

# MODELLING THE CONTROL OF WALKING IN INSECTS

Jeffrey Dean, Holk Cruse

Abteilung für Theoretische Biologie und Biokybernetik, Universität Bielefeld,  
Postfach 8640, D-4800 Bielefeld 1, FRG

## Abstract

The current state of control models for legged locomotion is discussed first in terms of general control requirements in order to illustrate the complexity of the problem and then in terms of a specific, kinematic model for leg coordination in the stick insect. The kinematic model is used to demonstrate that the coordinating mechanisms deduced from behavioral experiments are sufficient to qualitatively simulate normal step patterns. However, quantitative discrepancies indicate an important role for the dynamic factors not yet incorporated in the model.

## 1. Control Requirements for Legged Locomotion

Legs easily outperform wheels in climbing or travelling over uneven ground. This advantage is the reason why numerous laboratories devote much time and effort to designing walking machines and testing diverse control algorithms. However, progress has been slow despite numerous working prototypes--animals which walk using a variety of structures and mechanisms. Before examining the control of walking in the stick insect, it is useful to consider the general problem in order to appreciate why learning to walk has been so hard for machines and where a theoretical analysis runs into difficulties.

The first task to be solved by a walking system is easy to define: the legs must always be positioned to resist the effect of gravity and to maintain the distance between body and substrate within working limits. As a first goal in learning to walk upright, this task can be formulated as keeping the center of gravity above an area of support defined by the locations of the feet contacting the ground. Fulfilling this condition provides static stability even if the feet cannot actively grasp the substrate: the walker can halt its movement at any point and not fall over.

However, it is in the nature of legged locomotion that the feet vary their positions with respect to the center of gravity as they propel the body forward. Moreover, because the length of a leg is finite, each leg must be periodically lifted and returned

to where it can begin a new stance. Thus, each leg performs rhythmic step movements in which it alternates between stance, when it provides support and propulsion, and swing, when it returns to the starting point for the next stance.

This rhythmic stepping causes the relation between the center of gravity and the support area to vary continuously. Therefore, the concept of static stability must be augmented to include the notion of safety margins and the realization that maximum stability is only possible for slow speeds. The faster the system needs to move, the smaller the number of legs which can be kept in contact with the substrate at any moment. To increase speed still more, as in the faster gaits of vertebrates, static stability is completely abandoned in favor of dynamic stability. A fast-moving vertebrate uses the inertia of its body and limbs to pendulate from one unstable position to another.

Besides ensuring adequate support, the walking system must provide forward propulsion and allow for changes in speed and direction. These functions involve adjusting the magnitude and direction of the forces the legs apply to the substrate.

Thus, the criteria for successful walking are few and only basic physics is required. Nevertheless, theoretical approaches to walking have advanced more slowly than one might have expected. The problem lies in the complexity of the total system. First, the six legs of an insect theoretically allow nearly 40 million gaits--different sequences (stepfall patterns) of swing and stance in the six legs (McGhee, 1976). Second, each leg has three major joints which must be coordinated for proper stepping. Finally, legs in stance are mechanically coupled through the substrate and the body itself possesses additional joints. As a result, the relationship between what any one leg does and the global performance of the system is indirect. The set of possible step movements for each leg is enormous and what movements are appropriate for maintaining stability or achieving a change in direction depend upon the actions of the other legs.

## **2. Approaches to Modelling Leg Coordination of Walking Insects**

Before turning to a specific model for the stick insect, it is worthwhile to briefly review previous theoretical approaches to insect walking.

A deductive approach was followed by McGhee and his colleagues in a formal analysis of gaits for four and six-legged walkers (McGhee, 1976). The set of possible gaits, generated by combinatorial analysis of the corresponding finite state machine, was first reduced using the plausible assumption that all legs make similar movements. Then the remaining gaits were evaluated using a stability criterion defined as the minimum distance between the vertical projection from the center of gravity onto the substrate and the boundary of the area of support spanned by the feet. The gaits for slow walking identified by this procedure were not new: they were the same metachronal gaits typically used by many arthropods.

Relying upon the evaluation of a global parameter, such as stability, to evaluate gaits creates difficulties when step patterns must be generated because it requires a central processor which monitors the configuration and movement of all the legs. The complexity of biological walking systems would place an enormous computational burden upon such a central processor. In fact, behavioral observations discussed below indicate that control is decentralized, so that each leg, and possibly each leg joint or set of joints, has its own semi-autonomous controller, referred to here as the step pattern generator. These controllers interact with each other to generate appropriate step patterns.

The inductive approach, which begins with observed gaits and attempts to understand how these are generated, has a longer history. It has been applied to both physiological and functional control mechanisms. The latter application uses models on an abstract level to try to understand the control principles underlying walking (e.g. Box 3). The ultimate goal is a comprehensive model which provides a quantitative formulation of the control algorithms for specifying leg movements to achieve a particular behavioral performance. This is the approach followed here. The former application attempts to synthesize physiological information on neural properties and connectivity. The goal is to understand the neural mechanisms producing the observed pattern of muscle activation.

Only initial steps have been taken toward these goals. In the absence of a comprehensive model, attention has focussed on the generation of step rhythms. Models at the behavioral or functional level begin with coordination rules deduced from observations of walking insects. The model serves as a kind of shorthand for the behavioral description. For example, the observation that swings of adjacent legs tend not to overlap is used to postulate an inhibitory influence between the step pattern generators of adjacent legs. Such models can be used to test the completeness of hypotheses derived from behavioral data or, where relevant parameters cannot be precisely measured, evaluate the consequences of assuming different values for such parameters. This is the method used here and in numerous earlier models (review Cruse and Graham, 1985; Graham, 1985).

Models of the physiological mechanisms explicitly consider the neural origin of rhythmic stepping. They require information on neuronal properties and interconnections. Sufficient physiological information is available to construct realistic neural models for some rhythmic behaviors but not for walking. Efforts in this direction have been limited to the demonstration that simple arrangements of two or more neurons or neuron pools can produce alternating activity, which is taken to represent swing and stance (e.g. Brown, 1911, Wilson and Waldron, 1968) or a simple step cycle (Szkeley, 1968).

### 3. The Control of Leg Movement in the Stick Insect

#### 3.1. The Nature of the Step Pattern Generator for Individual Legs

Numerous investigators have shown that different legs may step with different frequencies (e.g. von Holst, 1935; Wendler, 1964; Foth and Bässler, 1985). Therefore, it appears that each leg possesses its own step pattern generator. Coordination of the legs, the focus of this paper, represents the coordination of these step pattern generators. Lower levels of control, which organize the movements of the different joints within a leg, and higher levels of control, which govern walking speed and direction, will not be considered.

An important issue for neurobiologists was the question of what anatomical elements participate in the step pattern generator. Simple neuronal models have often been advanced with the implication that central neural circuits can generate motor activity patterns sufficient for walking. Autonomous central pattern generators (CPGs)--neural circuits in the central nervous system (CNS) which can produce much or all of the normal motor output in the absence of patterned sensory input--have been characterized for many rhythmic behaviors (review Delcomyn, 1980). A central pattern generator for walking with this degree of autonomy has not yet been demonstrated conclusively.

Abstract descriptive models derived from behavioral observations do not explicitly consider the identity of the step pattern generator (e.g. Box 3). When applied to normal step patterns, models of this kind often make no formal distinction between an autonomous CPG and one dependent on feedback from the periphery (peripheral oscillator models). However, several control tasks, such as responding to external disturbances or maintaining gait continuity in starting and stopping, are more easily handled within the framework of a peripheral oscillator model. Most recent behavioral results have emphasized the role of sensory information in modulating the step pattern (review Bässler, 1987; Cruse, 1990).

These experiments show that the step pattern generator includes the peripheral sensory and motor elements. Changing the afferent input, by either altering the external conditions or manipulating leg proprioceptors, leads to changes in the spatial and temporal pattern of stepping. The step pattern generator is affected by the position of the leg and by the load it experiences. The force developed by the leg also reflects the load. Thus, leg movement is not merely the expression of endogenous activity in the CNS; the neuromuscular system of the leg itself is an important element in the step pattern generator. Further experiments suggest that while information on position and load is used to determine the transitions between swing and stance, the control system assumes the characteristics of a velocity controller in carrying out each movement (Dean and Cruse, 1986; Weiland and Koch, 1987).

These results, plus the absence of a robust CPG, have led most investigators to include the peripheral elements, both sensory and motor, as an integral part of the pattern generator and therefore an important factor in the interactions between leg

controllers. One consequence is that state variables such as leg position have been explicitly included in many recent models. A second consequence relates to possible analytical treatments. At the current level of understanding, a leg can be in one of two discrete states, stance or swing, in which different coordinating mechanisms are active. This formulation does not lend itself to simulating the step rhythm with smooth functions. In contrast, the neural correlates of these states, the activity in populations of neurons, make state transitions which are rapid but not instantaneous. As discussed below, the introduction of force as a state variable in models may create a continuous variable at the behavioral level and provide a bridge between these two viewpoints.

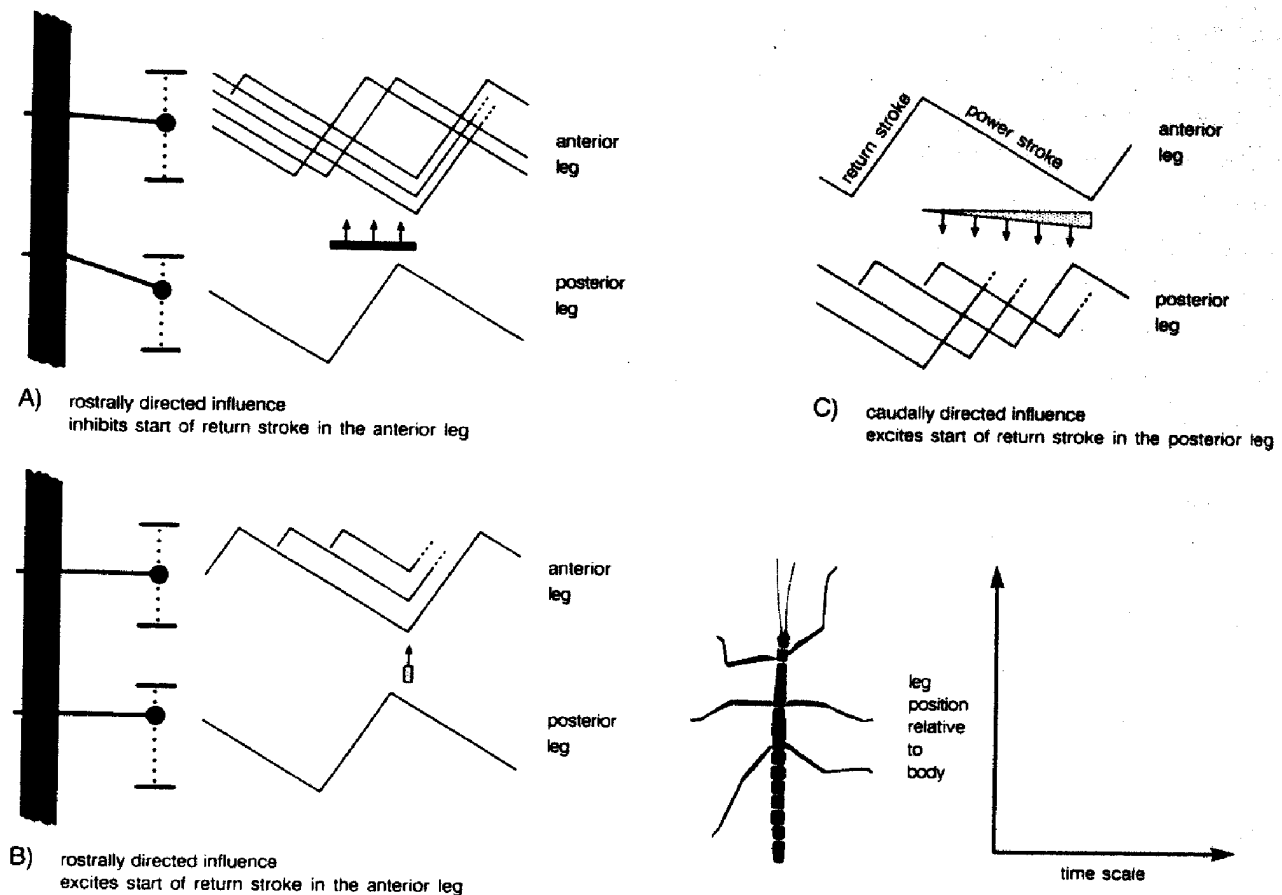
### 3.2. The Nature of the Mechanisms Mediating Coordination of the Legs

The ability of the step pattern generator to vary its activity in accord with the local state of the leg establishes a non-neural link between the legs. Through the mechanical coupling, the action of each leg affects the load on the other legs and this, in turn, can activate intraleg mechanisms which influence force development and step pattern.

However, the mechanical influences experienced by one leg are not tightly linked to specific actions by other legs, so they do not provide good information for global coordination. In fact, insects continue to produce coordinated stepping when mechanical coupling is reduced, as in supported walking on a treadmill, or eliminated, as in supported walking on a slippery surface. This finding demonstrates the existence of coordinating mechanisms mediated by the central nervous system. These mechanisms are the focus of the model studies described here. However, intraleg mechanisms responding to the current mechanical state continue to play an important role in leg coordination, as shown below. Some intersegmental mechanisms mediated indirectly by mechanical coupling are equivalent to influences transmitted through the CNS, particularly during slow walking.

Neurally mediated coordinating mechanisms appear to act only between adjacent ipsilateral legs and between the contralateral legs of each segment. Experimental results for the stick insect have identified six different mechanisms contributing to coordination among the legs either by influencing the step end-points (the anterior extreme position or AEP and the posterior extreme position or PEP) or by modulating the force exerted during stepping (reviews Graham, 1985; Cruse, 1990). The position and timing of the transition from stance to swing is crucial for maintaining adequate stability because this transition ends the support phase of the leg. The most important timing influences affect this transition (Fig. 1).

The three ipsilateral influences are asymmetric: within each pair of legs, one is the controlling leg or sender and the other is the controlled leg or receiver. One



**Figure 1.** Coupling mechanisms between adjacent ipsilateral legs of the stick insect measured in behavioral experiments. The range of movement of the two legs is illustrated at the left. The single trace in each part plots the movement of the controlling leg against time; upward change corresponds to forward movement of the leg. The multiple traces illustrate the way the influence modifies the movement of the controlled leg for different initial configurations. The duration and intensity of the influences are indicated qualitatively by the length and thickness of the bar or wedge: solid and open figures represent inhibition and excitation, respectively.

influence passes from front to rear. The farther the controlling leg retracts, the more it excites the adjacent caudal leg to begin a swing (Fig. 1c). Two others are rostrally directed. When the controlling leg is in swing, it inhibits the adjacent rostral leg from beginning a swing (Fig. 1a). When the controlling leg has completed its swing and begins active retraction, it excites the rostral leg to begin a swing (Fig. 1b). In the free-walking animal, both these rostrally directed influences are probably augmented by local mechanisms in the controlled leg: intrinsic responses to the load changes presumed to result from the actions of the controlling leg act in the same direction as these influences mediated through the CNS.

Contralateral coordination is weaker and less easily measured. The contralateral mechanisms have the same form as the ipsilateral mechanisms, but the interactions are symmetric. Both excitatory mechanisms identified for ipsilateral leg pairs also act within contralateral leg pairs. The strength of the coupling varies in dif-

ferent segments. The excitation at the start of stance is present in all segments; the position-dependent excitation has been clearly identified only for front and rear legs. Whether the third major ipsilateral mechanism, the inhibition during swing, also acts between contralateral legs is unclear. Experiments in which ipsilateral thoracic connectives are cut, so that each ipsilateral leg is solely dependent on its contralateral coupling for coordination, suggest that contralateral coordination is strongest between front legs and weakest between middle legs.

Two ipsilateral mechanisms affect the transition from swing to stance. The first is a spatial coordination which causes each leg to step to a position close behind the position of the next rostral leg (review Cruse, 1990); the leg moves to a target determined by proprioceptive information from the rostral leg. This mechanism is probably a special adaptation for animals walking on a patchy substrate. The information that the rostral leg possesses a foothold serves as a predictor that a neighboring leg can find a foothold if it steps close to this position. In this way, a support found by the front leg can be used successively by the ipsilateral middle and rear legs. This mechanism does not have a strong influence on timing because the duration of the swing is only weakly correlated with step amplitude, but it does re-establish normal spatial relationships between the legs following a disturbance. This targeting mechanism has not been found in either crayfish or locusts, animals for which finding adequate footholds is less critical. It has been considered for use in walking machines but not implemented (Donner, 1984).

The second influence on the transition from stance to swing serves to correct errors in leg placement. If a leg steps onto its rostral neighbor, then the tactile input from the rostral leg triggers a reflex causing the caudal leg to lift and step slightly to the rear (Graham, 1979).

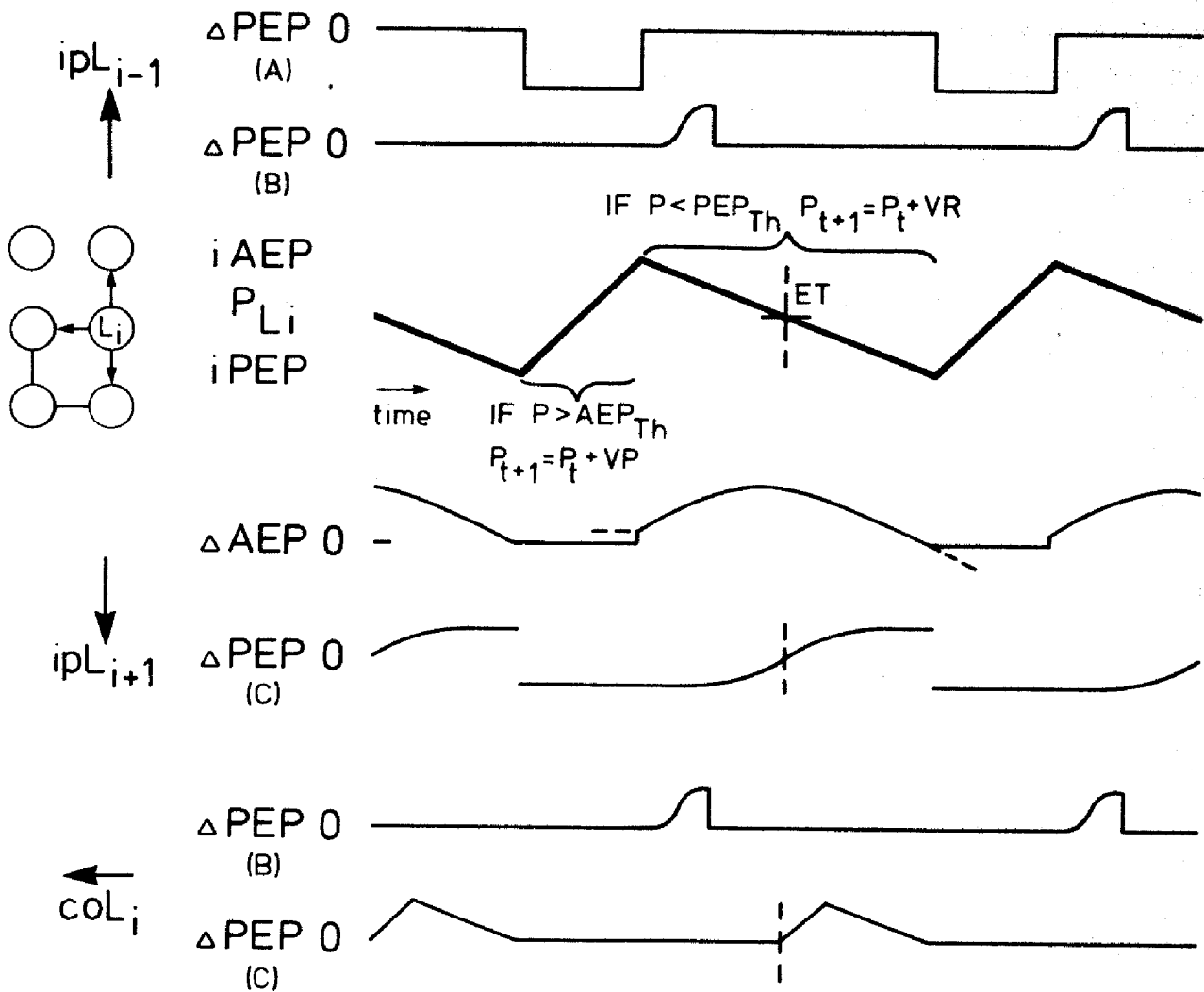
A final influence affects the force generated during the stance. When the controlling leg experiences a greater resistance and increases the force of its power stroke, then it also excites adjacent legs to exert more force. This interaction is active in both directions in all pairs of adjacent legs except the two rear legs.

#### **4. The Structure of the Model**

##### **4.1. The Nature of the Step Pattern Generator for Individual Legs**

To test the sufficiency of the mechanisms described above, the four timing influences were combined in a computer model which will be described in detail elsewhere. Here the model will be described briefly and then used to illustrate several features of the coordinating mechanisms.

In constructing a model (Box 3), it is first necessary to select decision rules for switching between swing and stance. Like other kinematic models with an explicit peripheral referent, the present model uses leg position for this purpose. The model



**Figure 2.** The step pattern generator for each leg, illustrated here for leg  $L_i$ , is simulated as a relaxation oscillator in which the variable corresponds to leg position ( $P$ ) and the two states correspond to stance and swing. In successive time steps, the leg position is compared with the current threshold to determine whether the leg should continue moving in the same direction or reverse direction; then the appropriate velocity input ( $VR$ ,  $VP$ ) is added. All six step pattern generators have the same intrinsic thresholds for ending stance ( $iPEP$ ) and swing ( $iAEP$ ). Each leg sends signals of different types to adjacent ipsilateral ( $ipL$ ) and contralateral legs ( $coL$ ). These signals depend upon the state, the leg position and the velocity inputs of the sending leg; they additively change the indicated thresholds of the receiving leg. The letters in parentheses denote the corresponding behavioral effects shown in Figure 1. The position  $ET$ , which determines when the position-dependent influences are neutral, moves rostrally with increasing retraction speed. The dashed lines for the influence on  $AEP$  indicate the course of the effect for stance positions rostral to the  $iAEP$  and caudal to the  $iPEP$ .

leg functions as a relaxation oscillator with threshold positions defining the endpoints of the two movements (Fig. 2). One simplification is the use of constant velocities during swing and stance to replace the forces actually developed by the muscles. This makes the transitions between phases instantaneous and not smooth. Coordinating influences are expressed as changes in the thresholds. This choice of state variable has the advantage that leg position is more easily measured than load. It is



supported by experimental findings showing shifts in step end-points depending upon the state of the controlling leg. Expressing the coordinating influence as a shift in a position threshold is natural for the targeting behavior where the position of the controlling leg is used to modulate the end-point of the controlled leg's swing, the anterior extreme position or AEP in forward walking. Expressing the rostrally directed inhibition as a shift in a position threshold also appears natural because the posterior extreme position (PEP) may shift caudally when the controlling leg prolongs its swing. For other influences not included in the present model, e.g. the intraleg responses to loading, the threshold would be more naturally expressed in terms of force vectors. The control system used by Donner (1984) is an example of using load and changes in load thresholds as the control parameter. A challenge addressed in the continuation of the present modelling is to reconcile these two formulations

#### 4.2. Implementation of the Coordinating Mechanisms

The model (Fig. 2) incorporates the ipsilateral and contralateral mechanisms shown in Figure 1 plus the targeting mechanism. The form of the influences is based on experimental findings, but some details and numerical parameters must be estimated. For example, the targeting influence does not appear to be equally strong for all target leg positions: extreme forward positions, which the caudal leg cannot reach, do not cause the leg to move as far forward as intermediate positions. Therefore, the targeting mechanism was modelled as a linear combination of movement to a fixed, slightly forward position when the target leg is far forward and movement to a position a constant distance behind the target leg when this leg is at or caudal to its mean PEP.

The rostrally directed inhibition (Fig. 1a) is represented by a step change in the PEP threshold. The size of this step cannot be determined from the experimental data because the disturbance involved in physically blocking the swing of one leg probably influences the behavior of the other legs. The size of the step determines the efficacy of the inhibition. Intuitively, it needs to be large enough that if two ipsilateral legs simultaneously approach their intrinsic PEP thresholds and the caudal leg begins its swing first, then the inhibition should keep the rostral leg in stance until this swing is completed. During this interval the rostral leg is compelled by the constant stance velocity in the model to continue moving to the rear. It appears that the inhibition active in fast walking must be nearly equal to the full step amplitude, but in fact less is required. The PEP change measured in the animal will be reduced because a real leg will begin to resist the forward movement and force a decrease in the retraction velocity. This effect is ignored in the present model. Furthermore, the threshold change required for adequate inhibition can be reduced in both model and insect because the excitation from the rostral leg will normally cause the caudal leg to advance its swing.

The strength of the other influences is also incompletely determined by the experimental results. The rostrally directed excitation (Fig. 1b) and the corresponding contralateral excitation are thought to be coupled to the beginning of active retraction in the controlling leg. In the stick insect, but not in the current model, the active retraction may begin with a delay after the leg steps onto the ground. To simulate this interval the influence used in the model includes a delay inversely proportional to retraction velocity.

The caudally directed influence (Fig. 1c) and the corresponding contralateral excitation present greater uncertainties. This mechanism should delay or advance the start of a swing by the caudal leg so that the swing is completed about the time that the rostral leg reaches its intrinsic PEP threshold. Therefore, the position of the controlling leg for which the effect is neutral depends upon the retraction velocity: when the insect walks faster, the swing must be triggered at more rostral positions of the controlling leg. Under the simplifying assumption of constant retraction and protraction velocities, the PEP of the controlled leg required for the leg to arrive at its AEP just as the controlling leg reaches its PEP can be determined as a function of the retraction velocity and the position of the controlling leg. The relation is a line between the following two configurations of controlled leg (the receiver,  $r$ ) and controlling leg (the sender,  $s$ ): ( $AEPr$ ,  $PEPs$ ) and ( $PEPr$ ,  $POs$ ), where  $PO$  is given by the distance the controlling leg retracts during a full-length swing of the controlled leg. (This line follows the margin of the shaded triangles in Figure 4a and continues to the AEP of the controlled leg.) For slow retraction speeds,  $POs$  is near the  $PEPs$ ; for equal protraction and retraction speeds, it is at the AEPs. An excitatory coupling following this minimal requirement, similar to the contralateral influence in Figure 2 or 4a, does not enforce strict alternation; it allows quite asymmetric phase relations because some leg configurations are not modified. The amount of the allowable asymmetry increases with decreasing walking speed.

For the symmetric coupling existing between contralateral legs, strict alternation can be achieved by letting  $PO$  approach the midpoint between AEP and PEP, rather than the PEP, as walking speed decreases. This change means that the mechanism begins to excite a swing in the controlled leg at more rostral positions of the controlling leg. The contralateral phase values observed in the stick insect lie between symmetric alteration and the extreme asymmetry allowed by the minimal form required to prevent overlapping swings.

The effects of using different forms for the threshold shift have also been investigated. The occurrence of in-phase steps by contralateral legs and the symmetry of the coupling suggest that the threshold shift for the controlled leg is never greater than the distance of the controlling leg from its own PEP. Thus, the threshold shift must have a maximum somewhere between the AEP and the PEP of the controlling leg.

In contrast, the coupling between ipsilateral legs is asymmetric and in-phase steps by adjacent legs are rare. Therefore, the relation between the threshold shift

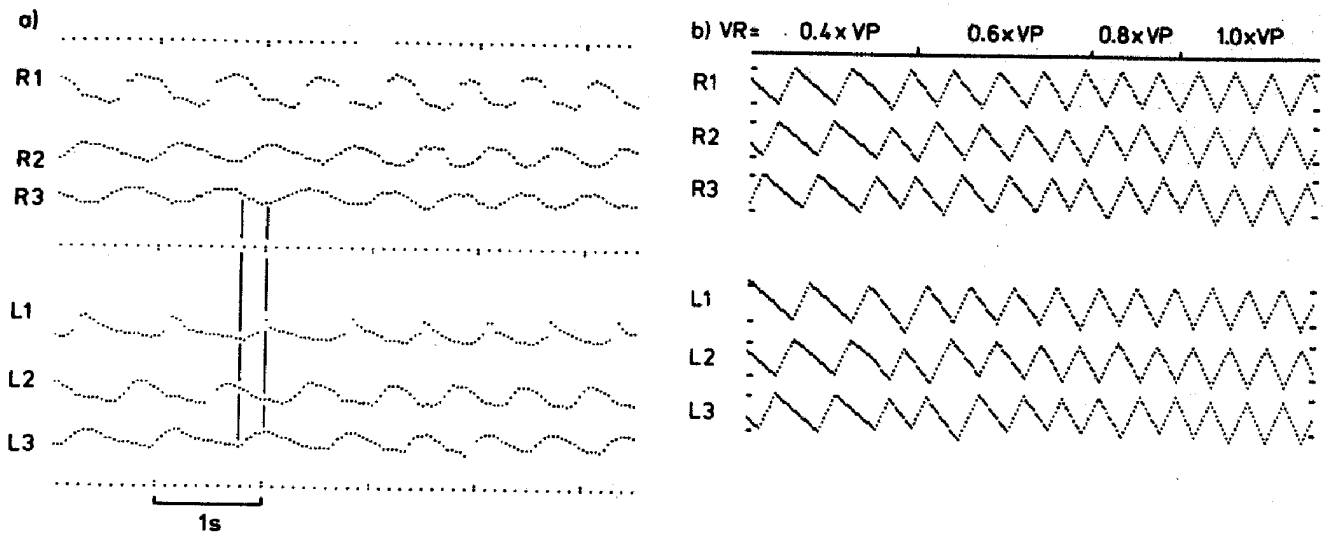
and the position of the controlling leg presumably differs from that of the contralateral mechanism. In particular, the excitation from the controlling leg appears to increase monotonically as the leg moves farther to the rear. To prevent this influence totally dominating other influences, the ipsilateral relation is given a sigmoid form (Fig. 2).

Ipsilateral phase relations typically show a single peak corresponding to asymmetric stepping. Therefore, as a first approximation, the relation between neutral position and retraction speed of the controlling leg can be represented by the minimum necessary to prevent overlapping swings. This is not completely realistic because there is a delay, during which both legs retract together, between the end of the caudal leg's swing and the start of the rostral leg's swing. Moreover, the quantitative relation between ipsilateral lag intervals and step period presents further complications which can be approximated but not completely resolved within the framework of the present model (see below).

## 5. Step Patterns Produced by the Model

### 5.1. General Features

The present model combining several coordinating influences qualitatively reproduces the temporal and spatial organization of step coordination in stick insects (Fig. 3). Unlike models based on a single mechanism (e.g. Graham, 1977; Cruse, 1979), the present model does not require a hierarchy of intrinsic rhythms in the segmental step pattern generators. It rapidly assumes a stable coordination from any starting configuration in a natural way. The coordination of ipsilateral legs is characterized by metachronal sequences of steps progressing from rear to front. When the contralateral position-dependent excitation uses a speed dependence like that used ipsilaterally, it does not enforce symmetric alternation. Histograms of contralateral phase values reveal a broad band of permitted phases. The width of this band can be reduced by letting the excitation begin at more forward positions of the controlling leg. Phase relationships observed in the animal suggest that the actual mechanism is somewhat more restrictive than the minimum requirement but not sufficiently restrictive to enforce symmetric alternation. Nevertheless, the model uses a similar speed-dependence for both ipsilateral and contralateral coupling on the grounds that the physiological mechanisms would be simpler if both influences share a common source. One consequence of this arrangement is a tendency for diagonal leg pairs to step nearly simultaneously, a coordination which has often been observed but is not a fixed rule (Graham, 1972; Hughes, 1952). Here, this pattern results from diagonal leg pairs being subject to a common influence from a third leg, as in the model of Graham (1977); it does not represent a coordinating mechanism connecting legs in diagonal pairs, as postulated by Cruse (1980).



**Figure 3.** Comparison of the step patterns produced by the model (b) with those of the stick insect (a). Each trace represents the position of a leg; the legs are designated as left or right and numbered from front to back. Upward change in a trace corresponds to forward movement of the leg. The results for the simulation show step patterns for several different retraction velocities (VR), expressed as ratios of the protraction velocity (VP).

Two differences between model and insect are worth mentioning. First, the simulated leg movements have the sharp, saw-tooth appearance characteristic of a relaxation oscillator, whereas the steps of the insect are more rounded. The latter correspond to rhythmic changes in forward velocity such that the velocity is slower when one or more legs are near a transition between swing and stance and faster when legs are in the middle of their retraction (Fig. 3b). The reduction in speed at the transitions may simply reflect low-pass characteristics of the skeletomuscular system, but it could also reflect neural delays necessary for processing local and inter-segmental coordination signals.

The second, related difference is that the natural speed dependence of the lag between steps by adjacent ipsilateral legs is only approximately duplicated by the model: the lag does not increase sufficiently for slow speeds. In the adult stick insect, the speed dependence lies between that of constant lag and that of constant phase. Swing duration is virtually independent of step period (Wendler, 1964; Graham, 1972), so the speed dependence primarily affects the duration of the stance overlap after the caudal leg completes its swing. Because retraction velocity is reduced during this interval, its duration has a relatively small effect on the spatial configuration of the legs: the mean AEP and PEP do not vary measurably with velocity. In the model, the neutral position for the ipsilateral position-dependent mechanism must change in order to allow for variable amounts of stance overlap. Because the retraction velocity

is constant, changes in lag correspond to large changes in this neutral position. Attempting to reconcile these factors within the framework of a model with constant retraction velocity leads to neutral positions forward of the AEP, a result which does not appear realistic. The relation used in the model is a compromise.

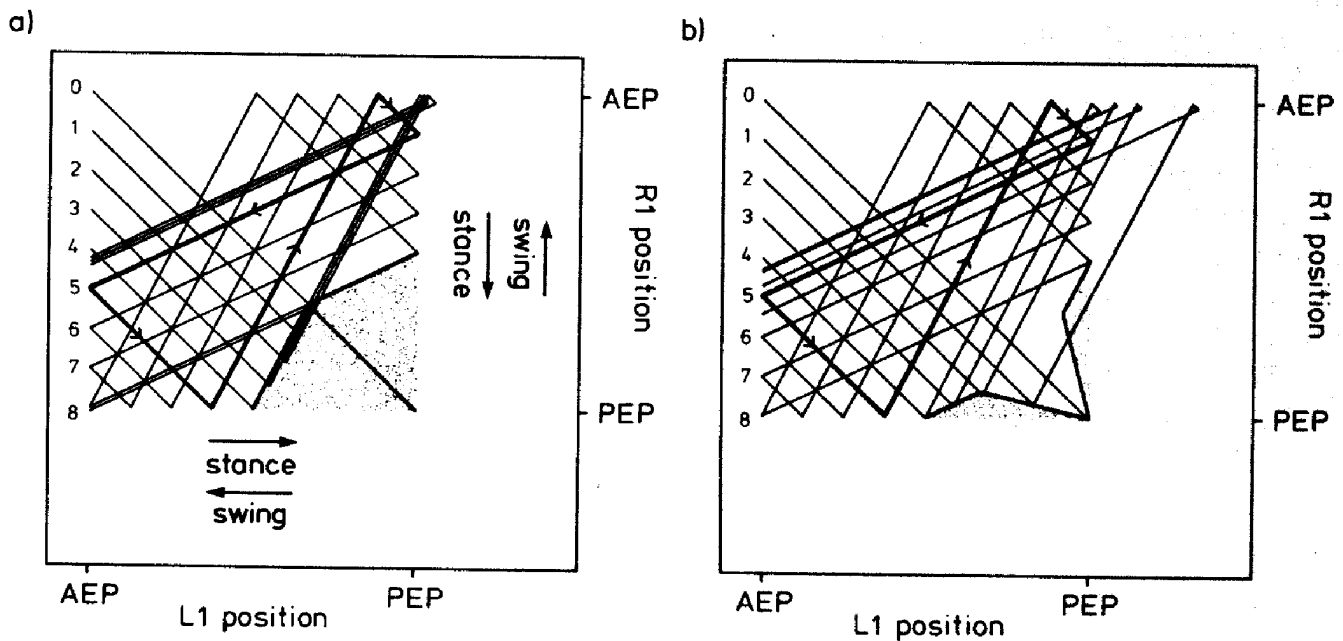
## 5.2. Effects of Coupling Strength on Contralateral Coordination

Behavioral experiments indicate that contralateral coupling is strongest between the front legs. When retraction velocities of left and right legs are equal, the strong form of the position-dependent influence (shaded triangles in Fig. 4a) used between front legs in the model is sufficient to ensure that swings of the front legs do not overlap (Fig. 4a). In contrast, the weaker coupling used between middle legs and between rear legs (e.g. shaded areas in Fig. 4b) does not suffice to prevent overlapping swings. However, the ipsilateral position-dependent mechanism, because it modulates the transition from stance to swing over a wide range of leg configurations, provides a tight ipsilateral coupling and imposes the alternation of the front legs on the other leg pairs. In order to reveal the effect of contralateral coupling in the other segments, the normal coordination must be perturbed by either placing the legs in unusual configurations or varying the retraction velocity of one or more legs.

One unnatural configuration is with symmetric positions of left and right legs in each segment. When a stick insect starts from such a configuration, segmental leg pairs often make several in-phase steps before switching to alternation. The model cannot produce sustained in-phase stepping unless the contralateral position-dependent influence is weaker than that of Figure 4a.

How the stick insect recovers from in-phase stepping is not well-studied. Here the model can generate predictive hypotheses. For example, when the hierarchy of coupling strengths is such that the contralateral coupling is strongest at the front, then the recovery begins at the front and propagates to the rear (Fig. 5a). Recovery is gradual in the example shown because the metachronal sequence facilitated by the ipsilateral configurations prevents the contralateral influence between the front legs from effecting a correction within one step. Nevertheless, alternation is achieved within a few steps. To allow still longer sequences of in-phase stepping, the strength of the contralateral coupling must be reduced. If the form of the influence is slightly modified or the amplitude is allowed to vary, then the switch from in-phase to alternate stepping in the front legs can occur abruptly in a manner often seen in the animal.

When the contralateral coupling is strongest at the rear, then alternation is established more slowly but the pattern is the same (Fig. 5b). The ipsilateral mechanisms used here again cause the recovery to depend upon the direction of change in the front legs. Recovery is slower because the coupling between the front legs is weaker. The strong coupling between the rear legs may mean that this pair achieves alternation about the same time as the front legs and before the middle legs.



**Figure 4.** Phase-plane representation of the coordination of a single contralateral pair of legs. The figure illustrates the effect of combining the position-dependent excitation with inhibition during the swing. In this simulation, one leg begins at its intrinsic AEP and the other leg at one of 9 positions from AEP to PEP. The ensuing step cycle is followed until the first leg returns to its AEP in order to measure the change in the spatial configuration produced by the coordinating mechanisms. Stable coordinations correspond to closed trajectories--those which return to the starting point; these are not stable attractors because the mechanism is neutral for some configurations. For leg configurations in the shaded areas, the position-dependent excitation from the controlling leg (the trailing leg--that farther from its intrinsic PEP), shifts the PEP threshold for the controlled (leading) leg in order to reduce (b) or avoid (a) swing overlap. The strong form alone (a) is sufficient to prevent overlapping swings and adding inhibition during the swing of the leading leg has no effect. Weaker coupling (b) does not excite a swing soon enough to prevent overlapping swings. Adding inhibition prevents overlapping swings by forcing caudal shifts in the PEP of the trailing leg for some starting configurations (e.g. trajectories 1-3).

The strength of the contralateral coupling between the middle legs appears less important. Keeping this coupling weak simplifies the use of an additive threshold computation because the middle leg PEP threshold is also subjected to three ipsilateral influences whereas the front leg PEP is subjected to only two and the rear leg PEP to just one.

The same qualitative result occurs when the contralateral coupling is measured by letting the legs of the two sides step with different frequencies. When the contralateral coupling is strongest at the front, the front legs make fewer overlapping swings than the middle and rear legs and vice versa.

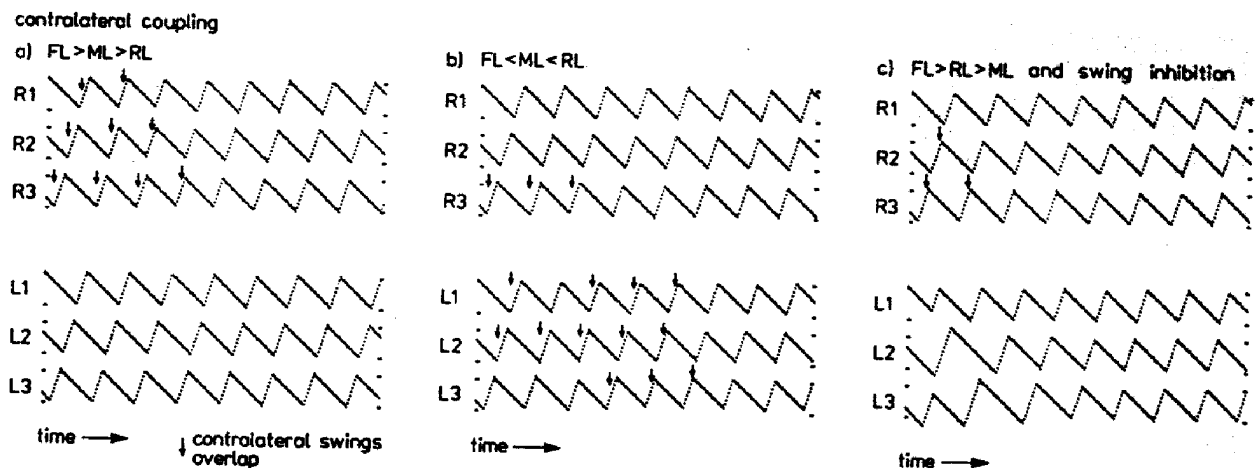
### 5.3. Effect of Adding Contralateral Inhibition on Contralateral Coordination

The behavioral evidence for the existence of an inhibition of swing during the swing of the contralateral leg is ambiguous. Adding this influence to the model strengthens the coordination of contralateral leg pairs by reducing the frequency of overlapping swings. When the inhibition is of the same strength as that on the ipsilateral side, it virtually excludes in-phase stepping. This change is particularly evident when the position-dependent excitation is weaker, as in middle and rear legs (c.f. Fig. 4a,b). The presence of the inhibition appears as a caudal shift in the PEP of the trailing leg when the difference between the positions of the two legs is small (trajectories 1 to 3 in Fig. 4b). When present in the front legs, contralateral inhibition virtually excludes gallops (Fig. 5c), sometimes at the cost of inducing overlapping ipsilateral swings. This neurally mediated inhibition could be duplicated by local mechanisms preventing a leg from beginning a swing if it is loaded.

## 6. Conclusion

In the introduction, several tasks were described which a successful walking machine must solve. The most basic is the provision of adequate support. For a large, heavy machine, falling is a failure and intensive effort must be invested to achieve fail-safe operation. For small animals, falling may have less serious consequences; therefore, the control system may accept a greater risk of falling in return for advantages in other respects. Both insects and smaller mammals often do stumble and fall, particularly when moving fast. The stick insect, the subject of the current study, probably is an animal for which falling is a constant risk and carries a high penalty. Crayfish use a different control strategy (see Müller, this section; Cruse, 1990) which appears appropriate where the consequences of inadequate support are less serious. The tolerance of such failures must be born in mind when considering the function of biological control systems and their possible use as models for technical systems.

Nevertheless, the control principles used by insects offer several advantages. One principle is the generation of an appropriate coordination through a combination of several mechanisms. Stability is obtained by combining local mechanisms intrinsic to each leg controller with coordination mechanisms mediated by the central nervous system. The local mechanisms appear necessary because the algorithms for the distributed control reduce but do not totally exclude the possibility that instabilities will occur, for example, through overlapping swings by adjacent legs. A second principle is that the central coordinating mechanisms themselves are redundant: for example, several different mechanisms encourage alternate stepping in adjacent legs. Some mechanisms, like the forward directed inhibition, serve as checks to prevent



**Figure 5.** Simulations of walks beginning with bilaterally symmetrical leg positions. This configuration leads to in-phase stepping (gallops). For the ipsilateral coupling used in the present model, the switch by contralateral legs from overlapping swings, marked by arrows, to alternation is more rapid when the contralateral coupling is strongest at the front (a). The strength of the contralateral coupling is expressed as a fraction of the minimum form required to prevent overlapping swings (e.g. Fig. 4a); the values for front, middle and rear legs were as follows: a) 1.0, 0.5, and 0.25; b) 0.25, 0.5, and 1.0, and c) 1.0, 0.25, and 0.5 with inhibition during the swing of the contralateral leg.

impending instabilities. Others, like the two excitatory mechanisms, are promotive in the sense that they establish leg configurations which are unlikely to lead to instabilities.

Some of these mechanisms have been incorporated into more recent, decentralized controllers for walking machines. Acknowledging a debt to the biological literature, Donner (1984) implemented a control system with rostrally directed inhibitory and excitatory influences for ipsilateral coordination. The resulting step patterns possess several features characteristic of insect walking but do show some irregularities. The present kinematic model demonstrates that the coordinating mechanisms identified in the stick insect suffice to produce robust and stable walking patterns. In particular, the caudally directed position-dependent influence, which modulates stepping over a wide range of leg configurations, provides a good, predictive mechanism for ipsilateral coordination. The elegance of walking machines can presumably be improved by incorporating these additional mechanisms.

However, the results also show the limitations of a kinematic model. Not all of the behavioral findings can be explained and several mechanisms are not easily incorporated. The mechanisms inhibiting a swing, both local and intersegmental, require a certain plasticity in the motor pattern so that modulations in step timing can be accommodated within the physical constraints on leg position and force. In the animal, this plasticity is provided by changes in velocity which reflect changes in



the muscle force available for support and propulsion as well as the mechanical coupling through the substrate. A more adequate model requires the incorporation of this dynamic information. Such a model of the dynamics would also facilitate treatment of influences related to the loading of the individual legs.

## REFERENCES

- Brown T.G. (1911) The intrinsic factors in the act of progression in the mammal. *Proc.Roy.Soc.B* 84, 308-319
- Bässler U. (1987) Timing and shaping influences on the motor output for walking in stick insects. *Biol.Cybern.* 55, 397-401
- Cruse H. (1979) A new model describing the coordination pattern of the legs of a walking stick insect. *Biol.Cybern.* 32, 1-7
- Cruse H. (1980) A quantitative model of walking incorporating central and peripheral influences. II. The connections between the different legs. *Biol.Cybern.* 37, 137-144
- Cruse H. (1990) What mechanisms coordinate leg movement in walking arthropods? *TINS* 13, 15-21
- Cruse H., Graham D. (1985) Models for the analysis of walking in arthropods. In: B.M.H.Bush, F.Clarac (eds) *Co-ordination of motor behaviour: 283-301* SEB Seminar 24. University Press, Cambridge
- Dean J., Cruse H. (1986) Evidence for the control of velocity as well as position in leg protraction and retraction by the stick insect. In: H.Heuer, C.Fromm (eds) *Generation and modulation of action patterns: 263-274.* Exp.Brain Res.Series 15. Springer, Heidelberg
- Delcomyn F. (1980) Neural basis of rhythmic behavior in animals. *Science* 210, 492-498
- Donner M.D. (1984) Control of walking: local control and real time systems. PhD Thesis. Carnegie-Mellon University, Pittsburg
- Foth E., Bässler U. (1985) Leg movements of stick insects walking with five legs on a treadmill and with one leg on a motor-driven belt. II. Leg coordination when step-frequencies differ from leg to leg. *Biol.Cybern.* 51, 319-324
- Graham D. (1972) A behavioral analysis of the temporal organisation of walking movements in the 1st instar and adult stick insect (*Carausius morosus*). *J.Comp.Physiol.* 81, 23-52
- Graham D. (1977) Simulation of a model for the coordination of leg movement in free walking insects. *Biol.Cybern.* 26, 187-198
- Graham D. (1979) Effects of circum-oesophageal lesion on the behaviour of the stick insect *Carausius morosus*. II. Changes in walking co-ordination. *Biol.Cybern.* 32, 147-152
- Graham D. (1985) Pattern and control of walking in insects. *Adv.Insect Physiol.* 18, 31-140
- Holst E. von (1935) Die Koordination der Bewegung bei den Arthropoden in Abhängigkeit von zentralen und peripheren Bedingungen. *Biol.Rev.* 10, 234-261
- Hughes G.M. (1952) The coordination of insect movements. I. The walking movements of insects. *J.exp.Biol.* 29, 267-284
- McGhee R.B. (1976) Robot locomotion. In: R.M.Herman, S.Grillner, P.S.G.Stein, D.G.Stuart (eds.) *Neural control of locomotion: 237-264.* Plenum, NY
- Szekely G. (1965) Logical network for controlling limb movements in urodela. *Acta Physiol.Acad.Sci.Hungaricase* 27, 285-289
- Weiland G., Koch U.T. (1987) Sensory feedback during active movements of stick insects. *J.exp.Biol.* 133, 137-156

- Wendler, G. (1964) Laufen und Stehen der Stabheuschrecke Carausius morosus: Sinnesborstenfelder in den Beingelenken als Glieder von Regelkreisen. Z.vergl.Physiol. 48, 198-250
- Wilson D.M., Waldron I. (1968) Models for the generation of the motor output pattern in flying locusts. IEEE Proc. 56, 1058-1064

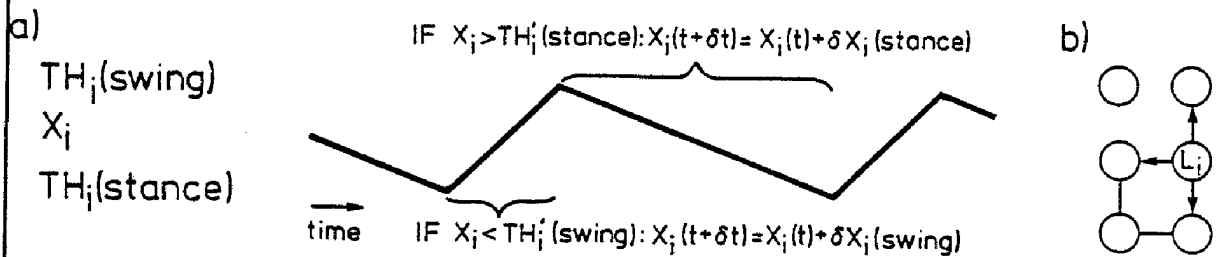
## BOX 2

## COMPUTER SIMULATION OF STEP MOVEMENTS AND INTERLEG COORDINATION USING RELAXATION OSCILLATORS

Jeffrey Dean, Uwe Müller, Holk Cruse

The step pattern generator for leg  $L_i$  is simulated as a relaxation oscillator with two states, corresponding to stance or retraction and swing or protraction, and two intrinsic thresholds (TH) determining the transitions between states (Fig. 1). The state variable and variable of integration can be interpreted as the movement phase and the position of the leg or as the type and magnitude of activity in circuits within the central nervous system which control leg muscles. In most models of arthropod stepping, interleg coordination mechanisms modify one or both thresholds of the controlled leg (the receiver), as in the example outlined below and the models presented by Dean and Cruse and by Müller (this section), but they may also affect the rate of change during one or both states. These signals depend upon the state, the variable of integration and the velocity inputs of the controlling leg (the sender).

Digital computer models decompose the simulation into a series of discrete time intervals. In successive time intervals, the effective thresholds (TH')



**Figure 1.** a) The oscillator consists of a state variable (S), a variable of integration (X), two inputs defining the rate of change of X during each state, and two intrinsic thresholds (TH(S)) used in determining the transition from one state to the next. The two inputs have opposite sign but can differ in absolute value. b) Each leg exchanges coordinating signals with other legs: only influences sent to adjacent legs are indicated.

## BOX 2

are computed. Then the variable of integration is compared with the effective threshold to determine whether to continue the same state or change states. Finally, the appropriate velocity input is added.

### Sample program structure

```
/* Set up and initialize variables. Here, TH(stance) < TH(swing),
so  $\delta X(\text{stance}) < 0$ . Define function(s),  $f_{ijk}(\text{state}, \text{position},
\text{velocity})$ , for coordinating influence(s) k of leg j on leg i */
```

```
/* Loop for calculating changes in leg position and state */
```

```
REPEAT UNTIL t => t end
```

```
  FOR i = 1 to NLEGS
```

```
     $TH'(S_i) = TH(S_i) + \sum_{j <> i} \sum_k f_{ijk}(S_j, X_j, \delta X_j)$ 
```

```
    IF  $S_i = \text{"stance"}$  THEN
```

```
      IF  $X_i < TH'(S_i)$  THEN  $S_i = \text{"swing"}$ 
```

```
    ELSE
```

```
      IF  $X_i > TH'(S_i)$  THEN  $S_i = \text{"stance"}$ 
```

```
       $X_i(t + \delta t) = X_i(t) + \delta X_i(S_i)$ 
```

```
    END
```

```
  t = t +  $\delta t$ 
```

```
END
```