QUANTITATIVE ANALYSIS OF WALKING IN A DECAPOD CRUSTACEAN, THE ROCK LOBSTER *JASUS LALANDII*

I. COMPARATIVE STUDY OF FREE AND DRIVEN WALKING

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SUMMARY

The study compares the relative validity of the data obtained from two experimental situations, i.e. free walking and driven walking, in relation to leg coordination in *Jasus lalandii* (Milne-Edwards).

The relationship between ipsilateral and contralateral legs during the forward as well as the backward walking sequences has been analysed in the two situations. They operate roughly in opposition. Although little difference in the mean phase values has been observed in the two experimental situations, the strength of coupling is greater in the driven walking animals.

The power stroke (PS) duration correlates well with the period, but the return stroke (RS) is more variable and varies according to the leg considered. The phase does not appear to be correlated with the step period during free walking, but is correlated in the treadmill situation.

Initially, several of the properties of the single motor unit discharges correlated with movement have identical mean values in both free and driven walking. However, several significant differences have been observed in the intra-burst organization. These differences indicate that the constraint of the treadmill decreases the variability of all parameters and produces a stable and more stereotyped walking pattern.

INTRODUCTION

Our knowledge of crustacean walking has increased steadily over the last 20 years, so that we are now able to define its main features in comparison with the walking of other arthropods (Clarac, 1982). Most of the recent work on interleg coordination has been done on the Brachyura (Burrows & Hoyle, 1973; Barnes, 1975; Sleinis & Silvey, 1980) and the Astacura (Parrack, 1964; Macmillan, 1975; Ayers & Davis, 1977; Grote, 1981; W. J. P. Barnes, in preparation). The Palinura, however, have not been well investigated although we know that several species of this group are able to walk for long distances during migration (Herrnkind, 1980). In these animals, the disposition of the five pairs of thoracic appendages is somewhat peculiar. The insertion of the front pair of limbs is such that they tend to move in parallel with the

rostrocaudal axis (Fig. 1), the back legs are perpendicularly disposed to the same axis, while the third pair of legs has an intermediate orientation. In a previous study we investigated the effects of faster stepping on the third pair in relation to the back legs in order to define the relative coordination of the ipsilateral limbs in Crustacea during backward walking (Chasserat & Clarac, 1980).

We have chosen the treadmill as an experimental system because of the simplicity in controlling the various walking parameters and the relative ease of recording data. Quantitative studies on free walking animals are more difficult.

Nevertheless one can argue that the 'treadmill situation' differs significantly from a free walking situation. Therefore, before making a study of the spatial and temporal walking parameters of a Rock lobster on a treadmill (see following paper), we have compared systematically the free and the driven walking conditions.

The present report is a comparative analysis of the temporal parameters from data collected in free conditions in an aquarium and on a treadmill where we have elicited forward and backward walking at speeds analogous to those observed in an aquarium. Leg movements and muscle discharges have also been compared in the two types of walking.

MATERIALS AND METHODS

The rock lobster, *Jasus lalandii*, was used in all experiments. Thirty experiments were performed in the driven walking situation and 20 on freely walking lobsters. Animals obtained from French sources (Cap Langouste, Nice) were maintained in a filtered running sea water system and fed regularly. Animals used were male or female and all weighed around 500 g; under water their weight can be divided by a factor of ten.

The five pairs of legs are used differently in walking; the front leg pairs 1 and 2 are mostly used in feeding, fighting or cleaning behaviour, their contribution to stepping is only accessory. The third pair participates much more in the walking pattern. However the main walking limbs are leg pairs 4 and 5 which have been recorded in every experiment, whereas pairs 3 and 2 were only occasionally studied. EMGs were recorded from the two antagonistic muscles controlling the most proximal joint (thoracico-coxal joint = T-C joint); the promotor which protracts the legs towards the front and the remotor which retracts them to the rear. The recording techniques used were identical to those described by Ayers & Clarac (1978). Each muscle is innervated by fewer than 10 motoneurones, although in a few favourable preparations it is possible to identify the discharge of single discrete motor units. In these rare cases, it has been possible to measure the duration of successive unitary bursts and to study the discharge frequency of single motor units. No recordings of inhibitory motor discharge such as those obtained by Ballantyne & Rathmayer (1981) were obtained here. Muscle activity was recorded simultaneously with the movement of the T-C joint using the transducer described by Marrelli & Hsiao (1976).

Experimental procedure

Free walking

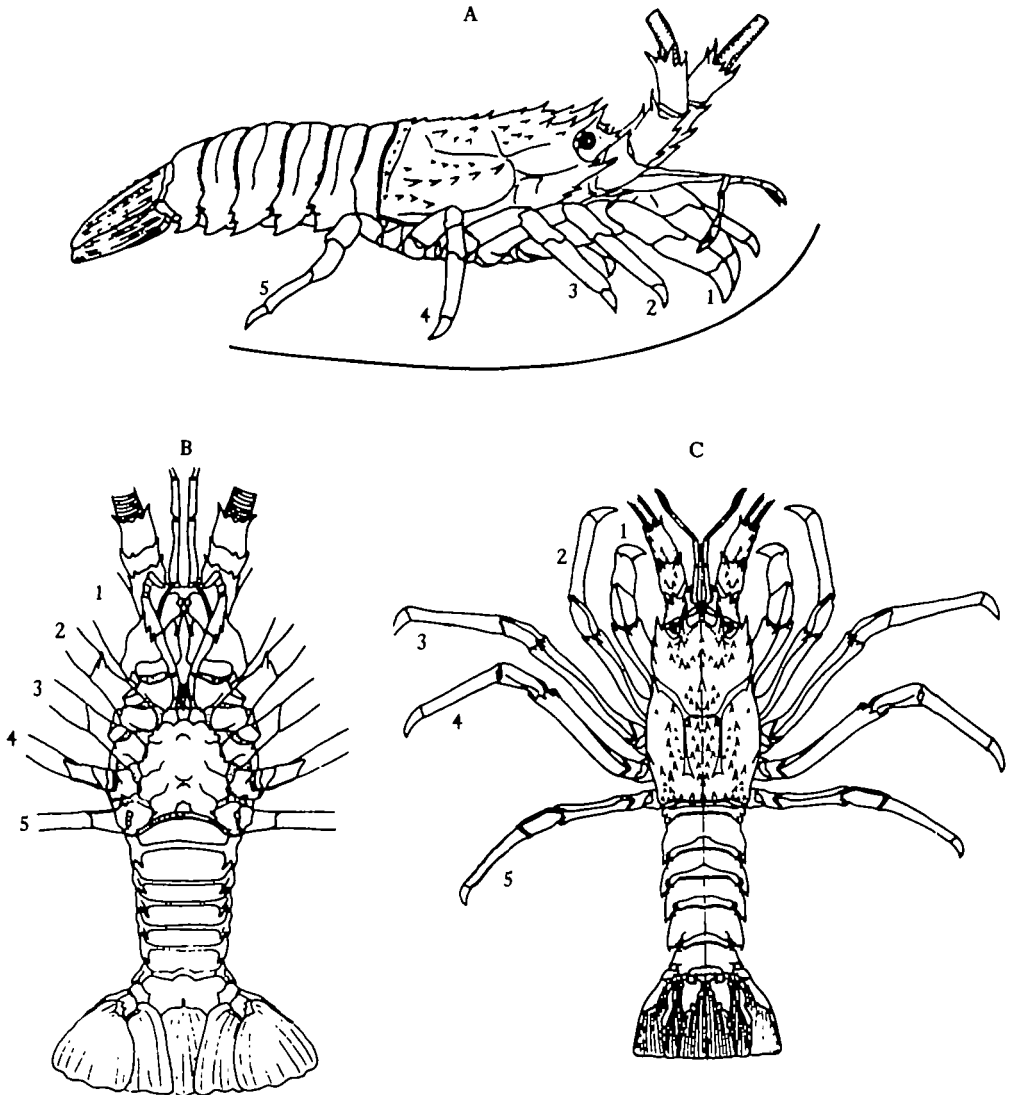Animals were placed in a round swimming tank, 2 m in diameter. The recording

Fig. 1. The rock lobster *Jasus lalandii* with its five pairs of legs, numbered 1 to 5. (A) Lateral view, (B) ventral view, (C) dorsal view.

wires glued to the coxopodite were connected to a styrofoam float which apparently did not restrict the animal's movements in any way. The float itself was connected to the electrophysiological apparatus by lightweight wiring.

The occurrence of walking seems to be dependent on the size of the experimental area. If it is too small the animal stays at rest and walks only rarely. If the diameter is large enough, however, the animal often walks around the perimeter and in all directions.

Driven walking

The animal was fixed on a treadmill in the way described by Chasserat & Clarac

(1980) using counterweights to offset the weight of the support and any effect it might have on the animal's posture. For the various quantitative analyses (period, burst duration, phase etc.) we took the onset of the powerstroke (PS) as the reference point in each walking cycle. This is in contrast to previous workers who have used the onset of the return stroke (RS) i.e. when the leg is lifted from the ground (Barnes, 1975; Graham, 1977; Wendler, 1966). We have chosen the onset of the PS because recent studies on leg movements in this animal show that the beginning of the PS is a much more stable point in the stepping cycle (Clarac, 1982). Furthermore, in recordings of EMG activity, the onset of PS is much more clearly defined. It seems that workers using cinematographic techniques have preferred to use the start of the RS because of its better definition in frame-to-frame analysis. As Macmillan (1975) points out, since the PS can be preceded by a long deceleration and by a pause time, it is difficult to visualize the exact point in the cycle when the leg makes contact with the ground.

EMG data were digitized before processing on a Digital MINC computer. All phase values were calculated using circular distribution methods (Batchelet, 1965) which are more suitable for cyclic phenomena and give both the mean phase and a concentration parameter (r). Dispersion about the mean is expressed by the circular standard deviation (c.s.d.). The concentration parameter ($0 \leqslant r \leqslant 1$) is a suitable measure of the % coupling between legs (Hughes, 1972).

RESULTS

If a rock lobster is able to walk freely in a small round aquarium it moves in every direction, investigating the surrounding area in a series of continuous walking sequences. However, it may also remain stationary without movement for several hours. We have been able to distinguish different types of walking behaviour that we have classified as follows:

(1) Stereotyped walking where the animal walks forward or backwards in a straight line, in the middle of the pool.

(2) Composite walking where the rock lobster changes its direction several times in the same sequence or when it walks obliquely using the legs of a trailing and a leading side, as in lateral walking.

(3) A further type of walking behaviour is observed when the animal moves around the perimeter of the aquarium. One difficulty in analysing sequences of this type is that often the legs of one side are touching the outer rim of the aquarium and this bilateral asymmetry can make the sequences somewhat difficult to interpret. Therefore, type 3 walking sequences have been taken into account only if they can be classified clearly into the first of second group above. Thus, we have divided our free walking data into two main groups:

(i) 'simple' or stereotyped forward or backward walking sequences which are composed of at least five consecutive steps;

(ii) complex walking patterns comprising all other types of walking behaviour.

For the first group, it has been possible to make a quantitative analysis while for the second we will present some qualitative data only.

'Simple' free walking analysis

During these sequences, the animal can take between five and 15 steps, using only the back legs, 3, 4 and 5. Legs 1 and 2 are most of the time held above the ground with the front part of the body raised up, while the uropods of the abdomen are dragged gently along the ground.

General features of interleg relationships

To study the relationship between legs during forward and backward walking, we recorded from the two proximal muscles (promotor, remotor) of the T-C joint. During forward walking the promotor acts as a return stroke (RS) muscle and the remotor as a powerstroke (PS) muscle. During backward walking their functions are reversed; the promotor becomes the PS muscle and the remotor the RS muscle.

Contralateral relationships. In a given sequence of forward walking, the promotor burst of the right leg 4 (R4) tends to remain more or less in antiphase with the remotor burst of the left leg 4 (L4) (Fig. 2). Several motor units discharge in each muscle and these may be tonic as well as phasic. Although a summation of all phase values gives a mean value of 0·47, this interaction is not very tight as is evident from the high c.s.d. value (0·17) and the wide spread (i.e. between 0 and 1) of phase values on the corresponding histogram. This variability in the phase coupling of L4 on R4 is further evident in the upper record of Fig. 2, where in the final step of the sequence, the two legs are actually in phase rather than in antiphase.

During backward walking, the shape of the bursts in legs R4 and L4 seems to differ from that during forward walking. At similar speeds the step period tends to be longer and each stroke appears to be more variable. Again both tonic and phasic units are activated. As is evident in the lower part of Fig. 2, the two legs are also loosely coordinated, operating in phase soon after the start of the record and out of phase at the end following an abrupt change in the middle of the record. The histogram of the phase values of all the sequences recorded gives a mean value of $0·22 \pm 0·17$, the c.s.d. being identical to that during forward walking (Table 1). These results indicate that, even in the most stereotyped sequences chosen deliberately, contralateral limbs during both forward and backward walking are not highly coupled (40 % coupling in the convention of Hughes, 1972). In a given sequence, the small number of backward walking steps in comparison to forward walking reflects the natural difference in occurrence of the two types of walking. Backward walking is often supplanted by an escape swimming behaviour involving the 'tail flip'.

Ipsilateral relationships. The relationships between legs on the same side during forward walking were also studied, again using the onset of remotor discharge as the reference point in each cycle. We investigated the phase of leg 5 in the leg 4 cycle and of leg 4 in the leg 3 cycle (Fig. 3). In both cases, the two pairs of legs are more or less in opposition as shown by the mean phase values, $0·46 \pm 0·12$ and 0·13, respectively (coupling in each case 77 %, Table 2). However, the histograms are sharper and much more symmetrically disposed around the mean than is apparent in the phase relationship of contralateral legs. The patterning of the remotor discharge appears similar in the three legs with the discharge duration being mostly shorter than the interburst interval. From Fig. 3, it appears that during forward walking the PS duration is very
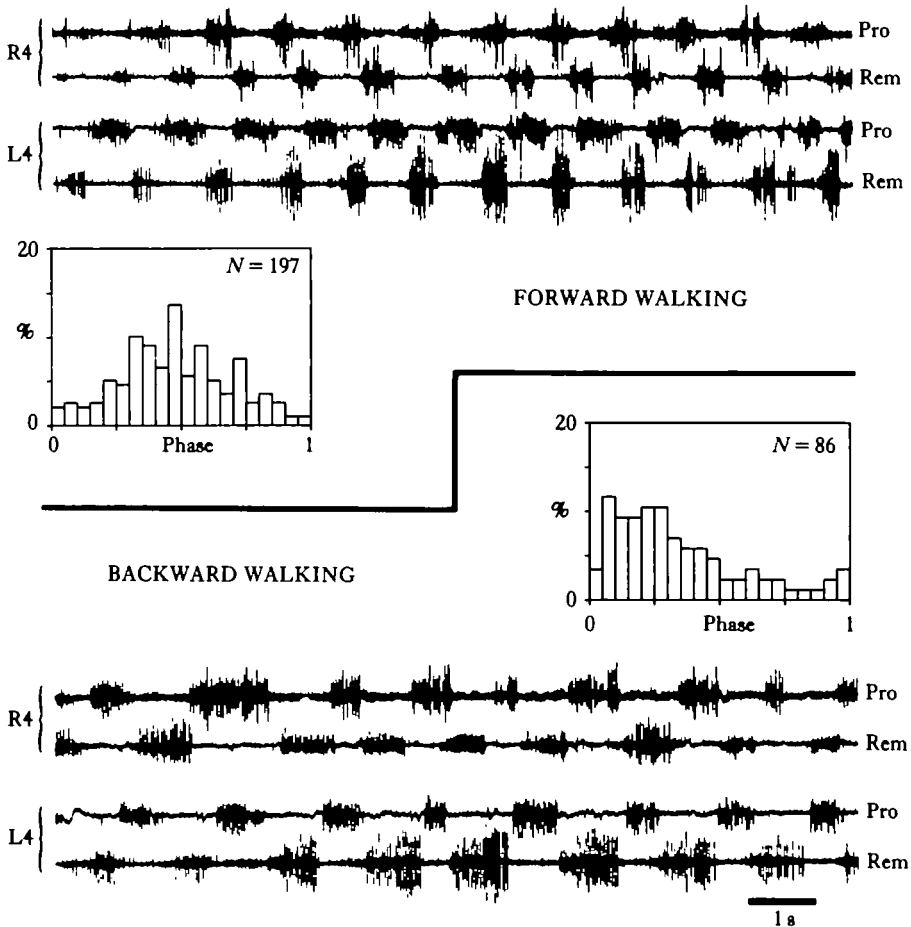
Fig. 2. Contralateral interleg mean phase values. Electromyogram recordings during forward and backward free walking. The remotor (Rem) and the promotor (Pro) are recorded for legs R4 and L4 (right and left 4th leg). Histograms present the phase of R4 in L4; the onset of the powerstroke being taken as the reference.

Table 1. *Mean contralateral phase (± 1 c.s.d.) and coupling (r × 100) in forward and backward free walking*

	N	Φ	% coupling
Forward walking	197	0·47 ± 0·17	39
Backward walking	86	0·22 ± 0·17	42

These values refer to the histograms of Fig. 2.

often shorter than the RS, even when step frequency is low (1 step s^{-1}). Furthermore, the three legs in all the sequences studied were found to step at the same frequency even though any sequence can start with the 3rd, 4th or the 5th leg.

During backward walking, the remotor discharge (now from the RS muscle) is dissimilar in its patterning for the three legs. In Fig. 3, for example, the remotor
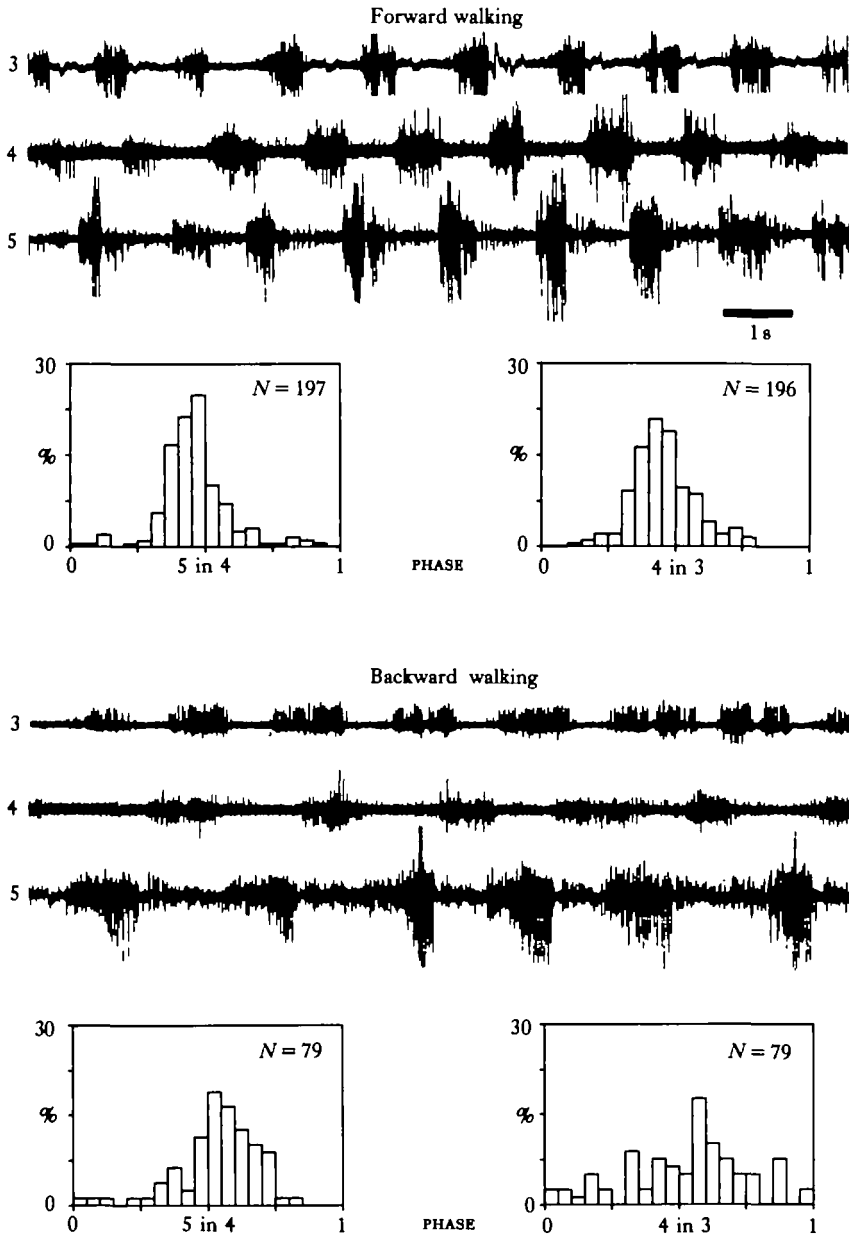
Forward walking

Backward walking

Fig. 3. Ipsilateral interleg mean phase values during free forward and backward walking. Simultaneous EMG recordings of remotors in legs 3, 4 and 5. Phase histograms show the percentage of occurrence for the ascending phase values distributed in 20 bins. The reference points measured are the onset of the powerstroke.

bursts of leg 5 have a high discharge frequency while those of leg 4 and 3 are lower. The phase between the back legs (5 in 4) is 0.56 ± 0.13 (67 %), the c.s.d. being analogous to the value obtained during forward walking. However, the interaction between leg 4 and leg 3 is of a different nature: most of the time leg 3 steps faster than

Table 2. *Mean ipsilateral phase (± 1 c.s.d.) and % coupling in forward and backward free walking*

		N	Φ	% coupling
Forward walking	5 in 4	197	0·46 ± 0·13	77
	4 in 3	196	0·46 ± 0·12	77
Backward walking	5 in 4	79	0·56 ± 0·13	67
	4 in 3	79	0·56 ± 0·18	37

From histograms of Fig. 3.

leg 4 and they are therefore in 'relative coordination' [as defined originally by Von Holst (1935) and studied by Chasserat & Clarac, (1980)]. This variability can be seen in Fig. 3, for example, where two consecutive remotor bursts can occur in leg 3 without a corresponding burst in leg 4. Although the mean phase value (0·56) obtained from the histogram is close to 0·5, as in forward walking, the shape of the distribution is much more dispersed (i.e. ±c.s.d.: 0·18) indicating a low degree of ipsilateral coupling (37 % coupling).

Influence of walking speed

In the different recorded sequences, step periods varied from 0·5 to 2·5 s during forward walking, and from less than 1 s to more than 3 s during backward walking. The mean period values were 1·38 s and 2 s respectively. To give some insight into the neural mechanisms underlying leg coordination, we have studied the relationship between remotor burst duration and step period. Fig. 4 demonstrates that this part of each cycle (RS for forward and PS for backward) is always positively correlated with the period. For legs 3 and 5, the relationship between remotor burst duration and period (R values between 0·72 to 0·85) remains very similar during both directions of walking and despite the fact that the muscle is involved in the swing phase during forward walking. For leg 4, however, the correlation coefficient differs greatly (both are significant) with the walking direction. This coefficient is of high value (0·827) when the remotor acts as a PS muscle, but is of low value (0·453) when the remotor is a RS muscle (Table 3).

Some authors have reported the presence of a descending metachronal wave in crustacean walking systems (Barnes, 1975; Sleinis & Silvey, 1980). The direction of such a wave is generally difficult to evaluate when examining classical gait patterns alone. Cruse (1979) has shown that the metachronal model of Wilson (1966) could be supported by a descending wave as well as by an ascending one. In order to demonstrate the presence or absence of a metachronal pattern in the rock lobster, we have plotted interleg ipsilateral phase against step period (Fig. 5). It is apparent that no significant correlation appears for the 4 in 3 phase (R = 0·08; P = 0·125) and only very weak values for the phase of 5 in 4 (R = 0·137; P = 0·027, Table 4). Although in the latter case there could be a tendency for a slight increase of the 5 in 4 phase with the burst period (i.e. an *anteriorly* directed metachrony), the degrees of significance we obtained for both coefficients are too low to permit us to conclude that there is a

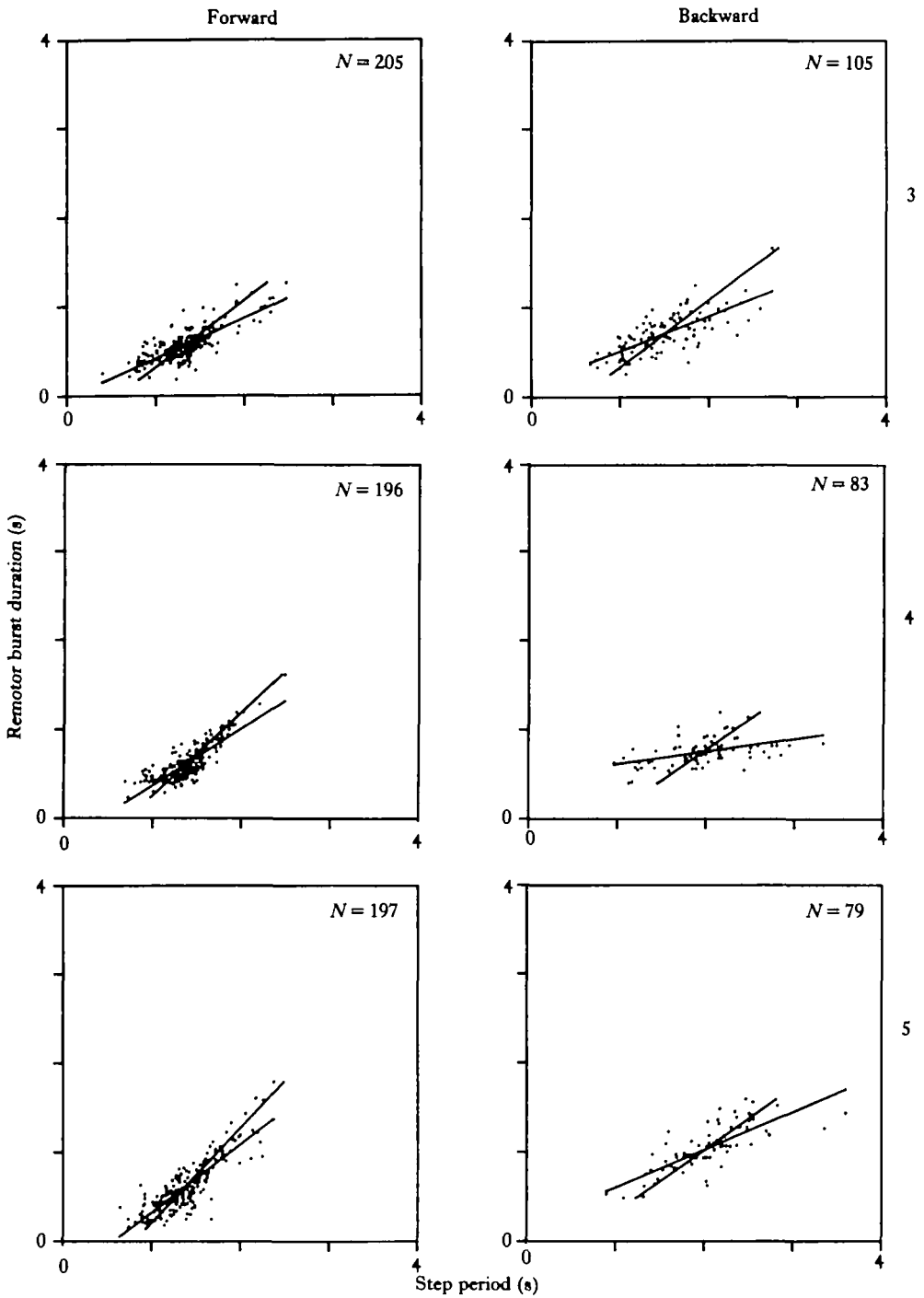Forward   Backward

Fig. 4. Correlation of the remotor burst duration *versus* step period for ipsilateral legs 3, 4 and 5 during free forward (powerstroke) and backward (return stroke) walking. All the coefficients are highly significant ($P \ll 10^{-4}$).

Table 3. *Statistical values from correlation analysis of Fig. 4*

		Forward walking	Backward walking
Leg 3	N	205	105
	R	0·775	0·720
	X̄	1·33 ± 0·32 s	1·50 ± 0·43 s
	Ȳ	0·57 ± 0·19 s	0·72 ± 0·23 s
Leg 4	N	196	83
	R	0·827	0·453
	X̄	1·38 ± 0·27 s	1·97 ± 0·47 s
	Ȳ	0·63 ± 0·20 s	0·76 ± 0·15 s
Leg 5	N	197	79
	R	0·849	0·777
	X̄	1·38 ± 0·32 s	2·02 ± 0·48 s
	Ȳ	0·62 ± 0·29 s	1·04 ± 0·26 s

N = Number of steps.
R = Correlation coefficient.
X̄ = Mean period (± 1 s.d.).
Ȳ = Mean remotor burst duration (± 1 s.d.).

Table 4. *Statistical values from correlation analysis of Fig. 5*

	Φ 5 in 4/step period 4	Φ 4 in 3/step period 3
N	197	196
R	0·137	0·08
X̄	1·39 ± 0·27 s	1·35 ± 0·31 s
Ȳ	0·46 ± 0·13 s	0·46 ± 0·13 s

N, R, X̄, Ȳ as defined in Table 3.

metachronal wave. This negative result does not mean that the metachronal pattern is not a property of rock lobster walking (see below and following paper). It may be that metachronicity is masked by other factors, at least in the current experimental conditions.

Complex free-walking

A rock lobster moves not only in stereotyped walking sequences but can also walk in every direction. Complex walking is difficult to quantify and therefore only a qualitative description will be presented here. When it walks, the rock lobster uses a variable number of legs. In a given sequence of stepping, the same leg can be involved in pulling or pushing the animal or may even be moved passively along the ground. The variability is evident in Fig. 6C, D. During the forward walking sequence in Fig. 6C, for example, all the legs are actively involved, but then the animal stops and starts to go backwards using fewer legs (i.e. R5, L4). In Fig. 6D, R3 is discharging weakly during a backward sequence, but as soon as the animal starts to move forward again, it becomes the major leg involved in moving the animal. In fact, the other side does not 'walk' at all (as seen by the steady state of the L4 remotor activity) and consequently the lobster turns to the left. In Fig. 6C, the transition between forward and backward is very sudden; the legs stopped in the order R3, L4, R5 and R4 (in other
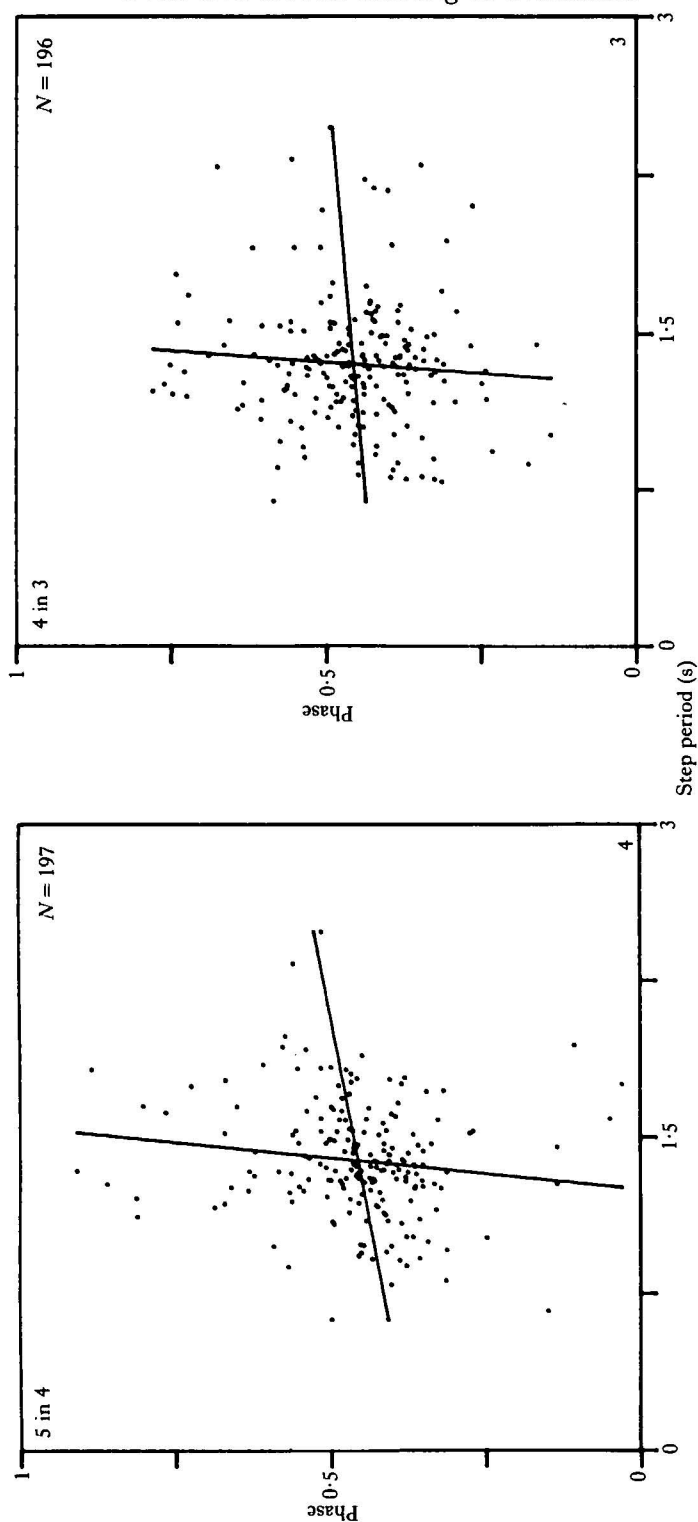
Fig. 5. Correlation of interleg ipsilateral phase (5 in 4 and 4 in 3) *versus* step period (4 and 3) during free forward walking. Both correlation coefficients are very close to zero and the regression lines are nearly perpendicular ($P \geqslant 0.03$ in both cases).
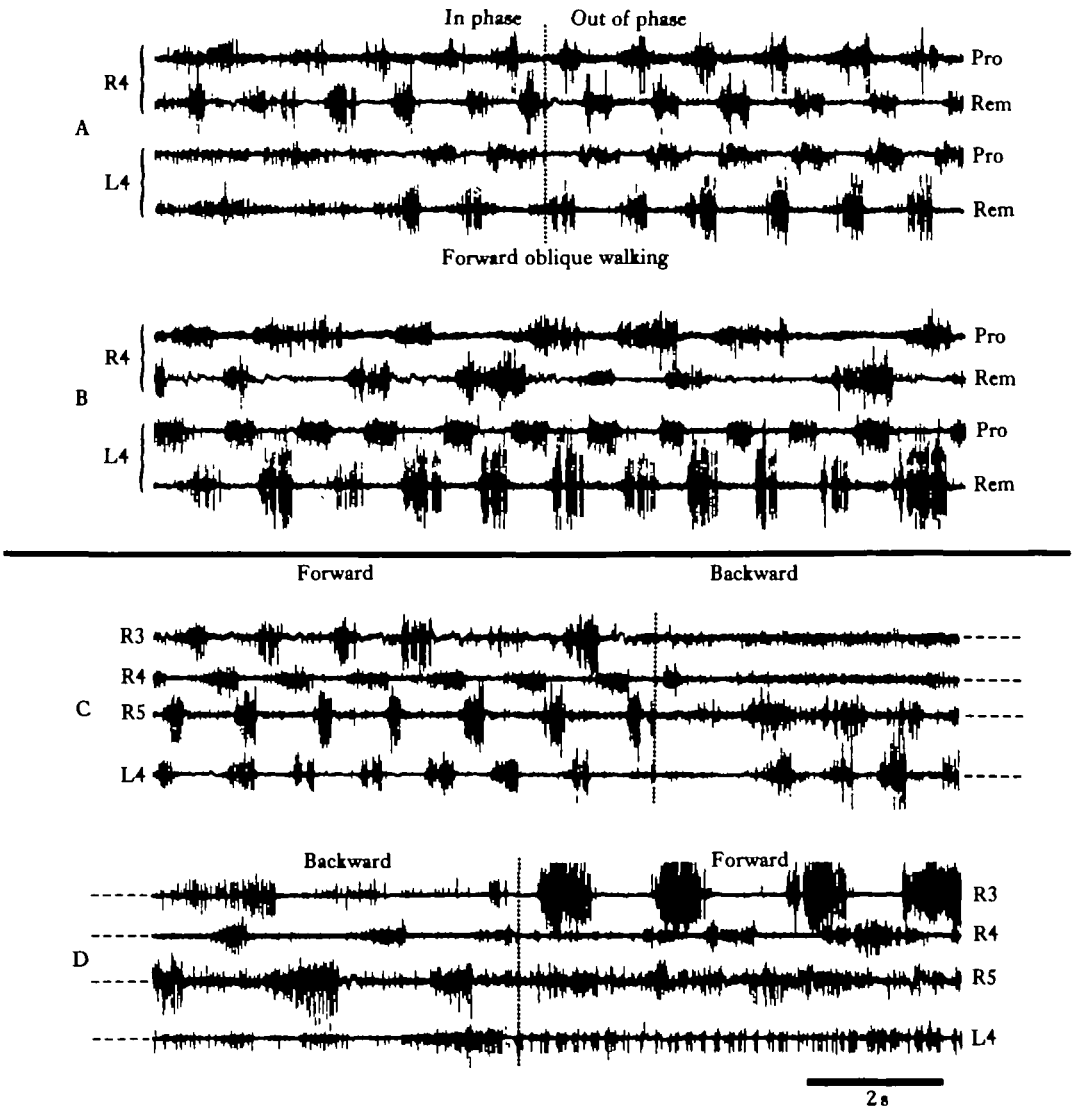
Fig. 6. Electromyogram recordings during free walking. The four records consist of simultaneous recordings from the remotor and promotor muscles of R4 and L4 (in A and B) and from the remotor muscles of R3, R4, R5 and L4 (in C and D). (A) Short sequence of in-phase forward walking followed by (dotted line) a typical alternating forward walking pattern. (B) Forward walking along a left oblique axis; this behaviour is very common in free animals. The left (leading) side has a stepping frequency higher than the right (trailing) one. (C) and (D) present a continuous complex walking sequence. It starts with several steps of forward walking involving all the legs recorded, then a sequence of backward walking occurs at a slower speed, followed by a series of steps of forward turning walking, the R3 directing the sequence.

sequences, the order could be completely different); the backward sequence does not finish abruptly but the onset of forward walking occurs suddenly and involves R3 only. The transition between walking sequences has also been studied in other arthropod groups (Land, 1972; Franklin, Bell & Jander, 1981; Delcomyn, 1982; Bowerman

1982) and these authors have already observed the complexity of such changes in types of walking behaviour.

If we consider more typical forward sequences, as in Fig. 6A and 6B, the interleg relationships are extremely variable. In Fig. 6A, leg R4 starts to walk before L4 which, for two steps, is in phase with the contralateral leg. Following this, the two legs tend to operate out of phase in the way described previously. The sudden transition from an initial in-phase to an antiphase coordination is due mainly to shorter R4 steps.

Often the animal walks in a direction other than in the anteroposterior one. If food is placed near the lobster, it will take the shortest route to its prey and this may involve walking obliquely. Such forward oblique walking is represented in Fig. 6B where the two sides step at very different frequencies; the left side making 11 very regular steps while the opposite side makes six irregular steps. In this case, the right side of the body is used partly as a trailing side and the left as a leading side. The discharges themselves are much more regular on the leading side, both tonic and phasic remotor units being used to activate the muscle. During this form of walking, the M-C joint, in addition to the T-C joint, is used to push or pull the animal along (Ayers & Clarac, 1978). An analogous record of activity is presented in Fig. 11C when the trailing side shows a great variability in strength and duration for both remotor and promotor bursts. The corresponding T-C joint movement is also very irregular in amplitude. These complex forms of walking demonstrate the capability of the two sides to operate independently although usually there remains a certain degree of coordination (defined as relative coordination). All degrees of this form of interaction can be encountered, ranging from a preferential phase relationship (although the legs may be operating at different stepping frequency) to complete phase drift.

Analysis of treadmill walking

If the rock lobster is placed above a treadmill, forward or backward walking can be elicited, depending on the direction of belt movement. Furthermore, it is possible to adjust the speed of the treadmill belt in order to elicit a walking speed analogous to that observed in free walking. To cover the range of different stepping periods observed in free walking, the speed of the belt was set at between 6 and 12 cm s^{-1}.

General features of the interleg relationships

Fig. 7 shows ipsilateral and contralateral relationships between the legs during driven forward walking (A and B) and during driven backward walking (C). Compared to free walking, ipsilateral leg coordination during forward driven walking appears much less variable (7A) because of the very regular step duration. Legs 5, 4 and 3 step very regularly. In addition, we have been able to record enough stepping sequences of leg 2 to be able to quantify the data of this limb also. Although leg 2 does not always display a strong remotor discharge, its timing is more or less correlated with the other legs. In this situation when there is a well defined type of walking movement, it is possible to determine the successive order of the leg stepping according to Parrack (1964). By referring to the onset of the PS, the sequential pattern observed most of the time is 2-5, 3 and 4. This means that the most common gaits are 2-5-3-4 or 2-3-4-5, the former gait having been already described in the Crustacea (see Clarac, 1982).
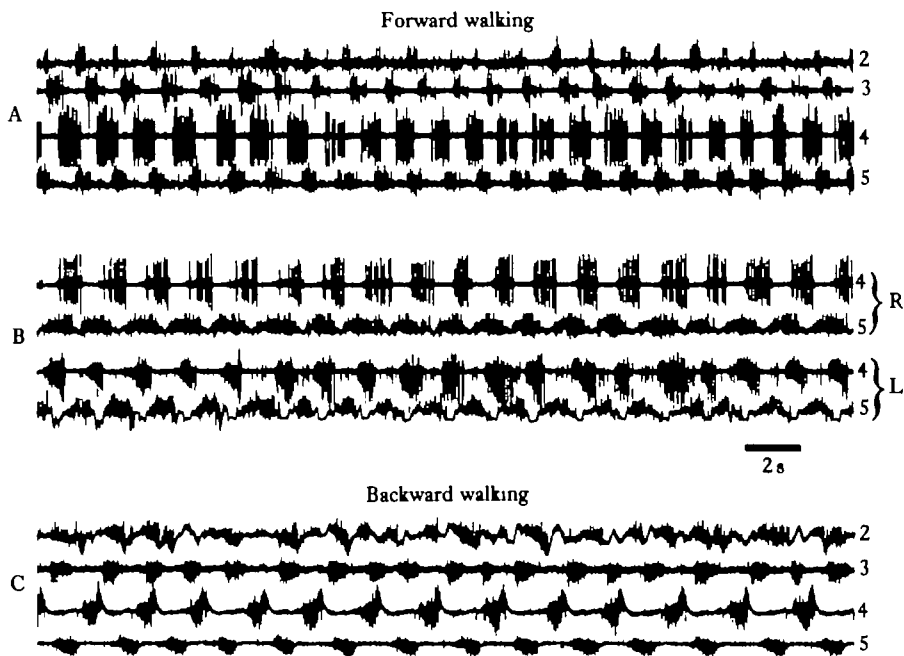
Forward walking

Fig. 7. Electromyographic recordings during driven forward (A and B) and backward (C) walking. The four traces consist of simultaneous recordings from the remotor muscle of the ipsilateral legs 2, 3, 4 and 5 (A and C) and from the contralateral ones R4, R5 and L4, L5 (B).

The ipsilateral leg 5-in-leg 4 and leg 4-in-leg 3 relationships have been quantified in Fig. 8. The legs stay more or less in antiphase although the absolute mean values are slightly different from those observed in free walking (see Fig. 3). However, the greatest difference is in the c.s.d. parameter which is two times less than during free walking and consequently the phase histograms show a correspondingly narrow distribution.

During a sequence of backward walking, the burst discharge and the timing of successive cycles also appeared to be very regular (Fig. 7C). Nevertheless, leg 2 is often only gliding on the belt while leg 3 is in relative coordination with leg 4 (Chasserat & Clarac, 1980). The histogram presented in Fig. 8 shows these differences clearly. Although the mean values are similar, i.e. 0·53 (leg 5 in leg 4) and 0·47 (leg 4 in leg 3), the c.s.d. of the latter value is double that of the former (Table 5).

The occurrence of relative coordination during backward walking is also observed in free walking (Fig. 3) and suggests that initially the nature of leg coordination is not altered in the treadmill situation.

If we consider contralateral coordination during driven forward walking, the relative stability of the step period on each side again makes the coupling more apparent than in free walking. The histograms (Fig. 8) lie mainly between values of 0·25 and 0·5 with c.s.d. analogous (0·08) to ipsilateral coordination. Thus, in forward
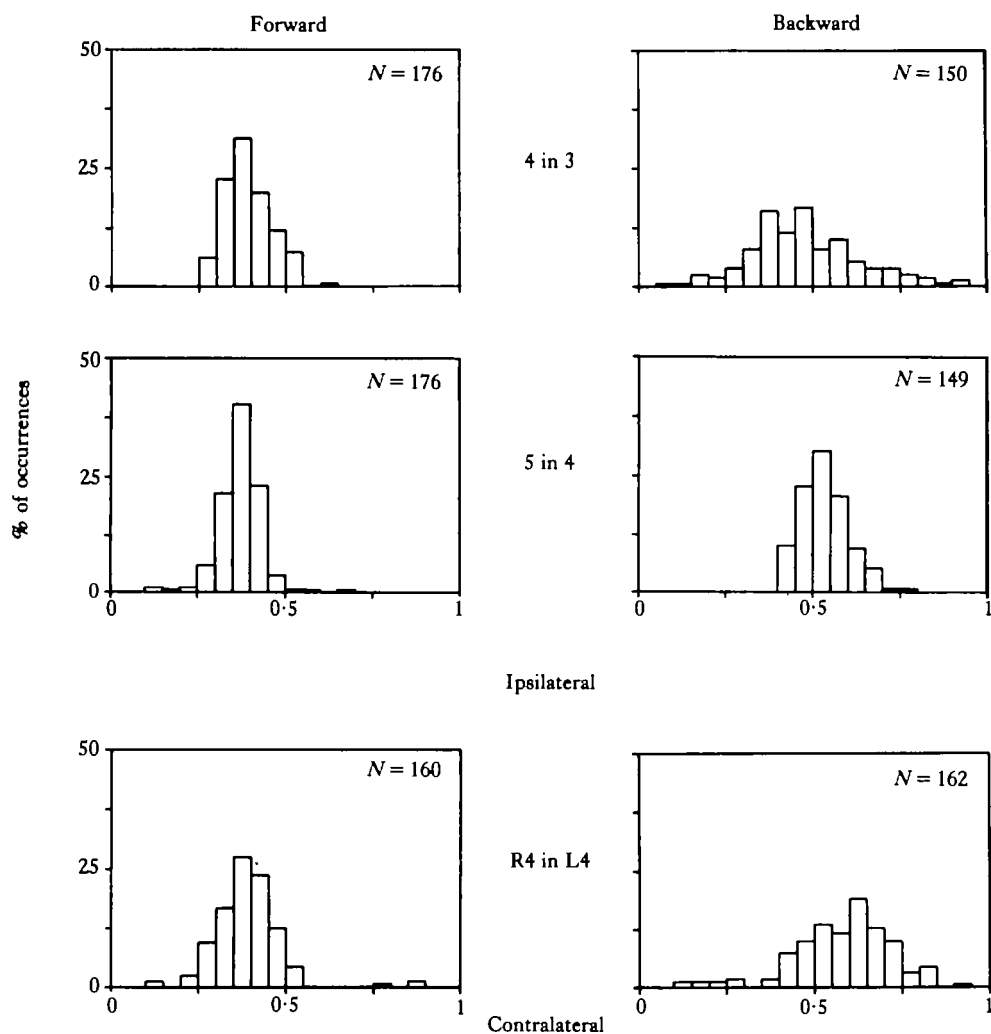
Fig. 8. Ipsilateral and contralateral interleg mean phase values during driven forward and backward walking. As in previous analyses, the onset of the PS burst has been taken as a reference.

Table 5. *Mean interleg phase (± 1 s.d.) and % coupling in forward and backward driven walking (from histograms of Fig. 8)*

		N	Φ	% coupling
	5–4	176	0·37 ± 0·06	93
Forward	4–3	176	0·39 ± 0·07	91
	4–4	160	0·38 ± 0·08	87
	5–4	149	0·53 ± 0·07	91
Backward	4–3	150	0·47 ± 0·14	61
	4–4	162	0·59 ± 0·12	70

Table 6. *Statistical values from correlation analysis of Fig. 9*

Legs		2	3	4	5
Forward walking	N	176	176	176	176
	R	0·353	0·696	0·917	0·753
	$\bar{X}$	1·18 ± 0·23	1·19 ± 0·21	1·19 ± 0·22	1·19 ± 0·21
	$\hat{Y}$	0·30 ± 0·11	0·55 ± 0·11	0·65 ± 0·17	0·61 ± 0·14
Backward walking	N	169	175	150	149
	R	0·890	0·837	0·438	0·471
	$\bar{X}$	1·87 ± 0·52	1·81 ± 0·48	2·11 ± 0·46	2·15 ± 0·48
	$\hat{Y}$	1·23 ± 0·48	0·78 ± 0·25	0·84 ± 0·10	0·96 ± 0·12

N, R, $\bar{X}$, $\hat{Y}$ as in Table 3.

walking the three pairs of back legs are operating in a clear and stereotyped manner. The contralateral relationships during backward driven walking (Fig. 8) also demonstrate a narrow range of phase values in comparison with free walking. Nevertheless the histogram is still more dispersed (i.e. a greater c.s.d.) than for forward driven walking. This could be explained by the relative coordination of 4 and 3 on each side.

Influence of the belt speed on leg coordination

As in free walking, we have studied the relationship between remotor burst duration and step period at different walking speeds of the treadmill. A comparison of the two directions of walking shows that, as in free walking, the cycle period of forward walking is generally shorter than in backward walking at the same belt speed. This can be seen in the Table 6 and in Fig. 9, where in the forward direction we have a mean value of 1·19 s for each step, while in the backward direction the front legs 2 and 3 step faster (1·8 s step^{-1}) than the back legs (2·1 s step^{-1}). The variability between the different step durations is two times greater for backward than for forward walking. The difference in period between front and back legs in backward walking can be explained by the position of the animal during this type of behaviour when the abdomen is completely flexed and is now anterior to the direction of movement. Legs 4 and 5 are held underneath the abdomen and directed forwards, while legs 2 and 3 serve more or less as counterweights to maintain the position of the animal. Due to their different orientation legs 2 and 3 sometimes step faster. The correlation co-efficients for forward as for backward walking are all significant but the values differ from one leg to another (Table 6). A comparison of the remotor correlation coefficient with the direction of walking for the different pairs of legs is shown in Fig. 9. The remotor burst duration of legs 4 and 5 is better correlated with the period when it acts as a PS muscle (in forward walking, R = 0·7–0·9) than when it acts as a RS muscle (backward walking, R = 0·4–0·5). Leg 3 remotor bursts are well correlated with the

Fig. 9. Correlation of the remotor burst duration *versus* step period for ipsilateral legs 2, 3, 4 and 5 during driven forward (powerstroke) and backward (return stroke) walking. Data from different 'physiological' ranges of belt speeds have been used for the calculations (6–12 cm s^{-1}). All coefficients are highly significant ($P \ll 10^{-5}$). Because of the difference in step duration, abscissa and ordinate time scale is double for backward walking.
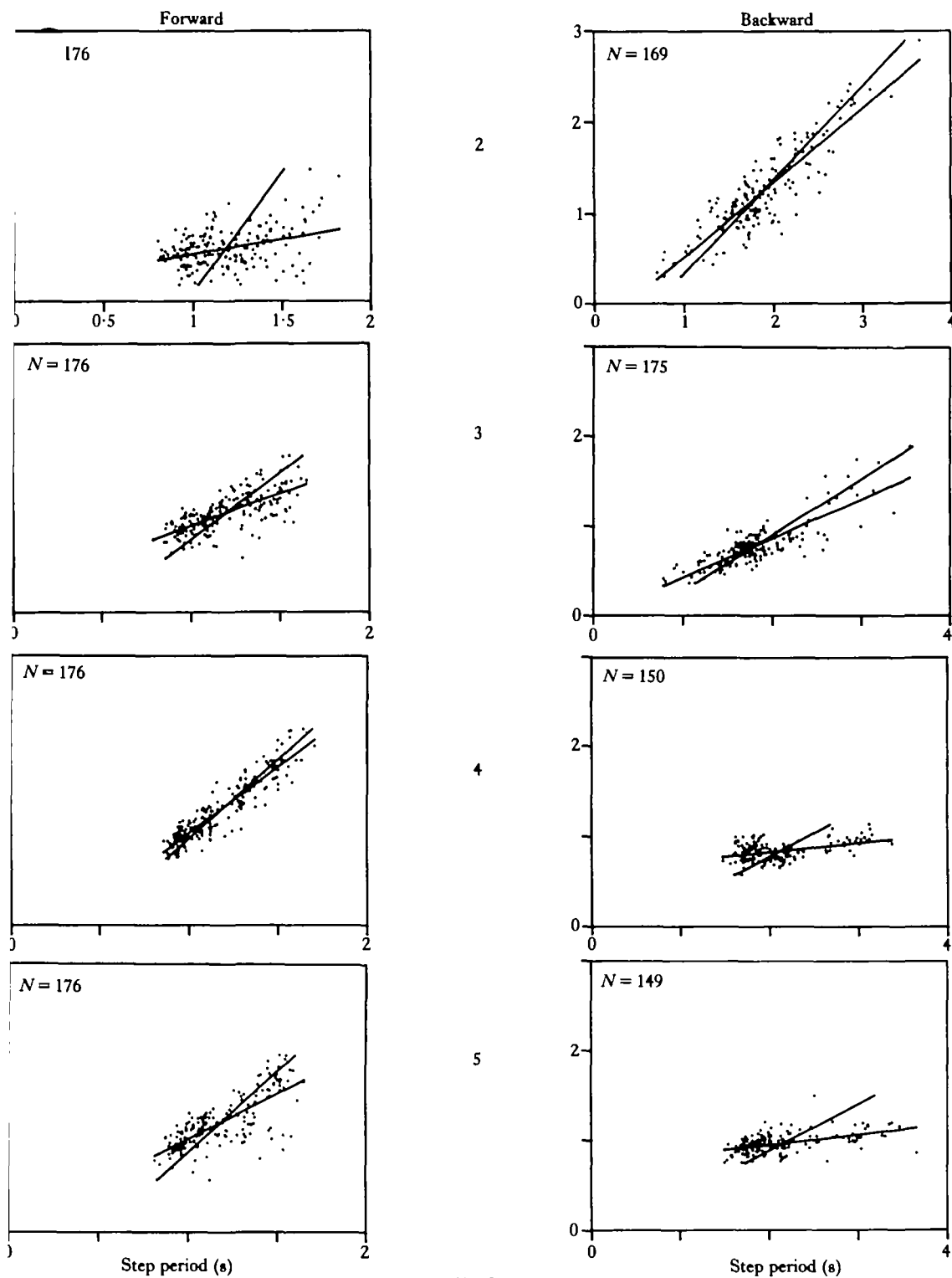
Fig. 9

period whether the direction is forward or backward. For leg 2, however, the co-efficients are reversed in that the remotor burst duration is better correlated with the period when it operates as a return stroke muscle (R = 0·89) than as a PS muscle during forward walking (R = 0·35).

In the treadmill situation, as for free walking, we have analysed the relationships between phase and step period. We subjected the animal to four different belt speeds (6, 8, 10 and 12 cm s^{-1}). Fig. 10 (top) shows a plot of leg 4 in leg 5 phase values *versus* the step period, mixing the data from the four different sequences. The bottom diagram has been constructed using the same data but expressed in a different way. The mean phase ($\pm$1 c.s.d.) was computed for each set of steps and plotted in the four categories of imposed belt speed.

As in free walking, the step period exhibited large fluctuations in duration even at a constant speed. A step period of 1·5 s for example can occur in any of the four imposed speed sequences. Nevertheless the results of this analysis in the treadmill situation demonstrate that there exists a metachronal mechanism in interlimb phase coordination whose short latency appears to be directed forward along the body. The weak correlation observed during free walking does suggest, however, that in the free condition a similar wave is present. A t-test performed on the four mean phase values shows that the leg 4 in leg 5 phase undergoes a significant decrease ($P \ll 10^{-4}$) as the imposed speed is reduced from 12 to 6 cm s^{-1} (data from Fig. 10).

Leg movements and muscle discharge during free and driven walking

Since leg 4 is the most commonly used limb and the most powerful in terms of displacement, we have correlated the motoneurone activity of its remotor and promotor muscles with the corresponding T-C movement. Fig. 11 gives examples of such recordings during various types of movement. When the animal moves in a straightforward manner, the amplitude of consecutive T-C joint movements is more or less constant and corresponds to 20°–30° of displacement. The transducer record shows a sharper peak at the end of the remotor burst than at the end of the promotor burst, indicating a slight deceleration towards the end of promotion. In Fig. 11A, the leg L4 performs a prolonged promotion (black star) as the animal turns to the right, then a new strategy is used on the left side with an increased discharge in the promotor muscle. The sequences can be even more complex. For example in Fig. 11B the animal starts to walk forwards but without apparent remotor bursting. In this case, the animal is propelled by the other legs and leg 4 is displaced only passively without powerstroke activity. (An analogous record is visible in Fig. 6D where leg 3 exerts the main forces while legs L4 and L5 are weakly activated.) After this short transition

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Fig. 10. Correlation of interleg ipsilateral phase (4 in 5) *versus* the leg 5 step period (upper diagram) and *versus* the imposed belt speed (12–6 cm s^{-1}, lower diagram) during driven forward walking. In the upper scattergram, each value of phase is plotted against the corresponding step period with a special symbol indicating the imposed belt speed (black square, 12 cm s^{-1}; open circle, 10 cm s^{-1}; black triangle, 8 cm s^{-1}; open diamond, 6 cm s^{-1}. $N = 156$; $R = 0·524$; $P \ll 10^{-5}$). The same symbols are used for the corresponding belt speed in the lower diagram. Each point represents the mean phase value computed for all the steps in each speed bin. The number of steps and the $\pm$1 c.s.d. bars are represented. The regression line of the phase *versus* the period and the phase *versus* the belt speed have the same slope, but this is merely because of the choice of the respective x-axis ranges ($N = 4$; $R = 0·993$; $P = 0·04$).
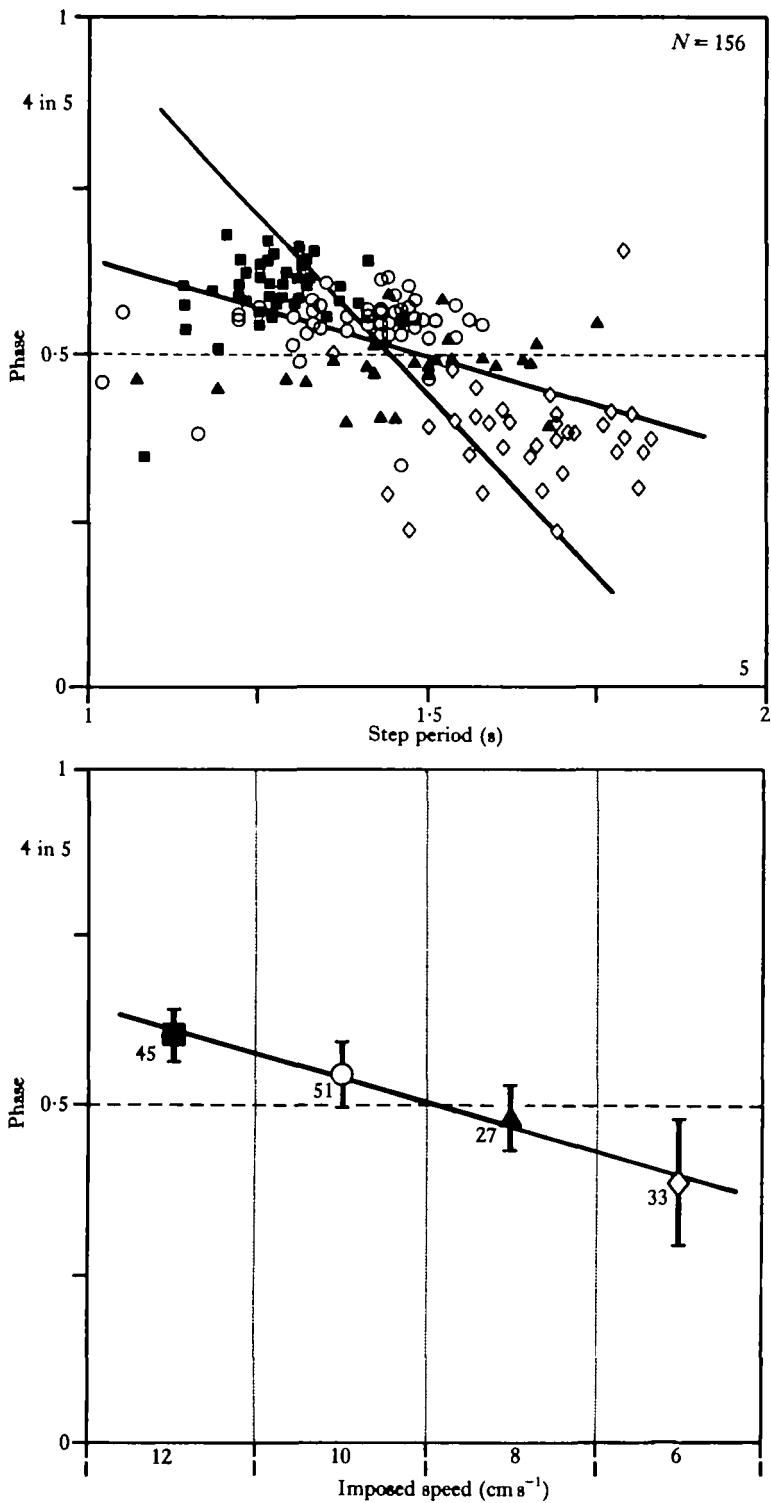
Fig. 10

period, leg 4 becomes involved in propulsive stepping activity. When the animal walks
obliquely as in Fig. 6B, the T-C movement is very irregular (Fig. 11C). There is a
large variability in the most anterior and posterior positions reached by the limb from
one step to another. This irregular movement is directly related to the intensity and
duration of remotor/promotor muscle discharge. The variation observed in remotor
activity suggests that the corresponding forces exerted by the limb also vary greatly
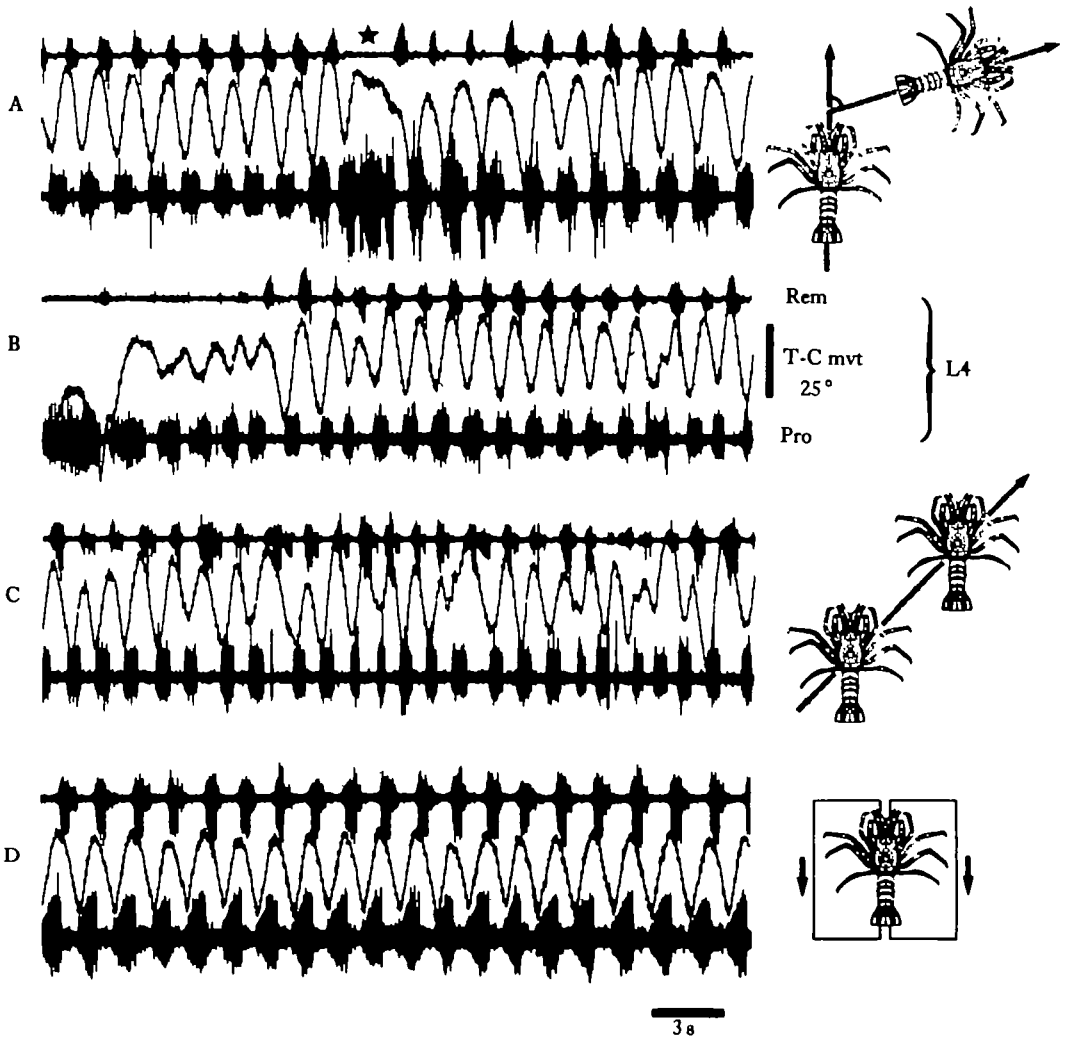from step to step.

Fig. 11. EMGs during free and driven forward walking. Simultaneous recordings of the remotor
(Rem) and of the promotor (Pro) muscle. The movement (mvt) corresponds to the T-C joint angle
of leg L4 (promotion is up and remotion is down). (A) Straight forward walking with a turn to the
right (black star). L4 makes a larger step with a long stride length. (B) Onset of a forward walking
sequence. The first five steps of leg 4 are performed passively, the remotor is not active while the
promotor continues to discharge in bursts. (C) Forward oblique walking (as in Fig. 6). Leg L4 is on
the trailing side; the muscle discharges and the movements are very irregular. (D) Forward driven
walking (at 12 cm s^{-1}). EMG activity and movements are very stereotyped.

Comparisons of T-C movement obtained on the treadmill and during free walking confirm that the shape, amplitude and the frequency of muscle discharge are more or less the same but that the treadmill tends to impose greater stereotypy.

To try to understand more precisely the organization of the motor output pattern responsible for the movement itself, we have compared single motor unit discharges (one tonic promotor and remotor unit and one phasic remotor unit) with movement in the two experimental situations. For this we have analysed 15 steps of rapid forward walking, firstly in free conditions and secondly on the treadmill with the belt set at $10 \, \text{cm s}^{-1}$ (see method of measurements in Fig. 12). Under these conditions several parameters of walking remain unchanged (e.g. T-C movement = $25\,°$, cycle period = $1 \cdot 2 - 1 \cdot 3 \, \text{s}$ in both cases). Table 7 summarizes the mean period and the mean spike frequency ($\pm$ s.D.) of each recorded unit over the 15 cycles in both situations. One can see that the dispersion around the mean period values during driven walking is much less than in free walking and is consistent with the greater variability of the step pattern observed during free walking.
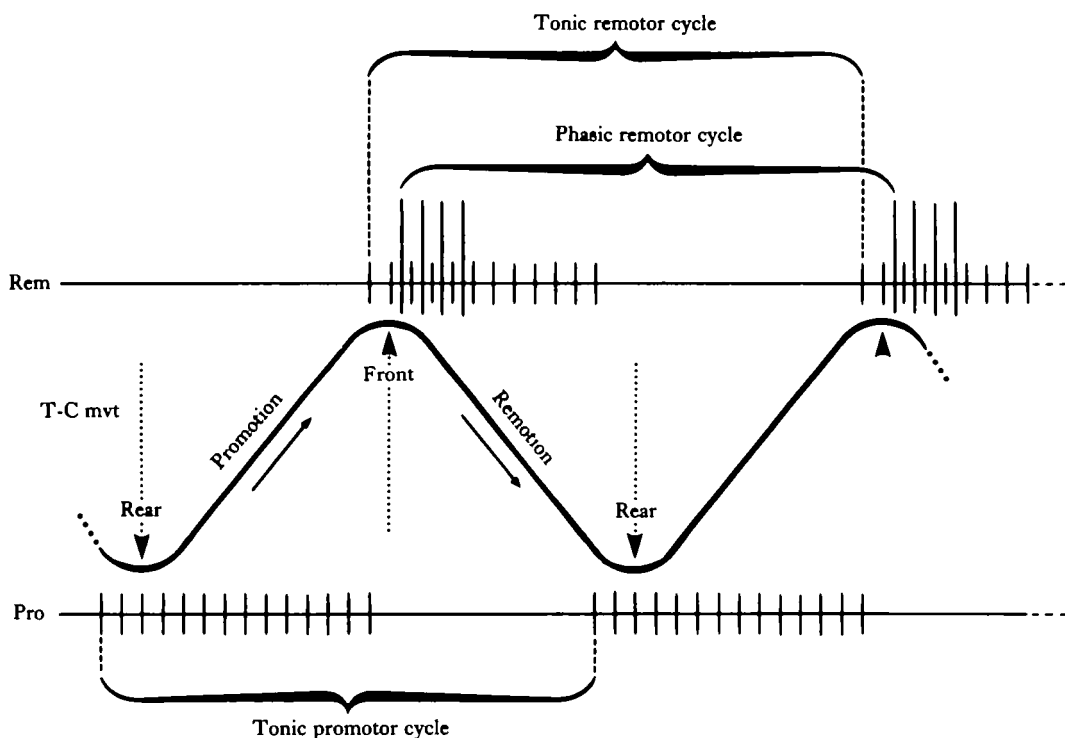

Fig. 12. Diagram illustrating the different measurement used for Figs 13 and 14. Cycles have been chosen from the first impulse of the motor burst to the first impulse of the next one, the promotor cycles being the reference. In the diagram of Fig. 13, the tonic remotor diagram has been displaced to the mean phase ratio, tonic Rem/tonic Pro. Diagrams for the phasic remotor have been displaced to the mean phase ratio, phasic Rem/tonic Rem. In Fig. 14 we have considered the mean value of the onset of the promotor and of the remotor tonic discharge with the T-C angular displacement (the rear point with the promotor and the front point with the remotor).

Table 7. *Mean values from the diagrams of Fig. 13*

Step periods		Free walking	Driven walking
Tonic promotor	N	15	15
	$\bar{X}$	1·22 ± 0·11	1·29 ± 0·03
	$\bar{F}$	63 ± 28	80·5 ± 36
Tonic remotor	N	15	15
	$\bar{X}$	1·22 ± 0·12	1·29 ± 0·05
	$\bar{F}$	55·6 ± 36	73·7 ± 41
Phasic remotor	N	10	15
	$\bar{X}$	1·21 ± 0·18	1·29 ± 0·04
	$\bar{F}$	41·5 ± 32	52·3 ± 37

N = Number of averaged cycles.
$\bar{X}$ = Mean period (s) ± 1 s.d.
$\bar{F}$ = Mean burst frequency (Hz) ± 1 s.d.

General intra-burst organization

Fig. 13 presents a complete analysis of spike occurrence and instantaneous frequency for the three units, recorded during their burst discharges. The different diagrams serve to emphasize the variation in the discharge of analogous units during free and driven walking. The main features are summarized as follows.

(i) The timing of successive bursts for all three motoneurones is relatively constant during driven walking but not in free walking (black dots).

(ii) The burst densities (% of spike occurrences in each phase bin) show little difference in their shape in the two situations for the tonic remotor and promotor units. In free walking the maximum spike density of both units is at the beginning of their bursts while the histograms for driven walking show maxima at about mid burst. Burst density for the phasic remotor motoneurone remains similar throughout both free and driven walking.

(iii) The instantaneous discharge frequency is the most variable parameter. In free walking it appears to be much more irregular and less related to the spike distribution than during treadmill walking. Although the first or second phase bins correspond to the highest frequency and burst density in the three units analysed, the remaining parts of the discharges show a great variability in frequency, with sometimes a complete inversion in relation to the number of spikes. Standard errors tend to become very large towards the end of the burst. During driven walking however, impulse frequency remains closely coupled to the burst density throughout the whole discharge. Standard error bars are very short in all phase bins, except for the somewhat irregular tonic remotor spikes occurring in the second half of each burst.

If one considers the mean discharge frequency of each unit (see Table 7), it appears that the same decreasing gradient (tonic Pro/tonic Rem/phasic Rem) exists in free as well as in driven walking, although all the numeric values are about 15 Hz more on the treadmill.

Relationship between muscular activities and T-C movements

In the two forward walking situations we have recorded EMGs concurrently with
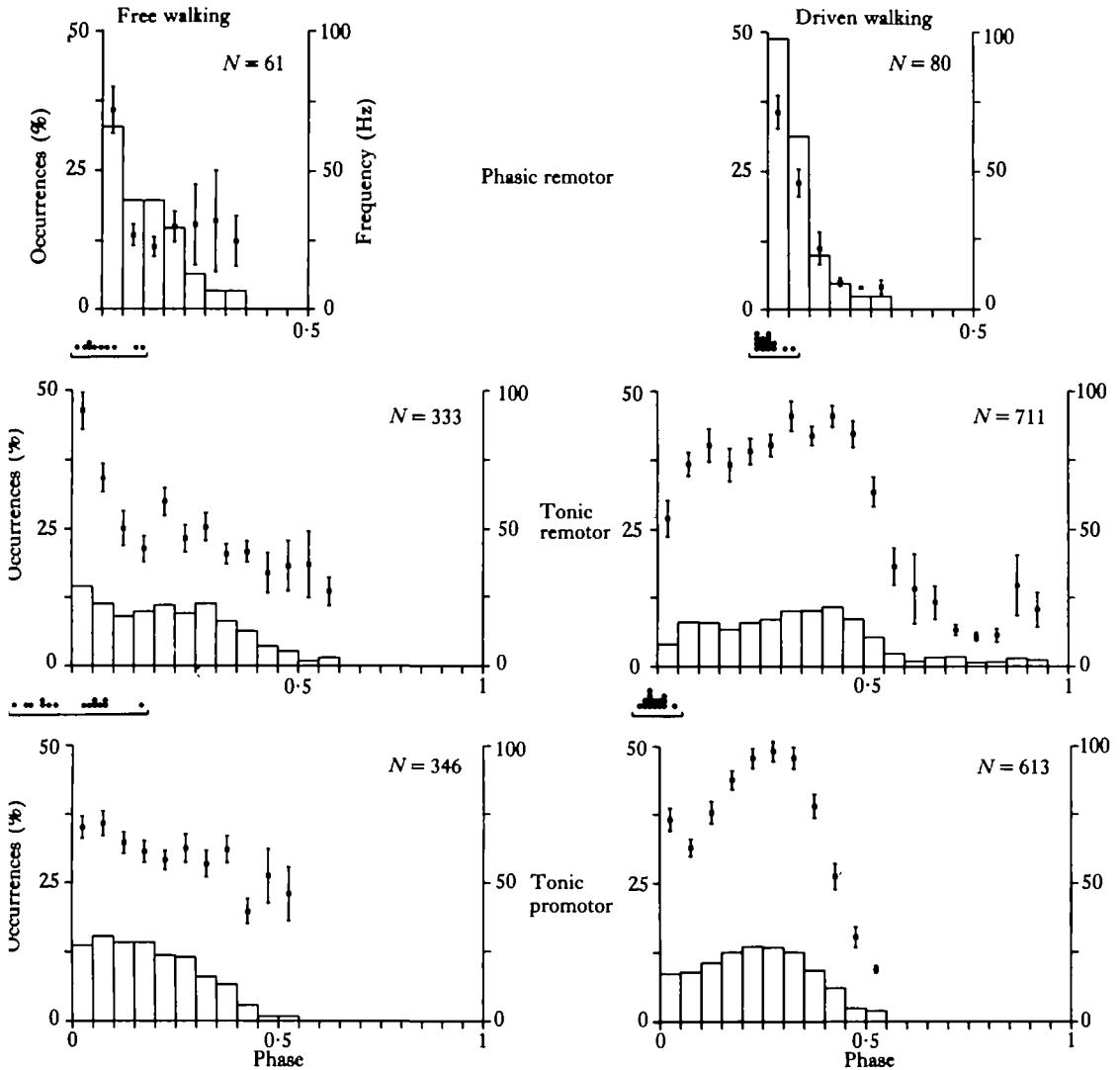
Fig. 13. Analysis of the phasic remotor, tonic remotor and tonic promotor discharge for leg 4 during 15 successive steps of forward walking in two different experimental conditions: on the left for a freely walking animal, on the right for an animal walking on a treadmill at an analogous speed (10 cm s^{-1}). Spike motor unit occurrences and instantaneous frequency have been plotted in the same diagram after normalization in phase units in order to compare the 15 steps. The left vertical scales are expressed as a percentage of occurrence of muscle spikes in the step phase; this represents a burst density histogram. The right vertical scales indicate the mean frequency of the discharge (±1 s.e.m. bars) for each phase bin (black square). In both situations, diagrams referring to tonic and phasic remotor units have been shifted to the right from the reference diagram of tonic promotor, in order to respect the real pattern averaged within the overall 15 steps analysed. The black dots under the zero point of the diagrams indicate the real phase ratio of the burst onset for the 15 successive steps. The phasic remotor discharged in only 10 steps from the 15 of the free walking sequence.

the angular excursion of the coxa and the duration of leg promotion and of leg remotion for individual steps. The phase ranges of the tonic promotor and remotor are displayed in Fig. 14 in the same shifted arrangement as in Fig. 13. It is clear that
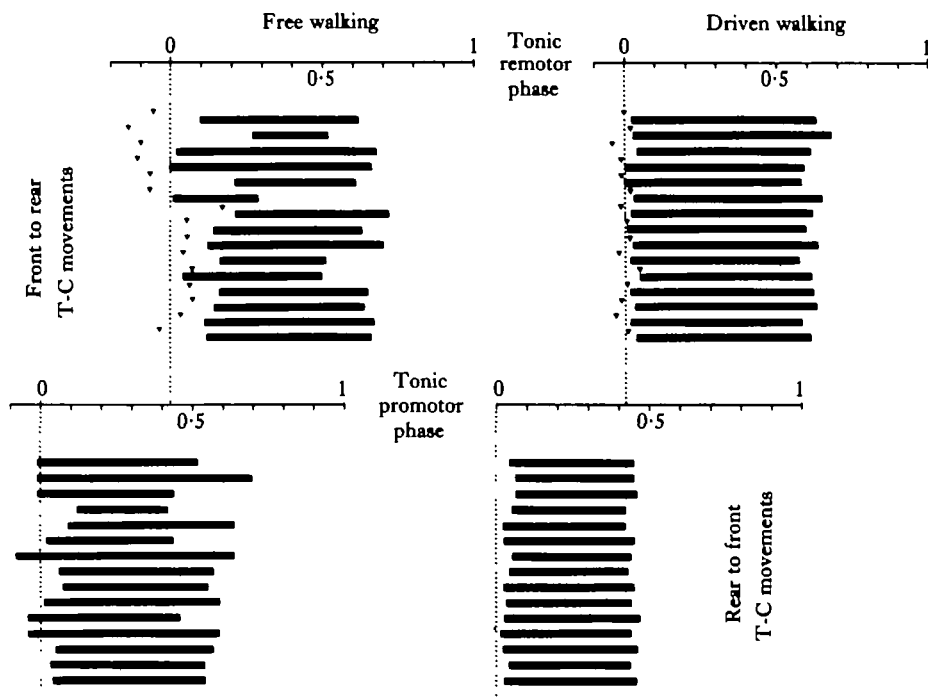
Fig. 14. Comparison in free and driven walking between the onset of the promotor (or remotor) discharge represented by a black triangle, with the corresponding T-C movement represented by a black bar during a sequence of 15 successive steps. The vertical dotted line, which corresponds to the beginning of the promotor (and of the remotor discharge), is the mean value for all the 15 successive cycles (see Fig. 12).

on the treadmill a leg promotion is perfectly correlated with the promotor burst as is leg remotion with the corresponding burst of the remotor (marked by a black triangle). The leg movement always starts at the beginning or shortly after the onset of unit discharge. The delay never exceeds $0 \cdot 1$ of a phase unit from one step to another (i.e. about 100 ms for the walking speeds used). In free walking, however, there is a great variability from one cycle to another in the firing positions of both remotor and promotor units relative to the movements they produce. Deviations can reach up to $0 \cdot 4$ phase units (about 500 ms). Moreover, in the 7th, 11th and 12th steps, promotion movement actually starts *before* the beginning of the promotor burst while in the 11th step remotion begins before the remotor unit discharge. Frequently, however, there is some delay between the burst and the beginning of the movement (up to 400 ms in the 2nd remotion); it is probably due to inertial effects.

Thus a comparison between unit discharges in the two situations reveals differences which are consistent with the differences in the other parameters described above. The greater variability observed in the free walking bursts is no doubt related to the pattern instability already described in this experimental situation. In driven walking, however, the stepping sequence is much more stereotyped, one step being nearly 'superimposable' upon the next one. This applies not only to the duration of each half

cycle, but also to the density and instantaneous frequency of spikes within individual bursts.

DISCUSSION

The main purpose of the present study is to try to quantify the behavioural motor strategies used by the same animal walking freely or on a moving treadmill in order to determine the reliability of the data obtained in the latter situation.

Efficiency of movement in free and driven walking

In Crustacea, the problem of loading seems to be crucial given that some animals live under water and others out of water while some crabs and crayfish are able to live in both media. A comparison of walking in these two situations has been made and there appear to be significant differences. Pond (1975) and Grote (1981) demonstrated that very little force is developed in a crayfish walking under water compared with the same animal walking on land; in the former medium, the number of legs used is less and their position different. The mutliplicity of appendages and the small amount of weight distributed among the standing legs is considerably reduced in the rock lobster. The problems of posture, support and balance that are mainly responsible for the prevalent alternating pattern mostly found in terrestrial Arthropods such as insects (tripod, Hughes 1952) and Arachnids (tetrapod), whatever their walking speed range, is less apparent in our experimental animal.

In treadmill experiments, the counter-balanced holding system permits the animal to move freely in the vertical direction so that it supports its own weight and can choose the convenient distance from the substrate. But attachment is rigid in the longitudinal and lateral directions. This restrains the animals posture and reduces the problem of right/left balance during walking. As we saw before, these postural problems are secondary here.

Another criticism often made is that there is no dynamic visual feedback in the restrained situation. Davis & Ayers (1972) have demonstrated that visual afferences from the surroundings could elicit short walking movements, but played only a weak role among the whole sensory input, particularly the proprioceptive information given by the belt displacement and transmitted by the legs' tips. One of the major arguments against the validity of treadmill walking data is that the animal walks passively, being entrained by the movement of the belt which drives the powerstroke. In reply to this suggestion, we demonstrated with Cruse (Clarac & Cruse, 1982) that at a given step frequency the forces exerted by the back leg pushing on the belt are of similar magnitude to those exerted on the substrate in free walking. We noted, nevertheless, that in free walking the forces differ greatly from one step to another, while in driven walking they stay very regular for a given belt speed. This confirms that the powerstroke occurring on the belt is performing an active locomotory role. Significant differences between driven motion and free walking are evident when comparing motoneurone discharge to ongoing movement. In driven walking, the discharge of the tonic and of the phasic units in relation to the movements are very well characterized. The activity is stable in frequency, in duration and in amplitude. In free walking,

however, the same parameters, despite having similar mean values, are very variable. For example, the smooth changes in the frequency discharges of bursts, obtained of the treadmill, could result from the continuous belt stimulation which produces a kind of steady state influence on all of the discharges. The difference in the burst structure and the presence of a maximum frequency in the middle of the discharges could come from the leg control system itself working as a servo-mechanism. During the PS when the leg is far from the 'desired' back point the ongoing movement is facilitated: however, when the leg nears this 'desired' point, the motor output is inhibited (see Cruse, Clarac & Chasserat, 1983).

The problem of T-C movement appears to be much more critical. The differences described between free and driven walking appear significant enough to require caution in interpreting data obtained from locomotion studies on Crustacea walking freely under water using motion film analyses. The important feature here is that the starting of movement is not always synchronized with the onset of the corresponding muscular burst. This observation supports our decision to use the EMG signals, since they are the most direct measure of the motor output pattern.

Comparison between temporal data obtained in free and driven walking

Correlation between the period and the burst duration

The PS duration is always correlated with the period whatever the situation: for the correlation between RS and period the results are more ambiguous.

In a recent review of insect walking, Delcomyn (1982) suggested that this parameter has received more attention than it is worth; we believe, however, that this parameter does have a real interest. As Delcomyn has pointed out, in Crustacea the status of this parameter is confused with respect to the contradictory data presented by several authors (see Clarac, 1982). For example, conflicting data have been published on the relationship between RS duration and step period (compare Ayers & Davis, 1977 with Macmillan, 1975; data in *Homarus*). Evoy & Ayers (1982) state that in the treadmill situation, the fact that the RS is not correlated with the period duration is due to the restraints imposed by the experimental situation. They suggest that an animal on a treadmill is somewhat like a free walking loaded animal. Our study suggests a similar conclusion (see following paper). On a treadmill, the animal is more regularly stimulated by its proprioceptors than in the free walking situation. Our results on leg 5 have shown that the remotor muscle, when it is acting as a RS muscle, is better correlated with the period in free walking (0·777) than in driven walking (0·471).

We have some evidence to suggest that whatever the period, the stability of the RS duration is due mainly to the degrees of force exerted during the PS (see Evoy & Fourtner, 1973, in the crab *Cardisoma*). If the leg does not play this role of support and is used more passively, the RS duration can vary either randomly or strictly with the period as it is used as a 'time regulator'. This stroke is primarily involved in maintaining a given coordination. An extreme situation of this arises when a leg is autotomized; before autotomy the RS is not correlated with the period, while after autotomy it is perfectly correlated (see Clarac, 1978). Analogous data have been described for the stick insect by Graham (1981), who demonstrated that on a light

treadwheel with no horizontal loading there is a close correlation with period. This

> also supported by walks on mercury (Graham & Cruse, 1981).

The present data appear to confirm the earlier findings (Clarac, 1982) that the variation in RS duration correlation characterizes the behavioural role of each leg. Burns (1973) in Orthoptera, Bowerman (1982) in a scorpion and Ward & Humphreys (1980) in a spider suggested from their correlation data that the first pair of legs is functionally different from the others in that it is used mainly in searching above the ground, i.e. it is more a 'sensory leg' than a leg used to propel the body. We reach the same conclusion with leg 2 in *Jasus* studied on a treadmill, where the RS is always perfectly correlated with the period. On the contrary, leg 4 is mainly used to propel the body and its RS is weakly correlated with period. In free walking, the forces are distributed between the back pairs of legs and therefore the correlation is not so apparent.

Interaction between legs

The different inter-leg temporal parameters studied here in many respects do not differ significantly in free and driven walking in *Jasus lalandii* as Macmillan has already observed for *Homarus* (1975). During forward walking in both cases, ipsilateral relationships are of the absolute type, whereas contralateral legs are very loosely coupled. During free backward walking as in driven walking, ipsilateral legs 5 and 4 are in absolute coordination, while all other limb coupling, both ipsilateral and contralateral, is of the relative type. The mean values of the phases are slightly different in the two situations, but this does not seem to be particularly meaningful because of the high degree of variability. Other authors have determined values which exhibit the same degree of variation as we have observed here (Macmillan, 1975; W. J. P. Barnes, in preparation, cited in Clarac, 1982). The main difference, then, between free and driven walking is in the dispersion of the mean values. The c.s.d. value is always halved in the latter case (there is just one exception, the 4 and 3 ipsilateral coupling during backward walking). The coupling data are summarized in Table 8.

For the crayfish and for *Homarus*, the different deviations given by previous authors demonstrated a better coupling for ipsilateral than for contralateral pairs of legs. The lone exception is the soldier crab, but this seems to be correlated to its anatomical lateralization even though it walks forward (Sleinis & Silvey, 1980). In a comparative study of crayfish walking, W. J. P. Barnes (in preparation) found an analogous variability in the mean phase values when the animal was walking freely in an aquarium or when it walked on a wheel that it moved by itself. The s.d. values displayed less variability when the animal was loaded. It could be considered, therefore, that an animal loaded and walking freely is analogous to an animal walking on a treadmill. Thus the mean phase value has only a real meaning when the c.s.d. parameters are low (under 0·10). In fact, a broad distribution, as has been observed in free walking, could be the expression of very different successive walking patterns during the analysed stepping sequence.

Considering these interactions between legs, one of the most interesting features observed is the occurrence of an ascending and/or descending metachronal wave. In free-walking *Jasus*, the phase between legs is not clearly linked with the period,

Table 8. *Summary of the different percentages of coupling in free and driven walking*

	Free walking	Driven walking
Forward	Ipsilateral 5–4:77 % 4–3:77 %	Ipsilateral 5–4:93 % 4–3:91 %
	Contralateral 4–4:39 %	Contralateral 4–4:87 %
Backward	Ipsilateral 5–4:67 % 4–3:37 %	Ipsilateral 5–4:91 % 4–3:61 %
	Contralateral 4–4:42 %	Contralateral 4–4:70 %

although this correlation becomes more visible during sequences on the treadmill. The greater stereotypy of the motor output could make the linkage between phase and period more apparent. However, the limited treadmill speed range studied in this report does not permit more extensive discussion of this point. It will be considered in greater detail in the following paper.

In conclusion, the treadmill situation not only elicits stereotyped and regular walking sequences, but, moreover, reinforces the interdependence of physical and temporal parameters involved in free walking behaviour. The constraint of the belt decreases the variability of all parameters, thereby enhancing stereotyped walking. However, this stereotypy can obviously be manipulated in a predictable manner by adjusting the belt speed. A free-walking animal, however, does not exhibit a great range of variation in walking speed. In the experimental situation of driven walking, we can vary the speeds thus producing speeds never observed during free walking. In this context the treadmill situation is advantageous; it can clarify some rules of walking which for the most part are masked during random, uncontrolled free walking (see Chasserat & Clarac, 1983, following paper).

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