

THE FORCES EXERTED ON THE SUBSTRATE BY WALKING AND STATIONARY CRICKETS

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SUMMARY

1. The gait and the protraction/retraction ratios (P/R ratios) for the cricket are described. They are essentially the same as for the cockroach and the grasshopper.

2. The vertical forces exerted on the substrate by all six legs of walking and stationary crickets are measured. On the basis of the 'forceprints' obtained and differences in P/R ratios among the legs of different thoracic segments, it is pointed out that all segments are not functionally identical. Specifically, the greater irregularity of the forceprints of the prothoracic legs, and the lower magnitude of peak force exerted on the substrate by the prothoracic legs suggest that the prothoracic legs are more involved in balancing or searching than in propulsion.

3. The metathoracic legs exert an increased vertical force on the substrate just before the initiation of protraction. This increase correlates with an extension of the leg apparently through extension of the femoral-tibial joint.

4. A slight decrease in the force exerted on the substrate by the mesothoracic legs occurs when the leg is at right angles to the body.

5. Placing or lifting one mesothoracic leg does not affect the force exerted by the contralateral mesothoracic leg in a regular way. This argues against mechanical interactions between the legs and in favour of theories invoking central generation of pattern.

6. At a stepping frequency of below 2 steps s^{-1} the shapes of the forceprints of all legs are no longer repetitive. Also, below 2 steps s^{-1} there is an increase in the variability of the peak force exerted on the substrate. It is possible that the animal switches to a more sensory sensitive mode below a step frequency of 2 s^{-1} .

7. During stationary periods the forces exerted on the substrate continue to show oscillations which may be metachronal. This suggests a mechanism whereby a central oscillatory mechanism can account for the behaviour of an animal starting to walk following such a stationary period.

INTRODUCTION

In order for an insect to move efficiently from place to place it must move its appendages in coordinated sequences and it must adjust to changing terrain. Classical studies on coordination have focused on analysis of gait, the sequence of leg move-

Table 1. *Characteristics of technique*

Item	Cruse (1976)	Harris & Ghiradella
Ability to resolve force components	All 3	Only vertical
Number of legs recorded simultaneously	1	6
Maximum displacement of force transducer	1 mm	0.05 mm
Time resolution of leg touchdown and lift	± 20 ms	± 17 ms
Sensitivity	20 mg	5 mg

Table 2. *Applications of technique*

Item	Cruse (1976)	Harris & Ghiradella
Insect used	Stick	Cricket
Maximum stepping frequency	2-3 s ⁻¹	15-20 s ⁻¹
Body weight (mean)	820 mg	435 mg
Filming speed	18 frames s ⁻¹	32, 60, 80 frames s ⁻¹
Used for determining		
Forces from insect walking horizontal, vertical and hanging	all 3	only horizontal
Torque at each joint	+	-
Coordination of legs	-	+
Variations at different stepping frequencies	-	+
Forces exerted by standing insects	-	+
Maximum force exerted by metathoracic leg, animal walking on horizontal plane	252 mg	220 mg

ments (Manton, 1973; Hughes & Mill, 1974). The regularities of these movements and their constancy in unrelated species has led to attempts to model and describe the gaits in terms of cybernetic rules of control (Graham, 1977*a, b*; Wilson, 1966). The regularity, simplicity, and elicibility of the gaits has led neurobiologists to utilize insect walking as a tool to explore the neural basis of behaviour (for reviews see Hoyle, 1976; Pearson & Duysens, 1976). The gait studies have described the mechanical movements of all six legs and the neurobiological studies have recorded the activities of a few muscles and nerves.

A major thrust of research in the coordination of insect walking has been to determine the role of sensory feedback in normal leg movements. Experiments involving amputations (Hughes, 1957; Delcomyn, 1971*b*; Wendler, 1966; Graham, 1977*a*), fixing the leg in rigid positions (Pearson & Iles, 1973; Graham, 1977*a, e*), and ablating sense organs (Wendler, 1966; Land, 1972; Wong & Pearson, 1978; Bassler, 1977) all show that the animal does normally utilize sensory information to adjust sequences of leg movements or to maintain rhythm and amplitude of leg movements. On the other hand, completely deafferented animals can make basic stepping movements and continue to show reciprocal activity in coxal levator and depressor motor neurones (Pearson & Iles, 1973). So although it has been shown that both central tapes (behaviours generated by central nervous components without requiring sensory feedback for their execution) and sensory feedback are involved in normal pattern generation, the contribution of each to normal walking remains to be elucidated.

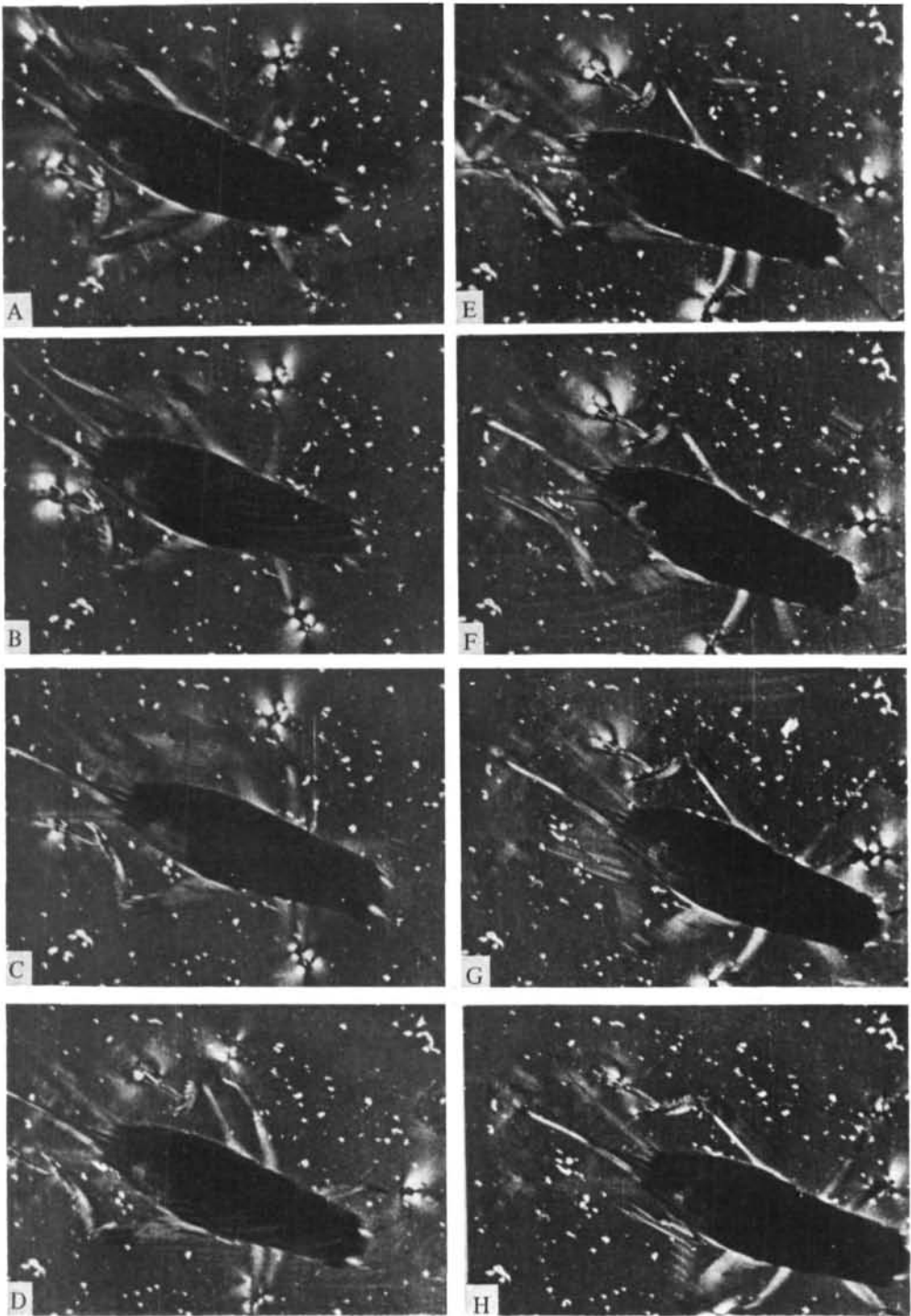


Fig. 1. Eight consecutive frames from 16 mm film of cricket walking across substrate between crossed polars. The white patches at each tarsus are the photoelastic signals; the area of each patch corresponds to the force exerted by that leg. Note the tripod stance in B and F. Note also the surge in the signal from the right metathoracic leg in E, just before protraction (F). The fine parallel lines (B, F and G) are film-processing artifacts. The fine white dots littering the surface are caused by depolarizing dust on the surface, most of which was deposited by the cricket on a previous passage. Note (by reference to these dots) that the printing frame was shifted after C. This passage was made at a stepping frequency of 5-8 steps s^{-1} . Time interval between frames is 16 ms.

To dissect the contributions of central tapes and sensory feedback to the coordination of walking, we need to know the normal leg movements of unrestrained insects and we also need to know how the animal maintains balance and produces propulsive forces. The leg movements have been characterized (Wilson, 1966) and Cruse (1976) measured the forces produced by the legs of a free-walking stick insect. By using strain-gauges he was able to measure the components of forces produced in the x , y and z directions from insects walking horizontally, vertically and hanging from a beam. The strain-gauge technology permitted recording from one leg at a time. This present study reports quantitative measurements of forces exerted on the substrate (in the vertical direction only) by all six legs of unrestrained walking and stationary crickets. For comparisons of this work and Cruse's see Tables 1 and 2.

MATERIALS AND METHODS

The recent work on insect walking has utilized large insects: the stick insect (Wendler, 1966; Cruse, 1976; Graham, 1972), the cockroach (Hughes, 1967; Wilson, 1966; Delcomyn, 1971*a, b*; Pearson & Iles, 1970, 1973) and orthopterans (Hoyle, 1964, Runion & Usherwood, 1968). For this work, adult female common house-crickets, *Acheta domesticus*, were used. Although the cricket can jump, it is not so specialized for jumping as other orthopterans, and field and laboratory observations suggest that the cricket prefers to walk rather than to jump. (In the laboratory the younger, smaller instars are more likely to jump than the older, larger instars.)

The technique used to measure the forces exerted by the crickets is photoelastic substrate transduction. A complete description of the technique is available elsewhere (Harris, 1978). Briefly, the passing cricket tarsus induces temporary strain birefringence in a polymeric (gelatin based) substrate. This birefringence is visible when the substrate is viewed in polarized light (Fig. 1). The area of the birefringence is quantitatively related to the stress (force per area) exerted on the substrate by the cricket tarsus (Harris, 1978). Dividing the stress by the area of contact gives the force exerted by the tarsus. It is important to emphasize that the animal does not noticeably indent or deform the substrate; the optical pattern results from induced strain.

Although the shape of the resulting pattern of birefringence can be utilized to determine the direction of applied stress (Harris, 1978), the area of the birefringence corresponds to the vertical component of the force independently of the other components (Harris, 1978). That the area corresponds to the vertical component is demonstrated by two experiments. Stress is applied to the substrate by a needle with an end of known area which slides freely in a glass sleeve held in a micromanipulator. The stress applied to the substrate depends, then, on the weight of the needle and the sine of the angle between the substrate and the needle (which can be adjusted by the micromanipulator). It has been found that the area of birefringence depends on the vertical component of the applied stress; that is, as the stress is applied at increasingly horizontal angles, the area of the birefringence decreases proportionally to the vertical component of the force and without regard to the horizontal component, which is increasing (Harris, 1978, fig. 4). The second experiment demonstrates that the horizontal component of the force does not cause

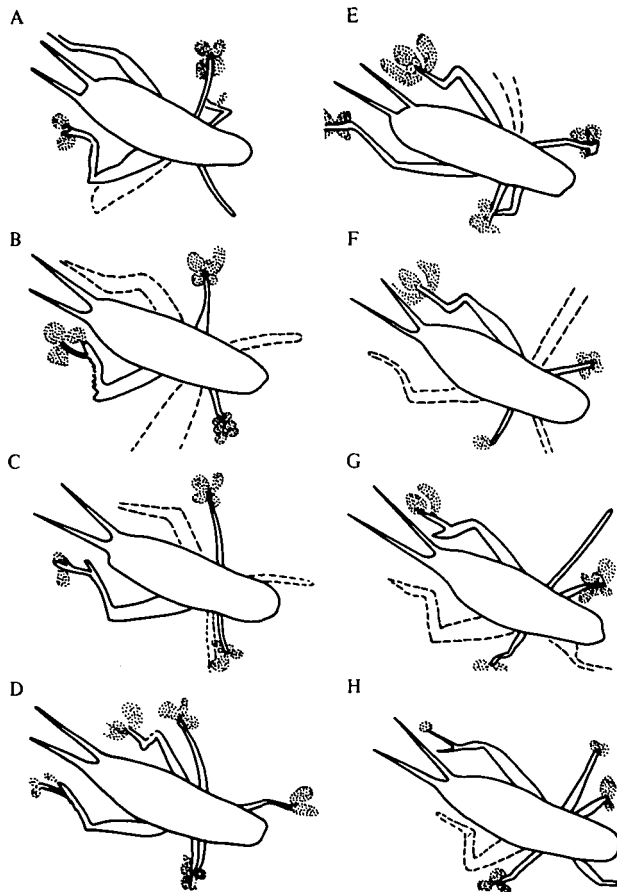


Fig. 2. Diagram of film sequence in Fig. 1. In this diagram, load-bearing legs are represented by solid lines, protracting legs are represented by dashed lines, and the photoelastic signal is represented by stipple.

distortion or misrepresentation of the vertical component of the force. If at each angle of setting of the micromanipulator, a compensatory weight is added which serves to keep the vertical component of the force constant while constantly increasing the horizontal component of the force, it is found that the area of birefringence remains constant.

Substrates were prepared as per Harris (1978), placed between crossed polars, and the cricket was allowed to walk freely on the substrate. The changing pattern of birefringence was recorded on film (Fig. 1). Generally it was arranged that the substrate was larger than the filming area. The animal was released at one end of the substrate and filmed as she walked through the area (4.5×7 cm) covered by the camera, an area large enough to photograph about three steps of all legs per passage. In this way, records have been made of many behavioural patterns such as animals standing still, walking at different speeds, turning, starting and stopping. As far as we could tell the animals were not obviously affected by either the bright light (necessary for filming in polarized light) or by the gelatin-based substrate. All experiments were conducted at ambient laboratory temperatures between 18.3 and

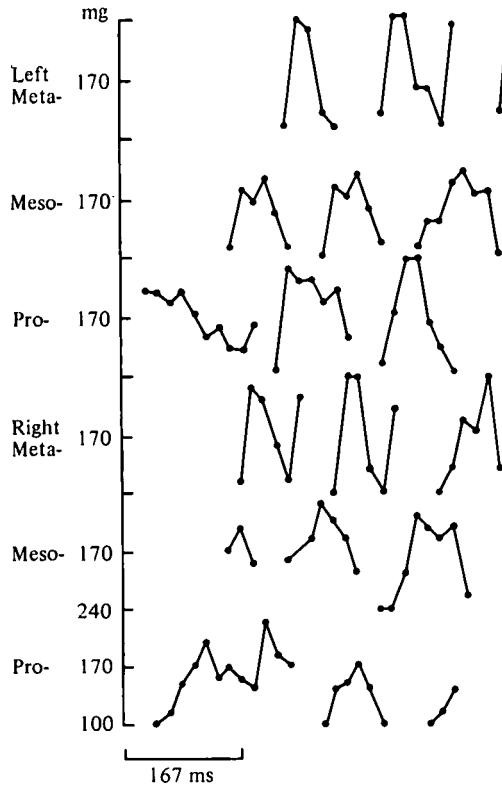


Fig. 3. Graphical representation of forces exerted on the substrate over 0.5 s by a cricket (including the sequence shown in Fig. 1). The forces are calculated from the area of birefringence measured for each foot in consecutive frames of the film. A break in the line represents protraction.

21.1 °C. A heat filter was placed between the light source and the stage to prevent heating of the substrate.

Since the photoelastic substrate technique measures stress (force per unit area) it is impossible to state the ultimate sensitivity of the technique for resolving *forces* (Harris, 1978). For the stresses applied by walking crickets, we could routinely measure differences in force of less than 2 mg. However, some error is to be expected from the photographic and analysis procedures and we therefore chose 5 mg force as a conservative estimate of sensitivity. Accuracy and repeatability of the interpretation were assured by calibrating each film as described below.

The pattern of birefringence was filmed on 35 mm Tri-X film at 48 frames s^{-1} with a Bell & Howell type A-7 camera and at 60 and 80 frames s^{-1} on 16 mm Tri-X film with an Arriflex camera. The films were processed in Diafine developer and the area of birefringence for each foot in each frame was measured on an International Imaging Systems false colour densitometer. The system was calibrated on each film by applying known stresses by a needle with an end of known area applied at varying angles as described above.

This paper reports the results of analysis of 38 such films representing 162 000 frames and over 400 steps. Fig. 3 gives a sample plot of the resulting data. Note that the

convention introduced by Wilson (1966) is reversed in that retractions are in black and protractions are represented by breaks in the line. In this way vertical deflexion can be used to indicate the magnitude of the vertical force exerted on the substrate.

RESULTS

(A) *Description of gait*

The gait of the cricket is essentially the same as reported for the cockroach (Delcomyn, 1971a), independent of speed over most of its range. Fig. 4 shows the angles swept by the legs. These are slightly more anterior than in the grasshopper (Burns, 1973). Figs. 5–7 illustrate the changes in the gait characteristics with increasing stepping frequency and consequent velocity. As was found to be the case with the cockroach (Delcomyn & Usherwood, 1973) and the locust (Burns, 1973), the duration of protraction is approximately constant for all velocities above two hertz and the duration of retraction varies with step frequency. Step frequencies were determined as an average for each passage of the cricket through the filming area rather than for each step. This has the effect of averaging over several steps the rapid changes seen in instantaneous velocity of the animal and reflects the time averaged rate of progress of the animal for that particular stepping frequency.

(B) *Forceprints*

Each passage of the cricket was plotted as in Fig. 3. Comparisons of these 'forceprints' for different animals and of the same animal walking at different speeds demonstrates that the shape of the forceprint is more consistent (i.e. the same shape occurs in all forceprints) for the mesothoracic and metathoracic legs than it is for the prothoracic legs for animals walking above 2 steps s^{-1} (Fig. 8). For animals walking slower than this frequency the forceprints are non-repetitive for legs of all segments.

A small dip usually occurs in the forceprint of the mesothoracic legs (Figs. 3, 8). This dip occurs when the leg is at $93 \pm 5^\circ$ to the central axis of the body. When the leg is bent, such as occurs when the animal is turning towards that side (i.e. not extended straight out from the body through all joints as is the case normally), the dip is not present.

In many cases there is a sudden increase in the force exerted on the substrate by the metathoracic legs one frame (17 ms) before the leg protracts (Figs. 3, 8, 9). Tracings of apparent leg positions from sequences with this 'surge' show that the leg extends slightly just before protraction. The amount of apparent extension correlates with the amount of increased force observed. This extension involves a change of, typically, about 20° in the apparent angle of the femoral–tibial joint, 15° in the angle of the tibial–tarsal joint, and sometimes 5° in the angle of the trochanteral–femoral joint (Fig. 9). From analysis to date it is not possible to say which, if any, of these apparent changes in leg angles is responsible for the observed increase in vertical force exerted just before protraction.

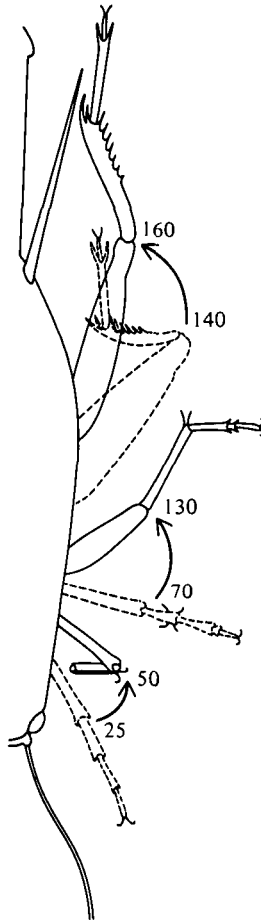


Fig. 4. Angles relative to body axis swept by legs during retraction. This data is taken from films made from above the animal, using polarizing optics, which does not permit resolution of the angles between segments of individual legs. Note that unlike the legs of other segments, the prothoracic flex legs during retraction.

(C) Walking behaviour

Fig. 10 is a histogram of observed walking speeds. The cricket walks between 2 and 10 steps s^{-1} on this substrate under experimental conditions. Speeds slower than 2 steps s^{-1} involve starts and stops and may correspond to the slow walking of cockroaches that Delcomyn & Usherwood (1973) termed 'ambling'. At speeds faster than 10 steps s^{-1} the cricket resorts to small hops interspersed with normal steps. From Fig. 10 it can be seen that adult female crickets walking on the substrate show a preference for walking about 4.5 steps s^{-1} .

The mean peak force (and standard deviation) exerted on the substrate as a function of stepping frequency is shown in Fig. 7. There is a small, but significant, change in peak forces at different speeds.

Diagrams like Fig. 3 can be used to look for effects of sudden shifts in weight borne by one foot that might be caused by lifting or placing a different foot on the substrate. From the geometry of the tripod gait, maximum effect might be expected

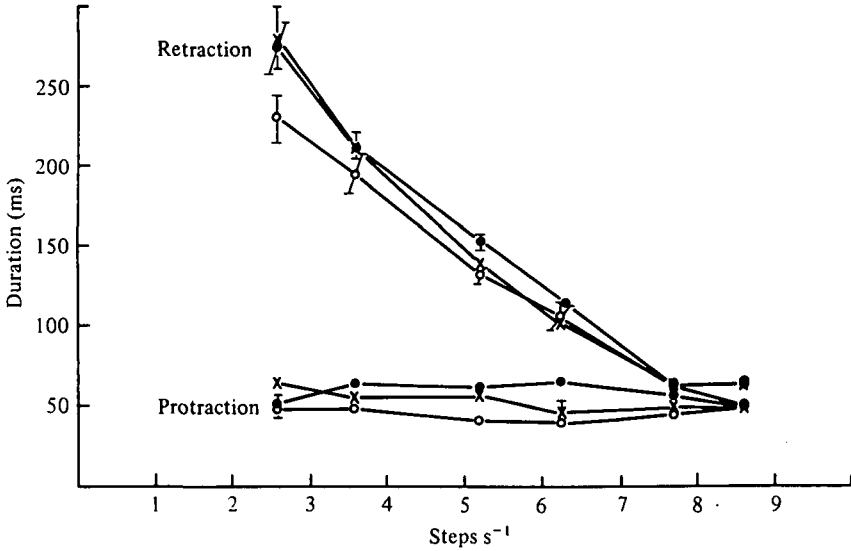


Fig. 5. Duration of retraction and protraction at various stepping frequencies. Data points not showing error bars had standard deviations too small to indicate.

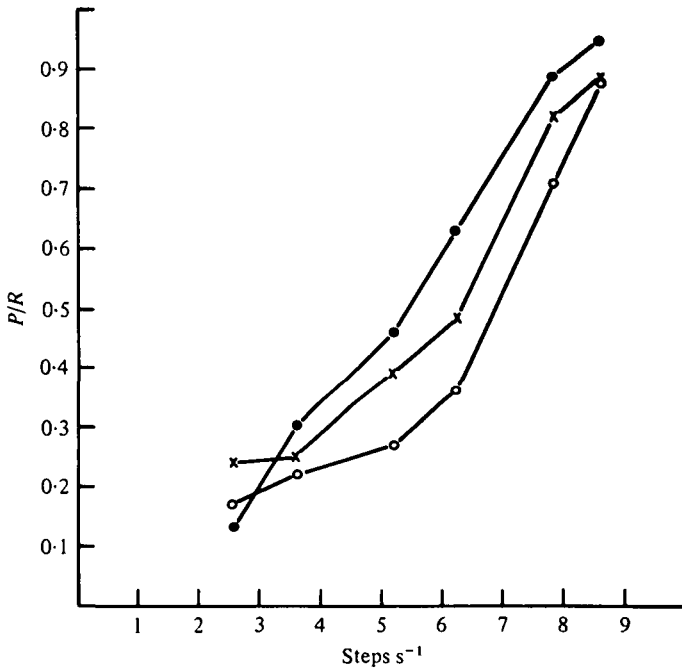


Fig. 6. Change in the *P/R* ratio (which is unitless) at various stepping frequencies. Since the data for this chart was obtained from the results of data shown in Fig. 5, there is only one data point for each stepping frequency.

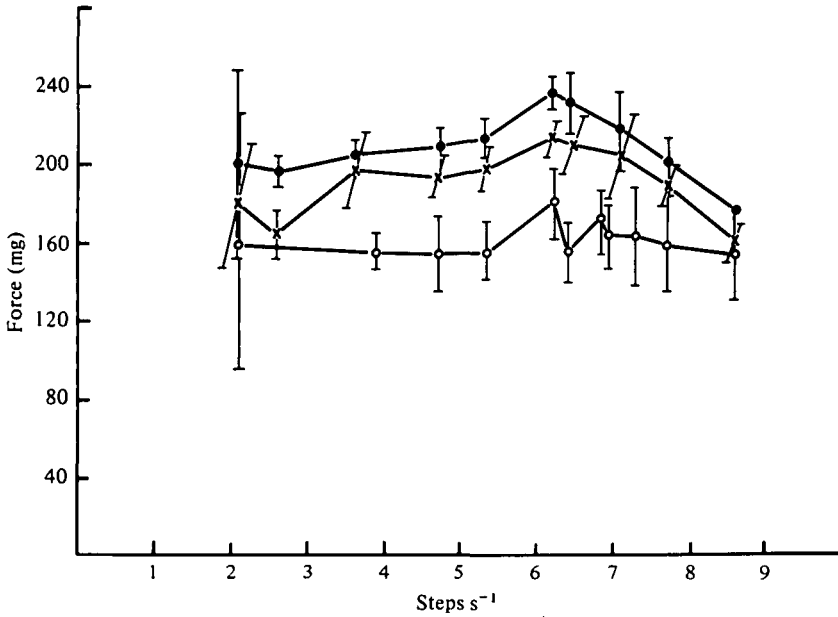


Fig. 7. Peak forces exerted on the substrate at various stepping frequencies. The dots represent the mean and the error bars indicate the standard deviation of the vertical component of the force. This figure represents the average highest force recorded for each leg at each stepping frequency without reference to when that peak force occurs in the retraction. For typical forceprints, see Figs. 3 and 8. ●, Metathoracic legs; ×, mesothoracic legs; ○, prothoracic legs.

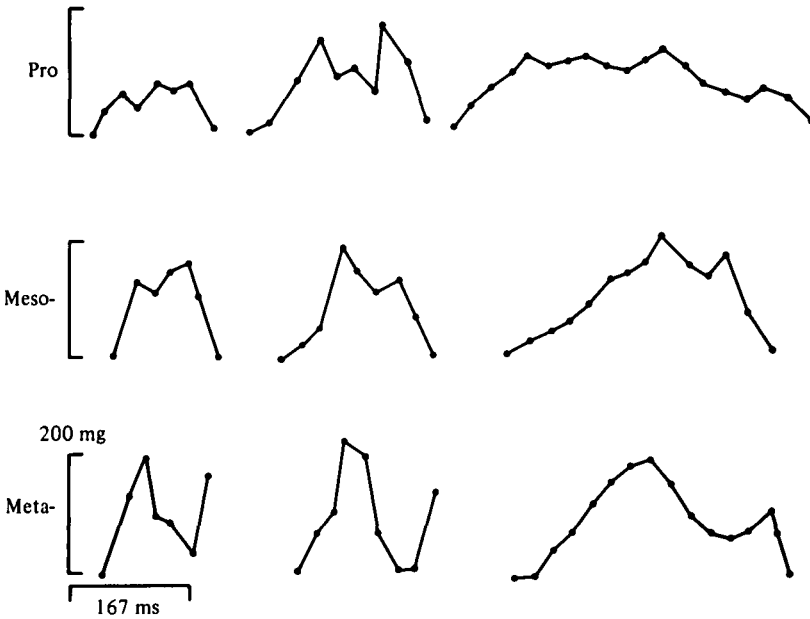


Fig. 8. Typical forceprints of legs of the three segments at three stepping frequencies (for average forces see Fig. 7). The three forceprints on the left represent a stepping frequency of about 7 steps s⁻¹, the middle three represent a stepping frequency of about 5 steps s⁻¹, and the three forceprints on the right represent a stepping frequency of about 3 steps s⁻¹. Note that the shape of the forceprints of each segment is distinctive and constant even at different stepping frequencies.

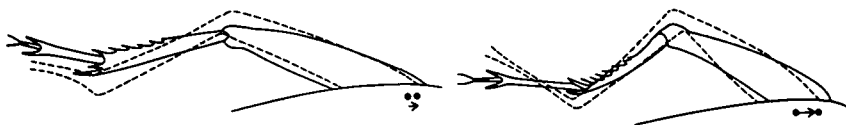


Fig. 9. Tracing of metathoracic leg position from one frame before protraction (solid line) and two frames before protraction (dashed line) from sequences showing a surge in the signal just before protraction. The tracings were superimposed to show that the leg has extended in that interval (16 ms). The arrow indicates how much the tracings had to be moved to superimpose them, which is how far the body had moved forward over the legs in that interval. These two examples represent the range of variability of leg extension and body movements of all examples examined.

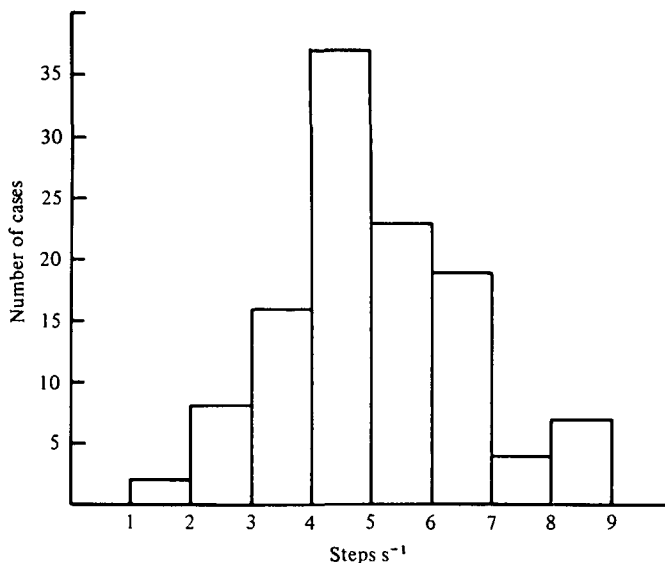


Fig. 10. Histogram of observed stepping frequencies for crickets walking on gelatin-based substrates. Each 'case' represents the average stepping frequency for one passage through the filming area consisting of at least three steps.

on one mesothoracic leg when the other is placed or lifted. Fig. 11 considers the effects on the weight borne by one mesothoracic leg when the other is placed or lifted. The effect can be seen to be small and irregular.

(D) *Standing metachrony*

Land (1972) raised the question of how the oscillations that produce stepping manage to keep in phase while the animal is temporarily stationary. To study this question, analysis was made of sequences in which the cricket stood still to find out if the usual shape of the forceprints occurs at the end of a standing period. Surprisingly, the force exerted on the substrate during stationary periods was not constant, but varied with an amplitude of about 20 mg and a frequency of about 5 Hz (Fig. 12). In many plots like Fig. 12 there appears to be a metachronal phase lag among the legs, and work in progress indicates certain fixed phasic relationships among the legs (Harris, in preparation), so this phenomenon is being called 'standing metachrony'. To demonstrate that there is a regular phase relationship among the forces

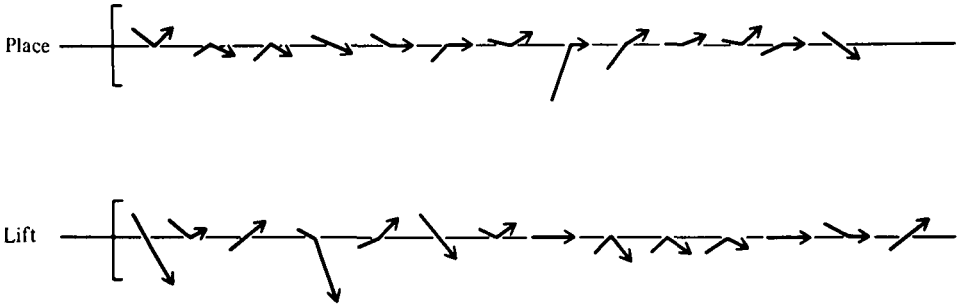


Fig. 11. Changes in the force exerted on the substrate by one mesothoracic leg when the other mesothoracic leg is either placed on the substrate or lifted from the substrate. Each arrow represents three data points from three consecutive film frames. The end of the arrow represents the frame before the opposite mesothoracic leg is placed or lifted, the middle of the arrow (where the arrow touches the line) represents the frame when the contralateral leg is lifted or placed, and the pointer on the arrow represents the frame after the contralateral leg is lifted or placed. A downward deflexion of the arrow means the force on the substrate increased, an upward deflexion means the force on the substrate decreased. Brackets represent 80 mg.

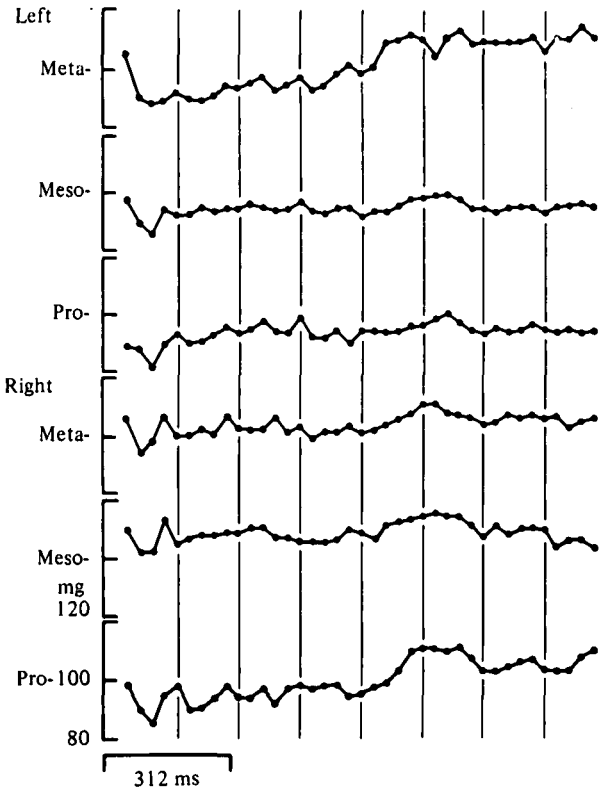


Fig. 12. Standing metachrony. Forces exerted on the substrate by a stationary cricket. Same conventions as Fig. 3.

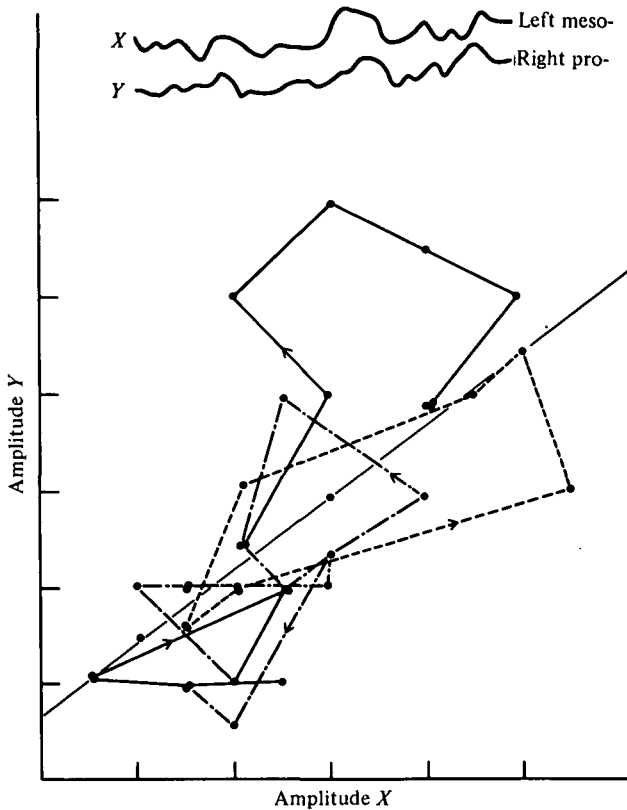


Fig. 13. The amplitude of force for two legs from Fig. 12 (the forceprint for the two legs is given at the top of the figure, drawn to a different scale than in Fig. 12). For each frame of the film, one data point is generated. The amplitude of force exerted by one leg is plotted on the abscissa and the amplitude of force exerted by the other leg is plotted on the ordinate. The data points so generated are connected consecutively. The presence of loops is indicated by marking the connecting loops differently; the direction of the loops is indicated by arrows. The narrow line represents the linear regression. For these two legs, the correlation coefficient is 0.73.

exerted on the substrate during standing metachrony, phase diagrams (Fig. 13) were constructed and correlation coefficients between two legs were calculated. It is not strictly correct statistically to calculate correlation coefficients between two potentially independent parameters, but while more sophisticated tests are being made (Harris, in preparation), the results obtained ($r = 0.60$ to 0.93) are at least suggestive.

Various arguments can be made from the shape and areas of the phase loops, but for this study it is sufficient to point out that the loops are present. The loops turn both clockwise and counter-clockwise which means the forces exerted by the legs vary regularly but drift in and out of phase. This may be therefore another example of 'gliding coordination' (von Holst, 1934), that is, incompletely coupled oscillation, frequently seen in other aspects of insect locomotion (Wendler, 1966).

DISCUSSION

The stepping behaviours of different segments are not identical. The metathoracic legs spend a higher percentage of the step cycle protracting than do legs of other segments (Fig. 6). The same was found for the cockroach (Delcomyn & Usherwood, 1973). Pearson & Iles (1970) found that the bursts to the metathoracic coxal levators were indeed longer than the bursts to the mesothoracic coxal levators in the cockroach. The longer protraction time may be necessary because the metathoracic legs are longer or because the mesothoracic and prothoracic legs may be more involved in balancing.

The greater irregularity of the forceprints of the prothoracic legs and the lower magnitude of peak force exerted on the substrate by the prothoracic legs (Fig. 7) suggest that the prothoracic legs are more involved in balancing or searching than in propulsion. The prothoracic legs protract and retract in the proper metachronal order (Fig. 3), but during each retraction there is greater variability in the pattern in the force exerted on the substrate than is seen in other segments. It is interesting to note that the prothoracic legs flex during retraction (Fig. 4) while the legs of the other segments extend.

Previous studies on the contributions of central and peripheral nervous elements to the generation of walking patterns have focused on the (larger) mesothoracic and metathoracic legs. It is possible that these studies are not generalizable to the prothoracic legs and that the coordination patterns of the prothoracic legs are considerably more sensitive to sensory feedback than the legs of other segments. This was suggested also by Burns (1973), who found greater variability in protraction and retraction durations in the prothoracic legs than in the legs of other segments. At very slow stepping frequencies (less than 2 steps s^{-1}) the forceprints of all legs show no repeating pattern, and resemble the forceprints of prothoracic legs. One possible explanation for this change from a systematic pattern of forceprints to a variable pattern is that at slower walking speeds the animal is now feeling her way more carefully; that is, that she is making use of sensory feedback to make fine adjustments in each retraction.

The differences in shapes of the forceprints of the legs from different segments could mean the legs behave differently and/or carry different loads. This means that a more careful definition of 'metachrony' needs to be made since it has been heretofore tacitly assumed that the legs of all segments are functionally identical. 'Metachrony' now should be seen to be simply the proper temporal sequence of stepping of the legs relative to each other, which is independent of detailed events during the protraction or retraction of any one leg.

There is a small but significant change in average peak force exerted on the substrate at different stepping frequencies (Fig. 7). It may be that the slight increase in force at rates faster than 5 steps s^{-1} is why the animal chooses to walk below this rate (Fig. 9). The decrease in force at still higher walking speeds may be due to effects of increased momentum, or perhaps to recruitment of new patterns of nervous stimulation which might, for example, result in the conversion of postural muscles to propulsive muscles thereby increasing efficiency. The peak forces reached by the legs of different segments are different. The peak forces reached by the metathoracic

legs are the highest and the prothoracic legs produce the lowest peak force. This serves as another illustration that the legs of the different segments are not functionally identical during normal walking. The difference in peak forces may be accounted for in part by the fact that the centre of gravity of the female cricket lies between the coxal articulations of the metathoracic legs, so the posterior legs must, presumably, carry a larger load. However, this is only a partial explanation, since what is being compared is the peak force exerted on the substrate, not the minimum force which would support the animal's weight; and in the case of the metathoracic legs, that peak force occurs early in the retraction.

A dip in the forceprint of the mesothoracic legs occurs when the leg is at right angles to the body and does not occur if the leg is bent at the femoral-tibial joint, when, for example, the insect is turning. These observations suggest that the dip is caused by a mechanical alignment of force angles such that the force vectors are momentarily reduced, rather than by a feature of the nervous-muscular system. Nonetheless, such a dip could serve as a sensory signal. Cruse (1976) found similar dips in some of the forceprints, and human dog forceprints also show a double peak in force exerted on the substrate (Alexander, 1977) but the causes are probably different.

The surge in force exerted on the substrate by the metathoracic legs just before protraction (Figs. 1(e), 3, 8, 9) is apparently caused by sudden extension of the femoral-tibial joint, sometimes with the involvement of other joints as well. The push resulting from this extension may be necessary to shift the weight the leg was carrying to a more anterior leg, or may be the result of a hurriedly completed retraction mediated by a reinforcing reflex (Pearson & Duysens, 1976). Again, it is possible that the sensory feedback from such an extension may signal other segments of the imminent lifting of the leg.

Forceprint details like the mesothoracic dip and the metathoracic surge occur during single retractions and therefore independent of protraction and retraction cycles. They are seen at all stepping frequencies (Fig. 8). The metathoracic surge appears to be largely mediated by the flexor and extensor muscles in the leg (so-called 'intrinsic' muscles), compared to retraction and protraction, which are more strongly mediated by coxal levators and depressors ('extrinsic' muscles). Since both 'intrinsic' and 'extrinsic' muscles are normally employed in walking, it is plausible that nervous control of walking in insects consists of two superimposed systems: a central pattern generator which mediates metachrony through coxal levators and depressors, and a system mediating complex balancing which acts through intrinsic leg muscles. Presumably, the second system is more sensitive to sensory feedback. According to this hypothesis, a mechanical model for an insect leg would be a rotating gear operating the coxal-femoral joint and a spring representing the tibial-femoral joint.

Support for this idea comes from a difference in the nervous stimulation patterns of the 'intrinsic' and 'extrinsic' muscles. Pearson & Iles (1970) found only phasic bursts to metathoracic coxal flexors and depressors (tonic stimulation occurred very rarely and then only at low frequencies of discharge). The bursts alternated between flexors and depressors and the frequency of bursts related directly to the rate of protraction and retraction. This is what would be expected in a pattern generator

On the other hand, Hoyle (1964), Ewing & Manning (1966) and Runion & Usherwood (1968) found that stimulation of the tibial flexors and extensors was continual and simultaneous to flexors and extensors. Specifically, phasic stimulation of tibial extensors and flexors through the fast excitatory nerve is involved in jumping. Tonic stimulation of tibial extensors and flexors through the slow excitatory nerve follows the pattern of force production from extension of the tibial-femoral joint (Runion & Usherwood, 1968). Further, Runion & Usherwood (1968) describe a reflex connection between the tarsal hairs and the tibial extensors, mediated through the slow excitatory nerve, which functions while the animal is stationary and which presumably therefore is involved in maintaining balance. Tonic stimulation and sensory feedback are just what would be expected in a system undergoing small and rapid adjustments, as would be the case in this postulated balancing system.

Pearson & Iles (1973) found that severing one of the two nerves carrying sensory information from the cockroach metathoracic leg did not abolish rhythmic leg movements nor prevent normal patterns of stepping. However, severing both nerves caused the animal to adopt an unusual posture and to walk with great difficulty, without being capable of normal adjustments, although using an apparently normal tripod gait. This lends additional support to the hypothesis that pattern generation and sensory feedback to muscles involved in balancing are anatomically separate, but neurologically superimposed systems.

To postulate superimposed pattern-generating and balancing systems offers a way out of a current dilemma. Sensory feedback has been shown to influence the cycle of protraction and retraction. Wong & Pearson (1976) found that trochanteral hair plates and cuticle stress receptors are normally involved in the timing of protractions. However, animals with ablated sense organs, and completely deafferented preparations can cycle approximately normally (Wendler, 1966; Pearson & Iles, 1973), so the sensory feedback is not required for central generation of stepping even though it may be normally utilized by intact animals. The finding in this study of varying forceprint details within normal metachronal steps suggests that central pattern-generation and sensory-feedback mechanisms are operating simultaneously but with different principal targets. This hypothesis would predict that deafferentation would not affect protraction and retraction (metachronal cycles) very much but would profoundly affect balancing.

The effect on the weight borne by one mesothoracic leg by lifting or placing the other mesothoracic leg on the substrate is small and irregular (Fig. 11). This equivocal result suggests that there is very little mechanical linkage (movement in one leg affecting sensory or motor inputs in the other) between these two legs and therefore argues against Pearson & Iles' (1973) third mechanism for coordination (indirect coupling of intersegmental reflexes by mechanical linkages). If metachronal rhythm is not established by mechanical interaction between legs, there are many other possibilities involving the central nervous system, including those requiring a central tape. Another argument for central generation of metachronal pattern is the low variability in peak force exerted on the substrate at slow walking speeds (but above 2 steps s^{-1}). This lack of variability could be explained by either a very sensitive feedback system or by the repetitive playing of a central tape. However, it seems likely that an animal responding to a sensory feedback system would show

more fluctuation than an animal responding to the repetitive playing of the same tape. At very slow speeds (less than 2 steps s^{-1}) there does appear to be a change in variability and this may signal the change to a more sensory-sensitive kind of walking. This is illustrated by the increased variability in peak force and in the nonrepetitive shapes of the forceprints. Delcomyn & Usherwood (1973) found a change in character in the burst patterns below 3–4 steps s^{-1} in the cockroach and suggested that below that frequency the animal used a different gait termed 'ambling'.

Pearson (1972) found that the coxal depressor in the cockroach spiked spontaneously at a rate of 5–30 Hz (his diagrams show a spontaneous rate of 3–4 Hz. This compares with the rate of about 5 Hz of the standing metachrony and suggests that the standing metachrony may be caused by the activity of the coxal levators and depressors working at levels too low to cause movement, but applying sufficient isometric pressure to be picked up by the substrate transduction technique. The preferred rate of stepping of the cricket in our conditions is around 4.5 steps s^{-1} (Fig. 10), which suggests that this rate of stepping may be generated by the spontaneous rate of the depressor motor neurones. Delcomyn & Usherwood (1973) found that the slow depressor motor neurone continued to spike for 15 min during a stationary period and only stopped spiking while the animal was crouched down with all its weight borne by the body instead of by the legs.

The standing metachrony is not the effect of a single leg oscillator because there is relative coordination with other legs. This suggests that oscillating programs persist during stationary periods. These oscillator programs may be either central oscillator programs or continuously active proprioceptive oscillator programs and may be linked individual segment oscillators (Graham, 1977).

Graham (1977) concluded that coordination of metachrony must be by sensory cues since a central pattern generating system would not know where the leg was positioned following a stationary period. However, the existence of standing metachrony suggests a mechanism whereby a central oscillatory mechanism may indeed provide the necessary information for starting up following a stationary period. To make an analogy, the cricket has its motor running and its clutch disengaged. This suggestion is consistent with the evidence discussed above that pattern generation is a centrally mediated event.

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