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# A Quantitative Model of Walking Incorporating Central and Peripheral Influences*

## II. The Connections between the Different Legs

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**Abstract.** Using the experimental results of Cruse and Saxler (1980a, b) and other authors (Graham, 1972; Pearson, 1972; Bässler, 1977, 1979) a quantitative model is developed in order to describe the behaviour of the systems controlling the leg movements of a walking insect. The whole model consists of six subsystems each of which controls the movement of an individual leg. The single subsystem (Fig. 1) consists of a central part which can assume two modes (protraction, retraction) the transition between which can be controlled by sensory influence. The central part produces the reference input for a feedback loop which controls the leg position. The reference input is however also determined by influences from other subsystems. Four different types of such connections are assumed to exist between the subsystems. Two of these produce alternating (t1, t3), two others "in phase" coupling (t2, t4) between the subsystems to be connected. These connections can transfer information originating from the central part as well as from the periphery of other subsystems. The model is capable of describing either quantitatively or qualitatively the experimental results of Cruse and Saxler (1980a, b) (see Figs. 3 and 4). In addition it is capable of describing the results of other authors, e.g. the temporal leg coordination of the free walking animal (Graham, 1972).

## Introduction

When an insect walks, the legs normally are moved in a well coordinated way and produce a temporal pattern of pro- and retraction movements typical for each walking speed. One might assume that this coordination between the different legs is produced by neuronal connections between neuro-muscular subsystems each of which controls the movement of its leg. The coordination might however also be produced by mechanical connections between the legs so that each individual leg reacts to load changes in the vertical and/or horizontal direction during the walk. It is shown by Graham and Cruse (in preparation) for stick insects that a proper pattern of temporal coordination can also be found when mechanical connections between the different legs are entirely excluded. Therefore such neuronal connections must exist. However, ideas concerning the quantitative nature of the neuronal connections between different subsystems are only published in the form of hypothetical models (Wendler, 1968, 1978; Graham, 1972, 1977b; Bässler and Graham, 1978; Cruse, 1979). Only in two cases has direct evidence been found for such connections in insects in terms of a phase response curve for legs operating with different step frequency (Graham, 1978) and by Pearson and Iles (1973) from electrophysiological experiments.

Apart from these results the only other indirect evidence on the nature of these connections comes from experimental work on the temporal coordination of legs of free walking animals or of animals with one or more legs amputated (for stick insects: Buddenbrock, 1921; Wendler, 1964; Bässler, 1972; Graham, 1972, 1977a; for other insect species: Hughes, 1952, 1957; Wilson, 1966 (see here for further references); Delcomyn, 1971a, b, 1973; Burns, 1973; Delcomyn and Usherwood, 1973; Pearson and Iles, 1973; Graham, 1978; Greene and Spirito, 1979; Spirito and Mushrush, 1979). As an alternative to amputation which may produce an entirely different behaviour pattern another method which places the animal in an unnatural behavioural situation but leaves it completely intact is used by Cruse and Saxler (1980a, b) following Wendler (1964).

An adult female stick insect (*Carausius morosus*) is fixed dorsally and walks on a treadwheel. When one

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leg is put on a platform standing beside the treadwheel, all the legs remaining on the treadwheel continue walking while the leg on the platform stands and develops a force which acts in vaposterior direction. This force is not constant but varies with time. In many of the possible experimental situations these force oscillations have the same frequency as stepping of the walking legs and are coordinated with them. As shown by Cruse and Saxler (1980a, b) these experiments can be performed with up to five legs on different platforms. The temporal coordination of the movement of the walking legs and the force oscillations in the standing legs is different for different combinations of standing and walking legs.

It is shown in Cruse and Saxler (1980a, b) that it is difficult to obtain necessary conclusions on the nature of the connections between the different subsystems. In this paper a model of the connections between the legs is described that correctly predicts the experimental results of Cruse and Saxler (1980a, b) and thereby shows those connections which are sufficient to explain the results.

Such a model calculation must first show that the different assumptions stated do not contradict one another. As there exists a large number of experimental results (ten different combinations of walking legs and legs standing on a platform were investigated) a comparison between experimental data and model values will be a good test for the validity of these assumptions. In addition to an agreement with the data of Cruse and Saxler (1980a, b) the model is also capable of describing the walking behaviour of an animal walking freely and at different speeds. Following Cruse and Saxler the ten different experimental situations are described by the underlined abbreviation of all those legs which are free to walk. The legs are abbreviated by an *L* or *R* showing left or right leg followed by the number 1 for front-, 2 for middle-, and 3 for hindleg. The experimental situation L1L2R1R2 means that frontlegs and middlelegs walk on the treadwheel, while both hindlegs stand on force transducers.

## Connections between the Six Subsystems

Before considering the nature of the connections between the six subsystems each of which controls the movement of a leg the subsystem itself must be defined. For this purpose in the preceding paper (Cruse, 1980, Fig. 1B) the hypothetical construction of each individual subsystem is given, which will be used in the following model (Fig. 1). The definitions, symbols and properties of the subsystem are the same as those given in the preceding paper (Cruse, 1980).

As discussed in Cruse and Saxler (1980b) one does not know how the connections between the subsystems depend upon the experimental situation. In addition to the assumption discussed earlier (Bässler, 1977; Cruse, 1980) that the individual subsystem consists of an oscillator which can be stopped by sensory influence according to the connections between subsystems the following assumption is made. It is assumed that those connections which originate from subsystems of walking legs are always the same regardless of the experimental situation. Basing on these two suppositions the following conclusions can be drawn from the experimental results.

To show the direction of an influence, a connection is described to run from a "controlling subsystem (leg)" to a "controlled subsystem (leg)". The experiments of Cruse and Saxler (1980b) show that there is a good coordination between both frontlegs when both are walking (L1L2R1R2, L1L3R1R3, L1R1) and no detectable coordination between both walking middlelegs and between both walking hindlegs when the frontlegs are standing (L2L3R2R3, L2R2) or between the hindlegs when the middlelegs are standing (L1L3R1R3). Thus a connection producing alternating coupling within one segment (i.e. between contralateral legs) exists only between frontlegs. (The alternating coordination between both hindlegs in the situation L3R3 does not contradict this assumption as discussed below.) To connect the other walking legs with the walking frontlegs there could exist either diagonal connections and/or connections along the body. As possible diagonal connections can be switched off without disturbing the coordination pattern on either side of the body (Graham, 1972, 1980b) connections producing alternating coordination along the body must exist. As the coordination in the situation L1L2R1R2 agrees with that of a normal walking animal while in the situation L2L3R2R3 both middlelegs show no detectable coordination the commands producing alternating coupling along the body under these experimental conditions must run from the frontleg to the ipsilateral middleleg. The results of situation L2L3R2R3 only show that between middleleg and ipsilateral hindleg connections exist but nothing can be said concerning the direction of this connection. As however the middlelegs are driven by the frontlegs and as the only connection between contralateral legs producing alternating coupling is found between frontlegs one must assume that these connections again run in posterior direction. A direct connection between ipsilateral front- and hindlegs is improbable because situation L1L3R1R3 shows that there is no detectable coordination between front- and hindlegs.

In the hypothetical model of Cruse (1979) two types of connections are assumed. The first one (called type 1) has the same properties as the connections just described. They determine the alternating coordi-

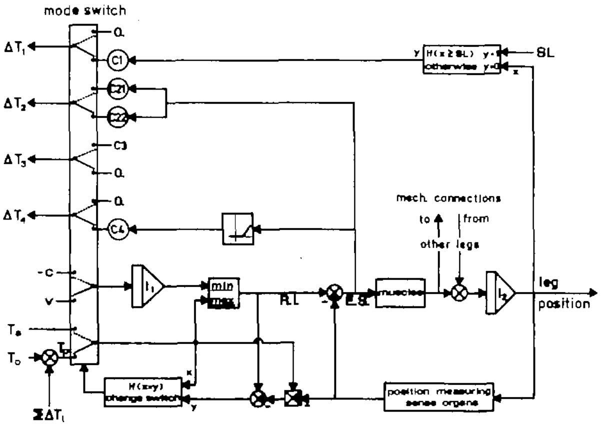

**Fig. 1.** The construction of an individual subsystem. For further explanations see text

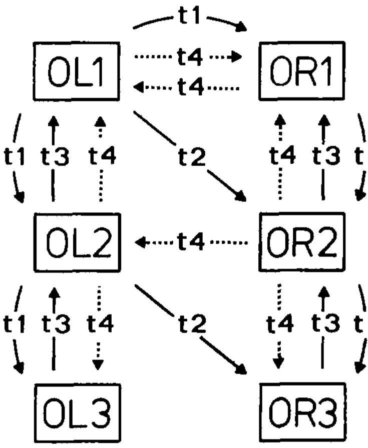

**Fig. 2.** Schematical diagram showing the different connections between the six subsystems. t1: decrease of threshold to release protraction (alternating). t2: decrease of threshold to release protraction (in phase). t3: increase of threshold to inhibit protraction during protraction of the controlling leg. t4: increase of force when the force of the controlled leg is increased strongly

nation between both frontlegs, between front- and ipsilateral middlelegs and between middle- and ipsilateral hindlegs in the following way. The position of the controlling leg is compared with a given threshold value. This value depends upon the walking speed and upon the pair of legs which are connected. It is called SL for both pairs of left legs, SR for both pairs of right legs and SL1R1 for both frontlegs. Their speed dependence is shown by Cruse (1979). In Fig. 1 as an example only SL is represented. If the position of the controlling leg was higher than SL then the comparator gives the output value 1, otherwise 0. This output value is weighted with the value $C_1$. If the controlling leg is in the retraction mode the value $\Delta T_1$ will be $C_1$ or zero, if it is in protraction $\Delta T_1$ will be zero. As shown by Cruse (1979) this connection causes the controlled leg to perform a cyclic movement which alternates with the controlling leg. In the closed loop model (Cruse, 1980, Fig. 1B) it also produces a force minimum in the standing leg because in the standing leg the output value of the integrator $I_1$ is larger than the value $T_p = T_0 + \Sigma \Delta T_i$ and therefore the reference input is determined by the latter value. The experimental results indeed agree with this assumption as the results of the situation L1L2R1R2 and L2R2 indicate influences from walking middlelegs on the force values of standing hindlegs. The results of the situations L1R1 and L1 indicate an influence from walking frontlegs on the force values of standing middlelegs. Therefore these "type 1" (or t1) connections are also incorporated into the model shown in Fig. 1. Figure 2 shows the position and direction of these type 1 connections.

To explain bimodal distributions in the experimental situations L1, L1L2, and L1L2L3 and to explain the alternating coordination between hindlegs which occurs in the situation L3R3, but not in the other situations with both hindlegs walking freely (L2L3R2R3, L1L3R1R3) the existence of diagonal "in phase" connections between the legs L1–R2 and between L2–R3 are assumed (Fig. 2, t2). Such connections (called type 2) were also postulated in the model of Cruse (1979) with respect to the behavioural observations of Buddenbrock (1921) and Graham (1972) that in free walking adult stick insects just these pairs of legs protract simultaneously over the whole speed range observed. In the open loop model (Cruse, 1979, 1980, Fig. 1a) a threshold change $\Delta T_2$ is produced which has the value $C_2$ when the controlling leg is in the protraction mode and is zero during retraction of the leg. In the closed loop model (Fig. 1) the value $\Delta T_2$ is proportional to the error signal ES (this corresponds to the force developed by the leg) with the proportional factors $C_{21}$ during retraction and $C_{22}$ during protraction mode.

Pearson and Iles (1973) in cockroaches proposed an inhibition of protraction between ipsilateral legs. Such a pathway has been experimentally confirmed in walking Katydids (Graham, 1978). In this insect the hindlegs often protract with approximately half the step frequency of the legs in front. In this situation middleleg periodicity is found to oscillate from step to step and shows the presence of an inhibiting influence from the hindleg which delays the end of retraction in the middleleg each time the rear leg protracts. These results could be interpreted as an increase of threshold in the controlled leg when the controlling leg protracts. In the closed loop model (Fig. 1) an increase of threshold also produces an increase of force in the standing leg. Such a force increase during protraction movement of a neighbouring walking leg was also observed by Cruse and Saxler (1980b) as shown in the following. The results of the situations L2L3R2R3 and L2R2 indicate such connections from middle- to ipsilateral frontlegs, those of the situation L1L3R1R3 and L3R3 those from hind- to ipsilateral middlelegs. These anteriorly directed connections produce an increase in the force of the controlled leg when the controlling leg protracts as the force maximum of the controlled leg occurs during or directly after the protraction of the controlling leg. Therefore, such connections (called type 3) are also assumed in the model (Fig. 2, t3). As shown in Fig. 1 the threshold is changed by the value $C_3$ when the controlling leg protracts and by zero when it retracts.

While the types of connection described above are in agreement with the coordination of the legs of a free walking animal, in many of the experimental results one finds coordinations which are in contrast to those of a free walking animal. Very often standing legs are "in phase" which would alternate in the free walking animal. This suggests another type of connection which constrains different pairs of legs to produce "in phase" coupled force oscillations. It is not possible from these experiments to determine between which pairs of legs these connections must exist as different combinations can explain the results.

As however in the experimental situation L2L3R2R3 there is a very strong coordination between both standing frontlegs but no detectable coordination between both middlelegs and between both hindlegs, such an "in phase" connection (type 4) must exist between both frontlegs in this experimental situation. Such a connection might disturb the coordination of a free walking animal. As such a coordination is only observed in standing legs which produce force values of about one order of magnitude higher than normal walking legs, this conflict could be avoided by the following mechanism. It is assumed that the force value of the controlled leg is influenced in proportion to the value of the force of the controlling leg but only when the force of the controlling leg is higher than a given threshold. This mechanism agrees with the observation of Bässler (1979) and Cruse and Saxler (1980a) that the force of a leg standing on a platform beside the treadwheel increases when the wheel is stopped. As by this experiment the situation of the standing leg itself is not changed, the result shows that from subsystems of legs which were walking before the stop occured influences on the subsystem of the standing leg must exist. Graham (1980a) showed that in this experiment the motor output of a walking leg in the retraction mode increases. Therefore this connection produces an increase in the force of the standing leg when the force of the walking leg is increased.

The factor of proportionality to produce $\Delta T_4$ is $C_4$ (Fig. 1) and the threshold value for the error signal to produce a value of $\Delta T_4$ different from zero is 3.5. This value is chosen to be somewhat higher than the highest error signal obtained in a "free walking leg". As said above except for their existence between the frontlegs no direct conclusion can be drawn from the experiments between which pairs of subsystems these type 4 connections may exist. Therefore in the model calculation the lowest number of connections necessary to describe the experimental results was used (Fig. 2, t4, dotted lines). But possibly this connection exists between all pairs of legs.

It follows from Fig. 2 that the scheme of Fig. 1 must be expanded for the frontlegs in the following way. First the subsystem of L1 produces two different output values $\Delta T_1$, one for L2 and another for R1. In addition, each frontleg subsystem receives two different input values $\Delta T_4$ one from the ipsilateral middleleg and another from the contralateral frontleg. To simplify the figure these paths are however not drawn in Fig. 1.

In the earlier models (Wendler, 1968, 1978; the peripheral version of Graham, 1972, 1977b; Cruse, 1979) the retraction speed (and therefore the corresponding force) was assumed to be constant for a given period length during the whole retraction stroke of the leg. This simplification allows one to neglect the mechanical connections between the legs during retraction. When however the force developed by the individual leg can vary during the retraction stroke this mechanical connection must be taken into account. This is achieved by summing the forces of all legs in retraction. The resulting force influences the individual leg. These influences work only during retraction of the leg which is not shown in Fig. 1 in detail.

## Results

The model was written in Fortran using a time raster of 20 ms. For simplicity all the six legs are assumed to develop about the same force. Therefore the walking speed in the different experimental situations and – for a roughly constant stride length – the period would be expected to depend upon the number of walking legs but this does not appear to be the case in the experimental results. To adapt the period values of the model to those obtained in the different experimental situations for each situation the force factor was changed correspondingly. For the same period length this value was thus greater the less legs were walking. Using the parameter values shown in Table 1 for the ten experimental situations the onset of the retraction of the walking legs and the phase position of the force maximum of the standing legs was calculated. Because of the discontinuous elements in the model most often no unique maximum appears but a more or less broad maximum range. In these cases the middle of such a

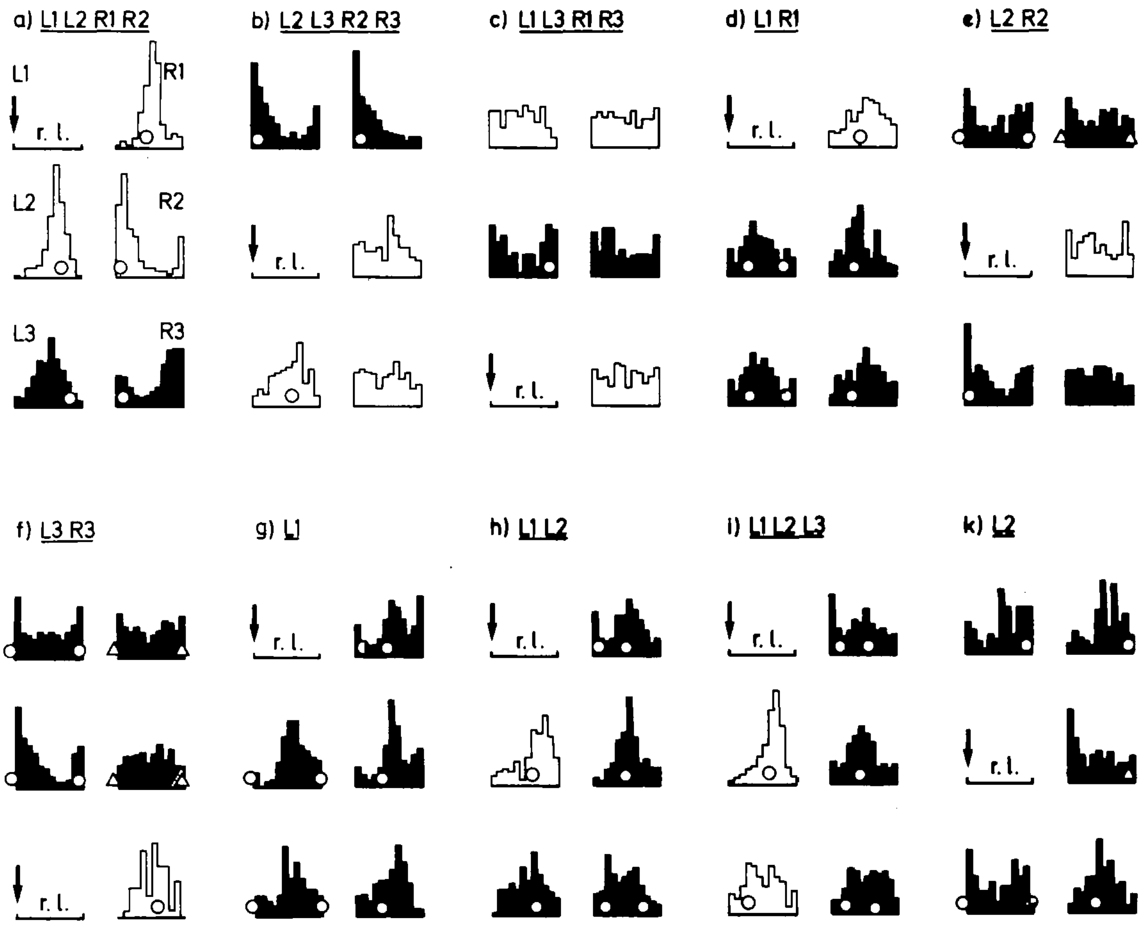

**Fig. 3a–k.** Comparison between some of the experimental values (maxima of the histograms) and the corresponding model values (white circles). The experimental results are shown in the following way. For each of the ten experimental situations the phase histogram of the investigated leg relative to a reference leg (r.l.) is shown. Reference point of a walking leg is the onset of retraction (in the reference leg shown by an arrow). Reference point of a standing leg is the force maximum. The histograms of walking legs are shown by white columns, those of standing legs by black columns. The histograms are normalized. Sample size, mean angle and circular standard deviation of the histograms can be found in Cruse and Saxler (1980b, Table 1)

range was used as maximum value. A comparison of some of the experimental and model results are shown in Fig. 3. For each experimental situation and for one reference leg the phase plots are given (black columns: force maximum distribution of standing leg, white columns: distribution of onset of retraction of walking leg). The white circles show the corresponding values obtained by the model calculation. If no circle is shown an equal distribution was obtained in the calculation. Very often the maximum appears at the beginning or the end of the cycle. To make the cyclic structure of these phase plots clearer in this case the circle is shown at both ends of the phase plot at the same phase values. Two circles at different phase values in the same distribution indicate two distinct maximum values. For the meaning of the triangles see below.

Concerning the results obtained by Cruse and Saxler (1980b, Table 1) with other reference legs the coordination of 120 pairs of legs were measured. 31 pairs of legs showed no detectable coordination. The remaining 89 pairs of legs showed all together 100 maximum values. (This means that in 11 cases bimodal distributions were obtained.) While the first can only be compared qualitatively with the model calculation the latter can be compared quantitatively in the following way. In 99 out of 100 cases the difference between

**Table 1.** The parameter values of the model shown in Fig. 1b which are used for the calculation. For the values of SL and $T_p$ see Cruse (1979)

$C_1 = -4.$
$C_{21} = 3.$
$C_{22} = 0.15$
$C_3 = 2.$
$C_4 = 0.2$
$T_a = 0.$

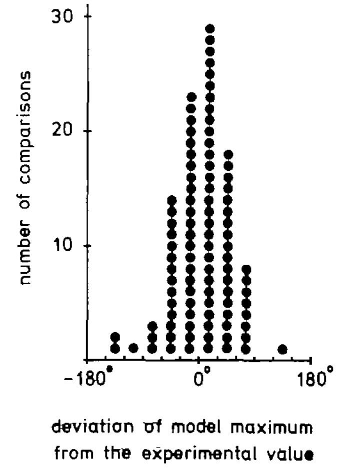

**Fig. 4.** A histogram showing the distribution of the differences between the 99 maximum values obtained by the experiments and by the model calculation. 45 out of the 99 maximum values used for this comparison are shown in Fig. 3

the maximum value in the experiment and in the model calculation was measured. The distribution of all these values is shown in Fig. 4. It has a mean value of 6° with a circular standard deviation of ±41°. If the model did not describe the experiments at all one would expect an equal distribution. The description is better, the more tightly these values are distributed around the zero value. In one out of these 100 cases the model showed no maximum where a small maximum value was found in the experiment (L1: R2–L1, the second leg is the reference leg). It should be mentioned that also the three most deviating values in Fig. 4 occur in the same experimental situation L1, the results of which are described as being somewhat ambiguous by Cruse and Saxler (1980b).

As described above the 31 cases without detectable coordination can only be compared qualitatively. In 24 of these the model also showed no coordination. In the seven remaining cases the model calculation showed a maximum. These were L1R1: L1–R1, L2R2: R1–L2, L3R3: R1–L3, R2–L3, L2: R2–L2, R1–R3, R2–R3 (the second leg is the reference leg). Four of these seven maximum values of the model are shown in Fig. 3 by triangles. In the situation L3R3 the model shows also a second mode value which is coupled with the movement of R3. The coupling between L3 and R3 in the model is weak as in this instance the coordination is gliding with an exclusion of simultaneous protraction. Therefore this second mode in the other legs has a very large circular deviation which is not expected to be detectable in the experimental results. In the corresponding experiments the circular standard deviations are also large, and it is not sensible to compare their mean values with the model values. This means that with the discrimination level chosen by Cruse and Saxler (1980b) in these seven cases the model does not describe the experiments. It may however be possible that a weak coordination exists which was not detected experimentally.

Finally it must be asked whether this model is also capable of describing the coordination pattern of a free walking animal. Calculations showed that this model can describe the coordination pattern in the same way as has been shown for the simpler model published earlier (Cruse, 1979). This is to be expected as the present model is based upon the structure of this earlier model.

In conclusion therefore one can say that except for one contradictory case and seven cases where no decision is possible the model describes quantitatively the coordination of the walking and standing legs in the ten investigated experimental situations. It also describes quantitatively the coordination pattern of free walking animals for a broad speed range and for various starting positions of the legs as described by Cruse (1979). Qualitatively the model describes the results of a series of several experimental results obtained by different authors as shown in the preceding paper (Cruse, 1980) in detail. However, the large number of results concerning the walking coordination of animals with different legs amputated (v. Buddenbrock, 1921; Wendler, 1964; Graham, 1977a) is not considered here but will be examined in a subsequent paper. The main problem will then be the question of how the amputation of a leg (normally cut off at the trochanter-femur-connection) can be represented in the model as part of the leg musculature and sense organs may still be intact.

## Discussion

Four different types of connections are assumed to exist between the six subsystems (Fig. 2). The actual realisation of these connections in the calculations is described earlier. However, the essential properties for which they are constructed are the following. The t1-connection decreases the threshold to release a protration and possibly (see below) decreases the propulsion force of the controlled leg in alternation (which does not necessarily mean a phase shift of 180°) with the controlling leg. The t2-connection has the same effect however "in phase" with the controlling leg i.e. during protraction of this leg. The t3-connection increases this threshold and possibly (see below) decreases the propulsion force of the controlling leg during protraction movement of the controlled leg. The t4-connection increases the force of the controlled leg when the force in the controlling leg becames large.

For all connections a change of the threshold value also means a change of the propulsion force of this leg only when the central part of the subsystem is near or at the end of the retraction phase.

Two of these connections produce an alternating coordination (t1, t3). Two others (t2, t4) are "in phase" coordinations. The effects of the connections depend upon the mode ("retraction", "protraction") of the controlling leg. The connections t1 and t3 are only meaningful when the controlling leg is walking but not when it is standing. While the connections t1, t2, and t3 are always active during normal walk the t4 connection is only used when the force developed by the controlling leg is relatively high. This means that the "in phase" influence between legs increases with increasing load. This also might be the reason for the nearly simultaneous protraction of contralateral legs when the animal has to drag a load or is walking vertically. All these connections influence the controlled subsystem at its threshold (which has to be reached in order to start protraction) and can influence the value of the reference input of the control loop. In addition to these connections the model also includes mechanical connections by which a leg is moved not only by its own forces but also by the forces developed by the other retracting legs. The model calculation gives not only the position of the walking leg but also the value of the force component parallel to the long axis of the body.

A detailed discussion between the other published models and a model similar to that described is shown earlier (Cruse, 1979). Therefore only two aspects will be described briefly. A principal difference between the model of Wendler (1968, 1978) and the peripheral ("POM") models of Graham (1977b) and Cruse (1979) is that in the first the other subsystems influence only the force value while in the latter models only the threshold values are influenced. In the present model both influences on force value and on threshold value of the controlled leg are possible. In the models of Graham (1972, 1977b) and of Wendler (1968, 1978) the connections point only in anterior direction which implies that the subsystem of a hindleg is the pacemaker. In contrast in the model of Cruse (1979) and the model presented here the subsystem of a frontleg acts as pacemaker. It might be that these two different types of models are equivalent hypotheses for different walking situations.

As mentioned in the preceding section the gain of the position controlling feedback loop must be higher when less walking legs contribute to the total propelling force. This indicates that to improve the model the negative feedback loop which here is assumed to be linear could be expanded to include an element which increases the gain of the loop in a nonlinear way. Such an element might be represented by the positive feedback loop including the trochanteral campaniform sensilla which was mentioned in the preceding paper (Cruse, 1980).

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