

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

II. SPATIAL AND TEMPORAL REGULATION OF STEPPING IN
DRIVEN WALKING

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SUMMARY

Spatial and temporal stepping parameters have been studied in a rock-lobster walking on a treadmill moving at a wide range of speeds. The stride and the return stroke (RS) duration remain more or less stable and independent of the belt speed. Nevertheless, these 'invariant' parameters can act as spatial and temporal buffers resulting in a very precise adjustment of individual steps.

A careful study of the power stroke (PS) duration demonstrates that the rock-lobster, although constrained to walk at an imposed belt speed, continues to correct its leg speed over a narrow range when the speed is considerably different from its natural one. Ipsilateral phases are always speed dependent, with an interleg ascending delay that is almost constant. The contralateral phase between legs of the same pair is approximately constant.

Some of the parameters described are greatly influenced by gradual or abrupt variations in the belt speed. For a given speed, there is no absolute significance in the step period and ipsilateral phase. At very slow speeds, the interleg relations are significantly changed and have been studied separately. The metachrony observed at other speeds is discussed in relation to data from other arthropods.

INTRODUCTION

Our comparative study of free and driven walking (Clarac & Chasserat, 1983) led us to the conclusion that analogous rules are applied to locomotory behaviour during these two situations. However, because of the natural narrow speed range used ($6\text{--}12\text{ cm s}^{-1}$), some essential points remain unclear – for example, metachronal patterns and regulating mechanisms. Therefore, a systematic study of the driven walking parameters will be presented in this report in which we vary all of the possible treadmill conditions. We used a larger speed range and the animals performed stepping sequences at unnatural rates and experienced smooth as well as abrupt changes

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of the imposed speed. In addition, a systematic analysis of spatial parameters has been carried out, measuring angular excursion of the leg and its tip displacement.

The following work attempts to present an exhaustive report on the interaction between spatial and temporal parameters throughout the coordination of rock-lobster locomotion. We have focused our study on the main functional leg pairs, the most posterior two pairs of legs (4 and 5).

MATERIALS AND METHODS

We present data from 20 experiments. Stepping sessions were elicited by using the standard conditions already described in the first paper. The leg tip was fixed at one point of a loop made of very fine thread and supported by light wheels. A multi-turn potentiometer was related by a light stick tethered at another point on the thread loop, above the water surface (Fig. 1B). The tension of the whole system was adjusted precisely in order to suppress nearly all artifact resistance, so that the leg could step naturally. Analogue data were translated in an A/D converter and stored on disc. A programme was used to detect the maximum and minimum values and to compute the value of step parameters (period, stroke duration, stride length, mean leg velocities during remotion and promotion, and occasionally pause times). The sampling rate was adjusted to obtain about 60 values within one step cycle so that the parameters were always computed with the same accuracy (e.g. ± 20 ms for a 1.2-s period, ± 50 ms for a 3.0-s period etc.).

Such a precision (1/60 of a cycle) was adequate in all cases to distinguish unambiguously the different parts of the step cycle duration. The determination of extremes in the signal were calculated with a margin of ± 1 mm (i.e. an error $< 2\%$ for a stride length of 10 cm). Data significance was estimated using standard statistical methods (mean, standard deviation, student *t*-test) and linear correlation analysis. Mean values are given with ± 1 standard deviation. The probability of a given confidence test is indicated when it concerns a critical result.

For each speed sequence on the treadmill, the greater available number of consecutive regular steps is taken for computer analysis and the few irregular steps occurring sometimes at the speed changes were not taken into account in the data analysis.

It is necessary to define some parameters used frequently in this report (see Fig. 1).

AEP and *PEP* are the anterior and posterior extreme positions of the forward walking legs, as first described in the insect by Bassler (1972). *AEP* corresponds to the

Fig. 1. (A) Typical multiple recording of the spatial and temporal parameters in a 4th leg (forward driven walking, 8 cm s^{-1}). From top to bottom: Rem, remotor muscle EMG (power stroke); T-C mvt, T-C joint angular excursion; Pro, promotor muscle EMG (return stroke); Leg mvt, leg tip position (linear stride). Maxima and minima in the latter trace mark the anterior and posterior extreme positions within the sequential steps (*AEP*, *PEP*). The six divisions displayed in the first cycle are described in the text (a to f). The convention for movement traces (promotion upward, remotion downward) is used throughout. (B) Lateral schematic view of the experimental system used to record the tip position of a stepping leg 4. (C) Dorsal view of the spatial excursion of a leg during a one-step cycle. Muscles, joints and dactyle positions as above. Note the leg extension at the end of RS (*AEP*) and the partial flexion of the M-C joint during the power stroke, which explains the linear stride from *AEP* to *PEP*.

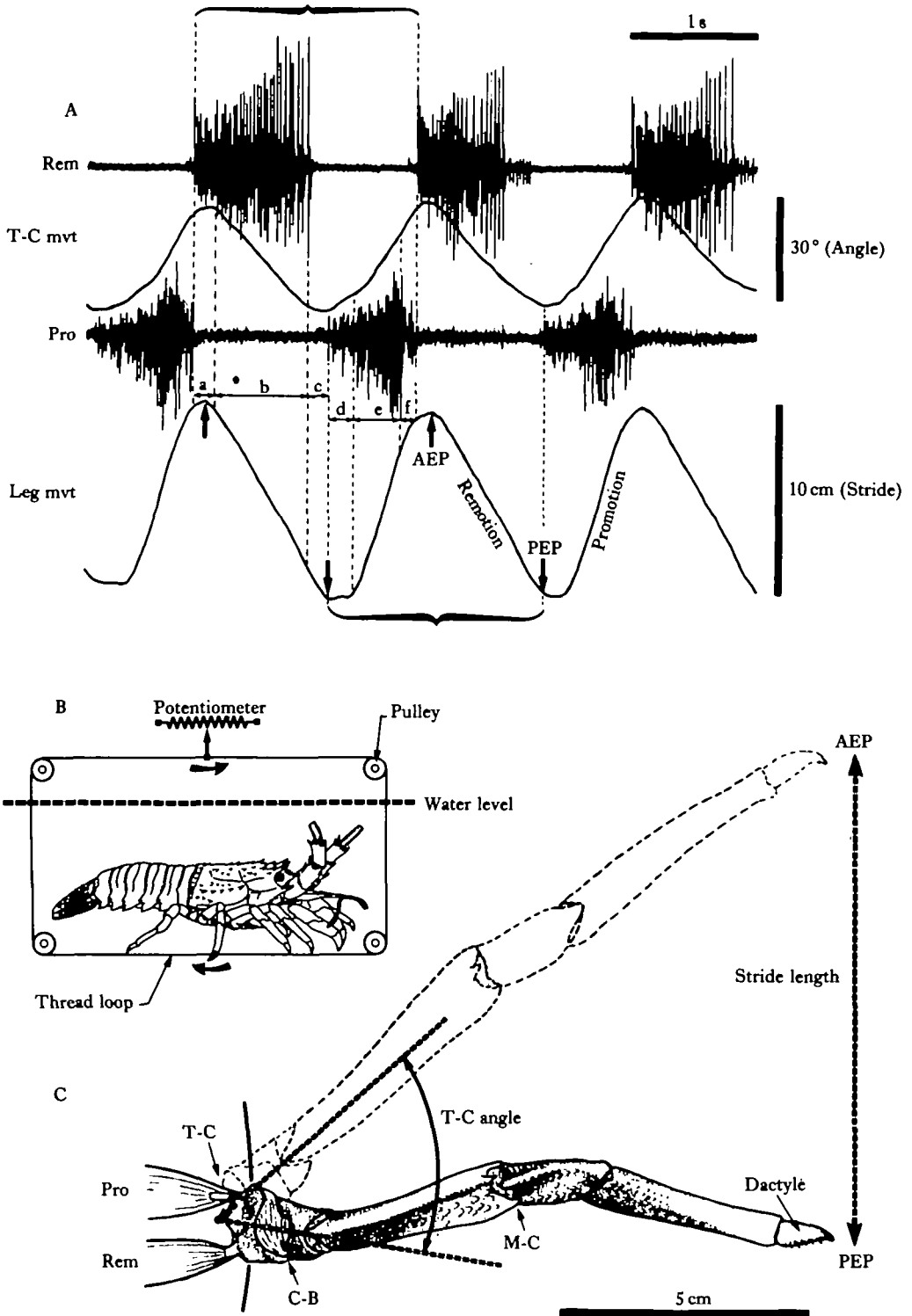


Fig. 1

point where the stepping leg touches the belt at the end of the return stroke (RS) and PEP refers to the point where it lifts off the belt at the end of the power stroke (PS). These points are expressed in centimetres and can be positive or negative relative to the thoracico-coxal joint (T-C) of the considered leg which is taken as the reference point on the body axis (Fig. 1C).

Stride length corresponds to the absolute distance covered by the leg tip when in contact with the belt (i.e. during the power stroke). For a given step, the stride is thus equal to AEP — PEP. In the signal of leg tip movement recording, power and return strokes are strictly defined as the step parts where the leg is moving relative to the body. Leg velocity during each stroke is calculated from the mean slope of the signal trace, when going upward (leg promotion) or downward (leg remotion), as in Fig. 1A.

Pause times. These were first described in *Homarus* by Macmillan (1975) and correspond in the leg tip recording to that part of the step where the leg remains immobile at AEP or PEP (a and d, respectively in Fig. 1A).

RESULTS

Walking parameters in a single leg

Description of the stepping parameters

Fig. 1A shows for three successive steps, an EMG recording of the two T-C joint muscles, the promotor and the remotor, with measurement of the T-C joint angle and with the stride covered by the leg tip. The T-C joint movement is well correlated with the remotor and promotor muscular activities during up and down deflection and is proportional to the real step length. Differences between leg tip and T-C movements are mainly due to inertial effects caused by the six joints of the whole leg. EMGs show that the onset of the PS (here in forward walking, the remotor burst) is much more sharply defined than the onset of the RS (here the promotor burst) (see 'Methods' in previous paper).

These recordings permit us to divide the step cycle into six parts that can be described as follows.

(a) The remotor begins its burst as the leg reaches its AEP. The leg touches the substrate (maximum peak) and starts its power stroke.

(b) and (c) form the power stroke where the leg tip moves on the belt at a constant speed. The remotor discharge stops at (b). In (c), the leg continues moving on the belt towards its PEP while the T-C joint remains immobile.

(d) corresponds to a short pause of the leg tip at its PEP. The promotor begins to fire (T-C joint promotion) but the dactyle does not move due to elasticity in the other leg joints.

(e) and (f) form the return stroke. The leg tip is not in contact with the belt and the leg velocity during this phase is not as constant as during the PS. It starts with a slight acceleration, then reaches its maximum value (at end of 'e') and decelerates at (f), just before the next peak of the signal (AEP of the next step).

In some cases a second pause can occur at this point just before the leg again touches the belt.

The T-C joint is mainly involved in generating the antero-posterior movement. A small angular excursion of about 30° can produce a large linear step length (about 10 cm) parallel to the body axis because of the movement of the other leg joints. There is a leg extension during the RS so that the dactyle reaches its AEP at the maximum radius (distance T-C dactyle, about 15 cm). During the PS, the radius is regularly decreased. When the leg tip is at PEP, the radius is only 12 cm. This mechanism is necessary to transform the angular T-C joint movement into a linear trajectory for the propulsive forces applied at the leg tip.

These kinetics are unique for the 4th leg which is a traction limb. The 5th leg has a propelling action, flexing during the RS and extending towards its PEP during the PS.

Imposed walking speeds and stepping parameters

The influence of belt speed upon the various step parameters is illustrated in Fig. 2. These data are from the same animal whose behaviour during driven walking sessions was particularly representative of the behaviour of all the animals encountered. The most significant result is the stability of the stride length whatever the imposed speed. The overall mean for the full sequence is 8.9 ± 1.4 cm. The return stroke also appears to have a constant duration of around 500 ms, except for a slight increase at the slowest speed (at 3 cm s^{-1}). The PS duration seems to follow a hyperbolic law.

The period includes both the PS and RS duration and the pause time occurring at the end of each stroke. The fact that the step period also shows a hyperbolic relationship to the imposed speed suggests that the pause times do not vary with speed. Their values are nearly constant; 200 ± 80 ms at the end of the PS and 125 ± 70 ms at the end of the RS (means ± 1 s.d. for three different animals). The mean leg velocity during PS is identical to the belt speed when in the 'physiological' range (7 to 11 cm s^{-1}). This result might appear to be obvious since the dactyle should move with the belt during the PS. In fact, because all values have very small s.d. bars, the data show clearly that mean PS speeds deviate slightly from the imposed belt speed (dotted line).

At slow imposed speed ($< 6 \text{ cm s}^{-1}$), the dactyle slips slightly on the substrate and its mean velocity appears to be greater than the belt speed. In the opposite case, at faster imposed speed ($> 12 \text{ cm s}^{-1}$), the animal leg can resist slightly against the belt movement and its mean speed appears to be slower than that of the belt. Of course, these corrections are small and Fig. 2 shows that the animal follows the imposed speed quite closely within the whole range.

The results obtained for the RS leg velocity are much less clear. It must be noted that the s.d. is obviously greater at any given speed. This suggests that if RS duration remains steady, RS leg speed appears to be very variable from step to step.

Leg stroke speed in RS seems to increase slightly with the imposed speed, but the variability within one speed class does not allow us to draw any conclusion about the nature of such a relationship.

The mean RS leg speed is always greater than the PS leg speed, even at the maximum imposed belt speed.

Systematic measurements of leg speed during RS have been made in three forward

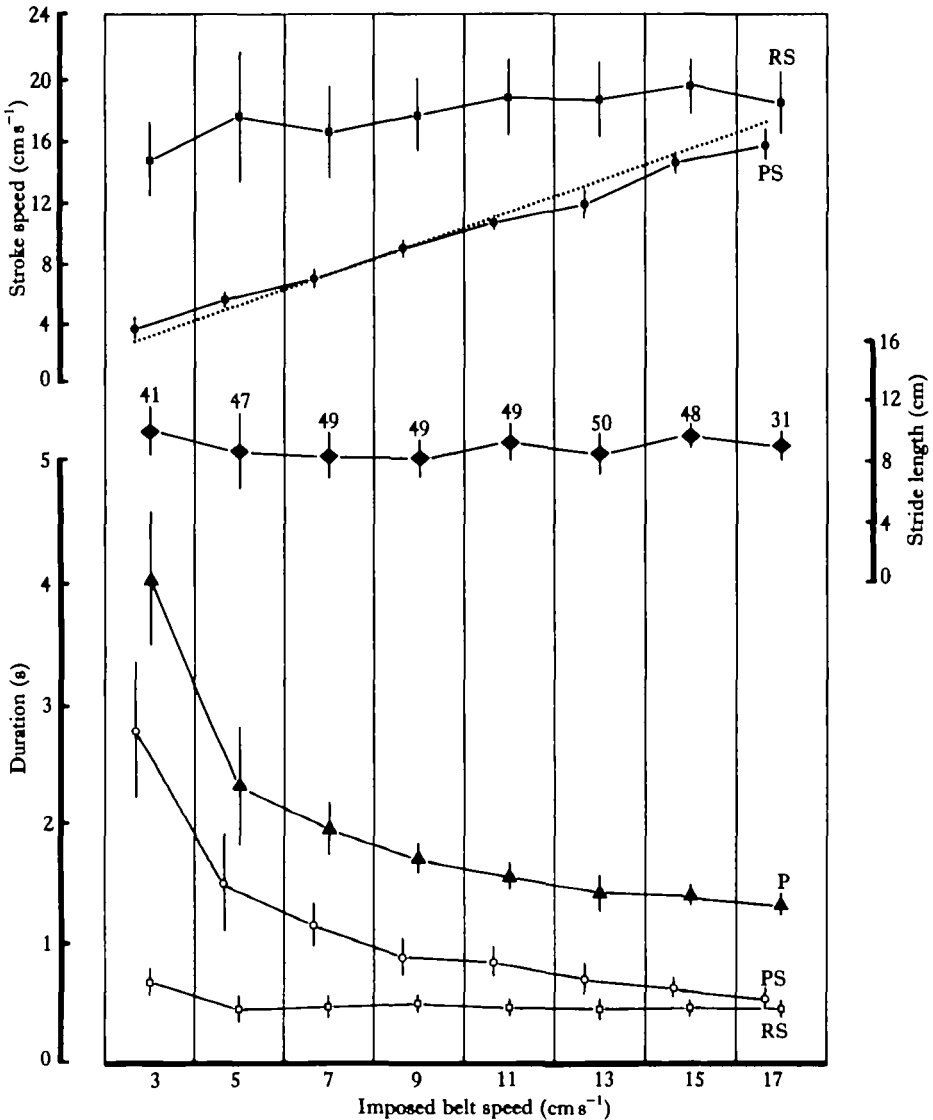


Fig. 2. Mean values (± 1 s.d.) of the step parameters for a forward walking rock lobster (Leg L4) at eight different imposed belt speeds (from 3 to 17 cm s⁻¹): (◆) stride length (from AEP to PEP); (▲) step period (time interval between the onset of two successive retractions); (□ and ■) stroke duration and leg tip speed in RS; (○ and ●) stroke duration and leg tip speed in PS. (Number of steps is noted near the stride value.) Periods are greater than the sum of PS and RS durations because they include pause times. The straight dotted line represents the belt speed.

walking animals, and in a backward walking one. Even after averaging, the values obtained confirm the great variability of this parameter. Comparing various experiments the RS speed can exhibit very different values for a given imposed belt speed. Behavioural observations show that it is often lower in backward than in forward walking.

Interleg relationships

Imposed speeds below 4 cm s⁻¹ generally induce a characteristic 'slow walking'

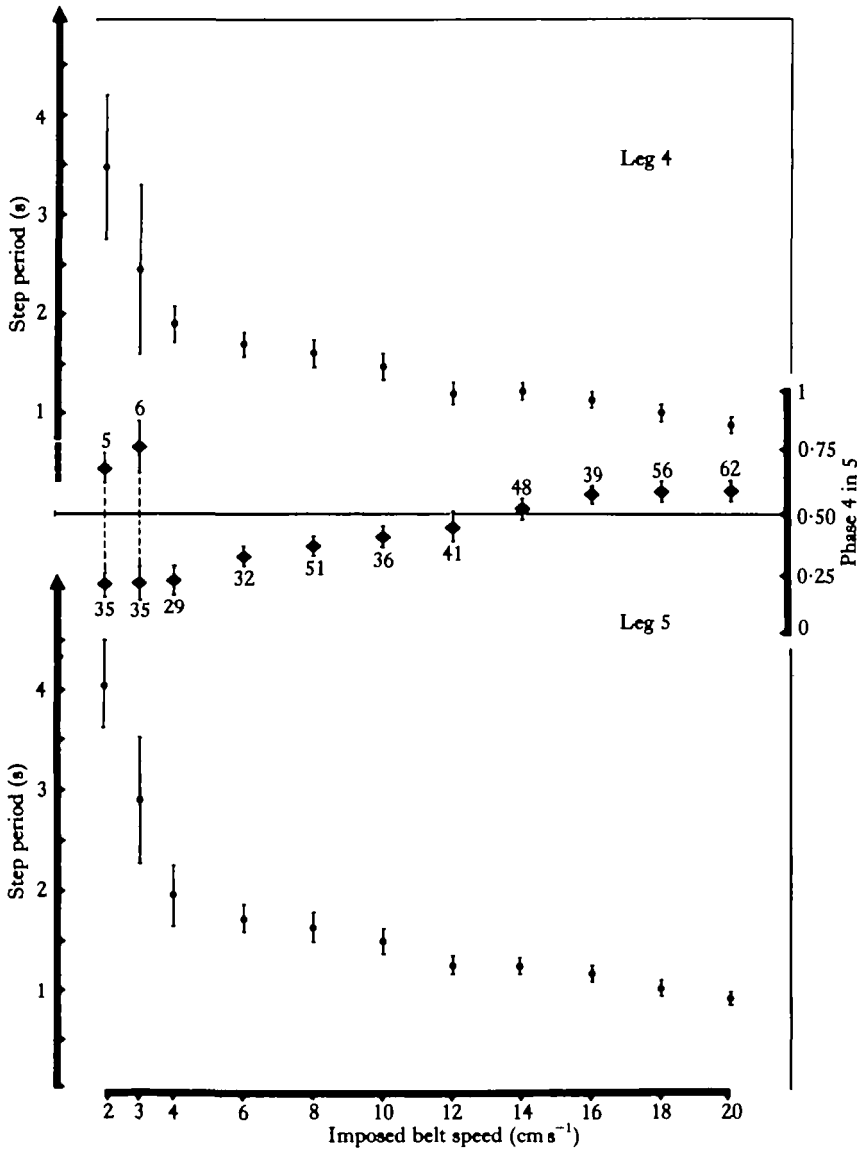


Fig. 3. Ipsilateral phase during forward driven walking. Step period of legs 4 and 5 on the same side and phase 4 in 5 plotted against the belt speed. The number of steps in each speed class is noted near the phase value. Eleven different speeds have been imposed, increasing from 2 to 20 cm s⁻¹. Every point is the mean value (± 1 s.d.). Note the bimodal distribution of phase at 2 and 3 cm s⁻¹, due to the relative coordination occurring between the 4th and 5th legs.

which needs to be examined separately. Let us first describe the ipsi- and contralateral leg relations at imposed speeds below 4 cm s⁻¹.

Ipsilateral legs

Results from legs 4 and 5 are presented for three different experiments (Figs 3, 4 and Table 1). In Fig. 3 stepping was performed up to 20 cm s⁻¹. The step period decreases with increasing speed in legs 4 and 5. No significant differences between

Table 1. *Ascending delay 5-4 and 4th leg period during forward driven walking*

Belt speed (cm s ⁻¹)	Leg 4 period (s)	Delay 5-4 (s)	Step number
2	3.87 ± 0.47	0.83 ± 0.12	30
3	3.09 ± 0.42	0.70 ± 0.10	20
4	1.97 ± 0.18	0.50 ± 0.12	24
6	1.77 ± 0.11	0.63 ± 0.09	32
8	1.67 ± 0.13	0.67 ± 0.08	90
10	1.50 ± 0.12	0.66 ± 0.08	69
12	1.27 ± 0.11	0.60 ± 0.07	40
14	1.28 ± 0.07	0.67 ± 0.06	43
16	1.20 ± 0.06	0.67 ± 0.06	30
18	1.09 ± 0.04	0.65 ± 0.05	50
20	0.97 ± 0.06	0.60 ± 0.06	45

Extra steps on 4 in 5 occurring at the three slower speeds have been excluded from the data.

them can be recorded for a given speed. The 4 in 5 mean phase shows a significant increase from 4 cm s⁻¹ (0.23 ± 0.06) to 20 cm s⁻¹ (0.59 ± 0.04). The phase *versus* speed variation appears to increase continuously until 16 cm s⁻¹ at which point a levelling off occurs. In Fig. 4 (upper left part), periods and the ipsilateral phase for L4 in L5 are plotted for each consecutive step throughout a continuous stepping sequence. Some random variations observed within a given speed are greater than the period differences due to the speed changes.

In order to relate the speed dependence to ipsilateral phase, the ascending interleg delay 5-4 was measured and the data are presented in Table 1. In the 6-20 cm s⁻¹ range the delay remains more or less stable at about 650 ms. A regression analysis of the delay 4-5 *versus* the period was performed on the 399 steps made at imposed speeds of 6 cm s⁻¹ and greater. The correlation coefficient ($R = 0.300$) is significant, but the regression line (delay = 0.08 × period + 0.53) has a very weak slope.

Contralateral legs

It can be seen in the lower left part of Fig. 4 that the phase R5 in L5 does not present any significant change with decreasing speeds (12, 8, 6 cm s⁻¹). The phase values are approximately 0.4, with a scatter that seems somewhat greater than for the ipsilateral legs. The legs R5 and L5 always have the same period at any imposed speed (Table 2).

Leg interactions during slow walking

When the belt is running slower than 4 cm s⁻¹ (2-3 cm s⁻¹ in Fig. 3 and 3-4 cm s⁻¹ in the right part of Fig. 4, 2-4 cm s⁻¹ in Table 1), the interleg relations are significantly altered. In this situation, the 4th leg commonly performs a double step in the ipsilateral leg 5 cycles, while contralateral legs R5 and L5 stay coordinated 1:1. The mean period durations between legs 4 and 5 become significantly different at slow speeds (0.46 s at 3 cm s⁻¹ and 0.55 s at 2 cm s⁻¹). Such a time difference has already been described between the step periods of the homolateral legs 3 and 4 in backward

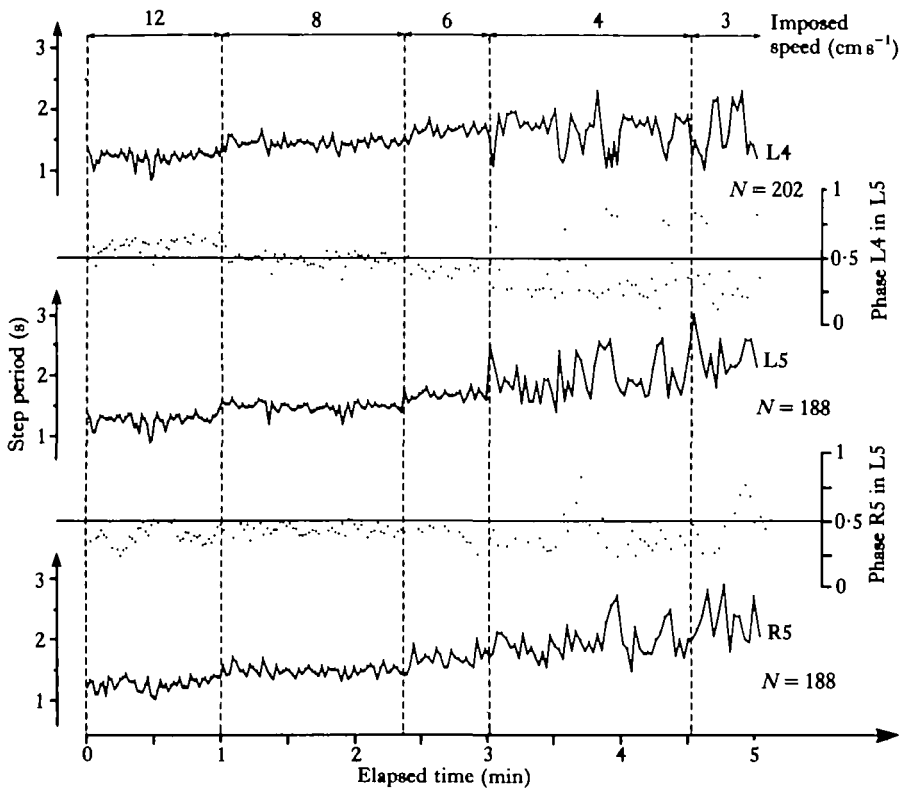


Fig. 4. Ipsi- and contralateral phase during forward driven walking. Step periods of legs L4, L5, R5 and phases L4 in L5 and R5 in L5 are plotted *versus* elapsed time. Each successive step is represented during a continuous walking session with five decreasing imposed speeds (from 12 to 3 cm s^{-1}). The small vertical bars mark the step timing in the continuous plot of periods.

driven walking and is closely linked to the occurrence of relative coordination (Chasserat & Clarac, 1980). The ipsilateral phase values exhibit a bimodal distribution with a 'preferred' phase corresponding to relative coordination. One of the 'preferred' phase values observed in Fig. 3 at 2 and 3 cm s^{-1} is not significantly different from a single phase value as observed at 4 cm s^{-1} (close to 0.20 in Fig. 3). As has been described in katydid walking (Graham, 1978*a,b*), we have also observed 'forbidden zones' of phase value less than 0.2 and greater than 0.6.

In Fig. 4 one can see that legs L4 and L5 also become relatively coordinated when the belt speed is decreased from 6 to 4 and then to 3 cm s^{-1} . Here again the period difference, which is less than 0.1 s at 6 cm s^{-1} when the two legs are absolutely coordinated, becomes 0.23 s at 4 cm s^{-1} and even 0.6 s at 3 cm s^{-1} , inducing double stepping of L4 in L5.

At these slow speeds the 'preferred' phase values (0.28 and then 0.26) follow the decreasing phase gradient observed within the decreasing speed sequence.

Although the two rear legs continue to walk in 1:1 coordination (the R5 and L5 mean periods do not differ significantly), the contralateral phase R5 in L5 becomes

Table 2. Mean values (± 1 S.D.) of the parameters plotted in Fig. 4, within the five classes of imposed speed (12 to 3 cm s⁻¹)

Belt speed (cm s ⁻¹)	Leg L4			Leg L5			Leg R5			Contralateral phase R5 in L5	Ipsilateral phase L4 in L5
	Step number	Period (s)	Step number	Period (s)	Step number	Period (s)	Step number	Period (s)	Step number		
12	49	1.23 \pm 0.11	49	1.23 \pm 0.11	49	1.24 \pm 0.11	49	1.24 \pm 0.11	49	0.39 \pm 0.07	0.58 \pm 0.05
8	57	1.47 \pm 0.09	57	1.47 \pm 0.09	57	1.48 \pm 0.08	57	1.48 \pm 0.08	57	0.43 \pm 0.04	0.47 \pm 0.05
6	23	1.67 \pm 0.09	23	1.71 \pm 0.18	23	1.70 \pm 0.12	23	1.70 \pm 0.12	23	0.38 \pm 0.06	0.38 \pm 0.05
4	53	1.70 \pm 0.28	45	1.93 \pm 0.31	45	1.96 \pm 0.26	45	1.96 \pm 0.26	45	0.38 \pm 0.12	(45) 0.28 \pm 0.07 (8) 0.78 \pm 0.06
3	20	1.72 \pm 0.38	14	2.32 \pm 0.31	14	2.31 \pm 0.33	14	2.31 \pm 0.33	14	0.47 \pm 0.20	(14) 0.26 \pm 0.08 (6) 0.77 \pm 0.06

very irregular and fluctuates within the full range 0 to 1. There is no forbidden zone in the contralateral phase. We have performed a correlation analysis with the data of Fig. 4, after exclusion of the 14 'extra steps' made by L4 at slow speed in the phase range beyond 0.75. The ipsilateral phase L4 in L5 is strongly correlated with the period (188 steps, $R = -0.630$, $P < 10^{-5}$), while the contralateral phase R5 in L5 does not show any significant correlation with the period (188 steps, $R = 0.067$, $P = 0.18$). If one considers now the interleg delay 5-4 (Table 1), it appears to decrease regularly at slow speeds (from 0.83 s at 2 cm s^{-1} to 0.50 s at 4 cm s^{-1}).

Between 4 and 6 cm s^{-1} , the mean period decreases slightly and becomes much more regular ($1.97 \pm 0.18 \text{ s}$ to $1.77 \pm 0.11 \text{ s}$). On the other hand, the interleg delay increases from 0.5 to 0.63 s and then remains steady at all greater imposed speeds. Such a break in the relationship between the ascending interleg delay 5-4 and the speed suggests that a different neural mechanism could underlie the ipsilateral phase control during slow walking. Again, the data of Table 1 were used for a regression analysis in the slow range ($2\text{--}4 \text{ cm s}^{-1}$: 74 steps). In this case, the interleg delay is strongly correlated with the period ($R = 0.782$) and the regression line (delay = $0.16 \times \text{period} + 0.20$) has a slope significantly greater than the one obtained at speeds above 6 cm s^{-1} .

Relative coordination between ipsilateral legs 4 and 5 can sometimes induce rather long stepping sequences of 'stereotyped' 2:1 coordination, where the 4th leg steps twice in each successive cycle of leg 5. Such a situation is shown in the upper left part of Fig. 5. The animal walks at 3 cm s^{-1} and the difference between mean periods of the 4th and 5th leg is 1.2 s (Fig. 5). The outcome of such a large time difference is that the coordination of the two legs is almost consistently 2:1. The two preferred phase values (0.20 and 0.65) and the T-C movement trace show how leg 4 acts spatially in performing the double steps (Table 3).

In fact, the 5th leg of the rock-lobster has a particular T-C joint position which allows the animal to take extremely long strides. At very slow belt speeds, the rear legs use this strategy in order to increase their period by increasing the time of ground contact (PS). This is not possible for leg 4, which would be physically hindered by the other stepping legs. Therefore, the 4th leg must lift off the belt, to start its RS before leg 5 has ended its ongoing PS and can thus perform a second step while leg 5 finishes its given cycle.

When the speed is rapidly increased to 8 cm s^{-1} (vertical dotted lines in Fig. 5), the animal immediately alters its stepping mode by reducing the stride of leg 5, while the mean period of leg 4 changes only slightly and is stable ($1.5 \pm 0.31 \text{ s}$ to $1.48 \pm 0.11 \text{ s}$). The two legs then continue to step in absolute coordination (1:1) and the phase 4 in 5 acquires a unimodal value (0.25 ± 0.04) slightly greater than the preferred one at 3 cm s^{-1} (0.20 ± 0.03).

This phenomenon, emphasized in Figs 3 and 4, supports the hypothesis of a stable forward directed interleg delay. The second phase mode observed at 3 cm s^{-1} is more scattered (0.65 ± 0.05). This suggests that the second step of each leg 4 doublet does not occur at random within the leg 5 cycle but is also probably controlled by other ongoing events.

The particular behaviour of the continuous double stepping of leg 4 in leg 5 can be exactly compared to the walking mode of the katydid in the 'systematic absences'

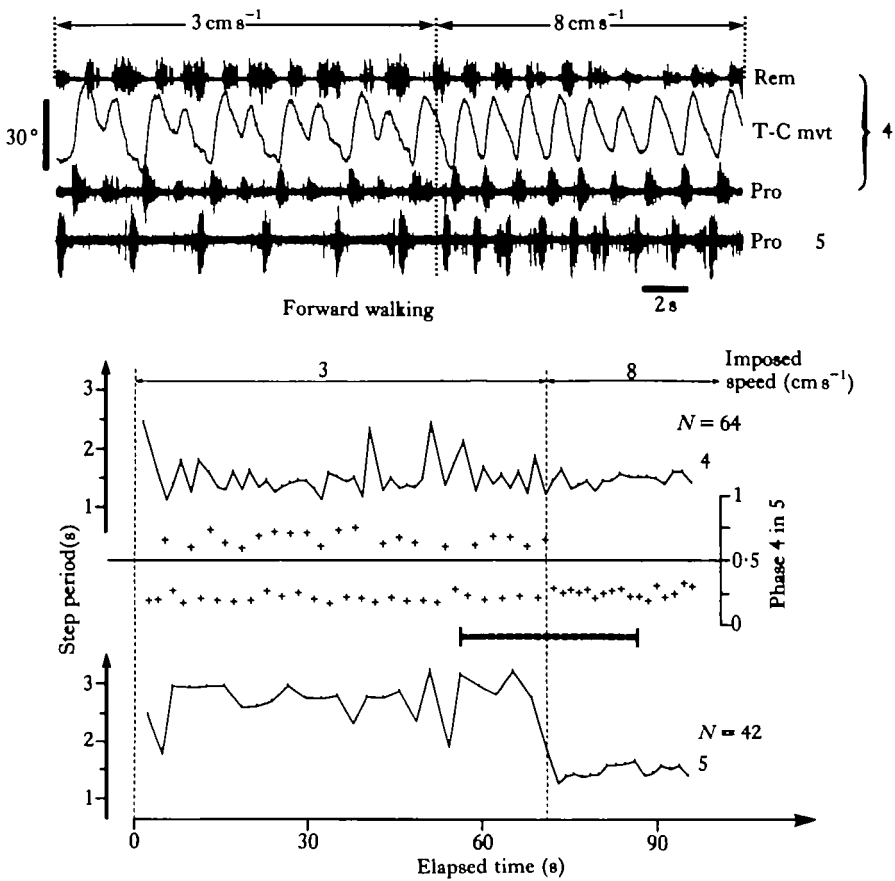


Fig. 5. Effect of an abrupt increase in imposed speed during forward driven walking. Lower diagram: same representation as in Fig. 4. Periods of ipsilateral legs 4 and 5, and phase 4 in 5 are plotted *versus* elapsed time. At 3 cm s^{-1} legs 4 and 5 behave in a particular fashion; their respective stepping frequencies are nearly in the 2:1 ratio and the phase has a bimodal distribution (0.20–0.65). As the belt speed changes to 8 cm s^{-1} both periods reach a common value and the legs go on walking in absolute coordination (1:1) with a phase lock at 0.25. The horizontal bold dashed line (about 30 s long) marks the sequence recorded above. Upper record: from top to bottom, remotor EMG T-C joint angular movement, promotor EMG of leg 4, and promotor EMG of leg 5 are simultaneously recorded in order to show the immediate transition from 2:1 to 1:1 coordination when the imposed speed is sharply increased from 3 to 8 cm s^{-1} (vertical dotted line).

Table 3. Mean values ($\pm 1\text{ S.D.}$) of the parameters plotted in the lower diagram of Fig. 5

Belt speed (cm s^{-1})	Leg 4 period (s)	Leg 5 period (s)	Phase 4 in 5
3	(47) 1.50 ± 0.31	(26) 2.70 ± 0.44	(26) 0.20 ± 0.03 (21) 0.65 ± 0.05
8	(17) 1.48 ± 0.11	(16) 1.50 ± 0.13	(17) 0.25 ± 0.04

situation (Graham, 1978*a,b*). In an analogous study, we can consider the rear leg 5 protractions as a natural stimulus in every second cycle of the next anterior leg 4. We plotted the changes in the period of leg 4 when stimulated, *versus* the phase occurrence

of the stimulus. The results from three different animals can be interpreted as a phase-response curve (see Fig. 6). This plot shows a very symmetrical scattergram, centred around the theoretical mid-point (phase = 0.5 and the period ratio = 1, i.e. no effect), with no value in the two zones 0–0.2 and 0.75–1. As phase has a circular distribution, this really corresponds to a single forbidden zone for values of phase <0.2 and >0.75 similar to that reported for katydid walking behaviour (Graham, 1978b). The correlation coefficient is highly significant (for 73 steps, $R = 0.790$, $P < 10^{-5}$) and the three data samples are evenly distributed. All these features show that the interactions between legs 4 and 5 involve a reciprocal influence, both excitatory and inhibitory,

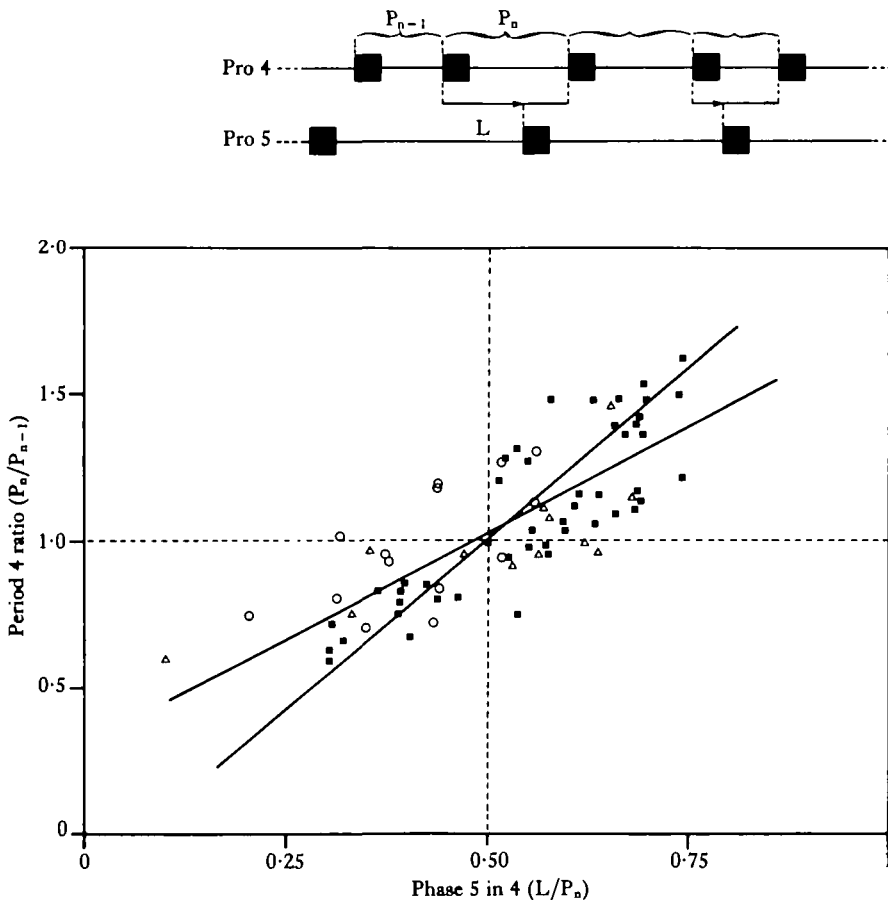


Fig. 6. Analysis of the functional relationship between ipsilateral legs 4 and 5 when stepping strictly in stereotyped 2:1 coordination. Leg 5 promotions are considered as a rhythmic stimulus occurring in every two cycles of leg 4. Top inset explains the measurements. P_n = ongoing period of promotor 4 (stimulated). P_{n-1} = preceding period of promotor 4 (unstimulated). L = latency of promotor 5 occurrence in the cycle of leg 4. Abscissae = phase 5 in 4 (L/P_n). Ordinate = ongoing effect on period (P_n/P_{n-1}). Dotted lines mark the phase 0.5 and the unit ratio (i.e. no change in period 4). Data from three animals under the same experimental conditions (1, black squares; 2, open circles and 3, triangles). The data points from the three animals fit well with the symmetrical organization of the scattergram. Regression lines are for the three animals. Correlation: $R = 0.790$, $N = 73$. General means (± 1 s.d.): $\bar{X} = 0.52 \pm 0.14$ (s). $\bar{Y} = 1.05 \pm 0.26$ (s).

and that the 'magnet effect' model first described by Von Holst (1943) accurately describes the coupling mechanism for the ipsilateral rear legs of *Jasus*.

Induced and spontaneous changes in the driven walking behaviour

All the results presented above come from walking sessions performed at constant speed. The perturbations observed at the transition points will now be systematically described. In most cases, the rock-lobster immediately adapts its walking mode to the new conditions imposed by the belt speed change. Even if the actual strategy must be radically altered, the adaptation can easily be carried out within one single step cycle (Fig. 5).

This is not always the rule, as illustrated in the records of Fig. 7. Here, a 2 cm s^{-1} change is imposed at two belt speed levels ($6\text{--}8\text{ cm s}^{-1}$ and $12\text{--}14\text{ cm s}^{-1}$). In both cases, the animal stops walking for a short time (about 5 s) and then resumes stepping at a higher frequency corresponding to the new belt speed. One can see that the first three steps in each restarting sequence of leg 4 are somewhat weaker in T-C angular movement as well as in PS burst intensity. Once the walking pattern is established (right and left parts in both records), the T-C angle does not change its value (about

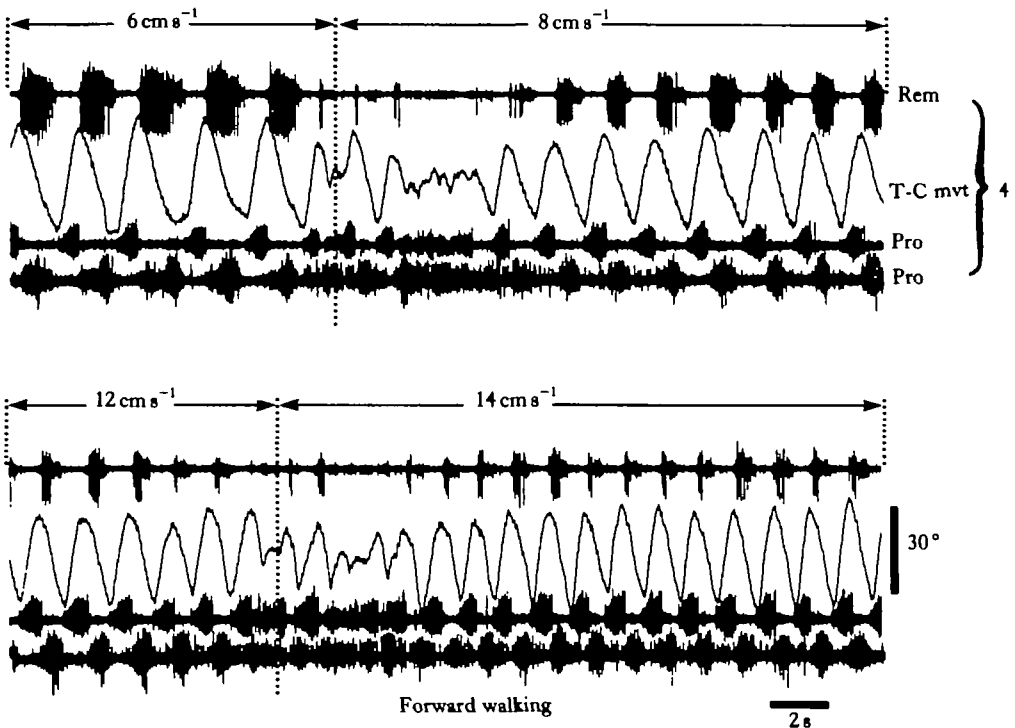


Fig. 7. Influence of imposed speed changes upon the amplitude of the T-C joint movement. EMG of remotor and promotor muscles and T-C movement of leg 4 and promotor of the homolateral leg 5. Upper, speed change from 6 to 8 cm s^{-1} ; lower, speed change from 12 to 14 cm s^{-1} . In both cases the adaptation to the new imposed speed is not instantaneous. The animal stops for about five steps and then resumes its walking with a convenient higher stepping frequency. Note that when the walking rhythm is stabilized, the angular excursion of the leg 4 T-C joint remains nearly constant whatever the speed.

30/35°) no matter what speed (6, 8, 12, 14 cm s⁻¹) is used. This can be extrapolated to the stride length which is also found to be an invariant parameter.

If we now consider the remotor discharges of leg 4, the burst intensity decreases gradually as the belt speed increases from 6 to 14 cm s⁻¹. This is consistent with the hypothesis of a position servo mechanism regulating the PS discharge; at slow speed the PS discharge is reinforced but at high speed it is partly inhibited (Clarac & Cruse, 1982; Cruse, Clarac & Chasserat, 1983).

Fig. 8 is a composite representation of averaged parameters (period and stride) and real values (AEP and PEP) within consecutive leg 4 steps in a walking sequence including progressive and abrupt speed changes. As already shown in Fig. 2, the mean stride remains more or less constant whatever the speed (either a gradual increase or the 20 to 8 cm s⁻¹ decrease), while the mean period changes significantly at any

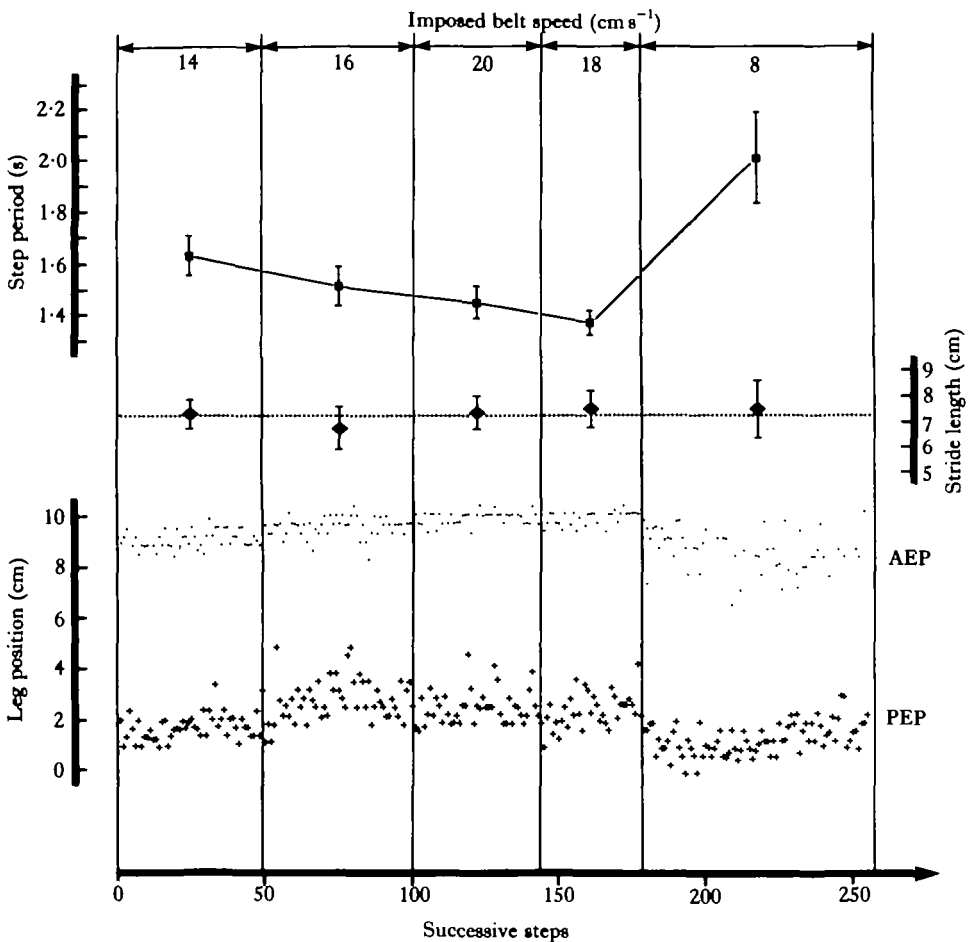


Fig. 8. Influence of imposed speeds upon the period, the stride length and the leg tip extreme positions of leg 4 during forward walking. AEP (.) and PEP (+) are plotted for each consecutive step of the walking sequence. Zero corresponds to the leg 4 T-C joint position along the body axis. Stride and period values are the computed means (± 1 s.d.) for all the steps performed at every speed. The dotted horizontal line indicates the general mean stride within the whole sequence (7.3 cm \pm 0.9).

change in the imposed speed. During this time the successive plot of leg 4 AEP and PEP within the sequence shows that both extreme positions are affected when the speed slows down abruptly. AEP and PEP are both shifted to the rear (more than 1 cm). In addition, a slight ascending position gradient appears from rear to front when the speed gradually increases from 14 to 20 cm s⁻¹. The PEP value appears to be rather broadly scattered around the mean position at any given speed, but the AEP seems to be more precisely distributed at high rather than at low speed.

If we examine Fig. 3 again, it appears that between 12 and 14 cm s⁻¹, the period of both legs remains steady (1.25 s) while the 4 in 5 mean phase undergoes a significant increase (0.45 to 0.52). On the other hand, at 2, 3, 4 cm s⁻¹ and at 16, 18, 20 cm s⁻¹ the phase has reached a limiting value (0.20 and 0.60) and no longer changes, but the step period continues to vary significantly in these speed ranges (see Fig. 3). In order to clarify these ambiguous observations, we have carried out the following experiment where the imposed speed increases gradually from 10 to 20 cm s⁻¹ and then decreases in 4 cm s⁻¹ intervals to 8 cm s⁻¹ (Fig. 9).

Periods of the ipsilateral legs 4 and 5 and the 4 in 5 phase are plotted for each of the 300 successive steps. At first sight, the period and phase *versus* speed appears to follow the previously described behaviour, but a careful study shows that this is not always the case (see Table 4).

(i) Stepping trials of 12 cm s⁻¹ and 16 cm s⁻¹ were carried out twice. The first time in the ascending speed gradient (1) and then again in the descending one (2). The period of legs 4 and 5 and the phase 4 in 5 have significantly different values in the two situations.

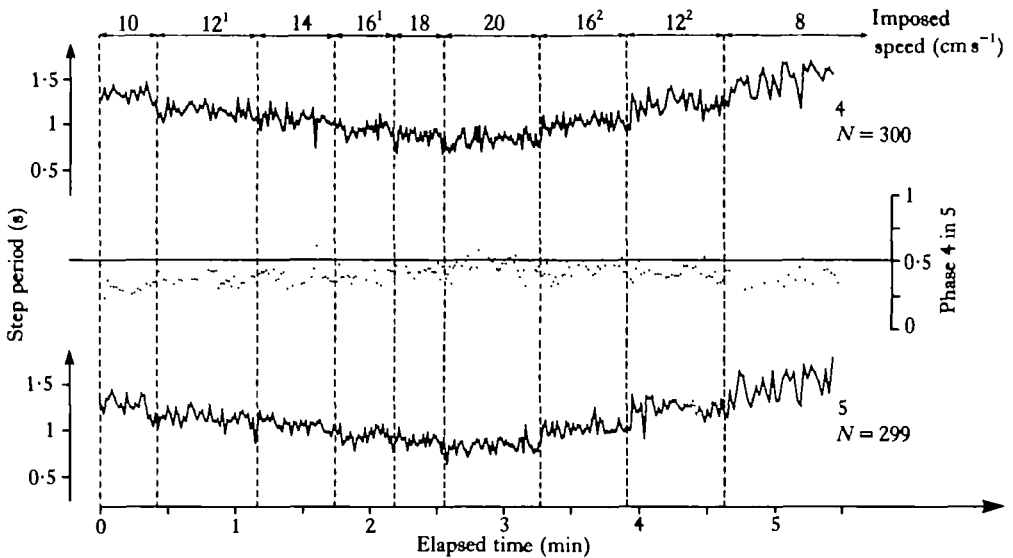


Fig. 9. Non-specific nature of period and phase values related to the imposed speed. Continuous sequence of forward walking, step periods of ipsilateral legs 4 and 5, and phase 4 in 5 are plotted *versus* elapsed time. The speed is increased from 10 to 20 cm s⁻¹ by 2 cm s⁻¹ increments and then decreases more sharply to 16, 12 and 8 cm s⁻¹. The small vertical bars on period plots mark the step timing as in Fig. 4.

Table 4. Mean values (± 1 S.D.) of the parameters plotted in Fig. 9, for each of the nine imposed speed classes

Belt speed (cm s ⁻¹)	Step number	Leg 4 period (s)	Leg 5 period (s)	Phase 4 in 5
10	20	1.32 \pm 0.07	1.27 \pm 0.10	0.28 \pm 0.05
12 ¹	40	1.14 \pm 0.07	1.13 \pm 0.08	0.33 \pm 0.05
14	33	1.05 \pm 0.09	1.07 \pm 0.06	0.36 \pm 0.07
16 ¹	27	0.95 \pm 0.07	0.95 \pm 0.08	NS 0.35 \pm 0.05
18	26	0.87 \pm 0.08 NS	0.90 \pm 0.06	0.39 \pm 0.04
20	49	0.85 \pm 0.07	0.85 \pm 0.07	0.43 \pm 0.06
16 ²	38	1.04 \pm 0.07	1.05 \pm 0.07	NS 0.42 \pm 0.06
12 ²	35	1.24 \pm 0.11	1.27 \pm 0.10	NS 0.40 \pm 0.05
8	32	1.50 \pm 0.14	1.51 \pm 0.16	0.37 \pm 0.06

The indices (1) and (2) for the speeds 12 and 16 cm s⁻¹ refer to first or second passage at these given speeds, as indicated on the speed scale of Fig. 9.

NS indicates that the difference between two mean values is not significant ($P < 0.01$).

(ii) From 14 to 16 cm s⁻¹, 20 to 16 cm s⁻¹ and from 16 to 12 cm s⁻¹ both 4th and 5th leg periods undergo a significant change, while the 4 in 5 phase remains stable.

(iii) From 18 to 20 cm s⁻¹ the opposite is true and L4 period is not significantly different while ipsilateral phase increases.

One cannot find any significant similarity between the step parameters of this animal and those of the rock-lobster of Figs 3 and 4 in any class of analogous imposed speed. Therefore, at a given speed, the step parameters seldom present identical values from one animal to another or even in the same animal during different walking trials. This suggests that such timing parameters have a degree of reliability when related to speed changes but can either be altered or not, depending on the kind of imposed speed variation (gradual or abrupt) and on their initial value.

The relative significance of both the step period and the ipsilateral phase is described in Fig. 10. In this experiment, the animal walks backward on the treadmill with an imposed speed fixed of 10 cm s⁻¹. Table 5 shows that, in the first 50 s of the sequence, the common period of both legs is stable (1.04 \pm 0.07 s) as is the 4 in 5 phase (0.70 \pm 0.05). Then the rock-lobster changes its walking mode spontaneously (black star in Fig. 10) by increasing the step period (1.27 \pm 0.16 s) while the belt speed remains constant at 10 cm s⁻¹. At the same time the phase of ipsilateral legs decreases (0.58 \pm 0.09).

During the last part of the sequence the step to step periods and the phase ratio become more irregular than in the first part, with the legs always stepping in absolute coordination.

In order to increase its period the animal can either modify the RS and/or PS duration. On the treadmill, an increase of the PS duration necessarily involves a

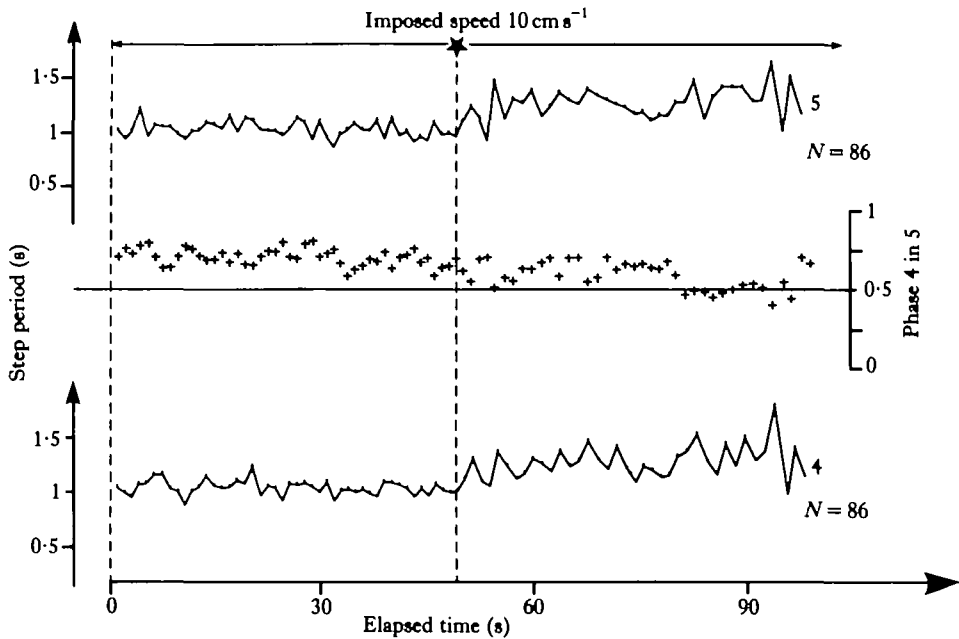


Fig. 10. An unusual backward driven walking sequence; periods of ipsilateral legs 4 and 5 and phase 4 in 5 *versus* elapsed time. Imposed speed is 10 cm s^{-1} for the whole session. At black star, the animal spontaneously slows its stepping rate. The period increases and phase decreases from 0.70 to 0.58.

Table 5. Mean values ($\pm 1 \text{ S.D.}$) of the parameters plotted in Fig. 10

	Step number	Leg 4 period (s)	Leg 5 period (s)	Phase 4 in 5
Before black star	46	1.04 ± 0.07	1.04 ± 0.07	0.70 ± 0.05
After black star	40	1.27 ± 0.16	1.28 ± 0.16	0.58 ± 0.09

The black star refers to the change in walking rate occurring spontaneously within the sequence.

greater stride, since the imposed belt speed remains unchanged. Such a behavioural feature is thus only possible if at least one parameter is changed (stride or RS duration). The two legs can use the same strategy to reach the new period or one leg can modify its stride while the other one changes its RS duration. When the reorganization of the stepping parameters produces a significant shift of interleg phase (as in Fig. 10), one can hypothesize that the alterations involved mainly the temporal rather than the spatial step components.

DISCUSSION

As presented in detail in the first paper (Clarac & Chasserat, 1983), walking on a treadmill is an active locomotion (Evoy & Ayers, 1982). Legs 4 and 5, which are the most active in walking, never remained passive on the belt throughout the different stepping sequences analysed (see Figs 2, 7 and 10).

The present data permit us to discuss the spatial and temporal relationships which govern the different parts of a step and, at another level, the mechanisms which coordinate the different legs.

The stepping period

The step period is a very complex parameter with spatial, temporal and force components. The force components have been studied elsewhere (Clarac & Cruse, 1982; Cruse *et al.* 1983), and we shall discuss separately the spatial and temporal factors before discussing their interactions.

Spatial parameters

The extreme positions of the legs are generally independent of the walking speed. The only significant change linked with the speed seems to be when an abrupt change occurs as in Fig. 8 (from 20 to 8 cm s⁻¹). These rapid changes create an uncommon behavioural problem for the animal. The observed instability of the extreme position that results could arise from massive proprioceptive flow due to the speed change. Considering the spatial dispersion of the extreme positions it appears that the AEP is always more narrowly distributed than the PEP. This is consistent with the results obtained by Graham & Cruse (1981) for the stick insect walking on mercury. Furthermore, Wendler suggested (1966) that the ground contact (i.e. AEP) could provide an essential timing signal within the step cycle by stimulating load receptors. Also, the analysis of Pearson & Duysens (1976) demonstrated that initiation of the swing phase was inhibited by the leg load during standing. They propose that at the PEP a position receptor sends an excitatory signal producing the leg swing, while inhibition is suppressed as the leg becomes unloaded. The necessary simultaneous occurrence of these two conditions could (if it applies to all the legs) explain the greater variability of PEP in rock-lobster stepping.

The stability of the stride is probably a general feature in multilegged animals. Nevertheless, no systematic study of the stride has been made in other arthropods over such a wide speed range. Since a constant stride normally produces a hyperbolic distribution of the PS duration and of the step period *versus* speed, this may be a general characteristic of arthropods where such relationships are commonly found.

The recent review of vertebrate locomotion (Grillner, 1981) shows that stride modification is a common strategy in human walking, while tetrapod mammals keep a more stable stride in the most common gaits (walk, pace and trot). Therefore, for a multilegged animal the stride of a given leg would be determined and limited by both the hindering presence of adjacent appendages and by activation of specific joint receptors such as those studied in the cockroach by Pearson (1972). Thus, it seems likely that the spatial parameters (AEP, PEP and stride) are under proprioceptive control and, indeed, our results show clearly that they are much more variable at slow speeds than at very high speeds (see the s.d. bars of mean strides in Fig. 3, and scatter of AEP in Fig. 8). This is consistent with the general distinction between the somewhat 'automatic' walking rhythm observed at high speeds in very excited animals, and the much more irregular and modulated ones which characterize very slow walking and explorative behaviour (the two walking modes of Kozacik, 1981).

Temporal parameters

Each stroke differs according to the variability of the imposed belt speeds.

RS components: above the treadmill, the RS duration for leg 4 remains stable for all except the slowest of imposed speeds (see Fig. 2). This differs from free walking and has already been discussed in paper I. The RS leg speed, on the contrary, is very variable from one step to another. This based upon a regulating mechanism intended for performance of a constant RS duration whatever the irregularities in stride length (see Figs 2, 8).

PS components: the PS duration and speed appear to be rigidly dependent on both stride and belt speed. At a given walking rate, the stride changes from step to step while the leg speed remains close to the imposed belt speed. For a given stride deviation ΔS , the hyperbolic function ($PS = S/V$) results in a larger deviation in PS duration at slower speed than at higher speed (note s.d. bars of open circles in Fig. 2).

In none of these experiments have we observed PS durations below 500 ms. If it is assumed that this empirical value is the lower permissible limit, this may explain why some rock-lobsters refuse to walk when the imposed speed overshoots 14 cm s^{-1} , while others can easily perform regular stepping at belt speeds of up to 20 cm s^{-1} . Indeed, the stride length of a given animal allows one to infer the maximum rate at which it will be able to follow the belt (e.g. in Fig. 2 the overall mean stride is 8.9 cm, corresponding to a maximum theoretical imposed speed of $8.9/0.5 \approx 18 \text{ cm s}^{-1}$; effectively, the animal stops walking at belt speeds beyond this value). The average stride length for a given animal in a given posture is a characteristic value related to its driven walking rate. Pause times are not correlated with the imposed speed, in forward walking, above 4 cm s^{-1} . The pauses at the end of either stroke can be compared with the results of Graham & Cruse (1981), who also found pause times (30–100 ms) in stick insects when walking on a mercury surface or on a wheel. These pauses seem to be a characteristic of slow walking arthropods, and their role is somewhat unclear. One possible explanation is that they correspond to an initial time during which the muscular power is partly absorbed by the leg joints, before producing the tip displacement.

Interaction between different parameters in the whole animal

The discussion of the spatial and temporal data organizing the successive steps in driven walking suggests a paradoxical conclusion. On the one hand, we defined the stride length and the RS duration as invariable parameters, on the other hand we say that they vary from one step to another.

In fact there is no contradiction if we take into account the levels of regulation. On average, the two values are invariant whatever the speed, but from step to step, due to the heterogeneous mechanical assemblage of individual limbs, the animal uses these two 'invariant' parameters to maintain a certain coordination. Then the mechanism organizing the stepping pattern can be described as a continuous balance between the following two sets of elements.

(i) *The spatial elements* (AEP-PEP and stride).

Because of their different lengths and spatial arrangement along the longitudinal

body axis, ipsilateral legs do not have similar mean strides. Mixed data from several animals give the following rough proportions. Taking the 4th leg stride as the reference (100 %), the stride of leg 2 is about 50 %, for leg 3 it is about 70 %, and leg 5 has a stride equal to that of leg 4 but extendable to 120 % at slow speeds. Thus the period value is the result of different proportions of each component depending on the considered leg. The PS duration is much longer in the rear legs than in the front ones. This phenomenon exists also in other arthropods. Several authors have reported that in some animals front legs spend more time elevated than on the substrate (Bowerman, 1977 in scorpion; Seyfarth & Bohnenberger, 1980 in tarantula; Burns, 1973 in the locust). Indeed, the second legs of a rock-lobster, when involved in stepping, play a 'tactile' role with a very short PS duration and a very long RS often followed by a pause time. In this peculiar case, the RS components are mainly responsible for the temporal regulation of the step (Clarac, 1982).

(ii) The remaining *temporal elements* of the step period (RS velocity, duration and pause time).

The PS duration of each leg is more or less fixed by both its stride and the imposed speed. The animal can modulate the RS velocity of a given leg, in order to adjust the RS duration to the convenient value, whatever the stride just performed in the current cycle (see the large s.d. bars of black squares in Fig. 2).

The precise adjustment with the neighbouring ipsi- and contralateral legs is realized by the addition, if necessary, of suitable pause times as 'waiting delays' for sensory signals coming from adjacent legs when switching from PS to RS (or the opposite). Any modification in period can obviously be performed by alteration of either PS duration, RS duration or a combination of both (Fig. 10).

This apparently independent control of the strokes has already been described in the turning movements of jumping spiders (Land, 1972). The rock-lobster and the jumping spider show analogous behavioural parameters (stride-constant turning behaviour performed by right and left sides walking in opposite directions). Land deduced from his data that each limb 'oscillator' must be more complex than a single relaxation oscillator. Therefore, he proposed a theoretical model where each leg was driven by two oscillators and a proprioceptive system able to 'memorize' the current leg position. Such regulation probably governs the slow walking behaviour of various lightly loaded arthropods. In these conditions, the legs can alter the time spent 'off ground' (i.e. the RS duration) without causing disturbances in their equilibrium. Also the step-by-step variability of the leg stride may be an essential feature related to the ability of these animals to walk on very uneven substrates. The treadmill situation emphasizes the necessity of controlling the 'off ground' components, since the belt stimulus fixes rather strictly the duration of the 'on ground' components (see paper I, Clarac & Chasserat, 1983).

Interleg functional relationships

Various coupling between legs

The previous paper shows that coupling is much looser in free than in driven walking. The present paper, on the effect of a large speed range, indicates that the ipsilateral and contralateral coupling are different in nature and this agrees with the

idea of individual commands for each side, as proposed by Graham (1977) in his model for stick insect walking. This idea is supported by the following observations. The rock-lobster can easily walk forward on one side and simultaneously backward on the other. This can appear in free turning or on the treadmill when right and left belts are moving in opposite directions. Similarly, driven walking can be elicited on one side while the other side remains standing on the non-moving belt (unpublished observation). The experimental data presented in this report also confirm the ipsi-contralateral coupling differences.

Ipsilateral phase for the rear legs is always dependent on speed, with an interleg ascending delay which is nearly constant. Neither the phase nor the period are representative of a given speed but phase never falls into the forbidden zone defined by the limits of <0.25 and >0.75 . For the contralateral phase all values can be attained (between 0 and 1) and whatever the speed the mean values are around 0.4. The presence of asymmetry again reinforces the idea of a dual command for right and left sides and explains why contralateral coupling can be sometimes very strong (Fig. 4 at 8 cm s^{-1}) or sometimes very weak as if each side were unsynchronized (Fig. 4 at slow speed). This kind of coupling can create very irregular periods, although no cycles are lost. This is particularly useful in free walking (see above), where the animal alters the relative frequency on either the right or left sides rather than the stride length. It seems useful to define the contralateral coupling as 'labile' in comparison to the rigid ipsilateral coupling (as did Graham, 1972, in the stick insect).

Metachronal sequences between ipsilateral legs

In paper I, we were not able to discuss metachrony because of the narrow range of values obtained, although its presence was suggested in the treadmill situation. Now with the large range of step periods the metachrony is obvious. Wilson (1966) in his insect model presented a rigid law concerning the metachronal wave. He later moderated this view after his study of the tarantula spider (1967) and he noted that the interleg latency was never stable but 'of insufficient variation to maintain phase constancy'.

In this regard, our results fit perfectly with the model since the 5 to 4 delay remains nearly invariable while phase 4 in 5 increases continuously with the imposed speed. The speed dependence of the 5 to 4 delay observed at very slow rates (Table 1) could be caused by the predominant influence of the peripheral system, which must reorganize the walking pattern based upon the lower critical phase value (0.2) imposed by the forbidden zone.

In contrast to the metachronal gaits, it has been proposed that arthropod gaits are basically tripod or tetrapod and that the phase between legs remains constant while the interleg delay and stroke duration vary. Animals with more than four walking leg pairs use the metachronal gait (Sleinin & Silvey, 1980; Barnes, 1975). Others exhibit a break in their stepping pattern using the metachronal mode at slow speed and the tripod (or the tetrapod) at fast speeds (Delcomyn, 1971; Spirito & Mushrush, 1979). Adult stick insects with a maximum speed of 10 cm s^{-1} walk metachronally up to 7 cm s^{-1} and then maintain an approximate tripod pattern from 7 to 10 cm s^{-1} (Graham, 1972).

In rock lobster, despite the continuous change of ipsilateral phase with respect to

speed, there is a tendency to maintain the phase values around 0.5 (i.e. the value characteristic of an alternating mode) in the natural speed range of free walking ($10\text{--}14\text{ cm s}^{-1}$ for the animal in Fig. 3, 8 cm s^{-1} for the animal in Fig. 4). Nevertheless, during faster walking, rock-lobsters depart from an alternating pattern and the phase continues to increase beyond 0.5. This suggests that the control system, at least in this case, is not able to deviate from the rules concerning RS duration and interleg delay constancy. This is also an explanation of why metachrony is not readily observed in free walking.

General characteristics of crustacean leg coupling

The data we have now accumulated on decapod walking still remain less in terms of numbers and variety of animals studied than those obtained on insect walking. (The data given here on crustacean walking seem interesting because they confirm the idea of the separation of this group from the other arthropods.)

Two main features typify crustacean walking:

(A) These animals can walk in all directions although each group seems to have a preferential walking direction. Crabs such as *Carcinus maenas* and *Maia squinado* which move laterally most of the time, can also easily walk forward or backward on a treadmill (F. Clarac, unpublished observations). Although *Homarus* walks mostly forward and backward, it can also walk perfectly in a lateral direction (Ayers & Davis, 1977). The rock-lobster can also walk in every direction, although forward walking seems to predominate under natural conditions.

(B) A complementary feature is that they use different numbers of legs for different walking sequences. *Homarus* uses its four pairs normally, and if it catches prey it walks only with its two back pairs of legs while the small chelae on the front pairs are used to grasp the prey. A crab uses mainly the 2nd, 3rd and 4th pairs; leg 1 being the chelae, while leg 5 is often specialized for swimming. The type of walking also changes with the number of legs used. When *Ocypode* walks very fast, it uses two legs only (Burrows & Hoyle, 1973). Palinura, for example *Iasus*, may walk with only the two back pairs during both free and driven walking, though in free walking the number of legs used often varies greatly due to the small forces required by the animal to propel its body.

Because of the wide variability of the walking pattern of Crustacea, it does not seem appropriate here to discuss the different gaits used. Consideration of all ipsilateral legs together gives a superficial view of the organization. On the other hand, it seems much more meaningful to consider the relation of pairs of legs since the coordination is essentially a successive rearrangement of timing and position between legs which can occur step by step.

An analysis of walking that describes each leg as an individual 'leg oscillator' with neuronal connection is difficult because of the great variability observed in leg co-ordination in free as well as in driven walking. Our study nevertheless reveals that:

(i) the greatest tendency is that neighbouring legs (intra- and intersegmental) must move more or less alternately;

(ii) in slow walking, turning or exploratory behaviour, any pair of adjacent legs (except the 4–5 ones) can occasionally move perfectly in phase.

From these observations one can hypothesize that both inhibitory and excitatory

influences may coexist within the oscillatory network, the strength of both effects being under the control of the whole system (central as well as peripheral).

The major difficulty when one tries to understand the neuronal coupling mechanisms from intact animals, is that the stepping sequences recorded are often the result of a stable equilibrium state between the different leg 'oscillators'. Description of 'relative' phasing between 'oscillators' when locked in a steady state cannot result in any information about the mechanisms responsible for such equilibrium.

For this reason the particular behaviour exhibited at slow speeds between leg 4 and 5 is of great interest. In Graham's (1978*a,b*) study on the katydid the leg 3 and 2 relationship corresponds to an inhibitory ascending model. Our scattergram is analogous to a 'magnet effect' model and involves excitatory and inhibitory pathways. This kind of interaction has been described at the neuronal level by Ayers & Selverston (1979).

In summary, two types of relationships have been studied using our experimental device:

- (1) The relationship between the belt speed and individual legs.
- (2) The relationship between the different legs.

This has given us some insight into the mechanism of leg coordination. In nature, rock-lobster walking presents a much larger repertoire of sequences: we hope that they will be found to follow the fundamental properties described here.

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