Simulation of Complex Movements Using Artificial Neural Networks*

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A simulated network for controlling a six-legged, insect-like walking system is proposed. The network contains internal recurrent connections, but important recurrent connections utilize the loop through the environment. This approach leads to a subnet for controlling the three joints of a leg during its swing which is arguably the simplest possible solution. The task for the stance subnet appears more difficult because the movements of a larger and varying number of joints (9–18: three for each leg in stance) have to be controlled such that each leg contributes efficiently to support and propulsion and legs do not work at cross purposes. Already inherently non-linear, this task is further complicated by four factors: 1) the combination of legs in stance varies continuously, 2) during curve walking, legs must move at different speeds, 3) on compliant substrates, the speed of the individual leg may vary unpredictably, and 4) the geometry of the system may vary through growth and injury or due to non-rigid suspension of the joints. This task appears to require some kind of „motor intelligence". We show that an extremely decentralized, simple controller, based on a combination of negative and positive feedback at the joint level, copes with all these problems by exploiting the physical properties of the system.

Introduction

The ultimate goal of neurobiological investigations is to understand how the brain contributes to the control of behavior. Brains, in particular mammalian brains, are considered to be the most complex systems in the world. Therefore, reaching this goal is surely not a simple task. Even so-called "simple" brains, for example those of insects, are far from understood. Important progress has been made with respect to specific, typically low-level questions by following a reductionistic approach. In our research, this approach is represented by the use of standard methods of behavioral physiology and neurophysiology to study aspects of insect walking. However, essential progress in understanding the whole system can only be expected if these reductionist methods are accompanied by the synthetic tools of simulation. By simulation studies, the separately investigated elements of the system can be put together in order to examine system properties which emerge from their interactions. Typically these syntheticstudies are done using computer simulations. However, many properties of the system including those of the environment in which the system is acting, cannot easily be simulated. Therefore in recent years so-called hardware simulations have assumed a more important role which means that the simulation takes the form of a real, physical robots. In our research on insect walking, we use both software and hardware simulations which, however, are always based on extensive experimental investigation of the biological system.

One important problem for the control of behavior is often neglected: the number of degrees of freedom provided by the body is usually greater than necessary for solving the task at hand. In this case, the task is ill-posed or underdetermined. This means that the control system can select among different alternatives, giving it some degree of autonomy. This problem appears in practically all natural control tasks, even apparently simple ones. For example, grasping a cup can be performed using very different arm postures and different movement trajectories of the hand to the cup. Or think of a bird building its nest. The general goal, i.e. the general form of the nest may be prescribed.

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But how a particular twig has to be fixed on a particular branch, cannot be determined in advance; it has to be decided in the actual situation. In other words, the system needs to have some "motor intelligence". This makes the investigation of such systems interesting, but also challenging. Because of the autonomy of a behaving animal, the experimenter has little direct influence on its behavior, and such a system is therefore not very appropriate for the traditonal input-output analysis.

Walking in a Natural Environment Requires Motor Intelligence

In this paper we concentrate on a seemingly simple behavior, namely the control of walking in insects. This is an ill-posed problem. Each of the six legs typically has three joints, which means that there are 18 degrees of freedom. The movement of 18 joints has to be coordinated in a sensible way in an environment which may change its properties drastically from one moment ot the next. Therefore, the control system has to react in an adaptive way to disturbances in order to perform a given task such as straight walking, for example. Comparable problems occur in human motor control. We are, however, usually not aware of these problems, because we do not usually consciously think about how to move the elbow or the shoulder when grasping a cup. Therefore the task seems to be simple. The difficulties, however, become immediately evident when one tries to construct a robot to solve this task. Even walking on a simple flat horizontal surface cannot be performed by present-day robots with the ease and elegance of "simple" insects.

Results from a large number of behavioral and neurophysiological studies suggest that the flexibility of the system controlling walking in insects is based on a far reaching decentralisation of the control structure. This decentralization has the advantage that two important questions can be considered separately. One refers to the control of the single leg and the other to the spatio-temporal coordination among the legs.

To date, the vast majority of investigations of the mechanisms underlying insect walking has focused on the behavior. The neuronal implementation of the reported control features is known only to a very limited extent. Therefore, in this paper the control system is described in the form of a model which summarizes the findings obtained from behavioral experiments. Although the model uses concepts and methods from the field of artificial neural networks, this should not be misunderstood asapplying to real neurons in the insect unless otherwise stated.

These simulations will show that the intelligence required to control complex behavior is not necessarily based on a complex control system. On the contrary, the control systems are quite simple and the "intelligence" relies on the exploitation of the physics of the system and the environment. These results may also be appropriate to help to understand other more complex behaviors.

Different Local Mechanisms Control the Coordination of Legs

It is known from the work of v. Holst (1943) and Wendler (1964) that the movements of individual legs are governed by independent control systems (for Crustaceans see Chasserat and Clarac (1980)). Each indvidual leg can step with its own rhythm. If the legs are only weakly coupled this leads to a behavior von Holst called relative coordination. Subsequent investigations (Wendler, 1964; review Bässler, 1983) showed that the whole system, that is, the leg and the accompanying neural control structures, forms a relaxation oscillator. During stance, the leg is on the ground, supports the body and, in the forward walking animal, moves backwards with respect to the body. The posterior transition point is called the posterior extreme position (PEP); it is determined in part by the position of the leg. At this transition, the behavior switches from stance to swing. During swing, the leg is lifted off the ground and moved in the direction of walking to where it can begin a new stance.

Although the legs are independent in principle, in the absence of strong disturbance during walking an insect typically shows a well defined stepping pattern. The tripod gait – front and rear leg of one side swing together with the contralateral middle leg -is usually said to be typical for insects. Graham (1985) has shown in detailed investigations of stick insects, that slowly walking animals or animals walking under load, generally adopt the tetrapod gait (Fig. 1). This appears to be also true

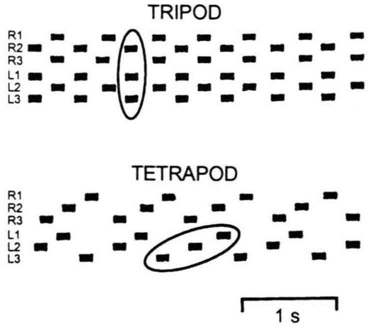

Fig. 1. The step patterns of a tripod (a) and a tetrapod (b) gait as produced by a stick insect. The six traces represent the six legs. Black bars correspond to swing movement. Legs are designated as left (L) or right (R) and numbered from front to rear. Left and right legs on each segment (e.g., L1 and R1) always have a phase value of approximately 0.5. The phase value of adjacent ipsilateral legs (e.g., L1 and L2) is 0.5 in the tripod gait but differs in the tetrapod gait (after Graham, 1985).

for insects other than stick insects. The tetrapod gait can be described as a wave of swing movements travelling along the body from rear to front.

How does this coordination occur and how is it stabilized after disturbances? Results from stick insects and other arthropods show that the coupling between neighboring legs can be described by simple rules (Cruse, 1990).

In all, six different coupling mechanisms have been found in behavioral experiments with the stick insect. These are summarized in Fig. 2. One mechanism (5 in Fig. 2a) serves to correct errors in leg placement; another (6) has to do with distributing propulsive force among the legs. These will not be considered here. The other four are used in the present model. The beginning of a swing movement, and therefore the end-point of a stance movement (PEP), is modulated by three mechanisms arising from ipsilateral legs: (1) a rostrally directed inhibition during the swing movement of the next caudal leg (Fig. 2b), (2) a rostrally directed excitation when the next caudal leg begins active retraction (Fig. 2c), and (3) a caudally directed influence depending upon the position of the next rostral leg (Fig. 2d). Influences (2) and (3) are also active between contralateral legs. The end of the swing movement (AEP) in the animal is modulated by a single, caudally directed influence (4) depending on the position of the next rostral leg. This mechanism is responsible for the

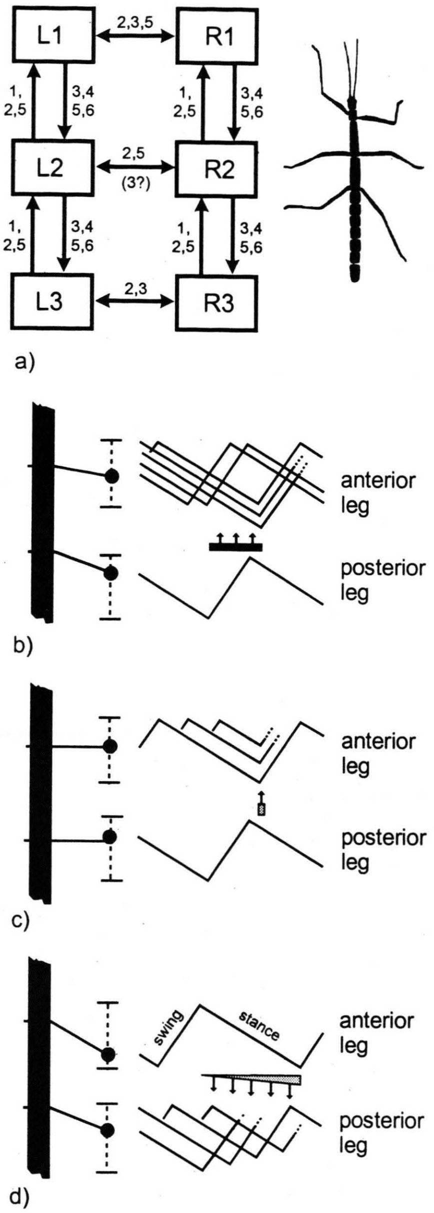

Fig. 2. (a) Summary of the coordination mechanisms operating between the legs of a stick insect. The leg controllers are labelled R and L for right and left legs and numbered from 1 to 3 for front, middle, and hind legs. The different mechanisms (1 to 6) are explained in the text and in (b–d). (b, c, d) Coordination between two ipsilateral legs. The upper trace of each panel shows the anterior leg. The influencing leg is drawn only once. Several traces for the influenced leg are presented to show the effect of the coordinating mechanisms at different phase relations. The durations and the intensities of the influences are roughly indicated by the length and the thickness of the bars and wedges, respectively. (b) the rostrally directed inhibitory influence is active during the swing of the posterior leg. (c) The rostrally directed excitatory influence is active at the beginning of the stance of the posterior leg (d) The caudally directed excitatory influence is active during the stance of the anterior leg.

targeting behavior – the placement of the tarsus at the end of a swing close to the tarsus of the adjacent rostral leg.

These interleg influences are mediated in two parallel ways. The first pathway comprises the direct neural connections between the step pattern generators. The second pathway arises from the mechanical coupling among the legs. That is, the activity of one step pattern generator influences the movements and loading of all legs and therefore influences the activity of their step pattern generators via sensory pathways. This combination of mechanisms adds redundancy and robustness to the control system of the stick insect (Dean and Cruse, 1995).

The simulations shown below demonstrate that these mechanisms deduced from behavioral experiments are sufficient to produce walks of the tripod or the tetrapod type and to stabiliz the coordinatione against disturbances. This result means that the gaits are not explicitly calculated, but emerge from the cooperation of these local rules.

The Control of the Quasirhythmic Movements of the Single Leg

An insect leg typically has three joints. The coxa-trochanter and femur-tibia joints, the two distal joints, are simple hinge joints with one degree of freedom corresponding to elevation and extension of the tarsus, respectively (Fig. 3). The subcoxal joint is more complex, but most of its movement is in a rostrocaudal direction around the nearly vertical axis. The additional degree of freedom allowing changes in the alignment of this axis is little used in normal walking, so the leg can be considered as a manipulator with three degrees of freedom for movement in three dimensions. As already mentioned above, the step cycle of the walking leg can be divided into two functional states, stance and swing. Already in 1911 based on his studies in cats, Brown proposed a simple system, for what is now called a central pattern generator, to control the switching between the two states, namely two mutually inhibitory neurones. Later this idea was expanded to include sensory input (Land, 1972; Bässler, 1986). By applying simple learning rules we found an alternative circuit which shows better stability against disturbances. The essential difference is replacing mutual inhibition with positive feedback for the stance subsystem and for the swing subsystem (Fig 4, selector net). To avoid unlimited growth of excitation, two neurones are provided with a nonlinear characteristic. For insects there are no physiological experiments to decide between the positive and negative feedback alternatives for controlling the stepping phases. Nevertheless, we decided to use the positive feedback version in our simulation for two reasons. First, indirect evidence of positive feedback in other systems exists for the leech (Kristan *et al.,* 1996) and for the stick insect (Kittmann *et al.,* 1996), and similar circuits are assumed to exist in mammalian brains (Houk *et al.,* 1993). Second, and more importantly, the positive feedback version provides better stability.

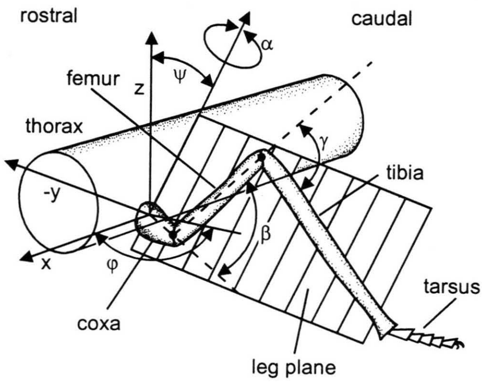

Fig. 3. Schematic model of a stick insect leg showing the arrangement of the joints and their axes of rotation.

The selector net decides which of the two "microbehaviors", stance or swing movement, will be performed. Two modules (or "agents") are responsible for the detailed realisation of these behavior, the swing net and the stance net. The task of finding a network that produces a swing movement seems to be easier than finding a network to control the stance movement because a leg in swing is mechanically uncoupled from the environment and therefore, due to its small mass, essentially uncoupled from the movement of the other legs. Therefore, we first will concentrate on the control of the swing movement.

The Swing Movement Can Be Controlled by an Extremely Simple Network

As a basis for the simulation, first the swing movements of walking animals have been investigated (Cruse and Bartling, 1995). The measured spatio-temporal trajectories of the tarsi have then been used to train an artifical neural network.

The geometry of the leg is shown in Fig. 3. As there are three joints to be controlled, the control network must have at least three output channels, one for each leg joint. A simple, two-layer, feedforward net with three output units and six input units can produce movements which closely resemble the swing movements observed in walking stick insects. The inputs correspond to three coordinates defining the actual leg configuration and three defining the target – the configuration desired at the end of the swing. In the simulation, the three outputs, interpreted as the angular velocities of the joints, dα/d*t*, dβ/d*t*, and dγ/d*t*, are fed into an integrator (not shown in Fig. 4) to obtain the joint angles. (In the animal, the movement of the leg itself can be considered as an integration of the muscle activities.) The actual angles resulting from the integration and any external disturbance are measured and fed back into the net.

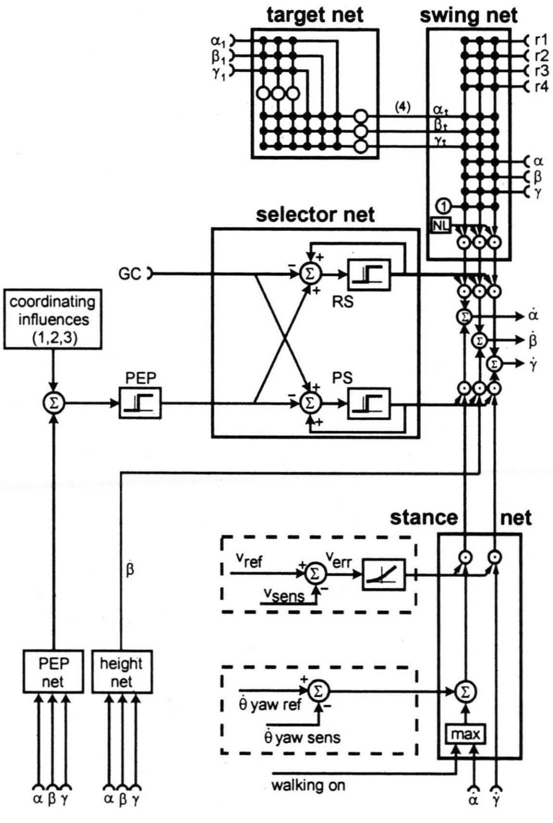

Fig. 4. The leg controller consists of three parts: the swing net, the stance net, and the selector net which determines whether the swing or the stance net can control the motor output, i.e., the velocity of the three joints, α, β, and γ. The selector net contains four units: the PEP unit signalling posterior extreme position, the GC unit signalling ground contact, the RS unit controlling the return stroke (swing movement), and the PS unit controlling the power stroke (stance movement). The target net transforms information on the configuration of the anterior, target leg (α_1, β_1, and γ_1) into angular values for the next caudal leg which place the two tarsi close together. These desired final values (α_t, β_t, γ_t) and the current values (α, β, and γ) of the leg angles are input to the swing net together with a bias input (1) and sensory inputs (r1–r4) which are activated by obstructions blocking the swing and thereby initiate avoidance movements. A non-linear influence (NL) modulates the velocity profile. For details see Cruse *et al.* (1996).

Through optimization, the network can be simplified to only 8 (front and middle leg) or 9 (hind leg) non-zero weights (for details see Cruse *et al.*, 1996). We believe this represents the simplest possible network for the task; it can be used as a standard of comparison with physiological results from stick insects. Despite its simplicity, the net not only reproduces the trained trajectories, it is able to generalize over a considerable range of untrained situations, demonstrating a further advantage of the network approach. Moreover, the swing net is remarkably tolerant with respect to external disturbances. The learned trajectories create a kind of attractor to which the disturbed trajectory returns. This compensation for disturbances occurs because the system does not compute explicit trajectories, but simply exploits the physical properties of the world. The properties of this swing net can be described by the 3D vector field in which the vectors show the movement produced by the swing net at each tarsus position in the workspace of the leg. Fig. 5 shows the planar projections of one parasagittal section (a) and one horizontal section (b) through the work space. The complete fields are similar to those shown by Bizzi *et al.* (1995) for the frog.

This ability to compensate for external disturbances permits a simple extension of the swing net in order to simulate an avoidance behavior observed in insects. When a leg strikes an obstacle during its swing, it initially attempts to avoid it by retracting and elevating briefly and then renewing its forward swing from this new position. In the augmented swing net, additional inputs similar to a tactile or force sensor signal such mechanical disturbances (Fig. 4, r1–r4). These units are con-

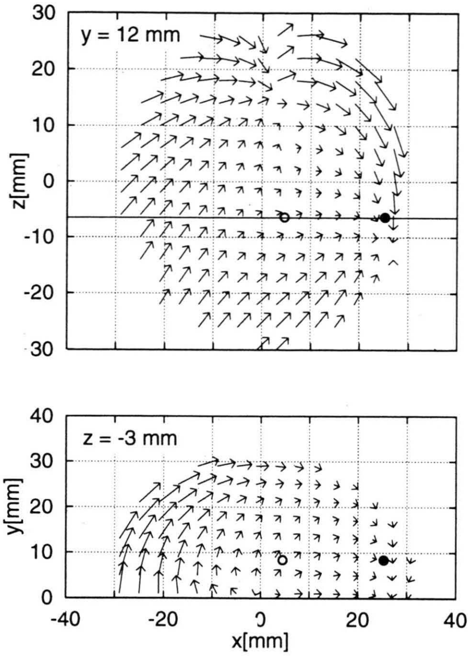

Fig. 5. Vector field representing the movement of the tarsus of a left front leg produced by the swing net. (a) Projection of a parasagittal section (y = 12 mm). (b) Projection of a horizontal section slightly below the leg insertion ($z = -3$ mm). Left is posterior; right is anterior. The average posterior extreme position (start of swing movement) and the average anterior extreme position (end of swing movement) are shown by open and closed circles, respectively.

nected by fixed weights to the three motor units in such a way as to produce the brief retraction and elevation seen in the avoidance reflexes.

In the model, the targeting influence (coordinating mechanism no. 4) reaches the leg controller as part of the input to the swing net (Fig. 4). These signals can be generated by a simple feedforward net with three hidden units and logistic activation functions (Fig. 4, "target net") which directly associates desired final joint angles for the swing to current joint angles of a rostral leg such that the tarsi of the two legs are at the same position (Dean, 1990). There is no explicit calculation of either tarsus position. Physiological recordings from local and intersegmental interneurons (Brunn and Dean, 1994) support the hypothesis that a similar approximate algorithm is implemented in the nervous system of the stick insect.

The Control Problems for the Stance Movement

The control of the stance movement appears to be more difficult. It is not enough simply to specify a movement for each leg on its own as in the case of the swing movement: the mechanical coupling through the substrate means that efficient locomotion requires coordinated movement of all the joints of all the legs in contact with the substrate, that is, a total of 18 joints when all legs of an insect are on the ground. The task is a nonlinear problem, because we have to deal with rotational movements. This is even more the case when the rotational axes of the joints are not orthogonal, as is often the case for insect legs and for the basal leg joint in particular. Another nonlinearity arises from the fact that the number and combination of mechanically coupled joints varies from one moment to the next, depending on which legs are lifted.

For straight walks, one could simplify the problem by assuming that the trajectories of the leg endpoint follow a straight line parallel to the long axis of the body. This assumption, however, is only approximately the case in normal walking. It definitely does not hold when the animal negotiates a curve, which requires the different legs to move along different arcs at different speeds. Superimposed on all these problems we have the above mentioned problem that the control system has to deal with extra degrees of freedom. This means that the control system has to decide, by applying some criteria, which of the possible solutions should be selected.

In machines, these problems can be solved using traditional, though computationally costly, methods, which consider the ground reaction forces of all legs in stance and seek to optimize some additional criteria, such as minimizing the tension or compression exerted by the legs on the substrate. Due to the nature of the mechanical interactions and inherent in the search for a globally optimal control strategy, such algorithms require a single, central controller; they do not lend themselves to distributed processing. This makes real-time control difficult, even in the still simple case of walking on a rigid substrate. Taking into account the much smaller bandwidth and the much slower computational speed of the biological systems compared to the technical ones makes real time control even more difficult.

Further complexities arise in more irregular, natural walking situations, making solution difficult even with high computational power. These problems arise, for example, when an animal or a machine walks on a slippery surface or on a compliant substrate, such as the leaves and twigs encountered by stick insects. Any flexibility in the suspension of the joints further increases the degrees of freedom that must be considered and the complexity of the computation. Further problems for an exact, analytical solution occur when the length of leg segments changes during growth or their shape changes through injury. In such cases, knowledge of the geometrical situation is incomplete, making an explicit calculation difficult, if not impossible. Such problems already arise during normal walking: the positions and orientations of the axes in the non-rigid joints may change due to load changes elicited by different orientation with respect to gravity.

Local Positive Feedback – the Solution?

Despite the evident complexity of these tasks, they are mastered even by insects with their "simple" nervous systems. Hence, there has to be a solution that is fast enough that on-line computation is possible even for slow neuronal systems. How can this be done? Several authors (e.g. Brooks, 1991) have pointed out that some relevant parameters do not need to be explicitly calculated by the nervous system because they are already available in the interaction with the environment. This means that, instead of an abstract calculation, the system can directly exploit the dynamics of the interaction and thereby avoid a slow, computationally exact algorithm. To solve the particular problem at hand, we propose to replace a central controller with distributed control in the form of local positive feedback (Cruse *et al.,* 1996). Compared to earlier versions (Cruse *et al.,* 1995), this change permits the stance net to be radically simplified. The positive feedback occurs at the level of single joints: the position signal of each is fed back to control the motor output of the same joint (Fig. 4, stance net). How does this system work? Let us assume that any one joint is moved actively. Then, because of the mechanical connections, all other joints begin to move passively, but in exactly the proper way. Thus, the movement direction and speed of each joint does not have to be computed because this information is already provided by the physics. The positive feedback then transforms this passive movement into an active movement.

This idea is supported by an earlier finding of Bässler (1976) showing a reflex reversal for the femur tibia joint which could be interpreted as a positive feedback (see also Schmitz *et al.,* 1995). Therefore, we decided to implement this solution for the control of the stance movement. There are, however, several problems to be solved. The first is that positive feedback using the raw position signal would lead to unpredictable changes in movement speed, not the nearly constant walking speed which is usually desired. This problem can be solved by introducing a kind of band-pass filter into the feedback loop. The effect is to make the feedback proportional to the angular velocity of joint movement, not the angular position. In the simulation, this is done by feeding back a signal proportional to the angular change over the preceding time interval.

The second problem is that using positive feedback for all three leg joints leads to unpredictable changes in body height, even in a computer simulation neglecting gravity. In the stick insect, body height is controlled by a distributed system in which each leg acts like an independent, proportional controller (Cruse, 1976; Cruse *et al.,* 1993). However, maintaining a given height via negative feedback appears at odds with the proposed local positive feedback for forward movement. How can both functions be fulfilled at the same time? To solve this problem we assume that during walking positive feedback is provided for the α joints and the γ joints (Fig. 4, stance net), but not for the β joints. The β joint is the major determinant of the separation between the substrate and the leg insertion in the body, which determines body height.

A third problem inherent in using positive feedback is the following. Let us assume that a stationary insect is pulled backward by gravity or by a brief tug from an experimentor. With positive feedback control as described, the insect should then continue to walk backwards even after the initial pull ends. This has never been observed. Therefore, we assume that a supervisory system exists which is not only responsible for switching on and off the entire walking system, but also specifies walking direction (normally forward for the insect). This influence is represented by applying a small, positive input value (Fig. 4, "walking on") which replaces the sensory signal if it is larger than the latter (the box "max" in Fig. 4, stance net).

To permit the system to control straight walking and to negotiate curves, a supervisory system was introduced which, in a simple way, simulates optomotor mechanisms for course stabilisation that are well-known from insects and have also been applied in robotics. This supervisory system uses information on the rate of yaw ("$d\theta_{\text{yaw sens}}/dt$", Fig. 4, stance net), such as visual movement detectors might provide. It is based on negative feedback of the deviation between the desired turning rate and the actual change in heading over the last time step. The error signal controls additional impulses to the α joints of the front and hind legs which have magnitudes proportional to the deviation and opposite signs for the right and left sides. In earlier versions, this bias was given to the front legs only. A much better behavior can be found when the bias is also given to the hind legs. With this addition and $d\theta_{\text{yaw ref}}/dt$ set to zero, the system moves straight (Fig. 6a) with small, side-to-side oscillations in heading such as can be observed in walking insects. To simulate curve walking (Fig. 6b), the reference value is given a small positive or negative bias to determine curvature direction and magnitude.

Finally, we have to address the question of how walking speed is determined in such a positive feedback controller. Again, we assume a central value which represents the desired walking speed v_{ref}. This is compared with the actual speed, which could be measured by visual inputs or by monitoring leg movement. This error signal is subject to a nonlinear transformation and then multiplied with the signals providing the positive feedback for all α and γ joints of all six legs (Fig. 4, stance net).

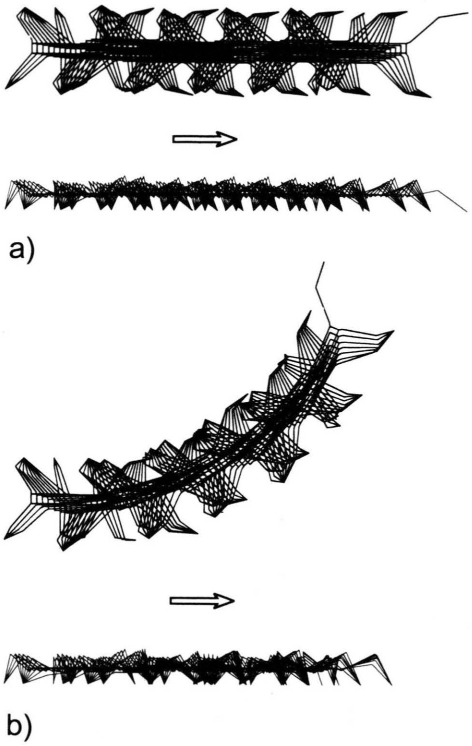

Fig. 6. Simulated walk by the basic six-legged system with negative feedback applied to all six β joints and positive feedback to all α and γ joints as shown in Fig. 4. Movement direction is from left to right (arrow). Leg positions are illustrated only during stance and only for every second time interval in the simulation. Each leg makes about five steps. Upper part: top view, lower part: side view. (a) Straight walking ($d\theta_{\text{yaw ref}}/dt = 0$). (b) curved walking ($d\theta_{\text{yaw ref}}/dt \neq 0$).

Local Positive Feedback Solves These as Well as Further Problems

As is shown in Fig. 6a for the case of straight walking, this network is able to control proper coordination. Steps of ipsilateral legs are organized in triplets forming "metachronal waves", which proceed from back to front, whereas steps of the contralateral legs on each segment step approximately in alternation. With increasing walking speed, the typical change in coordination from the tetrapod to a tripod-like gait is found. For slow and medium velocities the walking pattern corresponds to the tetrapod gait with four or more legs on the ground at any time and diagonal pairs of legs stepping approximately together; for higher velocities the gait approaches the tripod pattern with front and rear legs on each side stepping together with the contralateral middle leg. The coordination pattern is very stable. For example, when the movement of one leg is interrupted briefly during the power stroke, the normal coordination is regained immediately at the end of the perturbation. Furthermore, the model can cope with obstacles higher than the normal distance between the body and the substrate. It continues walking when a leg has been injured, such that, for example, half of the tibia is removed.

What about curve walking? The typical engineer's solution is to determine the curve radius and the center of the curve. With these values the trajectories of the different legs are calculated and then, using inverse kinematics, the trajectories for the joint angles are determined. In our case, too, a value is required to determine the tightness of the curve. This, however, does not need to quantitatively correspond to the curve radius. The value is only used as an amplification factor for the feedback loop of front and hind legs. This value can deliberately be changed from one moment to the next. No further calculations are necessary.

The introduction of the local band-pass filtered positive feedback in 12 of the 18 leg joints provides a control system which as far as we can see cannot be further simplified, because it is decentralized down to the level of the single joints. This simplification has the side effect that computation time can be minimized. The essential advantage, however, is that, by means of this simplification and the consideration of physical properties of the body and the environment, all problems mentioned above can easily be solved, although they, at first sight, seemed to be very difficult.

Unexpectedly, the following interesting behavior was observed. A massive perturbation, for example by clamping the tarsi of three legs to the ground, can make the system fall (Fig. 7). Although this can lead to extremely disordered arrangements of the six legs, the system was always able to stand up and resume proper walking without any help. This means that the simple solution proposed here also eliminates the need for a special supervisory system to rearrange leg positions after such an emergency.

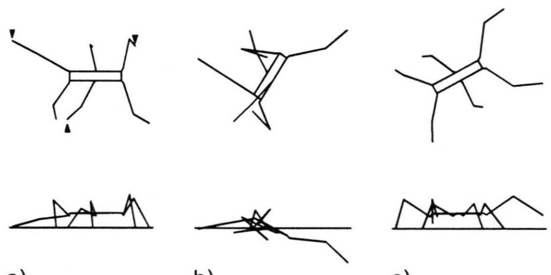

Fig 7. Righting behavior. (a) By clamping the tarsi to the ground (arrowheads), the system is made to fall leading to disordered arrangement of the legs (b). Nevertheless, the system stands up without help and resumes proper walking (c).

Conclusion

Considering all the problems a walking system already has to deal with under seminatural conditions, one is inclined to attribute such a system quite a high motor intelligence to such a system. We have, however, seen that the control system neither has to be very complicated nor does it require a centralized architecture. On the contrary, the seemingly most difficult problems are solved by the structurally most simple subsystems. This simplification is possible because the physical properties of the system and its interaction with the world are exploited to replace an abstract, explicit computation. No explicit internal world model is required. Thus, "the world" is used as "its own best model" (Brooks, 1991). This principle is implemented at several places in the control system.

(i) The quasi-rhythmic leg movements are not produced by a endogenous central oscillator. Instead they result from the interaction of the neuronal control system and the environment.

(ii) No explicit computation of the complete trajectory is necessary for the generation of the swing movement. Instead the instantaneous continuation of a movement is determined on the basis of the current sensory input values.

(iii) The discrepancy between the complexity of the task and the simplicity of the solution is most obvious in the case of the control of the stance movement.

Furthermore, the Walknet simulation shows that simple local rules can produce unexpected properties at the level of the whole system:

(a) the four local coordinating mechanisms produce tripod or tetrapod gaits which are stabile against disturbances, and (b) a combination of positive and negative feedback permits the control system to maintain body height and to right the body after a fall.

Outlook

The results presented are based mainly on behavioral experiments and software simulations. An earlier version has also been successfully tested using the six-legged TUM walking machine (Pfeiffer *et al.,* 1994; Pfeiffer and Cruse, 1994). One major disadvantage of our present simulation is its pure kinematic nature. To test the principle of local positive feedback at least for straight walking, we have performed a dynamic simulation for the six-legged system under positive feedback control during stance. The basic software was kindly provided by F. Pfeiffer, TU Munich. No problems occured. Nevertheless, a hardware test of the walking situations is necessary and is planned with M. Frik, University of Duisburg, and his robot TARRY (Frik and Amendt, 1995).

To date, learning the weights in the different subnets of Walknet has been done off-line. After being adjusted once, the weights cannot be changed by the system through online learning. As we have found such learning capabilities in the animals, we plan to introduce corresponding properties in Walknet. Another point is to add new behavioral modules for other body movements, such as feeding, body cleaning, or camouflage rocking (Pflüger, 1977) for example. This requires the introduction of an architecture which allows the system to decide between such modules. In a simple form this problem had to be solved for the swing-stance decision. Although not explicitely designed as such, the units of the selector net could be interpreted as a simple motivational system. Such motivational structures (see Maes, 1991) may help solve these problems. In other cases (e.g. rocking and walking), a decision may not be necessary and a simple summation, such as proposed by Steels (1994), may suffice.

All these structures are based on purely sensory driven subsystems. Many approaches, in particular those used in traditional AI, presuppose the existence of an explicit world model as a prerequiste to planning behavioral actions and deciding among different possible actions. Although it is very possible that truly cognitive systems require a kind of internal world model, it is an open question as to the complexity of behavior that can be produced without having a cognitive system. Therefore, we first concentrate on purely data-driven systems which have no explicit world model. However, this restriction will be relaxed in later stages. For example, a planned first step toward a world model will be to implement an internal model of the body. We argue that this is justified because the body is the nearest and the most important part of the external world of a brain. A special type of neural network to be used as a body model is already available (Steinkühler and Cruse, 1998), but up to now has been used here only as a technical device to simulate the kinematics of the body.

Neurophysiological investigations have not been considered above in detail. However, a comparison between the artificial neural system presented here and the results of neurophysiological investigations is desirable. What is known so far? Apart from the relatively well investigated motoneurones and a huge number of sensory neurons there are several groups of spiking interneurones, which presumably represent the first integrational layer for the sensory input (Burrows and Laurent, 1989). As a rough estimate each thoracic hemiganglion contains about 700 to 1000 spiking and nonspiking interneurones. About 50 nonspiking interneurons have been investigated in the context of walking movements. Fifteen of these neurons are also documented morphologically (Schmitz *et al.,* 1991; Büschges *et al.,* 1994; Wolf and Büschges, 1995). About 30 more interneurones have been shown to be activated in different ways during standing and walking (Kittmann *et al.,* 1996). The different neurones show quite different temporal behavior such as saw-tooth like, sinusoidal, or very short, pulse like activations or inactivations extending during the stance. A relatively large percentage of the neurones known up to now are coupled to the transitions between stance and swing. However, general principles, much less a functional circuit, are still unclear. Therefore, any attempt to directly correlate the artificial neurons of the Walknet with the neurons known from the neurophysiological investigations still appears very premature. However, we hope that these modelling studies will guide neurophysiological experiments and interpretation of the results.

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