COORDINATION OF LEG MOVEMENT IN WALKING ANIMALS

Holk Cruse
Dept. of Biol. Cybernetics, Fac. of Biology, and Center of Interdisciplinary
Research, University of Bielefeld, Fed. Rep. of Germany
E-mail: UBIOF140 at DBIUNI11

ABSTRACT

When a robot has to move in a locally uncertain environment, propulsion by means of walking legs is advantageous compared to a wheel driven system. However, the control of walking legs is more complicated. The question of how the movement of the different legs is coordinated will be investigated here. Three different solutions which have been developed during natural evolution will be compared. These are the walking systems of an insect, of a crustacea, and of a mammal. The results show that coordinating mechanisms differ considerably in these animals.

1. INTRODUCTION

An autonomous robot which has to move in an uncertain environment has to deal with the problem of how to perform a goal-oriented behaviour. This problem is a global one, meaning that the robot has to deal with the detection of possible paths and to decide which of these it should take. This includes the problem of obstacle avoidance. When the environment is "locally certain", as for example a semi-artificial environment with flat surfaces, the technical problem of how to move the body forward is comparatively simple and can be solved by driving the robot with wheels. If, however, the local structure of the environment is uncertain, i.e., consists of irregular terrain, a robot with walking legs is advantageous. Several attempts have been made to construct such a walking machine. Nevertheless, comparing the walk of a six-legged robot with that of an animal such as an insect, immediately reveals differences. The walking of an animal is much more versatile, and it appears to be more efficient and elegant. Thus it is useful to consider biological control mechanisms in order to apply these or similar mechanisms to the control of walking legs in machines. In the past, engineers have pointed out that little information is available on the biological control mechanisms, but this situation has changed recently. This paper provides a summary of the recent biological results focussing on data obtained from insects, crustaceans, and cat by means of behavioural methods.

2. CONTROL OF THE INDIVIDUAL LEG

The results to be described here mainly concern the coupling mechanisms between legs, i.e. those mechanisms that produce a proper coordination of the walking legs even when walking is disturbed. However, for this purpose it is necessary also to consider briefly how the movement of an individual leg is controlled. The mechano-neuronal system that produces this movement might be called the step pattern generator. To avoid a possible misunderstanding it should be stressed that it is completely open whether this step pattern generator contains an endogenous central pattern generator.

For simplicity, only forward walking will be discussed. The cyclic movement

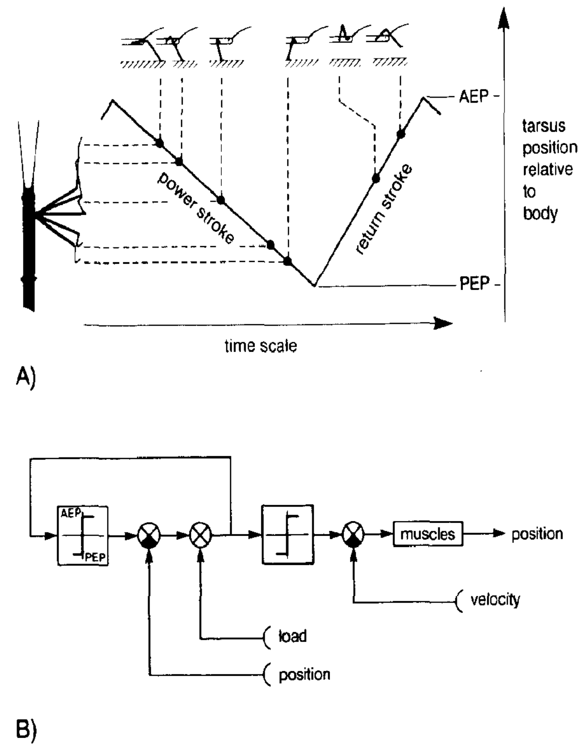


Fig. 1. (A) The cyclic movement of a leg consists of the power stroke during which the leg supports and propels the body and the return stroke during which the leg is swung back to the initial position. In forward walking the latter is called the anterior extreme position (AEP). The power stroke which then corresponds to a retraction movement of the leg ends at the posterior extreme position (PEP). Position of the leg always means the position of the leg tip relative to the body.
(B) Circuit model of the movement of a leg. The left hand part represents a hierarchically upper-level circuit which decides which of the two states, power stroke or return stroke, should be adopted by the system. The left relay characteristic produces the two alternative target positions, AEP or PEP, when its input value is positive or negative, respectively. The value of the target position is compared with the actual leg position. The result is also affected by signals from load-sensitive organs. The output of the decision circuit is considered as reference input for the second, lower-level circuit (right), a velocity controlling feedback system.

of a walking leg consists of two parts (Fig 1A), the power stroke (also stance phase or support phase) and the return stroke (also swing phase or recovery phase). During the power stroke the leg is on the ground where it can support and propel the body. In a forward walking animal this corresponds to a retraction movement of the leg. During the return stroke the leg is lifted off the ground and swung to the starting position for the next power stroke. In forward walking this corresponds to a protraction movement of the leg. The question of how to coordinate the movement of the individual joints of a leg will not be considered here. In the stick insect, which has been investigated in detail, the movement of the leg during both the power stroke and the return stroke is controlled by at least one servo-system. By means of negative feedback this servo-system regulates a parameter corresponding to the velocity of the leg (Cruse 1981, Cruse 1985b, Cruse and Pflüger 1981, Cruse and Schmitz 1983, Dean 1984, Schmitz 1985). This view was later shown to be true even for a single joint (Weiland and Koch 1987, Bässler 1988). With respect to the temporal pattern of stepping, the critical question is how the step pattern generator decides whether or not the transition from one mode (power or return stroke) to the other should be made. Experimental results have shown that for insects the most critical point is the transition from power stroke to return stroke. This seems to be intuitively clear as this transition terminates the support function of the leg; if performed at the wrong moment the animal may be left unsupported which may be hazardous. Nevertheless, the crayfish was found to use another solution (see below). In the stick insect, three parameters influence this transition: position, load, and phase in the step cycle of the other leg. The first two depend on proprioceptive information describing the state of the leg itself; these peripheral influences ensure that the leg only lifts off the ground when its position relative to the body is far enough to the rear and that it only lifts off when the load under which it stands is small enough (Bässler 1977, Cruse 1985c).

These results can be summarized by the circuit model shown in Fig 1B (Cruse 1985d). It consists of two parts. The first is a hierarchically superior circuit that decides which of the two states, power stroke or return stroke, the system should adopt. The relay characteristic produces the two alternative target positions AEP and PEP (anterior and posterior extreme positions, Bässler 1972) when its input value is positive or negative, respectively. The value of the target position is compared with the actual leg position. The result is also affected by signals from load-sensitive organs. The output of the decision circuit is considered as reference input for the second, inferior circuit, a velocity-controlling feedback system. A positive output value of the decision circuit corresponds to a movement in the anterior direction (positive velocity, return stroke) and a negative value to movement in the posterior direction (negative velocity, power stroke). Results reported by Bässler (1988) support the assumption that load-sensitive organs also affect the system on the lower level, which is however not shown in Fig 1B. The model could easily be reformulated in neuronal terms. The decison part can, for example, be represented by a bistable circuit as described by Land (1972) or Bässler (1986). Investigations of an intersegmental reflex - the TOT-reflex first described by Graham (1979) - show that the part of the system which decides on power or return stroke is hierarchically superior to that part which decides whether the individual leg walks forward or backward (Schmitz and Haßfeld 1989). This was also assumed to be the case for crustacea (Ayers and Davis 1977).

3. COORDINATION BETWEEN LEGS

The third parameter is of major importance here because it depends on coordinating influences: the transition from power stroke to return stroke of one leg also depends on the relative timing or the phase of the leg's movement to that of the other legs. In addition, direct peripheral influences from the sense organs of neighbouring legs might exist which are not involved in the step pattern generators of these legs. Not only are coordinating mechanisms known that influence the power-return stroke transition, but also mechanisms that influence the return-power stroke transition at the anterior extreme position (AEP) and mechanisms that influence the strength of the motor output during the power or the return stroke. The experimental data show no essential differences in the intraleg, peripheral influences among insects, crustacea, and even mammals. In contrast, comparative investigations have shown that the coordinating mechanisms are quite different for crustaceans, insects, and mammals (Cruse and Müller 1986, Cruse and Schwarze 1988, Cruse and Knauth 1989, Müller and Cruse 1991a, Cruse and Warnecke 1991). Thus the results obtained for the three most thoroughly investigated species, the crayfish, the stick insect, and the cat are discussed separately.

4. THE CRAYFISH

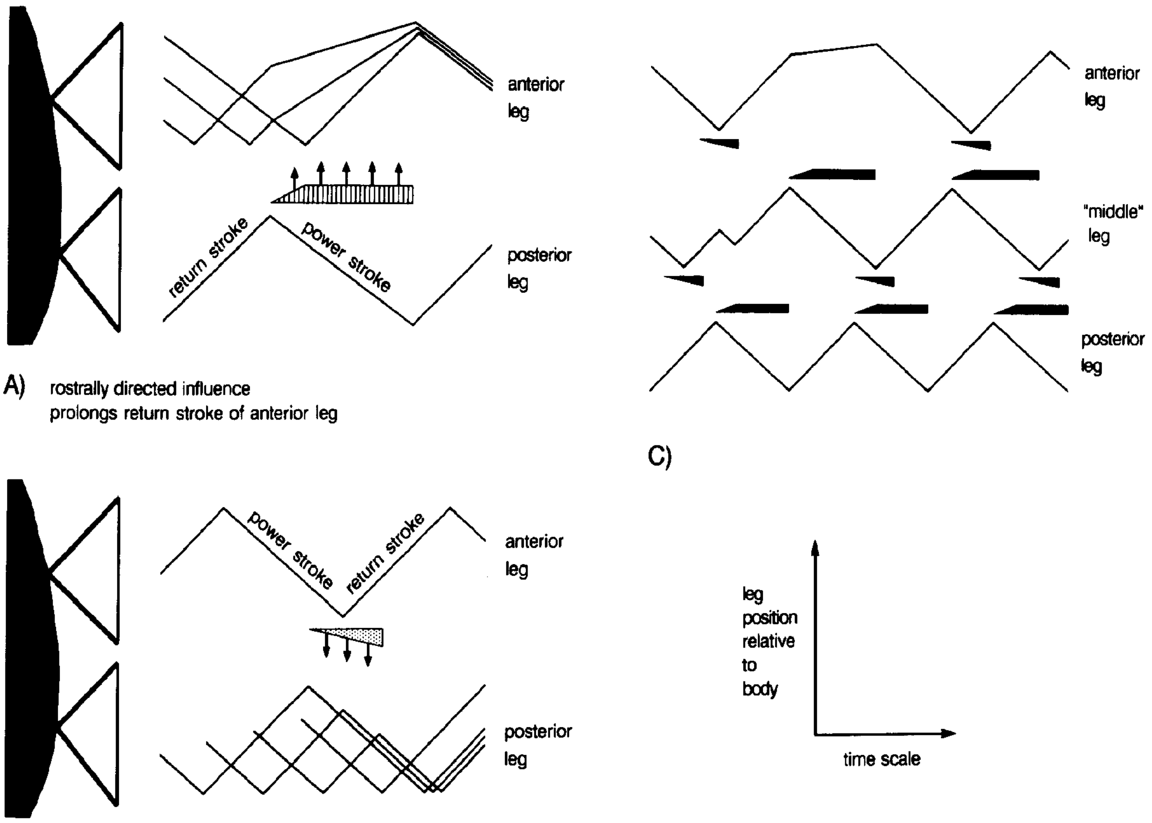
As a common feature it can be stated that in arthropods coupling between ipsilateral legs, i.e. legs on the same side of the body, is generally stronger than coupling between contralateral legs, i.e. legs on opposite sides of the body (rock lobster: Clarac and Chasserat (1983); crayfish: Müller and Cruse (1991a); stick insect: Dean and Wendler (1982), Foth and Bässler (1985b), Graham (1977a); cockroach: Delcomyn and Cocatre-Zilgien (1988); tarantula spider: Seyfarth and Bohnenberger (1980)). Therefore ipsilateral mechanisms are easier to investigate and will be treated first.

To begin with the crayfish, two coordinating mechanisms are found acting between neighbouring ipsilateral legs (Cruse and Müller 1986). These two influences are schematically presented in Fig 2. The two traces represent the movement of the two legs. Several phase situations are plotted in each sketch. They might be produced by a disturbance of the normal walk for example due to an irregular or slippery ground. One coordinating mechanism is only rostrally-directed. This is illustrated in Fig 2A: as long as the posterior leg performs a power stroke, the anterior leg has to perform or continue a return stroke. In addition the velocity of the movement during the return stroke is also decreased to some extent. Thus the return stroke can be prolonged so that normal coordination is regained in the next step. The horizontal striped bar indicates the time during which this mechanism is active. The intensity of the influence is roughly indicated by the thickness of the bar. The second influence is caudally-directed. This is illustrated in Fig 2B: when the anterior leg is near the end of its power stroke or at the beginning of its return stroke, an influence with increasing intensity has the effect of ending the return stroke and beginning the power stroke of the posterior leg, thus shortening the return stroke of this leg. As indicated by the stippled wedge, this influence ends abruptly about 200 ms after the beginning of the return stroke of the anterior leg. Both coordinating mechanisms influence the transition from return stroke to power stroke.

A crayfish has four ipsilateral legs. Thus two of these legs have both an anterior and a posterior neighbour. These "middle" legs might therefore obtain both influences which, depending on their temporal relation, could superimpose. When the middle leg obtains the signal from the anterior leg at the beginning of the power stroke of the posterior leg then in the middle leg a long return stroke can be produced which is interrupted by a short power stroke. This is shown for one example in Fig 2C. This indicates that in this situation the caudally directed influence is somewhat stronger. In this case the transition from power to return stroke is affected, which means that the PEP is shifted to a more rostral position. In any case both mechanisms act together in the same sense so that an incorrect phase relation between two legs is immediately corrected within the following step. Although for convenience the mechanisms are described as influencing the transition between the two states, this example also shows that the influence could also be described as facilitating one of the two states. As could be shown by means of a model calculation, each mechanism alone would be sufficient to produce a coordinated walk. In this respect the connections can be considered redundant.

An additional influence acting between adjacent ipsilateral legs of the lobster was described by Müller and Clarac (1990a,b) and was also found in the crayfish (Müller 1990). These authors electrically stimulated a leg nerve which containes fibres from a mechanical sense organ at the tip of the leg. The stimulus caused the adjacent leg to prolong its power stroke, or, if it was in return stroke, interrupt the return stroke and begin a power stroke. This coordinating influence was found to act in both anterior and posterior direction but it is open whether it plays an important role during normal walking.

To couple contralaterally neighbouring legs, i.e. legs of the same segment, the crayfish uses a mechanism which very much resembles the ipsilateral, caudally directed influence (Müller 1989, Müller and Cruse 1991 a,b). In contrast to the ipsilateral mechanism where the influence is only active during a small fraction of the whole step cycle (see



A) rostrally directed influence prolongs return stroke of anterior leg

B) caudally directed influence shortens return stroke of posterior leg

Fig. 2. Coordination between the ipsilateral legs of a crayfish (A, B). The upper trace of each shows the anterior leg. Each schema is drawn as if only one of the two coordinating mechanisms existed. In each case the influencing leg is drawn only once. For the influenced leg several traces are presented to show the effect of the coordinating mechanism. The duration and the intensity of the influences are roughly indicated by the length and the thickness of the wedges, respectively. A) The rostrally directed influence is active during the power stroke of the posterior leg. It prolongs the return stroke of the anterior leg and can also decrease the speed of the limb movement.
B) The caudally directed excitatory influence is active at the end of the power stroke and the beginning of the return stroke of the anterior leg. It "excites" the start of a power stroke in the controlled, posterior leg.
C) Coordination between three ipsilateral legs when both forward and caudally directed influences are active. The top trace shows the most anterior leg. The "middle " leg obtains a signal from the anterior leg which excites a power stroke. At the same time the middle leg obtains an influence from the posterior neighbour to perform a return stroke. As the latter signal at the very beginning is weak, the signal from the anterior leg "wins" until this influence ceases and the rostrally directed influence dominates (after Cruse and Müller 1986).

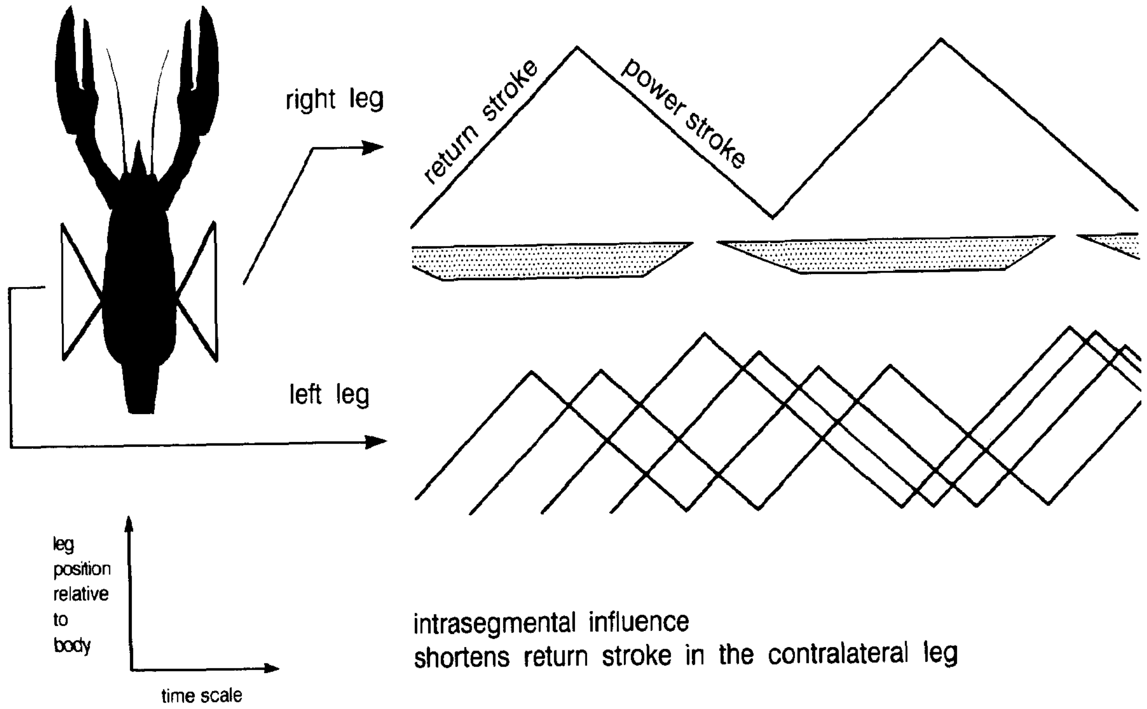
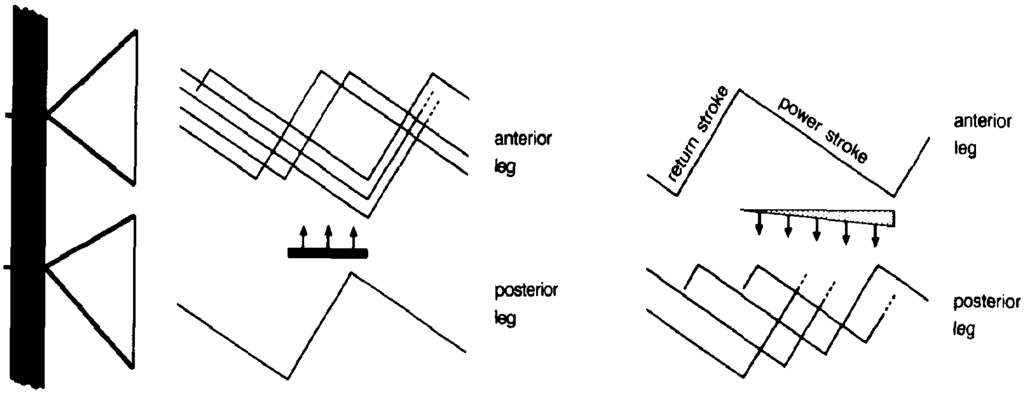


Fig. 3. Influences between two contralateral legs of a crayfish. The influences are assumed here to act only in one direction, from right to left. As in the ipsilateral caudally directed coupling mechanism (Fig 2B) the controlled leg is influenced to start a power stroke. Compared to the ipsilateral case the influence continues for a much longer part of the step period but the influence is weaker. Thus several steps could be necessary to retain the normal coordination and relative coordination might eventually be observed (after Müller and Cruse 1991a).

Fig 2B), the contralateral influence continues during most of the cycle (Fig 3). With the exception of a small phase range the return stroke of the other leg is always shortened. The effect is much weaker than ipsilateral influences. While in ipsilateral legs the effect of a disturbance is compensated within the following step, because of the weaker coupling in contralateral legs a disturbance results in a so called gliding coordination (the relative coordination of von Holst (1939)). This means that several steps are necessary to regain normal coordination. This contralateral influence acts in the same way in both directions but one leg might be somewhat more dominant. This dominance seems to be inherent to some extent but can additionally be influenced experimentally by inducing different turning tendencies by means of an optical stimulus. A gradient along the longitudinal axis was found in the way that anterior leg pairs show less strong coordination than more posterior pairs. In some cases the coupling between diagonally neighbouring legs was found to be stronger than between contralateral legs of the same segment. This result, however, does not require direct coupling connections between diagonal neighbours but can be explained on the basis of the above mentioned intersegmental contralateral influences (Cruse and Müller 1991b).

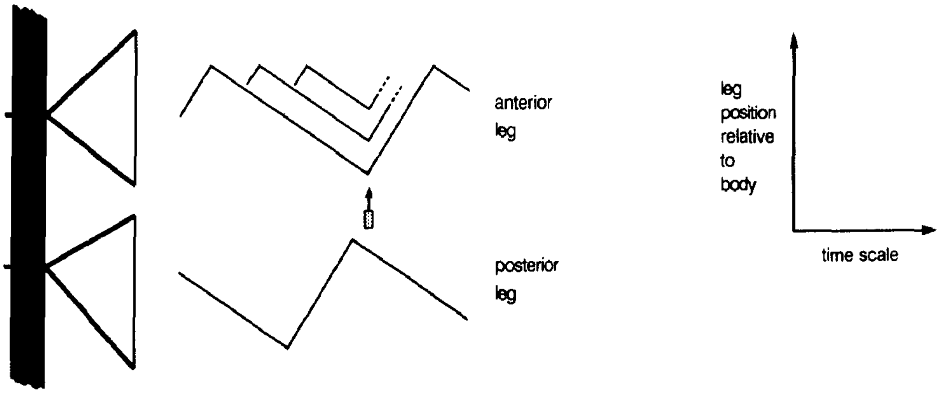
5. THE STICK INSECT

As mentioned above, quite different results were found concerning the coordinating mechanisms in the stick insect. Three different mechanisms influence the PEP, i.e. the transition from power stroke to return stroke. They are shown schematically in Fig 4. Two influences are rostrally directed.



A) rostrally directed influence
inhibits start of return stroke in the anterior leg

C) caudally directed influence
excites start of return stroke in the posterior leg



B) rostrally directed influence
excites start of return stroke in the anterior leg

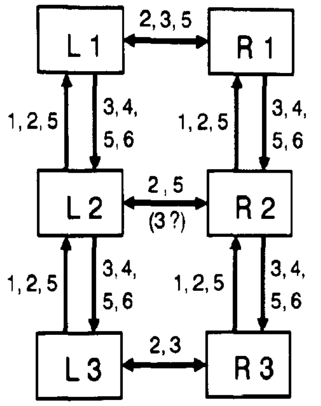
Fig. 4. Coordination between two ipsilateral legs of a stick insect (A,B,C). The upper trace of each shows the anterior leg. Each schema is drawn as if only one of the three coordinating mechanisms existed. In each case the influencing leg is drawn only once. For the influenced leg several traces are presented to show the effect of the coordinating mechanism. The duration and the intensity of the influences are roughly indicated by the length and the thickness of the bars and wedges, respectively.
A) The rostrally directed inhibitory influence is active during the return stroke of the posterior leg.
B) The rostrally directed excitatory influence is active at the beginning of the power stroke of the posterior leg.
C) The caudally directed excitatory influence is active during the power stroke of the anterior leg.
The terms "excitatory" and "inhibitory" are applied according to the effect on the start of the return stroke in the influenced leg.
The duration of the return stroke could not be shown to be influenced by these coordinating mechanisms. As it is not known in detail how the varying amplitudes are compensated return strokes are only roughly indicated (after Cruse and Schwarze 1988).

One (A) hinders a leg from starting a return stroke as long as the posterior leg performs its return stroke and may continue for about another 100 ms. This influence can prolong the power stroke (Cruse and Epstein 1982, Cruse and Schwarze 1988, Dean and Wendler 1982, Foth and Bässler 1985a). Experimental results indicate that this is done by shifting the threshold for beginning a return stroke to a more posterior position (Cruse 1985a). In contrast to this "inhibitory" influence the following two have an "excitatory" effect. The second rostrally directed influence (B) can elicit a return stroke in a leg when the posterior leg starts a power stroke (Cruse and Schwarze 1988). This influence shortens the duration of the power stroke. A third influence is caudally directed (C): the start of a return stroke of a leg is more strongly excited, i.e. occurs earlier, the farther the anterior leg is moved rearward during its power stroke (Cruse and Schwarze 1988, Dean and Wendler 1982, Foth and Bässler 1985b, Bässler et al. 1987). This has the effect that the posterior leg performs a return stroke before the anterior leg begins its return stroke. In the model shown in Fig 1B these influences can be imagined to change the AEP or PEP value of the relay characteristic, or, logically equivalent, to sum with positive or negative sign to the input of this characteristic. These three mechanisms are redundant in the sense that they produce the same effect: the nearly immediate re-establishment of coordination in the case of any disturbance.

In addition three other, less important coordinating mechanisms are found in the stick insect (Fig 5). One is probably a special development for an animal climbing on branches as it is not found in other animals such as locusts (Pearson and Franklin 1984) or lobsters (Cruse, Clarac and Chasserat 1983). The position where the hind leg finishes its return stroke is given by the actual position of the tarsus of the ipsilateral middle leg: the hind leg tarsus is placed immediately behind the middle leg tarsus (Cruse 1979a, Dean and Wendler 1983). Thus information on the spatial position of the middle leg tarsus relative to the body is given to the neuronal system controlling the movement of the hind leg. The same "targeting" occurs between middle and front leg and also between front leg and antennae (unpubl. observation). The main function of these mechanisms is presumably to help a leg find ground contact, an essential function when climbing on branches but trivial when walking on a continuous surface. However this mechanism also contributes to coordination. If any irregularities occur in the step of a leg, the targeting mechanism can shorten or prolong the return stroke of the next posterior leg in order to retain a normal coordination. It was shown in a neural network simulation that this mechanism can be realized by a simple system consisting of nine neurons,i.e., three sensory, three moto- and three interneurons (Dean 1990).

Another coupling mechanism is the so-called "coactivating" influence which affects the motor output during the power stroke (Bässler 1979, Cruse 1985a). An increase in the motor output of a leg induced, for example, by experimentally decreasing the speed of the retraction movement immediately leads to an increase in the motor output of neighbouring legs during their power stroke. In contrast to the influences discussed earlier which act only in one, either forward or rearward direction, the coactivating influence acts in both directions. It is therefore a mutual influence between all immediately adjacent legs with the single exception of the two hind legs. Thus, these coactivating mechanisms provide an increase in the propulsive force of the whole animal.

If the hind leg steps onto the tarsus of the middle leg, the hind leg often lifts off again and is replaced



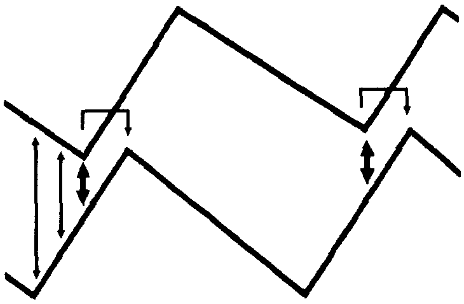
1. Return stroke inhibits start of return stroke
2. Start of power stroke excites start of return stroke
3. Caudal positions excite start of return stroke
4. Position influences position at end of return stroke ("targeting")
5. Increased resistance increases force ("coactivation")
6. Treading-on-tarsus reflex

Fig. 5. Summary of the coordinating mechanisms operating between the legs of a stick insect (modified after Dean 1989)

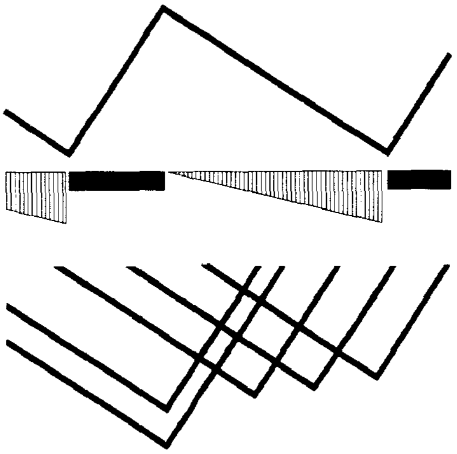
slightly posterior without an interruption of walking. This treading-on-tarsus or TOT reflex can also be elicited experimentally by touching the middle leg tarsus with a fine brush. If the tarsal stimulus on the middle leg is applied during the early return stroke of the hind leg, this return stroke is prematurely terminated (Graham 1979, Schmitz and Haßfeld 1989). The TOT reflex was also found between middle and front legs.

The coactivating influences are not the only contralateral effects. As was found for the crayfish, coupling between contralateral legs is weaker than that between ipsilateral legs. However, two of the three mechanisms found for ipsilateral legs also act between contralateral legs of the same segment. These are the two "excitatory" mechanisms shown in Fig 4B,C for ipsilateral legs; both elicit the start of a return stroke in the other leg (Cruse and Knauth 1989). The first influence increases the probability that the contralateral neighbour will start a return stroke when one leg has started a power stroke (corresponding to Fig 4B). This influence exists in all three pairs of legs: front, middle and rear. The second influence corresponds to that shown in Fig 4C. The farther back one leg has moved during its power stroke, the higher is the probability that the contralateral neighbour starts a return stroke. Indications of this mechanism have only been found for front and for hind legs. For contralateral legs the first mechanism seems to be of greater importance and evidence for the latter is only indirect.

As in the crayfish these contralateral influences, unlike the ipsilateral coupling, seem to act in both directions between the two legs of one segment. Asymmetrical stepping patterns, i.e. patterns where contralateral legs do not walk in an exact alternating mode (phase of 0.5) but show phase values of about 0.4 or 0.6, commonly occur in the stick insect (Graham 1972). This asymmetry can be influenced by altering the load of the legs (Foth and Graham 1983b). This indicates that in insects, too, one side can dominate the other. As the motor output is increased when the leg walks under load, this result also indicates that a step pattern generator which produces a stronger motor output also produces coordinating signals to other legs which are of higher intensity. This is supported by experiments considering the amplitude of force oscillations of a leg standing on a fixed platform while the other legs are walking (Cruse and Saxler 1980). The correlation between strength



A) influences between ipsilateral legs



B) influences between contralateral legs

Fig. 6. Schematic representation of the coupling influences between (A) ipsilateral legs and (B) contralateral legs of the cat.
(A) The coupling mechanisms between front (upper trace) and ipsilateral hind leg (lower trace). The distance between both legs (two-way arrows) has to be smaller than a given threshold to start the return stroke of the front leg. After some delay the hind leg finishes return stroke and starts power stroke (bent arrow).
(B) The coupling mechanisms assumed to exist between contralateral legs are shown as if they acted only in one direction, from the leg shown in the upper trace to that shown in the lower trace. Several traces are shown for the influenced, lower leg to illustrate the effects resulting from the coupling mechanisms. During the return stroke of the influencing leg (black bar) the power stroke of the influenced leg may be prolonged because the start of the return stroke is inhibited. During the power stroke of the influencing leg the influenced leg is excited to start the return stroke, which will occur the earlier, the farther the position of the influencing leg has moved backwards (wedge).

of motor output and of coordinating influences can also explain the following result obtained in the crayfish (Cruse and Müller 1986). When the movement of one leg was briefly stopped during the power stroke, the normal coordination was regained in a way that shows that the coordinating influences from this single leg dominate the neighbouring legs. This was astonishing at first sight because one would expect that the combined influences of all the other, well-coordinated legs should dominate the deviant leg.

6. THE CAT

Investigation of slow-walking cat (Halbertsma 1983, Cruse and Warnecke 1991) showed the following results. Influences between contralateral legs, i.e. both front legs or both hind legs, are stronger than those occurring between ipsilateral legs, i.e. front and hind leg of the same side. As mentioned earlier, this finding is markedly different to the findings in arthropods. Influences which coordinate front legs seem to be of the same kind as those for the hind legs. These influences are in general symmetrical, which means that the same type of influence acts from right to left leg and in the reverse direction. Two types of influences are described for contralateral legs: first, when the influencing leg performs a return stroke, the influenced leg is prevented from starting or continuing a return stroke. Second, when the influencing leg performs a power stroke, the probability that the influenced leg starts a return stroke is the higher, the farther the influencing leg has moved backwards during its power stroke. This is shown in Fig 6 and qualitatively agrees with the finding in the stick insect. The "inhibitory" influence which in the stick insect is assumed to inhibit only the start of the return stroke, in the cat also seems to inhibit the continuation of an ongoing return stroke, thus "exciting" the start of a power stroke. As in arthropods, there seems to be some asymmetry in the sense that the leg of one side may be somewhat more dominant, which would mean that there is no qualitative, but possibly a quantitative difference between the legs of a contralateral pair.

In contrast to contralateral coupling, the ipsilateral mechanisms are asymmetrical, i.e., a qualitatively different influence acts from front to hind leg than does in the reverse direction. The front leg is influenced to start a return stroke when the hind leg has approached the front leg to a given distance. It is not the position of the legs in the body-fixed coordinate system, but the position of both legs relative to each other that constitutes the decisive criterion for the front leg to finish its power stroke. The hind leg is influenced to start a power stroke after the front leg has begun its return stroke. The signal for the hind leg to finish return stroke may either be calculated from the position relative to the front leg, or, another possible interpretation may be that the start of the front leg return stroke as such serves as a signal for the hind leg to finish return stroke. In any case, the switch in the hind leg follows after some delay, thereby producing the "understepping" of the hind legs and leading to an obvious overlapping between return strokes of adjacent legs.

7. MODELS

A model of the coordinated movement of walking legs can be used in three ways. First, as a short description of the experimental results. Second, it can serve as a tool to predict experimental results which occur, for example, after a disturbance of the normal leg movement. Third, it can be used to test whether a hypothetical assumption concerning the nature of the underlying mechanism does not contradict natural behaviour.

The models proposed up to now for different arthropods (for review see Cruse and Graham 1985) do not describe the detailed movements in each joint of the legs but are concerned only with the projection of the line between the leg basis and the leg tip on the horizontal plane. This means that only the forward-backward component of the movement is taken into account. Each leg is considered as a relaxation oscillator which in all models corresponds qualitatively to the one shown in Fig 1B. The earlier models were hierarchically organized in the sense that the flow of information between two neighbouring oscillators was only unidirectional (Wendler 1968, Graham 1972,1977, Cruse 1979b). A model with mutual, though symmetrical influence was proposed by Wilson (1966) for the cockroach (see also Pearson and Iles 1973). For the rock lobster Chasserat and Clarac (1986) proposed a model for the coupling between two legs where both legs influence each other. This was used for coupling between ipsilateral as well as contralateral legs. A model which is based on detailed behavioural investigations was presented by Cruse and Müller (1986) for the ipsilateral legs of the crayfish which has recently been completed by Müller and Cruse (1991b) also for the contralateral legs. This model contains the asymmetrical influences between ipsilateral legs (Fig 2) and the symmetrical influences between contralateral legs (Fig 3), and is probably the first comprehensive model based on behavioural data.

On the basis of measurements of the above-mentioned force oscillations (Cruse and Saxler 1980) a hypothetical model was proposed for the stick insect by Cruse (1980a,b) which contains several types of influences running in different directions. At least on a qualitative level most of these assumptions could be supported by later experimental investigations as described above. Using these experimental results (see Fig 5 for a summary) an extensive computer simulation has recently been successfully completed by Dean (in press). This simulation contains all mechanisms shown in Fig 5 except for mechanism no. 5 and 6. As mentioned, all these models describe only the horizontal projection of the leg movement. Very recently a complete kinematic and kinetic 16-body model of the stick insect was constructed by Pfeiffer et al. (1989) which can now be used as a basis for modelling the real movement of the legs. However, this task requires further information not only on the vertical component of the movement (see following section), but also on the question of how to control the movement of the individual joints of a leg.

8. STARTING, TURNING AND HEIGHT CONTROL

An animal does not always walk. Therefore it has to be possible to activate and inactivate that neuronal circuitry that produces the walking movements. This circuitry can be imagined to consist of a system schematically represented by Fig 1B which has to be completed by the coordinating influences. An animal can start walking spontaneously or by being excited by different external, e.g. tactile stimuli. Some crustacea were found to be easily stimulated to walk when the legs of the animal are moved rearwards by moving the underground relative to the animal using a motor driven belt (Ayers and Davis 1977). Other species respond by a resistive force to this situation (U. Müller, unpublished observation) and the same was found for the stick insect.

When the standing stick insect is stimulated to walk, for example, by a tactile stimulus, all legs that are on the ground immediately start with caudally directed forces (Cruse and Saxler 1980, Bässler et al. 1985, for locust: MacMillan and Kien 1983). This is supported by observations of the starting behaviour (Dean and Wendler 1984). This can be interpreted as showing that the neural circuitry of each leg always starts in the state of power stroke when activated after a pause. This is, however, not generally the case. Land (1972) reported for the jumping spider that a leg can also stop the movement within a return stroke and later continue walking by completing the interrupted return stroke.

An animal does not always walk in a straight line. How is turning possible? When a stick insect walks in a moderate curve the coordination between right and left legs can be maintained and only the step amplitude, i.e. the distance between AEP and PEP, increases for the legs on the outside and decreases for those on the inside of the curve (Graham 1972). When the curve is narrow, right and left legs can become uncoupled and the outside legs walk with higher frequency (for stick insect: Jander (1985); for cockroach: Camhi (1988)). In extreme cases legs on one side can walk forward and those of the other side walk backward so the insect turns in place (for honey bee: Zolotov et al. (1975), for stick insect: own observation). However, for the cockroach turning in place only changes in step amplitudes have been recorded (Franklin, Bell and Jander 1981). They also found higher step frequencies in both front legs compared to middle and hind legs but no apparent decoupling between right and left legs.

The coordination of legs in a walking animal is discussed here only with respect to the movement in the forward-rearward direction, i.e. the horizontal component of the movement. When walking over an uneven surface, however, the legs have to act together in order to control the height of the body and coordinate the movement in the vertical direction. The behaviour of a stick insect walking over different obstacles (Cruse 1976) or standing on different forms of substrate (Cruse, Riemenschneider and Stammer, 1989) can be quantitatively described according to a hypothesis that each leg acts as a vertical "spring" which is independent of the other legs; thus the mechanical connections via the body are sufficient and no neuronal coupling between the legs is necessary to control body height.

9. CONCLUDING REMARKS

The results, which up to now have been mainly based on behavioural data, show that each walking leg can be considered as an oscillating unit with the properties of a relaxation oscillator. While the internal organization of this oscillator seems to reflect a hierarchical structure, the coupling between the different oscillators is organized in a non-hierarchical manner. The coupling between two such oscillators is not continuous as is the case in many mathematical descriptions of coupled oscillators. In contrast, the coupling between walking legs seems to be active only within selected phase ranges and "switched off" at other times. Ipsilateral influences are asymmetrical in the sense that rostrally directed influences are in general qualitatively different to caudally directed ones. Contralateral mechanisms seem to be symmetrical although quantitative differences can be found such that one side is able to dominate the other to some extent. There is a redundancy in the sense that different mechanisms produce basically the same result, namely a proper coordination between legs. The existence of several different mechanisms provides the possibility of a faster recovery of normal coordination after a disturbance. It also achieves a higher stability of the whole system. To obtain stable relationships earlier theoretical considerations on coupling mechanisms which acted only in one direction had to assume the existence of a hierarchy of eigenfrequencies in the different oscillators. This means that in insects for example front legs, if uninfluenced by coordinating signals, walked faster than middle legs and these in turn walked faster than hind legs (see Cruse and Graham (1985) for review). Because of the combination of different caudally and rostrally directed coupling mechanisms this assumption is no longer necessary.

The mechanisms seem to be quite different in different animals. Comparative studies showed that the mechanism in the crayfish and in the rock lobster are very similar (Clarac 1985). Forward-directed inhibitory influences were found for the stick insect, for the grasshopper (Graham 1978) and probably exist in the cockroach. One might speculate that the differences found between crayfish and stick insect reflect those between decapods and insects. What might be the reason for the different strategies used for the coordination of legs in crayfish and in stick insects? A basic difference is that maintaining the stability of the body position is much less a problem for the crayfish walking under water and using eight legs than for the stick insect walking on land with only six legs and climbing on branches. Therefore the stick insect is under much more constraint to keep as many legs on the ground as possible at each moment. Thus one might speculate that in stick insects coordination has to be obtained by a shorter or longer prolongation of the power stroke, whereas the crayfish can afford to solve the coordination problem by maintaining legs for a longer time in the return stroke. The latter might be the simpler task from the viewpoint of computation because (a) stability problems arising when changing the end of the return stroke might generally be less critical than those when changing the end of the power stroke and because (b) the control of the leg movement is easier during the return stroke when the movement of the leg is not mechanically coupled to the other legs.

A qualitative difference found between arthropods and the cat is that in the latter contralateral coupling is stronger than ipsilateral coupling. This might result from the fact that in the cat the coordination between ipsilateral legs allows both legs to perform overlapping return strokes, something that has been rarely observed in arthropods. What might be the reason for this difference? Simultaneous lifting of two ipsilateral neighbouring legs, in principle causes an instability of the body, particularly in a four-legged animal. Therefore one should assume that this situation is avoided by the system controlling leg movement. Nevertheless, the instability is much less of a problem for mammals, such as cats, than for the crayfish or the stick insect. In mammals generally right and left legs are arranged below the centre of body mass, in complete contrast to arthropods. Thus, in the cat, the horizontal projection of the lever arm, by which gravity rotates the body, is much shorter, and the body is, to a larger extent, also supported by the legs of the other side of the body. Thus, the cat can afford coordinating mechanisms that have the effect of ipsilaterally overlapping return strokes.

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REFERENCES

Ayers JL Davis WJ 1977. J comp Physiol 115, 1-27

Bässler U 1972. Kybernetik 10, 110-114

Bässler U 1977. Biol Cybern 25, 61-72

Bässler U 1979. Physiol Entomol 4, 193-199

Bässler U 1986. Biol Cybern 54, 65-69

Bässler U 1988. J exp Biol 136, 125-147

Bässler U Dübner C Fahrig T 1987. Zool Jb Physiol 91, 393-401

Bässler U Foth E Breutel G 1985. J exp Biol 116, 301-311

Camhi JM 1988. Experientia 44, 401-408

Clarac F 1985. In: Barnes, W.J.P. & Gladden, M.H. (Eds.) Feedback and motor control in invertebrates and vertebrates, Croom Helm, London, pp 379-400

Clarac F Chasserat C 1983. J exp Biol 107, 189-217

Clarac F Chasserat C 1986. Biol Cybern 55, 171-185

Cruse H 1976. Biol Cybern 24, 25-33

Cruse H 1979a. Physiol Entomol 4, 121-124

Cruse H 1979b. Biol Cybern 32, 107-113

Cruse H 1980a. Biol Cybern 37, 131-136

Cruse H 1980b. Biol Cybern 37, 137-144

Cruse H 1981. J exp Biol 92, 87-95

Cruse H 1985a. J exp Biol 114, 513-519

Cruse H 1985b. J exp Biol 116, 343-355

Cruse H 1985c. J exp Biol 116, 357-362

Cruse H 1985d. In: Gewecke,M. & Wendler,G. (Eds.) Insect Locomotion, Parey, Hamburg, Berlin pp 19-26

Cruse H Clarac F Chasserat C 1983. Biol Cybern 47, 87-94

Cruse H Epstein S 1982. J exp Biol 101, 161-170

Cruse H Graham D 1985. In: Bush, B.M.H. & Clarac,F. (Eds.) Co-ordination of Motor Behaviour, Soc. for Experimental Biology Seminar 24, Cambridge University Press, Cambridge, pp 283-301

Cruse H Knauth A 1989. J exp Biol 144, 199-213

Cruse H Müller U 1986. J exp Biol 121, 349-369

Cruse H Pflüger HJ 1981. J exp Biol 92, 97-107

Cruse H Riemenschneider D Stammer W 1989. Biol Cybern 61, 71-77

Cruse H Saxler G 1980. Biol Cybern 36, 159-163
Cruse H Schmitz J 1983. J exp Biol 102, 175-185
Cruse H Schwarze W 1988. J exp Biol 138, 455-469
Cruse H Warnecke H 1991. Exp Brain Res (submitted)
Dean J 1984. J comp Physiol A 155, 771-781
Dean J 1989. J exp Biol 145, 103-131
Dean J 1990. Biol Cybern 63, 115-120
Dean J 1991. Biol Cybern (submitted)
Dean J Wendler G 1982. J comp Physiol 148, 195-207
Dean J Wendler G 1983. J exp Biol 103, 75-94
Dean J Wendler G 1984. J exp Biol 110, 203-216
Delcomyn F Cocatre-Zilgien JH 1988. Biol Cybern 59, 379-384
Foth E Bässler U 1985a. Biol Cybern 51, 313-318
Foth E Bässler U 1985b. Biol Cybern 51, 319-324
Foth E Graham D 1983. Biol Cybern 48, 149-157
Franklin R Bell WJ Jander R 1981. J Insect Physiol 27, 249-255
Graham D 1972. J comp Physiol 81, 23-52
Graham D 1977. Biol Cybern 26, 187-198
Graham D 1978. J exp Biol 73, 159-172
Graham D 1979. Biol Cybern 32, 139-145
Halbertsma JM 1983. Acta Physiol Scand Suppl 521, 1-75
v.Holst E 1939. Ergebn Physiol 42, 228-306
Jander JP 1985. In: Gewecke,M. & Wendler,G. (Eds.) Insect locomotion, Parey, Hamburg, Berlin, pp 33-42
Land MF 1972. J exp Biol 57, 15-40
McMillan D Kien J 1983 Proc R Soc Lond B 218, 287-308
Müller U 1990 Thesis. Fac of Biology, Univ of Bielefeld
Müller U Clarac F 1990a. J exp Biol 148, 89-112
Müller U Clarac F 1990b. J exp Biol 148, 113-128
Müller U Cruse H 1991a. Biol Cybern (submitted)
Müller U Cruse H 1991b. Biol Cybern (submitted)
Pearson KG Franklin R 1984. Int'l J Robotics Res 3, 101-112
Pearson KG Iles FJ 1973. J exp Biol 58, 725-744
Pfeiffer F Weidemann HF Danowski P 1990. Proc of the 1990 IEEE Int Conf 3, 1458-1460
Schmitz J 1985. In: Gewecke,M. & Wendler,G. (Eds.) Insect locomotion, Parey, Hamburg, Berlin, pp 27-32
Schmitz J Haßfeld G 1989. J exp Biol 143, 373-388
Seyfarth EA Bohnenberger J 1980. Proc Intern Congr Arachnol 8, 249-255
Weiland G Koch U T 1987. J exp Biol 133, 137-156
Wendler G 1968. In: Marko,H. & Färber,G. (Eds.) Kybernetik 1968, Oldenbourg, München, Wien, pp 68-74
Wilson DM 1966. Ann Rev Entomol 11, 102-123
Zolotov V Frantsevich L Falk EM 1975. J comp Physiol 97, 339-353