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# A PHYSIOLOGICAL ANALYSIS OF WALKING IN THE AMERICAN LOBSTER (*HOMARUS AMERICANUS*)

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## CONTENTS

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The normal, unrestrained, forward walking of the lobster was studied with a closed-circuit television system and a video-tape recorder. A frame-by-frame analysis was undertaken and measurements made of unilateral stepping sequences, contralateral and ipsilateral phase relations between pairs of legs, the movements at the leg joints primarily involved in stepping and their differences in each of the four pereiopods.

The order of stepping was expressed in terms of the probability of any leg following any other leg and it was found that while there is a preferred order, there is considerable variation from the dominant pattern. The commonest deviations from the dominant gait are those involving the simplest types of re-ordering of the sequence. Pairs of contralateral legs show a strong tendency to alternate but all phase relations can occur. Similarly, while the ipsilateral legs show preferred phase relations, all possible relations do occur. The four pereiopods from anterior to posterior were found to have respectively, a pulling action, a combined pulling and rowing action, a rowing action and a combined pushing and rowing action. The same parameters of stepping were recorded from animals walking on a transparent, driven treadmill and, as no significant differences were found in comparisons with results from freely moving animals, subsequent results were obtained from animals walking on the treadmill where more detailed study and manipulation could readily be made.

The stepping action of the third pereiopod during forwards walking involves major movements about two joints whereas the other pereiopods move about three joints. Detailed study of the intra-leg activity was therefore confined to the third pereiopod where the simpler action considerably simplified the problems involved in collecting and analysing data.

Measurements were made of the angles swept out by the joints of the third pereiopod during movement. Electromyograms were recorded from the six muscles primarily responsible for these movements and from movement transducers placed at the joints. The duration of the movements and of the bursts of activity in the muscles and the interrelation between different muscle bursts were measured and a computer-aided analysis made to determine the characteristic features of the inter-burst relations during stepping. While there is considerable variability from step to step, the overall activity is relatively phase-constant over a wide range of stepping frequencies.

When some of the key parameters of normal walking had been characterized, changes designed to alter the sensory input to the system were imposed. Changes in the duration of the power stroke and return stroke fractions of the stepping cycle were found when the animal was induced to pull or carry a load. Because of this result, a series of modifications were applied to unloaded animals. These included splinting joints at abnormal angles, attaching prosthetic legs, harnessing legs up off the substrate and partial or total amputation. It was found that the normal phasing of leg movement is altered if the support function of any other leg is impaired and that the change is in a direction which would compensate for the loss of support.

This result was investigated further by loading animals in several different ways so that the power stroke or return stroke fraction of the cycle would be loaded differentially. Comparisons with unloaded animals demonstrated some previously undescribed changes in output in response to load. There is a marked reduction in the variability of the output irrespective of where a cycle is loaded, so that the burst structure during a loaded step becomes highly phase constant in most aspects. Other changes in overall burst structure are dependent on where the load is applied.

The significance of the results, and particularly of the previously undescribed responses to load, were discussed in the context of the role of sensory input in lobster walking.

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## 1. Introduction

One of the major areas currently under intensive investigation by behavioural neurophysiologists is the extent to which behaviour patterns are generated and modified by either preexisting behavioural scores within the nervous system or by sensory stimuli from the environment. The limits of the problem have been succinctly stated by Hinde (1970) as follows:

'The patterning of complex movements could be determined from the start in the central nervous system or could be adjusted by peripheral (proprioceptive or exteroceptive) stimuli received as a result of the earliest phases of the movement. Physiologists are largely concerned with experiments aimed at assessing the relative effects of central and peripheral factors.'

The comparative neurophysiologist has a particularly useful contribution to make because his studies bring him into contact with examples of a wide range of behavioural requirements which are met by very diverse neural systems covering the whole range of complexity. When a sufficient number of systems have been studied it should be possible to formulate some relations between behavioural requirements, centrally generated contribution and peripherally generated contribution.

Most studies which have used a physiological (as distinct from an ethological) approach to the problem of central–peripheral interaction have been limited to very small segments of behaviour (Kennedy 1967). It will not, however, be possible to formulate any general principles without more information about mechanisms underlying larger and more complex segments of behaviour. Most of the studies which are attempting to move to higher levels of complexity have been involved with activities like feeding, respiration and locomotion because rhythmicity has several important advantages. In general, rhythmic behaviours can be evoked reliably without the need for complex triggering situations. In many cases such parameters as frequency, amplitude and duration can be readily manipulated. The repetitive nature of the activity generates large samples of data which can usually be collected rapidly enough to avoid major changes in the endogenous state of the animal and such samples allow powerful statistical analyses to be used.

It has proved possible to study rhythmic activity in some detail in some simpler systems with relatively stereotyped outputs (Huber 1962, 1967; Miller 1966; Willows & Hoyle 1969; Wilson 1968) but it has proved more difficult to work with systems which might be expected to show more complex interaction with the environment (Barnes, Spirito & Evoy 1972; Clarac 1971; Davis 1969*a*, *b*, *c*; Pearson 1972; Runion & Usherwood 1966; Spirito, Evoy & Barnes 1972). It therefore seems desirable to increase the number of studies of systems at this level since they are most likely to reveal principles useful in moving to higher levels of complexity.

Walking behaviour is a rhythmic activity at the desired level of complexity. While there has been considerable study of insect walking mechanisms (Gray 1968; Pearson 1972; Wendler 1966; Wilson 1966*a*, *b*) the decapod crustaceans have received very little attention. The stepping order in macruran decapods, which appear to be very suitable for locomotory studies, has been described in several places but the descriptions are not in complete agreement and none goes beyond a simple level of analysis (Baldi 1936; Bethe 1930; Herter 1932; List 1895; Parrack 1964; Voelkel 1922).

The animal chosen for this study, the american lobster, is capable of navigating uneven surfaces quite rapidly (Herrick 1895, 1909), has a characteristically conservative crustacean

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motor innervation (Wiersma 1961), a typical decapod sensory system (Wales, Clarac, Dando & Laverack 1970) and the ganglia in the ventral nerve cord have already been studied with intracellular techniques (Otsuka, Kravitz & Potter 1967).

## 2. Materials and methods

### (a) *Animals*

Lobsters weighing about half a kilogram were purchased from a commercial supplier in Maine and transported by air express in ice-cooled containers. The animals were kept at 11 °C in a tank of seawater which was continuously circulated through a filter of gravel, fibre glass and activated charcoal. The lobsters were fed raw fish approximately once per week but otherwise the conditions of their confinement complied with those advised by the Maine Department of Sea and Shore Fisheries (Goggins 1960).

### (b) *Anatomy*

Observations on the muscles and nerves were made either from freshly dissected animals or from limbs fixed in Bouin's fixative and then dissected in 70 % alcohol. The nerves were studied by immersing the preparations in solutions of 5 % methylene blue diluted with seawater (Pantin 1946). Preparations prepared in this way were kept in a refrigerator at 5 °C for several hours. The staining solution was then replaced with fresh seawater and the preparation examined under a binocular microscope.

### (c) *Behaviour and physiology*

Video-tape records were made with a Bell and Howell video-recorder with a frame speed of 60/s of lobsters walking in a variety of situations. Animals were filmed from several different angles either in their large holding tank (180 cm × 90 cm × 50 cm) or in the smaller experimental tank (70 cm × 30 cm × 30 cm). A transparent acetate treadmill fitted inside the experimental tank allowed walking animals to be filmed from the lateral and ventral aspects simultaneously by means of mirrors. The mirror system also allowed the face of an oscilloscope to be included in the record for comparison of the timing of simultaneous physiological events. The video-recorder was equipped with a mechanism which allowed the record to be advanced frame-by-frame for detailed analysis of movements. The treadmill was driven by a continuously variable-speed motor so that animals walking on the treadmill could be readily kept in the centre of the recording field.

Electromyograms were obtained by inserting pairs of insulated copper wires (Belden, Chicago, 34 Nyclad) beneath the cuticle so that they made contact with the selected muscles. The actual position of the wires was checked by dissection after the experiments. The wires were waxed at the insertion point and connected to a wire harness on the animal's carapace. From there they were led to a.c. pre-amplifiers (Grass P8) and thence to an oscilloscope (Tektronix 565). The signals obtained were recorded either on magnetic tape or, for a permanent record, on photosensitive paper.

D.c. position transducers were often fitted across the joints to monitor movement. These were of a modified Sandeman (1968) type and detected the movement of a transmitter wire between two receiver wires. These transducers can be calibrated in position and adjusted so that they are operating within the approximately linear range of their response. When operating

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under seawater, however, the wire transmitter and receivers have to be rather large for an adequate signal. This means that they are very susceptible to extraneous mechanical movements and it is extremely difficult to keep them calibrated. They were therefore used only to give a non-linear indication of movement and finer analysis of movement was made from video-tape.

### (*d*) *Analysis*

The relations and durations of muscle bursts were measured directly from photosensitive paper and punched onto computer cards. Programmes for analysing the data stored in this way were written in Fortran IV and executed on an I.B.M. 360 computer.

## 3. ANATOMY

### (*a*) *General description of external anatomy*

*Homarus americanus* is a macruran decapod with the typical body divisions of cephalothorax and abdomen. It has a large pair of chelipeds immediately posterior to its mouth parts and a pair of pereiopods or walking legs on each of the last four thoracic segments (figure 1*a*). The

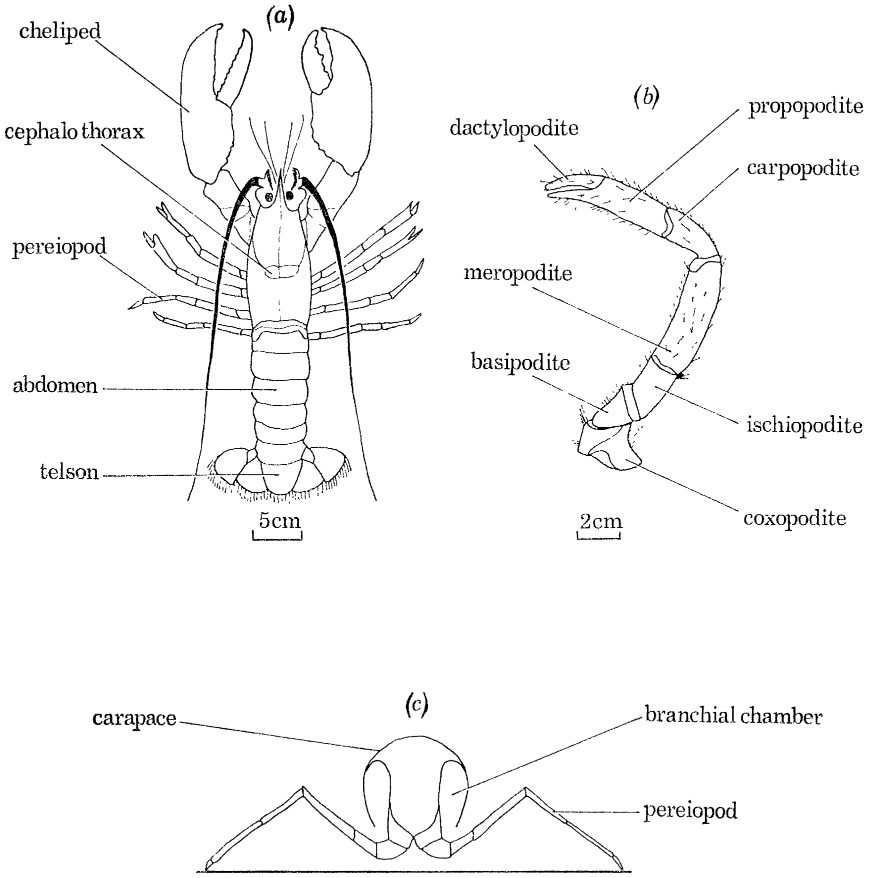

FIGURE 1. Diagrammatic representations of the general external anatomy of the body and the pereiopods. (*a*) Dorsal view of a lobster showing the main body divisions. (*b*) Anterior view of single right pereiopod showing the relations and relative dimensions of the segments. (*c*) Transverse section through the body showing relations of the legs to the body and branchial chamber.

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cephalothorax is entirely covered by the carapace which forms a protected gill chamber between the body and its inner surface. The pereiopods articulate with the body proper within this protected region and the body, rather than being propped up by the legs, is suspended from them (figure 1*c*). When the animal is moving, the weight of the body is normally carried entirely by the pereiopods but, when stationary, the telson and chelipeds may also rest upon the substrate.

TABLE 1. DIMENSIONS/mm OF CHELIPEDS AND LEGS FROM R.H.S. OF LOBSTER

(Mass: 0.4 kg; mid-line dorsal measurement: rostrum to end of carapace, 109 mm; rostrum to end of telson, 245 mm.)

| | | pereiopods | | | |
|---|---|---|---|---|---|
| | cheliped | 1st | 2nd | 3rd | 4th |
| coxa | | | | | |
| median axial length | 8 | 10 | 11 | 12 | 7 |
| lateral axial length | 15 | 8 | 9 | 10 | 7 |
| midpoint circumference | 56 | 41 | 40 | 40 | 34 |
| basis | | | | | |
| axial length | — | 14 | 14 | 14 | 10 |
| midpoint circumference | fused | 28 | 27 | 27 | 19 |
| ischium | | | | | |
| axial length | 35 | 16 | 15 | 14 | 9 |
| midpoint circumference | 56 | 22 | 21 | 22 | 18 |
| merus | | | | | |
| axial length | 50 | 41 | 37 | 30 | 25 |
| midpoint circumference | 60 | 24 | 23 | 23 | 20 |
| carpus | | | | | |
| axial length | 22 | 17 | 15 | 14 | 12 |
| midpoint circumference | 67 | 26 | 25 | 23 | 19 |
| propus | | | | | |
| axial length | 95 | 35 | 33 | 29 | 14 |
| midpoint circumference | 93 | 25 | 22 | 22 | 16 |
| dactylus | | | | | |
| axial length | 50 | 15 | 14 | 13 | 10 |
| midpoint circumference | 33 | 15 | 12 | 12 | 11 |
| total axial length | 190 | 121 | 116 | 115 | 105 |

The chelipeds and pereiopods are composed of seven segments each (figure 1*b*). Table 1 gives the dimensions of these segments in a typical lobster weighing 0.4 kg.

The seven joints in each leg operate as simple hinges. The mobility and range of movement of the leg arises from the offset of each hinge with respect to adjacent hinges, in gimbal-like fashion. When a lobster is in normal walking posture each of the four pereiopod pairs has a slightly different orientation with respect to the body. The first pereiopods, and to a lesser extent the second, have their axes angled anteriorly with respect to a transverse plane through their articulation with the body. The axes of the third pereiopods lie approximately in the transverse plane. The fourth pereiopods are angled posteriorly. These differences in orientation are mainly due to the positions of the coxal and basal hinges. The medial thoracico-coxal articulations of the four legs on a side are approximately 1 cm apart. As the series moves posteriorly the medial articulations are laterally displaced from the mid-line and the anterior offset of the lateral articulations becomes progressively less (figure 2*b*). In addition, the anterior articulation of the basis on the coxal rim becomes progressively more lateral as one shifts from the first pereiopod where it is located antero-medially to fourth where it is located antero-laterally (figure 2*a*).

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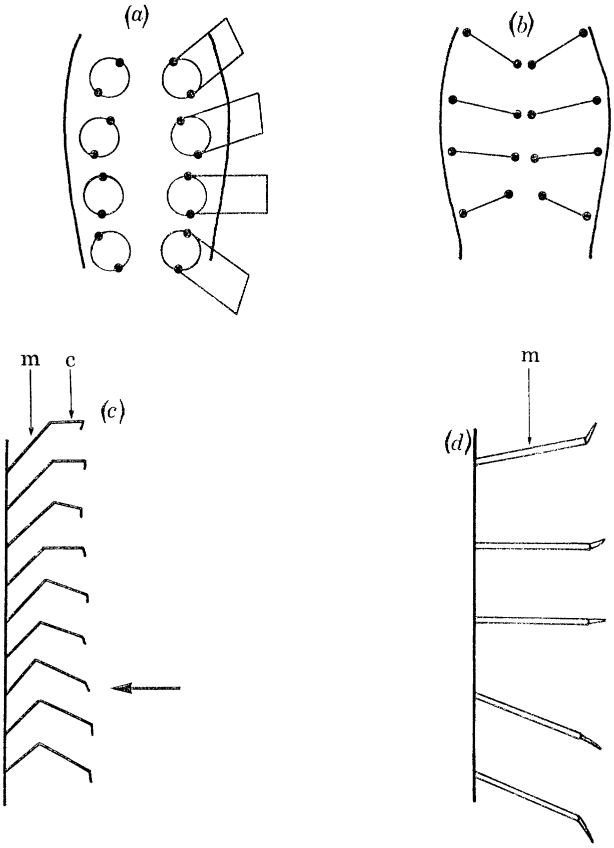

FIGURE 2. Diagrammatic representation of the alinement of the coxal and basal hinges. (*a*) Ventral view of animal showing the alinement of the coxo-basal hinges in the transverse plane. (*b*) Ventral view of animal showing alinement of coxal hinges in the transverse plane. (*c*) Posterior view of a retraction of the 3rd pereiopod. Arrow shows point where the leg was in the plane of the camera. m, baso-ischio-meral section; c, carpo-propo-dactyl section. (*d*) Ventral view of a retraction of the 3rd pereiopod. m, baso-ischio-meral section.

### (*b*) *Comparative movements of the four pereiopods*

The range of movement allowed around any particular joint is similar for each of the four pereiopods. However, because of the orientation of the coxo-basal articulations, the mechanical action required to sustain and propel the body mass is different for each leg. During a typical retraction the first pair of pereiopods move at both the thoracico-coxal and the mero-carpal joints so that propulsive forces may come from both joints (figure 3*a*). In the crayfish this has been termed a pulling action (Baldi 1936; Parrack 1964). The second pereiopod moves only slightly at the mero-carpal joints during retraction so that any propulsive forces developed must be generated mainly at the thoracico-coxal joints with the rest of the leg acting like a strut or oar. This action is therefore termed a combined rowing and pulling action (figure 3*b*). There is also some movement at the mero-carpal joint of the fourth pereiopod and its action is termed a combined rowing and pushing action (figure 3*d*). The simplest of the leg actions appeared to be in the third pereiopods where the mero-carpal angle appeared to be maintained approximately constant throughout retraction so that the leg functions as a rigid strut. This type of action is termed a rowing action. Because a rowing action would not pose the problem of propulsive force development at two joints simultaneously the third pereiopod was examined more closely.

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Because of the relatively large angle swept out by the leg and because the leg rotates as it retracts it is not possible to obtain a perpendicular alinement on the leg throughout its entire movement. The video camera was therefore alined in several different ways so that the leg would be approximately parallel to the field of the camera at the start, the middle or the end of the retraction. Figure 2*c* shows an example of a retraction movement of the third pereiopod filmed from behind and above. This movement was traced directly from a video-tape record. The arrow shows the position at which the leg is approximately parallel to the camera field. Figure 2*d* shows an example of a ventral view of the retraction movement of the third pereiopod also traced directly from a video-tape record.

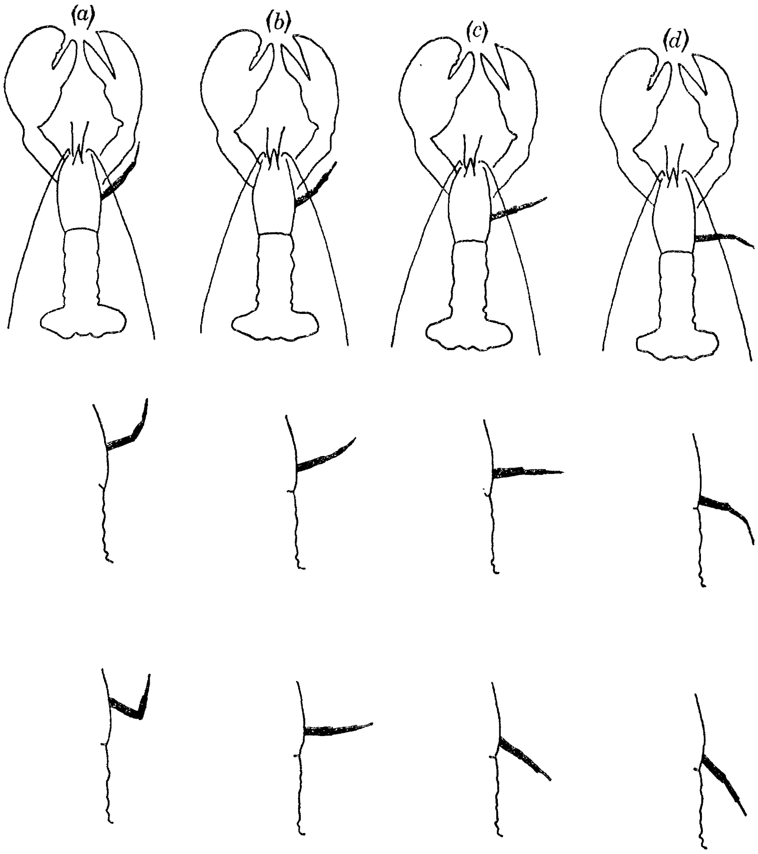

FIGURE 3. Movement of the periopods during retraction. Figures traced from video-records. Representation of the movement of the four pereiopods during a normal retraction showing how their actions differ.

This type of measurement indicated that the third pereiopod does execute a rowing action. The mero-carpal angle was found to be relatively constant during a retraction in forwards walking and this result will be described further at a subsequent point in the discussion.

Because it has a simpler movement than the other pereiopods the third pereiopod alone was used for the detailed anatomical and physiological analysis.

### (*c*) *External anatomy and range of movement at the joints of the third pereiopod*

#### (i) *Coxa*

The coxa is approximately cylindriform. When it is in the middle of its range of movement, the long axis of the cylinder runs dorso-ventrally. Its anterior wall is thickened and protrudes

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slightly where the basis articulates. A posterior concavity accommodates the anterior convexity of the immediately posterior coxa. The dorsal edge of the coxa dips down ventral to the two articulations both anteriorly and posteriorly so that both these borders of the coxa are joined to the body by large articulating membranes. In the third walking leg the coxal hinge is offset anteriorly from the transverse plane by 35° (figure 4*a*). The lateral articulation is also more dorsal than the medial articulation so that the hinge is offset from the frontal plane by 45° (figure 4*b*). Because the lateral wall of the coxa is longer than the medial wall its distal articulating face lies 35° from the frontal plane when the coxa is in mid-position. When the coxa is at the extreme anterior end of its range the positioning of its hinge causes the distal articulating face to project antero-ventrally. With the coxa in mid-position the articulating face projects

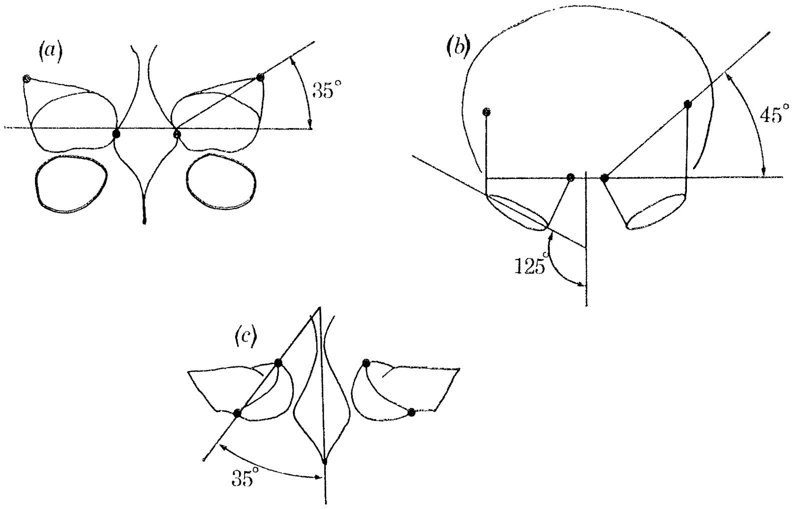

Figure 4. Diagrammatic representation of the alinement of the coxal and basal hinges. (*a*) Ventral view of the thoracico-coxal articulation of the 3rd pereiopod. (*b*) Transverse section through the body at the level of the 3rd pereiopod. (*c*) Ventral view of the coxo-basal articulation of the 3rd pereiopod.

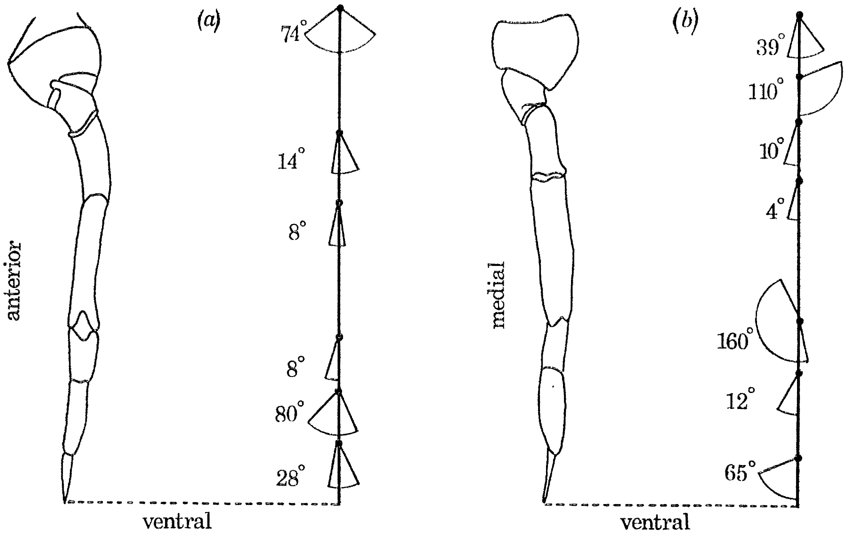

Figure 5. The range of movement at the joints of the 3rd pereiopod. (*a*) Medial view of the 3rd pereiopod held vertically below the body showing the range of movement in the sagittal plane. (*b*) Posterior view of the 3rd pereiopod held vertically below the body showing the range of movement in the transverse plane.

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ventro-laterally and when the coxa is fully retracted it projects ventrally, laterally and somewhat posteriorly.

Figure 5 shows medial and posterior views of the third pereiopod with the long axis of the leg held vertically below the body in order to illustrate the range of movement at each of the leg joints.

In moving from its extreme anterior to its extreme posterior position the coxa sweeps out an angle of approximately 74° in the sagittal plane (figure 5*a*). The same movement causes the body of the coxa to move through an angle of 39° in the transverse plane (figure 5*b*). The positioning of the coxo-basal hinge (figure 4*c*) together with the movement of the articulating face of the coxa allows the third pereiopod to operate with a rowing action because together they compensate for the lateral movement which must occur if the body is to move in a straight line with respect to a stationary *point d'appui* at the end of the limb. It therefore permits the mero-carpal angle to remain approximately constant throughout the range of coxal movement.

### (ii) *Basis*

The basis is a short, L-shaped segment with the short arm of the L forming a simple hinge with the coxa by means of two articulations on the distal articulating face of the coxa. With the coxa in the middle of its range of movement the basal hinge is also offset by 35° from the sagittal plane (figure 4*c*). With the coxa in mid-position the basis has a range of movement of approximately 110° in the transverse plane (figure 5*b*). This allows movement from vertically down below the body up to a position where contact between leg and carapace limits further dorsal movement.

The combination of coxal and basal hinge positioning produces axial rotation of the whole leg as it moves from an anterior to a posterior position and this is also necessary for the simple rowing action of the third pereiopod.

### (iii) *Ischium and merus*

The ischium is a short, rod-like segment with an oval transverse section, the narrower diameter of which lies antero-posteriorly. The baso-ischial joint is formed by two articulations at the extreme dorsal and ventral positions but the connecting rims of the two segments are very closely opposed along their entire circumference giving the joint a suture-like appearance. This joint structure limits movement at the joint to less than 15° in the frontal plane (figure 5*a*) and the basis and ischium tend to function as a single unit.

The merus which has the same cross-sectional shape and orientation as the ischium is the longest segment in the leg. Its articulation with the ischium is of the same type and orientation as the baso-ischial joint and, while it allows 8° of movement in the frontal plane, the merus functions, in most situations, as part of the baso-ischial unit (figure 5*a*). With the coxa in mid-range and the basal–ischial–meral unit in a normal walking position the long axis of the leg lies in the transverse plane and the merus runs at approximately 40° to the frontal plane.

### (iv) *Carpus, propus and dactylus*

The carpus is shorter than the merus and its cross-section more circular. Its two articulations with the merus lie in the frontal plane when the animal is in its walking posture with the leg in mid-range (figure 1*c*) so that its movement is then in the transverse plane. The range of movement possible at this joint is extremely large since it can move from a dorsal position a

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few degrees superior to the axis of the ischium-merus to a fully flexed ventral position limited only by its contact with the merus, a total range of 160° (figure 5*b*). In the common postural position the angle between merus and carpus is approximately 110° (figure 1*c*).

The propus is almost as long as the merus and has a similarly oval section. In the transverse plane of the leg the hinge between carpus and propus is at 90° to the mero-carpal hinge so that when the animal is in its walking posture with the leg in mid-range angular movement occurs in the frontal plane. With the leg in this position the propus can move from a position a few degrees posterior to the leg axis anteriorly through 80° (figure 5*a*).

The dactylus is a shorter, arrow-shaped segment connected with the propus by means of an anterior and a posterior articulation which allow it to move from a dorsal position in line with the leg axis ventrally through 65° (figure 5*b*). With the leg in the normal walking position the dactylus is held at an angle of approximately 145° to the propus.

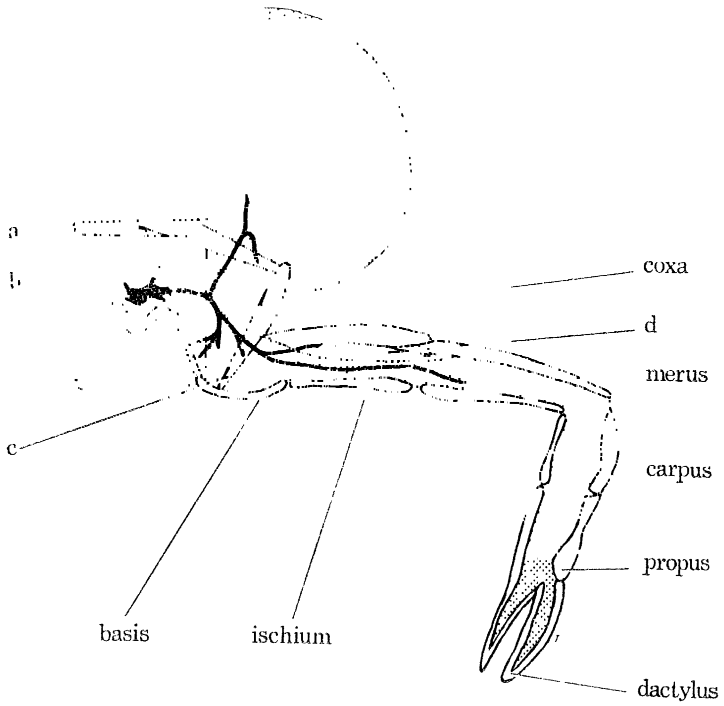

FIGURE 6. Diagrammatic representation of a pereiopod showing the types of muscles responsible for its movement. a, Extrinsic coxal muscles. Muscles which originate in the thorax and move the coxa. b, Extrinsic basal muscles. Muscles which originate in the thorax and move the basis. c, Intrinsic basal muscles. Muscles which originate in the coxa and move the basis. d, Intrinsic muscles in other segments. Muscles which originate in more peripheral segments and move the next most distal segment.

### (*d*) *Internal anatomy of the leg*

The general arrangement of the leg muscles can be seen in figure 6. The coxa is moved by extrinsic muscles with origins in the thorax. The basis is moved both by extrinsic muscles with origins in the thorax and by intrinsic muscles with origins on the coxa. All the other joints of the leg are moved by intrinsic muscles which have their origins in the segment proximal, and their insertions on to apodemes in the segment distal to the joint that they move (figure 6 shows one example, the rest of the intrinsic muscles are not shown). Although there is some separation of muscle bundles at the origins of some of the leg muscles, bundles which insert together to

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produce the same joint movement were treated as single muscles. Simultaneous myogram recordings from the region of different bundles supported this treatment and suggested that separate labelling was not warranted. Detailed analysis of the neuromuscular innervation may indicate that some further functional separation is necessary. Only the muscles involved in producing the specific stepping movements studied here are described.

### (i) *Coxa*

The coxa is moved by two protractors and two retractors. The two retractors are usually referred to as the posterior and anterior retractor muscles because of the relative position of their origins.

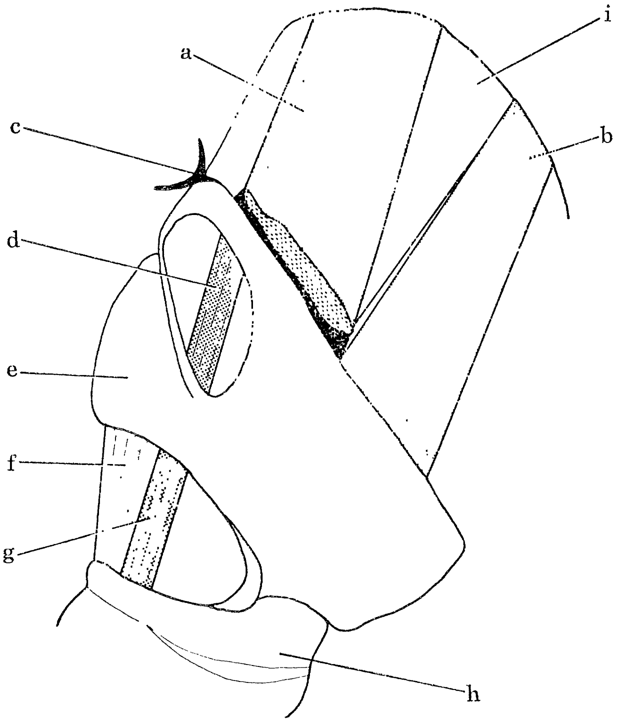

Figure 7. Lateral and slightly posterior view of the 3rd pereiopod on the left side of the animal. The arthrobranch and the articulating membranes between body and coxopodite have been removed. a, Posterior coxal retractor m. b, Anterior basal depressor m. c, Lateral hinge of coxopodite. d, Anterior basal elevator m (medial head). e, Coxopodite. f, Anterior coxal elevator m (lateral head). g, Anterior basal elevator m (medial head). h, Basipodite. i, Anterior coxal retractor m.

The posterior-coxal retractor muscle arises mostly from the interior surface of the lateral body wall just posterior to the opening for the pleurobranch. Its fibres run ventrally towards the coxa (figure 7) so that its medial surface forms part of the lateral limits of the thoracic cavity immediately superior to the leg it moves. A smaller number of the deeper, most posterior fibres arise from the lateral part of the anterior face of the endophragmal arch posterior to the leg. These fibres are posterior and medial to, but continuous with, those from the main origin. The muscle narrows slightly as it leaves the thoracic cavity and its fibres converge towards their insertion onto an apodeme along the extreme superior edge of the postero-lateral border of the coxa. As the muscle passes from the thorax to the leg it is the most superficial of the muscles beneath the posterior articulating membrane.

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The anterior coxal retractor arises from the posterior side of the anterior endophragmal arch and from the membrane connecting the arch with posterior arch and the sternal skeleton. The muscle becomes straplike as it runs from the thorax into the leg cavity, where it lies against the anterior surface of the posterior retractor (figure 7). It inserts along the same section of the coxal rim as the posterior retractor (figure 7). Since the two muscles insert together on to the coxa and the thoraco-coxal joint is a simple hinge they have similar actions. The slight difference in the position of their origins and the large angle of movement at the joint suggest that they may develop their maximum force over different sections of the coxal range. As suggested by Manton (1968), the difference in length may mean that one is more involved with high velocity length changes whereas the other is important in developing and sustaining high force with slower movements.

The anterior or superficial coxal protractor has its origin on the anterior endophragmal arch immediately medial to the membrane connecting the anterior and posterior arches which separates it from the origin of the coxal retractor. Its fibres run ventrally and slightly medially to insert on to an apodeme on the antero-lateral rim of the coxa close to its lateral articulation. It is the most superficial of the muscles beneath the anterior articulating membrane.

The posterior or deep coxal protractor has its origin on the anterior face of the posterior endophragmal arch in its most medial and ventral section where it meets the sternum. The fibres run an anteriorly and ventrally directed course across the coxal diameter to their insertion with the anterior protractor onto the rim of the coxa (figure 7). As with the two heads of the retractor muscle, the disparate origins and lengths of these two protractor muscles may indicate some separation of roles in protraction.

### (ii) *Basis*

The basis is moved by two depressors and two elevators. One muscle producing each movement is extrinsic, the other intrinsic.

The intrinsic posterior basal depressor originates from the interior surface of the coxa posteriorly and medially. The fibres converge as they run ventrally to insert on a small apodeme arising from the medial rim of the basis anterior to its posterior articulation with the coxa (figure 8). The anterior basal depressor muscle, an extrinsic muscle, originates in two heads anteriorly along an endophragmal spur from the sternum immediately anterior to the medial hinge of the coxa, and posteriorly from the medial edge of the posterior endophragmal arch. The fibres run ventrally to a long, thin apodeme which inserts on to the medial rim of the basis just anterior to the insertion of the posterior depressor (figure 8). Some of the more anterior fibres insert into a small apodeme immediately anterior to the main insertion. Although this muscle crosses two joints, its origin and insertions either side of the medial coxal articulation make it unlikely that it could exert significant torque on the coxa.

The anterior basal elevator, an intrinsic muscle, originates on the inner surface of the lateral wall of the coxa. Its fibres converge anteriorly and ventrally to insert onto the lateral rim of the basis immediately lateral to the anterior coxo-basal articulation (figure 9).

The posterior basal elevator originates on the posterior endophragmal arch just medial to the origin of the posterior coxal retractor muscle. The fibres run ventrally and slightly anteriorly to insert onto a long thin apodeme which attaches to the most lateral part of the basal rim. The origin and attachment of the muscle lie just slightly to either side of the transverse plane through the coxal hinge so it may possibly exert some torque about that joint as well. The

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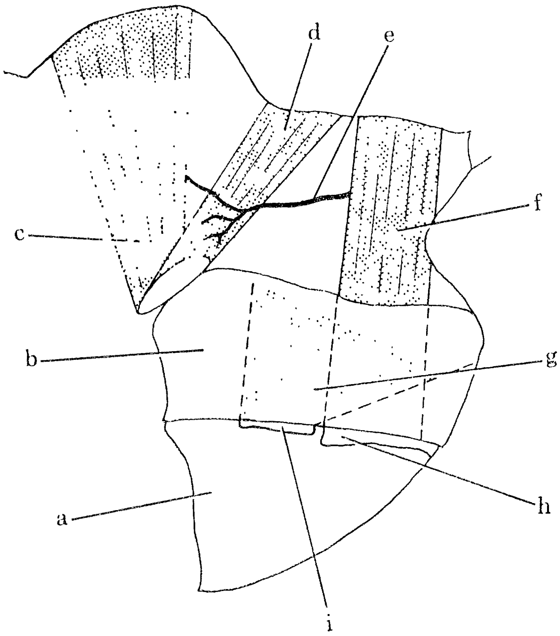

Figure 8. Posterior view of left 3rd pereiopod showing relation of posterior coxal muscles and posterior basal muscles. a, Basipodite. b, Coxopodite. c, Anterior coxal retractor m. d, Posterior coxal retractor m. e, Nerve to retractor muscles. f, Anterior basal depressor m. g, Posterior basal depressor m. h, Apodeme. i, Apodeme.

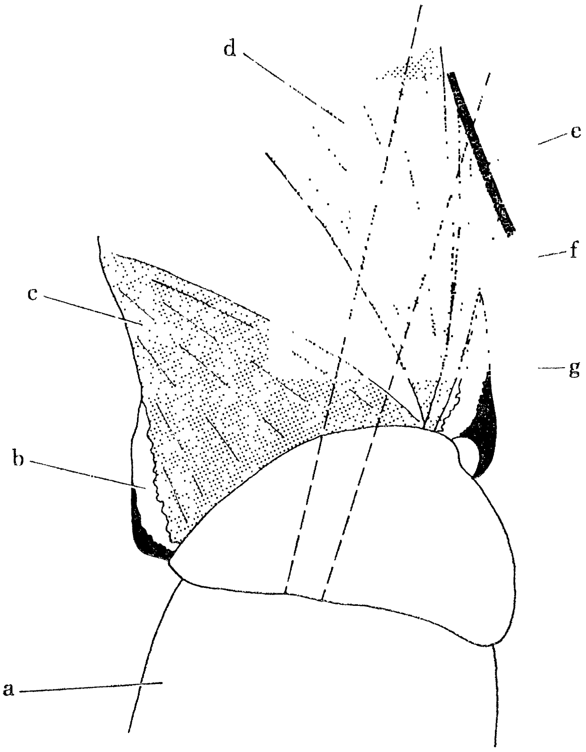

Figure 9. Antero-lateral view of the 3rd left coxopodite and basipodite with the anterior wall of the coxa removed. a, Ischiopodite. b, Remainder of the coxopodite. c, Anterior basal elevator m. d, Posterior basal elevator m. e, Sternum. f, Posterior basal elevator m. g, Position of the anterior basal depressor m (dashed lines).

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origin and insertion of the muscle lie almost in the same plane with the fulcrum in this case so that the muscle has an extremely poor mechanical advantage at that joint and it is only with the coxa in extreme protraction that it would be likely to exert any weak protracting effect.

### (iii) *Carpus*

The meropodite–carpopodite joint is moved by two antagonistic muscles but the merus also contains a small accessory flexor muscle and its accompanying receptors (Evoy & Cohen 1969).

The flexor of the carpus originates on the proximal two-thirds of the inner surface of the posterior wall of the merus. The more dorsal fibres converge ventro-laterally into the apodeme while the ventral fibres run dorso-laterally. The apodeme itself runs laterally and slightly dorsally to attach to the extreme dorso-medial end of the carpus (figure 10).

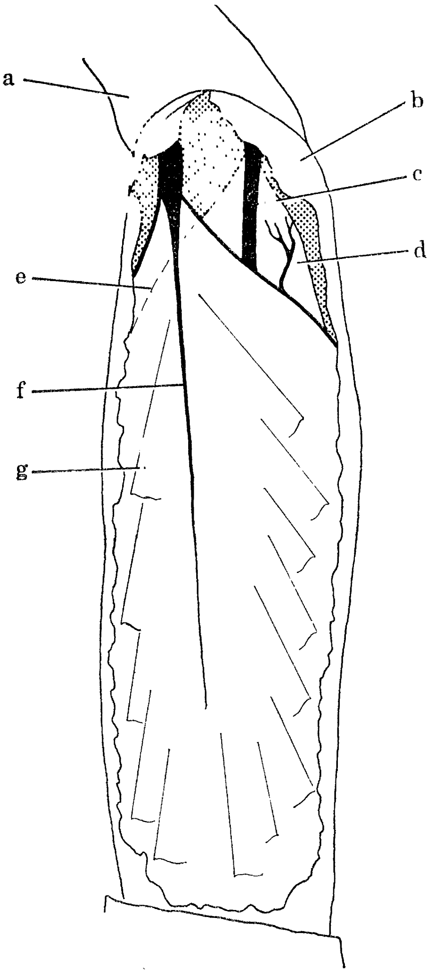

Figure 10. Posterior view of merus of left 3rd pereiopod. Posterior wall has been removed and the insertions of the flexor muscle fibres, which attach to it, cut. a, Carpopodite. b, Meropodite. c, Extensor apodeme. d, Extensor m. e, Position of the border of the extensor m (dashed line). f, Flexor apodeme. g, Flexor m.

### (iv) *Innervation*

The pedal nerve, which innervates the muscles of the leg, leaves the thoracic ganglion and takes a ventral and posterior course out of the thorax so that it passes through the anterior part

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of the endo-skeletal cavity above the coxa. It passes posterior to the anterior coxal protractor and a small branch runs to that muscle.

As the pedal nerve enters the coxa it divides into two branches. The more dorsal of the two passes posteriorly between the anterior basal depressor and the posterior coxal retractor to innervate the posterior surface of the retractor muscle (figure 8). The remainder of the nerve takes an axial course through the coxa and basis. A smaller branch from the axial nerve runs with the dorsal nerve to innervate the anterior basal depressor.

As the axial nerve traverses the coxa it lies lateral and anterior to the main blood vessel. The nerve passes anterior to the anterior basal depressor and gives off small branches to the rest of the muscles in the coxa and basis. As it enters the ischium it divides into three branches. An anterior branch runs along beneath the anterior or extensor surface of the leg and innervates the extensor muscle. A posterior branch runs beneath the posterior or flexor surface and innervates the flexor muscle. The third branch runs axially between the two muscles to innervate segments further out in the leg (figures 6 and 10).

## 4. Unilateral stepping sequences

It can be seen from the surveys of literature on walking in arthropods that one of the important measurements for comparison, for modelling and for a general understanding of locomotion is the stepping sequence which the animal uses and the frequency of occurrence of different sequences.

The simplest and most widely used method for recording stepping sequences has been that of choosing a point in the stepping cycle and recording the sequential occurrence of that point in successive legs. Theoretically it would be possible to do this for all the legs. If, as is the practice, each permutation is considered circular and expressed in order behind the same leg each time, there are seven! permutations of eight legs. For animals with six legs or more, consideration of stepping patterns produced by all the legs has been limited to comparatively short stepping sequences. Where longer sequences have been considered the analysis has been simplified by considering each side separately and obtaining the relationship between the two sides in other ways (Jacobi-Kleeman 1953; Parrack 1964; Wilson 1967). In these analyses a gait was defined for one side as any pattern arising from the repetitive or cyclic use of legs in which each leg is used once per cycle. The legs on the animal's right side were designated A, B C and D from anterior to posterior and a, b, c and d on the left side. The gaits were classified according to the order of stepping, the order always being expressed with the last leg stepping first. This treatment permitted easy recognition and classification of the gaits on one side as follows:

| gait number | order |
|---|---|
| 1 | DABC |
| 2 | DCAB |
| 3 | DACB |
| 4 | DBAC |
| 5 | DBCA |
| 6 | DCBA |

Such a treatment is a useful simplification but assumes *a priori* a basic cycle of four steps.

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In the present study this assumption was not made. The order in which legs were placed on the substrate to begin the power stroke was recorded in continuous sequences which were up to 100 or more steps on the treadmill and 7–20 steps in the large tank. The resulting sequences were considered two legs at a time and the number of occurrences of any given leg being followed by any other given leg scored. Thus, the sequence

DBCADB

would score

| | | | |
|---|---|---|---|
| B | follows | D | 2 |
| C | follows | B | 1 |
| A | follows | C | 1 |
| D | follows | A | 1 |

After a complete sequence (or set of sequences) from a single animal had been scored in this way the probabilities of each leg following each other leg were calculated. Table 2 shows an example of this type of probability calculation which uses 306 sequential steps recorded from the right side of an animal walking forwards on the treadmill with a third pereiopod mean step period of 1.56 s (s.d. 0.20). The results for each sequence analysed were summarized as shown in figure 11. The probability of any sequence can be readily calculated from this type of summary diagram and a dominant gait is apparent.

Table 2. Probability that a given leg will follow any other leg

| | following leg | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | A | | B | | C | | D | | |
| leading leg | score | *P* | score | *P* | score | *P* | score | *P* | total |
| A | 0 | 0 | 6 | 0.080 | 13 | 0.173 | 56 | 0.746 | 75 |
| B | 11 | 0.134 | 0 | 0 | 54 | 0.658 | 17 | 0.207 | 82 |
| C | 52 | 0.684 | 20 | 0.263 | 0 | 0 | 4 | 0.052 | 76 |
| D | 11 | 0.144 | 56 | 0.736 | 9 | 0.118 | 0 | 0 | 76 |

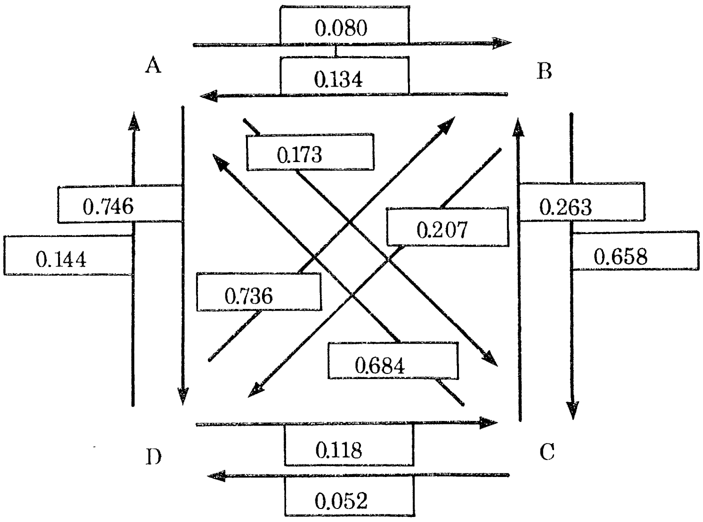

Figure 11. An example of the tabulation of the probability that any given leg will follow any other given leg. Stepping sequence from an animal walking on the treadmill. Mean period of the third pereiopod: $T = 1.56$ s; s.d. $= 0.20$. Number of steps 306. A–D are the pereiopods 1–4 respectively.

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Stepping sequences were taken from six different animals. Probability summaries were constructed from samples of stepping from both the left and right sides of animals moving freely in the holding tank or on the treadmill with a 30 % reduction in mean step period. In all situations the predominant gait on both sides was 5 and the relative frequency of occurrence of the six gaits similar to those represented in figure 11.

TABLE 3. EXAMPLES OF STEPPING SEQUENCES

| (*a*) on treadmill | | (*b*) free in tank | | (*c*) on treadmill | |
|---|---|---|---|---|---|
| right side | gaits | left side | gaits and transitions | right side | gaits and transitions |
| A | 5 | b | 5 | D | 5 |
| D | 5 | c | T (a 35) | B | 5 |
| B | 5 | a | T (a 35) | C | 5 |
| C | T | d | 3 | A | 5 |
| A | 6 | a | 3 | D | 5 |
| D | 6 | c | T (b 35) | B | 5 |
| C | T | b | T (b 35) | C | T (C 56) |
| B | 4 | d | 5 | A | 6 |
| A | 4 | b | 5 | D | ***T (D 36) |
| C | T | c | 5 | C | T (C 23) |
| D | 5 | a | 5 | B | 2 |
| B | 5 | d | 5 | D | 2 |
| C | 5 | b | | C | T (C 12) |
| A | 5 | c | | A | T (A 15) |
| D | 5 | a | | B | 5 |
| B | 5 | | | C | 5 |
| C | 5 | d | 5 | A | 5 |
| A | 5 | b | 5 | D | 5 |
| D | 5 | c | T (a 35) | B | 5 |
| B | 5 | a | T (a 35) | C | 5 |
| C | 5 | d | 3 | A | 5 |
| A | 5 | a | 3 | D | 5 |
| D | 5 | c | **T (b 35) | B | 5 |
| B | 5 | b | T (b 35) | C | T (C 56) |
| C | 5 | d | 5 | A | 6 |
| A | 5 | b | | D | 6 |
| D | 5 | c | | C | 6 |
| B | 5 | a | | B | 6 |
| C | T | | | A | T (A 26) |
| A | 6 | d | 5 | D | 2 |
| D | 6 | b | 5 | C | 2 |
| C | 6 | c | 5 | A | T (A 23) |
| B | T | a | 5 | B | 3 |
| A | 5 | d | 5 | D | 3 |
| D | 5 | b | 5 | A | 3 |
| B | 5 | c | *T (c 56) | C | 3 |
| C | 5 | a | 6 | B | T (B 35) |
| A | 5 | d | 6 | D | 5 |
| D | 5 | c | T (c 46) | B | 5 |
| B | | b | 4 | C | 5 |
| C | | a | 4 | A | 5 |
| A | | c | T (c 45) | D | 5 |
| | | d | 5 | B | 5 |
| | | b | 5 | C | 5 |
| | | c | | A | |
| | | a | | D | |
| | | d | | B | |

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The high probability of leg D following leg A suggested that perhaps the cyclic stepping pattern might show a tendency to start with a particular leg. The four permutations of the cycle are DBCA, ADBC, CADB and BCAD. The probabilities of each of these permutations was calculated for each of the stepping samples and the permutations ranked in order of probability. No consistent trend was found suggesting that there is an equal probability of the cycle starting with any leg.

The probability summaries indicated that deviations from the dominant gait do occur and it is of interest to determine the ways in which these deviations occur.

The method for doing this was to consider the samples in terms of the running gait by classifying all sequential sets of four steps. Sequences of four steps which had no repetition by any leg were labelled according to the six unilateral gaits and those which did not fit into the classification were marked T (table 3). When lobsters were walking forwards in a straight line all non-gait sequences observed were of the type in which one leg stepped twice (e.g. DACA, DABD) and higher orders of repetition were not observed (e.g. DADA). Sequences in which one leg steps twice can be classified in terms of the leg which steps twice, the identity of the other two legs which step and the order in which the four steps occur. These three parameters were combined into an easily derived notation in the following way.

All sequences with two steps by one leg contain three of the elements of two of the six gaits. Thus, DAAC contains three of the elements of D(B)AC which is gait 4 and three of the elements of DA(B)C which is gait 1. This sequence is therefore most closely related to gaits 1 and 4. Determining the two most closely related gaits defines the ordering of the elements in the sequence but does not distinguish between the two sequences which could produce this result, i.e. DAAC or DBBC. This distinction was made by including the identity of the leg which stepped twice. The sequence DAAC would therefore be rendered as

T(A14)

and the sequence DBBC as T(B14)

Examples of the gait and transition (T) sequences which result when stepping sequences are analysed in this way can be seen in table 3 (*b* and *c*).

It can be seen from the examples that as long as the animal maintains one of the true gaits no T sequences are observed. As soon as any deviation from a single true gait occurs at least one T sequence is observed. T sequences which contain no elements of the immediately preceding and following gaits may be constructed theoretically (table 4*a*) but while they may occur when an animal is clambering over obstacles they were rare in level walking in a straight line (< 1 % of T sequences counted). Consecutive pairs of T sequences in which the first contained elements of both the preceding gait and a new gait, and the second elements of the new gait and the following gait were observed in animals walking in a straight line (table 3*c* ***) but were uncommon (< 3 % of T sequences counted). Complex successions of T sequences which are unrelated to the preceding and following gaits would be generated if one or more legs stepped a disproportionate number of times in comparison with the remaining legs. The rarity of complexes of T sequences, together with the finding that the legs step approximately the same number of times during long sequences, indicates that stepping on either side of the animals tends to be evenly distributed in time among the four legs.

The most common change from one gait to another (approximately 60 % of all gait changes) produced only a single intervening T sequence (see table 3*b* *). Inspection of stepping sequences

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in which gait changes produce only one T sequence shows that this only occurs when two legs which step consecutively in the preceding true gait reverse their order in the following true gait. If the reversal is changed back the next time the legs step the common type of sequence shown in table 4*c* results. If, instead, the order continues to be reversed throughout the next cycle or two the type of sequence shown in table 4*d* results. If a pair reversal by one pair is followed by other pair reversals, such that the reversals are mutually exclusive, a pattern running through several different gaits separated by single T sequences results (table 4*e*).

The other commonly seen change from one gait to another (approximately 35 % of all gait changes) was a pair of T sequences both of which contained elements of the preceding and the following true gaits (table 4*f*). Inspection of stepping sequences which produce this result shows that it occurs when one leg moves two positions in the following cycle relative to its position in the preceding cycle(table 3*b***).

TABLE 4. ILLUSTRATIONS OF SOME TYPES OF STEPPING SEQUENCES AND THE GAITS AND ITERATIONS WHICH RESULT

| | | |
|---|---|---|
| (*a*) | c | 5 |
| | a | 5 |
| | d | T (c 36) |
| | b | T (c 45) |
| | c | T (c 45) |
| | c | 2 |
| | a | |
| | b | |
| | d | |

| | | |
|---|---|---|
| (*b*) | d | 5 |
| | b | T (a 15) |
| | c | TT (ac) |
| | a | T (a 36) |
| | a | 3 |
| | c | 3 |
| | b | |
| | d | |
| | a | |

| | | |
|---|---|---|
| (*c*) | D | 5 |
| | B | 5 |
| | C | T (C 56) |
| | A | 6 |
| | D | 6 |
| | C | 6 |
| | B | T (B 56) |
| | A | 5 |
| | D | 5 |
| | B | |
| | C | |
| | A | |

| | | |
|---|---|---|
| (*d*) | D | 5 |
| | B | 5 |
| | C | T (C 56) |
| | A | 6 |
| | D | 6 |
| | C | 6 |
| | B | 6 |
| | A | 6 |
| | D | 6 |
| | C | 6 |
| | B | T (B 56) |
| | A | 5 |
| | D | 5 |
| | B | |
| | C | |
| | A | |

| | | |
|---|---|---|
| (*e*) | C | 5 |
| | D | 5 |
| | B | T (B 25) |
| | C | 2 |
| | A | 2 |
| | B | T (B 26) |
| | D | 6 |
| | C | 5 (C 46) |
| | B | 4 |
| | A | 4 |
| | C | 5 (C 45) |
| | D | 5 |
| | B | 5 |
| | C | |
| | A | |
| | D | |

| | | |
|---|---|---|
| (*f*) | b | 5 |
| | c | T (a 35) |
| | a | T (a 35) |
| | d | 3 |
| | a | 3 |
| | c | T (b 35) |
| | b | T (b 35) |
| | d | 5 |
| | b | |
| | c | |
| | a | |

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This method of analysis cannot be used to draw conclusions concerning the functional relevance of gait changes. Its value is in indicating that changes from any current order are usually made by the simplest types of changes within that order rather than by complete re-ordering.

There are three important findings from the analysis of unilateral stepping sequences. The first of these is that the relative probability of any given sequence was similar on both sides of an animal, in two different recording situations and at two widely separated stepping frequencies. The second is that there is a dominant gait for the legs on a side. The third is that changes on a side are usually smooth since they are produced by the simplest types of re-ordering changes.

The findings are important for an understanding of the system but further information concerning the ratio of the duration of protraction to that of retraction ($T_p/T_r$ ratio) and the phase relations are also needed.

## 5. INTER-LEG RELATIONS

A more quantitative understanding of the coordination between legs was obtained by considering the phase relations between pairs of legs. Frame-by-frame video-tape records were used to measure the latencies between selected points in each cycle. The phase was calculated by taking the selected point in one leg (e.g. start of the power stroke) and measuring the latency to its occurrence in a second leg. This duration was then divided by the time interval between its occurrence in the first leg and its re-occurrence, i.e. the concurrent period of the first leg. This means that all references to phase relations and accompanying illustrations are concerned with proportions of step cycle rather than absolute units of time. Two points in the cycle were considered in this way: the start of power stroke (where the foot makes contact with the substrate), and the start of the return stroke (where the foot is lifted off the substrate).

The first series of phase measurements described below show the phase relations of the start of the power stroke.

The gait analysis showed that the dominant gait occurred on both sides of the animal so that it was important to obtain information about the phase relations between the two sides. Frequency histograms of the phase relations between the two legs of each segment of an animal walking freely in the large tank are shown in figure 12. Similar samples were taken from three different animals walking freely in the large tank or walking on the treadmill. In all cases the frequency distributions had modal classes close to 0.5 and the shape was similar to those shown. The distributions showed that while there was a tendency for legs to alternate almost all phase relations were observed.

Frequency histograms of the phase relations between ipsilateral pairs of legs from the left side of an animal walking freely in the large tank are shown in figure 13 and similar samples were made from the right sides of animals walking in the large tank. $\chi^2$-comparisons between samples from the left and right sides of animals with similar mean step durations (as measured at the third pereiopod) did not indicate significant differences. Similar samples were taken from three different animals walking freely in the large tank. The modal classes were the same or one class removed in all cases and all distributions were similar in shape to those shown in figure 13 indicating that while all ipsilateral pairs of legs have a tendency to preferred phase relations almost all phase relations were observed.

The sequential stepping analysis did not reveal any changes in the relative freqency of

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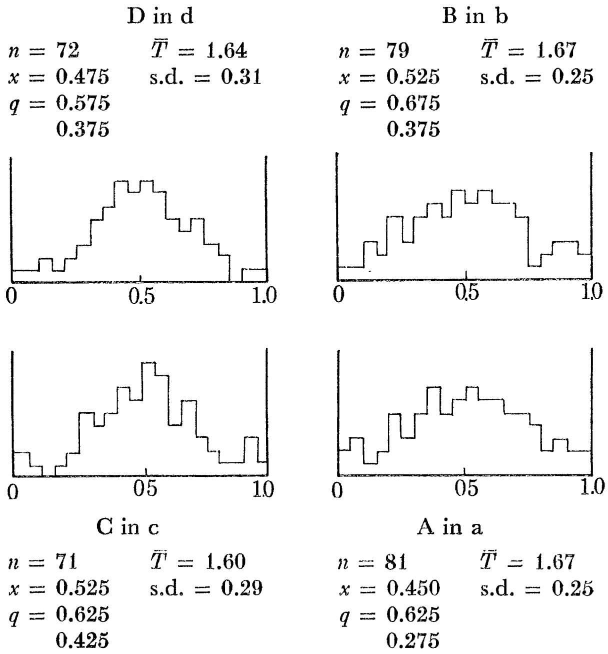

FIGURE 12. Example of the phase relation between the left and right pereiopods in each segment. The reference point for the relations was the start of the powerstroke. *T* is the step duration, *x* the modal class, *q* the quartile classes 25% above and below the modal class. Ordinate, 10 steps.

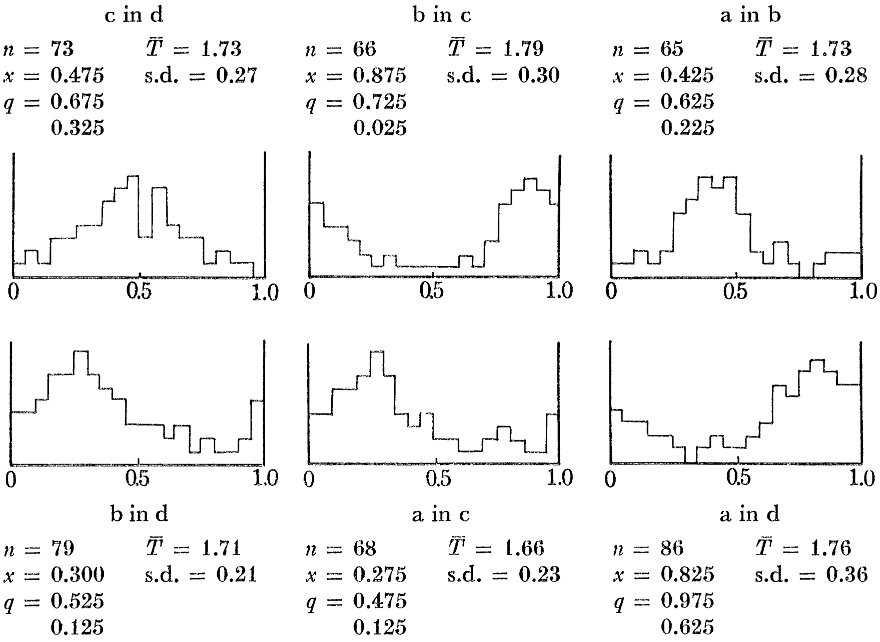

FIGURE 13. Example of the phase relations between pairs of ipsilateral pereiopods from the left side of an animal walking freely in the large tank. The reference point for the relations was the start of the return stroke. *T* is the step duration, *x* the modal class, *q* the quartile classes 25% above and below the modal class, Ordinate, 10 steps.

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occurrence of the six gaits for animals on and off the treadmill. As a further control for possible changes caused by walking on the treadmill, frequency histograms of the ipsilateral phase relations from animals walking on the treatmill were compared with those from animals walking in the large tank. The samples used in the comparisons were matched for stepping frequency. Samples from three different animals did not reveal significant differences in the frequency distribution as measured with a $\chi^2$-test.

Because of the variation in step duration, and of the animals' tendency to maintain step durations near the extremes of the range for relatively short periods, it was possible to obtain only short continuous sequences with significantly longer and shorter step durations for comparison with sequences from the middle of the range. The step durations of samples with 20–30 steps representing mean step durations of 15–20 % greater than and less than the mean value of the larger, non-selected samples (approximately 1.73 s) were compared for stepping frequency using a $t$-test. All the small samples selected in this way were shown to be significantly different in mean step duration and their phase frequency-histograms were then compared with those for the large, non-selected samples by using a $\chi^2$-test with Yates correction for small samples. In none of the four animals examined was any significant difference found in the phase frequency-histograms with changes in step duration.

The treadmill situation did not appear to cause any changes in the parameters concerned with inter-leg coordination which have been covered by this study. There remained, however, the possibility that the animals were being visually influenced by the treadmill and might not be able to produce the normal coordination without this input.

Davis & Ayers (1972) have shown that a moving treadmill marked with transverse black bars can evoke walking movements from lobsters but that the movements are not maintained if the animal is mechanically isolated from the treadmill by an intervening sheet of glass. The inference is that visual input has some function in the locomotory behaviour of the lobster but is not capable of maintaining the behaviour without additional sensory input.

To test whether a visual stimulus (from the animal moving relative to the ground or from the treadmill moving relative to the animal) is necessary for normal coordination a comparison was made between animals with plastic caps over their eyestalks and sighted animals. When placed in the large tank capped animals tended to walk more slowly than normal animals and they stopped more frequently. This made it difficult to gather samples of data for an analysis of the phase relations but small frequency distributions from such samples did not differ significantly from those examined previously for sighted animals. Capped animals walked readily on the treadmill and the range of stepping frequencies appeared to be normal. Phase frequency-distributions of the ipsilateral phase relations from a capped animal were compared with those from sighted animals and no significant differences were detected.

These results, together with those of Davis & Ayers (1972) suggest that visual input alone is insufficient to maintain locomotion in the absence of mechanical input but mechanical input without visual input can sustain normal locomotion. The mechanical input in this case may well arise from vibrations produced by the treadmill but the nature of the necessary sensory input was not investigated further in this study.

The importance of these results for this study is that they indicate that visual input is not necessary for normal coordination. This is an important factor for consideration when assessing how closely results from animals on the treadmill approximate to the normal locomotory situation.

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Up to this point, consideration has been given only to the phase relations of the start of the power stroke. The relations of that point in the cycle appear to be the same when an animal walks on the treadmill or with different mean step durations. The overall stepping pattern would, however, be altered considerably if the phase relations of the start of the return stroke changed.

Ideally, the most information concerning the relations between the start of the power stroke and the start of the return stroke in two different legs would be obtained if the two points were analysed simultaneously in both legs. Practically, this was not possible because camera positions which showed both points in two legs did not allow accurate determination of phase. The phase relations between ipsilateral pairs of legs were therefore determined by using the start of the return stroke as the reference point. Phase histograms constructed by using this reference point on sequences taken in the same situations as those described for the start of the power stroke were not significantly different from those for the start of the power stroke in any of the experimental situations.

The finding that the phase relations of the end of the return stroke remain the same in a variety of situations is a consideration for assessing the relative normality of results obtained on the treadmill. With information on the $T_p/T_r$ ratio the results of the phase relations obtained by using the two different reference points could be combined to construct modal stepping patterns.

Some measurements of the $T_p/T_r$ ratio were made directly from the video-tapes used for the phase relation determinations but, as mentioned above, this method was not highly accurate. For inter-leg phase relations the camera was always alined so as to give the best picture of the two legs whose phase relations were being examined when they were at the reference point being considered. This alinement did not usually favour a good view of the other reference point. A much more accurate measurement of the movement of a single leg (and hence its $T_p/T_r$ ratio) was obtained with close-up video-film sequences which precluded simultaneous measurement of its phase relations with other legs. The less-accurate $T_p/T_r$ values obtained directly from the phase analysis tapes agree well with those movements of a single leg. A discussion of the overall stepping pattern and the normality of the treadmill samples will therefore be taken up after the movements of a single leg have been analysed.

The analysis of sequential stepping showed that the dominant gait occurs some 60–70 % of the time but gave no information concerning the temporal arrangement of the four steps. The phase histograms must also reflect the dominant gait sequence and, since the distributions were generally unimodal and symmetrical, a gait constructed by using the modal classes gives a central measure of the temporal parameters of the dominant gait (figure 14). The histograms also showed that there is considerable variation around the modal class but do not indicate how this might occur.

There are two extreme possibilities. One is that the legs vary in a completely random fashion about the mean phase position. The second, already described for some insects (Wendler 1966), is that the phase drift is continuously in one direction but with the oscillations in the two legs coupled in a way that favours phase relations which produce the dominant gait (i.e. when those relations obtain the drift is slowed). Figure 15 shows examples of sequential phase relations.

Each sample plotted in this way was examined for trends by scoring the relation between all sets of three sequential steps according to whether the trend was continuously up (up–up), continuously down (down–down), upwards but reversing (up–down) or downwards but

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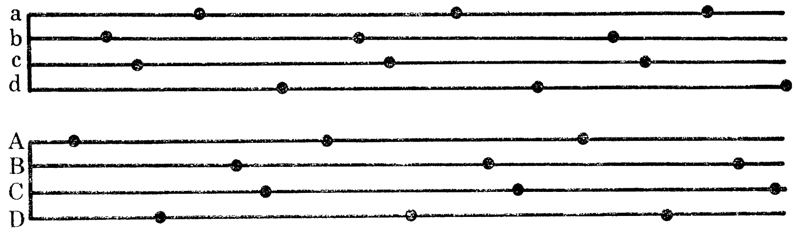

FIGURE 14. An example of a stepping sequence constructed by using the modal classes from a set of phase histograms such as those shown in figures 12 and 13.

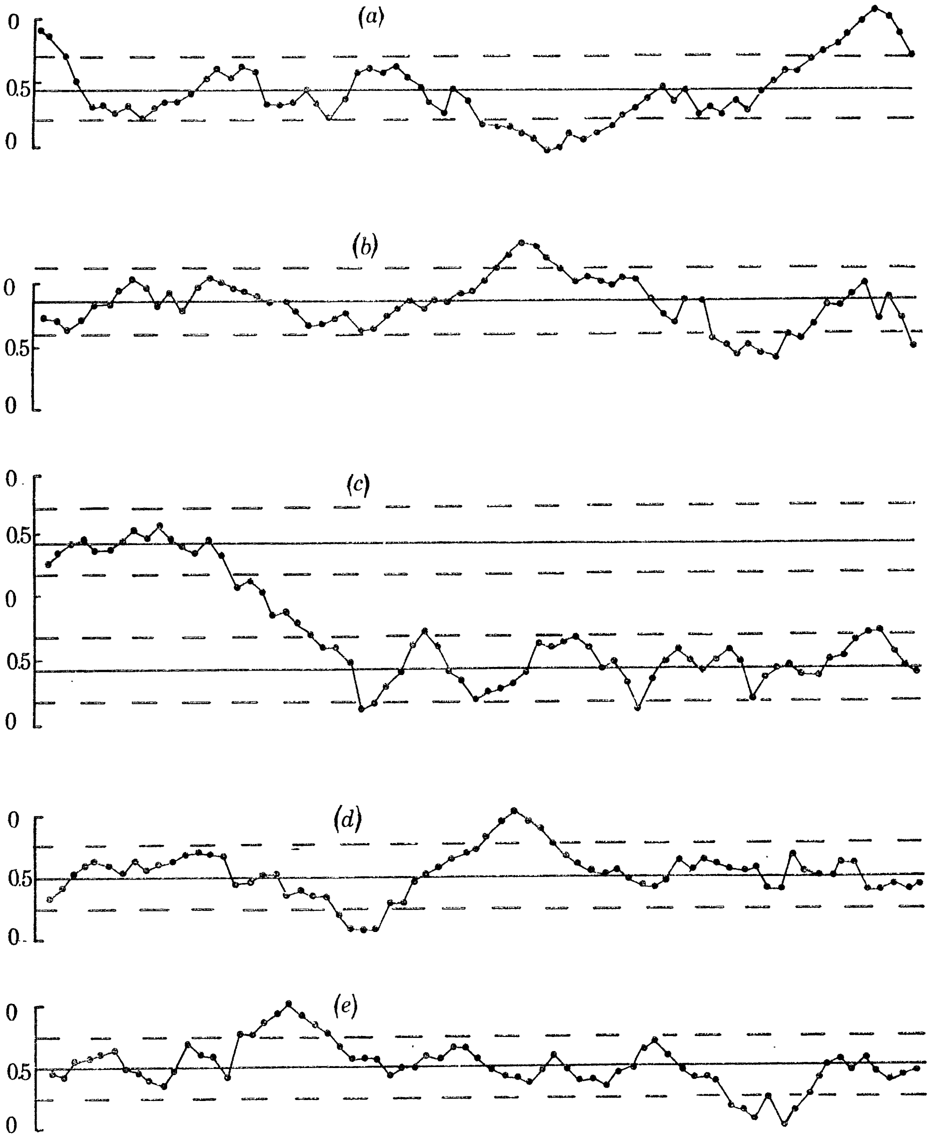

FIGURE 15. Examples of sequential phase relations between pairs of legs (phase reference point: start of power stroke). Ordinate shows phase relation. Continuous lines on abscissae show the position of the modal class (based on the larger histogram sample from which the example is drawn). Dashed lines on abscissae show limits of the population within 30–35 % of the mode (again based on the larger histogram sample from which the example is drawn). The dashed lines indicate the region in which the dominant gait may be formed with the least deviation from the mode. (*a*) B in D. Variation of the simpler type (see text). (*b*) B in C; variation of the simpler type. (*c*) A in D; example of 'gliding coordination' (see text). (*d*) C in c; variation of the simpler type. (*e*) D in d; variation of the simpler type.

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reversing (down–up). Table 5 shows the results of this type of analysis (together with the probability of each of the configurations) for four of the sequential plots in figure 15.

If the variation were completely random about the mean phase position the probabilities of each of the four configurations would be expected to be equal. It can be seen from table 5 that the probabilities of the down–down and up–up configurations are in all cases a little higher than those of the up–down and down–up configurations. This suggests that there is a tendency for short-term phase drifts in a rather slower oscillation about the mean phase position than would be produced by a completely random variation.

TABLE 5. EXAMPLES OF ANALYSIS OF TRENDS IN SEQUENTIAL PHASE PLOTS

| sequential plot (figure 15) | | up–up | up–down | down–down | down–up | total |
|---|---|---|---|---|---|---|
| *a* | score | 19 | 16 | 17 | 16 | 68 |
| | *p* | 0.279 | 0.235 | 0.250 | 0.235 | |
| *b* | score | 18 | 16 | 18 | 16 | 68 |
| | *p* | 0.264 | 0.235 | 0.264 | 0.235 | |
| *d* | score | 19 | 15 | 19 | 15 | 68 |
| | *p* | 0.279 | 0.220 | 0.279 | 0.220 | |
| *e* | score | 17 | 14 | 22 | 15 | 68 |
| | *p* | 0.250 | 0.205 | 0.323 | 0.220 | |

Reference to figure 15 shows that large drifts away from phase values which readily produce the dominant gait (see limits in figure 15) were usually of relatively short duration and were reversed by small increment corrections back towards the mean phase position. Correction back to the dominant gait region was sometimes made with the 'gliding coordination' described by Wendler but this was rare and not sustained (figure 15*c*).

The results of the sequential analysis indicate that the variation about the mean phase position is neither completely random nor of the gliding type. The results suggest that trends of phase progression are common but that these tend to be reversed short of phase reversal. The reversal of the short-term phase drifts occurs in such a way that the phase relations tend to be kept within the limits which readily produce the dominant gait. This may reflect a central tendency or a tendency imposed by mechanical requirements.

## 6. SINGLE LEG ANALYSIS

The third pereiopod was selected for detailed analysis because there appeared to be only limited movement at the mero-carpal joint during retraction of the leg. Because the third pereiopod rotates during retraction and because the leg sweeps through a relatively large angle during retraction it was not possible to obtain continuous measurements of the mero-carpal angle during a complete retraction. By alineing the video-camera for a particular point in the retraction it was possible to measure the mero-carpal angle at each point for a number of cycles and to obtain mean values for the angle. Figure 2*c* gave an example of a tracing of a retraction sequence obtained in that way. It can be seen that the method of measurement is probably accurate only within a range of about 5°. Table 6 shows examples of the mean mero-carpal angle during continuous stepping sequences measured at the start, middle and end of the retraction of the third pereiopod and measured from an animal walking on the tread-

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mill. The angle was also measured from animals walking freely in the large tank and the results were similar. The measurements indicated that, within the limits of the method, the mero-carpal angle of the third pereiopod is maintained relatively constant during protraction when the animal is progressing forwards in a straight line.

There are two important points which must be considered in making measurements of the mero-carpal angle. Whenever the animal shows any turning tendency or moves laterally while it moves forwards the mero-carpal angle changes and may change continuously throughout the retraction. In addition, the third pereiopod often loses traction and slips at the extreme end of retraction. This type of slip was seen both on the treadmill and in the large tank and when it occurs the mero-carpal angle undergoes a sudden, sharp extension as the leg elevates.

Table 6. Mean values for the meropodite–carpopodite angle

| point observed | number of steps in sequence | mean angle | s.d. |
|---|---|---|---|
| start of retraction | 20 | 110.8 | 3.6 |
| mid-retraction | 21 | 109.2 | 3.3 |
| end of retraction | 21 | 109.7 | 3.7 |

Problems similar to those encountered in measuring the angle of the mero-carpal joint were also found when measurements were made of the coxal and basal movements. The most accurate measurements were obtained by alineing the video-camera for one point in the cycle and measuring that point in a series of steps. Some measurements were made of the angles swept out during the movements but these were not as accurate because of the difficulty of measuring angles which were not in the plane of the camera throughout the cycle. Only a few relatively short continuous sequences were made of the angles swept out because sequences were usually broken up by steps or groups of steps which could not be measured accurately enough for inclusion.

Measurements were made from animals walking in the large tank and from animals walking on the treadmill where the sequential sequences were obtained.

### (*a*) *Coxa*

No movement was detected at the baso-ischial and ischio-meral joints during forwards walking in a straight line. The coxo-basal hinge permits only a few degrees of basal movement relative to the coxa in the frontal plane. This movement is limited to the extremes of the coxal range and occurs if the basis is elevated to an extreme position. Neither of these conditions obtain during forwards walking. This means that the angle that the baso-ischio-meral section makes with the body in the frontal plane depends essentially on the angle that the coxa makes with the body. Measurements were made of the extreme forward angle of the merus with the sagittal plane, the extreme backward angle of the merus with the same plane and the angle swept out. Figure 16 shows a sequence from an animal walking on the treadmill which shows simultaneous sequential measurements for these three parameters. Mean values for the two extreme angles and the angle swept out obtained from samples of stepping from animals walking freely in the large tank were compared with those from animals walking on the treadmill and walking on the treadmill with their eyes covered. No significant differences were found. Comparisons with the shorter sequences of faster and slower stepping using a *t*-test also revealed no significant differences. Similar results from two other animals confirmed that there is

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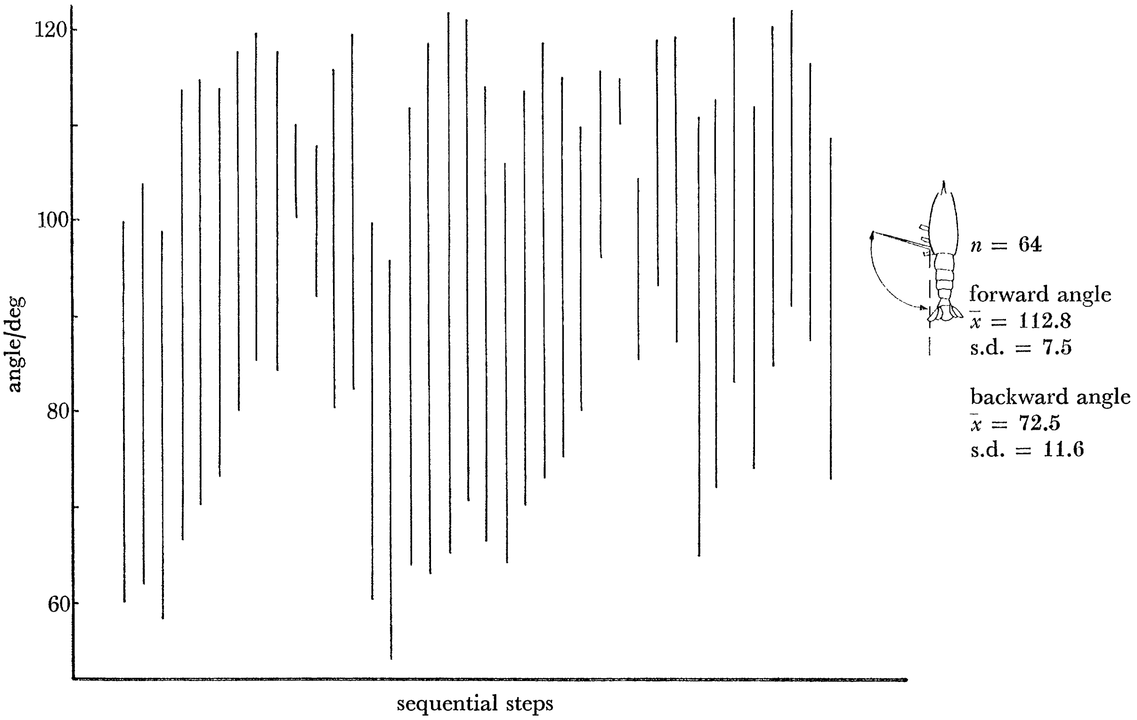

FIGURE 16. Angle swept out by the coxa of the 3rd pereiopod during a continuous sequence of stepping on the treadmill. Each line indicates the minimum backwards angle attained during the step and the maximum forward angle. Angles measured as indicated in the inset.

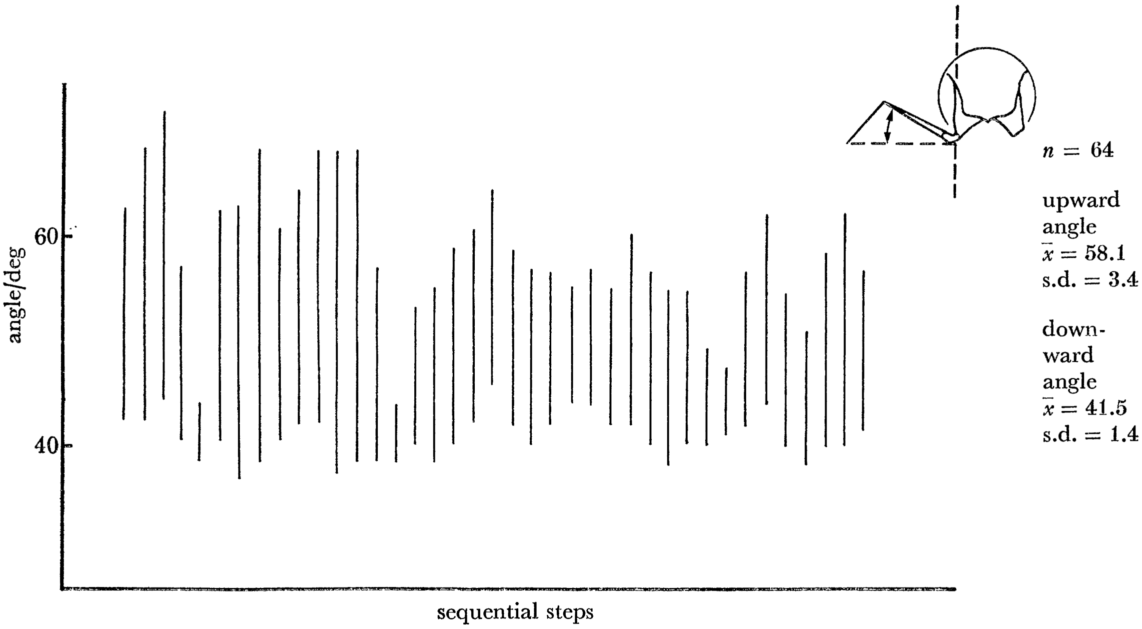

FIGURE 17. Angle swept out by basis of the 3rd pereiopod during a continuous sequence of stepping on the treadmill. Each line indicates the minimum downwards angle attained during the step and the maximum upwards angle. Angles measured as indicated in the inset.

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considerable variation not only in the angle swept out but also in the part of the available range in which the step occurs but also that the mean angles do not appear to change in the different experimental situations.

### (*b*) *Basis*

The movement at the other joint primarily involved in forwards walking was examined in the same way as the thoracico-coxal joint. The basal movement was measured by observing the angle that the ischio-merus made with the horizontal. The extreme upwards position, the extreme downwards position and the angle swept out were measured as for the coxal angles and figure 17 shows a continuous sequence from the treadmill. Comparisons of mean values for samples taken from animals in the different experimental situations were made with samples from free walking animals in the same way as for the coxa and no significant differences were found.

The relative lack of variation in the maximum downward angle is consistent with the finding that there is little movement at the mero-carpopodite joint during the power stroke.

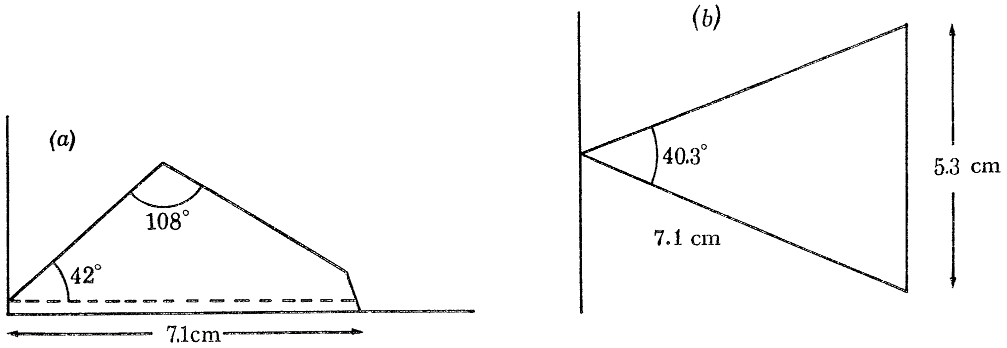

FIGURE 18. Calculation of mean effective leg length and mean leg span of the 3rd pereiopod using mean values for the length of the leg segments and mean angles between the segments during the power stroke. (*a*) Effective leg length. (*b*) Leg span.

### (*c*) *Whole leg movement*

Given the mean angles obtained for the merus in the transverse and frontal planes, together with the angle of the meropodite–carpopodite joint and the dimensions of the leg in walking posture, the span of the leg has a calculated value of 5.3 cm (figure 18). It is technically difficult to obtain accurate sequential measurements for the span with a filming technique but single, non-sequential samples from video-analysis were of the same order of magnitude.

The leg must decelerate, stop and reverse direction between the protraction and retraction sections of the cycle. The deceleration and subsequent acceleration at the end of the power stroke usually occurred over very few video frames (0.01–0.05 s) so that determining the division point was not usually difficult. The deceleration at the end of the return stroke was much more gradual and the leg often remained stationary for several frames before starting the power stroke acceleration. The start of the power stroke was also difficult to define since the leg often made contact with the ground moving only slowly and perhaps passively for several frames. Some slippage relative to the ground was also common during this initial contact period before the very obvious retraction acceleration started. Frames in the protraction–retraction interval where the leg was not clearly moving in either direction were counted separately as a pause.

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Figure 19 shows the total durations of a series of sequential steps of the third pereiopod from an animal walking on the treadmill. For consideration of the $T_p/T_r$ ratio in connexion with gross stepping movements the pause could be considered as part of the power stroke or part of the return stroke. If, during the pause, the leg is not making contact with the substrate then the pause correctly belongs in the 'off the substrate' fraction of the cycle, i.e. the return stroke. If, on the other hand, the leg is on the surface moving relative to the body then even if it is not propulsive at this time, in terms of the animal's progression it is part of the 'on the substrate' fraction of the cycle, i.e. the power stroke.

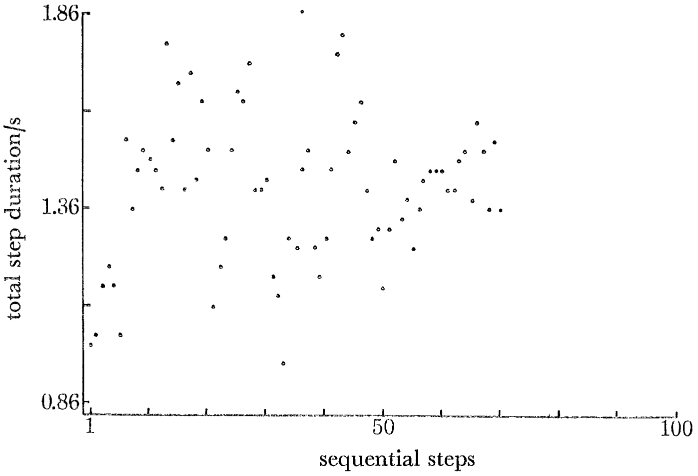

Figure 19. Total step duration of the 3rd pereiopod for 71 sequential steps. (Computer plotted graph.)

Observation suggested that most of the pause occurred with the leg on the surface or as contact was being made with the surface and for this reason the pause was tentatively included in the power stroke subject to further indications from observations on progression velocity and of myograms. This treatment of the pause and the rest of the retraction fraction of the cycle (figure 20) was somewhat supported by the finding that the pause tends to occupy a set proportion of the power stroke.

The power stroke (total 'on the substrate' duration) and return stroke durations for the sequence in figure 19 are shown to the same scale in figure 21 *b*, *c* and the manner in which they vary with cycle duration in figure 21 *a*, *d*.

In using the least squares regression lines of these two functions to calculate values for the $T_p/T_r$ ratio it is important to be aware of the limitations on accuracy imposed by the film-frame speed of 60/s. Having determined these limits it is necessary to consider whether changes close to or below the resolution of the measurements could be significant to the animals.

This can best be illustrated by taking an example of a cycle of 1.66 s duration. Such a cycle, which occupies 100 video-tape frames, might typically break down as follows

| fraction | frames |
|---|---|
| forwards movement | 40 |
| backwards movement | 57 |
| pause | 3 |

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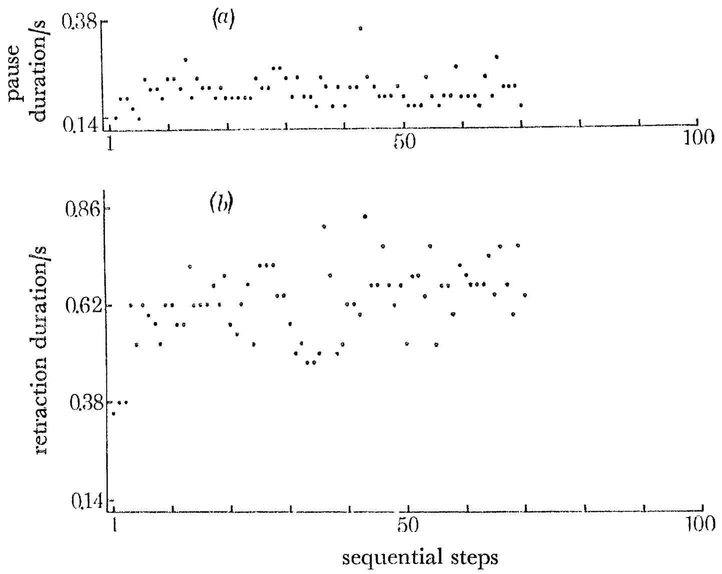

FIGURE 20. Same 71 sequential steps as illustrated in figure 19. (*a*) Duration of the pause interval of the 3rd pereiopod. (*b*) Duration of the 'on the substrate' fraction of the cycle of the 3rd pereiopod when the pause fraction is not included.

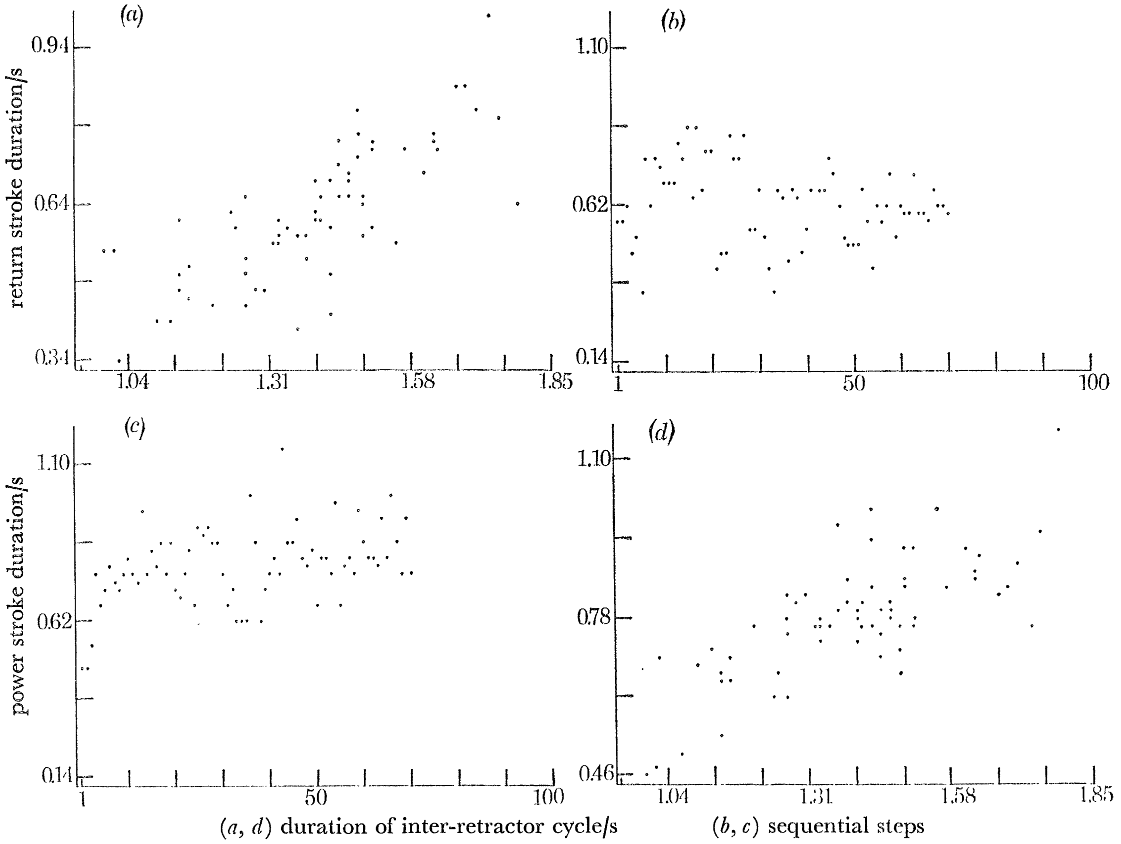

FIGURE 21. Same 71 sequential steps as illustrated in figure 19. (*a*) Relation between the return stroke duration and the duration of the whole cycle. (*b*) Duration of the return stroke interval of the 3rd pereiopod. (*c*) Duration of the power stroke (total 'on the substrate' fraction) interval of the 3rd pereiopod. (*d*) Relation between the power stroke duration and the duration of the whole cycle. ((*a*) $r = 0.78$, (*d*) $r = 0.73$.)

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or in terms of the power stroke and return stroke as

| | |
|---|---|
| protraction | 40 |
| retraction | 60 |

These values result in a $T_p/T_r$ ratio of 0.66. With a one-frame error in measurement the result would be

| | |
|---|---|
| protraction | 41 or 39 |
| retraction | 59 or 61 |

These values result in $T_p/T_r$ ratios of 0.69 and 0.63 respectively. The one frame error therefore produces a change of ± 4 % in the $T_p/T_r$ value for a change of ± 2.5 % in the return stroke duration and a change of ± 1 % in the percentage of the cycle occupied by the power stroke and return stroke. If these same values are used to calculate values for stepping parameters (with a value of 5.3 cm for the span) the results are as shown in table 7. It can be seen that the effect on the progression velocity for this magnitude of $T_p/T_r$ change is only ± 1 %.

Table 7. Changes in stepping parameters which result from small changes in the $T_p/T_r$ value

| step duration<br>s | step frequency<br>$s^{-1}$ | $\frac{T_p}{T_r}$ | stride<br>cm | progression velocity<br>$cm\ s^{-1}$ |
|---|---|---|---|---|
| 1.66 | 0.60 | 0.63 | 8.63 | 5.17 |
| 1.66 | 0.60 | 0.66 | 8.79 | 5.27 |
| 1.66 | 0.60 | 0.69 | 8.95 | 5.37 |

The distinction between the end of the power stroke and the start of the return stroke was usually clear between two frames but distinguishing between 'on' and 'off' is always liable to introduce a one frame error depending on where the frame division falls. The inclusion of the pause category was a reflection of the difficulty found in dealing with the return stroke/power stroke transition. It represents the possibility of a two frame error in the protraction/retraction measurement. If the errors add, then, in the example above there would be a change of ± 0.08 in the $T_p/T_r$ ratio.

It is clear that some of the pause category can be accounted for in terms of experimental error but that the duration of this part of the cycle is sufficiently large to indicate the possibility that it may have a real rather than just an experimental basis. This matter will be dealt with further in conjunction with evidence from myograms.

The regression lines from plots of power stroke against cycle and return stroke against cycle (e.g. figures 21*a*, *d*) were used to calculate $T_p/T_r$ at different stepping frequencies. The ratio showed some variation with stepping frequency but the direction of the change was not consistent. The mean values for $T_p/T_r$ at three different stepping frequencies (representing a 25 % and a 50 % change in cycle duration) determined for five samples of sequential stepping from one animal are shown in table 8.

It can be seen that the variation in $T_p/T_r$ values at each point is consistent with the limits of experimental resolution discussed above. It should be noted that the amount of change this variation produces in the progression velocity result is quite small ($< 10$ %) and thus completely dominated by the change produced by changes in stepping frequency. The results indicate that if there is a consistent change in $T_p/T_r$ with stepping frequency it is below the resolving

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power of the recording method used but that it is not, in any case, a significant factor in changing the progression velocity.

If this conclusion is correct it should be possible to make simple predictions concerning the progression velocity. With the previous findings of no significant change in the mean span of the third pereiopod or of the frequency distributions of the phase relationships with changes in stepping frequency there should be a simple linear relationship between stepping frequency and progression velocity. Video-tape recordings of short sequences of sequential stepping in a straight line in the large tank were analysed for distance progressed, time elapsed and number of steps taken. These measurements were used to calculate the mean stepping frequency and the progression velocity. Although this type of measurement cannot be made with a high

Table 8. Example of $T_p/T_r$ ratio at three different stepping frequencies

| | | | |
|---|---|---|---|
| $\dfrac{\text{step duration (from regression analysis)}}{\text{s}}$ | 1.00 | 1.25 | 1.50 |
| $\dfrac{\text{step frequency}}{\text{s}^{-1}}$ | 1.00 | 0.79 | 0.66 |
| mean $T_p/T_r$ (from regression analysis) | 0.69 | 0.70 | 0.71 |
| s.d. of $T_p/T_r$ | 0.10 | 0.14 | 0.05 |
| $\dfrac{\text{stride calculated with mean } T_p/T_r \text{ value and mean span}}{\text{cm}}$ | 8.957 | 9.010 | 0.063 |
| $\dfrac{\text{stride calculated with } T_p/T_r \text{ value one s.d. above the mean}}{\text{cm}}$ | 9.487 | 9.752 | 9.328 |
| $\dfrac{\text{progression velocity calculated with mean } T_p/T_r \text{ value}}{\text{cm s}^{-1}}$ | 8.957 | 7.117 | 5.981 |
| $\dfrac{\text{progression velocity calculated with } T_p/T_r \text{ value 1 s.d. above the mean}}{\text{cm s}^{-1}}$ | 9.487 | 7.704 | 6.156 |

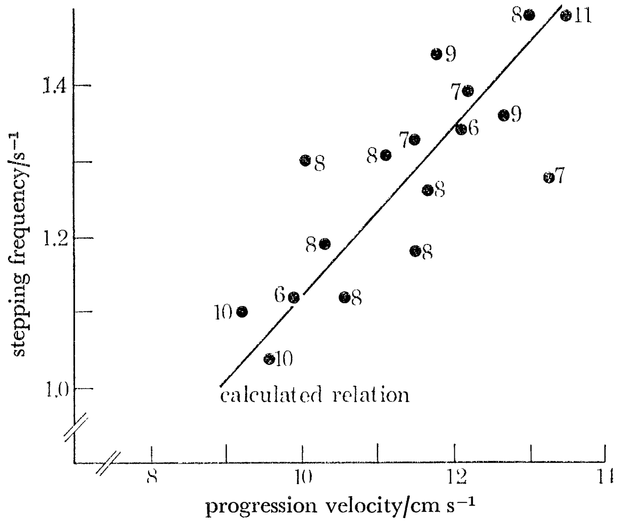

Figure 22. Example of the values obtained for progression velocity at different stepping frequencies of the 3rd pereiopod. Calculated linear relation was obtained by using the previously calculated mean values for the span and the $T_p/T_r$ ratio. Figures beside points refer to the number of steps counted for each point. The continuous line represents the theoretical relation obtained by using the $T_p/T_r$ ratio for unloaded animals and the calculated value for the span.

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degree of accuracy results from three animals showed a good agreement with the prediction. Figure 22 shows the results from one such animal compared with the linear relation obtained with a $T_p/T_r$ of 0.69 and a span of 5.6 cm.

The modal values from the phase histograms of the relations of the start of the power stroke and the start of the return stroke can be related using the $T_p/T_r$ value and a representative stepping cycle constructed. Figure 23*a* shows the stepping pattern which results and this reconstruction agrees well with short samples taken from animals which were walking with gait 5 (figure 23*b*, *c*).

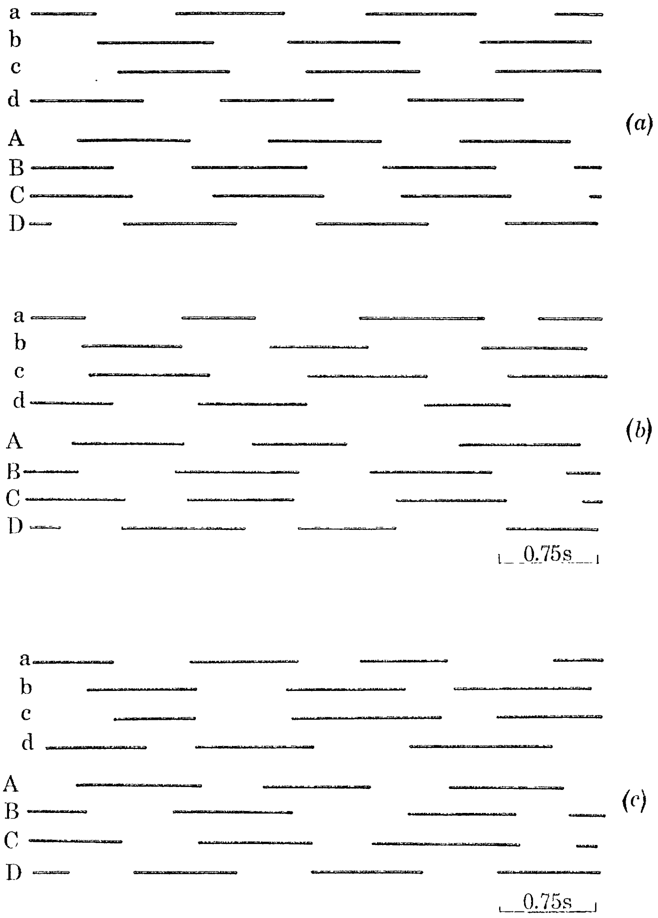

FIGURE 23. Reconstruction of stepping patterns by using constant $T_p/T_r$ and modal values from the phase histograms of phase relations at the start of the power stroke and the start of the return stroke. Lines represent contact with the substrate. (*a*) Reconstructed cycle. (*b*), (*c*) Examples of actual stepping patterns from animals using gait 5.

One hypothesis suggested by the stepping pattern produced by gait 5 is that the support and/or propulsive requirements are spread relatively evenly among the legs. If, in fact, only some of the legs which are on the substrate are involved in these activities then gait 5 places the other legs in favourable positions to assume these functions should it become necessary. Before summing up the characteristics of the lobster walking mechanism revealed by the analysis this aspect will receive some attention.

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## 7. Experimental changes to leg function

The most usual method for determining whether or not a leg normally provides support has been to amputate the leg and search for changes in the stepping pattern. The main problem with this method is that it is difficult to determine whether resulting changes are due to the change in support or to the amputation itself. Wendler (1964, 1966) approached this problem in *Carausius* by placing some of the legs on a stationary platform beside the body but found that legs supported in that way did not undergo stepping movements. In the experiments described here legs were harnessed to the carapace by means of a thread between the carapace and the merus. The length of the thread was adjusted so that the foot of the harnessed leg was a few millimetres off the substrate (figure 24*f*). This arrangement allowed the leg to move in a relatively normal manner; it could protract, retract, elevate and depress although the movements were somewhat reduced in amplitude. Animals with one leg harnessed in this way were able to progress without any noticeable increase in pitch or roll but they tended to progress more slowly than animals using all their legs. Measurements of the ipsilateral phase relations were made in the manner described previously but from animals with one leg harnessed. Two animals were examined and it was found that the harnessing of any single leg produced a

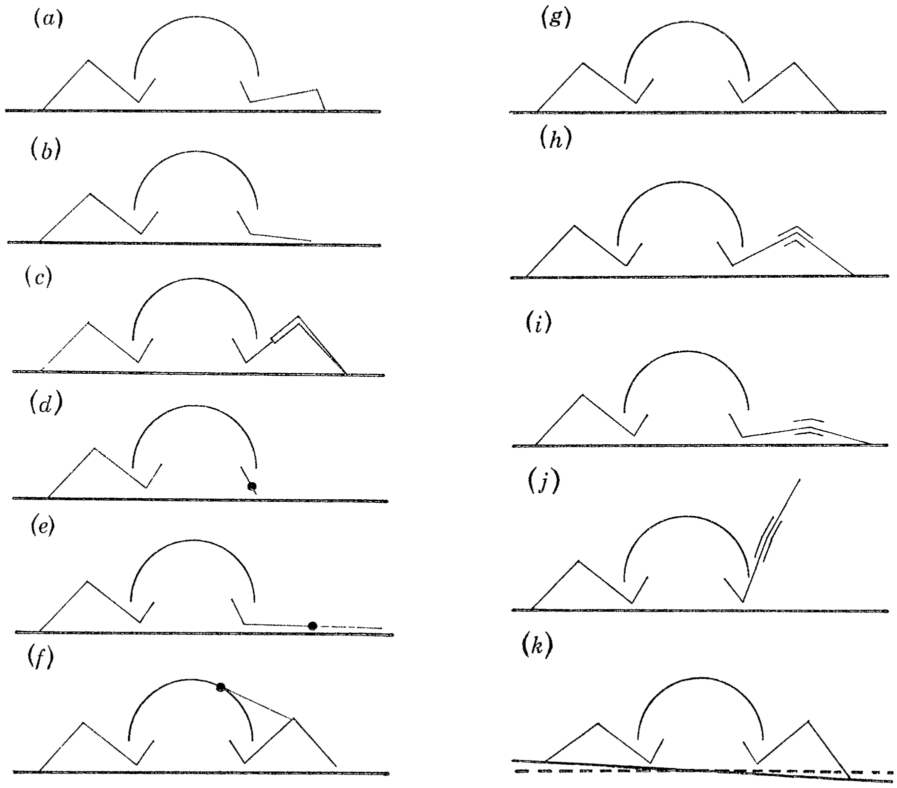

Figure 24. Diagrams showing experimental changes to 3rd pereiopod. (*a*) Mid-carpal amputation. (*b*) Mid-meral amputation. (*c*) Mid-meral amputation with prosthetic leg. (*d*) Amputation at baso-ischial joint. (*e*) Accessory flexor tendon cut. (*f*) Leg harnessed to the carapace. (*g*) Normal walking posture. (*h*) Mero-carpal joint splinted in a hyperextended position up to 120°. (*i*) Mero-carpal joint splinted in a hyperextended position of 140°. (*j*) Position assumed by the leg in a stationary animal when the mero-carpal joint is splinted at 180°. (*k*) Posture assumed when animal is standing or walking on a tilted treadmill.

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change in both $T_p/T_r$ ratio and the phase relations of the remaining three legs. Histograms of the phase relations between ipsilateral pairs were constructed with each of the four legs harnessed. These were used, together with the $T_p/T_r$ ratio, as previously described to construct modal stepping patterns. Figure 25 shows a comparison between a reconstruction of the normal stepping pattern and the ipsilateral stepping pattern from an animal with the third pereiopod harnessed (figure 25*b*) and the fourth pereiopod harnessed (figure 25*c*). The contralateral legs were also examined for changes. The changes in all cases appeared to compensate for the missing leg. Reference to the reconstructed stepping patterns suggests that the $T_p/T_r$ ratio of the remaining legs alters (although not necessarily by the same amount in each leg). The changes in all cases appeared to compensate for the missing leg. This agrees well with the finding that the centre of gravity of the submerged lobster is in the mid-line between the second and third pereiopods. It is not, however, clear from these experiments whether the compensation results from loss of support function or loss of propulsive function. This problem will be discussed further, but for present purposes the two will be considered together as the 'locomotory function' of the leg. In so far as disturbance of one leg results in changes in all the others the harnessing indicated that all the legs on a side participate in the locomotory function of that side. To investigate further the nature of the function and how the legs meet their requirement further experimental changes were made to the legs.

FIGURE 25. Reconstructed stepping pattern for the normal cycle compared with reconstructed ipsilateral stepping patterns from animals with one leg harnessed off the substrate. (*a*) Normal. (*b*) Third pereiopod harnessed off substrate. (*c*) Fourth pereiopod harnessed off substrate.

If the third pereiopod assumes any vertical load at its proximal end then force must be developed by the depressor muscle (at the coxo-basal joint) and the flexor muscle (at the mero-carpal joint). A theoretical construction of force vectors (figure 26) shows that the basal depressor force required to support a constant vertically directed load increases with increasing mero-carpal angle. A similar though rather more complex treatment could be made for the coxal muscles which will also require increasing force output for the same propulsive force if the mero-carpal angle is increased.

When the mero-carpal joint was fixed in hyper-extended positions (figure 24*h*) by means of a wire splint across the joint, the leg performed regular cyclic movements. The ipsilateral phase relations of an animal with the mero-carpal joint of the third pereiopod splinted between

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110° and 120° were not significantly different from those from a normal animal. A hyper-extension of 140° (figure 24*i*) caused changes in the stepping pattern as monitored by phase histograms. The changes were movements of the modal classes of the phase histograms in a direction which was typical of reduced locomotory function of the third pereiopod. The threshold angle for detection of the change was not investigated. The changes after the 140° hyper-extension could have been caused directly by the altered mero-carpal angle rather than by the inability of the muscles to function effectively with a reduced mechanical advantage. To test this possibility the leg was amputated at the mid-carpal level (figure 24*a*). Following this amputation the leg moved in regular cyclic fashion and during retraction the mero-carpal joint was maintained at approximately the normal angle. The ipsilateral phase relations in

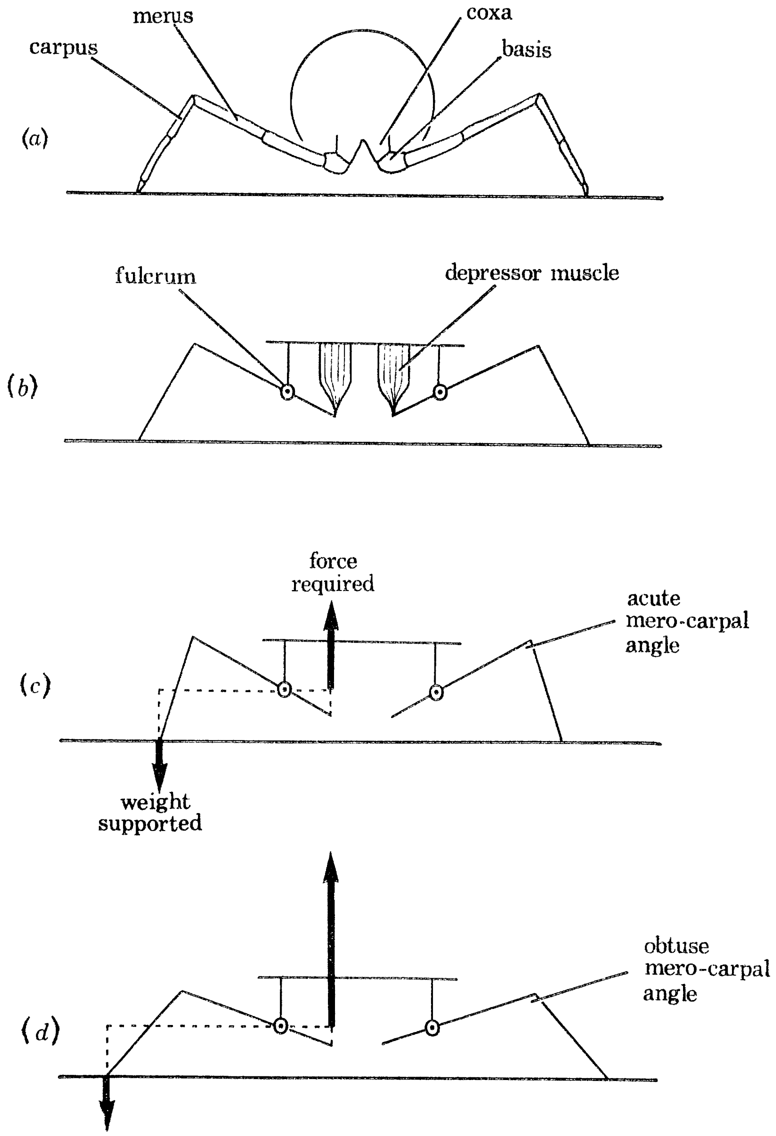

FIGURE 26. In the third pereiopod the mero-carpal angle is kept constant so that the leg acts as a rigid strut hinged at the coxo-basal joint (*a*, *b*). The depressor muscle acts at the joint to support the body mass as the contact point between the leg and the ground (*b*). If the mero-carpal joint is splinted through a range of angles the force that the depressor muscle has to develop to support a constant amount of body mass increase with increasing mero-carpal angle (*c*, *d*).

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this case showed the phase shifts typical of a reduced locomotory function in the leg. This suggested that the change to the mero-carpal joint was not a major factor in the reduced locomotory function seen after mero-carpal hyper-extension to 140°.

There still remained the possibility that the muscles require some pressure cue from the tip of the leg in order to function correctly and that for all the cases described where the locomotory function was reduced this pressure detection was disturbed by the experimental change. This possibility was tested by amputating the leg in mid-merus and attaching a prosthetic wire leg in place of the amputated segments (figure 24*c*). With the prosthetic leg on the third pereiopod the cyclic movement appeared to be normal and the ipsilateral phase relations were not significantly different from those of normal animals.

These experiments suggest that the leg may be depressed until resistance is encountered, irrespective of where this may be located in the range of movement available at the coxo-basal joint. This conclusion was supported by the finding that when the third pereiopod was amputated immediately distal to the basis, so that the remaining stump could no longer reach the substrate, the basis was depressed to the limit of its range during retraction (figure 24*d*). This conclusion has important implications for the function of the mero-carpal joint.

TABLE 9. ANGLE OF THE MERO-CARPAL JOINT ON A TILTED TREADMILL

| mero-carpal angle from stationary animal | mero-carpal angle from same animal when walking (mean of 10 steps) |
|---|---|
| 110° | 109.5° (s.d. = 1.20) |
| 115° | 115.4° (s.d. = 1.40) |
| 118° | 118.2° (s.d. = 0.70) |

The angle at the mero-carpal joint of the third pereiopod is maintained relatively constant during forwards walking and the experiments described above suggest that it is maintained against strong depressor activity. Within a limited range of mero-carpal angles (at least 69–120°) the actual size of the angle does not appear to be critical for the leg's normal locomotory function. Evoy & Cohen (1969) showed that the myochordotonal organ which is present at the joint could operate as part of a length-sensitive servo system. The setting of the mero-carpal angle is at least partially under statocyst control but there are probably other inputs to the system as well. The overall positioning of the mero-carpal angles determines not only an animal's clearance but also the span of the legs. The span of a leg affects not only the mechanical advantage of the altered leg, as described above, but also the mechanical advantage of other legs which may be using its support point as a fulcrum to unload other adjacent legs. These are important considerations for the stability of the walking animal. The setting of the mero-carpal joints may therefore be accomplished by some central mechanism sensitive to general stability factors and the experiments described above suggest that the mechanism may be separate from that responsible for producing the movements of forward stepping in the leg.

To test this hypothesis, the treadmill was tilted slightly to one side. The animals responded by altering both the coxo-basal angles and the mero-carpal angles so that the body tended to remain vertical (figure 24*k*). When an animal walked in this tilted position the mero-carpal angle of the third pereiopod was maintained at the new angle (table 9).

The hypothesis was supported further by another observation. The mero-carpal joint of the third pereiopod was fixed in extreme hyper-extension (approximately 180°). When the animal

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was stationary the leg elevated to an abnormal position against the body (figure 24*j*). When the animal started to walk forwards the leg was depressed against the substrate in regular cyclic fashion although, as discussed previously, its locomotory function was reduced. There was some tendency to hyper-elevation during the return stroke but it was not as extreme as that seen when the animal was stationary. No measurements were made to quantify this phenomenon but it was found to be quite reproducible in the five animals tested. It seems probable that the abnormal elevation was produced by disruption of the length-servo mechanism resulting from the extreme hyper-extension. The finding that this malfunction is overridden during locomotion suggests again that the locomotory mechanism for the leg is separate from the mechanism responsible for setting the mero-carpal joint.

The hypothesis concerning the length-servo mechanism and the conclusion that the leg may be depressed until it encounters sufficient resistance suggested an experiment involving both concepts. To prevent the accessory flexor muscle from affecting the mero-carpal angle the accessory tendon was cut where it passes beneath the articulating membrane at the distal end of the merus. After this operation the mero-carpal joint collapsed during the power stroke and the leg was depressed until the mero-carpal angle was 180° (figure 24*e*). If the mero-carpal joint was then bound at its normal angle the leg moved normally and in correct phase with the adjacent legs. The flexor muscle itself was not damaged because it was still able to develop tension and sham operations in which the membrane was opened but the accessory flexor left intact did not cause the collapse of the joint during walking. Similarly, damage to the MC1 chordotonal organ without damage to the accessory flexor did not cause the joint to collapse.

## 8. GENERAL CONCLUSIONS FROM VIDEO-TAPE ANALYSIS

By way of summary a subjective classification of lobster walking was made in terms of Manton's table of adaptation for speed and strength (Manton 1968). It is not possible to make a rigorous comparison since the present work is the first decapod study which deals with all the properties. The subjective decisions are made in comparison to decapods of similar size. Table 10 shows the results, which suggest that the lobster is not highly adapted for speed or strength. Manton suggests that animals which show this intermediate type of classification have the most versatile type of locomotion because specializations towards either extreme in any category tend to exclude the other possibility.

Some difficulty was found in discussing the support and propulsive functions of a leg. The two can only be readily separated when the static situation is considered (animal stationary or moving so slowly that the conditions for stability are essentially the same). In the dynamic situation it is probably only realistic to separate the two if this has some special relevance to the animal, e.g. where some legs support almost exclusively while others propel almost exclusively. The lobster does not appear to have a locomotion of this type. The dominant gait and the $T_p/T_r$ ratio produce a stepping pattern in which the functional requirements could be relatively evenly spread among the legs. The experiments in which legs were harnessed off the substrate suggests that all legs do participate in meeting these requirements but they do not determine whether all legs do so equally.

The problem of determining the importance of the locomotory function of a leg is that the results give no measure of how unevenly legs may contribute to the total requirement and still produce normal stepping patterns.

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At one extreme, the contributions can be made in a large number of different but equally effective ways so that the requirement from any single leg at any time may vary. In this case the deviations in gait and phase would probably represent mainly noise in the system. At the other extreme is the possibility that the normal locomotory function of any given leg is closely dependent on the normal functioning of all the other legs. In this case the deviations in gait and phase would probably represent necessary adjustments to changing support requirements.

Table 10. Classification of lobster walking

| Manton's suggested adaptations for speed | Manton's suggested adaptations for strength | comments on lobster | lobster classification | | |
|---|---|---|---|---|---|
| | | | speed | intermediate | strength |
| large promotor–remoter swing | small promotor–remotor swing | . | × | . | . |
| long leg length (large span) | short leg length (small span) | . | × | . | . |
| light slender legs | heavy stocky legs | . | × | . | . |
| markedly different segment diameters with large flexures | minimally different segment diameters with small flexures | . | . | × | . |
| light sclerotization | heavy sclerotization | . | . | × | . |
| long body segments | short body segments | as measured at articulation with body | . | . | × |
| long narrow muscles | short wide muscles | . | . | × | . |
| many extrinsic muscles | few extrinsic muscles | . | . | × | . |
| long intrinsic muscles crossing several joints | short intrinsic mucles crossing one joint only | . | . | × | . |
| dorso-ventral promotor–remotor swing | horizontal promotor–remotor swing | . | . | × | . |
| short duration pace | long duration pace | . | . | . | × |
| most legs off ground | most legs on ground | . | . | × | . |
| high $T_p/T_r$ (10/1), small | low $T_p/T_r$ (1/10), large | . | . | . | × |
| $\lambda$ (wavelength)† | $\lambda$ (wavelength) | gait makes $\lambda$ longer than the 4 leg segments | . | . | × |
| divergent leg gaits | convergent leg gaits | gait 5 produces convergence of legs | . | . | × |

† The number of segments between segments in phase.

The actual situation is unlikely to be at either extreme but some of the results from changes imposed on the system give indications about some of the constraints within these limits. The results of amputations and prosthetic leg attachments indicate that the mechanism for regulating the locomotory function of the third pereiopod is associated with the coxo-basal joint. The fact that the mero-carpal joint can be splinted over a wide range of angles ($<$ 120) thus producing a range of coxo-basal angles (figure 26) without changes in stepping pattern indicates that regulation of the locomotory function is not position dependent. As the mero-carpal angle is increased the force developed by the depressor muscle must increase for support of the same weight (figure 26) and a point is reached when it can no longer do so and the stepping pattern of adjacent legs starts to change. This suggests that each leg produces just exactly that amount of force which is consistent with a normal stepping pattern and that for each individual leg this may vary over a wide range. If a leg operating at maximum capability still does not meet its requirement for that step then the animal's stability is ensured by progressive changes in the stepping pattern.

There is quite an array of receptors associated with the coxo-basal region but those studied thus far appear to be involved with position detection. The above results suggest, however,

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that afferent information on muscle tension and loading could also be important. The myogram analysis was therefore designed to investigate further the effects of loading so that the discussion can be more profitably continued following the results of that analysis.

## 9. Myograms during walking

Both the coxal and the basal muscles presented particular problems for myogram recording. The coxal muscles are inaccessible in the region of their origins high up in the endoskeleton. Although they lie close to the surface as they pass beneath the thoraco-coxal articulating membrane recording from them in that region was also difficult. The coxo-basal muscles also present a problem because the coxo-basal membranes are small and the basal muscles do not pass close to the surface beneath them.

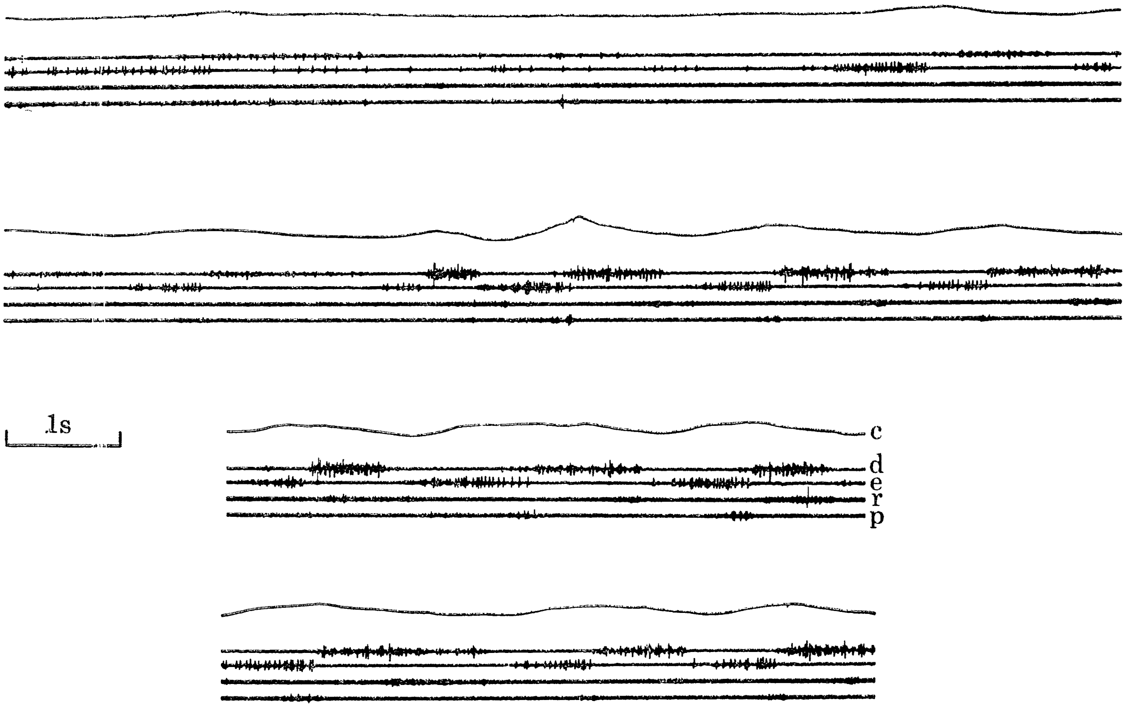

Figure 27. Electromyograms from four leg muscles showing bursting developing as walking starts. The top trace shows an analogue of the coxal movement with retraction causing a downward movement. Time calibration 1 s; c, coxal movement transducer; d, depressor muscle; e, elevator muscle; r, retractor muscle; p, protractor muscle.

The method used for most recordings and for all multiple channel recordings was that of inserting the leads through small holes drilled through the apodemes. This approach eliminated problems caused by differential movement and the apodemes provided firm insertion points. The method allowed multi-channel recordings from firm, movement-free insertions which lasted for periods of hours, or even days in some cases without the need for bulky attachment points. These advantages made this the method of choice in spite of the fact that the quality of the myograms was not as good as that of those obtained by recording through the membranes. The method also limited long-term records to muscles which insert through apodemes. Methylene blue staining indicated that apodeme and non-apodeme synergists have the same number of axons in all cases and short-term records from non-apodeme muscles indicated that during

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walking their activity is very similar to that of apodeme muscles in the parameters measured in this study. This aspect was not studied in detail.

Although there was background activity in leg muscles when the animals were stationary the activity was rapidly transformed to well-defined bursts when the animals started to walk (figure 27). The sharp definition of this activity into bursts allowed a detailed study of the relation between total excitatory muscle activity during walking.

Early experiments were limited by the equipment available to four channels of information but in later experiments as many as six muscle channels and two movement transducer channels were recorded simultaneously. The quality of recording on any individual channel varied considerably throughout the experiment owing to such problems as blood coagulation around the electrodes, movement artefacts, and mechanical damage to the low-conductance insulating material around the recording wires thus causing a loss of signal into the surrounding seawater. It was consequently unusual to have useful recordings from all channels simultaneously. By conducting a large number of experiments and continuing each experiment until all, or most, of the channels were active for at least part of the time it was possible to obtain samples of different combinations of some of the eight channels so that a composite picture of the total relation could be built up. To build a composite picture of intraburst relations, the burst parameters from usable channels in each experiment were measured and a note made when a parameter was unclear or unusable because of signal deterioration. The results were recorded on punched cards so that correlations between pairs of parameters could be run on the computer. Programs written in FORTRAN IV and executed on an I.B.M. 360 plotted a graph of the two parameters being considered, tested for correlation, determined the least squares regression line, and printed out general statistical information concerning the distribution of the two populations. The program was designed so that steps which lacked one of the parameters being considered were passed over. Mean values for the durations of bursts and their relations to any given point in the cycle provide information concerning the general structure of the muscle activity underlying a stepping movement by the leg. Figure 28 shows an example of the mean burst relations and the values used for its construction are given in table 11.

TABLE 11. INTRA-CYCLE PARAMETERS

| | $n$ | $\bar{x}/\mathrm{s}$ | s.d. |
|---|---|---|---|
| duration of cycle for sequences containing these parameters | 79 | 1.978 | 0.608 |
| retractor burst | 79 | 0.807 | 0.433 |
| protractor burst | 79 | 0.825 | 0.284 |
| start of cycle to start of protractor | 79 | 1.139 | 0.515 |
| depressor burst | 79 | 1.317 | 0.552 |
| start of cycle to end of depressor | 79 | 0.808 | 0.417 |
| duration of cycle for sequences containing these parameters | 50 | 1.843 | 0.517 |
| elevator burst | 50 | 1.230 | 0.430 |
| start of retractor to start of elevator | 50 | 0.616 | 0.201 |
| flexor burst | 50 | 0.775 | 0.226 |
| start of retractor to end of flexor | 50 | 0.733 | 0.250 |
| extensor burst | 50 | 0.969 | 0.430 |
| start of retractor to start of extensor | 50 | 1.290 | 0.370 |
| duration of cycle for sequences containing these parameters | 46 | 1.812 | 0.403 |
| coxal retraction | 46 | 1.100 | |
| start of retraction to start of retractor | 46 | 0.213 | 0.410 |
| basal elevation | 46 | 0.448 | 0.231 |
| start of retractor to start of elevation | 46 | 0.725 | 0.112 |

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In their gross relations to one another the bursts conform to the pattern that would be expected from the leg movement studies. The power stroke commences with activity in the depressor muscle which may be eventually effective in holding the foot against the substrate with sufficient force to start it moving relative to the body although the retractor burst has not yet started. The retractor activity occurs with the flexor activity so that forward propulsion and the necessary support at the mero-carpal joint appear to be provided together. The return stroke section of the step appears to be initiated by the elevator muscle and there is concomitant extensor and protractor activity.

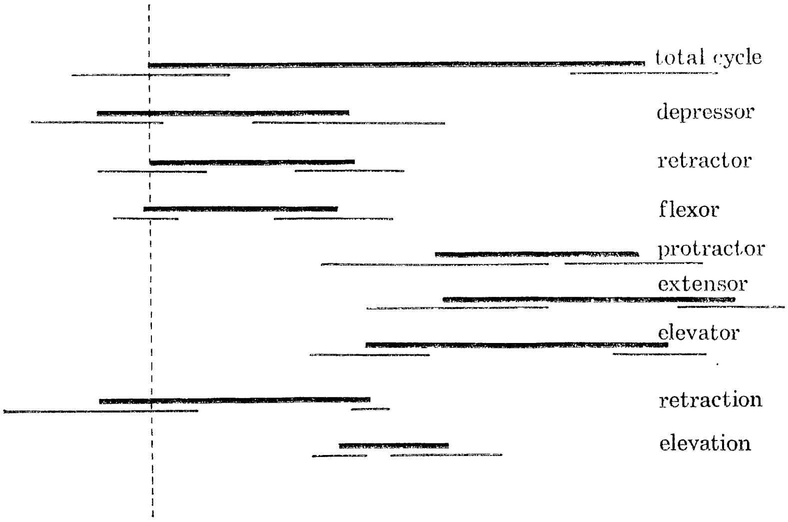

Figure 28. General relations of muscle activity and coxal and basal movement constructed by using mean values for burst durations and intervals to the start of the retractor burst given in table 11. Thick lines represent burst activity (or joint movement), thin lines represent standard deviations.

A study was made of the relation between bursts at different stepping frequencies. The behavioural studies showed that the animal appears to increase progression velocity by decreasing the power and return stroke proportionately. This suggested that a detailed study of burst relations could be made by plotting the onset (or termination) and duration of each burst as a function of cycle time. Cycle times were initially measured from two reference points: the start of the retractor burst or the start of the depressor burst. Since only steps in which the reference parameter for the cycle was absolutely clear could be used in the analysis it was important to use a point which was subject to as little signal-fade as possible. It was found that the start of the depressor burst was good in this respect and it is used in all the reconstructions reported here.

An example of the relation between a parameter and the cycle is shown in figure 29. Complete sets of relations for all the muscles studied allowed for construction of a representative cycle for any stepping frequency within the range of frequencies covered by the sample. The method relies heavily on the strength of the least-squares regression line. The sample sizes were generally large and except for muscle bursts which tend to run on into the opposite part of the cycle and the extensor burst, which is a special case, the regression coefficients were always high (the lowest seen was 0.59 but most were greater than 0.7). The gradient of each line was tested for significance at the 0.05 level and the 0.05 confidence limits calculated in each case.

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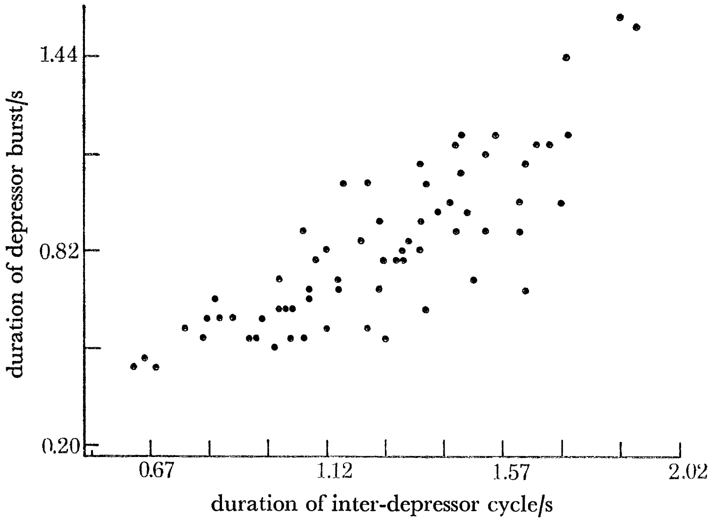

FIGURE 29. Example of computer plotted relation used for cycle reconstruction. Relation between duration of inter-depressor cycle and the duration of the depressor activity. ($r = 0.83$.)

TABLE 12. VALUES FOR RECONSTRUCTION OF BURST RELATIONS AT CYCLE DURATION OF 1.25 s

| | duration/s | phase |
|---|---|---|
| end of depressor burst | 0.801 | 0.641 |
| end of retractor burst | 0.773 | 0.618 |
| end of flexor burst | 0.748 | 0.599 |
| duration of interval between start of cycle and: | | |
| end of protractor burst | 0.244 | 0.195 |
| start of protractor burst | 0.890 | 0.712 |
| end of extensor burst | 0.650 | 0.520 |
| start of elevator burst | 0.769 | 0.615 |
| end of elevator burst | 0.363 | 0.290 |
| duration between start of extensor burst and start of cycle | 0.298 | 0.239 |
| duration of retractor burst | 0.588 | 0.471 |
| duration of flexor burst | 0.571 | 0.457 |

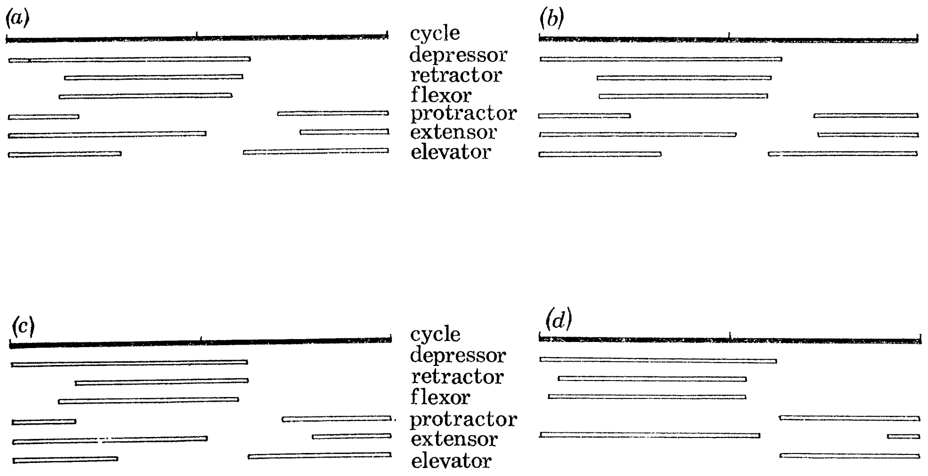

FIGURE 30. (*a*) Reconstruction of the phase relations between the muscles when the step duration is 1.25 s. (*b*) 1.0 s. (*c*) 1.5 s. (*d*) 1.5 s with a load of 30 gf attached to the carapace.

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Table 12 lists a set of values taken from a complete set of burst interrelations for a cycle duration of 1.25 s. The table also shows these same values expressed as a fraction of the cycle which allowed construction of the intracycle phase relations (figure 30*a*).

In attempting to correlate the cycle reconstructions with the information obtained from video-analysis some problems were encountered. If it is assumed that the protractor and retractor bursts are responsible for the basic divisions of power stroke, return stroke and pause seen in the video-analysis then the pause would occur in the region of the protractor–retractor overlap. This would leave a region between the end of the retractor burst and the start of the protractor burst unaccounted for. If the elevator, which is usually active during this time, does not actually lift the leg from the substrate before protraction starts then the period when neither protractor nor retractor is active would be seen as part of the power stroke. If these assumptions are made the reconstruction shown in figure 30*a* predicts a $T_p/T_r$ ratio of 0.80. If the elevator actually lifts the leg during the period when protractor and retractor are silent figure 30*a* predicts a $T_p/T_r$ of 0.95. Given the errors inherent in the video measurement a $T_p/T_r$ ratio of 0.80 could be considered as a possible approximation to the video result of 0.70 but 0.95 could not.

An alterantive hypothesis is that the video-analysis results reflect the activity of the depressor and elevator muscles. In this case the pause would be the result of depressor activity in the absence of retractor activity. The small overlap between depressor activity and elevator activity could be included in either power stroke or return stroke to give $T_p/T_r$ values of 0.60 and 0.66 respectively. These results are both within the range of possible approximations to the video result of 0.70.

The second hypothesis seemed the more likely for several reasons. First, the length of the presumed pause, as defined by depressor activity in the absence of retractor activity, agrees closely in its position in the cycle and in duration with the pause observed in the video-analysis. Furthermore, in the video-analysis, the pause was characterized by slippage, difficulty in determining whether some passive movement was occurring and the indeterminate relation between leg and substrate. All these factors could be predicted by depressor activity in the absence of retractor activity.

It was noted in the video-study that the termination of the power stroke was abrupt and easy to define because the leg was lifted rapidly from substrate. It has already been indicated that if the protractor–retractor relation defines the power stroke–return stroke relation, the interval where there is no activity in either muscle is assumed to be part of the power stroke. The elevator muscle activity would not therefore become effective until the protractor activity commenced. This long latency controlled by a third muscle would seem less likely to produce the sharp power stroke–return stroke division than the short latency, direct relation between elevator and depressor muscles. Because of these considerations, the depressor and elevator muscles were treated as the primary determinants of power stroke and return stroke.

Although the power stroke muscles (depressor, retractor, flexor) are active in the same part of the cycle they are not completely synchronous. The depressor starts firing before the other two but reference to original traces (figure 27) shows that the burst starts slowly with a low level of activity. The reconstruction shows that the depressor activity starts before the retractor activity at a time when there is still some elevator activity. At some stage during this depressor activity the leg will make contact with the substrate. It is probable that the point at which the leg starts to accept load is marked by the onset of flexor activity since if the leg accepts load

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concerted depressor activity in the absence of flexor activity would collapse the leg. The flexor and retractor become active together and complete their bursts before the end of the depressor. Reference to original traces again indicates that the leg does not collapse because the depressor burst trails off and the leg must therefore have been relieved of its load by that time or the depressor tension must have fallen to a very low level.

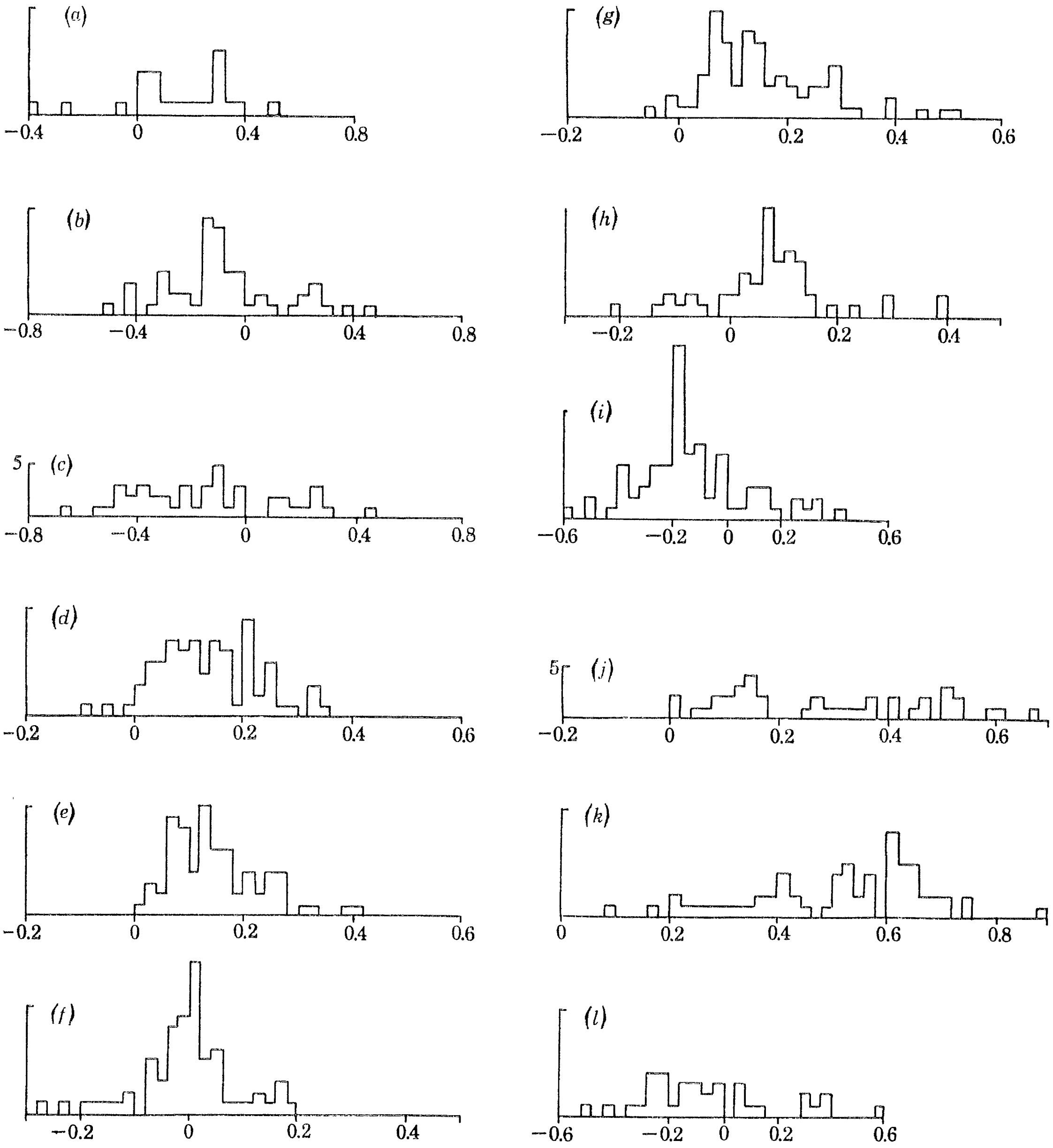

FIGURE 31. Histograms of normalized latencies between bursts from selected agonist muscles (*a*–*f*) and antagonist muscles (*g*–*l*) of an animal walking on the treadmill. Ordinate is 10 steps unless marked otherwise.

Agonist pairs: (*a*) Start of elevator to start of protractor. (*b*) Start of extensor to start of protractor. (*c*) End of extensor to start of elevator. (*d*) Start of depressor to start of flexor. (*e*) Start of depressor to start of retractor. (*f*) Start of flexor to start of retractor.

Antagonist pairs: (*g*) Start of depressor to end of protractor. (*h*) End of depressor to start of protractor. (*i*) Start of extensor to end of depressor. (*j*) Start of depressor to end of elevator. (*k*) Start of depressor to end of extensor. (*l*) Start of elevator to end of depressor.

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The return stroke is initiated by the elevator burst which tends to start its activity before the end of the depressor. The elevator activity does not become marked until the protractor muscle starts its burst. The activity of both the elevator and the protractor trail on into the start of the power stroke as defined above. Records of the activity show that the elevator and protractor activity is greatly reduced with the onset of the depressor and disappears shortly after the start of the retractor and flexor activity.

The extensor muscle activity differs from that seen in all the other muscles in that there is not a sharply defined burst of activity but rather a lower level of activity throughout almost the entire cycle. Apart from a short period around the end of the depressor the muscle is intermittently active throughout the cycle so that when it is indicated as being active in a cycle reconstruction it should be considered as a background discharge and not as a burst. The video-analysis indicated that the mero-carpal angle remains almost constant throughout the power stroke. Since the constant angle is maintained in spite of strong forces tending to alter it in either direction it is not surprising that the antagonistic muscles are active together and that one is active throughout most of the cycle.

The cycle reconstructions do not indicate the variation in burst relations around the mean square value given. Since the variation might change with alterations in stepping frequency or with other changes in sensory input it was derived in the following way. The duration of the interval between the two points in the cycle being considered was measured for each cycle and normalized by dividing by the cycle duration. This treatment, like that of the inter-leg phase relations, means that the latencies obtained are again expressed as proportions of step cycle rather than in units of time. The results were plotted on histograms and figure 31 shows some examples of agonist and antagonist relations. It can be seen from the histograms that all the relations show some scatter about the modal values but the least predictable relations are those where power stroke muscles run on into the return stroke or vice versa.

To test for changes in burst relations with changes in stepping frequency, burst reconstructions were made for other cycle durations in the same way. Figure 30*b*, *c* shows the structure of cycles with durations of 1.0 and 1.5 s.

A comparison of these two reconstructions with the reconstruction of the 1.25 s cycle shows that the bursts all maintain their phase relations over this range of stepping frequencies. When the normalized relations between agonists and antagonists were compared for slow and fast cycles from the same animal there was no significant difference in the histograms as tested with a $\chi^2$-test.

These results confirm that the conclusion of the video studies, that the lobster increases its progression velocity by decreasing power and return stroke proportionately, applies also to the intracycle parameters.

## 10. The effects of loading

With a spectrum of the characteristics of normal walking available for comparison the next step was to impose changes on the system and observe the results. Changing the loading on an animal is a relatively simple way of imposing physiological changes on to the system and the way in which the system responds to loading could be expected to provide further insight into the locomotory function of the legs.

When immersed in seawater the lobsters of the size used weigh 60–70 gf, about 12–15 % of their weight in air. Such animals are capable of pulling loads of 100 gf or carrying loads of up

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to 50 gf at progression velocities which are within the lower end of normal range. The animals were forced either to carry or to pull a load. Carried loads were either attached to the harness in the mid-carapace region in harnessed animals or attached to the carapace by wax or Plasticine in non-harnessed animals. Loads which were pulled were attached to a thread passing around the telson, the load being adjusted so that it hung over the end of the treadmill without resting on the floor of the tank.

No attempt was made to study the effects on walking of a series of increasing loads. When the loads carried were around 50 gf or more and the loads pulled around 100 gf or more serious perturbations were obvious. In the former case the animals would stumble so that their bodies often rested on the proximal segments of the legs – a condition which was not seen in unloaded animals. In the latter case the animals had trouble maintaining effective purchase on the treadmill. Loadings used were always well below levels causing gross changes in the ability to progress effectively. At the other extreme, a load of 10 gf did not produce any detectable changes in the parameters studied thus far. Loads used for the study were chosen from the middle of this range.

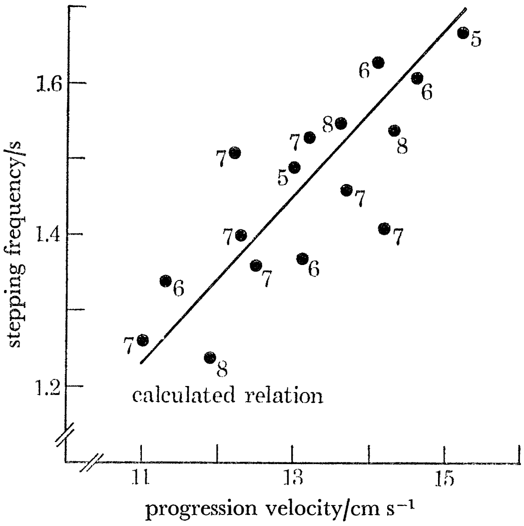

FIGURE 32. Relation between stepping frequency and progression velocity for an animal walking in the large tank with a load of 30 gf attached to its carapace. Figures beside points refer to the number of steps counted in each sample. The continuous line represents the theoretical relation obtained by using the $T_p/T_r$ ratio for unloaded animals and the calculated value for the span.

Figure 32 shows a result from a video-analysis of an animal carrying a 30 gf load walking freely in the large tank. The stepping frequency is in the lower part of the range seen in normal animals but the progression velocity for any given stepping frequency is the same. To test whether this progression velocity was produced in the same way as in unloaded animals the power and return stroke durations were again measured for the third pereiopod. Table 13 shows an example of power stroke cycle and return stroke cycle least-squares regression lines and $T_p/T_r$ ratio from an animal carrying a load of 30 gf on its carapace. These two results show that the gross features of progression are the same in loaded animals. To examine the details of inter-leg coordination, frequency histograms were made of the phase relations between the legs (figure 33). A $\chi^2$ comparison of these histograms with those from an unloaded animal walking with a similar mean step duration showed that they were significantly different.

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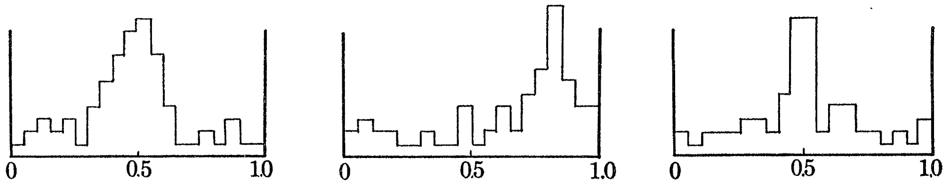
The comparison of the phase histograms from loaded animals (figure 33) with those from unloaded animals (figure 13) showed that the loading did not cause a shift in the position of the modal class but that the variation around the mode was sharply reduced. The differences in the shapes of the histograms were significant at the 0.05 level between adjacent legs but only significant at the 0.10 level between non-adjacent legs.

Table 13. Example of the relation of power stroke and return stroke: animal carrying a 30 gf load

(Power stroke against cycle $y = 0.55x - 0.06$; return stroke against cycle $y = 0.48x - 0.04$.)

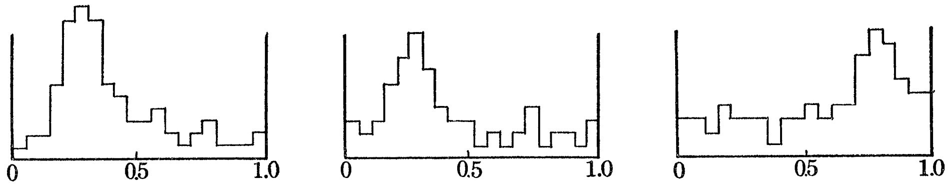
| step duration/s | $T_p$ | $T_r$ | $T_p/T_r$ | unloaded $T_p/T_r$ (mean of 5) |
|---|---|---|---|---|
| 1.00 | 0.43 | 0.61 | 0.70 | 0.69 |
| 1.25 | 0.55 | 0.75 | 0.73 | 0.70 |
| 1.50 | 0.67 | 0.89 | 0.75 | 0.71 |



c in d
$n = 73$ $\bar{T} = 1.73$
$x = 0.525$ s.d. $= 0.34$
$q = 0.675$
0.425

b in c
$n = 66$ $\bar{T} = 1.75$
$x = 0.825$ s.d. $= 0.35$
$q = 0.925$
0.725

a in b
$n = 65$ $\bar{T} = 1.75$
$x = 0.500$ s.d. $= 0.35$
$q = 0.625$
0.375



b in d
$n = 79$ $\bar{T} = 1.66$
$x = 0.275$ s.d. $= 0.19$
$q = 0.375$
0.175

a in c
$n = 68$ $\bar{T} = 1.62$
$x = 0.275$ s.d. $= 0.26$
$q = 0.425$
0.175

a in d
$n = 86$ $\bar{T} = 1.83$
$x = 0.775$ s.d. $= 0.42$
$q = 0.925$
0.625

Figure 33. Ipsilateral phase relations from an animal walking on the treadmill with a 30 gf load attached to its carapace. Reference point: start of power stroke. $T$, mean period; $x$, modal class; $q$, quartile classes 25% of the distribution above and below the modal class.

Intra-leg parameters of loaded animals were studied in the same way as for unloaded animals with burst durations being plotted as a function of cycle time. Figure 30*d* shows a burst reconstruction from an animal walking on the treadmill with a 30 gf load on its carapace for a step duration of 1.50 s. As was found for unloaded animals, the phase relations of the bursts were

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the same for cycle reconstructions at 1.25 and 1.00 s thus confirming the indication from the video studies that $T_p/T_r$ also remains relatively constant in loaded animals.

A comparison of cycle reconstructions for the same step duration from an unloaded animal (figure 30*c*) and a loaded animal (figure 30*d*) shows that there are some differences. The interval between the start of the depressor and the start of the flexor and retractor is considerably reduced so that although the duration of the bursts in both muscles increases, the interval between the end of their bursts and the end of the depressor increases slightly.

If the depressor produced significant tension in the absence of flexor activity the leg would collapse so that the changes in the flexor burst indicate that the leg assumes an effective supporting role at an earlier point in the cycle and maintains it for longer. The tendency for the protractor and elevator muscles to fire on into the power stroke section of the cycle is completely

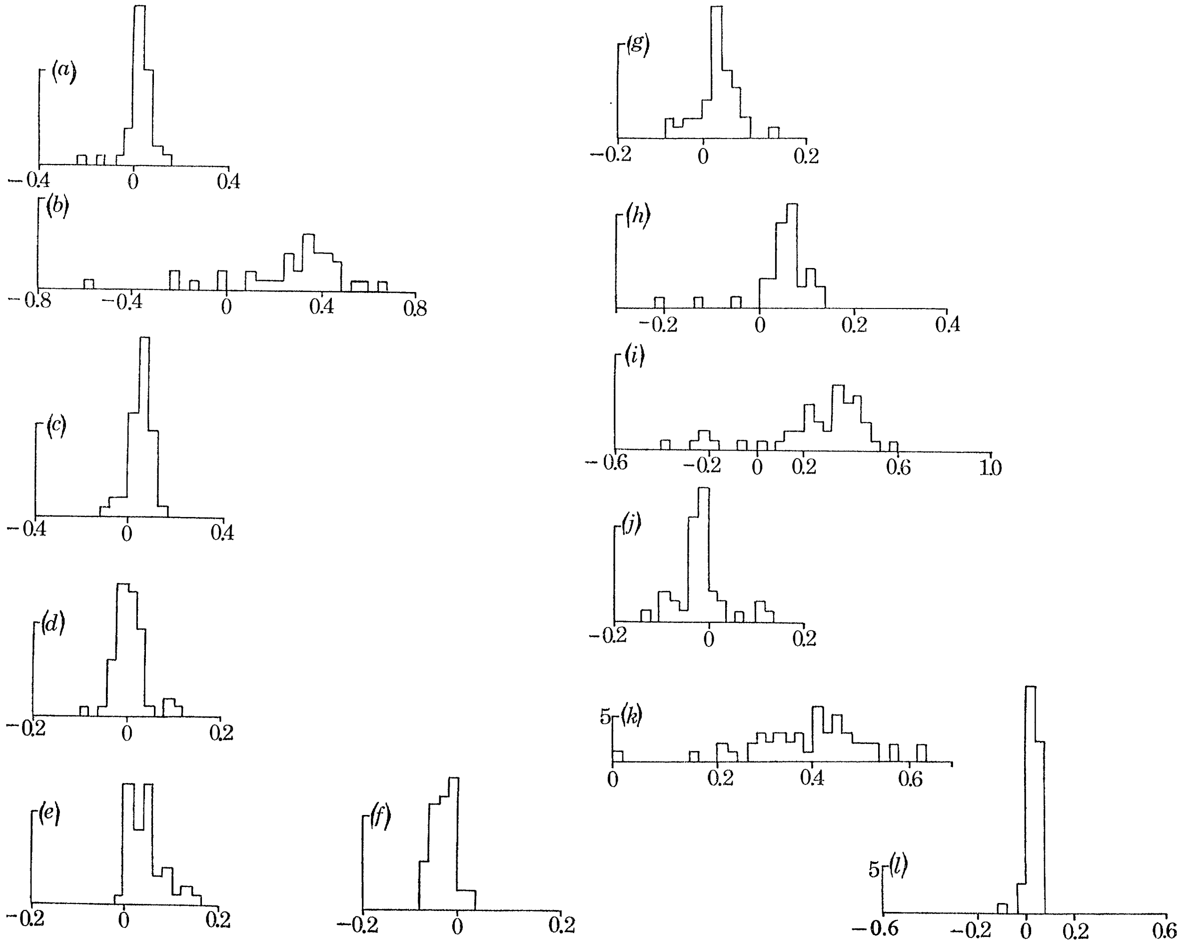

FIGURE 34. Histograms of normalized latencies between bursts from selected agonist muscles (*a*–*f*) and antagonist muscles (*g*–*l*) of an animal walking on the treadmill with a 30 gf load attached to the carapace. Ordinate is 10 steps unless marked otherwise.

Agonist pairs: (*a*) Start of elevator to start of protractor. (*b*) Start of extensor to start of protractor. (*c*) End of extensor to start of elevator. (*d*) Start of depressor to start of flexor. (*e*) Start of depressor to start of retractor. (*f*) Start of flexor to start of retractor.

Antagonist pairs: (*g*) Start of depressor to end of protractor. (*h*) End of depressor to start of protractor. (*i*) Start of extensor to end of depressor. (*j*) Start of depressor to end of elevator. (*k*) Start of depressor to end of extensor. (*l*) Start of elevator to end of depressor.

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eliminated and their bursts end with the commencement of the depressor. The protractor burst starts with the elevator so that its activity starts sooner than in the unloaded animal and occupies the whole of the return stroke interval. The extensor activity is prolonged almost to the end of the power stroke.

Taken together these changes mean that the cycle shows a cleaner demarcation between power stroke and return stroke and some increase in synchrony among agonists. To examine the variation in these relations, histograms were again plotted for the normalized intervals between agonists and antagonists (figure 34).

Table 14. Changes in intra-cycle structure with loading

| effect | example | cycle reconstruction comparison of figures | pair relation comparison of figures |
|---|---|---|---|
| silencing of a return stroke or power stroke burst which previously ran on into the power strike or return stroke | elevator–depressor | ↑ | 31l and 34l |
| change in relation causing synchronization of a burst to start and finish with agonist | protractor–elevator<br>depressor–flexor | | 31a and 34a<br>31d and 34d |
| where start or finish of one burst could occur either before or after the start or finish of another burst before loading the association becomes limited to one relative position | start of flexor to start of retractor | | 31f and 34f |
| agonists for which there is a change in relation but no marked reduction in variability | start of extensor to start of protractor | 30a and 30d | 31b and 34b |
| antagonist muscles for which there is a change in relation but no marked reduction in variability | start of extensor to end of depressor | | 31i and 34i |
| antagonist muscles for which a relation is maintained but variability is sharply reduced | end of depressor to start of protractor | | 31h and 34h |
| agonist muscles for which a relation is maintained but variability is sharply reduced | start of depressor to start of retractor | ↓ | 31e and 34e |

A comparison of muscle relations with the relations obtained for unloaded animals (figure 31) shows that the loading produced marked changes (table 14). Apart from the cases where the mode is displaced, as predicted by the cycle reconstruction, the most obvious change is the reduction in variability. In general, the change is more marked for agonist pairs than for antagonist pairs (with the exception of the start of the elevator to the end of the depressor) but the changes are not limited simply to the power stroke muscles, which presumably increase their activity in order to support and propel the increased load.

The lower limits of load which would produce the changes and the onset of the changes with increasing load were not studied. Samples of stepping from two animals carrying loads of 30 and 40 gf gave similar results. When the animals were made to pull loads of 40 and 80 gf the result was also similar. This latter finding is surprising since the direction of the forces on the animal could be expected to be rather different. Unfortunately the method of attaching the loads to be pulled was to hang the weight over the end of the treadmill and attach it to the telson by a thread. This method does not allow clear resolution of the forces so that a strong interpretation cannot be placed on this aspect of the results.

One important feature of the changes is the overall tightening up of intra-cycle relations particularly of the basic power stroke–return stroke relationship as reflected in the elevator and depressor muscles. One possible explanation is that the tightening up represents a direct

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effect of loading on the neural mechanisms responsible for intra-cycle relations. In all cases examined, the more precise phase relations caused by loading fell within the range of variability seen in the unloaded animals. It is therefore possible that in order to progress when loaded an animal is constrained to using only a small class of the intra-cycle patterns possible. Part of such constraint could be mechanical rather than neural and in this case at least some of the changes in intra-cycle parameters might be secondary rather than primary.

One way of approaching this problem was to try to separate loading effects by selective loading.

Loads which might be expected to affect the return stroke part of the cycle more than the power stroke were applied by attaching small loads between 5 and 10 gf to the merus with Plasticene or wax. It is apparent that a load applied in this way might also have some slight effect on depressor, flexor and retractor muscles. The method does, however, allow an entirely different form of loading and one which could be expected to have a direct and strong effect on the return stroke muscles.

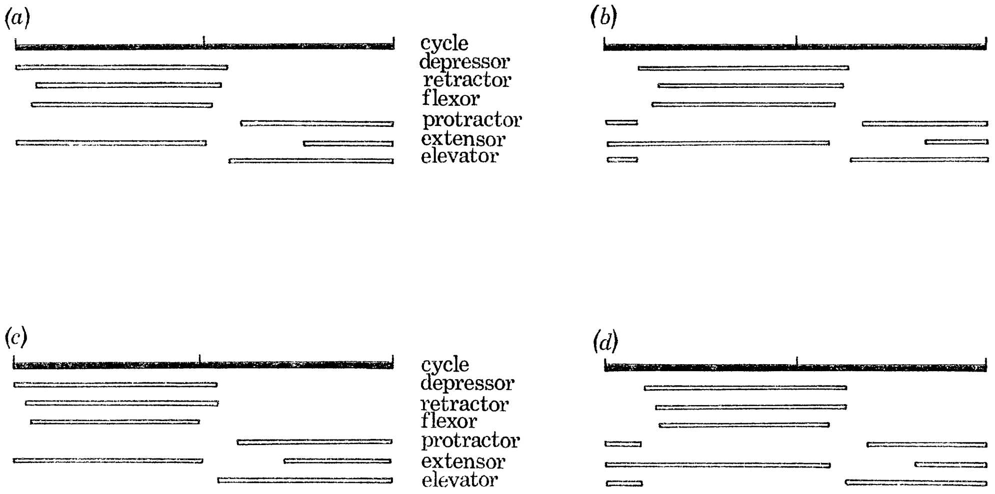

FIGURE 35. Reconstruction of the phase relations between the muscles of an animal with a load attached to the 3rd pereiopod. (*a*) Load 4.2 gf attached to the merus of the 3rd pereiopod; step duration 1.25 s. (*b*) The same reconstruction re-alined around a constant point for the depressor/elevator conjunction. The point of reference was taken from unloaded animals. (*c*) Load of 4.2 gf attached to the carpus of the 3rd pereiopod; step duration 1.25 s. (*d*) The same reconstruction re-alined around a constant point for the depressor/elevator conjunction. The point of reference was taken from unloaded animals.

Myograms obtained during samples of walking were analysed as described previously. Figure 35*a* shows a cycle reconstruction from an animal with a load of 4.2 gf attached to its merus. A close comparison of this reconstruction with that for the unloaded animal (figure 30*a*) shows that there has been a reduction in depressor duration and a decrease in the total elevator duration. Apart from these major changes in cycle structure, the gross relations between the bursts have been maintained. With loading on this part of the cycle the major changes are occurring in that part of the cycle which was chosen for alinement (the start of the depressor burst). The alinement of a basically stable cycle on the start of the depressor can therefore, in this case, give a false impression of a marked change in the whole of the cycle. To allow a more realistic comparison with a normal cycle, the end of depressor-start of elevator interface, which also gives a sharp and precise alinement point, was re-alined to the position where it

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would occur in a normal, unloaded cycle (figures 30*a*, 35*a*, *b*): all other elements were moved by the same amount so that *intra-cycle relations were not changed* (figure 35*b*)

When the re-alined reconstruction is compared with the unloaded reconstruction for the same step duration (figure 30*a*) it is apparent that this treatment illustrates more clearly the changes produced by merus loading. With the merus loaded, the protractor and elevator bursts run on into what would normally be part of the power stroke as they did in the unloaded cycle. When the merus is loaded, however, there is no depressor activity during this early power stroke period so that in terms of the definition of the cycle it becomes part of the return stroke which is thereby lengthened. It should also be noted that the activity of these two muscles no longer continues beyond the start of the retractor and flexor bursts.

When the normalized intervals for the burst relations (figure 36) are compared with those for unloaded animals it can be seen that there is once again a reduction in the variability of

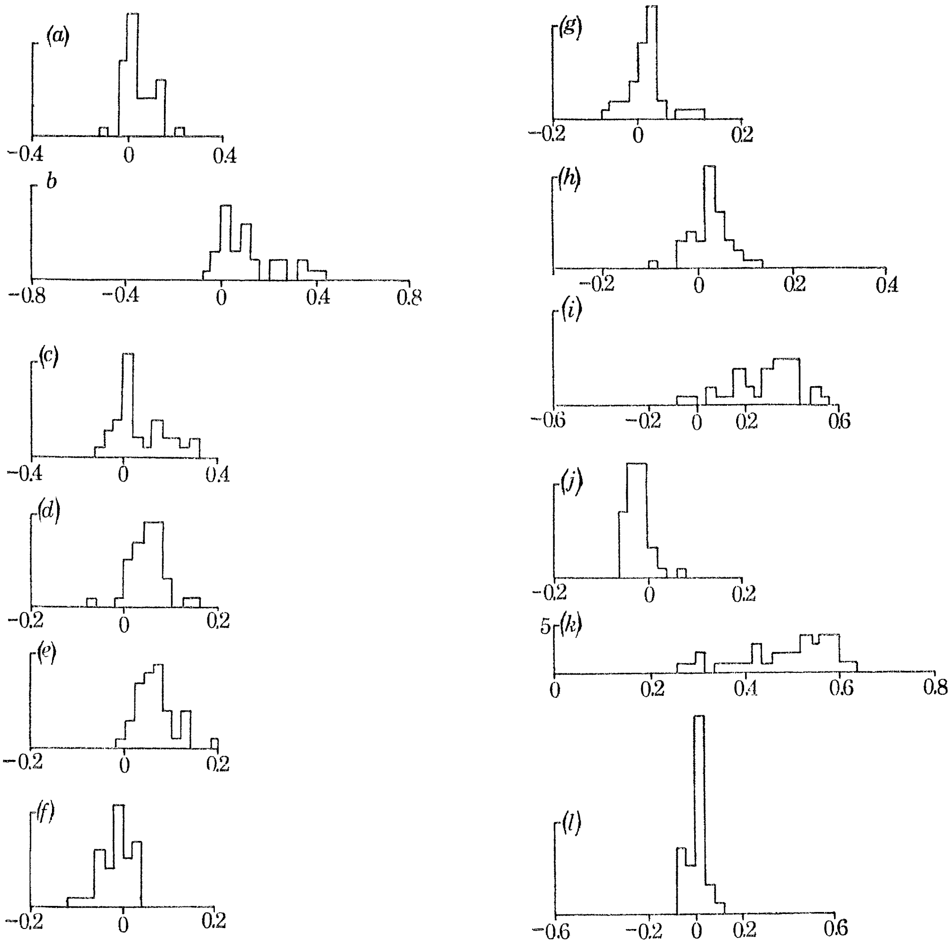

FIGURE 36. Histograms of normalized latencies between bursts from selected agonist muscles (*a*–*f*) and antagonist muscles (*g*–*l*) of an animal walking on the treadmill with a 4.2 gf load attached to the merus of the 3rd pereiopod (*a*–*f*) or the carpus of the 3rd pereiopod (*g*–*l*). Ordinate is 10 steps unless marked otherwise.

Agonist pairs: (*a*) Start of elevator to start of protractor. (*b*) Start of extensor to start of protractor. (*c*) End of extensor to start of elevator. (*d*) Start of depressor to start of flexor. (*e*) Start of depressor to start of retractor. (*f*) Start of flexor to start of retractor.

Antagonist pairs: (*g*) Start of depressor to end of protractor. (*h*) End of depressor to start of protractor. (*i*) Start of extensor to end of depressor. (*j*) Start of depressor to end of elevator. (*k*) Start of depressor to end of extensor. (*l*) Start of elevator to end of depressor.

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most of the relations. When they are compared with those for animals carrying a 30 gf load (figure 34) it can be seen that some of the new relations are very similar and that the transpositions of the modal values often agree closely. The types of changes seen in back-loaded animals (table 13) are also seen here but the magnitude and direction of the changes are not always the same.

The video observations from unloaded animals indicated that the mero-carpal angle is maintained relatively constant. Analysis of the angle between the merus and the vertical for back-loaded and merus-loaded animals showed that this is also true in these cases. This supports the hypothesis that the mero-carpal joint is set for position and is not affected by loads, at least within the range tested. To test this hypothesis further and to see if any additional separation of loading effects could be obtained, loads of 5–10 gf were attached to the carpus and the myograms obtained analysed.

Figure 35*c* shows a cycle reconstruction for an animal with a load of 4.2 gf attached to its carpus and figure 35*d* illustrates the cycle re-alined around the depressor/elevator conjunction. A comparison of the re-alined carpus-loaded cycle with the unloaded cycle (figure 30*a*) and the merus-loaded cycle (figure 35*a*) shows that the changes produced are the same as those produced by loading the merus. A similar comparison of the normalized intervals for the burst relations confirms this conclusion (figure 36).

It can be seen that a load on either the carpus or the merus causes the same general reduction in variability seen when loading the carapace. This does not eliminate the possibility that the effect is due to mechanical limitation to certain steps within the normal range. It suggests, however, that this explanation is less likely because the mechanical effects would be different in each of the three loading situations considered. It seems more likely that the changes are therefore due to some neural mechanism.

## 11. GENERAL CONCLUSIONS FROM LOADING EXPERIMENTS

The effects of loading appear to be of two types: those which occur irrespective of where the load is applied, and those which are sensitive to the position of the load.

In the normal cycle some muscles tend to start or finish with the agonist (figures 37*a*, *b*) and some tend to start or finish with the finish or start of activity in an agonist (figures 37*c*, *d*). Many burst relations of this type respond to any type of loading by maintaining phase position in the cycle but with sharply reduced variability. The simplest explanation for this would be in terms of direct phasic excitation and inhibition of the motoneurons. While some specific effects are seen which almost certainly occur in this way and the mechanisms could well be widely distributed, other types of changes suggest that the interaction is more complex. One of these is that some bursts are not drawn into synchronous starting or finishing relations but rather an existing short interval between burst onsets or completions becomes extremely phase constant (figure 37*e*). These results argue that in addition to any specific changes in burst relations due to the position of the load, there is a powerful general strengthening effect on a central mechanism which produces an output in which many components are phase locked. These results also suggest that some of this general feedback is to levels above the motoneurons.

Loading causes some bursts to maintain their unloaded relation to each other while both changing their phase within the cycle (figure 37*f*). In one case the start of one burst in part

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of the cycle is augmented by loading so that it starts when the other portion ends (figure 37*g*). While both these effects could be explained by a variation of the general tightening feedback mechanisms a simpler explanation is that there is direct elevation of the excitability of the motoneurons concerned. The relations of the muscle bursts at the return stroke/power stroke interface suggest that direct inhibition can occur also. In the unloaded animal the return stroke bursts run on into the depressor burst and even into the retractor and protractor bursts (figures 37*h*, *i*). Loading of the carapace silences the return stroke muscles during the overlap interval (figure 37*h*) whereas loading of the merus or carpus muscles silences the power stroke muscles during the same period (figure 37*i*).

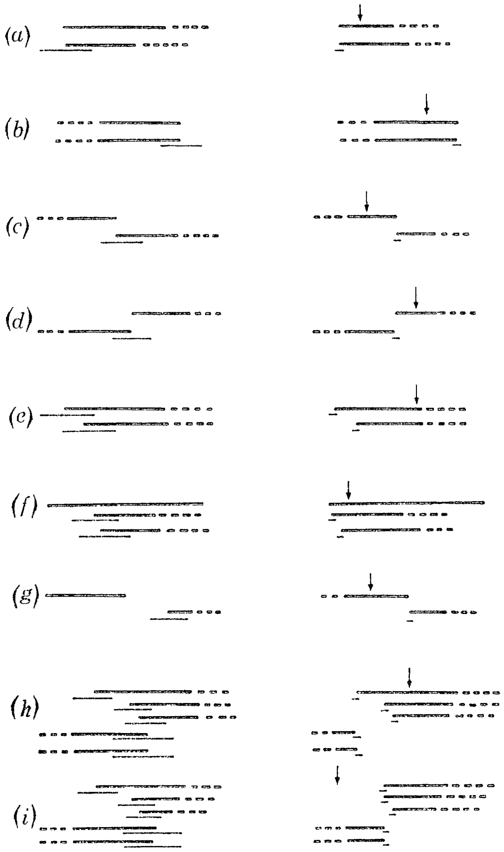

FIGURE 37. Summary of the types of changes seen in muscle burst relations with loading. Unloaded relations shown in the left column, loaded relations in the right. Muscle bursts are indicated by continuous (and dashed) lines. Variations in terminations and onsets are indicated below the bursts. Arrows indicate the part of the cycle which would receive the primary effect of the load.

## 12. DISCUSSION

Previous studies of walking in arthropods have, with a few exceptions, tended to analyse small stepping samples in detail. That approach generates very specific information about the samples but does not allow for generalized conclusions about the relation of the sample to the animal's total walking behaviour. The results here are based on mean phase, probabilities of sequences, least-square regression coordination and pooled results. This approach therefore allows for considerable insight into the system's variability but does not give specific details

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about how the variability relates to individual cycles. Since this is one of only a few studies which have approached arthropod walking in this way a first impression might be that the lobster system is more variable than the others studied. Without information of this type on the other systems this would not, however, be a valid conclusion. Until further studies of this type are made no direct comparison can be made between the variability of the various systems.

The finding of considerable variability in lobster walking poses the question as to whether or not it is functional. The limits of this problem can be seen in the two extreme views one might take. The first is that the variability is simply due to noise in the system. That argument would suggest that the animal can be supported and propelled adequately by a loosely controlled system and that the function of any given leg at any given time is not critical for the normal function of the whole. The second extreme is that *all* variation seen is a direct response to changing dynamic requirements. That argument would suggest that the function of any given leg is critical and that if it fails to meet its share of the total requirement other legs must compensate.

Both these extreme arguments appear unlikely but it is difficult to assess the relative contribution made by noise and by response to changing requirements. Removal of the functional input of any one leg produces a change in the functional output of the other legs. Loading also changes the functional output of the legs. Both these results suggest that there is considerable sensitivity to changing functional requirements. It is quite possible, however, that the mechanisms responsible for the adjustments do not become important until there are relatively large perturbations in the system.

The changes seen following loading have not been described previously and are important for any consideration of the role of sensory input to this system and possibly other locomotory systems. If the changes in the myograms are a result of mechanical restraints imposed by the loads, the chordotonal organs are strongly implicated (Burke 1954; Bush 1965*a*, *b*). If, on the other hand, the changes in leg movement are the result of the changed muscle output then tension receptors are implicated (Macmillan & Dando 1972).

The results suggest that sensory input is important in regulating the output of the lobster walking system during loading. Reflexes which could produce the type of change seen with loading have not been described in crustaceans. This may be due largely to an absence of detailed information about the functional relations between muscles which would indicate where to concentrate such an investigation. A relation between the carpopodite–propopodite and coxal innervated organ has been described briefly (Moody 1970) but no details are available. Some resistance reflexes which link the propopodite–dactylopodite chordotonal organs with the stretcher and bender muscles have also been described in crabs (Bush 1962) and crayfish (Muramoto & Shimozawa 1970). There is, however, evidence that resistance reflexes are suppressed by a central programme during walking (Barnes *et al.* 1972; Spirito *et al.* 1972) and from this it seems unlikely that they are involved in patterning. But, if central switching is capable of turning *off* reflexes which operate during imposed movement, it could presumably be capable of turning *on* reflexes which would operate only during centrally initiated movements. Thus the chordotonal organs would still have to be considered during any search for sensory input responsible for the load-induced changes. There is some preliminary evidence that some of the reflexes mediated by the tension receptors are not the same in active and imposed limb movements (Clarac & Dando 1973; Dando & Macmillan 1973).

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The present work provides the necessary functional information on muscle activity relations to direct a search for the significant sensory input and possible reflexes which it mediates.

Pearson (1972) studied the effect of load in cockroaches and found that it changed the frequency and intensity of the discharge in the loaded muscles. He also detected changes in the output to the return stroke muscles. In both respects the intraburst changes in the cockroach are similar to the interburst changes in the lobster. Pearson has some evidence that the changes are due to input from the campaniform sensillae which detect stress changes in the cuticle and in this respect also, the systems may be similar. As in the present study, the role of velocity-sensitive afference is ill-defined but there is evidence in the insect that while there is still a rhythmic motor output in the absence of chordotonal organ input (Pearson 1972; Pearson & Iles 1970) and the leg is still able to step, both posture and walking are affected (Usherwood, Runion & Campbell 1968).

It appears that the present system is similar in many respects to the cockroach walking system. This implies that on a central–peripheral scale it would be placed with systems which require considerable peripheral input in order to function in a non-constant environmental situation. Before a more concrete assessment of a central–peripheral scale can be made, it will be necessary to separate movement and tension effects, not only in this system, but in most other systems where sensory input has been shown to have any effect.

I should like to thank Dr Graham Hoyle for providing accommodation and facilities in his laboratory and also for his advice and encouragement throughout this work. For his valuable technical advice and assistance I am indebted to Mr Lee Vernon. I would particularly like to thank Dr Laurence Field and Dr Donald Maynard for many useful and stimulating discussions while the work was in progress. Thanks are also due to Dr Philip Grant, Dr Barbara Gordon-Lickey, Dr Donald Maynard and Dr Gernot Wendler who read and criticized various drafts of the manuscript and to Andria Sylvester who prepared the figures.

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