

# Insect walking is based on a decentralized architecture revealing a simple and robust controller

BY HOLK CRUSE\*, VOLKER DÜRR AND JOSEF SCHMITZ

*Abteilung für Biologische Kybernetik und Theoretische Biologie,  
Fakultät für Biologie, Universität Bielefeld, Postfach 10 01 31,  
33501 Bielefeld, Germany*

Control of walking in rugged terrain requires one to incorporate different issues, such as the mechanical properties of legs and muscles, the neuronal control structures for the single leg, the mechanics and neuronal control structures for the coordination between legs, as well as central decisions that are based on external information and on internal states.

Walking in predictable environments and fast running, to a large degree, rely on muscle mechanics. Conversely, slow walking in unpredictable terrain, e.g. climbing in rugged structures, has to rely on neuronal systems that monitor and intelligently react to specific properties of the environment. An arthropod model system that shows the latter abilities is the stick insect, based on which this review will be focused.

An insect, when moving its six legs, has to control 18 joints, three per leg, and therefore has to control 18 degrees of freedom (d.f.). As the body position in space is determined by 6 d.f. only, there are 12 d.f. open to be selected. Therefore, a fundamental problem is as to how these extra d.f. are controlled. Based mainly on behavioural experiments and simulation studies, but also including neurophysiological results, the following control structures have been revealed. Legs act as basically independent systems. The quasi-rhythmic movement of the individual leg can be described to result from a structure that exploits mechanical coupling of the legs via the ground and the body. Furthermore, neuronally mediated influences act locally between neighbouring legs, leading to the emergence of insect-type gaits. The underlying controller can be described as a free gait controller. Cooperation of the legs being in stance mode is assumed to be based on mechanical coupling plus local positive feedback controllers. These controllers, acting on individual leg joints, transform a passive displacement of a joint into an active movement, generating synergistic assistance reflexes in all mechanically coupled joints. This architecture is summarized in the form of the artificial neural network, WALKNET, that is heavily dependent on sensory feedback at the proprioceptive level. Exteroceptive feedback is exploited for global decisions, such as the walking direction and velocity.

**Keywords:** walking; insect; pattern generation; leg coordination; leg movement; gait

\* Author for correspondence ([holk.cruse@uni-bielefeld.de](mailto:holk.cruse@uni-bielefeld.de)).

One contribution of 15 to a Theme Issue ‘Walking machines’.

## 1. Walking behaviour: autonomous control of many degrees of freedom

The control of motor output is the basis of all actions, from reaching movements to a legged locomotion and a spoken language. In this article, we concentrate on walking. Controlling the legs for walking, at first sight, seems to be a rather trivial behaviour, partly because no one has to think consciously about how to move each leg joint when walking. Maintaining a desired walking speed feels easy, even when carrying fairly heavy weights or suddenly moving onto a different substrate. Maintaining course feels easy, even when the desired path is curved, if there are changes in slope, or if unpredicted obstacles require a brief detour. Despite the fact that control of walking is apparently simple to us humans, walking does require simultaneous control of many joints and, therefore, many degrees of freedom (d.f.) at the same time. Not only are there mechanical constraints that limit the possible simultaneous actions, but also these constraints are subject to a continuous change of internal and external variables. As a consequence, we will argue in the course of this review that walking indeed requires considerable ‘motor intelligence’, and it can be regarded as a paradigm for the control of motor behaviour in general.

### (a) *Controlling walking means dealing with redundancy*

In many biological motor systems, particularly in those controlling legged locomotion, the number of d.f. is larger than that necessary to perform the task. For example, a standing six-legged animal may keep five legs stable, while moving the sixth leg without lifting it off the ground. Thus, there may be a manifold of leg postures for a given kinematic boundary condition. Accordingly, coordinating several legs during forward propulsion requires the control system to select one out of many alternative movement sequences. Moreover, the selection criteria may be context dependent, like moving on different substrates may impose different mechanical constraints. For example, when running along a sandy beach, we move differently than when running along a paved road.

### (b) *Dealing with redundancy implies autonomy*

The ability to adapt quickly to unpredictable changes in an environmental condition, and to select appropriate motor actions in a context-dependent manner, implies that the system can follow self-contained rules and make its own decisions. Note that such rules need not be very sophisticated, and that decision-making is not necessarily a cognitive task. With ‘making a decision’ we refer to the action of selecting one out of at least two alternatives, mutually exclusive states in a context-dependent manner. Obeying self-contained rules literally means to be autonomous. Thus, autonomous behaviour is more than just being independent of an external energy supply, as the word is often used in robotics. Rather, it implies independence of external commands, e.g. those given to a machine by an operator.

### (c) *Autonomous systems are embodied and situated*

A part of the ascribed autonomy is the system’s ability to adapt to complex, often unpredictable, environments. Hence, an important aspect of autonomous behaviour is to make optimal use of the physical interactions between the body

and its environment. The second important aspect is the ability to exploit physical properties of the body, e.g. muscle properties for self-stabilization (see Geyer *et al.* 2003) to keep control as simple as possible. In addition to the kinematic constraints and mass distribution, which are set by the anatomy of the body, the muscles and tendons of a leg, as well as the mechanical coupling of several legs through the ground, determine the dynamic system properties that need to be considered during control of walking. Thus, the two important aspects of biological motor control are the ‘embodiment’ of the controller and the ‘situatedness’ or ‘embeddedness’ of the body in its environment (e.g. Brooks 1991; Pfeifer & Scheier 2001). Whereas embodiment refers to the significance of the physical properties of the body for the controller, i.e. the central nervous system, situatedness refers to the significance of a feedback loop via the real world, e.g. the impact that the body–substrate interaction has on the performance of the walking animal.

(d) *Behaviour is investigated first, followed by simulation studies and physiological experiments*

To investigate the underlying control system, we and others use the approach of studying insects at the behavioural level first, asking questions like: how do insects behave in specific environmental situations (e.g. when walking on a horizontal plane or horizontal path)? How do they react to specific disturbances applied by an experimenter (e.g. a brief interruption of a swing or a stance movement)? Typical measurement variables are kinematic parameters of the leg movement or forces developed by a leg. The results are then interpreted by the formulation of ‘rules’ that are assumed to describe the properties of the underlying control system. These rules, first formulated qualitatively, are then transformed into a quantitative model that serves as a testbed for the validity of these rules. Neurophysiological measurements, i.e. recording of electrical activity of nerve cells (or muscles), are used in the third step. In our approach, neurophysiological investigations come after the behavioural analysis, because it appears to be sensible to understand the global functional role of the intact neuronal machinery first, before diving into the much more detailed network level. Behavioural studies are not only appropriate to support neurophysiological studies by defining tasks to be investigated, but they can also directly support roboticists who may exploit these quantitative models. Thus, behavioural studies form a link between engineers and neurobiologists.

(e) *Only some selected biological systems have been investigated in sufficient detail*

Although many animals have body appendages that can be used for walking, only a few species are investigated in sufficient detail: in crustaceans, the crayfish and the lobster (with essentially four pairs of walking legs, i.e. eight legs; e.g. Clarac & Cruse 1982; Ayers 2002); in the six-legged insects, insect (Bässler 1983; Graham 1985; Cruse 1990; Bässler & Büschges 1998), the cockroach (e.g. Delcomyn 1987; Watson & Ritzmann 1998; Jindrich & Full 1999; Tryba & Ritzmann 2000; Noah *et al.* 2001*b*) and, to a minor extent, the locust (Burrows 1996). Some investigations of ants (e.g. Zollikofer 1994) and, more recently, of *Drosophila* (e.g. Pick & Strauss 2005), are also of interest. In four-legged animals,

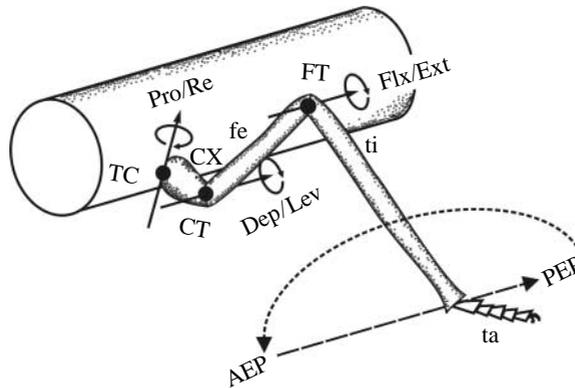


Figure 1. A simple model of a stick insect leg. Each leg can be modelled as a manipulator with three hinge joints, resulting in 3 degrees of freedom (d.f.). From the body towards the foot, the joints are called the thorax-coxa joint (TC), the coxa-trochanter joint (CT) and the femur-tibia joint (FT). The joint axes (solid arrows) account for protraction/retraction of the coxa (Pro/Re), depression/levation of the trochanter and femur (Dep/Lev), and flexion/extension of the tibia (Flx/Ext). The joint of the foot and the foot itself are neglected for simplicity. Each step cycle can be divided into two states: the stance movement on the ground (dashed arrow) and swing movement through the air (dotted arrow). The state transitions occur at the anterior extreme position (AEP) and posterior extreme position (PEP).

the dog and, mainly, the cat are of interest. Studies concentrating on neurophysiology but not so much on behaviour have also been done with mice and rats, and newts. The two-legged animal studied most is, of course, humans. However, most studies on humans concentrate on standing, on the control of upright posture or on handicapped people, e.g. paraplegic patients. However, the lower-level control problems, i.e. control and properties of individual muscles in the context of behaviour, have most intensively been studied in humans (Inman *et al.* 1981) and in cats (Pearson 1993*b*). Recently, the overwhelming importance of muscular properties to the control problem, in general, has also been shown for insects, in particular the cockroach (e.g. Full & Tu 1991; Full *et al.* 2002).

As mentioned, the most detailed studied insects are cockroaches and stick insects. Cockroaches are specialized to fast walking, up to 25 steps per second. At this high speed, proprioceptive input is of less importance and walking over rugged environment is mainly solved by exploiting the elastic properties of muscles. On the other hand, stick insects are adapted to walk and climb in more difficult environmental situations as, for example, climbing in branches. This behaviour requires a higher degree of sensitivity with respect to the ever-changing properties of the environment and needs a control system that is able to intelligently react to this information. As we are interested in studying the principles underlying autonomy and decision-making in neural motor control, we therefore decided to concentrate on stick insects, which will be the main subject in the rest of this article.

#### (f) *Modelling autonomous walking by behaviour-based, distributed ANNs*

In a walking insect, at least three joints per leg have to be controlled (figure 1): the thorax-coxa joint (TC-joint); the coxa-trochanter joint (CT-joint); and femur-tibia joint (FT-joint). The CT- and FT-joints are simple hinge joints with 1 d.f.

corresponding to levation/depression of the femur and extension/flexion of the tibia, respectively (figure 1). The TC-joint, which connects the leg to the body, is more complex, but most of its movement can be modelled by the rotation around a slanted axis. The two Euler angles that define the axis of protraction/retraction of the leg vary only little during normal walking (Cruse & Bartling 1995) and can be assumed constant. Thus, an insect has to control 18 joints in total, which, owing to their simplicity, result in an equal number of d.f.

In principle, there are two equally sensible ways of modelling hexapod locomotion based on biological findings. The first way is to assemble the known components of the nervous and musculoskeletal systems, to build an incrementally realistic model of a moving insect. An example of this approach has been presented by Ekeberg *et al.* (2004). The second way, as mentioned previously, takes the complementary approach of assembling logical components to model the system properties of the behaving animal. Here, we illustrate this behaviour-based modelling approach by explaining the control system WALKNET that governs a kinematic model of a stick insect (*Carausius morosus*). WALKNET is based on the behavioural rules that have been derived from the experimental studies on walking stick insects. Similar rules have been found for the walking crayfish (Cruse 1990) and cats (Cruse & Warnecke 1992). The core of WALKNET consists of a set of six single-leg controllers, each of which is built by a number of distinct modules that are responsible for solving particular subtasks. Some of these modules might be regarded as being responsible for the control of special ‘microbehaviours’; for example, a walking leg can be regarded as being in one out of two mutually exclusive states, namely performing a swing or a stance movement (figure 1). During stance (or power stroke), the leg maintains ground contact and is retracted to propel the body forward, while supporting the weight of the body. During swing (or return stroke), the leg is lifted off the ground and moved in the direction of walking, to touchdown at the location where the next stance should begin. Owing to the rhythmicity of insect gaits (e.g. Wilson 1966) and the alternating activation of antagonistic motor neuron groups in reduced preparations (e.g. Büschges *et al.* 1995), the two states of the step cycle of each leg are often treated as two phases of the same central motor pattern. Yet, behavioural experiments on the stick insect *C. morosus* show that a leg can be taken out of the normal stepping pattern and remain in the stance mode (Wendler 1964; Cruse & Schmitz 1983; Cruse 1985*b*). Other experiments even suggest that a walking leg ‘knows’ whether it is in a stance or a swing mode (Schmitz & Haßfeld 1989), indicating that swing and stance should be modelled as separate motor patterns—or states—which are activated one after another. Accordingly, the modules of WALKNET that control the leg movements during these two states are separate structures, and their outputs are gated by a third module that ‘selects’ which of the two modules has access to the motor neurons at a given time. Most components of WALKNET are artificial neural networks (ANNs; Cruse *et al.* 1998), mainly because ANNs provide an intuitive toolbox to assemble a networked control circuit that allows a reasonable structural comparison with network properties of the neural controller (for an introduction, see Cruse 2006), which shall be available shortly as an eBook.

The following three sections will introduce the main properties of WALKNET, each one dealing with a central problem in the physiology of a legged locomotion. Section 2 introduces the problem of timing the step cycles of several legs, making

them act as synergistic parts of a whole. In addition, it presents a solution to this problem without a central supervising instance. Section 3 is concerned with the generation of a manifold of targeted leg movements, as they occur during the swing component of a step cycle, but also during searching, grasping and grooming. Finally, §4 deals with the problem of controlling redundant d.f., for the example of coordinated control of several leg joints during stance.

## 2. Generating gaits: timing of stance–swing transitions

### (a) *Step cycles between neighbouring legs are coupled*

It is known since the work of [Holst \(1943\)](#) that the movements of individual legs are controlled by fairly independent control systems (see also [Wendler 1964](#)), for the stick insect ([Chasserat & Clarac 1980](#)) and the rock lobster. This appears to be a general principle, as similar experimental results on swimming fishes and walking dogs ([Holst 1939](#)) have also suggested the presence of a distributed, modular controller. Given certain experimental situations, neighbouring legs of walking animals show ‘relative coordination’, which indicates that each leg has its own inherent stepping rhythm and is only weakly coupled to its neighbouring legs. In insects, the degree of coupling between legs may differ between species, but may also depend on the locomotor context. In principle, coupling between step cycles of individual legs can be established via peripheral (sensory) or central (neural) feedback, but mechanical properties may also contribute.

### (b) *Coupling may depend on central and peripheral feedback*

Much has been argued about the extent to which sensory and central feedback loops contribute to the rhythmicity of locomotor activity (e.g. [Marder & Bucher 2001](#); [Prochazka \*et al.\* 2002](#); [Dürr \*et al.\* 2003](#)), and both physiological and simulation experiments have attempted to quantify their relative contribution to vertebrate walking (e.g. [Yakovenko \*et al.\* 2004](#)), vertebrate swimming ([Ekeberg & Grillner 1999](#)) or insect flight ([Pearson & Wolf 1987](#); [Wolf & Pearson 1987](#)). It is clear that there is an inherent rhythmicity to the central nervous system, as even reduced, deafferented preparations show alternating burst activity in antagonistic motor nerves, revealing enough similarity to normal motor patterns to be called ‘fictive locomotion’ (e.g. reviews by [Delcomyn 1980](#); [Grillner 1981](#); [Grillner \*et al.\* 1995](#)). However, each joint of an insect is equipped with several mechanoreceptors that are constantly signalling the joint’s angle, velocity, acceleration, torque or a mix of these magnitudes to the central nervous system, CNS, and their impact on pattern generation in insect locomotion is well established in stick insects (reviewed by [Graham 1985](#); [Bässler & Büschges 1998](#)), locusts (reviewed by [Burrows 1992, 1996](#)) and cockroaches (e.g. [Noah \*et al.\* 2001a](#); see also [Pearson 1993a](#); [Zill \*et al.\* 2004](#); [Büschges 2005](#)). Both peripheral and central feedback do exist and can be beneficial to a walking system. Central feedback may allow for fast predictive actions, while sensory feedback is a prerequisite for a fast context-dependent adaptivity of a motor program. Thus, from a behavioural perspective it is most interesting to determine which of the two types of feedback pathways are best suited in a given behavioural context.

In WALKNET, the quasi-rhythmic behaviour of the legs is due to the interaction of the six leg modules, i.e. coupling influences, and to closing the loop through the world. This agrees with the idea that behaviour is not only a product of neural activity, but also a product of the interaction between brain, body and environment (Chiel & Beer 1997). The possible role of central oscillators will be further addressed in §5.

(c) *Leg coupling aids stabilization and locomotor efficiency*

Coordinated action of the legs must account for at least two things. First, the timing of lift-off and touchdown in each leg must not impair the stability of the whole body. Hence, as the legs are retracted under the body, the number and pattern of the legs off the ground must ensure static or, at least, dynamic stability at any time. Second, the number of legs in stance determines the upper bound of propulsive force. Therefore, efficient timing and coordination of power and stance direction of all legs in stance must be controlled to ensure their synergistic action, e.g. to minimize strain across the body while maximizing propulsion.

As the step cycle of a walking leg can be divided into two functional states, stance and swing, an efficient coupling of neighbouring legs essentially concerns the correct timing of the state transitions. Accordingly, behavioural analyses of insect walking have often focused on the two kinds of state transitions. The first is the transition from swing to stance upon touchdown of the leg. This is a stabilizing transition that occurs at the so-called anterior extreme position (AEP). The second is the transition from stance to swing by lifting the tarsus off the ground. This is a destabilizing transition that occurs at the so-called posterior extreme position (PEP).

(d) *Six leg coordination rules govern leg coupling in stick insect walking*

Behavioural experiments on stick insects have established that the coupling between legs can be described by a set of six coordination rules, each of which is active only during certain fractions of the step cycle (see Cruse 1990, for review). Each rule can be viewed as an information channel, by which a leg signals its current state to its immediate ipsilateral and contralateral neighbours. Hence, the front and hind legs send information to two neighbouring legs, whereas the middle legs send information to three legs (figure 2). The six coordination rules described in the article are as follows.

Rule 1 *Suppress lift-off to avoid static instability.* Rule 1 exerts an inhibitory influence on anterior legs. During a swing movement, i.e. when a leg is lifted off the ground, it suppresses lift-off in the next anterior leg, thus, avoiding simultaneous protraction of ipsilateral neighbours. This rule has been implicitly derived from the observations on insects (Wilson 1966) and scorpions (Bowerman 1975) and experimentally characterized in grasshoppers (Graham 1978) and stick insects (Cruse & Epstein 1982). In stick insects, this rule has the highest efficacy, i.e. it is least violated (Dürr 2005a). In a robot, which must not fall over, this rule provides a simple means to avoid potentially harmful situations of static instability. In robots, this rule is often used to influence all three neighbouring legs, not just the anterior neighbour. Although this leg coordination

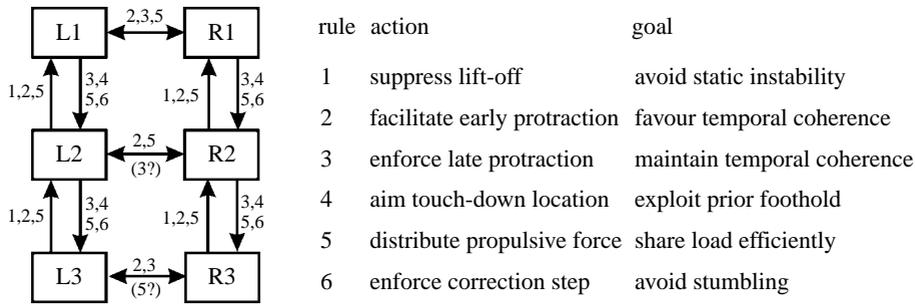


Figure 2. Known leg coordination rules that couple step cycles of neighbouring legs. Each of the six legs (boxes labelled L1 to L3 for the left front, the middle and the hind legs, respectively, and R1 to R3 for the corresponding right legs) signals information about its current state to its neighbours (arrows). The known coordination rules are numbered according to the list to the right. Numbers next to the arrows denote the rules known to be present in a given signalling pathway. The table lists actions and goals that can be associated with the experimental evidence. The corresponding behavioural findings in stick insects are: rule 1, return stroke inhibits start of return stroke of anterior leg; rule 2, start of power stroke excites start of return stroke of anterior leg; rule 3, increasingly posterior position excites start of return stroke in posterior leg; rule 4, tarsus position determines target posture of return stroke of posterior leg; rule 5, increased resistance increases force (co-activation) and increased load prolongs power stroke; and rule 6, treading-on-tarsus reflex.

mechanism appears to be ubiquitous among legged animals, it is yet a matter of debate to what extent it is mediated neurally. Experimental results on walking cats suggest that at least part of the coordination according to rule 1 is due to a local load-sensing mechanism that prohibits lift-off of a leg until it is sufficiently unloaded. This makes sense, as unloading of a leg typically signals that the body weight is maintained by the other legs. A recent modelling study on contralateral leg coordination in cat walking suggests that sensory information about ankle load is sufficient to maintain a stable coordination (Ekeberg & Pearson 2005).

**Rule 2** *Facilitate early protraction to favour temporal coherence.* Rule 2 exerts an excitatory influence on anterior legs. Upon touchdown of a leg, it facilitates lift-off of the next anterior leg. Thus, rules 1 and 2 act to couple a back-to-front sequence of swing movements, first by suppressing, then by facilitating a stance–swing transition in the anterior leg. Rule 2 has been shown in stick insects (Cruse & Schwarze 1988), where it also acts contralaterally (Cruse & Knauth 1989), although weaker than ipsilaterally (Dürr 2005a).

**Rule 3** *Enforce late protraction to maintain temporal coherence.* Rule 3 exerts an excitatory influence on posterior legs during late stance. The closer a leg gets to its normal lift-off position, the stronger is the facilitatory influence on the posterior leg in stance to undergo a stance–swing transition. By this influence, an anterior leg can enforce a swing movement, causing its rear neighbour to ‘catch up’ in order to maintain the rhythm. Like rule 2, this rule is active in stick insects (Cruse & Schwarze 1988), where it also acts contralaterally (Cruse & Knauth 1989).

- Rule 4 *Aim touchdown location to exploit prior 'knowledge' about foothold.* Rule 4 is a targeting mechanism that causes legs to be placed in very similar locations, i.e. to find foothold near to where the anterior neighbour is standing. In stick insects, the AEP of a protracting leg depends on the current posture of the next anterior leg (Cruse 1979; Dean & Wendler 1983). Three kinds of candidate interneurons that could mediate the required proprioceptive information to the next posterior leg have been recorded from the stick insect's thoracic ganglia (Brunn & Dean 1994).
- Rule 5 *Distribute propulsive force among the legs to share load efficiently.* Increasing load in one leg causes other legs to prolong stance, thus increasing the duty cycle of all legs, acting to distribute load among all legs in stance (Cruse 1985a; Schmitz 1993; Schmitz *et al.* 2000).
- Rule 6 *Enforce a correction step to avoid stumbling due to leg placement errors.* The treading-on-tarsus reflex is a sixth coordination rule, which becomes active if a leg steps on the tarsus of its neighbour leg (Graham 1979). In this case, the trod-on leg tells the one on top to step off. This reflex works both during forward and backward walking (Schmitz & Haßfeld 1989).

Note that the numbering of these rules above follows Cruse *et al.* (1995b).

(e) *Leg coupling gives rise to stable gaits, even without central patterning*

An interleg coupling is implemented in WALKNET by means of six almost identical single-leg controllers, each of which communicates its current state to its immediate neighbours (figure 2). The differences in the constraints acting during the two states (swing and stance) and in the conditions for their termination suggest that the leg controller consists of three separate control networks. The two low-level networks, a swing and a stance network, control the movement of the leg during swing and stance, respectively (figure 3). The transition between swing and stance is controlled by the selector module. This ANN receives sensory information about ground contact and, together with a sub-network that determines a normal lift-off position (PEP net in figure 3), information from other legs. The swing (see §3) and the stance networks (see §4) are always active, but the selector network determines which of the two networks actually controls the motor output. As experimental results on stick insects failed to demonstrate a robust central pattern generator (CPG) that produces strong intrinsic rhythms (Bässler & Wegner 1983), WALKNET uses only sensory information on ground contact to elicit a stance–swing transition, and it coordinates signals from neighbouring legs to elicit a swing–stance transition.

The coordinating signals from neighbouring legs that have been implemented are rules 1–4 of figure 2. As WALKNET is an entirely kinematic simulation, the effects of load, including rule 5, have not yet been implemented. Thus, the loading of the legs is not monitored by WALKNET, although it is known that the load affects the motor output during walking (Schmitz 1993) and influences stance–swing transitions (Schmitz 1993; Akay *et al.* 2004). Moreover, as WALKNET controls only three joints per leg, the lack of a tarsus precludes implementation of rule 6. Rules 1–3 all affect the timing of stance–swing transitions. In WALKNET, they are implemented by adding an offset to the PEP coordinates (figure 3), thus acting to shorten (rules 2 and 3) or prolong (rule 1)

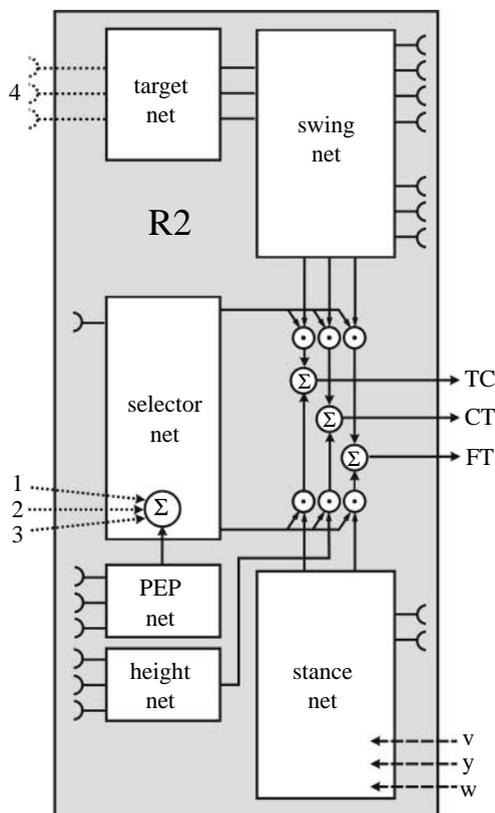


Figure 3. Implementation of coordination rules in WALKNET. Each single-leg controller (e.g. R2) consists of several ANN modules. The *swing* and *stance nets* generate leg movements during protraction and retraction, respectively. Their outputs set the joint angular velocities of the three leg joints (TC, CT and FT). They are gated by the *selector net* in a mutually exclusive manner. The state of the selector net depends on the sensory input from the own leg (half-circles inside the grey area indicate local sensory information) and the summed effects of the *PEP net*, coding the distance to the normal PEP, and weighted information corresponding to the coordination rules 1–3 (dotted arrows). Thus, rules 1–3 affect the stance–swing transition. Rule 4 acts via sensory information from the next anterior leg (dotted half-circles), which is transformed into a target posture by the *target net* (figure 5a). Thus, rule 4 affects the swing–stance transition. The *height net* controls the body clearance and affects only the CT-joint during stance. Except for the input to the target net and the coordinating influences 1–3, all sensory inputs are local. The stance net receives three global commands (dashed arrows): controlling body velocity ( $v$ ); yaw ( $y$ ); and forward walking ( $w$ ) (figure 6).

the stance period of a neighbouring leg. The targeting mechanism of rule 4 is implemented by a separate ANN in each single-leg controller, the target net (figure 3; Dean 1990), that transforms the joint angles of an anterior leg into appropriate target angles, i.e. into a desired posture of the posterior leg at touchdown.

Therefore, the leg coupling rules of WALKNET are mediated in two parallel ways. The first pathway models the direct neural connections between the single-leg step pattern generators (the single-leg controllers). The second pathway arises from the mechanical coupling among the legs (see §4). That is, the activity

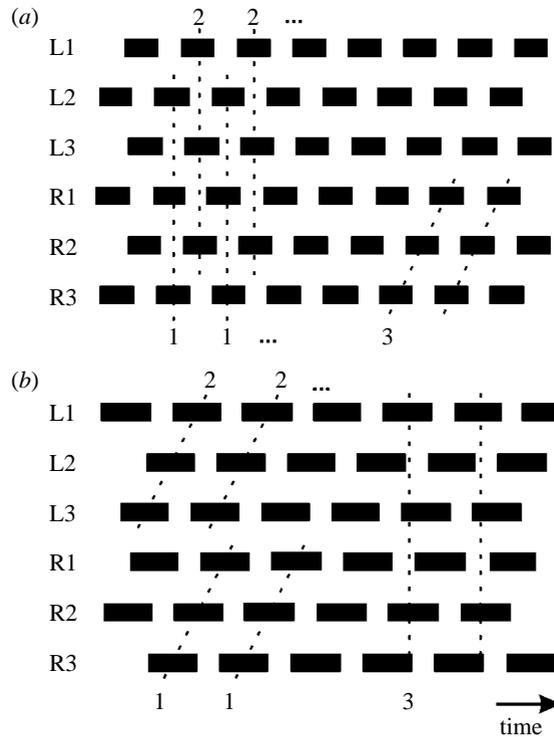


Figure 4. Coordination rules 1–4 are sufficient to generate typical insect gaits. A precursor model of WALKNET (Dean 1990; Müller-Wilm *et al.* 1992) was the first model to incorporate the leg coordination rules of figure 2. Like all subsequent versions, this model showed velocity-dependent gait changes that are the characteristic for insect walking. (a) If the reference walking velocity is high, the system generates a tripod gait with alternating tripods of L2–R1–R3 (dashed lines 1) and L1–L3–R2 (dashed lines 2). The black bars mark the stance periods of each leg, i.e. when a given leg is on the ground. (b) If the reference walking velocity is low, the system generates a tetrapod gait, in which always at least four legs are on the ground. The tetrapod gait is characterized by a back-to-front wave of stance movements on the right (dashed lines 1) and left sides (dashed lines 2). Identical footfall patterns can occur repeatedly in a tetrapod gait too (dashed lines 3), but they typically drift from one step to the next. Back-to-front waves can also be found in a tripod gait (dashed lines 3 in (a)), but stance periods of adjacent legs overlap less than in the tetrapod gait.

of one-step pattern generator influences the movements of all other legs in stance; therefore, it adds mechanical feedback to other step pattern generators via their local sensory inputs.

WALKNET reproduces the stick insect coordination of the legs when walking at different speeds on a horizontal plane (figure 4). The steps of ipsilateral legs, i.e. the legs on the same side of the body, are organized in triplets forming back-to-front waves, and the opposite legs approximately step in alternation. With increasing walking speed, the typical change in coordination from a 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 the diagonal pairs of legs stepping approximately together (figure 4b). At high velocities, the gait approaches the tripod pattern with front and rear legs on each side stepping in synchrony with the contralateral middle leg (figure 4a).

This is possible because swing duration is constant in the animal (Graham 1985) and velocity control has no impact on the swing module of WALKNET. Thus, the velocity-dependent adaptation of gait is not a result of a different central program, but rather the result of interacting local controllers. This is often called free gait control, the property of which becomes obvious when observing a very slowly walking animal, for example a grazing animal. For example, depending on the quite irregular body movement, the timing of individual steps of different legs may be quite irregular (for a range of long step patterns in stick insects, see Dürr 2005a). Generally, if irregular step patterns prevail during stable walking, they are an indication of a free gait controller, as modelled in WALKNET.

*(f) Strength of leg coupling is not constant*

So far, many experimental studies and all modelling studies concerned with leg coordination assumed that the strength of leg coordination remains stable in different behavioural contexts. Indeed, controllers such as WALKNET show that they can account for considerable adaptiveness of leg coordination (Kindermann 2002). Moreover, Espenschied *et al.* (1993) showed that rules 1–3 of figure 2 are fairly insensitive against minor changes in coupling strength and provide for stable gaits even if one of them is omitted at a time. Recent behavioural analyses of the transition from straight to curve walking in stick insects revealed that coupling strength is subject to considerable modulation and, thus, depends on the behavioural context (rules 1–3, Dürr 2005a; rule 4, Ebeling & Dürr 2006). As yet, it is unknown to what extent such modulation is a cause or rather a result of the corresponding changes in leg kinematics.

### **3. Protraction, searching, grasping or grooming: control of mechanically uncoupled leg movements**

*(a) Swing movements are mechanically uncoupled, regulated and targeted*

Controlling a swing movement is easier than controlling a stance movement, because a leg in swing is mechanically uncoupled from the environment and, owing to its small mass, essentially uncoupled from the movement of the other legs. Therefore, whatever a leg does during a swing movement, it has virtually no impact on the movements of the other legs.

According to figure 1, each stick insect leg can be modelled as a manipulator with 3 d.f. of rotation. As physiological experiments have shown that each one of these d.f. may show only a weak neural coupling to the two others (Bässler & Büschges 1998), the neural control network must have at least three pairs of motor outputs, one for each pair of antagonistic muscles per leg joint. For simplicity, each pair of these motor outputs is modelled in WALKNET as a single floating-point variable, allowing both negative and positive output. Thus, potential muscle co-contractions and resulting changes in leg stiffness are neglected.

Given the fact that stick insects regulate swing movements and compensate for external perturbations (Dean 1984), the neural network must receive proprioceptive sensory feedback to account for a closed-loop control. Moreover, because swing movements are known to be targeted towards a location near the foot of the next anterior leg (Cruse 1979), the network must also receive

information about a desired posture (rule 4 in figure 2; Cruse *et al.* 1984; Dean & Schmitz 1992).

(b) *A simple model for a networked control circuit underlying swing movements*

In order to achieve targeting and regulation of swing movements, the simplest model that has been proposed for modelling mechanically uncoupled leg movements is a two-layer feed-forward ANN with three output and seven input units, including a bias to model offset resting activation (Cruse *et al.* 1995a). Three sensory inputs correspond to three joint angles signalling the actual leg posture. Three further inputs receive target angles defining the desired posture at touchdown. In a detailed study using genetic algorithms, Linder (2002) could show that, for the middle leg, seven non-zero weights out of a total of 18 are sufficient to simulate typical swing movements. Inspection of six of these weights reveals that Linder's swing net consists of three negative feedback controllers, one for each joint, whereby the controller of the TC- (protraction) and the CT-joints (levation) are coupled via the seventh weight. This weight is responsible for changing from lelevation to depression. All 18 weights showed a small variability with the exception of this weight. This weight is responsible for varying the maximum height of the swing movement and might therefore be subject to a learning procedure that changes this weight depending on the ruggedness of the substrate. In a second approach using an antagonistic architecture, Linder was also able to propose a solution that self-stabilizes against disturbance, as, for example, synaptic drifts (see also Linder 2005) for a solution based on a spatial coding. The transformation of the anterior leg posture to the target angles of the leg is implemented by means of a simple feed-forward network (Dean 1990; target net in figures 3 and 5a).

The three outputs of the model are proportional to the angular velocities of the joints,  $\dot{\alpha}$ ,  $\dot{\beta}$  and  $\dot{\gamma}$  for TC-, CT- and FT-joints, respectively. In the kinematics simulation, they are formally integrated to obtain the current posture. The proprioceptive feedback then closes the control loop (figure 5a). Hence, the swing module can be viewed as a networked control circuit with integration properties. The weight matrix of the ANN sets the amount of interjoint coupling during a swing movement, i.e. the impact of movement in one joint on the movement of another joint.

This simple model can produce swing trajectories that closely resemble the swing movements observed in walking stick insects (Cruse & Bartling 1995). Moreover, it can account for terminal searching loops of the swing trajectory in case of lacking foothold. Thus, the swing and subsequent searching movements can be modelled by a single control circuit (Dürr 2001). This is considerably different from the separate search control strategy applied by Espenschied *et al.* (1996) to generate searching movements of a hexapod robot. However, note that modelling of searching movements requires more interjoint coupling than is present in Linder's solution mentioned previously. In other words, more weights than just Linder's seven need to be non-zero to account for reasonably large searching loops (Dürr 2001). Searching trajectories become even more realistic if the ANN structure is extended by antagonist outputs and additional sensory inputs, e.g. one that signals forward speed (Dürr 2005b). Recently, two alternative controllers have been proposed (Schumm & Cruse 2006).

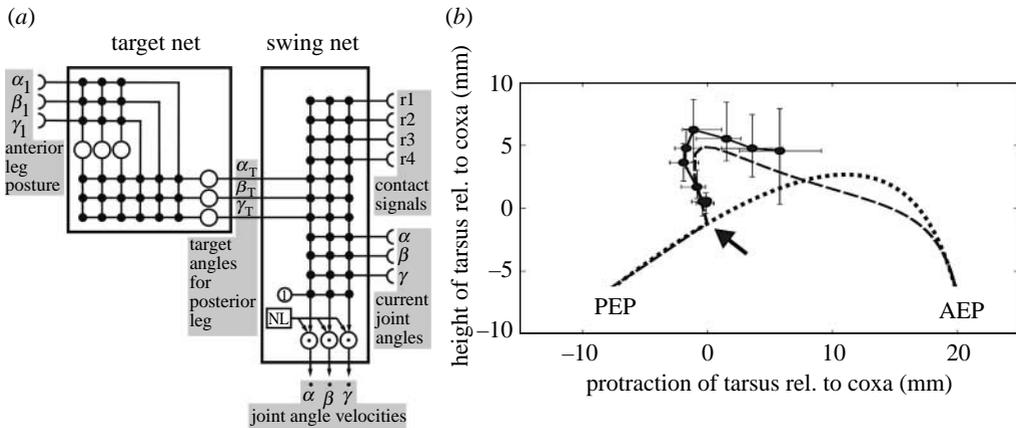


Figure 5. Modelling mechanically uncoupled leg movements with swing net. (a) Swing net is an ANN consisting of three neuroids, the output of which sets angular velocity of the TC- ( $\dot{\alpha}$ ), CT- ( $\dot{\beta}$ ) and FT-joint ( $\dot{\gamma}$ ). Each neuroid receives a weighted input (solid circles) from external sensors that signal the current joint angles ( $\alpha$ ,  $\beta$ ,  $\gamma$ ) and obstacle contact (r1–r4). A constant input models internal resting activation (1). Further inputs are the target angles ( $\alpha_T$ ,  $\beta_T$ ,  $\gamma_T$ ) from the target net. The control loop is closed via the leg itself, as movement changes the posture and, thus, the sensory input. The target net consists of six neuroids that receive sensory input signalling the current joint angles of the next anterior leg ( $\alpha_1$ ,  $\beta_1$ ,  $\gamma_1$ ). (b) Example trajectories of swing net, simulating normal protraction (dotted line) and an avoidance reflex (dashed line) upon obstacle contact (arrow). The reflex trajectory matches experimental results, i.e. average tarsus positions at different times (solid circles with error bars;  $\pm$ s.d.) after mechanical disturbance of a swing movement (adapted from Schmitz *et al.* 2001).

Despite its simplicity, the swing net not only reproduces the trained trajectories, but it is also able to generalize over a considerable range of untrained situations, demonstrating an important advantage of the ANN approach. Moreover, the swing net is remarkably tolerant with respect to external disturbances. The ability to avoid touched obstacles during swing (figure 5b; Schmitz *et al.* 2001) is a result of a simple extension of a swing net, namely the addition of four further sensory inputs that become activated in the case of a physical contact with an obstacle. The impact of each additional sensory input, with its specific weights on the output neurons, represents a simple implementation of distinct motor neuron activation patterns elicited by tactile hairs on the insect leg, as observed during avoidance movements (e.g. Siegler & Burrows 1986). When a leg of WALKNET strikes an obstacle during protraction, it is initially retracted and elevated, followed by the resumed protraction to overcome the obstacle (figure 5b). Indeed, the mechanical perturbation of the swing movement of a stick insect front leg typically causes a stereotyped avoidance movement, consisting of retraction, levation and flexion (Ebeling & Dürer 2006). The latter reflex is context independent and acts independently on each one of the three leg joints.

### (c) Similarities to grasping and grooming

Mechanically, uncoupled leg movements occurring in other behavioural contexts or in other insect species, are often quite similar to swing movements, in that they are targeted as well. For example, a fast retargeting of ongoing swing

movements can be observed in stick insects walking towards a vertical rod. In case an antenna touches the rod during the swing movement of the ipsilateral front leg, the trajectory of front tarsus can change rapidly to be redirected to grasp the rod, rather than to the normal target position on the ground (Dürr & Krause 2001). This indicates that the target information of the front legs can depend on the antennal mechanosensory input, a property that may be linked to the coordinated movement of antennae and front legs during normal walking (Dürr *et al.* 2001).

An example of a similar movement type in another insect is the hind leg grooming movement of a locust, in which the leg is targeted towards various locations on the body segments (Berkowitz & Laurent 1996) or the wings (Matheson 1997). These movements can be considered as being mechanically uncoupled in principle, since many of them do not lead to the contacts between leg and body surfaces. Grooming movements of locusts consist of an initial targeted trajectory followed by one or more tarsus loops. Thus, there is a considerable similarity to searching movements of stick insects that consist of a targeted swing movement with terminal searching loops. Moreover, as targeting of grooming movements is spatially continuous for stimulus locations along the forewing (Dürr & Matheson 2003) and animals successfully compensate for the external loads applied to the grooming leg (Matheson & Dürr 2003), the functioning of the underlying neural networks may not be so different from those of the stick insect swing and searching movements. Based on the fact that the contact between leg and body is not a prerequisite for the loop structure of a grooming movement, one may hypothesize that, when grooming, locusts really search for the source of the stimulus that disturbs them. Thus, grooming and searching could be variants of the same behaviour.

#### 4. Controlling propulsion: coordination of multiple legs during stance

##### (a) *Central processing can hardly account for required adaptiveness*

To control the stance movement, simple technical solutions can be found for straight walking on a flat surface (e.g. 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 sufficient to specify a movement for each leg on its own, because the mechanical coupling through the substrate implies that efficient locomotion requires the coordinated action of all the joints that connect the body to the ground, i.e. all joints of legs in stance. Thus, the action of up to 18 joints may need to be coordinated at any moment in time. However, the number and combination of mechanically coupled joints varies from one moment to the next, depending on the stepping pattern. Accordingly, the task to be solved changes continuously. Moreover, the control of a kinematic chain consisting of three rotational joints is a nonlinear task, particularly when the rotational axes of the joints are not orthogonal, as is the case for the TC-joint at the base of the leg. Further complexity is introduced not only by damping properties of muscles and joints, but also by changing segment lengths due to growth or injury.

In walking machines, the so-called force distribution problem, which occurs whenever two or more parallel kinematic chains are mechanically coupled via the ground, can be solved by computationally costly algorithms (e.g. Gorinevsky & Shneider 1990; Klein & Kittivatcharapong 1990; Gardner 1991). Such algorithms

take into account the ground reaction forces of all legs in stance and seek to optimize some additional criterion, such as minimizing the tension or compression exerted by the legs on the substrate. Owing to the nature of the mechanical interactions, and inherent in the search for a globally optimal control strategy, these ‘traditional’ algorithms require a single central controller, and do not lend themselves to the distributed processing. Accordingly, a neural implementation of such an algorithm would require the central nervous system to monitor and integrate information from all joints at the same time. In technical solutions, such central control makes real-time control difficult, even in the simple case of walking on a flat and rigid substrate. For a comparatively slow and inexact neural network of an insect, this is an even larger problem. Finally, under natural walking conditions, e.g. on leaves and twigs climbed by a stick insect, surfaces vary in slope, friction and compliance. In such cases, knowledge of the geometrical situation is often incomplete, making an explicit calculation difficult, if not impossible.

(b) *Positive feedback: not everything needs to be calculated*

Despite the evident complexity, the task to coordinate many joints during stance is mastered by insects without noticeable problems. Hence, there must be a solution that is fast enough for an online computation by an insect nervous system. How can this be done? Several authors (e.g. Brooks 1991; Pfeifer & Scheier 2001) have pointed out that not all desired information, e.g. the impact of one moving joint on another, need to be calculated explicitly by the CNS. Rather, much is made available by the interaction with the environment, e.g. due to mechanical coupling. Accordingly, instead of an abstract calculation, the nervous system may directly exploit the dynamics of the body–environment interaction.

To solve the particular problem at hand, WALKNET employs a strategy that is likely to be used by walking animals, in that it uses the distributed control in the form of local positive displacement feedback (Cruse *et al.* 1995c). A related form of positive feedback, but one that monitors force rather than a joint movement, is currently attracting much interest in the study of vertebrate motor control (e.g. Prochazka *et al.* 1997a,b) and self-stabilization (e.g. Geyer *et al.* 2003). Most direct evidence for a functional positive feedback loop during walking was provided by Donelan & Pearson (2004), who showed that load-sensing afferents (Ib-afferents) in the cat hind leg are part of a low-gain positive feedback loop that serves to reinforce ankle extensor activity during stance movements.

To understand the workings of positive displacement feedback, consider, for example, a standing human who begins to move one knee, while keeping both feet on the ground. Owing to the mechanical connections, all other joints of the moved leg, and even joints of the other leg, passively adjust to the active knee movement. The fact that the passive movements always maintain the mechanical integrity of the system may appear trivial to the human who moved its knee, but it is far from trivial to an engineer who attempts to control a multi-jointed leg. The example of a standing human is helpful to explain the principle of coupled joints; however, postural control of standing is quite different from control of movement. In standing animals, the local negative feedback control circuits act to compensate passive movements, maintaining the desired posture. In walking animals, a passive movement of a joint may indicate an active movement of

another joint, which should be assisted rather than counteracted. In conclusion, the angular velocities of mechanically coupled leg joints need not be computed explicitly, because this information is inherent to the biomechanics of the body. What is needed is a strategy that makes use of this inherent knowledge.

WALKNET exploits the body kinematics by a local positive displacement feedback mechanism. It occurs at the level of single joints, in that the current joint angular velocity is fed back to control the motor output of the same joint. Thus, positive feedback signals induce local assistance reflexes, where ‘local’ means that each feedback connection is confined to a single joint, although the initiating passive movement may have been caused by another distant joint. This assumption is justified by the experimental findings on stick insects (Bässler 1988; Schmitz *et al.* 1995). In the stick insect kinematics of WALKNET, this feedback is present in all TC- and FT-joints, i.e. all joints with a strong impact on propulsion and a low impact on the body height. Accordingly, the summed action of all local assistance reflexes supports propulsion in a given direction.

### (c) *Dealing with instability, height control and directional biases*

The proposed positive feedback mechanism requires several issues to be dealt with. The first is that positive feedback loops are prone to become unstable. Whereas in positive force feedback, the muscle properties may preclude instability, the positive displacement feedback of WALKNET is kept stable by bandpass filtering the feedback signal. Recently, this principle has been successfully tested in a dynamics simulation (Schneider *et al.* 2005) and on a single leg of a physical robot (Schneider *et al.* 2006). The so-called switched local positive velocity feedback controller switches from positive feedback to compliant motion depending on whether the joint produces a positive or negative mechanical power, respectively.

The second problem is that positive feedback on a joint that has an impact on the animal’s clearance leads to unpredictable changes in the body height. In stick insects, body height is controlled by a distributed system, in which each leg acts like an independent, proportional controller with nonlinear characteristics (walking animal: Cruse 1976a; Cruse *et al.* 1993; Diederich *et al.* 2002; standing animal: Cruse *et al.* 1989). Accordingly, the CT-joints, i.e. the joints with the largest impact on the body height, are not affected by positive feedback. Instead, a separate negative feedback loop controls the body height via the CT-joints.

The third problem concerns directional biases, e.g. when gravity opposes the walking direction on a steep slope. To avoid backward walking induced by gravity or even by small external disturbances, WALKNET uses a supervisory system that switches the entire walking system on or off, but also specifies the walking direction. This central bias in walking direction is caused by a constant, small, positive offset value (‘walking on’ in figure 6), which replaces the sensory signal if it is larger than the latter (‘max’ in figure 6).

### (d) *Course control*

Ideally, positive displacement feedback implies that the active movement at a single joint can determine the walking direction of the entire animal. This is because the induced passive movement of all other joints will be transformed into a supporting active movement. If the first joint to move was selected at random,

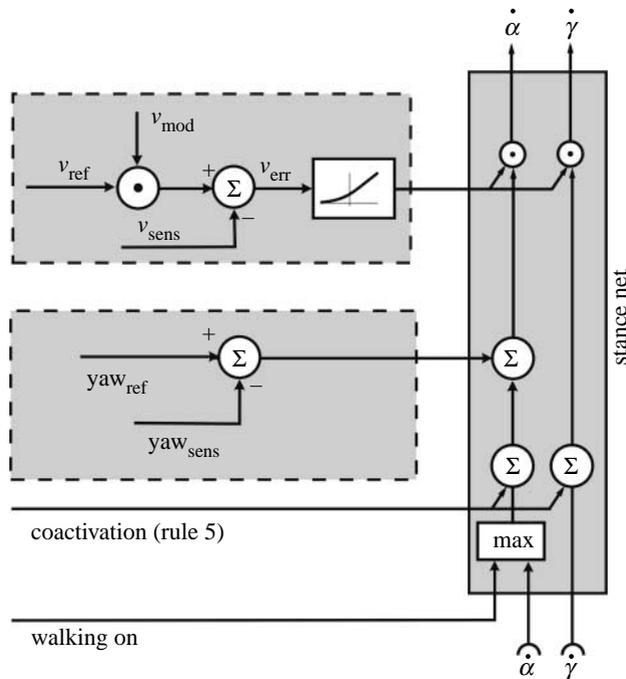


Figure 6. Modelling joint coordination during stance, using positive displacement feedback. The stance net consists of two output units that set the angular velocity of the TC- ( $\dot{\alpha}$ ) and FT-joint ( $\dot{\gamma}$ ) during stance. As the CT-joint mainly affects the height of the body relative to its feet, it is controlled by a separate ANN (height net in figure 3). The stance net receives sensory input from proprioceptors signalling angular velocities, i.e. closing a positive displacement feedback loop. In addition, it receives central commands that determine the velocity of forward translation ( $v_{ref} \times v_{mod}$ ) and yaw rotation ( $yaw_{ref}$ ). Both of these signals are subtracted from a corresponding sensory input signal, thus closing negative feedback loops. A ‘walking on’ signal sets a minimum retraction velocity (via a threshold operator ‘max’) to stabilize retraction against disturbances of the positive feedback signal. Coordination rule 5 can be partially modelled by adding a co-activation signal to the sensory input and by modulating the stance velocity via the  $v_{mod}$  input. Passive movements imposed on the TC- or FT-joint are sensed by the stance net and transformed into an active movement, implementing a local assistance reflex.

the body would probably not move forward along a straight path. In WALKNET, irregular movements are avoided, because (i) all legs initiate forward-directed propulsive forces at the start, as is the case in insects (Cruse & Saxler 1980) and (ii) a central yaw-control system maintains a desired course.

Insects respond to large-field visual motion stimuli with compensatory movements that act to cancel, or at least to reduce, the visual motion input by the so-called optomotor responses (e.g. Hengstenberg 1993). The optomotor response of stick insects to a rotating visual stimulus is to turn the entire body (e.g. Jander 1985). The curvature of the resulting walking path correlates with the stimulus velocity (Jander 1982) and various kinematic parameters of the leg movements change accordingly, the change of stance direction of the front legs being the fastest and strongest effect to occur (Dürr & Ebeling 2005). This suggests that descending visual interneurons primarily affect premotor networks of the front legs, thus initiating a turn by a change in the front-leg stance direction.

In WALKNET, course control is modelled slightly differently. It is implemented as a negative feedback control system that adjusts the stance velocity of all legs. Owing to its closed-loop nature, this system can compensate for unbalanced coupling factors or other inequalities between right and left legs. Assuming a descending signal from the visual system ( $\text{yaw}_{\text{sens}}$  in figure 6) that is proportional to the yaw-turning velocity, i.e. rotation around the body vertical axis, the deviation between the desired ( $\text{yaw}_{\text{ref}}$  in figure 6) and the actual headings is determined. This error signal is subtracted from the TC-joints of the front and the hind legs, with the opposite sign for left and right legs. If  $\text{yaw}_{\text{ref}}$  is set to zero, the system moves straight with small, side-to-side oscillations in heading such as can be observed in walking insects (Kindermann 2002). To simulate curve walking (figure 7), the reference value is given a small positive or negative bias to determine the curvature direction and magnitude. The model allows robust course control, albeit with the difference to the experimental findings that it includes direct signals to all legs at an equal rate. Recent results on phonotactic course control in crickets indicate that the overall turning tendency of the animal is the result of many brief and transient changes of the yaw rotation (Hedwig & Poulet 2004). Since the cricket ear is located in the front legs, one may speculate that the transient changes of the heading direction are driven by the altered stance direction of individual front-leg steps. If so, it would be reasonable to assume that both visual and acoustic course control relies on the modulation of prothoracic premotor networks.

(e) *Controlling walking speed*

To date, little is known about how insects sense their own walking speed, although, in principle, a simple neural network could transform the angular velocity of the TC-joints into a neural representation of forward speed forming a kind of odometer (but visual feedback might be used as well). In WALKNET, walking speed is determined by a negative feedback controller. Much like the negative feedback control of heading direction, forward speed is controlled by a negative feedback signal derived from the difference of sensed walking speed  $v_{\text{sens}}$  to the desired walking speed  $v_{\text{ref}}$ . This obtained error signal is subject to a nonlinear transformation and then used as a gain factor for the positive feedback signal to the TC- and FT-joints of all six legs (figure 6).

## 5. Discussion

(a) *WALKNET models many aspects of adaptive control of walking*

As mentioned in §2, the distributed processing of six coupled single-leg controllers allows WALKNET to generate a range of different gaits (figure 4). Rather than being centrally selected and controlled, the gait emerges as a result of the system properties. It depends on the external environmental situation, as well as on the descending steering commands and reference velocity. 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. The set of leg coordination rules of figure 2 has been exploited

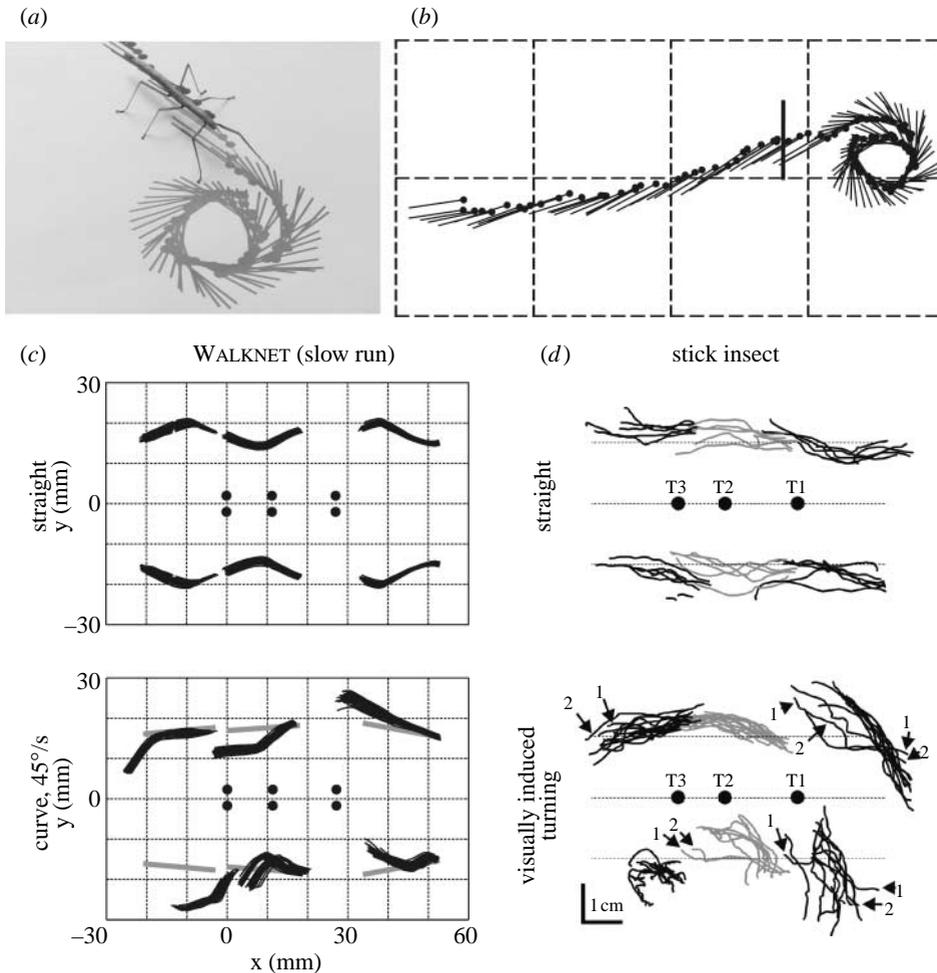


Figure 7. Comparison of walking stick insects with WALKNET: straight and curve walking. (a) Stick insects can negotiate fairly tight curves. Turning can be induced by a large-field visual motion stimulus. Here, *Carausius morosus* is standing on a printout of a recorded walking track. Same track as in (b), but printed to scale. (b) A walking track of 21.5 s duration, with each circle and line segment indicating the location of the head and orientation of the body's long axis, respectively. The vertical bar marks the instant when the visual motion stimulus began to move. (c) Stance trajectories of all six feet of the WALKNET simulation. Each bundle of black lines shows the movement of the foot during a single step. Walking direction is to the right. Solid circles mark the locations of the CT-joints. Top, straight walking row; bottom, curve walking during a right turn, i.e. with yaw-turning command  $yaw_{ref} > 0$  (figure 6). Straight grey lines mark the average AEP–PEP connection lines of the corresponding straight walk (above). Trajectories are more variable than during straight walking and appear more curved. (d) For direct comparison, stance trajectories of an unrestrained walking stick insect. Solid circles mark the thorax centre between the CT-joints. Top: straight walk; same trial as in (b), from the start of the recording until the onset of stimulus motion (7.5 s). Bottom: curve walk; same trial as in (b), from the onset of stimulus motion until the end of recording (15 s). Numbers indicate AEPs and PEPs of the first and second steps after stimulus onset, to illustrate the transition from straight to curve walking. Trajectories differ from (c), particularly for the steps of legs on the inside of the curve (bottom) and for the outer middle leg (data of (c) taken from Kindermann 2002, with permission; (b) and (c) adapted from Dürr & Ebeling 2005).

successfully by a number of hexapod walking machines (e.g. TUM walking machine: Pfeiffer *et al.* 1994, 1995; CWRU hexapod robot II: Espenschied *et al.* 1993, 1996; TARRY: Frik *et al.* 1999).

Compared to earlier versions of the WALKNET stance controller (Cruse *et al.* 1995*b*), the introduction of local positive displacement feedback permitted radical simplification, mainly because an apparently global problem is broken down into local components. WALKNET can cope with obstacles in the height range of the animal's clearance (Cruse *et al.* 1998). It automatically adapts to simulated injuries, such as the removal of half of the middle tibia (e.g. supplementary extension 3 of Dürr *et al.* 2003). Even in response to massive perturbations, for example after falling over, WALKNET resumes normal walking within a few steps. Thus, even extremely disordered postures that have never been encountered before can be managed autonomously (Kindermann 2002), i.e. without the need for a central command stage. Further extensive tests have been performed by Roggendorf (2005), including comparison with other solutions.

Central commands are only necessary to set the reference values for a heading direction and a desired walking speed, but not for selection of a given motor program, or by a selective modulation of low-level mechanisms. Autonomous walking behaviour may well be a matter of self-organized motor activity due to distributed local processing.

(b) *Real insects show more context dependency of control than WALKNET*

As yet, a number of problems remain, particularly the quantitative comparison of the real stick insect's walking performance with that of WALKNET (Kindermann 2002) reveals the shortcomings of the current model. For example, curve walking is possible and stance trajectories of WALKNET show many properties of stick insect trajectories (figure 7). Nevertheless, neither do the leg coupling strengths vary (Dürr 2005*a*), nor do the stance directions change as observed in the tight curves of the real stick insect (Dürr & Ebeling 2005). Moreover, backward walking would require a change of weights in all six swing nets and of the coordinating signals between legs. The walking situations that the model can master are impressive, given its simplicity, but by far not as extreme as those mastered by real insects. For example, crossing large gaps (Bläsing & Cruse 2004) or climbing high obstacles will require further elaboration of the control structure (Bläsing 2006) and, possibly, introduction of more elaborated sensory structures, such as insect antennae.

(c) *Insects carry active sensors: their eyes and antennae*

Indeed, the introduction of active sensors to a model like WALKNET bears much potential for the development of further adaptive mechanisms. The reason is that an active movement of a sensory organ reflects an intention of the animal, as it voluntarily directs the receptive field. The principal active sensory modalities are the tactile and the visual senses. In walking insects, tactile sensing is particularly important because insects can move their eyes only by means of head rotation or forward translation. The small displacements of the head render displacement by forward translation during walking the most important source for the self-generated visual image flow. In comparison with visual information processing, relatively little is known about tactile spatial information processing. In a recent

review, Staudacher *et al.* (2005) show that the range of behaviours in which antennal tactile information is important is remarkable. With respect to locomotion, antennae are used for the orientation relative to wind direction (Linsenmair 1973; Bell & Kramer 1979; Böhm *et al.* 1991) and gravity (e.g. Bässler 1971; Horn & Bischof 1983), for the detection of potential dangers (e.g. Gnatzy & Heußlein 1986; Stierle *et al.* 1994; Comer *et al.* 2003), the active exploration of the space ahead (e.g. Pelletier & McLeod 1994; Horseman *et al.* 1997; Okada & Toh 2000; Dürr *et al.* 2001) and the tracking of objects (Honegger 1981).

*(d) The properties of muscle affect the requirements on biological motor control*

A more general shortcoming is that up to now the solutions are only based on kinematic simulations and the forces developed by the insect have not been considered. For stick insects (Cruse 1976*b*; Bartling & Schmitz 2000) and cockroaches (Full *et al.* 1991; Ting *et al.* 1994; Jindrich & Full 2002), ground reaction forces of insects have been studied in a range of walking contexts. The results show that different legs make different contributions to the net ground reaction force vector. Moreover, these contributions are context dependent and change considerably between walking situations. For example, in stick insects, walking on horizontal planes, hind legs propel the body, middle legs mainly support and front legs often step irregularly, indicating that they may be used as feelers. When walking upside down along a horizontal beam, front and hind legs are used to carry the body weight, whereas middle legs additionally provide propulsive forces; in other situations, such as walking up a vertical wall, the results are less easily interpretable. As yet, it is not clear to what extent these different behaviours simply result from the changed geometrical situations with unchanged controller output (e.g. height control) and to what extent the controller adapts its output signals.

Furthermore, the passive properties of muscles are not regarded. As an extremely important contribution, Full, Blickhan and co-workers (e.g. Full *et al.* 1991; Blickhan & Full 1993; Jindrich & Full 1999, 2002) have shown that, in a fast walker, the mechanical, in particular the dynamical, properties of the system can be very appropriately described by a spring–mass model, i.e. an inverted pendulum with a point mass supported by a weightless spring. Such spring–mass models have self-stabilizing properties that may well be exploited to substantially decrease the control effort during hopping and running.

*(e) The relative contributions of central pattern generators and sensory feedback control remain elusive*

One result of this and related work is that the control of rhythmic movement of a complex system is possible without relying on central oscillators and fixed gait controllers. The reason for this is the interaction with the environment resulting from embodiment and situatedness. Thus, central oscillators are not required to control rhythmic movements of walking legs. Nevertheless, even if central oscillators are used to control the basic rhythmic movement of a leg, the problem of coordinating different joints of one leg during walking would remain. This is not a trivial task because, depending on the specific walking situation, there is considerable variation between the time course of the basic rhythm of swing and stance and the activation of different joint muscles (for a brief review,

see Cruse 2002). On the other hand, there are biological experiments that indicate that neural oscillators, the physiological equivalent of a central control circuit, do exist. Detailed studies have shown that separate oscillators can be found for each leg joint (e.g. Büschges *et al.* 1995; reviewed by Bässler & Büschges 1998). However, in order to produce a coordinated temporal sequence of joint movements, a proper sequence of load and position sensor signals would be necessary to trigger appropriate phase transitions of each joint oscillator (Akay *et al.* 2004). This induces the question of what might be the biological sense of such oscillators.

Based on a Brown half-centre oscillator, Cruse (2002) proposed a simple network that explains several findings observed in insects walking in different situations. It models the sensory–motor connection of each joint by means of antagonistic and time-dependent filters, two components that are missing in the WALKNET components: swing and stance nets. In contrast to a true CPG, this model does not produce a continuous oscillation as such, but only influences the next half-cycle. This is advantageous because its ‘predictive’ property is based on actual, local knowledge; therefore it avoids potentially inappropriate long-term predictions of a central oscillatory system with an inherent rhythm. As this network also generates motor patterns reminiscent of fictive motor activity, it provides for an alternative explanation of experimental results that have been interpreted as an indicator of a central oscillator.

However, there are other situations where a CPG is likely to be more appropriate than sensor-driven responses. For example, in emergency situations, the central system may be used to replace the ‘sensory-driven oscillator’. A dramatic case of such an emergency could be the loss of one or several sensors due to an injury. A less dramatic case, but for biological systems probably equally important, occurs when fast rhythms are to be produced as is the case in a fast running cockroach. Fast, here, is meant relative to the time delays resulting from the slow neuronal transduction; if sensory feedback is too slow, it may not be able to contribute to the production of the rhythmic output. Although such a central system might be inaccurate in the case of external disturbances, it may be better to use this approximate prediction than an exact sensor reading that comes too late. Note that this argument is usually not relevant for an artificial electronic system, because here transmission of signals is fast enough.

However, instead of using central oscillators as active devices to control motor output, they may be used in a more passive way, that is for predictive purposes. One way is to change sensory thresholds in a given time window (Degtyarenko *et al.* 1998). Moreover, central oscillators may be used on a longer time-scale to detect long-term deviations (e.g. in the case of sensory drift) by providing expectation values that could be compared with the sensory input. If a long-term deviation is detected, then this information can be used to read just the system via back-propagation mechanisms, for example (Kawato & Gomi 1992).

#### (f) Higher control centres

Following the behaviour-based approach (Brooks 1991), the control system WALKNET was constructed by interpreting the experimental outcomes as to result from a purely reactive system, i.e. a system without memory or internal world

models. This approach was, however, not followed in a strict sense as the positive feedback connections used in the selector net (figure 2) comprise a kind of short-term memory. Furthermore, other results (fig. 7 in Cruse *et al.* 1998) indicate that during swing movements, the reactions to obstacles depend on an internal state, which may be termed as ‘swing motivation’. Nevertheless, both results can be simulated by simple, hard-wired structures and may therefore still be described as belonging to a reactive type of systems. Assuming the presence of neural forward models, a given limb movement is an expression of an expected sensory experience, be it a contact event or lack thereof. Thus, behaviour will be changed whenever there is a discrepancy between the forward model prediction and the actual sensory input, the behaviour. A potential example of a behaviour governed by the forward model predictions is based on the recent results of Bläsing & Cruse (2004). They found that stick insects (*Aretaon asperrimus*) climbing over very large gaps respond differently to ground contact of a leg or of an antenna: whereas lack of ground contact at the end of a leg swing movement causes an immediate change in behaviour, lack of antennal contact does not, even if the antenna reaches below the walking surface at an edge. In this case, the cyclic antennal movement pattern could be interpreted to reflect the expectation of non-contact, whereas the stepping pattern of the legs would reflect the expectation of regular ground contacts.

Results like this suggest that future research should take into account the existence of forward models in insects, too (see Wolpert & Ghahramani 2000). Therefore, the model has to be expanded by motivational units and, possibly, by an internal body model (Cruse 2003) that may even allow the system to ‘invent’ new types of movements. As the first step, Roggendorf (2005) proposed a system that is able to look ahead for one or two steps to find alternative solutions for difficult situations. Therefore, insects, although often considered to be ‘simple systems’, provide an excellent domain for studying the principles underlying autonomous behaviour at the reactive and partly even at the cognitive level.

This work was supported by the Deutsche Forschungsgemeinschaft (DFG), more recently with grants Cr 58/9 and 58/10 to H.C. and J.S. and Du 380/1 to V.D., and SPARK (EC-IST programme) to H.C., V.D. and J.S. The authors thank A. Exter and T. Kindermann for their kind help with the figures.

## References

- Akay, T., Haehn, S., Schmitz, J. & Büschges, A. 2004 Signals from load sensors underlie interjoint coordination during stepping movements of the stick insect leg. *J. Neurophysiol.* **92**, 42–51. (doi:10.1152/jn.01271.2003)
- Ayers, J. 2002 A conservative biomimetic control architecture for autonomous underwater robots. In *Neurotechnology for biomimetic robots* (ed. J. Ayers, J. L. Davis & A. Rudolph), pp. 241–259. Cambridge, MA; London, UK: MIT Press.
- Bartling, C. & Schmitz, J. 2000 Reaction to disturbances of a walking leg during stance. *J. Exp. Biol.* **203**, 1211–1223.
- Bässler, U. 1971 Zur Bedeutung der Antennen für die Wahrnehmung der Schwerkraftrichtung bei der Stabheuschrecke *Carausius morosus*. *Kybernetik* **9**, 31–34. (doi:10.1007/BF00272558)
- Bässler, U. 1983 In *Neural basis of elementary behavior in stick insects*. Berlin, Germany; New York, NY: Springer.

- Bässler, U. 1988 Functional principles of pattern generation for walking movements of stick insect forelegs: the role of the femoral chordotonal organ afferences. *J. Exp. Biol.* **136**, 125–147.
- Bässler, U. & Büschges, A. 1998 Pattern generation for stick insect walking movements—multi-sensory control of a locomotor program. *Brain Res. Rev.* **27**, 65–88. (doi:10.1016/S0165-0173(98)00006-X)
- Bässler, U. & Wegner, U. 1983 Motor output of the denervated thoracic ventral nerve cord in the stick insect *Carausius morosus*. *J. Exp. Biol.* **105**, 127–145.
- Bell, W. J. & Kramer, E. 1979 Search and anemotactic orientation of cockroaches. *J. Insect Physiol.* **25**, 631–640. (doi:10.1016/0022-1910(79)90112-4)
- Berkowitz, A. & Laurent, G. 1996 Local control of leg movements and motor patterns during grooming in locusts. *J. Neurosci.* **16**, 8067–8078.
- Bläsing, B. 2006 Crossing large gaps: a simulation study of stick insect behavior. *Adapt. Behav.* **14**, 265–285. (doi:10.1177/105971230601400307)
- Bläsing, B. & Cruse, H. 2004 Mechanisms of stick insect locomotion in a gap crossing paradigm. *J. Comp. Physiol. A* **190**, 173–183. (doi:10.1007/s00359-003-0482-3)
- Blickhan, R. & Full, R. J. 1993 Similarity in multilegged locomotion: bouncing like a monopode. *J. Comp. Physiol. A* **173**, 509–517. (doi:10.1007/BF00197760)
- Bowerman, R. F. 1975 The control of walking in the scorpion. I. Leg movements during normal walking. *J. Comp. Physiol.* **100**, 183–196. (doi:10.1007/BF00614529)
- Böhm, H., Heinzl, H.-G., Scharstein, H. & Wendler, G. 1991 The course-control system of beetles walking in an air-current field. *J. Comp. Physiol. A* **169**, 671–683. (doi:10.1007/BF00194896)
- Brooks, R. A. 1991 Intelligence without reason. In *Proc. 12th Int. Joint Conf. on Artificial Intelligence (IJCAI-91, Sydney)*, pp. 569–595.
- Brunn, D. E. & Dean, J. 1994 Intersegmental and local interneurons in the metathorax of the stick insect *Carausius morosus* that monitor middle leg position. *J. Neurophysiol.* **72**, 1208–1219.
- Burrows, M. 1992 Local circuits for the control of leg movements in an insect. *Trends Neurosci.* **15**, 226–232. (doi:10.1016/0166-2236(92)90040-F)
- Burrows, M. 1996 *The neurobiology of an insect brain*. Oxford, UK: Oxford University Press.
- Büschges, A. 2005 Sensory control and organization of neural networks mediating coordination of multisegmental organs for locomotion. *J. Neurophysiol.* **93**, 1127–1135. (doi:10.1152/jn.00615.2004)
- Büschges, A., Schmitz, J. & Bässler, U. 1995 Rhythmic patterns in the thoracic nerve cord of the stick insect induced by pilocarpine. *J. Exp. Biol.* **198**, 435–456.
- Chasserat, C. & Clarac, F. 1980 Interlimb coordinating factors during driven walking in crustacea. A comparative study of absolute and relative coordination. *J. Comp. Physiol.* **139**, 293–306. (doi:10.1007/BF00610461)
- Chiel, H. J. & Beer, R. 1997 The brain has a body: adaptive behavior emerges from interactions of nervous system, body and environment. *Trends Neurosci.* **20**, 553–557. (doi:10.1016/S0166-2236(97)01149-1)
- Clarac, F. & Cruse, H. 1982 Comparison of forces developed by the leg of the rock lobster when walking free or on a treadmill. *Biol. Cybern.* **43**, 109–114. (doi:10.1007/BF00336973)
- Comer, C. M., Parks, L., Halvorsen, M. B. & Breese-Terteling, A. 2003 The antennal system and cockroach evasive behavior. II. Stimulus identification and localization are separable antennal functions. *J. Comp. Physiol. A* **189**, 97–103.
- Cruse, H. 1976a The control of body position in the stick insect (*Carausius morosus*), when walking over uneven surfaces. *Biol. Cybern.* **24**, 25–33. (doi:10.1007/BF00365591)
- Cruse, H. 1976b The function of the legs in the free walking stick insect *Carausius morosus*. *J. Comp. Physiol.* **112**, 235–262. (doi:10.1007/BF00606541)
- Cruse, H. 1979 The control of the anterior extreme position of the hindleg of a walking insect, *Carausius morosus*. *Physiol. Entomol.* **4**, 121–124.
- Cruse, H. 1985a Coactivating influences between neighbouring legs in walking insects. *J. Exp. Biol.* **114**, 513–519.
- Cruse, H. 1985b Which parameters control the leg movement of a walking insect? II. The start of the swing phase. *J. Exp. Biol.* **116**, 357–362.

- Cruse, H. 1990 What mechanisms coordinate leg movement in walking arthropods? *Trends Neurosci.* **13**, 15–21. (doi:10.1016/0166-2236(90)90057-H)
- Cruse, H. 2002 The functional sense of central oscillations in walking. *Biol. Cybern.* **86**, 271–280. (doi:10.1007/s00422-001-0301-2)
- Cruse, H. 2003 The evolution of cognition—a hypothesis. *Cogn. Sci.* **27**, 135–155. (doi:10.1016/S0364-0213(02)00110-6)
- Cruse, H. 2006 Neural networks as cybernetic systems. Brain, minds, and media. See <http://www.brains-minds-media.org/archive/289>.
- Cruse, H. & Bartling, C. 1995 Movement of joint angles in the legs of a walking insect, *Carausius morosus*. *J. Insect Physiol.* **41**, 761–771. (doi:10.1016/0022-1910(95)00032-P)
- Cruse, H. & Epstein, S. 1982 Peripheral influences on the movement of the legs in a walking insect *Carausius morosus*. *J. Exp. Biol.* **101**, 161–170.
- Cruse, H. & Knauth, A. 1989 Coupling mechanisms between the contralateral legs of a walking insect (*Carausius morosus*). *J. Exp. Biol.* **144**, 199–213.
- Cruse, H. & Saxler, G. 1980 Oscillations of force in the standing legs of a walking insect (*Carausius morosus*). *Biol. Cybern.* **36**, 159–163. (doi:10.1007/BF00365770)
- Cruse, H. & Schmitz, J. 1983 The control system of the femur-tibia joint in the standing leg of a walking stick insect *Carausius morosus*. *J. Exp. Biol.* **102**, 175–185.
- Cruse, H. & Schwarze, W. 1988 Mechanisms of coupling between the ipsilateral legs of a walking insect (*Carausius morosus*). *J. Exp. Biol.* **138**, 455–469.
- Cruse, H. & Warnecke, H. 1992 Coordination of the legs of a slow-walking cat. *Exp. Brain Res.* **89**, 147–156. (doi:10.1007/BF00229012)
- Cruse, H., Dean, J. & Suilmann, M. 1984 The contributions of diverse sense organs in the control of leg movement by a walking insect. *J. Comp. Physiol.* **154**, 695–705. (doi:10.1007/BF01350223)
- Cruse, H., Riemenschneider, D. & Stammer, W. 1989 Control of body position of a stick insect standing on uneven surfaces. *Biol. Cybern.* **61**, 71–77. (doi:10.1007/BF00204761)
- Cruse, H., Schmitz, J., Braun, U. & Schweins, A. 1993 Control of body height in a stick insect walking on a treadmill. *J. Exp. Biol.* **181**, 141–155.
- Cruse, H., Bartling, C., Cymbalyuk, G., Dean, J. & Dreifert, M. 1995a A modular artificial neural net for controlling a six-legged walking system. *Biol. Cybern.* **72**, 421–430.
- Cruse, H., Bartling, C., Dreifert, M., Schmitz, J., Brunn, D. E., Dean, J. & Kindermann, T. 1995b Walking: a complex behaviour controlled by simple networks. *Adapt. Behav.* **3**, 385–418.
- Cruse, H., Bartling, C. & Kindermann, T. 1995c High-pass filtered positive feedback for decentralized control of cooperation. In *Advances in artificial life* (ed. F. Moran), pp. 668–678. Berlin, Germany: Springer.
- Cruse, H., Kindermann, T., Schumm, M., Dean, J. & Schmitz, J. 1998 WALKNET—a biologically inspired network to control six-legged walking. *Neural Netw.* **11**, 1435–1447. (doi:10.1016/S0893-6080(98)00067-7)
- Dean, J. 1984 Control of leg protraction in the stick insect: a targeted movement showing compensation for externally applied forces. *J. Comp. Physiol. A* **155**, 771–781. (doi:10.1007/BF00611594)
- Dean, J. 1990 Coding proprioceptive information to control movement to a target: simulation with a simple neural network. *Biol. Cybern.* **63**, 115–120. (doi:10.1007/BF00203033)
- Dean, J. & Schmitz, J. 1992 The two groups of sensilla in the ventral coxal hairplate of *Carausius morosus* have different roles during walking. *Physiol. Entomol.* **17**, 331–341.
- Dean, J. & Wendler, G. 1983 Stick insect locomotion on a walking wheel: interleg coordination of leg position. *J. Exp. Biol.* **103**, 75–94.
- Detyarenko, A. M., Simon, E. S., Norden-Krichmar, T. & Burke, R. E. 1998 Modulation of oligosynaptic cutaneous and muscle afferent reflex pathways during fictive locomotion and scratching in the cat. *J. Neurophysiol.* **79**, 447–463.
- Delcomyn, F. 1980 Neural basis of rhythmic behaviour in animals. *Science* **210**, 492–498. (doi:10.1126/science.7423199)

- Delcomyn, F. 1987 Motor activity during searching and walking movements of cockroach legs. *J. Exp. Biol.* **133**, 111–120.
- Diederich, B., Schumm, M. & Cruse, H. 2002 Stick insects walking along inclined surfaces. *Integr. Comp. Biol.* **42**, 165–173. (doi:10.1093/icb/42.1.165)
- Donelan, J. M. & Pearson, K. G. 2004 Contribution of force feedback to ankle extensor activity in decerebrate walking cats. *J. Neurophysiol.* **92**, 2093–2104. (doi:10.1152/jn.00325.2004)
- Dürr, V. 2001 Stereotypic leg searching-movements in the stick insect: kinematic analysis, behavioural context and simulation. *J. Exp. Biol.* **204**, 1589–1604.
- Dürr, V. 2005a Context-dependent changes in strength and efficacy of leg coordination mechanisms. *J. Exp. Biol.* **208**, 2253–2267. (doi:10.1242/jeb.01638)
- Dürr, V. 2005b Nutzung taktiler Information von Antennen zur Laufbewegungssteuerung. In *Autonomes Laufen* (ed. F. Pfeiffer & H. Cruse), pp. 47–62. Berlin, Germany: Springer.
- Dürr, V. & Ebeling, W. 2005 The behavioural transition from straight to curve walking: kinetics of leg movement parameters and the initiation of turning. *J. Exp. Biol.* **208**, 2237–2252. (doi:10.1242/jeb.01637)
- Dürr, V. & Krause, A. 2001 The stick insect antenna as a biological paragon for an actively moved tactile probe for obstacle detection. In *Climbing and walking robots—from biology to industrial applications. Proc. 4th Int. Conf. Climbing and Walking Robots (CLAWAR 2001, Karlsruhe)* (ed. K. Berns & R. Dillmann), pp. 87–96. Bury St. Edmunds, London: Professional Engineering Publishing.
- Dürr, V. & Matheson, T. 2003 Graded limb targeting in an insect is caused by the shift of a single movement pattern. *J. Neurophysiol.* **90**, 1754–1765. (doi:10.1152/jn.00416.2003)
- Dürr, V., König, Y. & Kittmann, R. 2001 The antennal motor system of the stick insect *Carausius morosus*: anatomy and antennal movement pattern during walking. *J. Comp. Physiol. A* **187**, 131–144. (doi:10.1007/s003590100183)
- Dürr, V., Krause, A., Schmitz, J. & Cruse, H. 2003 Neuroethological concepts and their transfer to walking machines. *Int. J. Robot. Res.* **22**, 151–167.
- Ebeling, W. & Dürr, V. 2006 Perturbation of leg protraction causes context-dependent modulation of inter-leg coordination, but not of avoidance reflexes. *J. Exp. Biol.* **209**, 2199–2214. (doi:10.1242/jeb.02251)
- Ekeberg, Ö. & Grillner, S. 1999 Simulations of the neuromuscular control in lamprey swimming. *Phil. Trans. R. Soc. B* **354**, 894–902. (doi:10.1098/rstb.1999.0441)
- Ekeberg, Ö. & Pearson, K. G. 2005 Computer simulation of stepping in the hind legs of the cat: an examination of mechanisms regulating the stance-to-swing transition. *J. Neurophysiol.* **94**, 4256–4268.
- Ekeberg, Ö., Blümel, M. & Büschges, A. 2004 Dynamic simulation of insect walking. *Arthropod Struct. Dev.* **33**, 287–300. (doi:10.1016/j.asd.2004.05.002)
- Espenschied, K. S., Quinn, R. D., Chiel, H. J. & Beer, R. D. 1993 Leg coordination mechanisms in stick insect applied to hexapod robot locomotion. *Adapt. Behav.* **1**, 455–468.
- Espenschied, K. S., Quinn, R. D., Beer, R. D. & Chiel, H. J. 1996 Biologically based distributed control and local reflexes improve rough terrain locomotion in a hexapod robot. *Robot. Auton. Syst.* **18**, 59–64. (doi:10.1016/0921-8890(96)00003-6)
- Frik, M., Guddat, M., Karatas, M. & Losch, C. D. 1999 A novel approach to autonomous control of walking machines. In *Climbing and walking robots—and the support technologies for mobile machines. Proc. of the 2nd Int. Conf. on Climbing and Walking Robots (CLAWAR 1999)*, (ed. G. S. Virk, M. Randall & D. Howard), pp. 333–342. Bury St. Edmunds, London: Professional Engineering Publishing Limited.
- Full, R. J. & Tu, M. S. 1991 Mechanics of a rapid running insect: two-, four- and six-legged locomotion. *J. Exp. Biol.* **156**, 215–231.
- Full, R. J., Blickhan, R. & Ting, L. H. 1991 Leg design in hexapedal runners. *J. Exp. Biol.* **158**, 369–390.
- Full, R. J., Kubow, T. M., Schmitt, J., Holmes, P. & Koditschek, D. E. 2002 Quantifying dynamic stability and maneuverability in legged locomotion. *Integr. Comp. Biol.* **42**, 149–157. (doi:10.1093/icb/42.1.149)

- Gardner, J. F. 1991 Force distribution in walking machines over rough terrain. *J. Dynamic Syst. Meas. Control* **113**, 754–758.
- Geyer, H., Seyfarth, A. & Blickhan, R. 2003 Positive force feedback in bouncing gaits? *Proc. R. Soc. B* **270**, 2173–2183. (doi:10.1098/rspb.2003.2454)
- Gnatzy, W. & Heußlein, R. 1986 Digger wasp against crickets. I. Receptors involved in the antipredator strategies of the prey. *Naturwissenschaften* **73**, 212–215. (doi:10.1007/BF00417728)
- Gorinevsky, D. M. & Shneider, A. Y. 1990 Force control in locomotion of legged vehicles over rigid and soft surfaces. *Int. J. Robot. Res.* **9**, 4–17.
- Graham, D. 1978 Unusual step patterns in the free walking grasshopper. *Neoconocephalus robustus*. II. A critical test of the leg interactions underlying different models of hexapod co-ordination. *J. Exp. Biol.* **73**, 159–172.
- Graham, D. 1979 Effects of circum-oesophageal lesion on the behaviour of the stick insect *Carausius morosus*. I. Cyclic behaviour patterns. *Biol. Cybern.* **32**, 139–145. (doi:10.1007/BF00337390)
- Graham, D. 1985 Pattern and control of walking in insects. *Adv. Insect Physiol.* **18**, 31–140.
- Grillner, S. 1981 Control of locomotion in bipeds, tetrapods, and fish. In *The nervous system. Motor control* (ed. L. M. Brookhart & V. B. Mountcastle), pp. 1179–1236. Bethesda, MD: American Physiology Society.
- Grillner, S., Deliagina, T. G., Ekeberg, Ö., El Manira, A., Hill, R. H., Lansner, A., Orlovsky, G. N. & Wallén, P. 1995 Neural networks that co-ordinate locomotion and body orientation in lamprey. *Trends Neurosci.* **18**, 270–279. (doi:10.1016/0166-2236(95)93914-J)
- Hedwig, B. & Poulet, J. F. A. 2004 Complex auditory behaviour emerges from simple reactive steering. *Nature* **430**, 781–785. (doi:10.1038/nature02787)
- Hengstenberg, R. 1993 Multisensory control in insect oculomotor systems. *Rev. Oculomot. Res.* **5**, 285–298.
- Holst, E. v. 1939 Die relative Koordinationalen Phänomen und als Methode zentralnervöser Funktionsanalyse. *Erg. Physiol.* **42**, 228–306.
- Holst, E. v. 1943 Über relative Koordination bei Arthropoden. *Pflügers Arch.* **246**, 847–865. (doi:10.1007/BF01751829)
- Honegger, H.-W. 1981 A preliminary note on a new optomotor response in crickets: antennal tracking of moving targets. *J. Comp. Physiol. A* **142**, 419–421. (doi:10.1007/BF00605454)
- Horn, E. & Bischof, H.-J. 1983 Gravity reception in crickets: the influence of cercal and antennal afferents on the head position. *J. Comp. Physiol. A* **150**, 93–98. (doi:10.1007/BF00605292)
- Horseman, B. G., Gebhardt, M. J. & Honegger, H.-W. 1997 Involvement of the suboesophageal and thoracic ganglia in the control of antennal movements in crickets. *J. Comp. Physiol. A* **181**, 195–204. (doi:10.1007/s003590050106)
- Inman, V. T., Ralston, H. J. & Todd, F. 1981 *Human walking*. Baltimore, MD: Williams and Wilkins.
- Jander, J. P. 1982 Untersuchungen zum Mechanismus und zur zentralnervösen Steuerung des Kurvenlaufs bei Stabheuschrecken (*Carausius morosus*). Doctoral dissertation, University of Köln.
- Jander, J. P. 1985 Mechanical stability in stick insects when walking straight and around curves. In *Insect locomotion* (ed. M. Gewecke & G. Wendler), pp. 33–42. Berlin, Germany: Paul Parey.
- Jindrich, D. L. & Full, R. J. 1999 Many-legged maneuverability: dynamics of turning in hexapods. *J. Exp. Biol.* **202**, 1603–1623.
- Jindrich, D. L. & Full, R. J. 2002 Dynamic stabilization of rapid hexapedal locomotion. *J. Exp. Biol.* **205**, 2803–2823.
- Kawato, M. & Gomi, H. 1992 The cerebellum and VOR/OKR learning-models. *Trends Neurosci.* **15**, 445–453. (doi:10.1016/0166-2236(92)90008-V)
- Kindermann, T. 2002 Behavior and adaptability of a six-legged walking system with highly distributed control. *Adapt. Behav.* **9**, 16–41.

- Klein, C. A. & Kittivatcharapong, S. 1990 Optimal force distribution for the legs of a walking machine with friction cone constraints. *IEEE Trans. Robot. Automat.* **6**, 73–85. (doi:10.1109/70.88119)
- Linder, C. R. 2002 Self organisation in a simple task of motor control. In *Proc. Seventh Int. Conf. on Simulation of Adaptive Behavior: from animals to animats* (ed. B. Hallam, J.-A. Meyer, G. Hayes, J. Hallam & D. Floreano), pp. 185–194. Cambridge, MA: MIT Press.
- Linder, C. 2005 Self-organization in a simple task of motor control based on spatial encoding. *Adapt. Behav.* **13**, 189–209.
- Linsenmair, K. E. 1973 Die Windorientierung laufender Insekten. *Fortschr. Zool.* **21**, 59–79.
- Marder, E. & Bucher, D. 2001 Central pattern generators and the control of rhythmic movements. *Curr. Biol.* **11**, R986–R996. (doi:10.1016/S0960-9822(01)00581-4)
- Matheson, T. 1997 Hindleg targeting during scratching in the locust. *J. Exp. Biol.* **200**, 93–100.
- Matheson, T. & Dürr, V. 2003 Load compensation in targeted limb movements of an insect. *J. Exp. Biol.* **206**, 3175–3186. (doi:10.1242/jeb.00534)
- Müller-Wilm, U., Dean, J., Cruse, H., Weidemann, H. J., Eltze, J. & Pfeiffer, F. 1992 Kinematic model of stick insect as an example of a 6-legged walking system. *Adapt. Behav.* **1**, 155–169.
- Noah, J. A., Quimby, L., Frazier, S. F. & Zill, S. N. 2001a Force detection in cockroach walking reconsidered: discharges of proximal tibial campaniform sensilla when body load is altered. *J. Comp. Physiol. A* **187**, 769–784. (doi:10.1007/s00359-001-0247-9)
- Noah, J. A., Quimby, L., Frazier, S. F. & Zill, S. N. 2001b Force detection in cockroach walking reconsidered: discharges of proximal tibial campaniform sensilla when body load is altered. *J. Comp. Physiol. A* **187**, 769–784. (doi:10.1007/s00359-001-0247-9)
- Okada, J. & Toh, Y. 2000 The role of antennal hair plates in object-guided tactile orientation of the cockroach (*Periplaneta americana*). *J. Comp. Physiol. A* **187**, 849–857. (doi:10.1007/s003590000137)
- Pearson, K. G. 1993a Common principles of motor control in vertebrates and invertebrates. *Annu. Rev. Neurosci.* **16**, 265–297. (doi:10.1146/annurev.ne.16.030193.001405)
- Pearson, K. G. 1993b Common principles of motor control in vertebrates and invertebrates. *Annu. Rev. Neurosci.* **16**, 265–297. (doi:10.1146/annurev.ne.16.030193.001405)
- Pearson, K. G. & Wolf, H. 1987 Comparison of motor patterns in the intact and deafferented flight system of the locust. I. Electromyographic analysis. *J. Comp. Physiol. A* **160**, 259–268. (doi:10.1007/BF00609731)
- Pelletier, Y. & McLeod, C. D. 1994 Obstacle perception by insect antennae during terrestrial locomotion. *Physiol. Entomol.* **19**, 360–362.
- Pfeifer, R. & Scheier, C. 2001 *Understanding intelligence*. Cambridge, MA: MIT Press.
- Pfeiffer, F., Weidemann, H. J., Eltze, J. & The, T. U. M. 1994 The TUM walking machine. In *Intelligent automation and soft computing. Trends in research, development and applications*, vol. 2 (ed. M. Jamshidi *et al.*), pp. 167–174. Albuquerque, NM: TSI Press.
- Pfeiffer, F., Eltze, J. & Weidemann, H. J. 1995 Six-legged technical walking considering biological principles. *Robot. Autonom. Syst.* **14**, 223–232. (doi:10.1016/0921-8890(94)00031-V)
- Pick, S. & Strauss, R. 2005 Goal-driven behavioral adaptations in gap-climbing *Drosophila*. *Curr. Biol.* **15**, 1473–1478. (doi:10.1016/j.cub.2005.07.022)
- Prochazka, A., Gillard, D. & Bennett, D. J. 1997a Implications of positive feedback in the control of movement. *J. Neurophysiol.* **77**, 3237–3251.
- Prochazka, A., Gillard, D. & Bennett, D. J. 1997b Positive force feedback control of muscles. *J. Neurophysiol.* **77**, 3226–3236.
- Prochazka, A., Gritsenko, V. & Yakovenko, S. 2002 Sensory control of locomotion: reflexes versus higher-level control. *Adv. Exp. Med. Biol.* **508**, 357–367
- Roggendorf, T. 2005 Comparing different controllers for the coordination of a six-legged walker. *Biol. Cybern.* **92**, 261–274. (doi:10.1007/s00422-005-0546-2)
- Schmitz, J. 1993 Load-compensating reactions in the proximal leg joints of stick insects during standing and walking. *J. Exp. Biol.* **183**, 15–33.

- Schmitz, J. & Haßfeld, G. 1989 The treading-on-tarsus reflex in stick insects: phase-dependence and modifications of the motor output during walking. *J. Exp. Biol.* **143**, 373–388.
- Schmitz, J., Bartling, C., Brunn, D. E., Cruse, H., Dean, J., Kindermann, T., Schumm, M. & Wagner, H. 1995 Adaptive properties of “hard-wired” neuronal systems. *Verh. Dt. Zool. Ges.* **88**, 165–179.
- Schmitz, J., Schumann, K. & Kamp, A. v. 2000 *Mechanisms for self-adaptation of posture and movement to increased load. Abstract viewer/itinerary planner*. Washington, DC: Society for Neuroscience.
- Schmitz, J., Dean, J., Kindermann, T., Schumm, M. & Cruse, H. 2001 A biologically inspired controller for hexapod walking: simple solutions by exploiting physical properties. *Biol. Bull.* **200**, 195–200.
- Schneider, A., Cruse, H. & Schmitz, J. 2005 A biologically inspired active compliant joint using local positive velocity feedback (LPVF). *IEEE Trans. Syst. Man Cybern. Part B Cybern.* **35**, 1120–1130. (doi:10.1109/TSMCB.2005.850147)
- Schneider, A., Cruse, H. & Schmitz, J. 2006 Decentralized control of elastic limbs in closed kinematic chains. *Int. J. Robot. Res.* **25**, 913–930.
- Schumm, M. & Cruse, H. 2006 Control of swing movement: influences of differently shaped substrate. *J. Comp. Physiol. A* **192**, 1147–1164.
- Siegler, M. V. S. & Burrows, M. 1986 Receptive fields of motor neurons underlying local tactile reflexes in the locust. *J. Neurosci.* **6**, 507–513.
- Staudacher, E., Gebhardt, M. J. & Dürr, V. 2005 Antennal movements and mechanoreception: neurobiology of active tactile sensors. *Adv. Insect Physiol.* **32**, 49–205. (doi:10.1016/S0065-2806(05)32002-9)
- Stierle, I. E., Getman, M. & Comer, C. M. 1994 Multisensory control of escape in the cockroach *Periplaneta americana*. I. Initial evidence from patterns of wind-evoked behavior. *J. Comp. Physiol. A* **174**, 1–11. (doi:10.1007/BF00192001)
- Ting, L. H., Blickhan, R. & Full, R. J. 1994 Dynamic and static stability in hexapedal runners. *J. Exp. Biol.* **197**, 251–269.
- Tryba, A. K. & Ritzmann, R. E. 2000 Multi-joint coordination during walking and foothold searching in the blaberus cockroach. I. Kinematics and electromyograms. *J. Neurophysiol.* **83**, 3323–3336.
- Watson, J. T. & Ritzmann, R. E. 1998 Leg kinematics and muscle activity during treadmill running in the cockroach, *Blaberus discoidalis*: I. Slow running. *J. Comp. Physiol. A* **182**, 11–22. (doi:10.1007/s003590050153)
- Wendler, G. 1964 Laufen und Stehen der Stabheuschrecke: Sinnesborsten in den Beingelenken als Glieder von Regelkreisen. *Z. vergl. Physiol.* **48**, 198–250. (doi:10.1007/BF00297860)
- Wilson, D. M. 1966 Insect walking. *Annu. Rev. Entomol.* **11**, 103–122. (doi:10.1146/annurev.en.11.010166.000535)
- Wolf, H. & Pearson, K. G. 1987 Comparison of motor patterns in the intact and deafferented flight system of the locust. *J. Comp. Physiol. A* **160**, 269–279. (doi:10.1007/BF00609732)
- Wolpert, D. M. & Ghahramani, Z. 2000 Computational principles of movement neuroscience. *Nat. Neurosci.* **3**, 1212–1217. (doi:10.1038/81497)
- Yakovenko, S., Gritsenko, V. & Prochazka, A. 2004 Contribution of stretch reflexes to locomotor control: a modeling study. *Biol. Cybern.* **90**, 246–155. (doi:10.1007/s00422-003-0449-z)
- Zill, S., Schmitz, J. & Büschges, A. 2004 Load sensing and control of posture and locomotion. *Arthropod Struct. Dev.* **33**, 273–286. (doi:10.1016/j.asd.2004.05.005)
- Zollkofer, C. P. E. 1994 Stepping patterns in ants I. Influence of speed and curvature. *J. Exp. Biol.* **192**, 95–106.