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DACTYL SENSORY INFLUENCES ON ROCK LOBSTER LOCOMOTION

I. INTRASEGMENTAL AND INTERSEGMENTAL LEG REFLEXES DURING STANDING AND WALKING

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Summary

1. Recordings of activity of the rock lobster dactyl sensory nerve during walking on a driven belt showed that the receptors of this nerve were mainly active during the power stroke when the leg was loaded. This nerve contains in particular the afferent fibres of the funnel canal organ (FCO) which are bimodal sensillae located in the cuticle of the dactylopodite of crustacean walking legs.

2. In the standing animal, brief electrical stimulation of the dactyl nerve had an influence on the proximal leg muscles of the stimulated leg. The promotor and levator muscles were excited and the remotor and depressor muscles were inhibited.

3. The opposite reaction was observed in adjacent ipsilateral legs in response to stimulation of a middle leg: the promotor and levator were inhibited and the remotor and depressor excited.

4. The resulting movement by the stimulated leg was stereotyped and always consisted of a lift-off from the substratum and a slight shift in the forward direction. The response in the adjacent legs was not powerful enough to elicit a movement.

5. In the walking animal the response of a single leg was dependent on the phase at which a stimulus arrived during the step cycle: during a power stroke (PS) this cycle was interrupted and a return stroke (RS) was initiated and continued. A stimulation at the normal switch from PS to RS had little effect, whereas a stimulation at late RS very often delayed the start of the following PS. Opposite reactions were given by the adjacent unstimulated legs: an RS was interrupted and a PS initiated or prolonged by the stimulus.

6. A comparison between ipsilateral walking legs showed the existence of some obvious differences: legs 4 and 5 were able to reset the walking pattern of all the

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legs, whereas the more anterior leg 3 returned to its old trajectory after stimulation and thus had no influence on the other legs.

Introduction

Various studies have demonstrated that in arthropods peripheral receptors have fundamental effects on patterns of rhythmical behaviour such as walking or flight (see Wendler, 1974; Bässler, 1977; Barnes, 1977; Pearson *et al.* 1983; Zill, 1986; Clarac, 1985; Möhl, 1985). Recent research has mainly been carried out on isolated preparations (for reviews, see Delcomyn, 1980; and on Crustacea, Sillar and Skorupski, 1986; Chrachri and Clarac, 1987) and, in most of these, the rhythmic activity obtained was quite different from that observed in a normal behavioural context (see Hedwig and Pearson, 1984; Pearson and Wolf, 1987). In a reconsideration of the classical experiment by Pearson and Iles (1973), often referred to as an example of a centrally produced rhythm, Zill (1986) showed that the behaviour of a decapitated cockroach resembled that of righting rather than walking. This and other very informative experiments have highlighted the role of sensory feedback in the organization of locomotor behaviour (Bässler and Wegner, 1983; Dean, 1984; Cruse, 1985*a*,*b*; Zill, 1986).

In crustaceans, most of the receptors controlling walking are mechanoreceptors with proprioceptive functions. Chordotonal organs span each joint of the legs, acting as movement and position detectors. The thoraco-coxal muscle receptor organ (TCMRO) at the base of the leg, which measures the angle of the thoraco-coxal (T-C) joint, and the myochordotonal organ (MCO), which monitors the movements of the mero-carpopodite (M-C) joint, are neuromuscular structures. The cuticular stress detectors (CSD), which monitor mechanical deformation of the exoskeleton, are comparable to the campaniform sensilla of insects (Bush and Laverack, 1982; Clarac, 1985). Most investigations of the physiology of crustacean proprioceptors have been performed on restrained animals or, more recently, on isolated crayfish ganglia (Sillar and Skorupski, 1986; Skorupski and Sillar, 1986; Sillar *et al.* 1987; Chrachri and Clarac, 1987). The findings are not necessarily those to be found in restrained preparations, as demonstrated in the stick insect (Bässler, 1977; Cruse and Schmitz, 1983).

Only a few data are available on crustaceans demonstrating the influence of sensory input on the walking pattern in the intact animal: Klärner and Barnes (1986) showed that the CSD_2 of crayfish monitors the stance phase of a leg during locomotion and has an influence on interleg coordination, but they did not investigate the effects of phase-dependent stimulation on the walking pattern. In crustaceans another type of mechanoreceptor, termed the funnel canal organ (FCO), is located at the terminal segment of each walking leg (dactyl). An anatomical and ultrastructural study of these sensilla in the walking legs of the crab (Gnatzy *et al.* 1984; Schmidt and Gnatzy, 1984) has demonstrated that each of them consists of two mechanosensitive and 17–24 chemosensitive sensory cells. About 470 of these sensillae are located on the dactylopodite of a single leg. The

mechanoreceptive part of the sensillum is vibration-sensitive (Barth, 1980) and it has been shown that mechanical or brief electrical stimulation of the sensillae during walking can produce dramatic, phase-dependent effects on the muscle burst pattern of the stimulated leg, and also on the burst patterns induced in adjacent legs (Libersat *et al.* 1987*a*,*b*).

The present study investigates the role of sensory feedback in walking in the rock lobster *Jasus lalandii*. In comparison with crabs, this animal offers two major advantages for such experiments. First, it can walk properly on a motor-driven belt, even for several hours, so that it is possible to obtain long walking sequences at a constant speed. This is a necessary condition for a quantitative analysis. Second, it is possible to record the electromyographic (EMG) activity of the walking muscles, and to compare it with the leg movements parallel to the body axis using position electrodes.

Materials and methods

Experimental apparatus

Adult rock lobsters were used in all experiments. The animals were fixed at the carapace in a seawater-filled aquarium, using a universal joint (adapted from W. J. P. Barnes, personal communication) and a holder which was counter-balanced, so that the animals were able to carry their own weight. The flexible suspension allowed the animals slight scope for movement in all three dimensions but prevented rotations around the vertical axis. This significantly increased the frequency and duration of successful experimental walks. Only forward walking at a constant belt speed of $8\,cm\,s^{-1}$, similar to normal free walking (Clarac and Chasserat, 1983), was analysed.

Some experiments on standing animals were performed using a low-friction acrylic surface as substratum. In all other experiments the animals walked on a motor-driven belt.

Recording of leg positions and EMG activity

The ipsilateral legs of rock lobsters were labelled 1–5 from the front. Very often only legs 4 and 5 walked continuously, whereas their front neighbours produced more irregular steps, like searching movements. This tendency increased from rear to front. Therefore, we considered only the back three walking legs, without differentiating between the two sides of the animal. The positions of the three ipsilateral legs 3–5 were continuously recorded, using specific transducers developed by Cruse and Müller (1984), with which the position of an electrode can be measured within a high-frequency low-voltage electrical field (40 kHz, 1 V), generated in the aquarium. Electromyograms (EMGs) of 1–4 of the main proximal muscles involved in forward walking were recorded in parallel with the leg movements (Chasserat and Clarac, 1983). The muscle appendages in the animal's body at the insertion of leg 4 are shown in Fig. 1A. The antagonistic promotor (PRO) and remotor (REM) muscles move the leg rostrocaudally along the axis of the thoraco-coxopodite (T-C) joint. In contrast, the antagonistic levator

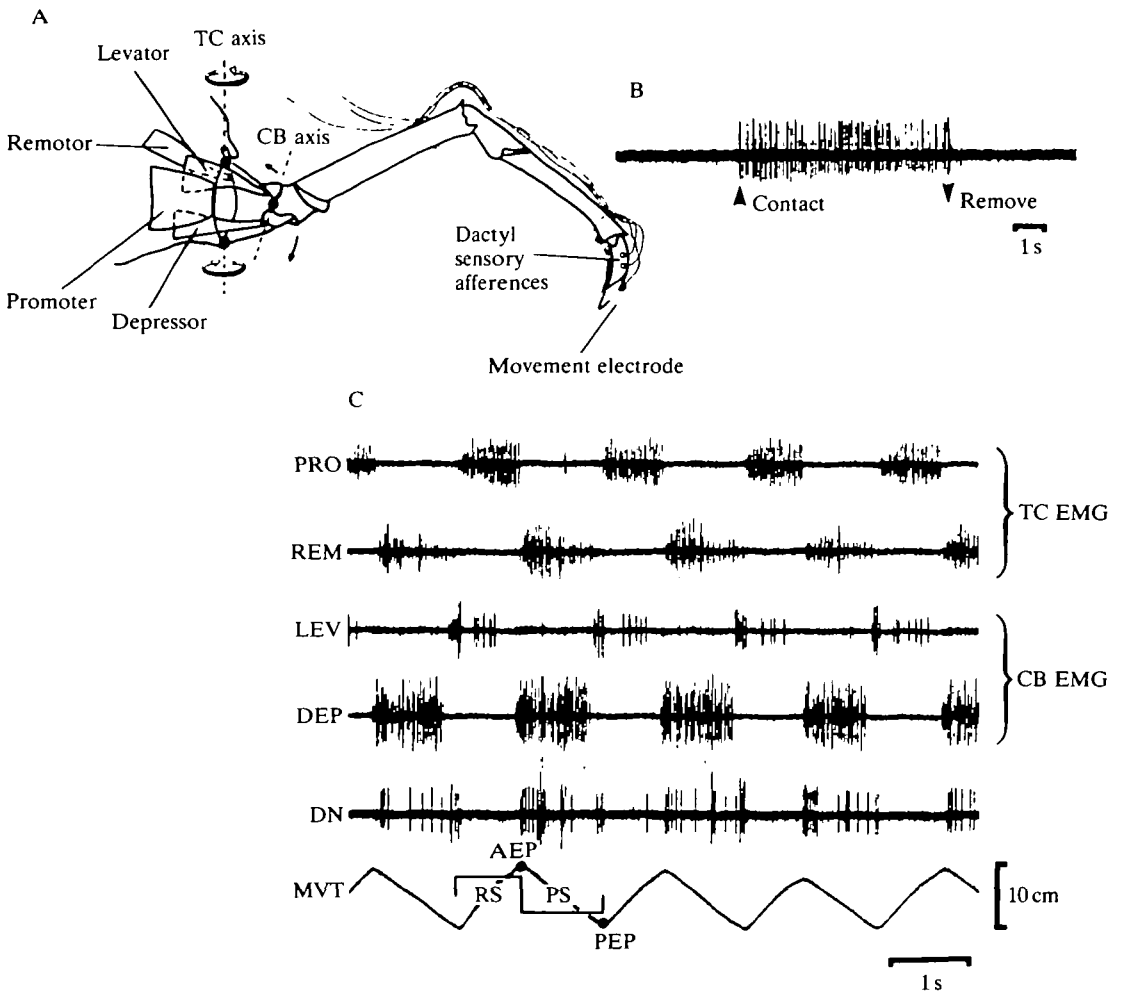

Fig. 1. Method for recording dactyl nerve (DN) activity, muscle EMGs and leg movement. (A) Arrangement of the four muscles recorded within the coxa (T-C: thoraco-coxal, C-B: coxo-basipodite limb axis). (B) Extracellular recording from the DN when the dactyl was deformed with a tweezer-tip. (C) Single leg activity pattern during forward, driven walking. The time is given on the abscissa. The upper four traces show the EMG discharge from the recorded muscles. Trace 5 is the summed potential of the dactyl nerve activity. In trace 6 the ordinate gives the stride amplitude of the movement (MVT). Upward deflection indicates return stroke (RS), downward deflection power stroke (PS). AEP, anterior extreme position; PEP, posterior extreme position.

(LEV) and depressor (DEP) muscles move the leg dorsoventrally along the axis of the coxo-basipodite (C-B) joint.

The leg movements and EMGs were recorded using nickel wires (100 μm in diameter, insulated except for the tip). The position electrodes were fixed at the dactylopodite (see Fig. 1A) using cyanoacrylate glue (Eastman 910 adhesive).

Pairs of EMG electrodes were inserted through small holes made at the muscle insertions, and fixed at the coxa.

Recordings of the dactyl sensory nerve

Extracellular recordings of the dactylopodite receptor activity were obtained from the central sensory nerve using silver wires (120 μm in diameter, insulated with PTFE to their tips). Pairs of electrodes were inserted through small holes made in the cuticle of the dactylopodite (see Fig. 1A), adjusted until the sensory discharge correlated with the mechanical stimulation of the dactylopodite, and then fixed in place. We believe that the main activity was caused by stimulation of the funnel canal organs, but we recorded and stimulated the central sensory nerve of that segment, labelled dactyl sensory nerve (DN). One example is shown in Fig. 1B. The dactylopodite of leg 4 was mechanically stimulated with a tweezer-tip. The DN responded with a tonic discharge during the whole period of stimulation. Depending on the position of the recording electrodes, the signal varied between experiments from the discharge of pairs of units, to the discharge of a whole population of units. All three electrode wires were fixed to the leg with small pieces of adhesive tape, care being taken that leg movement was not inhibited. The three wires were bundled together with plasticine and fixed, allowing some freedom of movement, to the holder.

A typical pattern obtained with the experimental apparatus is shown in Fig. 1C for a recording from leg 4. In medium-speed forward walking, the EMG activity of the promotor is in phase with the levator activity. These muscles mainly produce the return stroke (RS), in which the leg lifts off the ground and produces a forward-directed movement, represented in the movement trace (MVT) at the bottom of the pattern by an upward deflection. Antagonistically to this movement, the remotor and depressor muscle activities are in phase, forming the power stroke (PS), in which the leg supports the body and moves posteriorly. This movement is represented on the movement trace by a downward deflection. The switch point between RS and PS is the occurrence of the anterior extreme position of the leg (AEP), whereas the switch point between PS and RS is the occurrence of the posterior extreme position (PEP). We defined the period (PER) as the time interval between the occurrence of the AEP of one step cycle and the following AEP. The fifth trace shows the activity obtained from the DN. Receptor activity is limited to the PS, when the leg is loaded and has ground contact.

Electrical stimulation of the DN

We used brief electrical stimulation of the DN as a means of disturbing the walking pattern and observed the way in which the legs reacted to this disturbance and returned to their normal coordination. Electrical stimuli were applied through the electrodes positioned within the cuticle of the dactylopodite. In preliminary experiments, pulse trains were varied between 10 and 200 ms with a single pulse duration of 0.5 ms at 80 Hz. Standard conditions in all other experiments were train durations of 100 ms, and all the other conditions were as described above.

The intensity of the stimulation was always kept slightly above the threshold for eliciting reflex responses in the leg, as monitored myographically and by measuring the leg movements. The threshold ranged from 3 to 7 V peak-to-peak, depending on the quality of preparation. Under these conditions the leg response was always very stereotyped and consisted of a lift-off and a forward-directed movement, whereas the general walking behaviour was not affected. Simply increasing the stimulation amplitude (>15 V peak-to-peak) leads to qualitatively different behaviour (like startle responses and escape reflexes). In all cases these strong stimulations disrupted the walking behaviour. Trains of electrical stimuli were applied every 15 s. This corresponds to a stimulation occurring approximately every tenth step, at a random point within the cycle. All data were stored on tape and analysed using a graphic tablet connected to an Apple microcomputer.

Calculation of phase–response curves

We performed a set of quantitative analyses by evaluating the phase–response curves (PRC, see Stein, 1976, for a detailed description) of the effects described. With this method the changes in the period of an oscillation elicited by stimulation were plotted against the phase in which the stimulus occurred. The shape and the slope of the PRC yield a quantitative description of the effects of sensory stimulation on the pattern generator. In separate experiments, legs 3, 4 and 5 were stimulated and the reactions of the legs themselves as well as those of the unstimulated neighbouring legs were observed. Using the method of Möhl (1985) we measured the step duration in the cycle during stimulation and during the two following cycles (see, for example, Figs 7–9). We intended to examine whether the effect observed led to a resetting of the pattern (a phase shift of all oscillators) or whether the stimulation affected the pattern only for a short interval and was corrected during the subsequent steps. In all cases the abscissa was the phase of the appearance of the stimulation in the 'normalized' period. This normalization of the period was necessary, because it is not advisable to use a reference which is itself influenced. We therefore calculated the normalized period for each stimulation by averaging the preceding 8–10 steps of the undisturbed walk.

Trigonometric regression of PRCs

As PRCs are circular functions, it is not appropriate to use linear or polynominal regressions. We therefore fitted the data by determining the regression curves of the first three Fourier coefficients (Yamanishi *et al.* 1979):

$$p(x) = 1/2a_0x + \sum_{k=1}^{3} [b_k\cos(2\pi kx) + c_k\sin(2\pi kx)] .$$

Constants a_0, b_k and c_k were determined to minimize the square error (SE):

$$\mathrm{SE} = \sum_{n=1}^{m} |p(x_n) - y_n|^2$$

between the fitted values $p(x_1),p(x_2),..,p(x_m)$ and the averaged data points $y_1,y_2,..,y_m$.

Results

Intrasegmental effects of DN stimulation

When an animal was standing motionless on a horizontal plane, tonic activity of the depressor muscle was always visible. The levator muscle was almost inactive, and the promotor or remotor muscles could be active, depending on the leg position relative to the body axis. A stimulation of the DN with a pulse train slightly above threshold (more than 20 ms) always led to an excitation of the promotor and levator and an inhibition of the depressor muscles, as shown in two different examples in Fig. 2A,B. Because of the inactivity of the remotor muscle during the recording, no evidence for an inhibitory influence on this muscle can be seen in the two examples. Other recordings, including the muscle recording during walking in Fig. 4A, showed, however, that such an influence exists. The resulting leg movement was a lift-off and a slight shift in the rostral direction with an average latency of about 150 ms after stimulus application. After this reflex the leg was able to return to its previous position (especially when longer pulse trains were applied).

Dependence on stimulus duration

Stimulation of the DN with a train duration longer than 10 ms excited the promotor and levator and inhibited the remotor and depressor muscles in all preparations tested, as shown in Fig. 3A. Whereas the durations of the levator and depressor responses showed a clear dependence on the stimulus duration, this was not the case for the promotor and remotor. Fig. 3B shows the spatial leg response

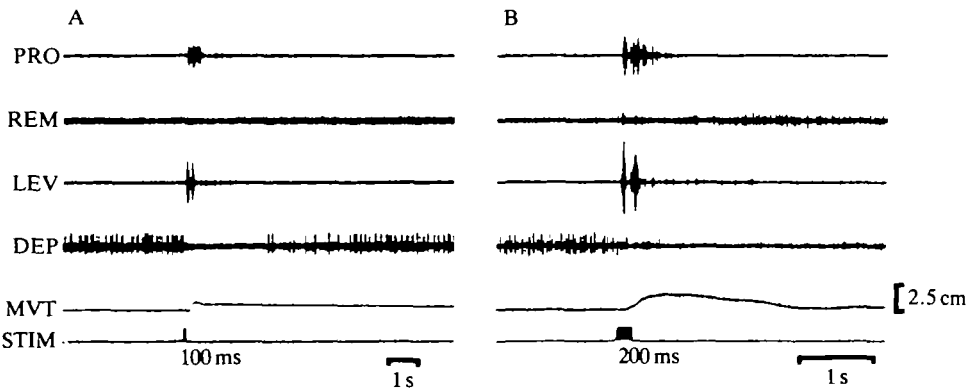

Fig. 2. Two examples of the response of a single leg to an electrical stimulation of DN in the standing animal, positioned on an acrylic surface. Trains consisted of 0.5 ms pulses at 80 Hz with an amplitude of 6 V peak-to-peak. The upper four traces correspond to those in Fig. 1C. Trace 5 (MVT) is the leg movement, trace 6 is the stimulus mark. (A) 100 ms, (B) 200 ms train duration. Note the different time scales.

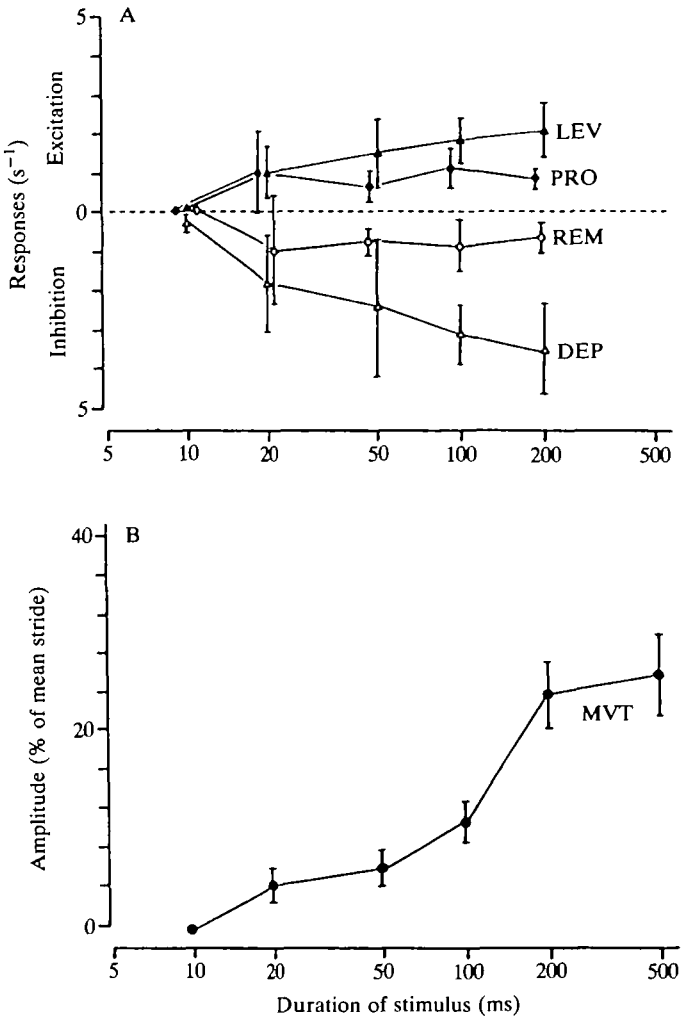

Fig. 3. Dependence of leg response on stimulus train duration. All stimulus parameters except the train duration were the same as those given for Fig. 2. Each point represents the mean value (±S.D.) of 10–25 observations. In A the dashed horizontal line indicates no changes in muscle activity. Values above that line indicate an increase, below a decrease, in the discharge activity in response to stimulation. In B the ordinate gives the ratio of the reflex amplitude to the average stride length during walking.

(as a percentage of the mean stride length, 10 cm) as a function of the stimulus duration, for stimuli lasting 10–500 ms. The amplitude of the resulting movement was independent of the initial position of the leg, but strongly dependent on stimulus duration. The threshold varied between 10 and 20 ms. With a stimulus lasting longer than 500 ms, no increase in amplitude was observed, but a very irregular movement of the leg occurred, as described above. Among the various experimental conditions we used, the stimulus duration of 100 ms was the most

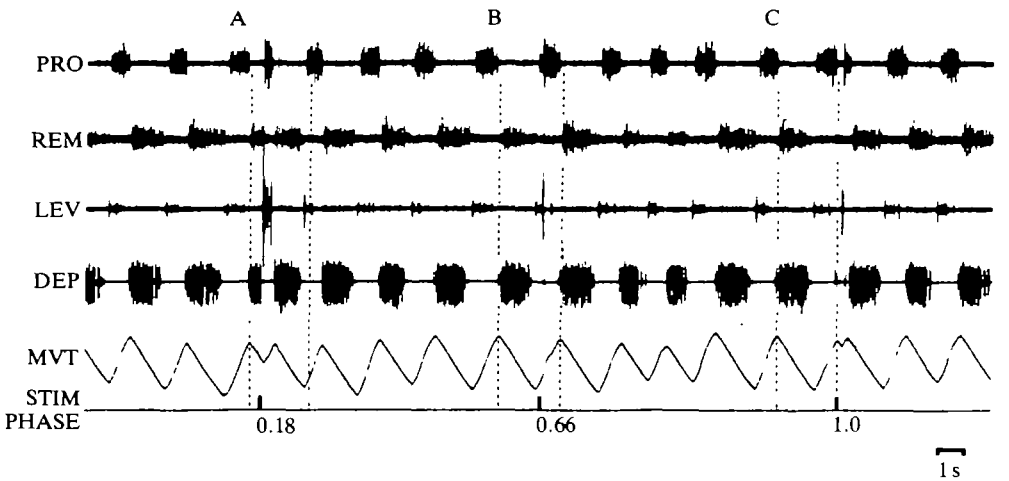

Fig. 4. (A–C). Three examples of the response of a single leg to DN stimulation during walking. The belt speed was $8\,cm\,s^{-1}$. The four upper traces show muscle recordings, the fifth trace shows the continuous leg movement and the bottom trace is a stimulus mark. The values below the stimulus mark represent its phase during the normalized period, which is indicated by the dashed lines (calculated from the mean of 25 undisturbed steps). Phase calculation was also normalized (delay of stimulus/mean period).

efficient for eliciting a repeatable response. We therefore chose it as the standard condition for all subsequent experiments.

Electrical stimulation was applied randomly during the step cycle to an animal walking on a driven belt, as shown for leg 4 in Fig.4. In Fig. 4A the stimulus was delivered during the early PS, just after the AEP. After a short latency, an excitation of the promotor and levator and an inhibition of the remotor and depressor muscles were visible. These results are similar to those described above, when the animal was standing motionless on a horizontal plane (Fig. 2), but here an additional inhibition of the remotor is visible. A change in the direction of the movement was observed. The RS began before the normal switch point (PEP) was reached. The period decreased, and the oscillation of the whole leg was advanced by the stimulus.

Fig. 4B shows the response of the same leg to a stimulus given just after the PEP had been reached. The muscle response corresponds to the first stimulus, but now the leg was in the early part of the RS. At this stage of the movement the remotor and depressor muscles were already inhibited. In addition to the normal promotor and levator output, the stimulus activated a set of units in both muscles that were not activated in undisturbed walking. This appeared more clearly in the reaction of the levator muscle. The result was an increase in the velocity of the RS but no change in the period length.

Fig. 4C shows a situation in which the stimulus was delivered at the switch from RS to PS. The muscle responses were similar to those shown in Fig. 4A,B. Again

the leg switched from PS to RS. Here, in contrast, the start of bursts in the remotor and depressor muscle was inhibited and delayed. This resulted in an increase in the period and a delay of the oscillation.

Intersegmental effects of DN stimulation

In the standing animal, muscle reactions of the ipsilateral neighbouring legs were examined. Fig. 5 shows responses of leg 4 and those of the ipsilateral neighbouring legs 3 and 5 to a stimulation of the DN of leg 4 when the animal was positioned on a horizontal plane. Stimulations with train durations of 100 or 200 ms led to an inhibition of the depressor muscle of leg 4, as observed in the previous experiments. In contrast, an excitation of the depressor muscle was observed in the neighbouring legs in response to stimulation of leg 4. This intersegmental reflex was also observable in the restrained animal when the dactylopodite was stimulated mechanically. The response to electrical stimulation seemed to be dependent on stimulus duration, but no detailed analysis was carried out.

In the walking animal, in addition to the muscle reactions, movements of the neighbouring legs occurred when leg 4 was stimulated at different points in the step cycle (Fig. 6A–F). Antagonistic behaviour was visible in immediately neighbouring legs, as expected from the results obtained when the animal was standing. Fig. 6B shows, as an example, that the stimulated leg itself reacted to the stimulus by ending the PS and starting the RS before the normal switch point was reached. The two neighbouring legs, in contrast, ended the RS and started the PS before reaching their normal switch point. In the posterior neighbouring leg 5, the reaction was therefore opposite to that of leg 4 but it was strongly phase-dependent and uniform, as can be seen from the sequential comparison in

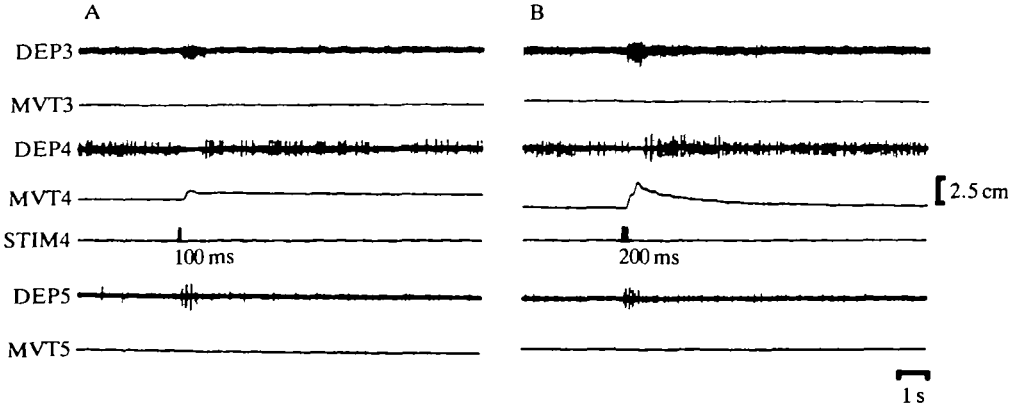

Fig. 5. Two examples of the response of adjacent legs 3 and 5 to stimulation of leg 4 in the standing animal. From top to bottom the traces show the EMGs of the depressor muscles (DEP) accompanied by the position signals (MVT) for each of the three legs. The fifth trace is the stimulus mark of leg 4. All stimulus parameters except for train duration were the same as those given in Fig. 2. (A) Train duration 100 ms. (B) Train duration 200 ms.

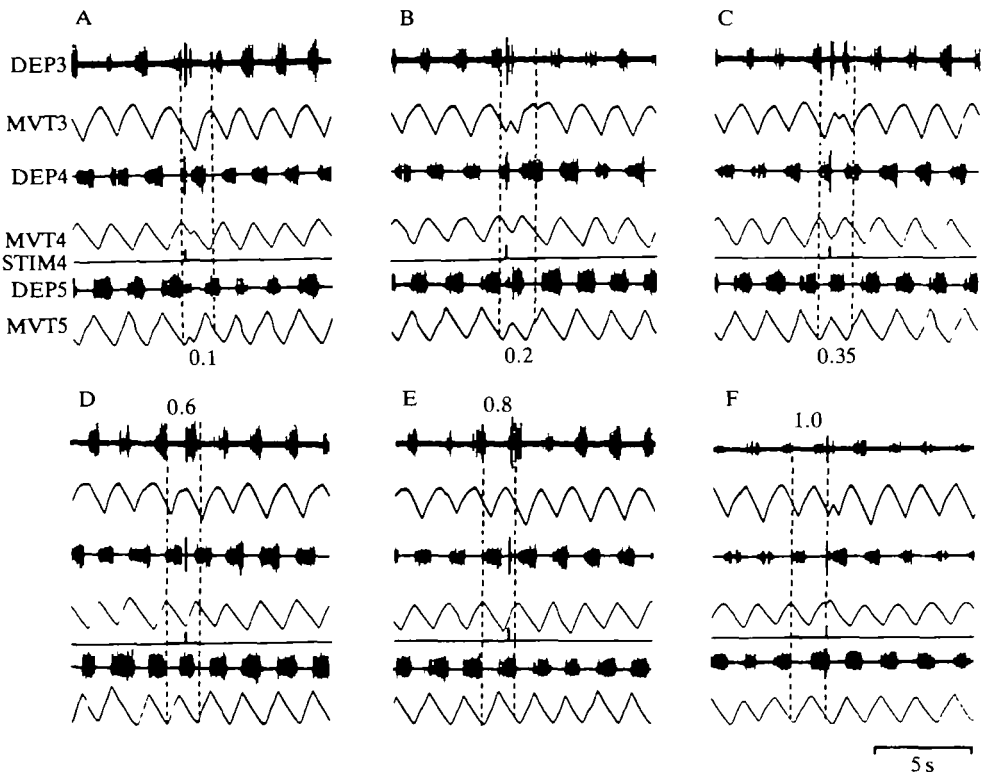

Fig. 6. (A–F). Six examples of responses of legs 3–5 to a stimulation of leg 4 in the walking animal. The traces in each example correspond to those in Fig. 5. The values below the traces in A–C and above in D–F represent the stimulus phase in the normalized period duration, which is indicated by the dashed lines (calculated from the mean of the previous 10 undisturbed steps). The figure shows six different situations with an increasing delay between the onset of the step cycle of leg 4 and the onset of the stimulation.

Fig. 6A–F, trace 7. The behaviour of leg 3 seemed to be more complex, but exactly the same general rule could be applied: when leg 3 was in PS, stimulation of its posterior neighbour led to a prolongation of the PS. When leg 3 was in RS, stimulation of leg 4 interrupted the RS and started the PS of leg 3. The behaviour of the depressor muscle was the same as that described above.

PRCs of the intra- and intersegmental effects of DN stimulation

Stimulation of leg 4

Leg 4 can have influences in both the anterior and the posterior direction. Fig. 7D–F shows the reactions of leg 4: the stimulation in Fig. 7D in the first part of the PS (between 0 and 0.325) led to a decrease of the period duration. Third-order polynomials were fitted to the data as described in Materials and methods. In the first part of the cycle (between 0 and 0.2) a zone was observed with a strong

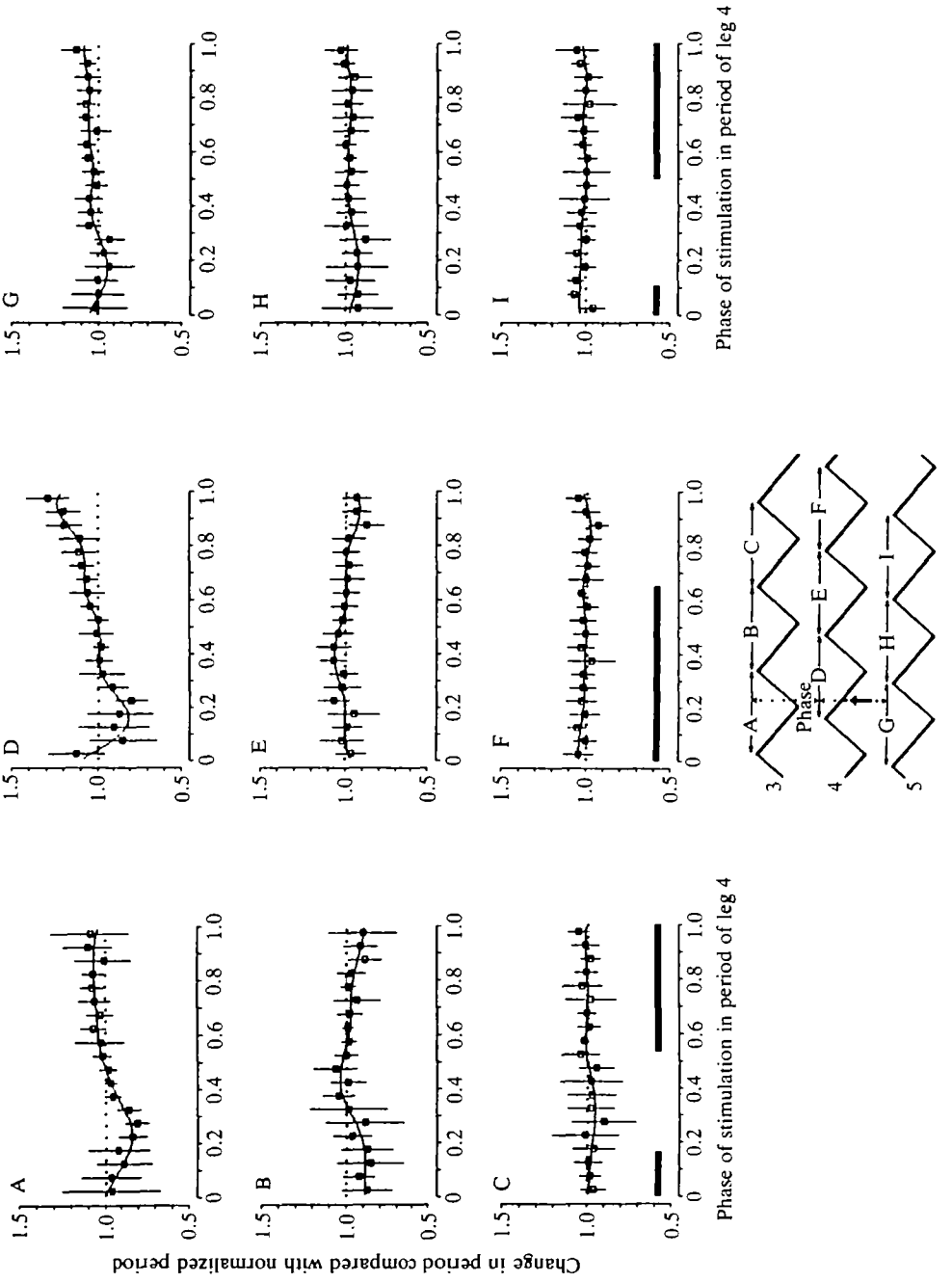
A
B
C
D
E
F
G
H
I
1.5
1.0
0.5
0
0.2
0.4
0.6
0.8
1.0
Change in period compared with normalized period
Phase of stimulation in period of leg 4
Phase
3
4
5

Fig. 7

Fig. 7. Dependence of the step period of legs 3 (A–C), 4 (D–F) and 5 (G–I) on the phase in which a stimulus was applied to the DN of leg 4. In each case the abscissa gives the phase of the stimulus in the normalized period of leg 4, calculated from the mean of the 10 undisturbed steps before stimulation. The ordinate shows the changes in period, compared to the normalized period. Values below 1.0 indicate a decrease in the period duration and therefore an advance of the oscillation. Values above 1.0 indicate an increase in the period duration and a delay of the oscillator, compared to the expected (unstimulated) cycle. The first row (A,D,G) shows the changes in the step during stimulation, the second row (B,E,H) shows the changes in the first step after stimulation and the third row (C,F,I) shows the changes in the second step after stimulation. Each point is an average of 5–20 single measurements within an interval of 0.05 units. Vertical bars indicate the standard deviation. Third-order polynomials were fitted to the data, as described in Materials and methods. Horizontal bars above the abscissa indicate that the leg in question was in the power stroke. Gaps between the bars indicate a return stroke. Between the application of the stimulus and a visible reaction of the stimulated leg a latency of about 150 ms was observed (as mentioned earlier in connection with Fig. 2). This latency advances the shape of the phase–response curves by approximately 15 % of the normalized step cycle.

negative slope, below −2.5. This zone corresponded to the transition from RS to PS and also showed a transition between prolongation and shortening of the period measured. This negative slope turned into a positive slope of up to 1.5 in the range 0.2–0.4. During the late part of the PS (in the range 0.325–0.525) no difference was visible between the measured and the expected period, corresponding to a slight slope, scattered around the zero point. During the RS (above 0.525) an increase in the cycle duration with a positive slope of up to 1.2 was observed.

In the first step after stimulation of leg 4 in Fig. 7E no significant deviation from the expected period duration was observed between 0 and 0.3. The slope turned from a weak positive value (below 0.5) to a weak negative value (above −0.5) at a phase value of 0.4, accompanied by a slight decrease in the step period in the second part of the cycle.

In the second step after stimulation of leg 4 in Fig. 7F no significant deviations from the expected period duration were observed in any part of the cycle. The slope of the calculated regression curves showed a scatter between −0.5 and +0.5 throughout the cycle. This shows that any reaction of the leg itself to the stimulus is terminated within two step cycles. Additionally, Fig. 7C,F,I serves to monitor the amount of statistical noise superimposed on all the PRCs.

In Fig. 7A–C the reactions of the unstimulated leg 3 to the phase of stimulation of leg 4 are plotted. As described in connection with Fig. 6, this led to a decrease in the period duration during the RS in leg 3 (ranging from 0 to 0.45). Corresponding to Fig. 7D–F, a zone with a negative slope (up to −1) is followed by a zone with a positive slope (up to 1). During the PS of the step cycle (above 0.525), the cycle duration was slightly prolonged in comparison with the unstimulated case, whereas the slope was approximately 0.

The first step of leg 3 after stimulation of leg 4 in Fig. 7B for the first part of the cycle (between 0 and 0.325) also showed a shorter period than expected. The slope

changed from zero to positive values of up to 1.4. During the second part of the RS (between 0.35 and 0.65) the regression curve was horizontal and no deviations from the expected period were visible. During the whole PS (above 0.65) a decrease in the period was observed along with a weak negative slope of up to −0.5.

In the second step of leg 3 after stimulation of leg 4 (Fig. 7C) a scattering of the regression curve around 0 appeared for all phase values.

The reactions of the unstimulated leg 5 are shown in Fig. 7G–I. Stimulation of leg 4 also had the effect of decreasing the period duration in leg 5 during the RS, as shown in Fig. 7G,H in the case of the period during stimulation and the subsequent period. In both cases the effects were weak and limited to the first part of the RS (between 0.1 and 0.3). Above this point the slope was approximately 0 for the whole range of phases observed. This was also the case with the whole second period of leg 5, shown in Fig. 7I.

Stimulation of leg 5

Unlike leg 4, with which we have been dealing in the former experiments, leg 5 has no posterior neighbour. The reactions of the stimulated leg are plotted in Fig. 8G–I: in the first part of the cycle (between 0 and 0.125) of Fig. 8G a zone with a strong negative slope (below −3) can be observed, which again corresponds to the transition between RS and PS. In the phase interval between 0.15 and 0.55 the period shortened and had a minimum at 1.25. The slope then increased with values between 1.5 and 0.5. During the late part of the PS and during the transition between PS and RS (between 0.55 and 0.75) we obtained a slope of approximately 0. Again no obvious differences between the measured and the expected period were seen. During the RS of the step cycle (above 0.725) we measured an increase in the period duration with a positive slope of up to 1.5.

In Fig. 8H,I no significant deviation from the expected period duration was observed in the first and second step of leg 5 after stimulation at any point in the step cycle. The slope scattered around 0 for all phase values. In this leg the reactions were therefore limited to the step cycle during stimulation.

In Fig. 8D–F the reactions of unstimulated leg 4 to stimulation of leg 5 are plotted. As observed with leg 5 in the first part of the step cycle, a strong negative slope of up to −2 appeared. Unlike in leg 5, this corresponds to the transition between PS and RS in leg 4. In the range 0.125–0.425, when the leg was in an early RS, the period was shortened and a positive slope with values of up to 1 was observed. At the transition between RS and PS (in the range 0.45–0.75) the slope of the regression curve was 0. Above a phase value of 0.75 a positive slope of up to 1 was again apparent.

The zone of negative slope (up to −1) is also visible in Fig. 8E for the first step of leg 4 after stimulation of leg 5 (between 0 and 0.25), but it is weaker than in the previous cycle. Above 0.25 the slope became slightly positive. During the later parts of the step cycle (in the range above 0.5) no obvious difference could be found between the expected and the measured period durations.

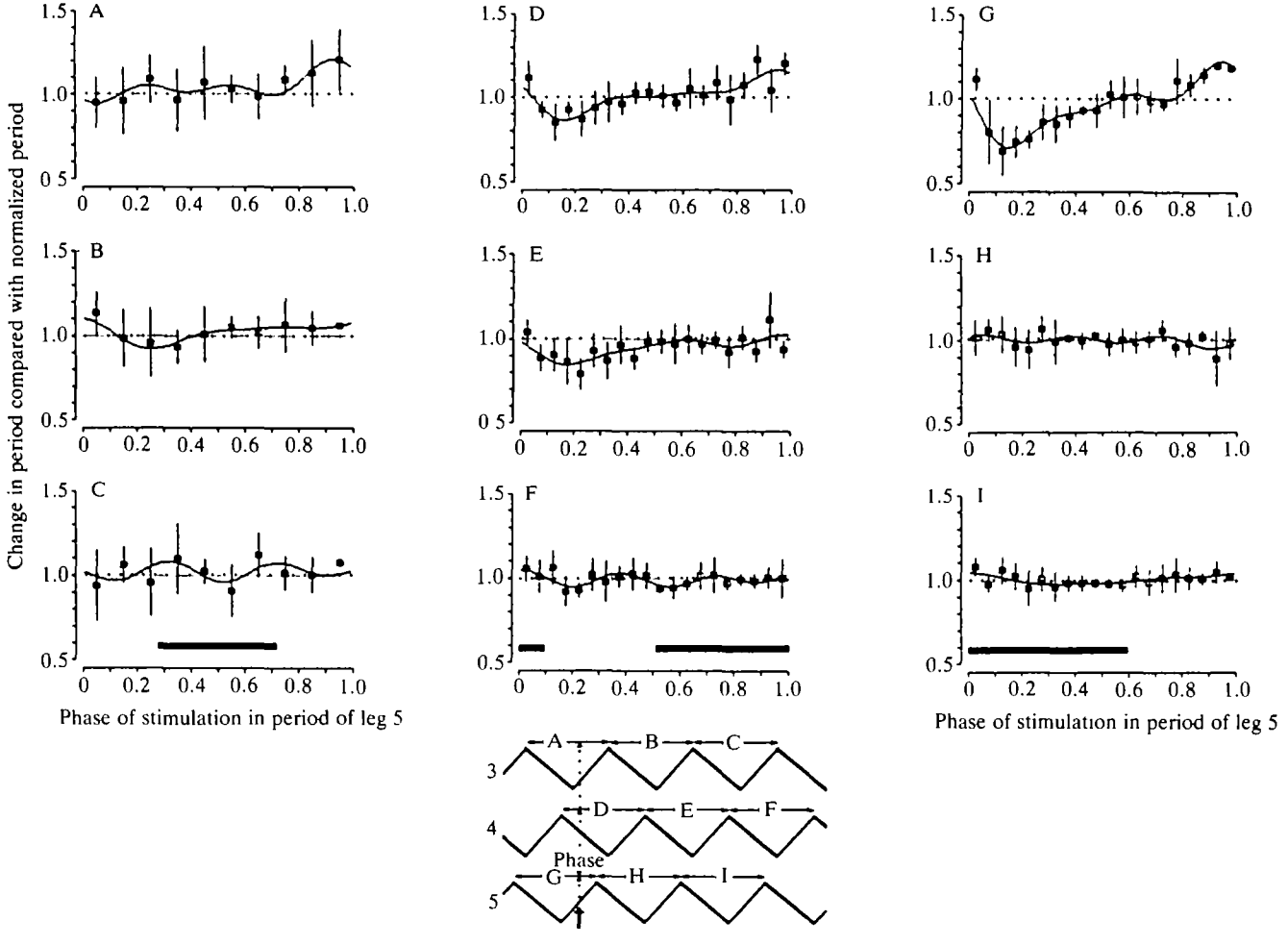

Fig. 8. Dependence of the step period of legs 3 (A–C), 4 (D–F) and 5 (G–I) on the phase in which a stimulus was applied to leg 5. In each case the abscissa is the phase of the stimulus in the normalized period of leg 5. All other parameters were the same as those given for Fig. 7, except for the average interval in Figs. 8A–C, which was 0.1 units.

In the second period of leg 4 after stimulation of leg 5 no significant deviations from the expected period duration are seen (Fig. 8F). The slope of the regression curve scattered around 0 for all phase values. Any reactions of the leg to the stimulus are therefore completed within two step cycles.

Leg 3 is positioned next but one to the stimulated leg 5. Fig. 8A–C shows the reactions of this leg. For reasons mentioned in Materials and methods, few data could be obtained here, so the interval width was doubled. These data have to be interpreted with caution in view of their high variability, as indicated by the standard deviation.

During most of the step cycle during stimulation (between 0 and 0.7) the data are scattered around 1, so no effects of leg 5 on leg 3 were demonstrable. With the beginning of the RS of leg 3 (above 0.7) a lengthening of the period appeared, similar to that observed in the other two legs.

In the first period in leg 3 after stimulation, the regression curve in Fig. 8B fitted the data well, showing that the behaviour of this leg was similar to that of leg 4. Again a zone of negative slope existed in the first part of the step cycle (between 0 and 0.25). This led to a slight decrease of the period within the range 0.1–0.4, followed by a weak increase during the rest of the cycle.

The variability of the data for the second period of leg 3 shown in Fig. 8C resulted in unsatisfactory fitting. It was therefore impossible to prove whether the period duration was affected.

Stimulation of leg 3

Unlike the two posterior legs, leg 3 showed no dramatic decrease in the step period. An increase in the period was measurable only at the transition from RS to PS (ranging between 0.8 and 0.1). This does not mean that leg 3 was not affected by stimulation. On the contrary, a strong reaction of the leg to stimulation was observed, but the leg very often remained at its AEP until the next step cycle began. Some cases were observed, but not analysed, where the leg paused for two or more cycles. For the first and second periods after stimulation no dependence of the leg reactions on the measured phase was observed.

The measurements of the reactions of leg 4 in Fig. 9D–F and leg 5 in Fig. 9G–I show that no strong reactions occurred in the posteriorly positioned legs on stimulation of leg 3. In all cases the values scattered around 1, indicating that no differences exist between the investigated and unstimulated step cycles.

Discussion

The results demonstrate that stimulation of the dactyl sensory nerve leads to a very stereotyped and uniform reaction in the leg affected. Fig. 4 shows that in all the cases studied excitation of the promotor and levator muscles and inhibition of the antagonistic remotor and depressor muscles were induced. Although the muscle responses were very consistent, the resulting leg movement was dependent on the state of the leg during stimulus application: if a PS was being performed, it

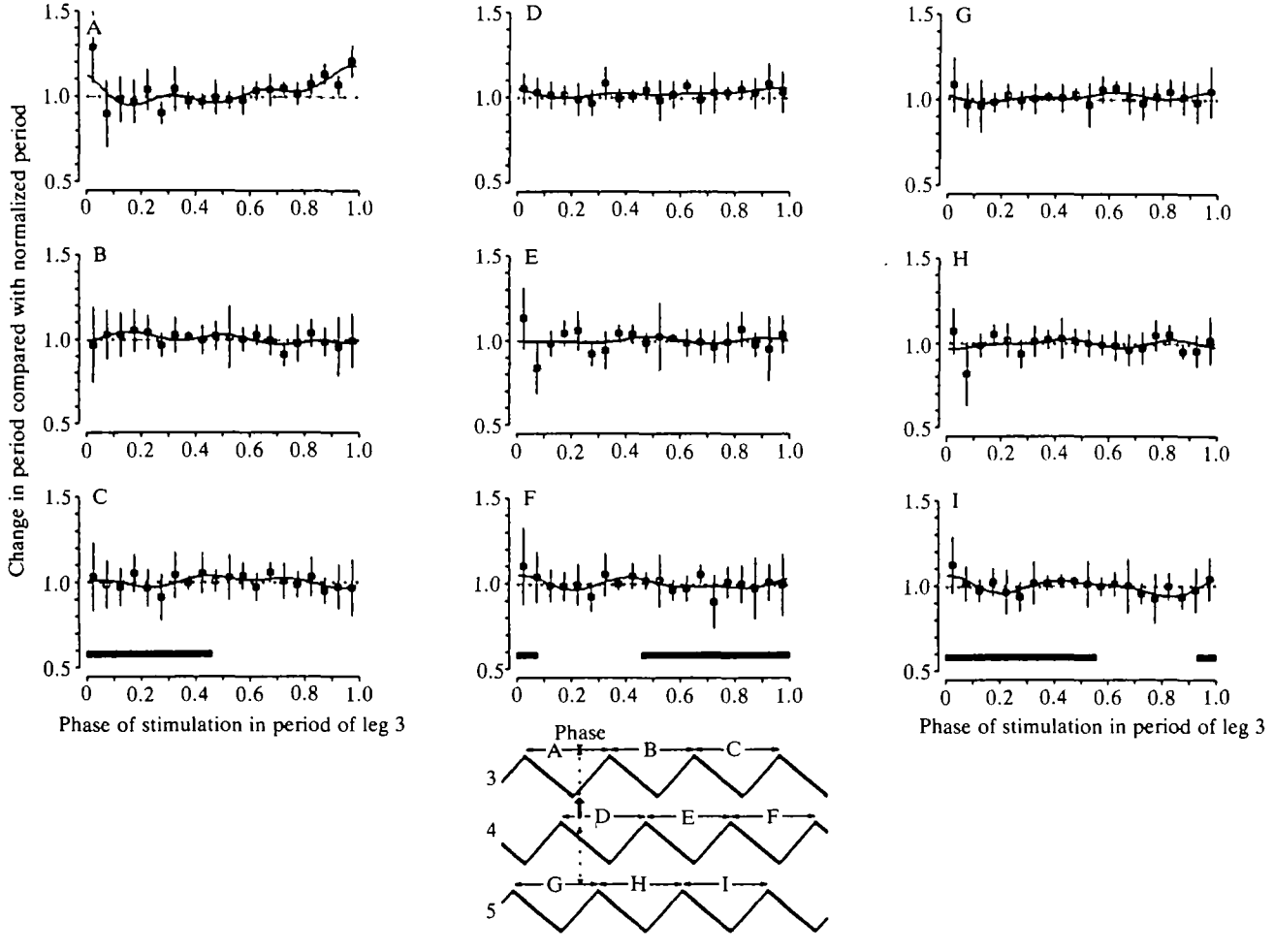

Fig. 9. Dependence of the step period of legs 3 (A–C), 4 (D–F) and 5 (G–I) on the phase in which a stimulus was applied to leg 3. In each case the abscissa gives the phase of the stimulus in the normalized period of leg 3. All the other parameters were the same as those given for Fig. 7.

was interrupted and an RS was initiated. This corresponds to the situation shown in Fig. 2, where the animal was standing motionless on a horizontal plane. Fig. 3 demonstrates that the contribution of the reflex itself to the stride length was less than 25 %, even in the cases with the strongest stimulation. Nevertheless, during walking, in approximately 95 % of all the cases observed, the leg maintained the new movement until the normal switch point was reached. The stimulation therefore induced a switch from PS to RS. This is supported by the finding that in the walking animal at the PEP, when the leg normally switches from PS to RS, stimulation had no additional influence on the step cycle. During the RS, stimulation could increase the velocity of the movement, owing to the additional excitation of the promotor and levator muscle. At the AEP, which is the switch from RS to PS, stimulation was found to delay the start of the new PS.

The unstimulated neighbouring legs consistently showed the opposite behaviour to that of the stimulated leg: excitation of the depressor muscle was observed and, judging from the movement traces (for example Fig. 6B, leg 5), the remotor was excited and the promotor and levator muscles were inhibited. Again the movement produced was dependent on the state of the legs when the stimulus occurred.

Phase shift and directionality of leg reflexes

Although the basic reactions of ipsilateral legs 3 and 5 were qualitatively the same as those described in leg 4, quantitative analysis in the form of the PRCs in Figs 7–9 shows the existence of obvious differences among the three legs investigated. As shown in Figs 7 and 8, the response of a single leg was not necessarily limited to the period during stimulation. Compensatory effects can occur, or the leg reaction can be split into two cycles. To establish the overall influence on a given leg, it was therefore necessary to add the PRCs of the three measured cycles (and, for reasons of standardization, to subtract the offsets):

$$p(x_k) = p(x_0) + p(x_1) + p(x_2) - 3\,.$$

This procedure was carried out with the calculated regression curves and is presented in Fig. 10A–C. Each figure shows the added responses of a stimulated leg 3–5, together with those of its unstimulated neighbours. The scaling of the abscissa corresponds to that in Figs 7–9. The phase shift which results from stimulation is plotted on the ordinate.

Descending influences

The data in Fig. 9 showing stimulations of leg 3, which are summarized in Fig. 10A, indicate that the only reactions that occurred were those of leg 3 itself. This leg responded by prolonging its step cycle (which caused a phase delay) only when the stimulus was delivered during the transition from RS to PS. When the stimulus was delivered in earlier parts of the cycle, no deviation from the normal step duration was observed. This seems to indicate that leg 3 is very insensitive to stimulation of its DN. In fact, the movement traces of leg 3 in all cases showed a

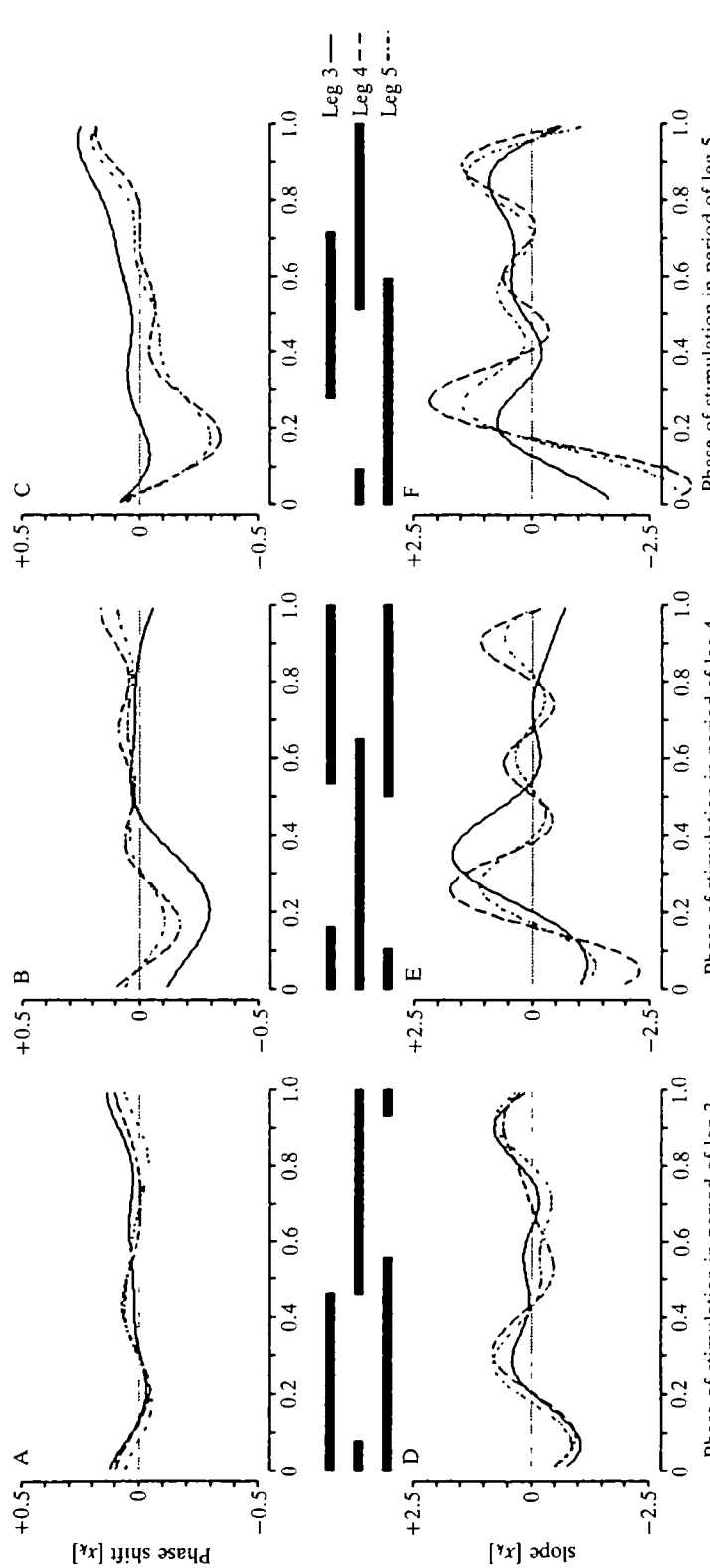

Fig. 10. Calculated phase shift and slopes for the experiments shown in Figs 7–9. Polynomials were fitted to the data, as described in Materials and methods. Each of the resulting curves is the sum of the phase–response curve during stimulation and those of the first and second step cycles after stimulation. (A) The resulting phase shift of legs 3–5, after stimulation of leg 3. (B) The phase shift of legs 3–5 after stimulation of leg 4. (C) The phase shift of legs 3–5 after stimulation of leg 5. (D–F) Slopes of the curves in A–C. The abscissa and all the other parameters except for the ordinate were the same as those given for Fig. 7. The horizontal bars between the first and second rows show the phase relationships between the power strokes of the three legs, measured during normal walking. Gaps between the bars show phase relationships between the return strokes.

clear response, as was the case with the other legs. This apparent contradiction can be explained by the finding that leg 3 compensates for the disturbance by a pause in the movement at the subsequent AEP. Such pauses at either the AEP or the PEP have been described previously by Chasserat and Clarac (1983) and serve, even during undisturbed walking, to synchronize the walking pattern. Moreover, in some cases, stimulation of leg 3 just before the AEP was reached led to a pause in its movement for one or two step cycles. In all cases the onset of a new cycle of leg 3 took place in the normal phase relationship to its posterior neighbouring leg. Posterior legs 4 and 5 showed no obvious responses to stimulation of leg 3. In addition, the first and second cycles after stimulus application showed no deviation from the normal step duration for any of the three legs investigated. These results show that leg 3 exerts no pronounced posteriorly directed influences in this situation.

Ascending influences

Fig. 10C summarizes the results for the stimulation of leg 5 given in Fig. 8. In contrast to the other results, all three legs investigated showed responses to a stimulation of leg 5. During the first part of the step cycle during stimulation, leg 4 followed the advance of leg 5, whereas leg 3 showed no obvious reaction. In the second part of this cycle leg 3 followed its posterior neighbours in a prolonged step cycle.

The behaviour of leg 4 paralleled that of leg 5 (Fig. 10C) and the two PRCs were nearly identical throughout the whole phase interval. Leg 5 therefore influenced the anteriorly positioned neighbouring leg 4 directly, and its next nearest neighbouring leg 3 either directly or (more likely) indirectly through its influence on leg 4. It is, in turn, not influenced by legs 3 and 4, so that the resetting of the whole stepping pattern was stable.

Ascending and descending influences

Fig. 10B summarizes the results given in Fig. 7 for the stimulation of leg 4. In this case influences may occur in both the anterior and posterior directions. Again, as with leg 5, all three legs investigated were influenced by stimulation of leg 4. In contrast to the stimulation of leg 5 shown in Fig. 10C, only the decreasing part of the period was stable, whereas much of the increase of period during the RS will be preadjusted, presumably by influences from leg 5. (This is very obvious in the case of leg 3, where the lengthening was nearly completely compensated.)

Only leg 5 showed some decrease in the period duration, as for leg 4. In the second part of the step cycle in Fig. 10B leg 5 showed only slight lengthening of the step cycle. This presumably explains the compensation observed in legs 3 and 4.

To sum up, this comparison among the three legs yields some useful basic information about how the walking legs in the rock lobster return to their stable state after disturbances of the walking pattern. Leg 3 has hardly any influence on the posteriorly positioned neighbouring legs, but is strongly influenced by them Disturbances of leg 3 will be compensated within the next but one step. In contrast

to these results, the resetting of the rhythm of leg 5 is stable and leads to compensatory movements in the other legs. Leg 4 is able to influence both neighbouring legs 3 and 5, but this is not a complete reset, as slight compensatory effects occur in the first step of leg 4 after stimulation. These compensatory effects are probably induced by the strong influence of leg 5.

Though the results clearly show intersegmental influences of DN stimulation, the question remains whether the observed effects were due to an interleg coordinating mechanism or whether they were secondary effects, resulting from interference with the normal movement of the legs. There are two main possibilities. (1) When a leg loses ground contact after stimulation, the other legs have to carry an additional load. The observed discharge of the depressor muscles as well as the leg reactions could thus result from changes in the load on individual legs and would be only an indirect effect. (2) The adjacent leg reactions may have resulted from intersegmental reflex pathways activated directly by DN stimulation of a single leg. If an unstimulated leg performs a PS, it will be prolonged; whereas if this leg performs an RS, it will be interrupted and the PS initiated. Since, in the normal walking pattern, neighbouring legs alternate in antiphase, this type of opposite coupling could be useful for stabilizing leg coordination.

The results presented in the following paper (Müller and Clarac, 1990) demonstrate clearly that intersegmental reflexes were generated by stimulation of the DN, but an additional indirect effect due to changes in leg loading cannot be excluded on the basis of the present data.

The problem of adequate stimulation

We used electrical stimulation of the DN to disturb a stable walking pattern. Certainly this method is not appropriate for characterization of the physiology of a receptor. This is, however, not particularly relevant to the present study, since it deals mainly with the effects that can be obtained with this type of stimulation. One of the main problems is the risk of stimulating not only the dactyl sensilla, but also other sense organs innervated by the DN (mainly hairs and the chemoreceptors of the funnel canal organs), and also neighbouring muscles, inducing co-contractions or other artefacts. These possibilities were excluded for the following reasons. (1) Recordings from hairs located on the cuticle of the dactyl were considerably smaller than those from the mechanosensitive part of the funnel canal organs. When applying an electrical stimulation comparable to that used in the described experiments, no leg response was observable. (2) The axons of afferents from the chemoreceptive part of the funnel canal organs are, in general, considerably smaller than those from the mechanosensitive part (M. Schmidt and W. Gnatzy, cited in Libersat *et al.* 1987*a*). Because of the low level of stimulation used in our experiments, it seems unlikely that the chemoreceptive part of the sensilla was responsible for the observed effects. (3) The dactyl sensilla, unlike other receptors such as the CSD or muscle receptors, are positioned far distal to the main leg muscles. When applying an electrical stimulation, no movements of the P-D (pro-dactylopodite) joint were observed, so this objection can be

overruled. (4) As observed in preliminary experiments, and in *Carcinus* (Libersat *et al.* 1987*a*) and isolated preparations of the crayfish thoracic ganglia (A. Chrachri and D. Cattaert, unpublished observations), a brief electrical stimulation of the DN produces reflexes similar to those produced by mechanical stimulation of the dactylopodite.

The advantage of electrical stimulation is that it can be used to apply short temporally and quantitatively defined pulses at specific phases in the movement pattern without any experimentally induced mechanical obstruction of the leg movements. The discharge of the DN is periodically modulated (Fig. 1B). Therefore, stimulations lasting longer than a fraction of the step cycle (which is usually the case with most types of mechanical stimulation) would be less appropriate for a functional analysis of the receptors' influence on the walking pattern.

Comparison with other results

The reflexes described here are very similar to those described in crabs (Libersat *et al.* 1987*b*), crayfish (Chrachri and Clarac, 1987) and *Homarus* (D. Cattaert, personal communication). Slight differences may exist in the case of crabs, presumably because walking is organized differently in crabs (which are lateral walkers) and rock lobsters.

Similar leg reflexes have been described in the stick insect: Graham (1979) and Schmitz and Haßfeld (1989) have described the treading-on-tarsus (TOT) reflex, which also acts intersegmentally. When, during walking, the tarsus of a middle leg was stimulated with a brush, the hind leg interrupted its RS and repositioned itself. This phase-dependent reflex is active only at the transition from RS to PS.

A second reflex, called compensatory leg placement (CLP, Fricke and Schmitz, 1988), can be observed in the standing stick insect. When the tarsus of any single leg is stimulated with a brush, it lifts from the ground and remains in a sustained extension. When an adjacent leg is stimulated additionally, this leg also lifts, while the first leg is replaced on the ground.

The reflex described for rock lobsters always produces a switch from the power stroke to the return stroke. Similar effects have been described in the stick insect (Cruse, 1985*b*; Bässler and Wegner, 1983) and in earlier comparisons between the reflexes of the cockroach and those of the cat (Pearson and Duysens, 1976). In all these cases, however, the reflexes were induced by an unloading of the leg, whereas in the present study we excited load-sensitive receptors.

In vertebrates, electrical stimulation of sense organs can also produce leg reflexes: Lennard (1985) has examined the influence of both cutaneous and muscle nerve stimulation on monopodal swimming movements in the turtle. Both types of stimulation were found to have similar, phase-dependent effects on the swimming pattern. A stimulation during the PS shortened the cycle and a stimulation during the RS lengthened it. Whereas cutaneous stimulation is not able to reset the rhythmic pattern during subsequent cycles, muscle nerve stimulation leads to a stable reset of the whole pattern.

Forssberg *et al.* (1976) and Forssberg (1979) have described a reflex in cats, called the stumbling corrective reaction. When an electrical stimulation was applied to the dorsum of the paw during flexion of the limb, it increased this flexion by inducing an additional excitation of the flexor muscle. A similar stimulation applied during the extension had no influence on the leg trajectory. A painful stimulus applied during the extension phase interrupted it, however, and caused the limb to flex, while the contralateral leg interrupted its RS and supported the body.

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