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Hexapod Walking: an expansion to Walknet dealing with leg amputations and force oscillations

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Abstract The control of the legs of a walking hexapod is a complex problem as the legs have three joints each, resulting in a total of 18 degrees of freedom. We addressed this problem using a decentralized architecture termed Walknet, which consists of peripheral pattern generators being coordinated through influences acting mainly between neighbouring legs. Both, the coordinating influences and the local control modules (each acting only on one leg), are biologically inspired. This investigation shows that it is possible to adapt this approach to account for additional biological data by (1) changing the structure of the selector net in a biological plausible way (including force as an analog variable), (2) introducing a biologically motivated coordination influence for coactivation between legs and (3) adding a hypothetical influence between hind and front legs. This network of controllers has been tested using a dynamic simulation. It is able to describe (a) the behaviour of animals walking with one or two legs being amputated and (b) force oscillations that occur in a specific experimental situation, the standing legs of a walking animal.

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1 Introduction

Analysis of the behaviour of animals may provide information concerning the underlying control system. A critical tool in understanding the function of such a control system is to rebuild it in simulations. The specific behaviour investigated here concerns hexapod walking characterized by the task of controlling 18 joints, i.e., 18 degrees of freedom (three joints in each of the six legs). This is an interesting case study because insects, for example stick insects, are able to adapt their walking behaviour to unnatural or disturbed situations (e.g., amputation of a leg). A system controlling complex behaviour may involve different levels: there is a low-level reactive control resulting in an ordered movement of the joints, but there may as well be a higher or cognitive level in which a representation of the body and its surrounding is established and which can be used to plan further actions.

In our approach we try to develop simple and only reactive models. An important issue of the underlying approach is modularity: a centralized control architecture may be too complex and would demand great computational power which seems to be inappropriate when regarding the insect and its nervous system. Furthermore, modular architectures appear to better compensate disturbances. An earlier model (Dürr et al. 2004) was able to simulate a range of walking behaviours and therefore to give a possible explanation for the generation and control of gaits. The model is built up out of local modules (one pattern generator for each leg) which are driven by sensory signals and which can influence each other. This system, called Walknet, is based on biological findings and will be introduced in Sect. 2.

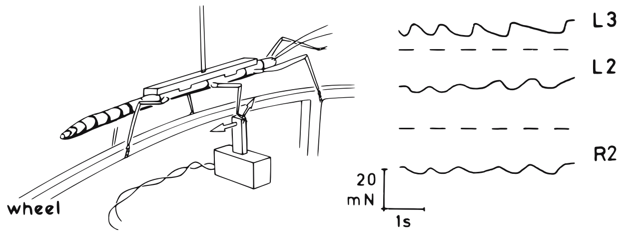


Fig. 1 Experimental setup for the biological experiments (*left*); force oscillations in the standing legs (*right*, both middle legs are standing): upper trace shows the movement of the walking hind left leg (*L3*), other traces show force oscillations in the standing middle legs (*L2, R2*); (figure after Cruse and Saxler 1980b)

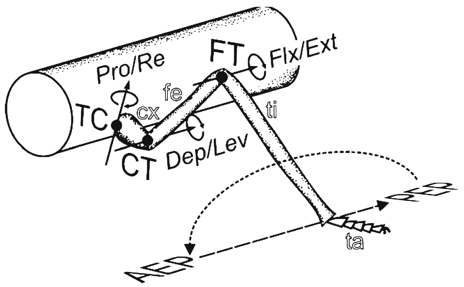


Fig. 2 A schematic drawing of a leg of a stick insect. It consists of four functional segments: coxa (*cx*), femur (*fe*), tibia (*ti*) and tarsus (*ta*). As a simplification the leg can be modeled as a manipulator of three segments connected through hinge joints: the thorax-coxa joint (*TC*, in the figure the axis of the joint is shown; the joint angle is labelled α.), coxa-trochanter joint (CT = β) and femur-tibia joint (FT = γ) (from Dürr et al. 2004)

Two qualitatively quite different results found in biological experiments can however not be entirely simulated by Walknet. First, insects can deal with amputation of one or two legs. Graham investigated (Graham 1977) a variety of different combinations of legs being amputated. For the insect, autotomy of a leg is a natural process and the effect of removing one or two legs seems to be little. The insects only reduce their velocity and the step pattern is adapted to result in a stable gait.

Second, Cruse and Saxler (1980a,b) performed experiments where a stick insect walked on a treadwheel and one or more of the legs were standing on separate platforms equipped with force transducers. Standing on the fixed platform, the leg developed forces that usually oscillated in the rhythm of the other walking legs (see Fig. 1). In experiments with a diversity of configurations of standing legs the coactivation in the neighbouring legs was observed, resulting in an in-phase relation of the force oscillations in the standing legs in most of the cases.

In this paper we want to describe the refinement of Walknet in order to describe these additional biological findings not covered by the earlier version: we introduce the analog-selector which incorporates position and load signals of the controlled leg. It is not a simple state switch as the selector net used in the earlier version, but is providing two analogous motor commands which can be used to drive the intensity of the motor output. In addition, we introduce a new coordinating influence between hind and front legs which depends on the load on the middle leg and implemented a load influence. The model is an extension to the original model (Cruse et al. 1998; Dürr et al. 2004) and can also generate stable gaits even in cluttered environments. We tested our model in two situations to see whether the extended version is sufficient to simulate the behaviour observed in experiments with the insect. To this end, we examined (1) the coactivation of standing legs of a walking animal (2) and tested whether and how the new model can deal with extreme disturbances: the amputation of legs.

The results show that minor changes are sufficient to describe the behaviour of insects observed in quite specific situations.

Being able to explain the reaction to such disturbances is considered a strong support to Walknet, a neural network based hypothesis concerning the control of hexapod walking.

2 The Walknet

The Walknet (Dürr et al. 2004) comprises a neural network which is able to control a six-legged walker. Its function is inspired by data conceived from experiments with stick insects. In this paper only aspects that are relevant in our context will be addressed (for further details see (Dürr et al. 2004), the model is formally defined in the appendix). The Walknet represents an autonomous agent in a virtual environment. It controls the legs of the agent to obtain a walking behaviour. The agent is therefore embodied—it has a body and six legs, each consisting of three main parts (coxa, femur and tibia in Fig. 2) which are coupled through three hinge joints. The morphology of the body and its segments as well as the orientation of the axes of the joints are comparable to those found in the stick insect. Furthermore, the virtual animal is able to act on its environment by controlling the joints and to sense its surrounding through sensors.

A main aspect of the Walknet is its decentralized modular architecture. Each leg has its own controller. The controller can be in one of two states:

- The leg is in protraction (‘swing’): the leg is lifted off the ground and swings from its posterior extreme position (PEP) to the front. During this phase the leg is aiming at the current PEP of the rostral leg to find a secure footstep.

- The leg is retracting (‘stance’): after touching the ground at the anterior extreme position (AEP) the leg is moving backwards with respect to the body—in this way pushing the body to the front and moving the whole animal forward.

The control of the three joints of the leg in either of the two states is accomplished through two separate modules: the swing net and the stance net. The controller determines in which of the two states the leg shall be depending on the current state and the current sensory signals (like position of the leg)—therefore it is called the selector net (Fig. 3). The two modules controlling the leg, the swing-net and the stance-net, are both implemented as neural networks. The swing-net is a simple, one layered neural network generating the trajectories to a target point by exploiting the loop through the world. Control of retraction is more difficult: all standing legs are mechanically coupled through their contact to the ground forming closed kinematic loops. Moving one joint has an effect on all the other joints. To cope with this problem, the different joints are treated differently in the retraction phase: the coxa-trochanter joint (CT, see Fig. 2), which is mainly responsible for holding the body in a specific distance over the ground (Cruse et al. 1989, 1993; Cruse 1976b), is driven through a simple negative feedback controller (as can be found in Diederich et al. 2002): depending on the current angles of the CT and femur-tibia joint (FT) of the leg the feedback controller steers the joint to an angle which results in the specific body height. To control the thorax-coxa joint (TC) and the FT we use a different approach, termed local positive feedback control (Kindermann 2002). This is based on the idea that the additional external force provided by the other legs to a joint is used to control the motor output during the next timestep. This can be thought of as a prediction of the external force during the next timestep. This approach avoids explicit computation of the consequences of moving one joint and afterwards trying to counteract them in another leg. Instead, we use the body as its own model (Brooks 1991).

2.1 The analog-selector

The selector module controls the switch between swing and stance mode and thereby controls the rhythm of a leg. In the earlier version as used in Walknet (Cruse et al. 1998) the selector net was driven by two inputs, a contact sensor that monitors when the leg has ground contact and a sensor that observes whether the leg has reached a given posterior extreme position (PEP) or not. The detailed connections are shown in Fig. 3. This figure also shows that each of the two output units, comprising a Boolean variable and controlling swing or stance, is stabilized by means of a positive feedback loop.

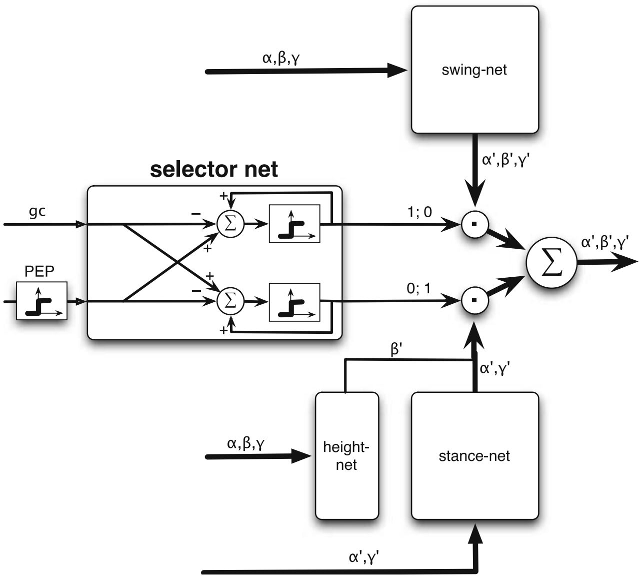


Fig. 3 The earlier Selector acting as a switch as used in the former Walknet

The analog-selector (see Fig. 4) introduced here is a refined version of this original selector module. The following changes are introduced:

- Instead of using a simple contact sensor, (Fig. 3, ground contact, gc) to initiate the transition from swing to stance, the load of the leg is measured (as proposed by Beckers 2002). The essential difference is that load comprises an analogous signal and not a Boolean variable as in the first version.
- To initiate the transition from stance to swing in the earlier version leg position has to reach a given threshold position (PEP). In the new version an analogous value is applied: The difference between the current leg position and the threshold (PEP) is measured and used as a signal to influence the selector net.
- Correspondingly the output variables are no longer Boolean truth values, but are analogous motor commands. The Heaviside characteristics necessary to limit the positive feedback loop have therefore been moved into the feedback loop.
- In the earlier version, the signals from the ground contact sensor and from the PEP sensor were used to turn the output of both the swing net and the stance

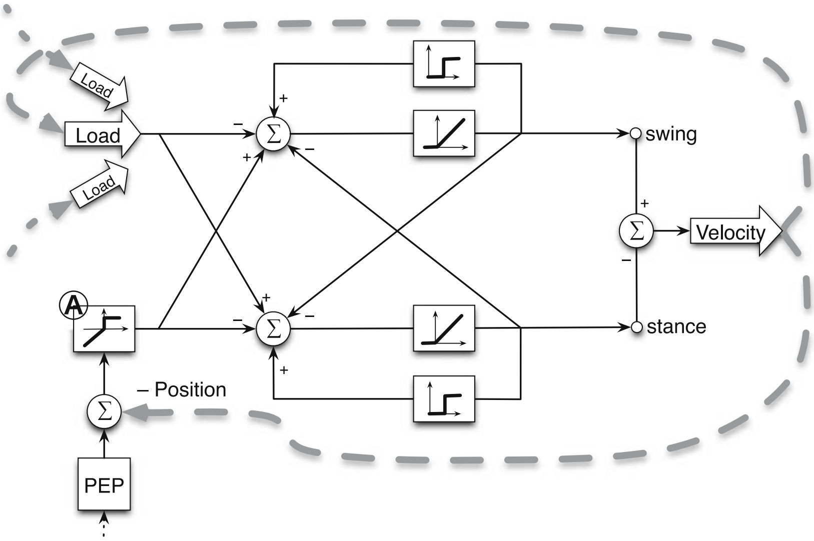


Fig. 4 The wiring of the analog-selector: *upper left* load input; *lower left* position input and PEP which can be influenced through the coordination influences. The two outputs (*right*) represent analogous control signals for the stance or swing movement, stance and swing, respectively

net on or off. Appropriate selection of weights guaranteed that for each moment in time only one of the modes was active. In the analogous version this connectivity was maintained in principle but recurrent inhibitory connections have been added. They form a winner-take-all like network similar to that used to control a pair of antagonistic muscles (to avoid too much cocontraction of the outputs (see Cruse 2002)). In the simulation the outputs are used as a gain for the output values of the swing-net and the stance-net, respectively.

To explain the switching behaviour, a complete cycle from stance to swing and back again shall be described: a standing leg contributes to carrying the weight of the body and to the movement of the body. Putting load on the leg (Fig. 4, upper left, input “Load”) leads to a stance movement: the leg pushes downwards and begins to retract—resulting in the forward movement of the body. At the same time carrying load inhibits the swinging of the leg. But how can the mode change to swing? Moving backward the leg approaches its posterior extreme position (PEP): as long as the leg is in front of the PEP, a small negative value (the difference between PEP and current leg position) is routed to the network (Fig. 4, lower left). But passing the PEP this difference is raised to a fixed positive value (see characteristic Ⓐ in Fig. 4) so that a swing movement will be started. During swing the leg is aiming at its AEP (given through the PEP of the anterior leg). Reaching the AEP, the leg is put on the ground and is therefore loaded. As a consequence the analog-selector changes back to stance.

Introduction of sensors for position and load to the simulation is plausible, because such sensors for position (Bässler 1977) and load [(Zill et al. 2004; Duysens et al. 2000); stick insect: (Cruse 1985a,b); cockroach: (Pearson 1972)] can be found in insects and have been shown to influence the walking behaviour. The incorporation of these sensors into the simulation allows to analyze whether the sensory signals are essential and helpful.

2.2 Coordination influences

To guarantee proper walking, the legs are coordinated. In the Walknet, coordination influences exist which mainly act on the switching from stance to swing by moving the PEP. As a result they prolong or shorten the retraction phase. There is not a preprogrammed phase relation between the legs.

The basic rules are (derived from experiments with the stick insect, see Dürr et al. 2004):

1. From rear to front: if the sender leg is swinging, the receiver leg should not start to swing. This avoids static instability.
2. From rear to front: on touch down of the hind leg, the anterior leg is stimulated to start swinging. This favours temporal coherence.
3. From front to rear: while the anterior leg is approaching its PEP, it is stimulating its posterior neighbour to swing, so when the anterior leg starts to swing, the posterior leg has already finished its swing movement. This is maintaining temporal coherence.
4. Aiming behaviour: the AEP of a leg is determined by the current position of the anterior leg.
5. Propulsive force is distributed on neighbouring legs.
6. Another rule, the treading-on-tarsus reflex will not be considered here (see Schmitz and Haßfeld 1989).

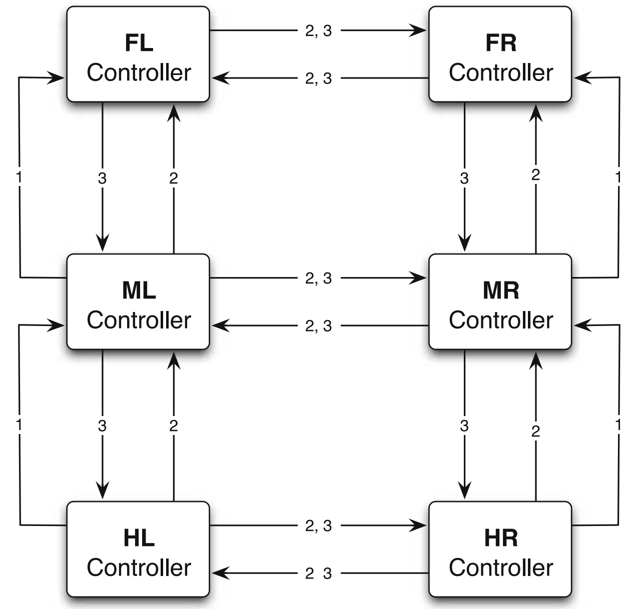


Fig. 5 The coordination rules 1,2 and 3 interconnect the selector nets and regulate their phase relationships through prolonging or shortening the stance phase by relocating the PEP. Legs are abbreviated by F (*front*), M (*middle*), and H (*hind*) as well as L (*left*), and R (*right*)

Rule two, three and five are assumed also to operate between contralateral legs (Fig. 5). In earlier simulations, application of rule 1 to 4 have been tested in detail (Kindermann 2002; review Dürr et al. 2004). The results have shown that these rather simple rules are sufficient to generate a stable walking behaviour: after randomizing the positions of the legs, a simulated animal can nearly immediately (in one or two steps) return to a stable gait.

In the actual study rule 5 has been applied to the model and the effects are analysed and compared to the biological data (see Sect. 5). Rule 5 states that loading of a leg of an insect by an additional weight leads to a specific reaction: after surpassing a certain threshold the leg activates the neighbouring leg and tries to share the additional load on these (Cruse 1985a; Schmitz 1993): a coactivation in the neighbouring legs can be measured.

This coactivation influence is transposed to our model in the following way. In the analog-selector (see Fig. 4, top left) not only the load of the controlled leg influences the analogous output command, but also the load on the neighbouring legs (which, in the animals, may be registered via the campaniform sensilla): when the load on a neighbouring leg exceeds a given threshold, the controlled leg receives a signal that corresponds to the load value. This rule is acting between neighbouring legs (from front to back, from back to front and contralateral). As a consequence the leg is forced to retract stronger (resulting in a higher output value).

Increasing the activation of the stance output makes the latter less sensitive to influences from the PEP input. Thus, this simulation may also account for the result of (Schmitz et al. 1998) who found a coordination influence acting on the timing of the switching behaviour.

Furthermore we analysed the effect of an additional coordination influence between hind and front legs: In the autotomy experiments the insect can adjust to the amputation of a middle leg and adapt stable phase relationships between hind and front leg. To simulate this behaviour, We introduced a coordination influence between hind and front leg (see Fig. 6) and analysed if the introduction of this additional rule leads to more stable gaits and phase relationships compared to the original Walknet: while the hind leg is in swing mode a switch to swing mode in the front leg is inhibited by prolonging retraction of the latter (this coordination influence corresponds to coordination rule 1 described earlier in this section) and is therefore called rule 1HF, as it acts from hind to front leg. This coupling between the two legs should however influence the walking behaviour only if the middle leg on the same side is missing. In an intact animal this influence must be overruled as otherwise front and hind leg could not protract in-phase as they do in a tripod gait. Biological experiments have shown that a normal stepping behaviour can be reestablished again in an animal after amputation of a leg when the remaining part of the amputated leg is supported by a kind of prosthesis which helps to carry some weight of the body (Wendler 1964). Therefore, load appears to play a crucial role in the recognition if a leg is present. We utilized the load input of our selector module to counteract this new coordination influence (see Fig. 6): when the middle leg contributes in carrying load, the rule 1HF is turned down, but in all other cases, i.e., when there is no middle leg or the middle leg is not standing, the rule is effective and inhibits start of protraction in the front leg while the hind leg is protracting.

3 The simulation environment and the simulated insect

For our simulation experiments we use Breve in version 2.3 (Klein 2003). Breve is an integrated environment, built upon OpenGL for the visualization and using the ODE library for the simulation of the dynamics. Simulations are composed in Breve in an object-oriented scripting language called Steve: the main purpose of the Breve environment is the modeling and simulation of decentralized systems and autonomous agents. The scripting language therefore supports setting up such

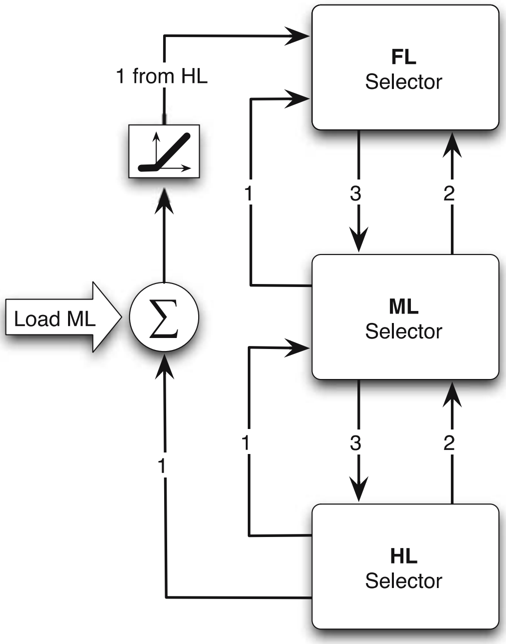


Fig. 6 Coordination influence between hind and front leg (1HF): it has the same effect as rule 1, but is suppressed if the middle leg is loaded

agents on an abstract level and the Breve engine provides the visualization and simulation of effects and behaviour. An agent is assembled through simple geometries which can have physical properties (mass, friction, ...) and are coupled through joints or springs. The physical properties of these can be altered, too (type of joint, working range, axis orientation, elasticity, damping, ...).

The physical properties and dimensions of our model of a six-legged walker with three hinge joints for each leg are derived from the stick insect. The model is building up a kinematic chain, suspended to a simple virtual environment. The tarsi of the stick insect allow the stick insect to hold itself down on the ground and to resist very high (a multiple of its own weight) forces. In the simulation this is recreated through springs attaching the tarsi to the ground when the leg is standing (to avoid high transverse forces these springs need a high damping and their maximum force is restricted). The ability to adhere to the ground is important for the stabilzation of the walking and standing stick insect (see Kindermann 2002, in experiments on slippery surfaces the animal's legs' straddled and the insect fell). Particularly in the amputation experiments this has shown to be significant. The model was tested with different distributions for the center of gravity: on the one hand a uniform distribution was used in which the center of gravity was identical with the geometric centre. In the other case the centre of gravity was shifted backwards as found in the adult stick insect. The two different mass distributions have lead to similar results. Therefore in the following only the results for one mass distribution will be shown: we selected the uniform mass-distribution, which is better suited for comparing and relating the results to work on other insects or robots which usually have a more uniform distribution (in the one case where the results differ this will be explicitly mentioned).

For the generation of the walking behaviour, following the architecture of Walknet we drive the joints by velocities (these come from the stance- or swing-net not explicitly shown in Fig. 4, see Dürr et al. (2004) and Fig. 3). The velocities are desired velocities for the joints. Instead of directly driving the joints with accelerations (which would be possible using the Breve environment), the acceleration that is necessary for a joint to reach the desired velocity is computed by the simulation environment for each time step. The resulting torques and ground contact forces are comparable to those found in a walking animal (Cruse 1976a). To exclude unnaturally high accelerations in the simulation when controlling the joints, an upper limit for the accelerations of the joints was introduced: the produced torques in the joints are therefore kept in a reasonable range: Analysis of the torques showed that the upper limit was never reached during walking. All tests have been performed with this new version of Walknet.

4 Amputation experiments

In a kinematic simulation (Kindermann 2002) the Walknet has shown to be able to generate different walking behaviours. It can account for walking at different velocities and gaits (tetrapod, tripod), for negotiating curves, for climbing obstacles up to the height of the whole animal, and for walking on uneven surfaces or in disturbed situations with a changed body geometry (shortening of a leg) (Kindermann 2002). In the following, using a dynamic simulation, the performance of the simulated insect will also be explored when missing one or more legs.

4.1 Biological experiments and simulation methods

Amputation of a leg appears to be an extreme intervention to an animal. Nevertheless, in the natural habitat of the stick insect we often find insects missing one or even more legs. If necessary, the insect even can detach a leg itself, called autotomy. In experiments with the stick insect *Carausius morosus* Graham (1977) has shown that *Carausius* is still able to adopt a stable walk after loosing one leg: the animal adjusts the phase relationships of the remaining legs and slows down—in most cases (referring to how many and which legs were removed) the animal immediately alters its behaviour and remains stable.

Graham examined the free walking behaviour of first instar nymphs. He recorded their movement and analyzed the videos frame by frame to determine the phase relationships between the legs and their velocities. In undisturbed walking he observed in 95% a tripod gait, i.e., a phase relationship of 0.5 between neighbouring legs. In diverse experiments he removed one or more legs by holding the leg at the mid-point of the femur until autotomy occured. After the amputation of the leg he again recorded the walking behaviour immediately, 5 min later, and two days later. The recordings at different times after the amputation showed no significant changes so learning could be excluded. Graham reported one exception: after the autotomy of one hind leg the contralateral phase relationship between the middle legs changes during the first five minutes. This means that in this case the insect is not at once able to adopt a stable gait. In all other cases the animal instantaneously adapts the phase relationships on both sides. The result is an adjusted walking speed and, as a consequence, a tetrapod gait (phase relationship between ipsilateral legs differs from 0.5).

Grahams' observations and results with the insect will be used as a benchmark for our model and his results for the different leg configurations will be reported in comparison to our results.

The phase relationships observed in the simulations are compared to the experimental data by Graham (Graham 1977) in Table 1. For each examined situation (a–g) the first line denotes the involved legs (examined leg in relationship to reference leg, phase is in [0,1]), followed by results from Grahams biological experiments, and at last phase relationships from the Walknet simulation. The phase relationships (considered leg in relation to reference leg) are specified by three numbers: a mean phase value, a concentration value (as a measure for circular standard deviation; Batschelet 1965) in brackets and the number of steps used for the analysis. In some cases bimodal distributions were observed and the results are shown apart.

In addition to the phase values stability is registered in the simulation and is used in the following way as a measurement for the performance. The stability refers to the degree of variation in body height: when the insects body is nearing the ground (the insect is tumbling) or even touching the ground (the insect crashes down) the insects' gaits will be called unstable. When, however, the walking insect is able to maintain its body position and the body height alters only slightly (and rhythmically), we will speak of a stable gait. As a quantitative measure for stability of the simulated insect we use the height of the coxae of the stick insect for the different walking situations (mean values and standard deviations) as shown in Table 2. The standard deviation represents the amount and strength of up and down movements of the body. A low standard deviation means the body is quite stable. As controls we use the normal walking behaviour of an intact animal (Table 2, tetrapod and tripod; see Figs. 7, 8, 9, 10).

After the amputation of a leg the animal is artificially decelerated: the gain factor representing the velocity of the retraction movement is externally set down to a lower value. In the simulation, the lower velocity for the one leg amputees was set to the value which was used to produce the tetrapod gait in the simulation with all legs intact. The decrease of velocity was observed by Graham in the amputation experiments as well as in other experiments involving disturbed walking. For example, in climbing over gaps a deceleration immediately after the animal stepped with one leg in the gap—i.e. when a leg receives no ground contact—has been observed (Bläsing and Cruse 2004).

In the following sections, some specific examples will be described in detail.

4.2 Single leg pro- and metathoracic amputees

After autotomy of a front leg the insect immediately slows down and alters the phase relationships to a tetrapod pattern (only in a few of Grahams experiments the animals maintained a tripod gait). These results can be recreated through our model: in the simulation the virtual intact animal walks freely and after some time one leg is removed. In Fig. 7a the height of the coxa is shown in different cases. Simulation of a tetrapod gait of the intact animal is shown by dashed lines. After the amputation (solid line) the position is lowered by about 1.3 mm (see Table 2). The simulated animal is walking steadily.

The model's walking velocity is decreased which results in new phase relationships for a stable gait. The phases are changed because lowering the velocity leads to longer duration of the retraction whereas the duration of the protraction remains unchanged. The phase relations found in the simulation between the remaining legs, as can be seen in Table 1c and d, are comparable to a tetrapod gait and therewith to those found by Graham (By externally setting a higher speed the animal can be forced to a tripod gait even with a missing front leg. This means that at some points in time only two legs are standing on the ground. But the animal remains stable in the simulation as has been found in the rare observations

Table 1 Comparison of phase relationships in different walking situations of results obtained from experiments with the stick insect done by Graham (1977) and data from the Walknet simulations: first line denotes the involved legs (examined leg in relationship to reference leg, phase is in [0,1]), followed by results from Grahams' biological experiments, and at last phase relationships from the Walknet simulation

	Phase relationships					
Walking situation	Right phase	*n*	Left phase	*n*	Across phase	*n*
(a) Tripod gait	*HR:MR*		*ML:HL*		*HR:HL*	
Experimental observations	0.52 (0.93)	60	0.48 (0.92)	60	0.51 (0.90)	64
Simulation results	0.54 (0.99)	43	0.46 (0.92)	43	0.49 (0.95)	43
(b) Tetrapod gait	*HR:MR*		*ML:HL*		*HR:HL*	
Experimental observations	0.63 (0.94)	44	0.37 (0.94)	43	0.35	44
					0.65	
Simulation results	0.71 (0.98)	89	0.29 (0.98)	89	0.35 (0.97)	41
					0.63 (0.95)	48
(c) Amputation FL	*HR:MR*		*ML:HL*		*HR:HL*	
Experimental observations	0.63 (0.89)	43	0.39 (0.81)	47	0.63 (0.77)	43
Simulation results	0.66 (0.98)	42	0.34 (0.98)	42	0.54 (0.97)	42
(d) Amputation HL	*MR:FR*		*FL:ML*		*MR:ML*	
Experimental observations	0.63 (0.92)	21	0.32 (0.95)	21	0.23 (0.89)	21
Simulation results	0.63 (0.96)	37	0.31 (0.99)	37	0.22 (0.95)	37
(e) Amputation ML	*HR:MR*		*FL:HL*		*HR:HL*	
Experimental observations	0.60 (0.82)	28	0.37 (0.64)	29	0.31	26
					0.62	26
Simulation results	0.66 (0.98)	33	0.23 (0.63)	33	0.58 (0.94)	33
Without 1hf coordination	0.65 (0.97)	41	0.06 (0.97)	41	0.65 (0.96)	41
(f) Amputation of both front legs	*HR:MR*		*ML:HL*		*HR:HL*	
Experimental observations	0.71 (0.89)	65	0.31 (0.98)	62	0.49 (0.73)	63
					0.65	
Simulation results	0.70 (0.98)	25	0.29 (0.99)	25	0.53 (0.98)	25
(g) Amputation of both middle legs	*HR:MR*		*ML:HL*		*HR:HL*	
Experimental observations	0.78 (0.94)	39	0.25 (0.94)	41	0.50 (0.88)	40
Simulation results	0.74 (0.97)	44	0.27 (0.96)	44	0.52 (0.89)	44

The phase relationships are specified by three numbers: a mean phase value, a concentration value (see Appendix) in brackets and the number of steps used for the analysis. In some cases bimodal distribution were observed and the results are shown apart. In (f) the center of mass is lying between middle and hind legs

of such a behaviour in animals.). The footfall pattern in Fig. 7b shows the adjustment after the amputation. The amputation of the leg results in lowering the height of the coxae in all legs because fewer legs have to carry the weight of the body. But the decrease is very small.

Considering the weight distribution in the stick insect, it is not surprising that the animal can walk with a missing front leg because the front legs are mostly used for searching movements.

Simulation of a missing hind leg showed that the animal can walk in a stable way, too (see Table 2). It adopts adequate phase relationships to compensate for the missing hind leg. Both cases (hind and front leg amputation) differ in the simulations only in the time immediately following the amputation. After a front leg amputation the animal immediately adapts its gait. In the case of a missing hind leg the insect needs a few steps to compensate. As can be seen in Fig. 8, the insect topples and doesn't walk stably in the next 8 to 10 steps. This problem could have been solved if an stronger deceleration had been used. But even without a central influence adapting the velocity, the simulated animal can recover: it stands up and the phase relationships between the legs get tuned just after a few steps.

These results match Grahams' observations: for hind leg amputations he observed significant variations in the phase relationship of the middle legs. These changes could be explained in two ways: on the one hand it can be argued that the insect needs time to adapt to a stable gait. On the other hand removing a hind leg significantly destabilizes the animal. This does not lead to a stable stepping pattern after a short adaptation phase but forces the animal to continuously re-adjust its gait. Both explanations match the results of our simulations: after a hind leg amputation the animal requires a few seconds before adopting a stable gait and the hind leg amputation impairs the stability more than removing a front leg (as can be seen in Fig. 8, the simulated animal

Table 2 Heights of the coxae of the simulated stick insect for different walking situations (mean values ±SD). (For further explanation see text)

	Mean height of coxa (standard deviation) in (mm)					
Gait	FL	ML	HL	FR	MR	HR
Tripod	12.62 (±0.99)	12.32 (±0.56)	12.02 (±0.45)	12.63 (±0.98)	12.33 (±0.55)	12.03 (±0.45)
Tetrapod	12.16 (±0.68)	11.90 (±0.37)	11.63 (±0.33)	12.16 (±0.67)	11.90 (±0.36)	11.64 (±0.34)
Amputation FL	11.27 (±0.96)	11.39 (±0.44)	11.52 (±0.36)	11.30 (±0.91)	11.43 (±0.39)	11.56 (±0.39)
Amputation HL	11.78 (±0.54)	11.51 (±0.34)	11.24 (±0.51)	11.83 (±0.60)	11.56 (±0.37)	11.28 (±0.49)
Amputation ML[a]	10.61 (±1.70)	10.23 (±1.44)	9.85 (±1.31)	10.91 (±1.45)	10.53 (±1.18)	10.15 (±1.06)
Amputation ML	11.12 (±0.79)	11.11(±0.55)	11.09 (±0.60)	11.23 (±0.71)	11.21 (±0.45)	11.20 (±0.54)
Amp. FL & FR[b]	10.98 (±1.01)	11.27 (±0.35)	11.57 (±0.39)	10.95 (±1.07)	11.25 (±0.42)	11.54 (±0.34)
Amp. ML & MR	10.94 (±0.83)	11.10 (±0.45)	11.26 (±0.76)	10.95 (±0.85)	11.11 (±0.47)	11.27 (±0.77)

[a] without additional coordination rule one acting between front and hind leg (rule 1HF), as described in Sect. 4.3

[b] mass distribution shifted backwards resulting in a center of gravity lying between middle and hind legs—in all other cases a uniform mass distribution is used

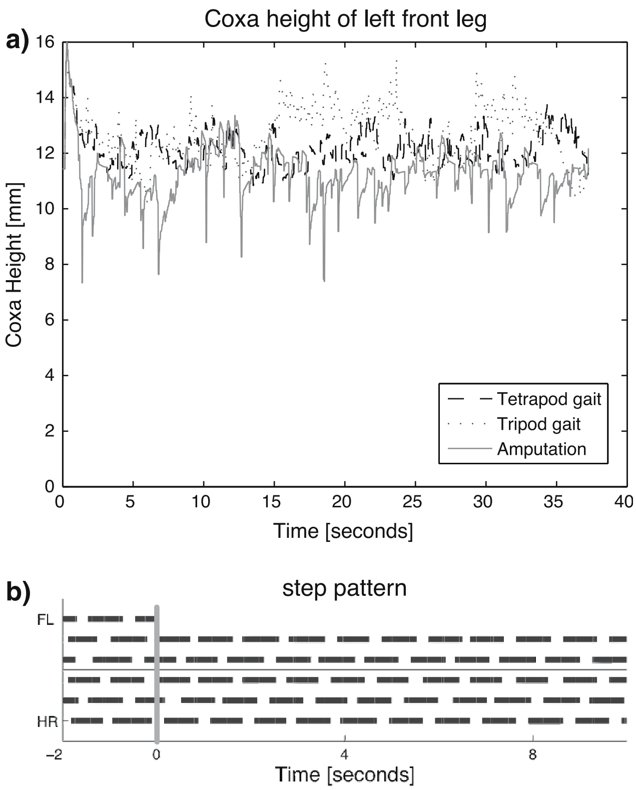


Fig. 7 Simulation results (front left amputation): **a** height of the front left coxa; *dotted line* intact animal, tripod gait; *dashed line* intact animal, tetrapod gait; *continuous line* left front leg amputee. **b** footfall pattern, the stance phases of the legs shown as black bars versus time (0 is time of amputation of the front left leg, marked through the *grey line*); legs shown from top to bottom: left front leg (*FL*), left middle leg, left hind leg, right front leg, right middle leg, right hind leg (*HR*)

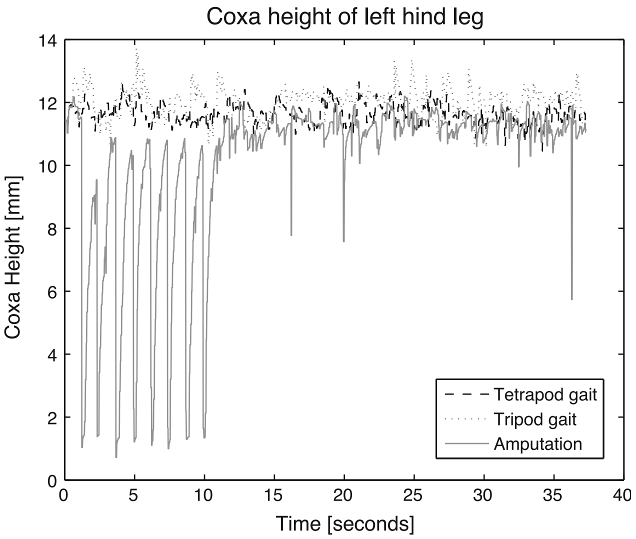


Fig. 8 Simulation results (amputation of left hind leg): height of the hind left coxa; *dotted line* intact animal, tripod gait; *dashed line* intact animal, tetrapod gait; *continuous line* left hind leg amputee. In the hind leg amputee the animal is stumbling the first steps immediately after the amputation—as was reported in the biological experiment. This can be seen in the figure where the body height is significantly dropping during these

stumbled during the next 40 steps twice and as a consequence altered its stepping pattern, not shown). In order to compare the results of the coxa heights we excluded the first twelve seconds in this case and only take the afterwards stable walking animal into account (in all the other cases the adaptation of the phase relationships is included in Table 2).

Delcomyn reported similar adaptations to amputation of a hind leg in slow walking cockroaches (Delcomyn 1991b): EMG recording from free walking cockroaches after a hind leg amputation reveal an adaptation of the activity pattern which he ascribes to the loss of sensory feedback from the amputated leg. He regards these findings as a strong support for the influence of sensory input from the leg on the walking behaviour of slow walking cockroaches, most probably true for insects in general, which is a key assumption for constructing local, peripheral controllers like the ones found in the Walknet.

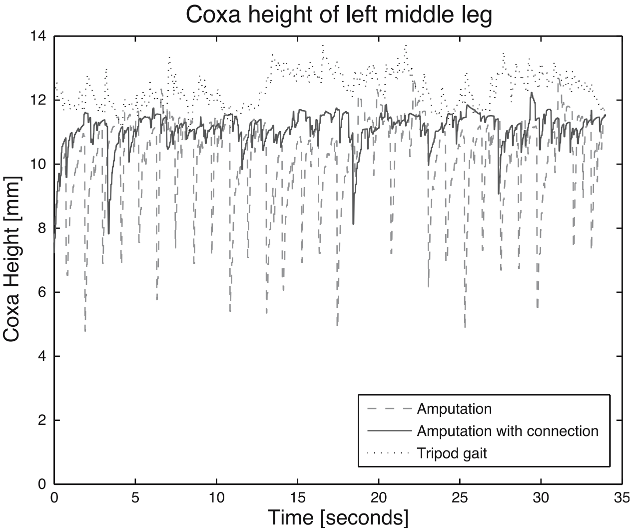


Fig. 9 Simulation results (amputation of middle left leg): height of the middle left coxa (in total about 35 steps are shown); *dotted line* intact animal walking in tripod gait as reference; *dashed line* left middle leg amputee, influence 1HF not active; *continuous line* the same with influence 1HF active

4.3 Removal of a mesothoracic leg

In the biological experiments, the loss of a middle leg causes a phase shift in the relative timing of the ipsilateral front and hind leg. The animal's velocity decreases and as a result the stepping pattern is changed (Graham 1977; Wendler 1964).

The earlier version of the model only produces random phase relationships between front and hind leg on the injured side leading to an unstable gait, incomplete protraction movements and continuously changing phase relations (see Fig. 9, dashed lines).

Therefore, we analysed if the introduction of an additional coordination influence between hind and front leg (influence 1HF) affects the walking behaviour, leading to a stable gait which is comparable to that found in the insect. As explained in Sect. 2.2, the hind leg influences the PEP of the front leg by shifting its PEP backward, when the hind leg is protracting. The introduction of rule 1HF did not change the behaviour of the intact animal in the simulation.

However, when a middle leg has been amputated, a stable gait is also adopted in the simulated animal (see Fig. 9, solid line). The positions of the coxae are slightly lowered and the coxae show only small up and down movements (see Table 2) and comparable phase relationships (Table 1e).

For slow walking cockroaches similar observations had been made by Delcomyn (1991a) who recorded EMGs of cockroaches after amputation of a middle leg and analysed phase relationships between the legs. The insect was surprisingly less impaired by the amputation of a middle leg than by the amputation of a hind leg: Being in a tripod gait pattern, the middle leg is, when in stance, the only supporting leg on that side. Therefore, one would suspect that loss of a middle leg would be a greater mechanical challenge to the insect. In Delcomyns' experiments the insects were not stronger impaired by the loss of a middle leg and the middle leg amputation was handled by the cockroach in a very similar way as a hind leg amputation. An additional influence as the presented rule 1HF might explain this adaptation.

4.4 Amputation of two legs

In his experiments with stick insect which lost two legs, Graham distinguished between the loss of transverse legs (one front and the contralateral hind leg) and all the other cases (namely loss of both front, both middle, both hind legs and one front plus the contralateral middle leg and one middle in addition to the contralateral hind leg). After loosing two legs the animal can not lift more than one leg of the ground at the same time without tumbling. Therefore, the animal has to decrease its velocity to avoid toppling. Again, the slowing down mainly affects the retraction movement.

As an example for a two-leg amputee the amputation of both middle legs will be mentioned (see Fig. 10): without the distant coordination between the hind and front leg (influence 1HF, introduced in Sect. 4.3) the animals' movement is not coordinated (not shown). With the additional coordination rule the animal is able to walk slowly and steadily (Fig. 10). The standard deviation seems to be very high and seems to suggest an instable gait in comparison to a tetrapod gait. But the high standard deviation can be explained by continuous, rhythmical up and down movements which have a low amplitude. The high SD does not result from stumbling or crashing for short moments (A frequency analysis of the up and down movements showed that most of this movement arises from frequencies which are lower then the step frequency. Removing these low frequencies and considering them as necessary due to the changed body geometry would lead to a standard deviation which is only half as high.).

Our model can account for two of the results shown in Grahams' experiments involving the amputation of two legs (see Tables 1f, g, 2). Problems, however, arise in amputations involving the hind legs and in amputations of one front and the contralateral middle leg—the resulting gaits are not very stable and in some of them no

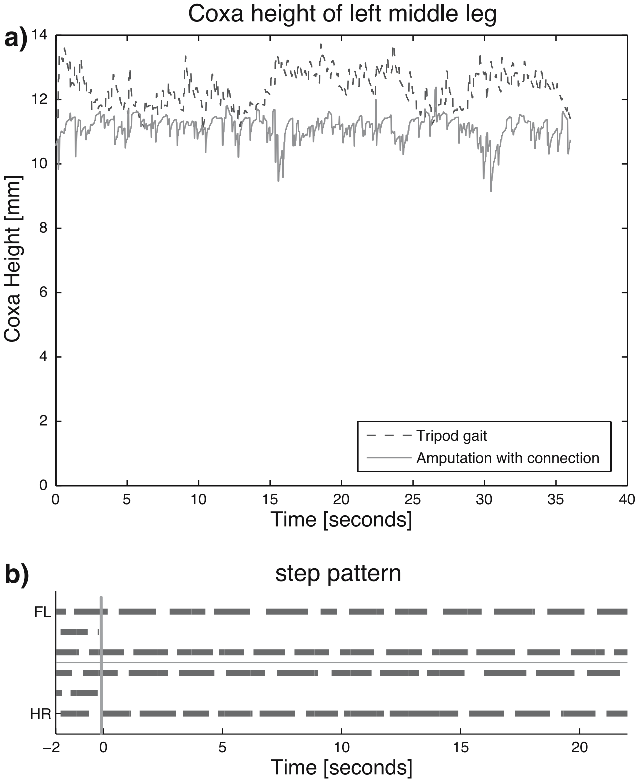


Fig. 10 Simulation results (amputation of both middle legs): **a** height of the middle left coxa; Both middle legs are amputated (*continuous line*); intact animal walking in tripod gait (*dashed line*). Influence 1HF activated in both cases. **b** footfall pattern, the stance phases of the legs shown as *black bars* versus time (0 is time of amputation of the legs, marked by the *vertical grey line*); legs shown from top: left front leg (*FL*), left middle leg, left hind leg, right front leg, right middle leg, right hind leg (*HR*)

constant phase relationships were adapted (these cases and possible solutions will be briefly discussed in Sect. 6).

4.5 Stump movements

Graham (1977) and Wendler (1964, 1966) reported—but only for a few cases—the movement of the middle leg stump: Wendler observed that the intact front leg and the stump of the middle leg start to protract at about the same time. A corresponding result could be found in the simulation.

Similarly, in crustaceans the leg stumps were moving in-phase with the next intact anterior leg (Clarac and Chasserat 1979). Delcomyn observed in EMG recordings of free walking cockroaches similar dependencies: After amputation of a hind or middle leg the movement of the stump seemed to be coupled to the anterior leg (Delcomyn 1991a,b). In the simulation, this results from the fact that the stump of the missing leg just flips very quickly to the front and the anterior leg starts its swing movement (initiated through the distant coordination influence 1HF from hind to front leg): front leg and middle leg stump start to protract nearly at the same time.

4.6 Summary

To summarize: the Walknet model can compensate loss of a single hind leg and amputation of one or both front legs by decelerating. The coordination influences are in this cases sufficient to adopt a stable gait through adapting the phase relationships only between neighbouring legs.

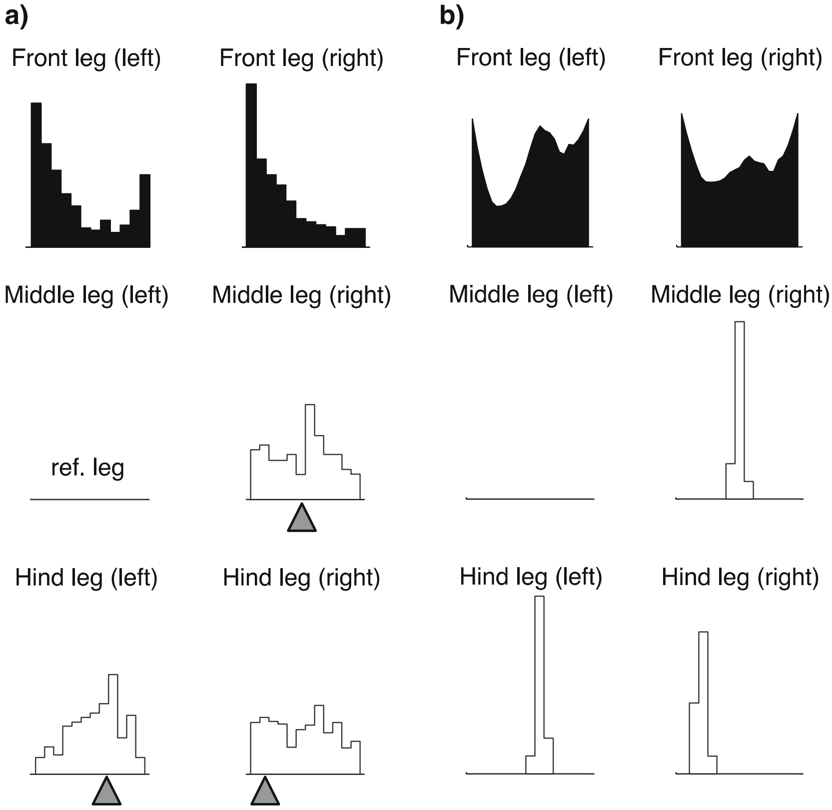
For the autotomy of one or both middle legs the former Walknet was not able to reproduce the performance of the stick insect after loosing a middle leg but produced only degenerated and instable gaits. An additional coordination influence is needed to account for this data: a coordination influence similar to rule 1 was implemented between hind and the ipsilateral front leg (rule 1HF). With this additional influence the Walknet can also account for amputations of the middle legs.

5 Sharing load on neighbouring legs

Cruse and Saxler (1980a,b) analysed forces in standing legs of walking stick insects. The insect walked on a treadwheel while one or more of the legs were standing on separate platforms. The forces of the legs were recorded using force transducers: the standing legs produced oscillating forces in the rhythm of the walking legs (see Fig. 1). Cruse and Saxler analysed this oscillations in a set of experiments with a diversity of configurations of standing legs: a coactivation in neighbouring legs was observed, which results in most cases in an in-phase relation of the force oscillations in the standing legs. In some situations also out-of-phase oscillations or double frequency oscillations have been reported. Such force oscillations have also been found in lobsters (Cruse et al. 1983).

The earlier Walknet could not simulate such a variation of the motor output. As this is possible for the new analog-selector and after the introduction of rule 5, these experimental results provide another benchmark for our model. In short: rule 5 states that loading a leg of an insect by an additional weight leads—when exceeding a certain threshold—to an increased activation in the neighbouring legs (Cruse 1985a; Schmitz 1993) and the neighbouring legs produced higher retraction forces (see coordination rule 5, Sect. 2.2). In extreme cases this influence would force the neighbouring legs to retract in-phase.

Fig. 11 **a** Data from experimental situations (after Cruse and Saxler 1980a,b) and **b** simulation results for both front legs standing. Phase histograms of the beginning of the retraction in the walking legs (*white*), force histograms of the maximum force in the standing legs (*dark*), reference leg (*ML*) starting with the beginning of the retraction movement. *Triangles* below the abscissa of the experimental results denote the mean values of the simulation. For the simulated animal not a force histogram is shown but the progression of the produced forces (smoothed mean values)



A quantitative comparison between model and experimental results appears difficult, because (1) phase relationships depend on walking velocity which has not been provided by Cruse and Saxler and (2) Cruse and Saxler reported the occurrence of force maxima and only in some examples the detailed time course of the force. Still, the following three experiments show the qualitative capability of the model to describe the biological results.

In the first example two front legs are standing whereas the other legs are walking undisturbed (see Fig. 11). In the simulation (Fig. 11b) as in the experimental situation (Fig. 11a) the left middle leg is used as reference. In the simulation, a strong correlation has been found with respect to the walking legs. The force distributions are similar to the distribution of the force maxima found in the biological experiments in which, as to be expected, the data are much more scattered. This leads to a very flat distribution in the right hind leg as this is not directly coupled to the reference leg. The force distributions in the front leg show a strong in-phase correlation ($r = 0.76, P < 0.01$) in the simulation. This result qualitatively agrees well with the biological findings (see Fig. 11a). For the biological data this is shown in a more indirect way, because—as mentioned—only the occurrences of the force maxima have been plotted there. These, however, are in good agreement with the simulated results (see maxima in Fig. 11b, front legs).

In the second example, both front and both middle legs walk, whereas both hind legs stand on fixed force transducers. The phase values of the simulated legs (arrow heads in Fig. 12a, and histograms in 12b) qualitatively agree with the biological data (apart from a somewhat smaller delay between right and left legs). The forces in the hind legs show alternating time courses (correlation $r = -0.63, P < 0.01$). This agrees with the biological findings. However, in the simulation two force maxima in the left hind leg are observed, whereas only one was found in the biological data.

In the simulations the threshold necessary for the coactivation has to assume a higher value for the hind legs compared to the middle and front legs. This appears to be plausible because in the forward walking animal the hind legs have to carry most of the weight, while the front legs are mostly used for searching movements.

Regarding the last case, in which only the two front legs are walking whereas both middle legs and both hind legs are standing (see Fig. 13), an in-phase relation between the forces exerted in the standing legs can be observed while the front legs are alternating. The latter can also be found in the simulation (Fig. 13b). With respect to the four standing legs, the simulations show

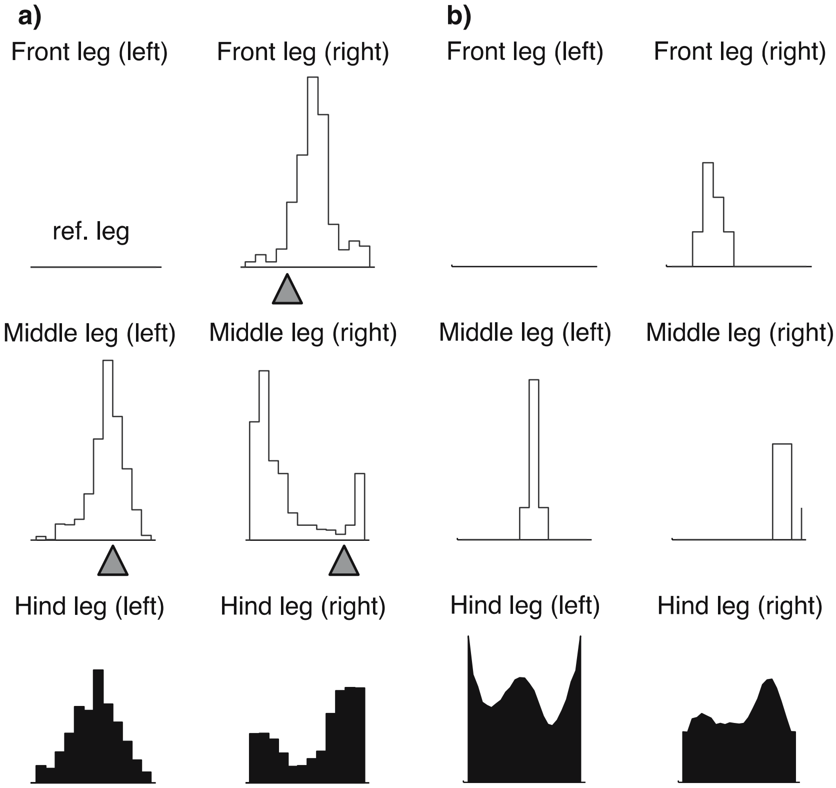


Fig. 12 **a** Data from experimental situations (after Cruse and Saxler 1980a,b) for both hind legs standing. The *grey triangles* represent the mean of the corresponding onset of retraction in the simulation. **b** Simulation results for both hind legs standing. Phase histograms of the beginning of the retraction in the walking legs (*white*), force histograms of the maximum force in the standing legs (*dark*), reference leg (*FL*) starting with the beginning of the retraction movement. For the simulated animal not a force histogram is shown but the progression of the produced forces (smoothed mean values)

a double peak in the time course of the forces which is in phase in all four legs. In the biological data, only one peak is obvious. However, for the left middle leg and the left hind leg the second small peak at phase 0 (or 1) may correspond to the second maxima found in the simulation. Also, Cruse and Saxler reported that they frequently found two distinct force maxima during one phase.

Simulation of the last two examples (Figs. 12, 13) shows that the parameter describing the coactivation threshold, has to be selected from a small range. Using one threshold which can account for all the described cases makes the selection of this threshold sensitive: on the one hand the threshold should be smaller than the acting load in the second case (both hind legs are standing, Fig. 12). On the other hand this threshold should be exceeded when more legs are standing as in the last case (middle and hind legs are standing, Fig. 13). The threshold chosen is only a small amount greater than the load produced in a hind leg with both hind legs standing. The model shows the above explained behaviour for the two standing hind legs: they produce alternating forces. When the middle legs are standing in addition, the middle legs begin to coactivate and try to share the load on the neighbouring legs. As a result the hind legs have to carry additional load from the middle legs, the threshold is exceeded and the hind legs are coactivated, too. The standing legs are steering to an in-phase relation. Once this is adopted the relationships did not change because the sharing of the load on the neighbouring legs between the standing legs gets balanced—we observe an in-phase relationship of the forces in the standing legs (pairwise correlations between the forces in the standing legs are all greater than 0.83, $P < 0.01$) .

The production of the force in the standing legs can qualitatively be reproduced by our model. The results support the existence of a coactivation influence. Other cases observed by Cruse and Saxler are in qualitative agreement with our simulation results (not reported here).

6 Discussion

The simulation of six-legged walking investigated here comprised an extended version of Walknet, a controller that is based on detailed behavioural studies of insect walking. Three expansions are introduced: a new coordination influence acting between hind and front leg (1HF, Fig. 6), an implementation of a coactivation-influence to share load on neighbouring legs, and a new, analogous version of the selector net (Fig. 4). The latter controls (1) whether the leg is in swing mode or stance mode and

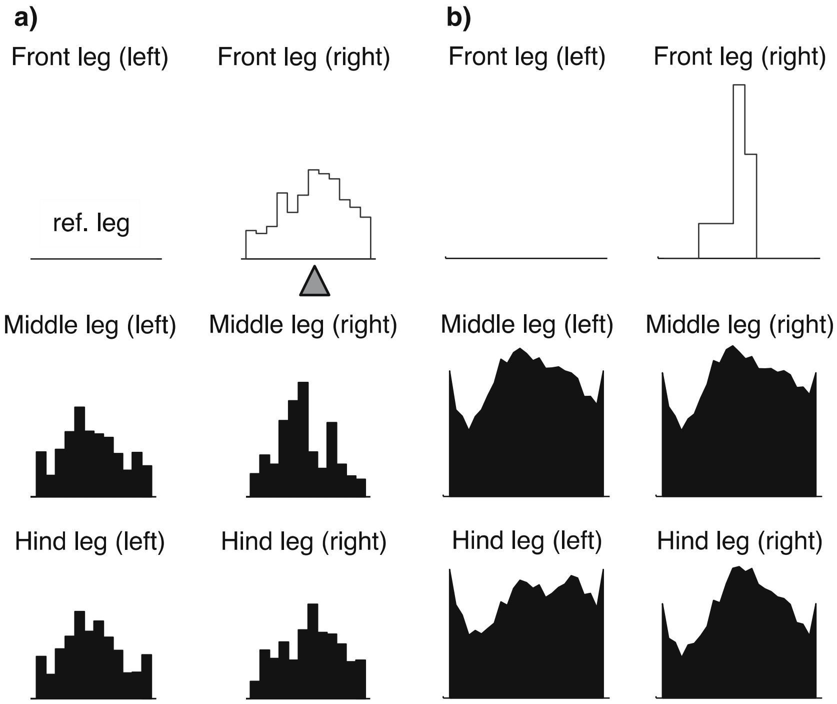


Fig. 13 **a** Data from experimental situations (after Cruse and Saxler 1980a,b) for both middle and hind legs standing. The *grey triangles* represent the mean corresponding onset of retraction in the simulation. **b** Simulation results for both hind and middle legs standing. Phase histograms of the beginning of the retraction in the walking legs (*white*), force histograms of the maximum force in the standing legs (*dark*), reference leg (*FL*) starting with the begin of the retraction movement. For the simulated animal not a force histogram is shown but the progression of the produced forces (smoothed mean values)

(2) provides a gain factor for the motor output in both modes.

This extended Walknet controller drives a simulated body whose dynamic properties are simulated in a virtual environment. With these expansions the controller can cope with a large number of leg amputations. The detailed behaviour is compared with data obtained from biological investigations (Graham 1977; Wendler 1964) and in the shown cases in good match. Comparable phase relationships and a comparable performance was observed—interestingly the results can be compared also qualitatively with respect to how strongly the phase relationships between the different legs are coupled (see Table 1, concentration values, and Table 2 for the performance results).

The introduction of a new coordination influence which suppresses the lift-off of the front leg while the hind leg is in swing mode showed to be sufficient to produce a stable gaiting pattern for the amputation of one or two middle legs and has therefore proven to be a simple and adequate solution.

An influence acting between hind and front legs had already been discussed by Wendler (1968), but in this approach the connection was not suppressed by a load signal of the middle leg: it simply was chosen to be weaker than the corresponding influence between direct neighbours.

Other cases involving amputations of two legs could not be emulated by our model. Especially, cases where one hind leg is missing (the biological experiments for this cases do not show very stable walking behaviour, either). Due to the mass distribution the slow walking animal is falling backwards. To avoid tipping over, greater forces in the front leg would be required pulling the body downwards and an abdomen which can support carrying the weight as known from the animal (Kindermann 2002). Additional coordination influences between non-neighbouring legs seem to be required. Some tests with an additional coordination influence (similar to the 1HF rule) between a hind leg and the contralateral middle leg significantly stabilized the walking animal when amputating a hind leg and lead to a stable gait. Our model can account for all amputations of one leg and the amputation of both middle legs.

The new selector net allows a qualitative explanation of a whole set of experiments which could not be described by the earlier Walknet: when an animal walks while one or more legs stand on a platform fixed relative to the body, the standing legs develop forces depending on the walking rhythm of the other legs. This effect can be reproduced by our simulation.

To achieve a more quantitative description, a coactivation has been introduced which forces neighbouring legs to participate in carrying the weight if a leg is experiencing too much load. Cruse and Saxler (1980a,b) analyzed ten configurations of standing legs in detail. Roughly speaking these could be divided in three groups. Six of their experiments resulted in an in-phase coupling between the standing legs (e.g., both front legs standing), two lead to alternating forces in the standing legs (e.g., both hind legs standing)—in all these the phase relationships between the walking legs were comparable to that in undisturbed walking—and the last two cases were completely uncoordinated (with both middle legs standing there was no coordination between front and hind legs). We tested all these cases and were able to reproduce the biological results qualitatively. We chose three cases which were then examined quantitatively in more detail: on the one side we presented a typical case (Fig. 11), and then the two most critical cases (Figs. 12, 13) with respect to the selection of the threshold in the hind legs (we left out a presentation of an uncoordinated case which would not allow further insights). Using one threshold value in all three cases, the results of our model are in good agreement with the experimental data.

This coactivation rule, based on results of (Cruse 1985a), was called rule 5, but was later renamed 5a, because (Schmitz 1993) observed a backward shift at the PEP of the posterior leg when loading a given leg which itself was called rule 5b. Our simulation appears to cover both effects.

The implementation of the extended Walknet and of the analog-selector on a walking robot is ongoing work. It will be performed in cooperation between biologists and engineers to analyse the transferability of the biological insights and to support these as general applicable and scalable influences for the coordination of leg movements.

This investigation has shown that due to three extensions, namely changing the structure of the selector net in a biologically plausible way (using analog instead of Boolean variables), introducing a biologically motivated coordination influence for the coactivation between legs as well as an hypothetically assumed influence between hind and front legs, it became possible to account for additional biological data through the Walknet model.

Acknowledgments This work has been supported by the EC-IST SPARK project and by the Deutsche Forschungsgemeinschaft (DFG, grant Cr 58/10-1).

Appendix

In the following we will give a formal mathematical description of the walknet controller and describe how the controller calculates the steering signals for the different joints. In our approach not all variables can be computed through a simple mathematical formula. Instead, the inputs for the controller are determined by the loop through the world: These signals are not computed directly, but result from the interaction of the virtual insect with the surrounding environment.

We introduce the different formulas describing the controller in the same order as the simulation computes them:

1. Collect the sensory values (load, joint angles and position).
2. Apply the coordination rules to calculate the current posterior extreme position for each leg and to compute the coactivations between the legs.
3. Evaluate the current state of the selector for each leg.
4. Modulate the joint velocities of the swing- and the stance-net by means of the selector outputs.

Besides the calculation of the current posterior extreme position, which is determined by the coordination influences, the other calculations are equal for all the legs and have to be computed individually for each leg. In the following all these functions will therefore be subscripted throughout the appendix with i ∈ {FL, ML, HL, FR, MR, HR} denoting the leg.

A. Sensory signals

The simulation provides the controller with the sensory signals—they result from the movements of the joints (controlled by the controller) in interaction with the body, with each other and with the environment. Each leg has a position: we define the position in a local frame of reference with respect to the body oriented to the front. The position is one-dimensional and describes the position of the tarsus in the direction of the body long axis. The anterior extreme position defines the origin while the normal posterior extreme position is located at −10.

$$pos_i(t), \quad t \in \mathbb{N}_0 \tag{1}$$

The joint angles (orientation of joint axes as in Fig. 2):

$$\alpha_i(t), \quad \beta_i(t), \quad \gamma_i(t), \quad t \in \mathbb{N}_0 \tag{2}$$

The load acting on the leg is determined through a simulated sensor which mimics the function of the campaniform sensilla in the insect. The sensor is mainly influenced by the torque in the beta-joint. Its values are linearly connected to the torque. The scale of the load is arbitrarily chosen (usually the load of a standing leg has a value of 12–24):

$$load_i(t), \quad t \in \mathbb{N}_0 \tag{3}$$

B. Coordinating influences

The coordination rules influence the current posterior extreme position. The current PEP is used by the selector to decide if the leg shall switch from stance to swing mode. Three influences were used in this implementation and an additional influence had been introduced:

1. From rear to front: if the sender leg is swinging, the receiver leg must not start to swing. In the model the value determining the strength of the swing value in the selector of the posterior leg for the prior timestep pushes the current PEP backwards.
2. From rear to front: at touch down of the hind leg, the anterior leg is stimulated to start swinging: this is implemented by using the stance value of the posterior leg, observing when this position value is rising which is detected by a bandpass filter: when the stance value rises the current PEP is, for a short time, moved more to the front.
3. From front to rear: while the anterior leg is approaching its PEP, it is stimulating its posterior neighbor to swing, so when itself starts to swing, the posterior leg has already finished its swing movement. Rule three uses a threshold function—after the sender leg moves behind a threshold, it increases the current PEP in the receiver leg (moving it to the front):

$$thr_i(pos_i(t)) = \begin{cases} 0 & pos_i(t) > -3.3 \\ -3.3 - pos_i(t) & pos_i(t) \in [-3.3, -5] \\ 1.7 & -5 > pos_i(t) \end{cases} \quad \text{for } t \in \mathbb{N}_0 \qquad (4)$$

Rule two and three are assumed also to operate between contralateral legs (Fig. 5). The new rule 1HF resembles a coordination influence of the first type: the swing value of the hind leg shifts the current PEP backwards. But this influence is modulated by the load signal of the middle leg—the shift of the current PEP is weighted (multiplied) with the load on the ipsilateral middle leg.

The weights used in the simulation for the influences are (in fact, the selection of the weights is not critical):

- For rule 1 $w_1 = -0.2$.
- Rule 2: Between ipsilateral legs, directed to the front $w_{2f} = 0.4$. Between contralateral legs (the influence is known to be weaker): $w_{2c} = 0.2$.
- For rule 3: Between ipsilateral legs, directed to the posterior $w_{3b} = 0.5$. Between contralateral legs (the influence is known to be weaker): $w_{3c} = 0.3$.

Now the current posterior extreme positions can be computed (shown for the left side—the influences are symmetrical and the right side is therefore straightforward. For $t = 0$: $cur\_PEP_i(0) = -10.$):

$$\begin{aligned} cur\_PEP_{FL}(t) = -10 & \\ & + w_1 * swing_{ML}(t-1) \\ & + w_1 * swing_{HL}(t-1) * load_{ML}(t) \\ & - w_{2f} * bp_{ML}(stance_{ML}(t-1)) \\ & - w_{2c} * bp_{FR}(stance_{FR}(t-1)) \\ & - w_{3c} * thr_{FR}(pos_{FR}(t)), \\ cur\_PEP_{ML}(t) = -10 & \\ & + w_1 * swing_{HL}(t-1) \\ & - w_{2f} * bp_{HL}(stance_{HL}(t-1)) \\ & - w_{2c} * bp_{MR}(stance_{MR}(t-1)) \\ & - w_{3b} * thr_{FL}(pos_{FL}(t)) \\ & - w_{3c} * thr_{MR}(pos_{MR}(t)), \\ cur\_PEP_{HL}(t) = -10 & \\ & - w_{2c} * bp_{HR}(stance_{HR}(t-1)) \\ & - w_{3b} * thr_{ML}(pos_{ML}(t)) \\ & - w_{3c} * thr_{HR}(pos_{HR}(t)), \\ & \text{for } t \in \mathbb{N} \end{aligned} \qquad (5)$$

Rule 5 (propulsive force is distributed on neighbouring legs) has been discussed in detail in Sect. 5: It does not influence the current PEP, instead it directly influences the behavior of the analog-selector (see 2.1): in the same way as load on a leg is activating its selector, load from the neighbouring legs coactivates the selector, when the load on the neighbouring leg exceeds a threshold. For the different leg pairs there are different thresholds, when the leg should start to coactivate the neighbouring legs:

- For front legs: $co\_thr_{FL/FR} = 24$.
- For middle legs: $co\_thr_{ML/MR} = 28$.
- For hind legs: $co\_thr_{HL/HR} = 32$.

Using this value the coactivation of the legs can be decided (for $t \in \mathbb{N}_0$):

$$\text{coactivation}_i(\text{load}_i(t)) = \begin{cases} 0 & \text{load}_i(t) < co\_thr_i \\ \text{load}_i(t) & \text{load}_i(t) \geq co\_thr_i \end{cases} \qquad (6)$$

When distributing this coactivation influence to the neighbouring legs this coactivation is weighted by $w_5 = 0.4$.

C. The Analog-selector

The analog-selector controls how strong the leg is in stance and swing mode by computing two variables representing the activation of each mode, relying on sensory signals and the current state (see Sect. 2.1 and Fig. 4).

An important relation is the position of the leg in stance mode in relation to the current PEP which, when reached, triggers the switch to swing mode. This relation is calculated as the difference between current position and calculated current PEP (Eq. 5). When, however, the leg is moving behind its current PEP, the positive value is artificially raised to a constant value. In this way the switch from stance to swing is boosted (for $t \in \mathbb{N}_0$):

$$\Delta pos_i(t) = cur\_PEP_i(t) - pos_i(t)$$
$$pep\_dist_i(pos_i(t)) = \begin{cases} \Delta pos_i(t) & \Delta pos_i(t) < 0 \\ 20 & \Delta pos_i(t) \geq 0 \end{cases} \tag{7}$$

The outputs of the analog-selector can be calculated (integrating equations 3, 6, and 7, for $t \in \mathbb{N}$. For $t = 0$ $stance_i(0)$ and $swing_i(0)$ are both 0.). For the stance mode:

$$\begin{aligned} stance_i(t) = {} & load_i(t) \\ & + \sum_{\text{j neighbour of i}} w_5 * coactivation_j(t) \\ & + stance_i(t-1)/8 \\ & - pep\_dist_i(pos(t)) \\ & - swing_i(t-1)/15 \end{aligned} \tag{8}$$

For the swing mode:

$$\begin{aligned} swing_i(t) = {} & -load_i(t) \\ & + swing_i(t-1) \\ & + pep\_dist_i(pos(t)) \\ & - stance_i(t-1)/3 \end{aligned} \tag{9}$$

D. Motor primitives

The swing and the stance movement are controlled by individual simple perceptron-like networks. The networks compute velocities for the joints which are modulated by the analog-selector.

The stance movement is computed as a constant value controlling the velocity of the alpha-joint, a negative feedback mechanism for the movement of the beta-joint to maintain the height whereas the gamma-joint does not change:

$$stance\_net_i\left(\begin{pmatrix} \alpha_i(t) \\ \beta_i(t) \\ \gamma_i(t) \end{pmatrix}\right) = \begin{pmatrix} -0.12 \\ -0.1 * \beta_i(t) - 0.05\gamma_i(t) \\ 0 \end{pmatrix} \quad \text{for } t \in \mathbb{N}_0 \tag{10}$$

The swing movement is calculated:

$$\begin{aligned} swing\_net_i\left(\begin{pmatrix} \alpha_i(t) \\ \beta_i(t) \\ \gamma_i(t) \end{pmatrix}\right) = {} & \begin{pmatrix} 0.1572 \\ 0.1258 \\ 0 \end{pmatrix} \\ & + \begin{pmatrix} -0.25 & 0 & 0 \\ -0.51 & -0.2 & 0 \\ 0 & 0 & -0.28 \end{pmatrix} \\ & * \begin{pmatrix} \alpha_i(t) \\ \beta_i(t) \\ \gamma_i(t) \end{pmatrix} \\ & \text{for } t \in \mathbb{N}_0 \end{aligned} \tag{11}$$

This corresponds to a simple version where the AEP is fixed and not determined by the target-net.

E. Control of the joints

The joints are controlled using joint velocities. This are calculated by modulating the stance- (Eq. 10) and the swing-network (Eq. 11) through the corresponding analog-selector signals (Eq. 8, respectively, Eq. 9):

$$\begin{aligned} \begin{pmatrix} \dot\alpha_i(t) \\ \dot\beta_i(t) \\ \dot\gamma_i(t) \end{pmatrix} = {} & stance_i(t) * stance\_net_i\left(\begin{pmatrix} \alpha_i(t) \\ \beta_i(t) \\ \gamma_i(t) \end{pmatrix}\right) \\ & + swing_i(t) * swing\_net_i\left(\begin{pmatrix} \alpha_i(t) \\ \beta_i(t) \\ \gamma_i(t) \end{pmatrix}\right) \\ & \text{for } t \in \mathbb{N}_0 \end{aligned} \tag{12}$$

The angular velocities are used to control the joints.

References

Bässler U (1977) Sense organs in the femur of the stick insect and their relevance to the control of position of the femur-tibia-joint. J Comp Physiol A 121:99–113

Batschelet E (1965) Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. A.I.B.S. monograph

Beckers U (2002) Die Kontrolle sechsbeinigen Laufens: Erweiterung des Simulationssystems Walknet zur quantitativen Beschreibung verschiedener biologischer Experimente. Master's thesis, Department of Biological Cybernetics, University of Bielefeld

Bläsing B, Cruse H (2004) Stick insect locomotion in a complex environment: climbing over large gaps. J Exp Biol 207: 1273–1286

Brooks RA (1991) Intelligence without reason. In: Myopoulos J, Reiter R (eds) Proceedings of the 12th international Joint conference on artificial Intelligence (IJCAI-91), p 569–595, Sydney, Australia, Morgan Kaufmann publishers Inc.: San Mateo, CA, USA. ISBN 1-55860-160-0.

Clarac F, Chasserat C (1979) Experimental modification of interlimb coordination during locomotion of a crustacea. Neurosci Lett 12:271–276

Cruse H (2002) The functional sense of central oscillations in walking. Biol Cybernet 86:271–280

Cruse H (1976a) On the function of the legs in the free walking stick insect *Carausius morosus*. J Comp Physiol 112:235–262

Cruse H (1976b) The control of the body position in the stick insect (*Carausius morosus*), when walking over uneven surfaces. Biol Cybernet 24:25–33

Cruse H (1985a) 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 (1985b) Which parameters control the leg movement of a walking insect? I. Velocity control during the stance phase. J Exp Biol 116:343–355

Cruse H, Saxler G (1980a) The coordination of force oscillations and of leg movement in a walking insect (*carausius morosus*). Biol Cybernet 36:165–171

Cruse H, Saxler G (1980b) Oscillations of force in the standing legs of a walking insect (*Carausius morosus*). Biol Cybernet 36:159–163

Cruse H, Clarac F, Chasserat C (1983) The control of walking movements in the leg of the rock lobster. Biol Cybernet 47: 87–94

Cruse H, Riemenschneider D, Stammer W (1989) Control of body position of a stick insect standing on uneven surfaces. Biol Cybernet 61:71–77

Cruse H, Schmitz J, Braun U, Schweins A (1993) Control of body height in a stick insect walking on a tread-wheel. J Exp Biol 181(1):141–155

Cruse H, Kindermann T, Schumm M, Dean J, Schmitz J (1998) Walknet - a biologically inspired network to control six-legged walking. Neural Netw. 11(7-8):1435–1447 ISSN 0893-6080. http://dx.doi.org/10.1016/S0893-6080(98)00067-7.

Delcomyn F (1991a) Perturbation of the motor system in freely walking cockroaches. II. The timing of motor activity in leg muscles after amputation of a middle leg. J Exp Biol 156: 503–517 ISSN 0022-0949 (Print)

Delcomyn F (1991b) Perturbation of the motor system in freely walking cockroaches. I. Rear leg amputation and the timing of motor activity in leg muscles. J Exp Biol 156:483–502 ISSN 0022-0949 (Print)

Diederich B, Schumm M, Cruse H (2002) Stick insects walking along inclined surfaces. Integr Comp Biol 42(1):165–173

Dürr V, Schmitz J, Cruse H (2004) Behaviour-based modelling of hexapod locomotion: Linking biology and technical application. Arthropod Struct Dev 33(3):237–250

Duysens J, Clarac F, Cruse H (2000) Load-regulating mechanisms in gait and posture: comparative aspects. Physiol Rev 80:83–133

Graham D (1977) The effect of amputation and leg restraint on the free walking coordination of the stick insect *Carausius morosus*. J Comp Physiol A 116(1):91–116

Kindermann T (2002) Behavior and adaptability of a six-legged walking system with highly distributed control. Adapt Behav 9(1):16–41

Klein J (2003) breve: a 3D environment for the simulation of decentralized systems and artificial life. In: ICAL 2003: Proceedings of the eighth international conference on Artificial life, pp 329–334, Cambridge, MIT ISBN 0-262-69281-3

Pearson KG (1972) Central programming and reflex control of walking in the cockroach. J Exp Biol 56:173–193

Schmitz J (1993) Load compensatory 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, von Kamp A, Kindermann T, Cruse H (1998) Adaptations to increased load in a control system governing movements of biological and artificial walking machines. In: Blickhan R, Nachtigall W (eds) BIONA reports 13: Motion Systems

Wendler G (1964) Laufen und Stehen der Stabheuschrecke Carausius morosus: Sinnesborstenfelder in den Beingelenken als Glieder von Regelkreisen. Z vergl Physiol 48:198–250

Wendler G (1966) The coordination of walking movements in arthropods. Symp Soc Exp Biol 20:229–259

Wendler G (1968) Ein Analogmodell der Beinbewegungen eines laufenden Insekts. In Kybernetik 1968, Beihefte zu "elektronischen Anlagen", Bd. 18, 68–74. Oldenbourg, München, Wien, 1968

Zill S, Schmitz J, Büschges A (2004) Load sensing and control of posture and locomotion. Arthrop Struct Dev 33:273–286