent on where the force is applied to the cuticle. This diversity of the 60 or so sensory cells (Clarac, 1976) may well give a detailed picture of the direction and magnitude of forces acting on a leg. The CSD2 units are most sensitive to stimulus frequencies between 10 and 30 Hz. This range probably allows a detailed coding of the time course of the forces exerted since crayfish rarely take more than one steps⁻¹.

Protective function

Proprioceptors can be involved in reflexes preventing potentially damaging overloading. Thus, lyriform sensilla in the tibia of spider legs elicit synergic reflex activity of patella muscles when the metatarsus is moved perpendicular to the main movement plane of the tibia–metatarsus joint. This prevents damaging forces at this joint (Seyfarth, 1978). Similarly, CSD1 prevents the accidental autotomy of crab legs by inhibiting the anterior levator muscle when the breakage plane is in danger of rupturing (Findlay, 1978).

By causing the leg to be lifted when strong forces are acting on the sense organ, CSD2 activity may prevent excessive loading of a leg. Natural loading was mimicked by twisting a wire round a crayfish leg. When the compliant cuticle of CSD2 was constantly depressed in this way, most crayfish lifted the leg up for some time. The anterior levator muscle may have been activated in these animals, for a weak reflex of this muscle was elicited in tethered crayfish by depressing the compliant cuticle of CSD2.

Coordination of legs

When animals move over heterogenous ground, which they frequently do, they probably rely on detailed proprioceptive feedback during walking to make the proper adjustments in their stepping pattern.

Some observations suggest that, in decapod crustaceans, load-sensitive proprioceptors influence interleg coordination during walking. (i) If the fourth leg of a crayfish, lobster or rock lobster is amputated, the stump retains its normal phase relationship to leg 5 during forward walking but moves almost in phase with leg 3 (Clarac & Barnes, 1985; MacMillan, 1975; Clarac & Chasserat, 1979). (ii) When a prosthesis is fixed to the amputated leg so that it can touch the ground during the stance phase, the phase relationships of adjacent pairs of legs become approximately

normal again (Grote, 1981; Clarac & Barnes, 1985; MacMillan, 1975). (iii) If all legs of a rock lobster are autotomized, the stumps move almost synchronously (Clarac & Chasserat, 1979). Interestingly there is a behaviour pattern in some decapod crustaceans where legs do move almost synchronously and are not exerting force. The animal stands on the fourth and fifth legs, holding the front legs off the ground and moving them in a slow, oscillatory wave, which may support gill ventilation (Pasztor & Clarac, 1983).

In conclusion, there seems to be an ascending influence of proprioceptors which are stimulated by loading of the walking legs. Loading of a leg seems to be a natural stimulus for CSD2, which would be a good candidate to influence interleg coordination. However, no evidence of interleg reflexes, which could be involved, was found. This may be due to the severe restriction of the animal and its legs during the experiments (see Materials and Methods).

When a wire was fixed round the CSD2 of a fourth leg, the activity of the sense organ was much more evenly distributed throughout the stepping cycle than before, and at the same time the relative and absolute time lags between stepping of legs 3 and 4 were more variable. This again corroborates the hypothesis that CSD2 is involved in the ascending pathway influencing the coordination of adjacent legs during walking. High activity of CSD2 may signal that the leg is being loaded and the swing phase of the anterior leg can begin. If the activity of CSD2 no longer corresponds to the loading of leg 4, the coordination of legs 3 and 4 is weaker.

It is most unlikely, however, that CSD2 is the only proprioceptor involved in the coordination of walking. Other mechanoreceptors may give additional information about the loading of a leg. Legs need to be coordinated in space as well as in time. Cruse, Clarac & Chasserat (1983) showed that the position of a leg is important for the timing of swing and stance phase in the rock lobster.

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