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1998 Special Issue

Walknet—a biologically inspired network to control six-legged walking

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Received and accepted 30 April 1998

Abstract

To investigate walking we perform experimental studies on animals in parallel with software and hardware simulations of the control structures and the body to be controlled. Therefore, the primary goal of our simulation studies is not so much to develop a technical device, but to develop a system which can be used as a scientific tool to study insect walking. To this end, the animat should copy essential properties of the animals. In this review, we will first describe the basic behavioral properties of hexapod walking, as they are known from stick insects. Then we describe a simple neural network called Walknet which exemplifies these properties and also shows some interesting emergent properties. The latter arise mainly from the use of the physical properties to simplify explicit calculations. The model is simple too, because it uses only static neuronal units. Finally, we present some new behavioral results. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: Walking; Leg coordination; Positive feedback; Six-legged robot; Stick insect; Situatedness; Decentralized control

1. Introduction

The investigation of animal behavior is not only interesting with respect to specific solutions to specific problems (e.g. how to solve the figure–ground problem in vision or how to navigate in an unknown environment), but, on a more general level, to understand how an autonomous system should be constructed. Autonomy as understood here does not simply mean, as it often does in robotics, energy autonomy, but, as it is used commonly according to its literal meaning, not depending on commands given by an external system such as an operator. Thus, an autonomous system here means a system which follows self-contained rules. The construction of an autonomous system is, of course, a far reaching goal, but as a first step in this direction, such a system should show adaptivity to changing environmental situations. This is usually meant in the sense of being able to learn, which in turn means being able to make structural changes such as changes in synaptic weights. However, even hardwired systems with no learning can show considerable adaptability in the sense that they change their behavior in accord with changing environmental conditions. Therefore, in order to find out how far we can get with hardwired systems, online learning will be

precluded here and postponed for a later stage of investigation. Thus learning is only used here to train the networks in separate, off-line training procedures.

1.1. Walking: a nontrivial behavior

What kind of behavior should we look at? From a cognitive standpoint, walking seems to be rather uninteresting (i.e. to be a specific solution to a specific problem) because it appears to be a fairly automatic behaviour. We do not have to think consciously about moving the joints when walking. Nevertheless, we will argue that walking in a natural environment requires considerable ‘motor intelligence’ and can be regarded as a paradigm for control of behavior in general. First of all, walking, as almost all behavior, has to deal with redundancy. In most biological systems for motor control, particularly those concerned with walking, the number of degrees of freedom is normally larger than that necessary to perform the task. This requires the system to select among different alternatives according to some, often context-dependent optimization criteria, which means that the system usually has to have some autonomy. Therefore, the experimenter does not have direct control of some important inputs to the motor system. Further, such natural systems are physical systems ‘situated’ in complex, often unpredictable environments, which means that any movement may be modified by the physics of the

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system and the environment. In turn, adapting to real environments requires the use of sensory information about the environment and the results of the system's actions. Together, these two factors create a loop through the environment which means that the actual behavior is determined by the properties of the environment as well as those of the walking system. Despite these experimental and theoretical difficulties, the complexity makes the study of motor mechanisms especially challenging, particularly because they illustrate to a high degree the task of integrating influences from the environment, mediated through peripheral sensory systems, with central processes reflecting the state and needs of the organism. In a walking insect at least 18 joints, three per leg, have to be controlled. Because the environment may change drastically from one step to the next, and, as will be discussed later, even the geometrical properties of the body may change, the control of walking is all but a trivial task.

As will be shown, one important biological principle for solving these problems is to use a fairly decentralized control structure. This raises the question of what kind of architecture might be used. Several have been proposed. The so-called subsumption architecture as proposed by Brooks (1986) uses an arrangement of control units which work in parallel but control their output in a hierarchical manner. The behavior-based approach (Brooks, 1991; Maes, 1991) is less strict and allows other influences, including additive and subtractive or inhibitory influences, between the units. Steels (1994) proposed that pure summation alone occurring at the motor units might solve a large number of problems. We will not restrict ourselves in advance to one such principle, but will apply an architecture which is supported by the experimental results, i.e. is based on real behavior. As the following brief overview shows, all principles mentioned earlier will be applied.

The control system explained here consists of a number of distinct modules (or agents in the sense of Minsky, 1985) which are responsible for solving particular subtasks. Some of them might be regarded as being responsible for the control of special 'microbehaviors': for example, a walking leg can be regarded as being in one of two states, namely performing a swing movement or a stance movement. During stance, the leg is on the ground, supports the body and, in the forward walking animal, moves backwards with respect to the body. During swing, the leg is lifted off the ground and moved in the direction of walking to where it can begin a new stance. These two 'microbehaviors' are mutually exclusive. A leg cannot be in swing and in stance at the same time, a situation also holding for many 'macrobehaviors' such as fight or flight, for instance. Therefore, the control structure has to include a mechanism for deciding whether the swing or the stance module is in charge of the motor output. To solve this problem, a simple network, based on positive feedback, is used. This network works like a 'two-way' subsumption system, although there is no direct suppression and subsumption influence (see Section 2.1).

There are other cases where several modules can act fairly independently from each other. It is known from the work of von Holst (1943) (for stick insects: Wendler, 1964) that the movements of individual legs are controlled by independent control systems. Our experiments have shown that the coordination between the legs which is necessary to stabilize a given gait pattern occurs only during limited time windows (review Cruse, 1990). Influences arise from one or more neighboring legs and from several different mechanisms. In our case these different effects are simply summed up (see Section 2.2). The goal of finding a controller as simple as possible was achieved largely by taking into account the physical properties of the system and its interaction with the world. As proposed by e.g. Brooks (1991) the physical properties may be exploited to replace an abstract, explicit computation (see Sections 2.3 and 2.4).

2. Walknet

2.1. Control of the step rhythm of the individual leg

As mentioned earlier, the step cycle of the walking leg can be divided into two functional states, stance and swing. The anterior transition point, i.e. the transition from swing to stance in the forward walking animal, is called the anterior extreme position (AEP) and the posterior transition point is called the posterior extreme position (PEP). Differences in the constraints acting during the two states and in the conditions for their termination suggest that the leg controller consists of three separate control networks. Two low-level networks, a swing network and a stance network, control the movement of the leg during swing and stance, respectively [Fig. 2(b)]. The transition between swing and stance is controlled by a selector network [Fig. 2(b)]. (This separation may only be justified on a logical level; it need not correspond to entirely distinct circuits in the nervous system.) The swing network and the stance network are always active, but the selector network determines which of the two networks controls the motor output.

To date there is little evidence for a strong central pattern generator and robust endogenous rhythms for walking in stick insects. Bässler and Wegner (1983) could find no walking motor output unless at least one leg was intact and walking so it could provide afferent activity. Büschges et al. (1995) found that pilocarpin, a muscarinic acetylcholine antagonist, applied to the deafferented nerve cord elicits alternating activity in antagonistic motor pools at each leg joint and occasional walking-like coupling between the motor pools of different joints. However, the rhythms may be weak and highly variable and the activity of motoneurons controlling different leg joints is usually not coordinated as it is in walking. In other arthropods (crayfish, Chrachri and Clarac, 1990; locust, Ryckebusch and Laurent, 1993) pilocarpine elicits endogenous rhythms which better

resemble the motor output of walking. Their frequency is, however, much lower than that of normal stepping. In summary, it is not clear whether these oscillations contribute significantly to normal walking. In contrast, a variety of results do show that leg position and ground contact are critical parameters (e.g. Wendler, 1964; Bässler, 1977; Cruse, 1979; Cruse, 1985b; Dean and Wendler, 1982, 1983; and Section 4). To match these experimental results in our simulation, sensory input is used to select between swing and stance. (For a detailed simulation study of the effect of changing the relative contributions of central and peripheral influences see Beer and Gallagher, 1992).

In the selector net positive feedback from each of the two output units stabilizes the activity of whichever output unit is active. Activity in a sensory input causes a transition by inhibiting the active output unit and exciting the inactive one. The sensory input is either ground contact (see Section 4 for details) or the position of the leg tip. The latter depends in a nonlinear way on the position of the leg joints. The results obtained in behavioral experiments have been implemented in a two layer feedforward net (PEP Net) which contains three input units for the three joint angles, two hidden units, and one output unit determining the distance to the PEP threshold value.

2.2. Coordination between legs

In all, six different coupling mechanisms have been found in behavioral experiments with the stick insect. These are summarized in Fig. 1. Another recently described mechanism will be explained later (Section 4). One mechanism [6 in Fig. 1(a)] serves to correct errors in leg placement; another (5) 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; (2) a rostrally directed excitation when the next caudal leg begins active retraction; and (3) a caudally directed influence depending upon the position of the next rostral leg. 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 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

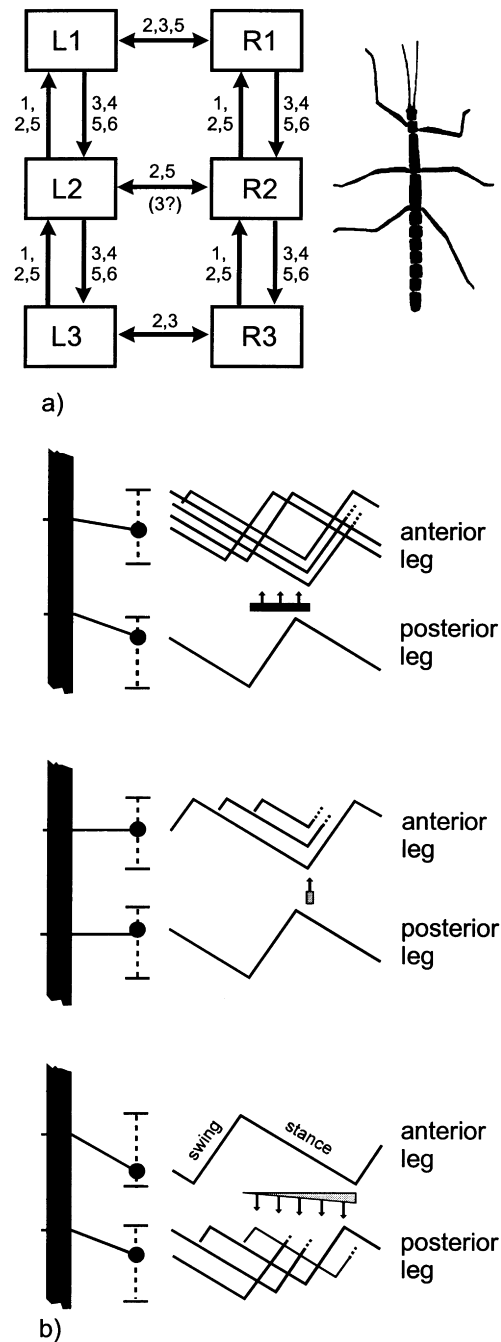


Fig. 1. Summary of the coordination mechanisms operating between the legs of a stick insect. The leg controllers are labelled R and L for right and left legs and numbered from 1–3 for front, middle, and hind legs. The different mechanisms (1–6) are explained in the text. (b) Illustrates the mechanisms 1–3 as shown from above to below.

pathways. This combination of mechanisms adds redundancy and robustness to the control system of the stick insect.

2.3. Control of the swing movement

The task of finding a network that produces a swing movement is simpler than finding a network to control the

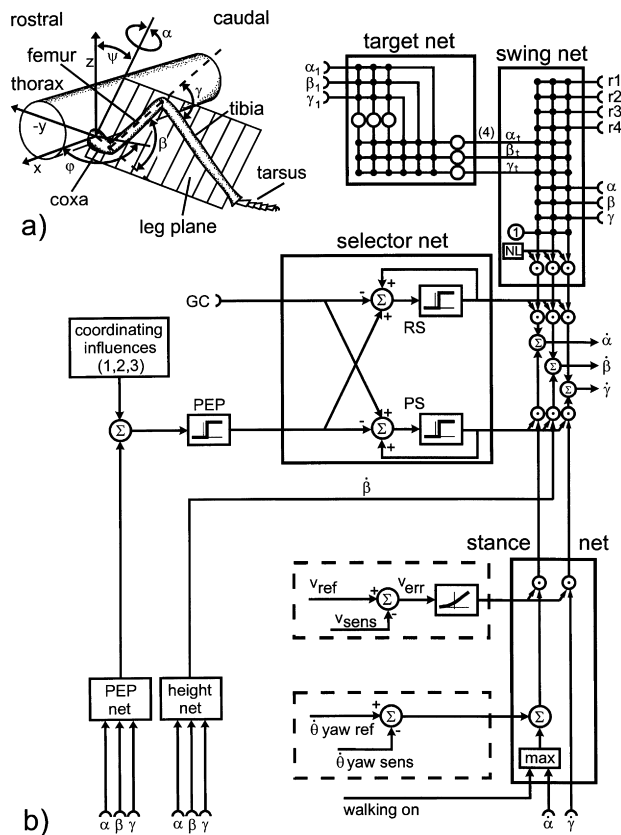


Fig. 2. Summary of leg geometry and control networks for the model. (a) Schematic model of a stick insect leg showing the arrangement of the joints and their axes of rotation. (b) The leg controller consists of three parts: the swing net, the stance net, and the selector net which determines whether 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 transfers 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_1 , β_1 , γ_1) 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 four sensory inputs (r_1 – r_4) which are activated by obstructions blocking the swing and thereby initiate different avoidance movements. A non-linear influence (NL) modulates the velocity profile. For details see Cruse et al. (1996).

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. The geometry of the leg is shown in Fig. 2(a). 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. 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. Thus, 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 (Cruse and Bartling, 1995). 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, $d\alpha/dt$, $d\beta/dt$ and $d\gamma/dt$, are used to control the joints. The actual angles are measured and fed back into the net.

Through optimization, the network can be simplified to only eight (front and middle leg) or nine (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. 3 shows the planar projections of one parasagittal section (a), and one horizontal section (b) through the workspace. 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, an additional input similar to a tactile or force sensor signals such mechanical disturbances at the front part of the tibia [Fig. 2(b), r_1] or the femur [Fig. 2(b), r_2]. These units are connected by fixed weights to the three motor units in such a way as to produce the brief retraction and elevation seen in the avoidance reflex. Other reflexes can be observed when the tibia is mechanically stimulated laterally (r_3) or when the femur is touched dorsally (r_4). These reflexes have been implemented in an analogous manner [Fig. 2(b)].

In the model, the targeting influence reaches the leg controller as part of the input to the swing net [Fig. 2(b)]. These signals can be generated by a simple feedforward net with three hidden units and logistic activation functions [Fig. 2(b), 'target net'] which directly associates desired final joint angles for the swing to current joint angles of a

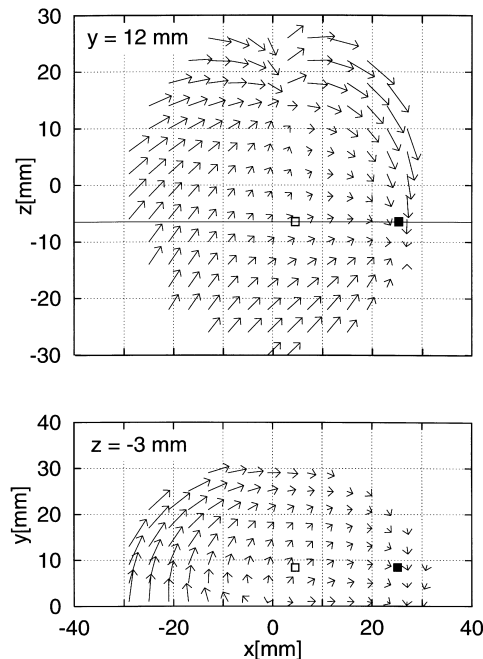


Fig. 3. Vector field representing the movement of the tarsus of a left front leg produced by the swing net. (a) Projection of a parasagittal section ($y = 12$ mm). (b) Projection of a horizontal section slightly below the leg insertion ($z = -3$ mm). Left is posterior, right is anterior. The average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

rostral leg such that the tarsus of the posterior leg is moved in the direction of that of the anterior leg. Compared with a first version (Dean, 1990) the new target net has direct connection between the input and the output layer. 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.

2.4. Control of the stance movement and coordination of supporting legs

For the stance movement, simple solutions can be found for straight walking on a flat surface (Müller-Wilm et al., 1992). In more natural situations, the task of controlling the stance movements of all the legs on the ground poses several major problems. It is not enough simply to specify a movement for each leg on its own: 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. However, the number and combination of mechanically coupled joints varies from one moment to the next, depending on which legs are lifted. The task is quite nonlinear, particularly 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. A further complication occurs when the animal negotiates a curve, which requires the different legs to move at different speeds.

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.

Further complexities arise in more complex, natural walking situations, making solution difficult even with high computational power. These occur, 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.

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, 1997) 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 with 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. 2(b), 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.

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. Body height of the stick insect is controlled by a distributed system in which each leg acts like an independent, proportional controller. 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. 2, stance net), but not for the β joints. The β joint is the major determinant of the separation between leg insertion and substrate, which determines body height. The value for the β joint is given by a three layered feedforward network (height net) with three input units (α , β , γ), five hidden units and one output unit. This net has been trained using the known leg geometry and approximates data from Cruse et al. (1989), where force–height characteristics of the standing animal have been measured.

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 experimenter. 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. 2(b), ‘walking on’] which replaces the sensory signal if it is larger than the latter [the box ‘max’ in Fig. 2(b), 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 stabilization that are well-known from insects and have also been applied in robotics. This supervisory system uses information on the rate of yaw [yaw_{sens} , Fig. 2(b), 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 legs which have magnitudes proportional to the deviation and opposite signs for the right and left sides. With this addition and yaw_{ref} set to zero, the system moves straight [see

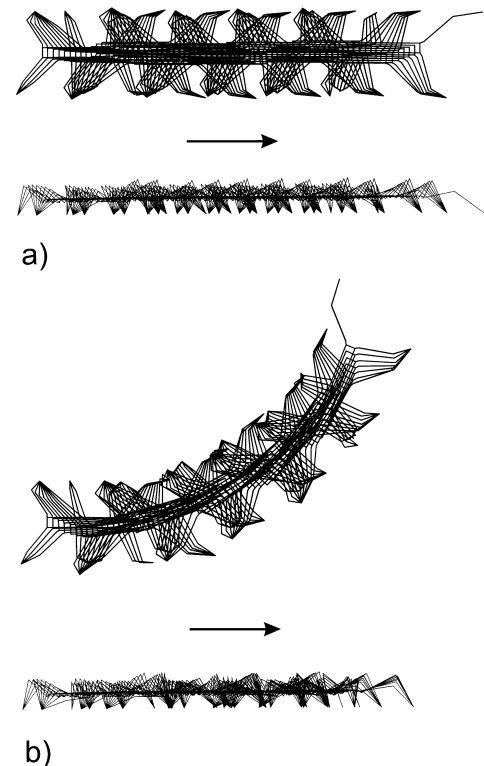


Fig. 4. Simulated walk by the basic six-legged system with negative feedback applied to all six β joints and positive feedback to all α and γ joints as shown in Fig. 2(b). Movement direction is from left to right (arrow). Leg positions are illustrated only during stance and only for every second time interval in the simulation. Each leg makes about five steps. Upper part: top view, lower part: side view. (a) Straight walking ($\theta_{\text{yaw ref}} = 0$); (b) curved walking ($\theta_{\text{yaw ref}} \neq 0$).

below, Fig. 4(a)] with small, side-to-side oscillations in heading such as can be observed in walking insects. To simulate curve walking, 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. 2(b), stance net].

One major disadvantage of our 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 occurred. 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).

3. Behavior of walknet

As a first step, i.e. before the planned implementation in a real robot, the behavior of Walknet was tested quantitatively in a software simulation. As the control principle relies on the existence of a body, the mechanics of the body had to be simulated, too. For this purpose, a recurrent network, called MMC, has been developed (see Steinkühler and Cruse, 1998) which will not be explained here. It suffices to say that it consists of a 78 unit, recurrent network with a Hopfield-like structure augmented by some nonlinear elements. The network represents the configuration of the central body and the six legs, each consisting of three elements [coxa, femur, tibia, see Fig. 2(a)]. The network can adopt a state representing any geometrically possible position of this 19 body system. After a not too large external disturbance the system always relaxes to a state which correspond to a geometrically possible configuration. In this way, it behaves like a mechanical device in which the joints are provided with adjustable springs. The new position depends on the old body position and the influence of the disturbance. The output values of the Walknet controller are then considered as such ‘disturbance’ influences and in this way move the simulated body. This is a purely kinematic simulation, i.e. no inertia and no forces are taken into account.

For the simulation of the body we had to decide whether to adopt the situation of a typical robot with no suckers at the leg tips, i.e. a leg which cannot develop forces pulling vertically on the surface, or whether to simulate an insect which, due to its complex tarsal morphology with adhesive structures, can develop pulling forces. As we primarily are interested in animal walking we chose for the latter. Under these conditions, stumbling occurs very rarely. To quantify instabilities during walking, we decided, somewhat artificially, that an unstable condition occurs if two neighboring legs are lifted off at the same time. For an intact insect and our simulation this is not necessarily a critical situation, but this measure allows an at least rough estimate of the stability of a corresponding walking machine without suckers. An insect can only fall, and did so in our simulations, when the vertical projection of the center of gravity of the body does not lie inside the support polygon for a certain time.

The evaluation of these data is not straightforward. Therefore, we consider three classes of behavior: (i) no problems, meaning that our criterion is never violated. This means that the insect, the simulation and a machine (without suckers) is stable. (ii) Short problems, meaning that the criterion is violated for not longer than the duration of one swing. This means that the insect and the simulation, but possibly not the machine, are still stable. (iii) Severe problems mean that the criterion is violated for longer than one swing duration. This may be critical for the insect and the simulation, but certainly is critical for the machine.

Like the earlier version (Cruse et al., 1995) this model shows proper coordination of the legs for straight and

curved walks at different speeds on a horizontal plane [Fig. 4(a)]¹. 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 this tetrapod to a tripod-like gait is found: front and rear legs on each side step together with the contralateral middle leg. Step amplitude is constant (approximately 20 mm) for all speeds. In relation to the distance between front and middle leg coxa (16 mm) and that between middle and hind leg coxa (11 mm) these step amplitudes are considerably larger than in most robots.

The second test considered complete amputation of one leg. Amputation can be easily simulated by holding the leg lifted in swing at a fixed position. In addition, for the amputated leg, the ipsilateral coordinating mechanism no. 1 for the amputated leg as sender has to be switched off. This has been done with front, middle, and hind legs. Of course, our artificial criterion was nearly always violated because the ‘amputated’ leg was always in swing. But no truly unstable configurations occurred due to the adhesion of the stance legs to the ground. However, in contrast to the findings with leg amputation in stick insects (Graham, 1977), the phase relations between legs did not change. This shows, as will be mentioned in Section 5, that the organization of Walknet is still too simple.

It has been argued that an important advantage of the positive feedback principle is that it can cope with changes in body geometry such as sudden changes of leg length, for example. This could be shown in simulation by cutting the tibia of the front, middle, or hind leg. For these tests, stability was considered during about 10 steps following a test ‘amputation’ performed during walking. The walks always started from a constant position. After about four steps the tibia was cut by a given amount. The results depend very much on walking speed. For a swing–stance ratio of 0.3, stable walks (criterion ‘no problems’) continued when the tibia was shortened by up to 67%, 75% or 62% (front, middle, hind leg, respectively). For a swing–stance ratio of 0.4 these threshold values were 53%, 67% and 54%, respectively. For even higher speeds (swing–stance ratio of 0.5) the threshold values were less than 33%. The main reason for this dependence is that at the higher walking speeds the system adopts the tripod gait, which is generally less stable than the tetrapod gait.

In a similar manner, walking over obstacles of different heights was investigated. Using our classification, the results in Fig. 5 show that there is no problem for all walks when the obstacle height is about 30% of normal body–ground distance. About 50% of the walks are still stable when the obstacle height is about equal normal body–ground distance. When the height of the obstacle was three times the normal body height or more, an increase in the

¹ For animation see <http://www.uni-bielefeld.de/biologie/Kybernetik>

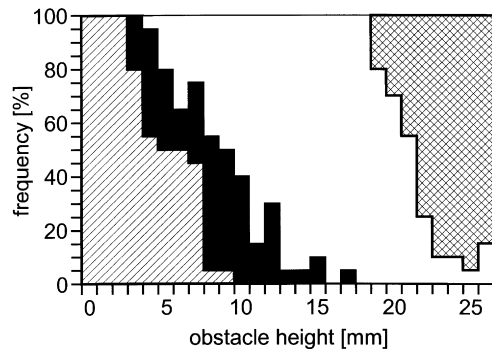


Fig. 5. The percentage of walks with no problems (hatched), short problems (black), severe problems (white), and failures (cross-hatched) over obstacles of different heights (abscissa). Normal body-ground distance is 6 mm. Swing-stance ratio 0.3.

percentage of 'failures' could be observed. In these cases the walking system did not walk over the edge but turned away from the obstacle. These results are fairly independent of the walking speed investigated (0.3–0.5). Again, however, it should be mentioned that our stability criterion may be a good estimate for a walking machine without ground adhesion, but it is unnecessarily high for real animals.

Finally, curve walking has been investigated and compared with results obtained from stick insects. A kind of minimal model presented in an earlier simulation (Cruse et al., 1996) showed that curve walking was possible when the input from the curve controller was given only to the α joints of both front legs. Detailed investigation, however, showed that the behavior of the simulation closely resembles that of the stick insect when the α joints of all three leg pairs are used [Fig. 4(b)].

Several studies on curve walking by stick insects have been performed. Graham (1972) investigated step timing in spontaneous turning by free walking animals, but did not measure geometrical leg parameters. In subsequent studies by Jander (1982) and in own experiments curve walking was elicited by the optomotor response, i.e. by placing the animals in a vertically striped drum which could be rotated at different speeds to elicit more or less tight curves. In Jander's study the animals walked freely on a motor driven ball (a locomotion compensator); in our experiments the animals walked with the body fixed above a styrofoam ball (diameter 195 mm, 4.7 gm; Dean and Schmitz, 1992) supported by an air cushion.

As in straight walking, two questions are of main interest. One concerns the coordination between legs, the other the trajectories performed by the individual legs. The investigations have shown that coordination corresponds to that of straight walking unless the curve is very tight. Only for curves with radii less than 7.5 cm, did adult stick insects use relative coordination, with the outer legs stepping faster than the inner legs Jander (1982). In the simulation presented here, we investigated only curves with a radius larger than 6.0 cm, where step coordination between right and left legs remains 1:1.

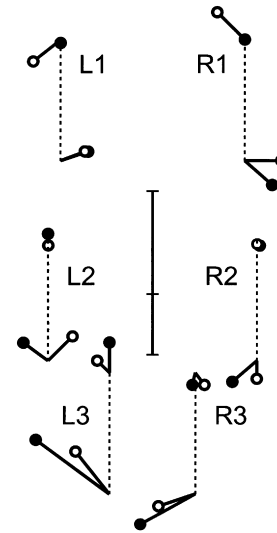


Fig. 6. Comparison of step extreme positions in curve walking for the insect and the model. The solid vertical line represents the thorax; tic marks indicate the positions of the basal leg joints. The dotted lines connect mean AEP and PEP for straight walking (L1, L2, L3 — left front, middle, and hind legs, respectively; R1, R2, R3 — right legs). The open circles are the mean endpoints for adult stick insects walking in curves to the left with a radius of curvature between 4.5 and 12.5 cm (adapted from Jander, 1982); the filled circles are the corresponding values for the model for a radius of curvature of 7.5 cm. For clarity, the paths of the middle legs are shifted away from the body and those of the hind legs are shifted closer to the body.

With respect to the movement of the individual leg, the changes in the AEP and PEP, which may or may not change step amplitude, and the form and speed of leg movement are of interest. Comparison of leg speed and step amplitude between these experimental results and the behavior of the simulation shows good agreement in the range investigated. Outer legs move faster and have a greater step amplitude than inner legs. Despite the larger step amplitudes, the stance duration of the outer legs in the model is shortened compared with straight walking, but this shortening is fairly well compensated by a correspondingly longer swing duration. This means that changes in the temporal parameters induced by curve walking are much smaller than changes in geometric parameters like step amplitude.

As a general result the changes in AEPs are smaller than those of PEPs during curve walking for both model and experimental studies. A quantitative comparison between the results of Jander (1982) is shown in Fig. 6. Changes in PEP agree qualitatively except for the PEP of the inner middle leg. In Jander's as in our own insect studies this leg's PEP shifts towards the body, whereas in the model it shifts away from the body. The reason may be that the center of rotation is more rostral in the model than in the insect.

For middle and hind legs the changes in AEP are very similar (Fig. 6). An obvious difference is found for the AEPs of the front legs. Jander found, at least for tight curves (radius <15 cm), that the AEP of the inner front leg moves away from the body and to the rear, whereas the

AEP of the outer front leg shifts towards the body and rostrally. In the model the qualitative changes point in the same direction, but the quantitative changes are much smaller and not visible in Fig. 6. Together the changes in AEP and PEP change the orientation of the tarsus path relative to the body of the insect. During stance the inner front leg is pulled diagonally toward the body while the outer front leg is pushed away from the body. As a consequence, the PEP moves nearer to the body or further away, respectively. These PEP shifts are present in both Jander's data and our own. The AEP shifts are more prominent in Jander's experiments because he investigated very tight curves ($r < 6$ cm). This means that for negotiation of very tight curves the AEPs of the front legs requires a special input which does not yet exist in the Walknet version. Also, the PEP net of these leg controllers would have to be trained to cope with the PEP ranges necessary for these tight curves. Without these extensions it was not possible to bring Walknet to walk in curves with a radius smaller than $r = 6.0$ cm, as the animals can.

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. Although this can lead to extremely disordered arrangements of the six legs, the system was able to stand up on its own and resume proper walking. To investigate this behavior more systematically we performed the following test. The simulation started at randomly chosen leg positions. After having reached a stable walk, the simulation was momentarily halted. During the pause, the state of each leg was switched randomly between swing and stance and all of the 18 leg joints were changed randomly such that all possible joint positions were equally likely. Then, the height controller was switched off until all six coxae had contact with the ground. In this state normal behavior of all controllers was switched on again and the behavior of the system was observed. Of 1000 tested cases 78% resumed proper walking with no problems (9%) or short problems (only during the first step) (69%). In 95% stable walking (no or short problems) was gained at least during the second regular step. About 5% required 3–7 step cycles to regain normal walking. This means that the simple solution proposed here also eliminates the need for a special supervisory system to rearrange leg positions after such a catastrophe.

4. New results

Although Walknet copes with a number of behavioral results found in the stick insect, there are new results (and some old ones) which cannot be reproduced by this system. One will be explained in more detail. In Walknet, it is assumed that the end of swing is determined by a sensory stimulus affecting the tarsal mechanoreceptors (and possibly load receptors, too). As soon as this stimulus is above a given threshold, the selector net is forced to switch from

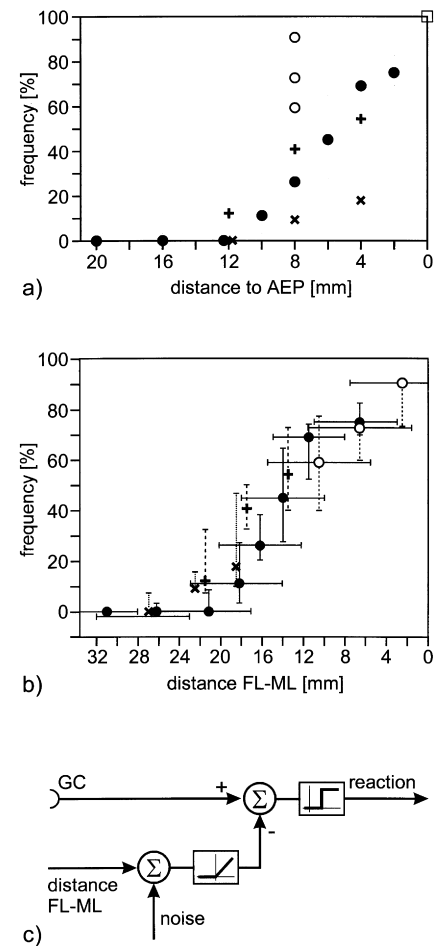


Fig. 7. (a) The dependency of the frequency of the grasping reaction of the middle leg tarsus on the test substrate's position relative to its normal AEP (distance in mm). The conditions are: (1) normal walking for a range of substrate positions at 2 mm intervals (closed circles); (2) for one test position when the swing of the middle leg is prolonged artificially by 500, 750 or 1000 ms (open circles, from bottom to top); and (3) for three test positions when the front leg stands on a fixed platform 1 mm (x) or 6 mm (+) behind its AEP. (b) The results from part (a) plotted versus the distance between ipsilateral front and middle leg tarsi. The vertical lines show the 25% and 75% quartiles for each test condition; the horizontal lines indicate the extreme values in middle to front leg distance. (c) A simple circuit which can describe these results and may replace the simple ground contact (GC) input to the selector net shown in Fig. 2. For further explanation see text.

swing to stance. In the animals, however, the situation is not as simple. This may not be unexpected because any arbitrary mechanical contact in the early swing, for example, should be considered an obstacle rather than a stimulus to finish swing. So one might assume that there is some internal state, an 'expectation value' or conversely, a value for 'swing motivation,' which tells the system whether a given stimulus should be treated as an obstacle or as ground contact.

How do the animals behave? When a possible substrate, for example a round wooden rod, is held at different positions in the swing trajectory of a leg, the probability it will be grasped by the tarsus to end swing is very low when the rod is in the caudal 40% of the step range, but the probability

increases about linearly to 100% as the position approaches that of the normal AEP [Fig. 7(a), closed circles]. This raises the question of how this decreasing swing motivation is produced? Experimental results showed that it is not simply the position of the leg, because the results for a given leg position is different when the swing duration is artificially prolonged by about 500, 750 or 1000 ms [Fig. 7(a), open circles]. This result also shows that another possible parameter, namely time elapsed since the beginning of the swing, cannot be the only relevant parameter, because these prolonged swing movements far exceeded the duration of a normal swing (150–200 ms). If time were the only parameter, the probability of ending swing should have been high for all three cases.

A third experiment hinted at a solution. One can easily manipulate the position of a leg of an insect walking on a treadmill by placing this leg on a platform fixed beside the treadmill. If this platform is held far enough in the anterior range of leg movement, this leg remains standing on the platform, while the other five legs continue to walk (Wendler, 1964). There are reasons to believe that this leg is in a walking rather than in a standing mode (Schmitz, 1985). When the basic experiment is repeated with a middle leg, and the position of the ipsilateral front leg is manipulated as described, the middle leg shows reactions which not only depend on its own position, but also on that of the front leg [Fig. 7(a), crosses, xes] behind its normal AEP. These results suggest that it is the distance between front and middle leg which determines the ‘motivation’ for the middle leg to accept a stimulus as ground contact, a hypothesis which can quantitatively describe all our data. This is shown in Fig. 7(b) where all data are plotted versus the distance between front and middle leg.

How might the probabilistic property found in these experiments be introduced into the network model? The simple static neurons used in Walknet up to now cannot do this. However, this behavioral reaction can be described most simply by the following assumption [Fig. 7(c)]: an interneuron provides a noisy measure of the distance between front and middle leg. The sum of both is rectified such that no negative excitations can occur at the output. This value inhibits the sensory input from the tarsal receptors. In this way the probability for a tactile input to exceed threshold and elicit a grasping reaction increases with the activity level of the neuron representing the distance.

At least qualitatively this result fits result of Brunn and Dean (1994) and Brunn (1998), who found an interneuron which increases its activity the closer both neighboring legs approach each other. This neuron in turn inhibits the protractor motoneurons and excites the retractor motoneurons, and thus can contribute to the transition from swing to stance.

5. Discussion

The model proposed here is based as far as possible on

data obtained from biological experiments, particularly from behavioral studies. The neurophysiological investigations are still in a state where not enough information is available to bridge the gap between the properties of the individual neurons (for review see Bässler, 1993; Bässler and Büschges, 1998) and the behavior observed. On the contrary, we hope that the modelling studies will guide neurophysiological experiments and interpretation of the results. Nevertheless, to match the basic architecture of the real system as closely as possible, our model is based on the artificial neural network approach.

Many neurophysiologists argue that real neurons are much more complex than those static ‘neuroids’ used for this simulation. This is, of course, completely justified, but in the early stages of investigation a model need not provide an exact copy of the original. A model should be, in the words of Einstein, as simple as possible, but not too simple. Whether or not it is too simple can only be decided a posteriori. Therefore our goal is to look for simple models which still show the system properties of interest. The Braitenberg (1984) vehicles already show that simple feedforward systems, when equipped with a body and placed in a real environment, can show quite complex behavior. This is the case because even a static feedforward system, being ‘embodied’ and ‘situated’, forms, together with the environment, a recurrent system and therefore constitutes a system with rich dynamic properties. Therefore we use recurrent architectures only if they appear to be necessary (or helpful).

To control the individual leg, no explicit central controllers in the sense of central oscillators are used. Rather the oscillations result from the cooperation of different subsystems and the physical world. Using a central controller might even worsen performance if such an autonomous central controller sometimes favors actions conflicting with those favored by the present control model relying directly on the physical properties of the system. Our results are sensible for slow walkers, where slow neuronal conduction speeds do not play a critical role. For fast walkers, which cannot rely on temporally adequate sensory input, central oscillators might be the better solution. On the other hand, Jindrich and Full (1998) show that, in a fast walker, the mechanical, in particular the dynamical properties of the system may well be exploited to substantially decrease the control effort. This may also be true in slow walking systems where the dynamics are important as, for example, in larger animals or in humans walking in a predictable environment.

One subsystem, the swing net, consists of an extremely simple feedforward net. More difficult problems have to be solved by the stance system, the second subsystem of the leg controller, particularly, if the geometry of the system may change due to growth, injury, or non-rigid suspension of the joints. Solving these complex tasks represents quite a high level of ‘motor intelligence’. However, this does not require a complicated, or a centralized control system. Due to its extremely decentralized organization and the simple type of

calculation required, the solution using local positive feedback permits very fast computation. 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. Thus, ‘the world’ is used as ‘its own best model’ (Brooks, 1991). Our solution also provides an example of how information about the environment may not be available to a passive system waiting for sensory input, but it is available to an active system.

Some central commands from a superior level are still required. These are necessary to determine the beginning and end of walking as well as its speed and direction. However, these commands do not have to be precisely adjusted to the particular configurations and states of all the legs; an approximate specification is sufficient for the positive feedback control. For example, turning does not require explicit calculation of leg trajectories using, for example, the desired curve radius and the geometrical parameters of the legs. Simple proportional commands to the legs are sufficient.

To describe the probabilistic behavior found in some experiments [Fig. 7(a) and (b)], namely the reaction to ground contact, neurons with noisy input had to be introduced. The variability in interpreting a sensory stimulus as either an obstacle or a suitable substrate depending on the position of the rostral leg represents a new coordinating mechanism not listed in Fig. 1.

This new coordinating mechanism has not yet been introduced to Walknet. There is another important result which cannot be simulated in the present Walknet version. In the experimental situation described earlier — the insect walks on a treadwheel with five legs and one leg stands on a fixed platform — the force this leg produces is not constant but oscillates in the rhythm of the other walking legs. This is not peculiar to stick insects (Bässler, 1979; Cruse and Saxler, 1980), but appears to be a basic property of biological walking systems because it has also been described for the rock lobster (Cruse et al., 1983) and for the cat (Grillner and Rossignol, 1978). This finding means that coordinating influences can directly affect the motor output. This is not possible in Walknet. A way to solve this problem has already been considered in a model approach by Cruse (1983). Following this approach, coordinating influences from one leg may not only influence the motor output of a second leg, but may also be transmitted to a third leg. In this way phase shifts found after amputation of a leg may be explained (Cruse, 1983) which is also not possible with Walknet (see earlier) as it stands. An alternative, but related approach, was given by Kimura et al. (1993).

6. Related work

Very impressive work has been performed by Beer and colleagues. As shown in a series of papers (for a review see Beer et al., 1997), these authors developed a six-legged robot which is, as is our approach, based very much on

results taken from insect investigations. They applied coordinate mechanisms no. 1, 2 and 3 (Fig. 1). For the control of the individual leg, they introduced two reflexes we have not applied to our system up to now. One is the searching reflex which elicits searching movements of the leg when it does not find ground contact at the end of swing. This is an important reflex which we also plan to introduce after we have completed a detailed investigation of this reflex in stick insects. The second reflex is called the stepping reflex. When one leg has been moved by an external disturbance in a horizontal direction by a sufficiently large distance, the leg is lifted off the ground and moved back to a normal position. This has been observed in standing locusts (Zill, 1993). In walking cockroaches, a stepping reflex has been observed (Zill, 1993) when the leg has been pulled in posterior direction at the very end of the stance. This reaction had been studied in detail in the stick insect and it could be shown that unloading the leg elicits a swing movement, but only in the posterior part of step range (Cruse, 1985b). Therefore, the primary signal appears to be the change of load, most probably measured by the campaniform sensillae, rather than a change in position. As we considered only the kinematics in our model, this reflex has not yet been introduced. Another ‘stepping reflex’ has been found in the form of the TOT reflex described earlier [mechanism no. 6 in Fig. 1(a)], which has not been incorporated in any of the models.

A third reflex described in Espenschied et al. (1996) corresponds to our reflexes r1 and r2. In the robot of Espenschied et al., it allows the leg to clear obstacles of about 1/3 of body-ground distance by repeated reflex activation. In the height control system of this robot, the set point of the height controller is adjusted to cope with different obstacles (the maximum height is about body-ground distance). Our controller is simpler insofar as no changes of the setpoint are used. Instead, the height net provides a soft and nonlinear characteristic which was sufficient to clear obstacles as shown in Fig. 5.

Two other basic differences are the following. While our simulation is still a purely kinematic system, the robot of Espenschied et al. has to act in the real world and, therefore, has to deal with dynamics. For this purpose these authors introduced passive and active compliance, i.e. a spring at the tibia and negative feedback position controllers at each joint. The passive element is an elegant and simple solution copying the elastic properties of muscles. The active part, i.e. the negative feedback controller, has been applied in a similar way in the TUM walking machine (Pfeiffer et al., 1994). This matches some experimental findings from stick insects (e.g. Cruse, 1985a) and locusts (Zill, 1993), but disagrees with others. Bässler (1976, review 1993); Schmitz et al. (1995) found that during stance positive feedback is present at the femur–tibia joint. These latter results form the basis of our positive feedback controller. It is still an open question how to combine these at first sight contradictory results. For very large disturbances in the robot of

Espenschied et al. the compliance is again decreased to protect the system from damage (a similar protective reflex had been used in the TUM walking machine mentioned earlier). The second basic difference is that Espenschied et al., as does the TUM walking machine, use traditional engineer's solutions to control the movement, whereas Walknet consists completely of simple static neurons. A neural network controller has, however, been applied by Beer et al. (1992) to control a six-legged walking robot with legs each having two degrees of freedom. This network uses dynamic neurons, some of which have pacemaker properties, to control the stepping rhythm.

Acknowledgements

This work was supported by the Körber Foundation and DFG grant no. Cr 58/g-1.

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