Reprinted from Co-ordination of Motor Behaviour.
Edited by B.M.H. Bush and F. Clarac.
Society for Experimental Biology Seminar 24.
Printed in Great Britain at the University Press, Cambridge.

MODELS FOR THE ANALYSIS OF WALKING IN ARTHROPODS

HOLK CRUSE and DON GRAHAM

284 A model describing onset of return stroke
289 A model describing position of the leg
295 Comparison between different models
299 Conclusion

Mathematical models describing a particular behaviour are sometimes regarded as the playthings of scientists and as such are sometimes considered to have little merit when compared with the noble task of acquiring experimental data. Furthermore, the opinion is sometimes expressed that the development of a model does not lead towards progress in research because the model only describes facts which are already known or it may contain arbitrary hypothetical assumptions which anyway have to be tested in a real experiment. This view might be justified if the model is very simple, i.e. when the behaviour of the model can be determined easily without any calculation, although even in this case models represent an important abstraction process for dealing with problem situations. If the system under examination is considered in more detail and therefore the hypotheses by which the system is described become more complicated, the properties of such a system may no longer be intuitively recognized. However, the behaviour of the hypothetical system has to be known in order to prove or disprove the hypothesis when testing it in an experiment. Thus, in the case of a complicated system a quantitative mechanical or mathematical formulation of the hypotheses (i.e. a model) is necessary in order to calculate the behaviour of the model and compare it with the behaviour of the real biological system. This can be done in two ways: either by testing whether a new concept is inconsistent with known data, and thereby rejecting the hypothesis, or by looking for as yet untested properties of the model. In the latter case the model is used as a predictor and generates new experiments which act as a test of its validity.

The system which controls the movement of six or more walking legs of arthropods is - for the authors at least - such a complicated system. The whole system consists of several control units (one for each leg) which are not of simple structure, and may be somewhat different for the different legs. In addition these units are coupled together in order to produce coordinated walking, and also, diverse coupling mechanisms may exist. The assumption that this system is not a simple one is supported by the fact that at least seven models exist for insect walking behaviour. Three of them are sufficiently well defined to be termed mathematical and include simulations of the model walking behaviour. One of these has been particularly successful in describing a wide range of experimental data and we would like to use it, initially, to illustrate the value of modelling in a design or quasi-evolutionary context and show how the predictions of such a model can be examined experimentally.

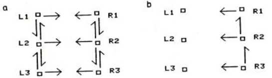
A model describing onset of return (recovery) stroke

Let us suppose we have a framework to which we can attach legs. Each leg is assumed to be able to step at regular intervals with slight variability in the cycle duration. If six legs are arranged around the body we have a primitive walking system. Due to the slight variability in cycle time the legs take up many different time relationships, and occasionally two or three adjacent legs may lift together and the body will be unsupported and may drag on the ground. At other times several legs may produce their power stroke together and the body will move rapidly forward, but then most of those same legs will lift together and dump the body on the ground. For some of the time, however, the adjacent legs may not lift together and some steady forward progress is possible.

How can we improve on this situation? Perhaps the prevention of adjacent legs from lifting at the same time would be sufficient. We can do this by letting the first leg to step insist that its immediate neighbours remain in their power stroke (see Fig. 1a). With these constraints the system adopts a step pattern in which support is never entirely lost and uses a rather variable but relatively stable supporting gait, although some legs are conspired against by their neighbours and may have difficulty in making a recovery stroke for several steps of the other legs. This problem is alleviated if one leg always cycles more slowly than all the others. This can be produced in the model by increasing the stride length, or making the leg recover (protract) more slowly. All the other legs will take their timing from the slowest leg and, provided that the protraction duration is significantly shorter than the retraction, a metachronal rhythm is established along the body axis. The waves of protractions appear to run posteriorly if a front leg steps most slowly and anteriorly if a hind leg is the controlling element of the system. Under this last condition, Fig. 1b shows the coupling pathways that control the timing in this particular configuration where R3 is the slow stepping leg. Those directed to the rear and from left to right in Fig. 1a are redundant as long as the right hind leg is the slowest stepping element. This simple concept produces patterns of behaviour which are consistent with many experimental observations of insect walking behaviour.

In this example we have assumed that all the legs have similar but not identical cycle durations. What predictions does this simple "inhibitory"model make if there are large differences in cycle duration? Two concepts are implicit in this model: (1) the leg has an inherent or natural frequency of stepping and (2) this can be altered (at the end of the power stroke) by an influence from specified other legs. Consider just two legs interacting with each other. If one leg is stepping very slowly then the faster leg may step one or more times before any coordinating influence is imposed on it. If the controlled leg is about to lift, and the warning - "I am now lifting off" - is received in time, it will be delayed. As a consequence, the controlled step will exhibit a lengthened power stroke and a longer than normal cycle duration. Thus, under certain conditions of relative timing it would be possible to observe a sequence

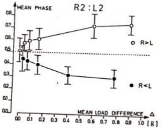
Fig.1. A hypothetical walking machine consisting of 6 legs all stepping with slightly varying step frequency. (a) Has inhibiting connections between nearest neighbour legs which prevent an adjacent leg from beginning a recovery (protraction) stroke when the controlling leg is being recovered. (b) Shows the functional or effective connections that are active when the hind leg on the right (R3) is attempting to step more slowly than the rest (in the coordinated condition all legs are forced to adopt the same step frequency as the controlling leg). It is assumed that legs are servo-controlled during the power stroke so that the system is capable of walking both up and down inclined surfaces.



of short-long or short-short-long in the duration of the controlled leg cycle, and this is produced by a significant displacement of the leg towards the rear in the controlled step if the anterior extreme position remains constant. Thus an increase in stride length is observed for every step on the controlled side in 1:1 walking but only in the controlled step for 1:2 or 1:3 walking.

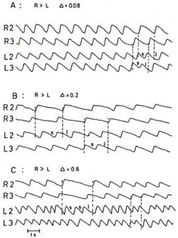
In order to examine such a prediction experimentally, a search must be made for animals which have legs that step with cycle ratios of 2 or 3 to 1. Surprisingly, there are such animals. The locust Romalea is one example (Burns, 1973), and another is the grasshopper Neoconocephalus robustus (Graham, 1978a). Alternatively, one can either modify an animal to induce such stepping - the work of Runion & Usherwood (1966) suggests that this can be achieved by cutting the chordotonal organs which control femur-tibia position in the locust - or distort the behaviour of an intact animal. It is possible to produce such a distortion by giving some of the legs more work to do and thereby reduce their frequency of stepping. The simplest experimental configuration is to let the animal walk with left legs on a free treadwheel while the right legs walk on a treadwheel with a resistance to rotation equivalent to a walk up a steep hill (Foth & Graham 1983b).

Fig.2. Plot of mean phase across the body for the middle legs of an adult stick insect walking on separate tread-wheels for right and left legs. The wheels can be loaded differently by friction at the wheel hub. The open circles are for friction greater on the right than on the left side and closed for left more heavily loaded than right. Only 1:1 stepping ratios are analysed for phase in this figure. Load difference (Δ) of 1.0g force = 10 mN. (From Foth & Graham, in press).



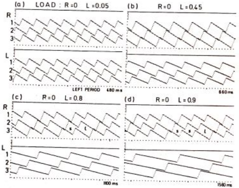
Under this light friction load (on one side) the step pattern remains 1:1, but asymmetry is present across the body. The asymmetry becomes more extreme as the load is increased (Fig. 2). If the friction loading is transferred to the other side the reverse asymmetry appears. When the load on one side is increased further, the ratio of stepping becomes 2:1 or 3:1 and sequences of the kind predicted by the model begin to appear (see Figs. 3 and 4). These sequences provide support for the model described above; had they not appeared the model would have had to be rejected.

Fig.3. Leg movement records for three different animals showing the effects of friction loading. Forward movement or recovery stroke is measured upward. Examples of 2:1 and 3:1 stepping ratios appear under high differential loads. Short-long sequences of step period and stride length are observed frequently and are marked (s) and (l), respectively. The controlling leg cycle that is assumed to generate them is defined by vertical dotted lines. The controlling leg is always on the right in these particular examples. The side with higher friction is always the controlling side. Load difference (Δ) of 1.0g force = 10 mN. (From Foth and Graham, 1983b).



Finally, let us briefly describe an alternative model using excitatory coupling. Simple excitatory coupling is obviously disastrous in the walking model given earlier, as all the legs would tend to protract together. However, such coupling might solve the problem of avoiding simultaneous lifting of adjacent legs if the excitation is applied after a delay, of a duration equal to the length of the protraction stroke of the controlling leg. Such a model would encourage the alternation of adjacent legs, and shows a stable coordinated pattern of the kind observed in insects if a hind leg steps more rapidly than the other legs. In the new experimental situation just described this would give long-short or long-long-short sequences in the controlled leg and a reduction in step amplitude on the controlled side. This has not been observed experimentally.

Fig.4. Four different step patterns simulated by a model analogous to the model of Fig. 1b.(a) Shows 1:1 stepping with almost equal friction on the two sides. (b) Shows 1:1 stepping with larger differential. Notice the distortion in stride length as the left side in this simulation delays the protraction of the right side. In (c) the friction difference is large enough to permit 2:1 stepping. Notice short-long sequences on the controlled side (right). (d) Is an example of 3:1 stepping with short-short-long sequences. Period of the loaded side and the friction loading in gm-force units is given for each simulation. (From Foth and Graham, 1983b).



A model describing position of the leg

So far we have shown on a simplified level what kind of influences could exist between individual legs, and how two models can be tested by examining a particular feature of the model behaviour, preferably using experimental data beyond the range of that used to initially create the model. Now we shall examine in more detail how the movement of an individual leg could be controlled. To do this we will refer also to the research on crustaceans whose behaviour appears to be closely related to that of the insects.

In both stick insects (see Bässler, this volume) and the lobster (Cruse et al., 1983) the return stroke and power stroke phases can be prolonged indefinitely. Therefore one can assume that there exist anterior and posterior reference points, and the leg switches from power stroke to return stroke, or vice versa, when such a point is reached.

The basic model (Fig. 5) consists of a detector measuring the leg position, a comparator (1) which "compares" this with a reference signal by means of a subtraction, and an integrator (7) representing the transformation from force to position. The two reference points are AEP (anterior extreme position) and PEP (posterior extreme position), respectively. The difference between the value of the reference point and the value of the actual leg position may be called "error signal" (ES). This value is transformed by means of several influences (see below for details) to the so called control signal (CS), the value of which is important for the system in two ways: first, when the control signal is zero, the reference is switched to its alternative state and the leg begins to move in the opposite direction. This gives a rhythmic movement which can be experimentally prolonged by blocking the movement of the leg (Wendler, 1964; Cruse & Saxler, 1980; Dean & Wendler, 1982). The model could be considered as a negative feedback system which produces its own reference input. Second, the CS provides the intensity of the input to the integrator (7). We assume that the two antagonistic muscles are not active at the same time. Therefore, the return stroke muscles are only excited by positive CS values, and the power stroke muscles only by negative CS values which are mediated by the two rectifier characteristics (6) which have opposite sign. The characteristic of the return stroke muscles in addition shows saturation, i.e. the output cannot overcome a definite maximum value even if the input value increases further (for explanation of the symbols see also Fig. 9).

The ES acts together with three other inputs to produce the CS. The central excitation (CE, 2) is assumed to come from higher centres. It is a non-rhythmic input and controls the walking speed. Increased CE values decrease the duration of the leg cycle by increasing the motor output. The other influences (load and coordinating inputs) will be described later.

Several authors (for reviews see Clarac, 1981; Evoy & Ayers, 1982) have measured the duration of return stroke (RS) and power stroke (PS) and determined their dependence on walking speed. Conflicting results were found for the dependence of RS duration on speed. In some experiments return stroke duration was constant at all speeds; in others it was correlated with speed. As proposed by Evoy & Ayers, we shall assume that this property depends directly on the propulsive loading conditions.

Propulsive load feedback from the leg proprioceptors are assumed to affect the motor output (3). If the effect of the increased load is to increase the error signal ES (increase gain), then we can simulate the increase in motor output produced by stress detecting sense organs. Furthermore, if the load effects are tonic (low pass filter) and the muscles have an upper limit of tension (saturation characteristic, 6) then the period dependence of the RS duration (RSD) can be simulated. (In fact, increased horizontal or propulsive load slows down the leg movement during the power stroke by direct mechanical influence; this effect is also considered in the model calculation (Cruse, 1983) but for clarity is omitted from the diagram). It should be mentioned that instead of assuming a tonic load influence which affects the gain factor, the load might alternatively influence the control signal CS additively. This fits the experimental results if one further assumes that either the load feedback channel or the CS unit itself has passive oscillating properties as a second order low pass filter. Strong excitation during PS would then lead to a strong overshoot with opposite sign ("negative rebound") during RS. By this mechanism an increase of load produces a stronger excitation of RS muscles. These assumptions are sufficient to describe the experimental results. The model predicts that for small loads RSD decreases with increasing speed and for high loads RSD is short and constant (Fig. 6). This prediction is in agreement with the experimental results for the rock lobster if one assumes that walking on a motor-driven belt corresponds to a high loading parallel to the walk surface. This assumption is supported by the observations of Clarac & Cruse (1982) on force measurements. This hypothesis predicts that RSD should decrease as load is applied. The

Fig.5. Wiring diagram of the model. 1, comparator; 2, gain influence of central excitation, CE; 3, gain influence of load; 4, additive influence from anterior leg supporting in-phase coordination; 5, additive influence from posterior leg supporting anti-phase coordination; 6, recovery stroke muscles (and related neurones) having the characteristic of a rectifier with saturation; 7, integrator transforming force to position; CS, control signal; LPF, low pass filter. For further explanation see text.

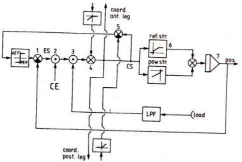
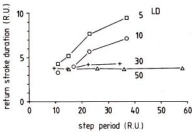


Fig.6. Return stroke duration versus step period (given in relative units R.U.) derived from the model of Fig. 5. The correlation between both values increases with decreasing load (LD, relative units).

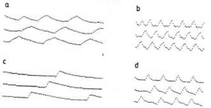


decrease of RSD after application of load is directly confirmed for crayfish (Cruse & Müller, 1984) and is also found for stick insects (Foth & Graham, 1983a, b).

As summarised by Bässler (this volume), several independent observations show that while the best known coupling interactions in insects clearly travel anteriorly, there are also certain influences which pass to the rear (Bässler & Wegner, 1983) and loading information which travels in all directions (Cruse, 1985a). Crustacea are particularly interesting in this respect for they do not show the inhibition of an anterior return stroke by blocking the posterior return stroke as clearly as it was found in insects. One reason for this may be the weaker coupling between legs which makes such an experiment more difficult to assess. The decreased coupling may follow from the lesser importance of stability in an animal which is supported by water and has 8 or 10 legs rather than 6.

One experiment in Crustacea which sheds a new light on the earlier amputation experiments of Wendler (1964) is that of Clarac & Chasserat (1979). When several legs are amputated their stumps move "in phase" with the next anterior intact leg. This influence clearly acts in a rearward direction, with decreasing strength for increasing distance from the intact leg. These results are similar to the observation that adjacent standing legs in a walking insect oscillate "in phase". This suggests that unloaded legs (amputated) may receive a posteriorly directed excitatory coupling. This would indicate that the insect middle leg amputation experiments could be explained by an excitatory (synchronising) influence from the more anterior leg.

Fig.7. Coordination of three ipsilateral (intact) legs. Upward deflection corresponds to return stroke movement. Abscissa is time in relative units. Upper trace shows the more anterior leg. The parameter central excitation (CE) increases from left to right, the parameter load (LD) increases from above to below.



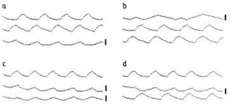
These experiments justify the inclusion of such an excitatory pathway in the leg control model. We assume that these backward directed "in phase" or "coactivating" influences are proportional to the motor output of the controlled leg (4). The rectifier means that only negative values of the CS of the controlling leg (which occur during PS) can influence the controlled leg. This additive influence tries to persuade the controlled leg to perform a PS as well.

Clarac & Chasserat (1979) also reported a coupling mechanism producing alternating coordination between a stump and its neighbouring intact leg. This influence acts in a forward direction, and we assume that it does not influence the motor output of the controlled leg but only shifts its PEP threshold rearward (5). This is analogous to the forward directed inhibitory coupling proposed by Graham (1978b) from the slow stepping of grasshopper hind legs; however the phase response curve found in the Crustacea (Chasserat & Clarac, 1983) shows both excitation and inhibition, depending on the relative phase, while that for the insect only showed inhibition.

The first task of the model is to demonstrate that the assumptions are sufficient, i.e. whether it can describe the normal walking behaviour of the animal. Fig.7 shows that an Apple II computer simulation of the model under different conditions of input (CE) and load can produce either metachronal or alternating behaviour. This shows that these two types of behaviour do not need different models.

In Fig. 8 the "amputated leg" configuration is shown and is in agreement with the experiments of Wendler (1964) and Clarac & Chasserat (1979). The model also has the property that a simulated leg produces

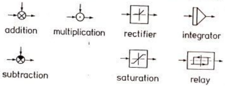
Fig.8. Coordination of three ipsilateral legs as in Fig. 7, but with different legs amputated (marked by vertical bars).



oscillating forces when placed on a fixed platform (Clarac & Cruse, 1982), and can show relative coordination (not shown here). Recent experiments showed that the end point of the PS is influenced as described by coordinating signals, by load and by position signals. However, during the PS (Cruse, 1985b) and also during the RS (Dean, 1984), not position but velocity seems to be the controlled variable. This would lead to a change in the model. Position is still used as a parameter for the decision to stop PS or RS, but no more as a parameter of a position feedback loop. Instead, an additional negative feedback channel acting on CS monitoring leg velocity is required. With this assumption, the ES value represents the reference input for this new velocity control loop. As velocity does not decrease during the PS or during the RS, but rather is kept constant (as is the motor output), one can assume that the reference input is also constant. Therefore in such an updated model the ES value is assumed to be transformed by a simple relay characteristic (without a hysteresis as that shown in Fig. 9) to a +1 or -1 value for RS and PS, respectively.

One can see from these examples that it is possible to prove the sufficiency of a hypothesis by a simulation. It is more dangerous if one attempts to do this by a "word" model, and misunderstandings may occur unless the model is very simple. The model is also predictive and could therefore be tested against new experimental observations. In one case (coordinating influences) a new test was affirmative and in the other case (position control) was shown to be a false premise. A positive result does not imply that the hypothesis is "true", but only means that one has been unable to show that it is false, in this particular experiment. The hypothesis is "supported", which means it will be used for further consideration and tests. In the foregoing example it has been shown that synchronising influences between adjacent legs, which are only exposed by amputation or standing leg experiments, need not be incompatible with the stronger inhibitory influences from the rear which define the normal walking pattern. Intuitively, one might have assumed that these two influences were incompatible within one model structure.

Fig.9. The symbols used for presentation of models in Fig. 5 and Fig. 10. The characteristics (rectifier, saturation, relay) show the transformation of an input to an output value and are usually used to describe nonlinear transformations. The input value appears on the x-axis, the output value on the y-axis. A rectifier transforms positive values without change (straight line with slope +1). Negative input values, however, produce zero output. For example, a spiking neuron has rectifier properties as it produces only (positive) spike frequencies, negative ones do not exist. A saturation transforms small input values without change, but the output value cannot exceed a given maximum value even if the input value is still increased. For the description of the relay characteristic see the text. The output of an integrator is the mathematical integral of the input value. A zero input, therefore, holds the output value at its momentary level.



Comparison between different models

In the final part of this report we will examine several models which are sufficiently well described to be illustrated by a common set of symbols. These symbols are shown in Fig. 9, but the 'relay' characteristic requires some further explanation. This characteristic produces only two discrete output values, a positive or a negative one. For very high input values only the positive output value is produced, and for very low input values only the negative output value. For middle range input values either the positive or the negative output value is produced, depending upon the previous history of the system as indicated by the arrows. A switch from the negative to the positive output value can only occur when the input overcomes the upper threshold value and vice versa.

Models of different authors are shown in Fig. 10. In all models shown in this figure the output value of the relay characteristic is used as the input of an integrator. The integrator output is fed back onto the relay characteristic. This loop forms an oscillator which produces a sawtooth like output. In Fig. 10 the feedback loop is drawn above the relay characteristic and the integrator when the oscillator is considered to be endogenous, or below these two units when the feedback signal is considered to come from sense organs. Fig. 10 does not show which legs are connected by coordinating signals since (a) this information would need considerable enlargement of the drawings and can easily be found in the original papers, and (b) not all authors provide sufficient detail concerning these questions.

The model of Wendler (1968, 1978) is based on peripheral (position) feedback. The position of the leg provides the coordinating signal which acts on the input of the integrator in the other legs. Therefore by motor output during PS and RS can be influenced but AEP and PEP are not changed. The model of Delcomyn (1971) does not treat coordinating influences. It consists of a central oscillator which as mentioned above is composed of the relay characteristic and the integrator. The model of Pearson & Iles (1971, 1973) is identical to that of Delcomyn but in addition considers coordinating influences and sensory feedback (load). Both influences act on the central oscillator at the output of the integrator, i.e. they influence both motor output and the state of the oscillator. The model considers only ipsilateral coordination and produces strong alternation between the legs.

In the model of Graham (1972, 1977) in its "peripheral oscillator model" (POM) version, the coordinating influences act in front of the relay characteristic, rather than after it as in Wendler's model. This appears to be an important concept which is incorporated in all later models, and indicates that the whole cycle of leg activity is moved in time relative to the other legs. Another unique feature of the Graham model is the presence of delay oscillators in the interleg coordinating connections (not shown in Fig. 10). These are used to generate the two gaits found in first instar stick insects. In biological terms these delays could be derived proprioceptively from the movement of the controlling leg and do not require a separate oscillator.

The model of Bässler (1977) contains a central oscillator which is influenced by coordination signals and by peripheral influences, both of which act in front of the relay characteristic, at the point where peripheral influences can interrupt the oscillation. The origin of the coordinating signals is not specified in detail but one possible influence is mentioned. During the return stroke (RS) of a leg the start of RS of the next anterior leg is hindered. In Fig. 10 the model is simplified to a two state model ("power stroke", "return stroke"). Originally it contained, as an essential property, the possibility of three or more consecutive states. This, however, is difficult to describe with the symbols used here. A special feature of this model is the "programme dependent reflexes" (see Bässler, this volume); for the sake of simplicity these have not been included in the diagram.

In 1979 Bässler proposed another model which also covers the same essentials as his 1977 model. As in the models of Delcomyn and of Pearson & Iles, the generation of a central rhythm is assumed. However, it is left open whether this rhythm is produced by an endogenous oscillator, or by rhythmic influences from other legs, or by both. Therefore, this central unit is drawn as a black box ("oscill."). The output value of the central unit produces a return stroke when positive and a

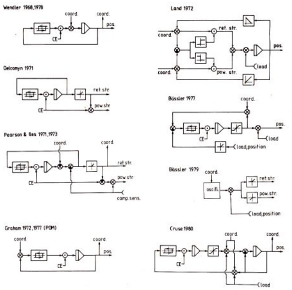


Fig.10. Wiring diagrams of models proposed by several authors which describe control of leg position in walking arthropods. Abbreviations: coord., coordinating influences; pos., position; pow.str., power stroke; ret.str., return (=recovery) stroke; camp.sens., campaniform sensilla. For further explanation see text.

power stroke otherwise. Sensory information is added onto this output value. In this way, a strong enough sensory stimulation can hold the leg in prolonged power stroke or return stroke, and the leg still produces a rhythmically modulated motor output, of the kind reported in the "saluting behaviour" of stick insects (Graham & Bässler, 1981), or in the standing leg of the walking insect (Bässler 1979; Cruse and Saxler, 1980; Clarac & Cruse, 1982).

A model proposed by Cruse (1980) contains a position controlled feedback loop and is shown in Fig. 10 in a somewhat simplified form. The reference input value in the servo-system is produced by the relay characteristic and the integrator. Coordinating influences depending upon the position of other legs act on the reference input value and on the oscillator in front of the relay characteristic. Increasing the load of the leg has qualitatively the same effect. Thus the beginning of protraction is inhibited when the leg is under load. This property is also part of the models of Pearson & Iles and of Bässler. The second integrator serves to transform force into position, as described in the models shown in Fig. 5. The same interpretation is possible for the integrators used in the models of Wendler and Graham. Concerning coordination, four different mechanisms are assumed for this model: (a) ipsilateral, anteriorly direct inhibitory influences; (b) ipsilateral, posteriorly directed excitatory influences; (c) coactivating influences between neighbouring legs along and across the body and (d) excitatory influences across the body. Experimental support exists for (a-c) but inhibitory rather than excitatory coupling has been demonstrated for across the body connections by Foth & Graham (1983b).

In 1972, Land proposed a model describing the control of leg movement of spiders. Like the model of Pearson & Iles (1973) it was originally given in neuronal terms. In Fig. 10 it is simplified by taking only its forward walking abilities into account. As in the model of Bässler (1977) two independent subsystems, for PS and for RS, are used. They obtain input from coordinating signals (which are not specified in detail) and from position sense organs. The latter are separated into two antagonistic parts. One records values proportional to position which range between zero and a maximum value, whereas the other records values which decrease from maximum to zero with increasing position value. (These two parts could be represented by hair-plates positioned at the posterior wall and the anterior wall, respectively, of the basal leg segment). The

output values of the two subsystems, for PS and RS, are compared. If the output of the power stroke subsystem is higher than that of the return stroke subsystem, the effect of the latter on the integrator is diminished by multiplication by zero. This means that a power stroke is performed. As soon as the inputs to the other subsystem are stronger, the movement is reversed. In the second half of one state the subsystem needs appropriate coordinating input to keep itself in this state. Load cannot influence the transition from PS to RS but influences only the motoneurones themselves. In the original model, the decision is not made by the two-state relay characteristic as shown here, but by two neurones with mutual inhibition. This is interesting as this system could produce "central oscillations" when deafferented, but this property is not used in the intact system.

Conclusion

In some instances, the models propose different logic circuits to describe the same behaviour, in others the models are designed to describe different sets of experimental results. The latter is particularly true of the later models since the quantity of new experimental data has increased dramatically in recent years. We have tried here to stress the qualitative differences between the models, as a guide to the development of experiments which may reject a given model assumption, and have attempted to present a symbolic framework to assist in identifying the distinctive features of each model. Models which attempt to describe the whole behaviour of the biological system become cumbersome, and it is probably most effective to model selected parts of the system. Thus one should not necessarily reject a model because of its limitations in completeness but rather make use of those parts which appropriately describe the components of the system. Thus, new models can build "upon" the concepts of older ones, and a process of evolution under the selection of experimental tests can take place.

REFERENCES

Bässler,U. (1977). Sensory control of leg movement in the stick insect Carausius morosus. Biol. Cybern. 25, 61-72.

Bässler,U. (1979). Interactions of central and peripheral mechanisms during walking in first instar stick insects, Extatosoma tiaratum. Physiol. Entomol. 4, 193-199.

Bässler,J. & Wegner,U. (1983). Motor output of the denervated thoracic ventral nerve cord in the stick insect Carausius morosus. J. exp. Biol. 105, 127-145.

Burns,M.D. (1973). The control of walking in Orthoptera. J. exp. Biol. 58, 45-58.

Chasserat,C. & Clarac,F. (1983). Quantitative analysis of walking in a decapod crustacean, the rock lobster Jasus lalandii. II. Spatial and temporal regulation of stepping in driven walking. J. exp. Biol. 107, 219-243.

Clarac,F. (1981). Decapod crustacean leg coordination during walking. In: Locomotion and Energetics in Arthropods, eds. C.F. Herreid & C.R. Fourtner, pp. 31-71. Plenum Press, New York.

Clarac,F. & Chasserat,C. (1979). Experimental modification of interlimb coordination during locomotion of a crustacean. Neuroscience Letters, 12, 271-276.

Clarac,F. & Cruse,H. (1982). Comparison of forces developed by the leg of the rock lobster when walking free or on a treadmill. Biol. Cybern. 43, 109-114.

Cruse,H. (1980). A quantitative model of walking incorporating central and peripheral influences. I. The control of the individual leg. Biol. Cybern. 37, 131-136.

Cruse,H. (1983). The influence of load and leg amputation upon coordination in walking crustaceans: a model calculation. Biol. Cybern. 49, 119-125.

Cruse,H. (1985a). Coactivating influences between neighbouring legs in walking insects. J. exp. Biol. 114.

Cruse,H. (1985b). Which parameters control the leg movement of a walking insect? I. Velocity control during stance phase. J. exp. Biol. (In press).

Cruse,H., Clarac,F. & Chasserat,C.(1983). The control of walking movements in the leg of the rock lobster. Biol. Cybern. 47, 87-94.

Cruse,H. & Epstein,S. (1982). Peripheral influences on the movement of the legs in a walking insect Carausius morosus. J. exp. Biol. 101,161-170.

Cruse,H. & Müller,U.(1984). A new method measuring leg position of walking crustaceans shows that motor output during return stroke depends upon load. J. exp. Biol. 110, 319-322.

Cruse,H. & Saxler,G. (1980). Oscillations of force in the standing legs of a walking insect (Carausius morosus). Biol. Cybern. 36, 159-163.

Dean,J. (1984). Control of leg protraction in the stick insect: a targeted movement showing compensation for externally applied forces. J. comp. Physiol. A 155.

Dean,J. & Wendler,G. (1982). Stick insects walking on a wheel: perturbations induced by obstruction of leg protraction. J. comp. Physiol. 148, 195-207.

Delcomyn,F. (1971). The locomotion of the cockroach. J. exp. Biol. 54, 443-452.

Evoy,W.H. & Ayers,J. (1982). Locomotion and control of limb movements. In: The Biology of Crustacea, vol. 4, Neural Integration and Behaviour, eds. D.C. Sandeman & H.L. Atwood, pp.61-105. Academic Press, New York.

Foth ,E. & Graham,D. (1983a). Influence of loading parallel to the body axis on the walking coordination of an insect. I. Ipsilateral effects. Biol. Cybern. 47, 17-23.

Foth,E. & Graham,D.(1983b). Influence of loading parallel to the body axis on the walking coordination of an insect. II. Contralateral effects. Biol. Cybern. 48, 149-157.

Graham,D. (1972). A behavioural analysis of the temporal organisation of walking movements in the 1st instar and adult stick insect. 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. (1978a). Unusual step patterns in the free walking grasshopper Neoconocephalus robustus. I. General features of the step pattern. J. exp. Biol. 73, 147-157

Graham,D. (1978b). Unusual step patterns in the free walking grasshopper Neoconocephalus robustus. II. A critical test of the leg interactions underlying different models of hexapod coordination. J. exp. Biol. 73, 159-172.

Graham,D. & Bässler,U. (1981). Effects of afference sign reversal on motor activity in walking stick insects (Carausius morosus). J. exp. Biol. 91, 179-193.

Land,M.F. (1972). Stepping movements made by jumping spiders during turns mediated by the lateral eyes. J. exp. Biol. 57, 15-40.

Pearson,K.G. & Iles,J.F. (1971). Innervation of coxal depressor muscles in the cockroach, Periplaneta americana. J.exp. Biol. 54, 215-232.

Pearson,K.G. & Iles,J.F. (1973). Nervous mechanisms underlying intersegmental coordination of leg movements during walking in the cockroach. J. exp. Biol. 58, 725-744.

Runion,H.I. & Usherwood,P.N.R. (1966). A new approach to neuromuscular analysis in the intact free-walking preparation. J. Insect Physiol. 12, 1255-1263.

Wendler,G. (1964). Laufen und Stehen der Stabheuschrecke: Sinnesborsten in den Beingelenken als Glieder von Regelkreisen. Z. Vergl. Physiol. 48, 198-250.

Wendler,G. (1968). Ein Analogmodell der Beinbewegungen eines laufenden Insekts. In: Kybernetik 1968, Beihefte zu "elektronische Anlagen" 18, pp. 68-74. Oldenbourg, München, Wien.

Wendler,G. (1978). Erzeugung und Kontrolle koordinierter Bewegungen bei Tieren-Beispiele an Insekten. In: Kybernetik 1977, ed. G. Hauske & E. Butenandt, pp. 11-34. Oldenbourg, München, Wien.