

A Quantitative Model of Walking Incorporating Central and Peripheral Influences^{*}

I. The Control of the Individual Leg

H. Cruse

Fachbereich Biologie, Universität Kaiserslautern, FRG

Abstract. A quantitative hypothesis is presented modelling the neuromuscular subsystem which controls the walking movements of a single leg of an insect. The model shows how central and peripheral influences can act together to produce walking movements. The subsystem of one leg consists of a central part producing reference input for a negative feedback loop which controls the position of the leg. The means by which the peripheral signals influence the central part of the model is constructed so that intact sense organs play the decisive role in controlling the walking rhythm of the leg. However, the rhythm can be produced by the control part alone, acting as a safety device if sense organs are destroyed. Using this model a series of experimental results obtained by several authors can be described.

Introduction

Several qualitative or quantitative hypotheses exist describing the control of movement of an individual leg in walking (Wendler, 1968, 1978; Delcomyn, 1971; Pearson and Iles, 1970; Pearson, 1972; Graham, 1972, 1977; Bässler, 1977, 1979; Bässler and Graham, 1978; Cruse, 1979a). All authors assumed that six individual subsystems exist each of which controls the movement of one leg. Each model of such a subsystem is designed to describe some definite experimental results. Recently new results have been published and as none of the hypotheses mentioned is capable of describing all the experimental results, a new hypothesis is presented in this paper concerning the control of the movement of an individual leg. This model is able to describe the results both qualitatively and quantitatively as far as the experimental results allow. These results are consecutively numbered from 1 to 17.

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Many of these results deal with the role of sensory afference in the control of the walking rhythm. They often appear to be contradictory. On one hand the sense organs seem to have a decisive influence on the rhythm generating part of the subsystem (2, 3, 5, 6, 8, 13) while in other experiments the influence of the same sense organs seems to be very small (1, 4, 7, 9).

(1) In cockroaches Pearson and Iles (1970) showed that after complete deafferentation a central rhythmic motor outflow still exists which strongly resembles that of the intact walking animal.

(2) Pearson (1972) and Pearson and Iles (1973) showed for fixed and partly deafferented cockroaches that stimulation of the trochanteral campaniform sensilla increases the retracting force and at the same time inhibits protraction in the same leg.

(3) Also for free walking stick insects Bässler (1977) could show that a stimulation of the trochanteral campaniform sensilla prevents the leg from starting a protraction although the other legs keep on walking.

(4) When most of the trochanteral campaniform sensilla are destroyed the leg movements show more or less normal behaviour. The same is true when after destruction of the campaniform sensilla the trochanter is stimulated in the same way as in the experiment (3) (Bässler, 1977).

(5) In another experiment with stick insects the femoral chordotonal organ is operated on in such a way that it records a bent femur-tibia-joint when in reality this joint is stretched and vice versa. In this situation the cyclic movement of the leg can be stopped during protraction. This can be interpreted as an interruption of the transition from protraction to retraction (Bässler, 1967; Graham and Bässler, 1980).

(6) After the same operation (only in the hindleg) the transition from retraction to protraction mode is inhibited (Bässler, 1977).

(7) When however the receptor apodeme of the femoral chordotonal organ is cut (Bässler, 1973) no

strong effects on the movement of the single leg can be seen.

(8) In stick insects the coxal hair rows and hair fields were manipulated so that they signal the leg being always in an anterior position. The leg can move normally but it often stops in the fully retracted position, indicating that the probability of the retraction – protraction transition has decreased (Bässler, 1977).

(9) When these coxal hair rows and hair fields are destroyed (Wendler, 1964; Bässler, 1977), only small effects on the movement of the single leg can be seen. In addition no such effects as reported above (3, 5, 6, 8) can be seen when the hair rows and hair fields at the coxa and the trochanteral campaniform sensilla are destroyed and the apodeme of the chordotonal organ is cut (Cruse and Pflüger, in preparation).

(10) Pearson (1972) in cockroaches found an increase of motor output when the animal had to drag a weight over a horizontal plane. Although he showed that there is a direct positive feedback influence from the trochanteral campaniform sensilla (which are assumed to measure the force applied on the leg) on the motoneurons this feedback is not necessarily the basic cause for the increase of motor output. The loading of legs may not be increased by the horizontal force directly but by an increase of muscle force which itself produces stronger stimulation of the campaniform sensilla. (This interpretation would mean that the existence of the positive feedback loop only increased the gain of the whole system but would not be the basic cause for increase of muscle force.)

(11) Graham (1980) showed for stick insects that when walking on a treadmill and the wheel is stopped during the retraction phase the motor output of the leg increases.

(12) The forces developed at the different joints of the legs during walking have been investigated (Cruse, 1976). The time course of the forces depends upon which leg is under consideration and the walking situation. E.g. it was shown that during the retraction movement forward forces can be developed. This suggests that protractor muscles are generating larger forces than the retractor muscles during the early part of the retraction stroke.

(13) When the stick insect walks on a treadmill and one leg is put on a platform standing beside the treadmill, all the remaining legs continue walking. However, the leg on the platform remains standing if the position of the leg is far enough in front of the posterior extreme position of the leg (Wendler, 1964; Bässler, 1967, 1979; Cruse and Saxler, 1980a, b). As in the case of (6) and (8) this can be interpreted as evidence that the sense organs record the posterior extreme position not being reached and constrain the

central part of the subsystem to stay in the retraction mode.

(14) If in these experiments the position of the standing leg is near to or even in front of its anterior extreme position, this influence is stronger than any coordinating commands arising from other legs, or “protraction commands” arising from a possible central oscillator. It is assumed that such coordinating commands consist of a change in the threshold to initiate protraction (Graham, 1972, 1977; Bässler, 1977; Cruse, 1979a). With this assumption these results show that the amount of change of threshold must be limited.

(15) In the same experiment one finds the backwards acting force of the standing leg being decreased which results in a force minimum at the time when a protraction is expected. This can be seen most clearly in the hindlegs of the experimental situation L1L2R1R2 where the legs L3 and R3 are standing on force transducers (Cruse and Saxler, 1980b, Fig. 1). This is shown more clearly in similar experiments by Bässler (1979) with *Extatosoma tiaratum*, which show all transitional stages from only small decrease of force to development of anteriorly directed forces, short lifting of the leg and real protraction movements. This result suggests that the commands starting a protraction also effect the force value developed during the retraction stroke.

(16) In these experiments the forces of the standing legs are about one order of magnitude higher than the forces developed by a leg during normal walking (Cruse, 1976; Cruse and Saxler, 1980a, b).

(17) Finally, as reported by Bässler (1979) and Cruse and Saxler (1980a, b) the forces developed by a leg standing on a platform beside the treadmill are modulated in the walking rhythm of the other legs.

The Model

Are the force oscillations of a standing leg (17) the product of a central oscillator of the subsystem itself or the product of rhythmical influences from the subsystems of the other walking legs? As discussed by Cruse and Saxler (1980a, b) there are two alternatives. (a) The subsystem consists of an oscillator which itself can be stopped by sensory influence or (b) the subsystem consists of an oscillator which goes on oscillating although the leg performs no movements. In the first case the force oscillations of a standing leg found in the experiments of Cruse and Saxler (1980a) must be interpreted as being initiated by subsystems of walking legs, thus the subsystem of a standing leg can only transfer information obtained from other subsystems. In the second case the force oscillations might also be

produced by the active “central” oscillator of the leg itself.

An attempt will be made to describe the results using the first hypothesis (a). The individual subsystem is assumed to function as an oscillator in the following way. The output value of the oscillator corresponds to the position of the leg. When the “posterior threshold” T_p [which equals T_0 (Cruse, 1979a), if no influences from other subsystems are present; for details see below] is reached a protraction movement is initiated. The protraction movement is stopped when the “anterior threshold” T_a is reached. This corresponds to a model described by Cruse (1979a) which is shown in Fig. 1A. Although the results of Bässler (1967, 1977) show that the movement cycle of a leg may consist of several parts in the simplified version treated here only the two modes “protraction” and “retraction” are considered. The two modes of the subsystem are selected by the position of the “mode switch”. This switch therefore has only the two positions protraction (dotted lines) and retraction (solid lines). The speed of leg movement during protraction is given by the fixed value $-c$, the speed during retraction by the variable v . These values are integrated giving the value of the leg position. The integrator possesses an upper and lower saturation level. By a comparator the real leg position is compared with the threshold value T_p or T_a . If the threshold is reached the mode switch is changed to the next mode.

Several results (10, 11, 16) can be interpreted by the assumption that the leg movement is not the result of open loop control as assumed in the model of Fig. 1A but by closed loop control with negative feedback. The existence of a negative feedback loop controlling the position of the femur-tibia-joint of a walking *Carausius morosus* has already been shown by Cruse and Pflüger (1978). All three results (10, 11, 16) can be explained by assuming a negative feedback loop controlling the position of the leg in the horizontal plane. During the retraction mode the reference input (R.I.) increases in the same way as the output value of the subsystem described in Fig. 1A and therefore its actual output (leg position) is increased. When the difference between reference input and actual output (error signal E.S.) is increased by an external load, the force is also increased. When the leg is held near the anterior extreme position the error signal is very large and as a consequence a high force is produced. Therefore the model (Fig. 1B) has been expanded so that the output value of the model shown in Fig. 1A is used as reference input (R.I.) for a position controlling feedback mechanism. As a consequence the information from the sense organs measuring the position of the leg has to be subtracted from the reference input value to close the feedback loop and this difference is

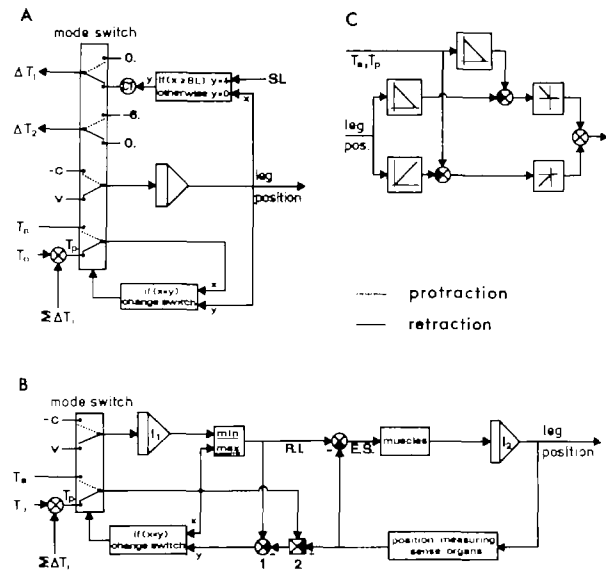


Fig. 1A–C. The model of an individual subsystem A as described in an earlier paper (Cruse, 1979a) and B as described here. The detailed construction of element 2 of B is shown in C. For explanations see text

given to the comparator which controls the mode switch. How could the latter be performed in detail? As shown by Bässler (1977) (4, 7, 9) and Cruse and Pflüger (in preparation) (9) the legs show more or less normal walking behaviour if those sense organs are ablated which, when intact, can strongly inhibit the transition from one mode to the other. Together with the results of Pearson and Iles (1970) (1) this indicates that a central oscillator exists but it can be stopped by sensory influence (Bässler, 1977). Following the assumption of Bässler (1977, Fig. 10) “afferences signalling the step-part not being finished” are subtracted from the output value of the integrator which here corresponds to the reference input R.I. This occurs in the subtracting element 1. With this circuit the threshold value can only be reached when the leg position is at its T_p position (or T_a position during protraction) although the reference input value is its upper limit.

How could these afferences be produced? It is assumed that position detecting sense organs record the difference between the actual leg position and the T_p value during retraction (during protraction the T_a value). This is symbolized in Fig. 1B by the element 2. The sense organs measuring the angular position of a joint are often arranged in the form of two populations of cells, one of which is stimulated as the angle increase while the other is stimulated as the angle decreases. This is obvious in the case of hair fields e.g. on the coxa and on the trochanter which are arranged on the opposite sides of the joint. It may also be the case for chordotonal organs as has been shown in crustaceans

by Mill and Lowe (1972) and for some units in the femoral chordotonal organ of locusts (Burns, 1974). This antagonistic structure is used for the detailed construction of elements 2 as shown in Fig. 1C. The anterior and posterior coxal hair fields could be used as an example. The anterior hair fields are stimulated as the leg moves forward (Fig. 1C, upper channel). In contrast the posterior hair fields are stimulated as the leg moves to the rear (Fig. 1C, lower channel). Concerning the subtraction postulated above these position values should be subtracted from the threshold values T_a or T_p . However, because of the inversion in the upper channel the threshold values must also be inverted. The upper channel excites the common output only when the leg position value is smaller than the threshold value and the lower channel excites the output value only when the leg position value is larger than the threshold value. This is achieved by the two rectifiers at the end of each channel.

The system shown in Fig. 1C has the same overall effect as a simple subtraction of the position value from the threshold value. However, it incorporates the assumed antagonistic structure of the sense organs and it has the property that destruction of the sense organs does not influence the essential function of the system as a whole (Fig. 1B). When the sense organs are ablated the system shown in Fig. 1C always produces a zero output value. Then the value of the reference input alone is able to determine the change of the mode switch to continue the cyclic movement of the leg. Therefore, this model corresponds to a central oscillator which at the end of each mode can be stopped by sensory influence. In this way the model shows a safety system whereby the intact animal operates with strong sensory influence, but is still able to function when the sense organs are destroyed. The possible role of the campaniform sensilla in this model are discussed later. This model with a central oscillator and a following position controlled feedback loop as described above can explain the results (1, 5–9, 11–14, 16) but it still does not show force oscillations as reported by Bässler (1979) and Cruse and Saxler (1980a, b) (15, 17).

Before examining this problem I wish to consider how the cyclic movement of a leg could be influenced by other legs to bring the legs into proper coordination. It is assumed here that the most important point where the movement cycle of a leg can be influenced by other subsystems is the beginning of protraction. This is in agreement with observations in the experimental situation presented by Bässler (1979) and Cruse and Saxler (1980a, b) where a protraction movement of the leg standing on the platform can be initiated when the platform is moved somewhat to the rear (however still in front of the T_p position). In addition such a protraction movement is coordinated

with the movements of the walking legs. For further arguments see Graham (1977) and Graham and Cruse (in preparation). Therefore it is assumed that there exist influences from other subsystems which change the threshold value about the value ΔT_i . All such influences from the different other subsystems are summed up to the value $\Sigma \Delta T_i$. Therefore the T_p value is calculated as to $T_p = (T_0 + \Sigma \Delta T_i)$. A "protraction command" from another subsystem would make the threshold value smaller than T_0 which means that the protraction is initiated when the leg is somewhat in front of its T_0 position. Therefore the real "posterior extreme position" (PEP) normally differs from the T_0 position which describes the PEP of the leg were it not influenced by other subsystems. The PEP normally assumes the momentary value of T_p . However, the protraction commands from other subsystems cause instantaneous changes in the value of T_p . Under this condition PEP may take a value between the values of T_p before and after such a transition. [Principally the same is true for the "anterior extreme position" (AEP) of a leg (Cruse, 1979b). This mechanism seems mainly to play a role when walking over irregular surfaces. In this model, for simplicity, the AEP is assumed to coincide with the value T_a .] This coupling between the subsystems is identical to that assumed in the model proposed by Cruse (1979a).

The result (15) cannot be explained by the model shown in Fig. 1A as here the change of the threshold does not change the actual force value. Also the feedback loop as described up to now (Fig. 1B) cannot describe such results. As in this experiment the leg position is constant a force change in this model can only occur when the value of the reference input R.I. is changed. As mentioned above the influences from other subsystems to change the threshold seem to be correlated with the changes of the force values. Therefore it is assumed that these threshold changes also influence the value of the reference input R.I.

If the threshold value itself ($T_p = T_0 + \Sigma \Delta T_i$) were used as a reference input this effect could be qualitatively described because with a standing leg (constant actual value) and a changing reference input one would obtain changes in the value of the error signal and therefore in the force value. However, in a normal walking leg the retraction force would be large at the beginning of retraction and fall continuously down to zero to the end of the retraction mode. This is not in agreement with experimental results of Cruse (1976) (12). It also would not explain the results obtained by Pearson (1972) (10) and Graham (1980) (11) on increasing the load. Therefore during the retraction mode the threshold value ($T_p = T_0 + \Sigma \Delta T_i$) is used as reference input only when it is smaller than the output value of the integrator I_1 . During the protraction mode

not the minimum but the maximum value has to be used as reference input as the output value of the integrator I_1 is then higher than the threshold value T_a . In Fig. 1B this is symbolized by the box labelled minmax.

The twofold influence of the value T_p being used in the model as threshold value and as reference input value seems to occur in a similar way to that observed experimentally by Pearson and Iles (1973) (2). But in this case the influences come from the same leg. To include the Pearson and Iles observations the model has to be expanded as follows. A value proportional to the output from the campaniform sensilla of the same leg might be added to the value T_p . By this circuit a leg under load would not start protraction although it may have reached the normal posterior extreme position. This means that, on the negative feedback loop controlling the position, there is superposed a positive feedback loop which is excited by the measured force value. For simplicity this system has not been inserted in this model. Except for gain changes it has no essential influence on the behaviour of the system with respect to the experimental results of Cruse and Saxler (1980a, b) which are compared quantitatively with the behaviour of the model in a following paper (Cruse, 1980). This enlargement of the model would qualitatively describe the results (2), (3), (4), and (10).

The antagonistic protracting and retracting muscles are lumped together in Fig. 1B but it should be mentioned that the activation of pro- or retracting muscles is not synonymous with the pro- or retraction mode which in the animal is defined by the beginning and end of tarsal contact and in the model by the position of the mode switch. It was shown by Cruse (1976) that during the early part of the retraction movement the protractor muscles can overcome the retractor muscles and produce forces on the substrate against the direction of motion of the body.

To translate force into position a second integrator I_2 is used in the model. This agrees with experimental results of Graham and Wendler (cit. Wendler, 1978, Fig. 6), but nevertheless is probably a simplifying assumption.

The connections between the six subsystems can be assumed to work in the same way as those proposed in an earlier model (Cruse, 1979a) one subsystem of which is shown in Fig. 1A. In this case the behaviour of the model with the new subsystem (Fig. 1B) is, in principle, the same except for a possible small change in the parameter ranges (Cruse, 1979a, Table 1). In the following paper (Cruse, 1980) the number of connections between the six subsystems is enlarged in order to describe quantitatively the results shown by Cruse and Saxler (1980a, b).

Discussion

The model presented here shows how the central and the peripheral influences could act together in order to produce walking movements. The subsystem consists of a central part producing reference input for a following negative feedback loop which controls the position of the leg. Both the central part and the feedback loop are controlled by sensory influence. In the model which corresponds to the intact animal the sensory influence completely controls the central oscillator. When however in the model all sense organs are removed the central oscillator alone determines the cyclic rhythm. When not influenced by other subsystems the model produces a somewhat higher frequency. In contrast to this in the locust flight system ablation of sense organs produces a decrease of frequency (Wilson, 1961). However, in rocking movements of stick insects the frequency was increased after removal of position measuring sense organs (Pflüger, 1977). Similarly for walking movements of Katydid's Graham (1978a, b) concludes that the stepping frequency of a leg is decreased by sensory influences from other legs.

It should be mentioned that in both situations (intact and removed sense organs) the real walking rhythm is determined by the inner state of the subsystem as well as by influences from the other subsystems. In the model the central oscillator does not cause the force oscillations found by Cruse and Saxler (1980a, b) in the standing leg of a walking insect. These oscillations are interpreted as the results of influences arising from other subsystems.

The model as shown in Fig. 1B is designed to possess only position sensitive organs. As described in the text also the force sensitive organs can be built into the model in a corresponding way. In this enlarged form the model is capable of describing qualitatively the experimental results and their interpretations as indicated in the introduction by the numbers 1–17. Its ability to describe some of these results quantitatively is shown in a subsequent paper (Cruse, 1980).

The way in which the peripheral signals influence the central part of the subsystem is constructed so that the position measuring sense organs give informations to the CNS not about the position itself but the deviation of the actual position from the "desired" position. So the system is relatively insensitive to destruction of these sense organs. The influence of the wing stretch receptors of locusts on the flying frequency can be interpreted in a similar manner. After ablation of these sense organs nearly no effect could be seen (Wilson, 1961) although signals on deviations from the "desired" wing position produce a significant effect (Wendler, 1978).

The model has a property similar to an essential property of a model proposed by Land (1972). In his model the individual subsystem is required to remember exactly the final leg position after the end of a walk. This is an important requirement in the description of the walking pattern of jumping spiders as the movements of a leg after a stop of seconds or minutes continue as if there was no interruption even when the direction of motion is reversed. Although this has not been investigated in insects, one can assume that the behaviour of insects in this respect is not too different from that of jumping spiders. In the model proposed here during retraction (stance phase) also the position of the leg is "remembered". During protraction (swing phase) the similarity depends upon whether stopping the whole subsystem means that the mode switch is held in the last position or that the input values v and c are switched to zero. In the second case also during swing phase the actual position is "remembered". In the first case only the mode is "remembered". According to Bässler (1967, 1977) the leg cycle does not consist of only two but several separate parts and in this case the subsystem would be very similar to that proposed by Land (1972).

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Prof. Dr. Holk Cruse
 Fachbereich Biologie der Universität
 Postfach 3049
 D-6750 Kaiserslautern
 Federal Republic of Germany