Full-length review

Pattern generation for stick insect walking movements—multisensory control of a locomotor program

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1. Introduction

The study of the neuronal basis of walking has attracted many investigators. This derives in part from the fact that the results of studies on the generation of walking movements are of general interest for two reasons. (1) In comparison to other rhythmic movements, walking movements must be performed in a very flexible way to adapt to irregularities of the ground. Additionally the temporal and spatial relationships between the different legs and between the different joints of each individual leg change, when the animal changes its walking gait or its movement direction. This implies that the neural system generating the motor output pattern for walking movements must exhibit a marked flexibility. (2) The results on walking pattern generation are relevant to applied sciences. For example, rehabilitation methods (in particular the technology for functional electrical stimulation) [102] or the construction of walking machines (e.g., Refs. [46,99,103]) need a detailed knowledge of mechanisms of the ‘real’ system.
More and more results indicate that the principles of walking-pattern generation seem to be very similar for different, if not all, legged animals (cf. Refs. [94,95]). Therefore, principles found in insects may also be relevant for mammals and man. Since insects are much easier to investigate, the knowledge about walking-pattern generation is more detailed for these animals than for many mammals. This article summarizes the results obtained from investigations on the generation of leg movements during walking in the stick insect, one of the most thoroughly studied examples. It updates previous reviews [5,71].

The stick insect walking system might as well be of general interest for another reason: today, it is generally accepted that all rhythmic movements are generated by central pattern generators (CPGs) whose actions can be modified and adjusted by sensory (peripheral) influences.

The detailed neuronal basis of the interactions of central and peripheral mechanisms are only starting to emerge for most rhythmic movements [94,96]. In the stick insect walking system, peripheral influences have been shown to be very important in sculpturing the motor output towards the functional walking pattern. There are preparational advantages, like the possibility of stimulating sense organs, that enable the investigation of the interactions of central and peripheral mechanisms in this system in an easier way than in other rhythm generators. Up to now most investigations concentrated on this aspect on the operational level. But during the last years, knowledge about the structure and actions of the central neuronal networks emerged as well.

Walking studies on stick insects have a fairly long tradition. Stick insects (phasmids) form a group of approximately 2500 species, including the largest insect species, that provide advantages for the investigation of walking movements due to their long legs. Stick insects are slow climbing animals that are mainly active at night. Their habitat is the crowns of trees and bushes in tropical and subtropical regions. The first paper on the generation of walking movements in stick insects was published in 1921 [21]. Since then most work was done on the stick insect Carausius morosus (Fig. 1), but sometimes also larger species, like Cunuculina impigra were used.

The strategy used in the investigations of walking-pattern generation in stick insects was a top-down analysis. It can be divided into three stages (for details see Ref. [5]): (1) Quantitative description of the behavior; (2) Relating the behavior to systems that are unambiguously defined on the operational level (on the basis of the operations they perform). In other words, one tries to demonstrate that the behavior in question is generated by identifiable subsystems. As an example: the coordinated movements of all legs was related to the action of six single-leg-pattern-generators and coordinating pathways between them (see Section 2); (3) Elucidation of the neural basis of these specified subsystems.

2. Movement of all legs

Initially, the movements of all legs have been described quantitatively on three levels: (1) movement, (2) torques in single joints [39] and (3) the activity of identified motor neurons (summary in Ref. [5]). The results are mentioned here in detail only if they are indispensable for the causal analysis.

According to the strategy used the first question of the analysis was: What is the overall structure of the walking pattern generating system? The answer should relate the movements to certain identifiable systems (stage 2, see Section 1). In most rhythm generating systems, it was the first step of this kind of analysis to relate the movement to

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Fig. 1. The stick insect C. morosus. Body-length (excluding antenna) approximately 7 cm.
central elements (CPGs) and sensory mechanisms (e.g., Ref. [82]). In case of the stick insect walking pattern generation, all investigators first wanted to know whether all legs are controlled by (i) one pattern generator that acts like a ‘master-center’ or (ii) whether each leg is controlled by a separate system which is partially independent from the control systems of other legs? The term ‘pattern generator’ is understood here to encompass all sensory and central nervous structures responsible for generating and timing the motor output. Because it includes all conceivable functional mechanisms, it does not preclude certain of these mechanisms as, e.g., the term CPG would have done. But it needs in a second step a clarification of the mechanisms involved (see Section 3).

This first question was mainly addressed by behavioral studies. First evidences for alternative (ii) came from amputation or lesion experiments (e.g., Refs. [21,70,119,120]). Very clear results on this question derived from a study, in which a stick insect was fastened above a light treadwheel [63]. The wheel consisted of two independent halves which the animal could turn with five of its legs. One leg rested on an additional motor-driven conveyor belt (Fig. 2A). When the animal walked with its five legs on the wheels at a constant velocity, one could make the belt velocity either similar to or faster or slower than the wheel speed. When the belt was moved slower than the wheels, the leg on the belt made fewer steps than the legs on the wheels. When the belt speed was higher than the wheel speed, the leg on the belt took more steps than the legs on the wheels. In all these cases the ‘belt leg’ remained coordinated with the other legs (Fig. 2B). Electrophysiological records showed that the leg on the belt actively walked (Fig. 2C).

From these and similar approaches it became evident that each leg must have its own pattern generator for walking movements. The walking movements of all six legs thus result from the action of six pattern generators of equal importance (each responsible for the movements of a single leg) and coordinating pathways between them (Fig. 3). The very stereotyped leg movements of this animal give the impression of being the result of a unique command structure. However, they are obviously not produced by a hierarchical structure. Furthermore, the fact that the step rhythm of the ‘belt leg’ was influenced by the belt speed shows that a walking-pattern generator for a single leg can be influenced by changing external conditions, i.e., the action of its central elements is influenced by sense organs.

Where is the walking-pattern generator of a particular leg situated? This question was first answered for the forelegs. A stick insect possessing only forelegs can perform walking movements when the prothoracic ganglion (which innervates the forelegs) is either connected to the intact suboesophageal ganglion (the second head-ganglion beside the brain) or to the rest of the thoracic and abdominal nervous system. Apparently the prothorax contains all neuronal and sensory structures sufficient for the generation of walking movements. Subsequent investigations showed that similar conclusions are valid for the other thoracic segments as well, i.e., that each thoracic ganglion contains its own walking pattern generating network [13,6,34].

What kind of walking movement is produced by the pattern generator of a single leg? To tackle this question, all legs except for the two legs of the segment under study were amputated and the animal was then fixed above a treadwheel. Under these conditions forelegs walked only forwards. Hindlegs walked mostly backwards and middle legs walked both forwards and/or backwards. Results of various other experiments as well suggested that the inherent walking direction of the foreleg pattern generator may be forwards and that of the hindleg pattern generator

Fig. 2. A stick insect is fastened above a double treadwheel. The left hindleg is moved by a motor-driven belt. (A) Experimental situation. (B) Movements of the left foreleg (L1), middle leg (L2) and hindleg (L3) when the belt speed is slower than the wheel speed. Up represents forward movement (swing) of each leg. (C) Records from the protractor and retractor coxae motor neurons of the right hindleg (on the slowly moving belt) and from retractor coxae motor neurons of the ipsilateral middle leg (gives the stepping frequency of the legs on the wheel). A bar in the top trace shows the occurrence of the hindleg swing phase [63].
Although this review mainly focuses on the generated patterns of the stick insect, the marked influence of coordinating influences among different legs on the movement of the individual leg needs at least a short introduction to this problem. Further details on this very thoroughly investigated subject can be gathered elsewhere (e.g., Refs. [43,46,71]). During walking, the stick insect is able to perform two different walking gaits, the tetrapod and tripod gait [69], which are very similar to walk and trot in quadruped animals. The coordinating mechanisms between legs were investigated by disturbing the system in different ways during walking (e.g., Fig. 2). Investigations conducted mainly by Don Graham, Holk Cruse and co-workers, revealed that there are at least three different mechanisms that coordinate the movements of neighboring legs during walking. One mechanism, for example, guarantees that when one leg performs a swing phase the next anterior leg cannot start a swing. A second mechanism allows the generation of a swing phase in a leg, when the posterior neighbor starts the stance phase (see Ref. [43] for summary). On the basis of these mechanisms, analogue or computer models for leg coordination that were constructed used the concept of a relaxation oscillator to represent the control mechanisms for an individual leg (e.g., Ref. [44]). With these simulations, the conclusion that the walking system consists of six independent oscillators for each leg with coordinating pathways between them was tested. All these models showed that in fact, the two gaits can be generated by specific interactions between six individual walking-pattern generators (for summary of the different models see Refs. [5,43]). In other words, the temporal sequence of the movements of all legs can be explained by the actions of a distributed command structure consisting of six more or less independent walking-pattern generators and at least three different kinds of coordinating pathways between them (Fig. 3). Based on these findings a very ‘stick-insect-like’ walking machine was constructed [99,100].

3. The general structure of a walking-pattern generator for a single leg

**What are the functions of sense organs and central neuronal elements in the walking-pattern generator of a single leg?** The first step in answering such a question was to denervate the central nervous system and to determine, whether the isolated CNS is able to generate a rhythmic motor output resembling the motor output during walking. In all cases the isolated thoracic CNS was able to generate the rhythmic alternating activity of antagonistic motor neuron pools of each single leg joint with variable burst durations, rapid transitions between the activity of antagonists and a termination of bursts after some time [18] (Fig. 4A). Similar results are also known from the cockroach, e.g., for the activity of the motor neuron pools innervating the coxal muscles (e.g., Ref. [92]). However, in the stick
insect, the deafferented thoracic CNS is not able to generate ongoing motor activity coordinated from cycle to cycle between motor neurons in the different joints of the same leg, or between corresponding motor neurons of other legs [18].

Similar conclusions arose from a pharmacological approach, in which long-lasting rhythmicity in leg motor neuron pools was elicited in single isolated thoracic ganglia or the whole denervated thoracic nerve cord of arthropods in the presence of muscarinic agonists, e.g., oxotremorine or pilocarpine (e.g., crayfish [36,37]; locust [106]; manduca [83]; stick insect [34]). In stick insects the rhythmicity induced in the excitatory motor neurons (insects have also inhibitory motor neurons) is regular and shows a rapidly changing alternation of very low frequency between the activity of antagonistic motor neuron pools of each leg joint (Fig. 4B–C) [34]. Most of the time, the activity in motor neuron pools of different leg joints is not coupled from cycle to cycle (see also below) and may even have different frequencies for individual leg joints (Fig. 4C,D). Corresponding motor neuron pools of adjacent legs tend to be active in phase (Fig. 4B), a coordination that is not present in stick insect walking. However, spontaneous recurrent patterns of coordinated activity (SRP) occur sometimes in the motor neuron pools of the adjacent leg joints [34]. Three different SRPs have been described and each of them shows a fixed coordination of the motor neuron pools of the leg joints in one leg. Their specific coordination resembles the one occurring during step phase transitions in forward and backward walking. For example,
SRP1 reflects the basic motoneuronal activity pattern as occurring during the transition from swing to stance (e.g., Fig. 5C,D) and SRP3 the transition from stance to swing in forward walking. The generation of SRPs can be released by sensory signals, e.g., SRP3 is elicited by flexion signals from the femur–tibia joint, i.e., elongation of the femoral chordotonal organ (see Fig. 8A) [32].

A careful comparison of many parameters of the pilocarpine induced rhythms outside the SRPs (e.g., dependence of burst duration upon cycle period, relative phase of different bursts) with the corresponding parameters during walking did not show similarities to normal walking pattern except the regular alternation between the activity of antagonistic joint motor neuron pools. Apparently, the stick insect thoracic CNS is unable (except for the SRPs) to produce a coordinated motor pattern for several leg joints.

In summary, these results indicate that the basic alternation of activity in the antagonistic motor neuron pools of each leg joint is produced by a central rhythm generator for each joint. One could argue, however, that the CNS would in principle be able to produce a coordinated walking-like motor output for all leg joints, in case the proper modulatory conditions were present. However, this argu-

Fig. 5. (A) Scanning electron microscopic view of the ventral coxal hair plate of the stick insect middle leg (Bar 50 μm; from Ref. [26]). C-coxa; JM-joint membrane; T-thorax. (B) Walking stick insect with manipulated sense organs of the right middle leg. The hair plates at the thoraco–coxal joint (the basal leg joint) were manipulated in a way that they continuously signaled a protracted leg position (see text, from Ref. [4]). (C) Occurrence of spontaneous recurrent patterns (SRP1, indicated by black bars) of motor activity in the motor neuron pools supplying the two proximal leg joints during pilocarpine induced rhythmicity (from Ref. [34]). Pro, protractor coxae; Ret, retractor coxae; Lev, levator trochanteris; Dep, depressor trochanteris. (D) Schematic drawing of motor neuron activity during SRP1 (see text, from Ref. [34]). SDTr, slow depressor trochanteris; FDTi, fast depressor trochanteris; SETi, slow extensor tibiae; FETi, fast extensor tibiae motor neuron.
ment does not interfere with the above conclusion on the existence of individual central rhythm generator for each leg joint (see also [74,87,93]), although it cannot be falsified at present. Furthermore, the above results are in agreement with evidence presented in Section 2. Support comes as well from the fact that in the isolated CNS a central rhythm generator for rocking movements (rhythmic side-to-side movements of the whole leg) can operate functionally producing a well coordinated motor output between the different motor neuron pools and between different legs [18]. Furthermore, in a given pilocarpine-preparation, different types of SRPs are reliably generated that each represent the coordination during either forward or backward walking. All this evidence indicates as well that the walking-pattern generator of a single leg is a modular system, which contains central rhythm generating networks for each leg joint.

What kind of feedback is involved in pattern generation? A step consists of two parts: stance and swing. Stance is the power stroke of the step cycle, swing is the return stroke. In a forward walking animal, stance is the retraction of the leg with the tarsus on ground, and swing is the protraction of the leg through the air. All legs that are in stance at the same time are mechanically coupled via the substrate, and the swing is usually performed with constant velocity in the most often used tetrapod gait [49,71]. Therefore, the main working points for timing influences are the transitions between both phases (e.g., Ref. [42]). We shall first consider the stance–swing transition. This transition is influenced (i) by sense organs measuring position, (ii) by sense organs measuring load and (iii) by coordinating influences from the other legs (see above and Ref. [43]).

First indications about the role of sense organs in the generation of walking derived from the investigation of leg movements in walking animals with surgically manipulated sense organs [2,4,42,119]. Sense organs that measure the position of the thoraco–coxal joint (Fig. 5A, see also Fig. 8A for leg anatomy) were surgically manipulated in such a way that they continuously signalled a protracted leg position regardless of the actual leg position. Such an operated leg moved backwards during stance phase as far as anatomically possible (Fig. 5B). Often, it did not release the ground at the end of stance phase. The leg was pulled off the ground with a distinct jerk by the activity of the other legs. As stick insects grasp the ground during stance phase, this result indicated that stance could not be terminated. Apparently, stance phase is normally terminated only, when the sense organs signal that the normal posterior extreme position (PEP) has been reached. Similar results were obtained by continuously stimulating load measuring sense organs, i.e., the campaniform sensilla on the trochanter [4].

These and other experiments revealed that each of three influences, i.e., (i) position information, (ii) load information and (iii) coordinating signals from the other legs can trigger a stance–swing transition provided the transition is not inhibited by action of the other two kinds of influences. This interaction is also most obvious from a sudden decrease of load triggering a swing with increasing probability the more posterior the leg position is [42]. No evidence was found that the transition from stance to swing is determined by a hierarchical command structure. The influences triggering the stance–swing transition also affect the actual ‘strength’ of the stance phase motor output (detailed discussion in Ref. [7]). This is especially obvious, when one of these influences inhibits the beginning of a swing phase. For example in Fig. 2C, the activity in retractor motor neurons of the ‘belt-leg’ is modulated in the stepping rhythm of the ‘wheel legs’. The same phenomenon is obvious (i) when one leg is placed on a stationary platform outside a walking wheel (like the middle leg in Fig. 6) and no longer walks because the platform is too far anteriorly [47]. The backward directed force exerted on the platform then oscillates in the stepping rhythm of the other legs. (ii) The mean force is much higher in this situation than the force exerted on the ground in free walking. Apparently the higher the load a leg has to overcome the higher the force a leg exerts [42]. (iii) When the platform is moved backwards the force exerted on it decreases. The more normal PEP is approached the smaller is this force [42].

![Fig. 6. Targeting response. The animal walked on a wheel. The right middle leg stood on a stationary platform. The black dots show the position of the middle leg tibia in different experiments, the circles the mean position of the swing phase endpoint of the right hindleg. The leg positions are shown for one experiment (modified from Ref. [40]).](image-url)
Apparently, coordinating influences, position and load information are all superimposed and convey two principal functions: (i) the result of this superposition determines the strength of the motor output during stance, and (ii) when the result of this superposition drops below a certain threshold the pattern generator switches from stance phase motor output to swing phase motor output. This is the property of a relaxation oscillator or a bistable system. These results again indicate that the walking pattern generator contains bistable systems. The occurrence of SRPs in the pilocarpine-preparation supports this idea as it indicates that the coordination of the different leg joints during step-phase transitions are partly centrally pre-programmed (Fig. 5C,D).

In fact, the characteristics of the stance–swing transition share similarities to the actions of a relaxation oscillator as does the generation of the motor output in deafferented preparations (for a further discussion see Section 5). Often the reciprocal inhibition model [77,121] or the half-center model ([19,87]; see also Ref. [97]) are used as a model for a relaxation oscillator, but other models are conceivable, too (e.g., Refs. [41,42]). In the following model (Fig. 9), we consider reciprocal inhibition.

Transition from swing to stance phase. This is more complicated than the transition from stance to swing. First, the control of the leg during the performance of a swing has to be considered. By applying external forces to a leg during swing, it became clear that both velocity and position of movement are controlled. The velocity of the movement is controlled by a servomechanism in a way that the tarsus may reach its target point even if some backward directed force acts on the leg [49]. Position

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**Fig. 7.** One-leg-preparation. The animal possesses either only one foreleg or only one middle leg. Body and coxa of that leg are restrained so that only coxa–trochanter (arrow) and femur–tibia joint (triangle) (both with axes of rotation perpendicular to the drawing plane) as well as the tarsus (dot) can be moved. Due to restraining the leg can only move in the vertical plane. (A) Movement sequence during a downward searching movement. The animal is seen from front. (B) Movement sequence during a stance of walking on a treadband (solid). Dotted: position of the leg after surgically crossing the receptor apodeme of the femoral chordotonal organ (see text; combined from Refs. [84,10]). (C) Motor activity in the muscles and motor neuron pools supplying the coxa–trochanter joint (Lev, levator trochanteris) and the femur–tibia joint (Flex, flexor tibiae; Ext, extensor tibiae) of the stick insect middle leg during a sequence of searching movements. (D) Motor activity in the muscles and motor neuron pools supplying the coxa–trochanter joint (Lev) and the femur–tibia joint (Flex, Ext) during walking. The bottom trace gives the horizontal component of tibial movements monitored by a photodiode attached to the tibia close to its distal end (from Ref. [76]).
information is used to determine the endpoint of leg swing. The mechanism that determines the endpoint of the swing phase is the so-called targeting response [40,51]. Free walking stick insects set the tarsus of a middle or hindleg at the end of swing phase down right behind the tarsus of the ipsilateral anterior neighbor leg (Fig. 6). The adaptive purpose of this response is obvious for a climbing animal. Where the anterior leg has found a solid foothold, the hindleg will most likely also find one just behind [40].

The targeting response depends on sensory signals about the position of the anterior tarsus that is provided by sense organs signalling the position of the thoraco–coxa, the coxa–trochanter and the femur–tibia joints (for anatomy see Fig. 8A). Removal of one or several of these sense organs for example in the middle leg alters the endpoint of the hindleg swing in a predictable way [45,50]. A number of intersegmental interneurons has been identified in the resting, i.e., standing animal that transfer position-information from sense organs in individual leg joints from one leg to the neighbor ganglion [20,27]. As yet, however, no data were presented concerning the question, if and how in the walking animal these and/or other interneurons are involved in this information transfer. More detailed information on the network topology of intersegmental information flow via intersegmental interneurons and their interaction with local, intraganglionic neuronal circuits has been gathered in the locust (for review see Ref. [25]).

Some information on the mechanisms controlling the swing movement and its end (the swing–stance transition) also come from investigating leg movements that are generated, when during swing a leg is unable to overcome an obstructing force (e.g., when it hits a solid obstacle with its tibia). Swing stops, the leg is retracted a bit and moved forward again in a somewhat more elevated position. This can happen several times with a frequency of 3–4 Hz until the obstacle is surmounted [41]. The interjoint coordination during this motor output was investigated in the so-called one-leg-preparation (Fig. 7A,B), in which the animal possesses only one foreleg [84,15,10] or one middle leg [76] that can be moved in the vertical plane only.

In this preparation the leg generates very stereotyped searching movements (Fig. 7A,C) [10] when it does not find contact, and it performs walking movements when a treadboard is placed underneath (Fig. 7B,D) [10]. If an obstacle is introduced into the movement plane of the leg during searching movements, the femur–tibia joint is flexed by a strong activation of the flexor tibiae muscle as soon as the obstacle is touched. At the same time, the tarsus is curled like during grasping the ground. This is irrespective of what part of the leg (femur, tibia or tarsus) touches the obstacle or of whether this happens during an upward or a downward movement. When the leg is removed from the obstacle by this flexor activation (e.g., when the tibia touched the obstacle during an upward movement), flexor activation stops as soon as the contact with the obstacle is lost. In all other instances the flexor activation continues.

As can be shown by ablation experiments this response is mainly triggered by the campaniform sensilla on the trochanter. These campaniform sensilla measure amount and direction of load that is applied to distal parts of the insect leg (e.g., Refs. [79,55,124]).

The obstruction of searching movements during a downward movement simulates some to extend the situation at the end of leg swing and the beginning of stance. As soon as the tarsus hits the ground the flexor creates some force and the tarsus grasps the ground. This increases the load which further increases the stance phase motor output (see above).

4. The detailed structure of a walking-pattern generator for a single leg

Section 3 has shown that every leg joint possesses its own rhythm generating network. One such network seems to be a modular system the central rhythm generating (or bistable units) of which are strongly influenced by sensory information (see also Refs. [10,74]). In this section it will be shown that sensory information is not involved only in the transitions between stance and swing and vice versa, but it also plays a role in coordinating the activities of the different neuronal joint oscillators. The whole picture is summarized in Fig. 9, the details of which are explained in the following.

By ablating, surgically manipulating or artificially stimulating sense organs a variety of sensory influences were described in the one-leg-preparation described before [10]. (i) sensory signals from each sense organ can modulate the activity of motor neurons of several joints and thus contribute to their coordinated activity. (ii) The motor neurons of a particular joint are influenced by several sense organs. This means that the system is highly redundant, and therefore ablation of a particular sense organ has often only a weak or no effect. (iii) Most of these sensory influences work only in the actively moving animal. They are not present or much weaker in inactive, i.e., resting animals. This means that these influences are based on neuronal structures that allow state-dependent alterations in their input–output characteristics. This and the fact, that many of the responses are of a complex structure, i.e., they might reflect the release of certain activity phases of central rhythm generators, suggests that they might be different from simple reflexes. Therefore they are called reflex-like.

Two of these reflex-like influences have already been mentioned above: (1) stimulation of the campaniform sensilla excites flexor and retractor unguis (claw curling) motor neurons and (2) proprioceptors at the thoraco–coxa (basal) leg joint signalling a protracted leg position inhibit releasing the ground by continuously activating the retractor unguis motor neurons. In the following some more examples for reflex-like modules are given.
(3) In the active animal sensory signals from the coxa–trochanter joint, signalling a levation of the trochanter excites the extensor and a signalled depression excites the flexor motor neurons [10]. In the inactive animal, no response in extensor and flexor motor neurons is present to this kind of stimulus [114].

(4) The movement in the coxa–trochanter joint and the femur–tibia joint is strongly affected by surgically altering sensory information provided by the transducer of the femur–tibia joint, i.e., the femoral chordotonal organ [4] (Fig. 8A). Due to the insertion of the receptor apodeme on the tibia, the femoral chordotonal organ is stretched by a flexion of the joint and released by an extension. It is possible to disconnect its receptor apodeme from the tibia and fix it to the tendon of the flexor tibiae muscle (see Fig. 8A, dotted line). After this surgical manipulation (named ‘crossing the receptor apodeme’) the chordotonal organ signals the opposite of the real movement because the receptor apodeme now inserts ventral to the axis of rotation. A leg manipulated in this way is maximally elevated in the coxa–trochanter joint (approximately to a vertical position above the head) during leg swing, with the femur–tibia joint fully extended (Fig. 7B, dotted). At irregular intervals the coxa–trochanter joint is briefly depressed (see also Ref. [72]). Very rarely the tarsus touches the treadband during these depressions. When this happens the tarsus grasps the treadband and a stance phase is performed. In most cases the leg stops moving the band when the femur–tibia joint is rather flexed, but the tarsus does not release the band towards the end of the stance phase, as usual [10].

These experiments show that signals from the femoral chordotonal contribute to interjoint coordination. During leg swing in a surgically manipulated leg, the incorrect chordotonal organ information signalling a flexed femur–tibia joint excites the levator motor neurons, whereas the incorrect information about an extended femur–tibia joint at the end of stance phase inhibits levation and inhibits the cessation of claw curling. The latter is similar to the results of manipulating the coxal hair plates shown in Fig. 5A. This interjoint influence of signals from the femoral chordotonal organ on the activity of motor neurons moving the coxa–trochanter joint can also be demonstrated in restrained active animals (Fig. 8B) [78] and during pilocarpine induced rhythmicity of the otherwise isolated mesothoracic ganglion [32]. At present some of the neuronal pathways contributing to these interjoint influences are known. Pathways from the femoral chordotonal organ to the motor neurons supplying the coxa–trochanter joint are both monosynaptic and polysynaptic, involving intercalated nonspiking interneurons. These interneurons are only partly specific for these pathways, as some of them affect also extensor and flexor motor neurons (see Section 5 and Refs. [30,78]; see also below).

(5) Another example of a reflex-like influence (in this case on motor neurons of the same joint) is the so-called ‘active reaction’ in the femur–tibia joint [3,8]. This motor response is only generated in the active animal. The active reaction represents mainly the reversal of a strong resistance reflex that is generated in the inactive, i.e., resting animal. In the inactive animal, elongation of the femoral chordotonal organ (which signals a flexion movement) strongly excites the motor neurons of the extensor tibiae muscle and inhibits motor neurons of the flexor tibiae muscle (Fig. 10B, first and second elongation stimulus; summary in Refs. [5,11]). In the active animal, however, the same elongation of the femoral chordotonal organ releases the opposite response, i.e., the active reaction (Fig. 8C, Fig. 10B, third stimulus).

The active reaction consists of two parts. (i) The first part is in simplified terms an assistance reflex and reflects a positive feedback (Fig. 8B,C, Fig. 10): elongation of the chordotonal organ, that signals joint flexion excites flexor motor neurons and inhibits the extensor motor neurons. At the same time the retractor unguis muscle (curls the claw) develops force [104]. The active reaction is only generated in a distinct range of rather slow movements at the fCO [8]. In the closed loop system, i.e., when the femoral chordotonal organ is stimulated by the movement of the joint itself, this positive feedback would accelerate any slow flexion movement. On the other hand, fast flexion movements would not be accelerated and would even be slowed down by the excitation of extensor motor neurons occurring in response to fast velocities [8]. Because it is only expressed with relatively slow velocities, the positive feedback during the first part of the active reaction causes a velocity control for flexion movements [8,118]. Simulation studies additionally showed that in walking positive feedback during stance phase of the legs helps to adjust and synchronize the movement parameters of all legs being on ground at the same time. This is important, because relative to the body, the tarsi of all these legs must

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**Fig. 8.** (A) Schematic drawing of a stick insect middle leg showing location and insertion of the femoral chordotonal organ and its receptor apodeme as well as the insertion of the tendons of the flexor and extensor muscles. The dashed part of the receptor apodeme represents the situation after it had been surgically fixed to the flexor tendon (see text). (B) Responses of extensor tibiae (Ext, recorded from nerve F2), levator (recorded from nerve C1) and depressor trochanteris (recorded from nerve C2) motor neurons in the active animal to stimulation of the femoral chordotonal organ. Ramp-and-hold stimuli corresponding to a change in joint angle from 120 to 60° were applied to the receptor apodeme of the femoral chordotonal organ. The arrows mark reflex reversals, i.e., ‘active reactions’ (AR) in extensor motor neurons (see C and text; from Ref. [78]). (C) Motor and muscular activity during the active reaction. Recordings of the activity of the extensor motor neurons (Ext nerve), the force of the flexor tibiae muscle (Flexor force) and the force of the retractor unguis muscle (Ret unguis force) in response to elongation of the femoral chordotonal organ corresponding to a flexion movement of the femur–tibia joint from 140° to 60° (from Ref. [8], modified).
move with the same velocity and parallel to each other [111]. We describe the neural basis of this reflex reversal in Section 5. (ii) When the chordotonal organ signals a fairly flexed joint position (Fig. 8C) the forces of the flexor tibiae and the retractor unguis muscles suddenly decline and the extensor motor neurons are strongly activated [8]. This transition from part 1 (flexor excitation) to part 2 (extensor excitation) is independent of ramp velocity and occurs at a distinct position of the receptor apodeme [8]. This forms a position-dependent endpoint control for flexion movements. The force of the retractor unguis muscle in the foreleg drops at the same time as the flexor force, i.e., the tarsus would release the ground. Therefore the transition from part 1 to part 2 of the active reaction can be considered to contribute to the stance–swing transition during walking.

Simulation studies [14] showed that the position-dependent, rapid transition from the first to the second part of the active reaction can only be adequately modeled, if a bistable system (or a relaxation oscillator) is introduced, e.g., by a mutual inhibition between two neurons (for details see Section 5). The neural network generating the active reaction should therefore contain a neuronal constellation able to function as a bistable system. This bistable system must also receive input from the campaniform sensilla on the trochanter, since electrical stimulation of these sensilla affects the generation of active reactions [8]. It is therefore in accordance with the experimental results when we assume that there is only one bistable system present in the femur–tibia joint. Perhaps it is the same system that is involved in the rapid transitions between flexor and extensor bursts in deafferented preparation. In the model of Fig. 9 we used mutual inhibition, but other mechanisms are conceivable, too.

How can we deduce a consistent model from these results for a detailed structure of a pattern generator? At first we have to take into account that a bistable system as discussed for the active reaction must also be present in the control system of the coxa–trochanter joint (and also in the subcoxal joint) because the motor output to the levator and depressor muscles suddenly switched from levator to depressor activity and vice versa in all cases in the active animal (e.g., Refs. [10, 34]). Since the oscillations of the motor neurons supplying the different joints appear to be independent from each other most of the time in deafferented preparations, there should be different bistable systems or rhythm generating networks for each leg joint. Fig. 9 presents a schematic model that is in agreement with all influences so far described for the forward walking animal. Additionally, a negative feedback loop from movement detectors of the coxa–trochanter joint is drawn to the network generating the motor output of the same joint. This loop stabilizes the body-to-ground distance [48, 119].

The model consists of three central relaxation oscillators (or bistable systems), one for each joint. In the schematic drawing only the two more distal joint oscillators for the coxa–trochanter and femur–tibia joint are shown. This is because most results on sensory influences came from the one-leg-preparation and in this preparation only these two joints can be moved. The three relaxation oscillators are weakly centrally coupled to each other in order to account for the generation of spontaneous recurrent patterns of coordinated activity (SRP) occurring in the pilocarpine preparations [34]. Sense organs are coupled to the oscillators in the ways described above. Due to the schematical presentation of the relaxation oscillators, the sensory influences in Fig. 9 are also schematically drawn in a way as if there were only direct excitatory influences. To generate a motor output the system must be activated by higher centers. To determine the walking direction perhaps also some of its modules and connections have to be tuned.

In this system of coupled oscillators there is no superior system that decides, when stance movement is finished and swing movement begins (or vice versa) and that deter-
mines the set-points of the subordinated servomechanisms. Such a system was originally proposed by Cruse [42] and it is used for the control of a hexapod walking machine [46,99]. In contrast to this theoretical proposal, the experimental results point in the direction that a transition, e.g., from stance to swing phase can be triggered by each of the single-joint oscillators. When one of the single-joint oscillators reaches its threshold it 'relaxes', i.e., it switches to its other state. This influences the other oscillators partly via endogenous pathways (possibly common interneurons in both oscillators, see Section 6) and partly via interjoint reflexes and via campaniform sensilla in a way that they also 'relax'. When, for example, in the one-leg-preparation (Fig. 7B) the tarsus touches the treadband at the end of swing phase, flexor (and retractor unguis) motor neurons are activated. The increased load further activates the flexor and the 'femur–tibia oscillator' switches to flexor activity. The flexion of the femur–tibia joint then activates

Fig. 10. (A) Schematic drawing of the network topology of the neuronal network controlling the extensor portion of the femur–tibia joint (modified from Refs. [11,31]). The numbers (1–5) indicate the different levels of interaction between parallel antagonistic information (see text). SN = sensory neuron, SIN = spiking interneuron, NSI = nonspiking interneuron, MN = motor neuron, CI = common inhibitory motor neuron 1. (B) Transition of the actions in the femur–tibia joint control network from the 'resistance reflex mode' of the inactive stick insect to the 'active reaction mode' of the actively moving stick insect. The changes in network function are expressed by the motor activity of the extensor motor neurons in response to stimulation of the femoral chordotonal organ (fCO) showing either the resistance reflex (RR) to elongation of the chordotonal organ (inactive stick insect) or the active reaction (AR, active stick insect, taken from Ref. [31]).
the levator muscle, etc. When the tarsus does not find contact, the depression of the coxa–trochanter joint activates the flexor and a coordinated searching movement occurs (Fig. 7A). In this modular system none of the single-joint oscillators is superior and none subordinated a priori. For example, a stance phase can either be terminated by a decrease of load or by a flexed femur–tibia joint or by a strongly elevated coxa–trochanter joint. It depends upon the actual situation which is the leading oscillator. This is again an example for a distributed command structure.

The reflex-like influences seem to work in the same way during walking as well as during searching movements. This suggests that the same neuronal network is in charge of generating both movements. Sensory inputs from the periphery are determining what kind of movement is
generated. Thus, the walking- and searching-pattern generator seems to be a modular system composed of endogenous modules, i.e., rhythm generators, each responsible for a single joint and a larger number of reflex-like modules that organize the coupling of these individual leg joint oscillators for a given task.

The model of Fig. 9 describes the current knowledge on the combination of all the modules so far described for the generation of the motor pattern during forward walking and searching of a single leg, especially for the one-leg-preparation. Backward walking was not studied in much detail [73,113]. But in principle this model could also produce a backward walking motor output, when some of its connections are altered. At present, the scheme shown can be taken as being the end of stage 2 of the top–down strategy (see Section 1). We have traced the generation of walking movements back to the action of modules that can be defined on the operational level. The next step was to unravel the neuronal networks and mechanisms underlying the action of the different modules described above.

5. Neural basis of the active reaction

We started the analysis of individual modules of the leg walking system (Fig. 9) with the analysis of the neural basis of the active reaction in the femur–tibia joint. Fig. 10A summarizes our current knowledge on the topology of the neuronal network controlling the tibial extensor motor neurons. By now, the detailed analysis has concentrated on the extensor portion of the femur–tibia joint control system, because the innervation of the flexor tibiae muscle is the extensor portion of the femur–tibia joint control system [80,81]. The information of some 80 of its approximately 500 sensory cells [29] is relevant for the functioning of the femur–tibia control network in the inactive and active animal [86,101]. The afferents influence each other by presynaptic inhibition via intercalated interneurons [108]. (2) Chordotonal organ afferents make either direct excitatory or delayed inhibitory projections (most likely via intercalated interneurons) onto 11 identified non-spiking interneurons (e.g., Fig. 11B) [28,109,110]. In addition they make direct connections with tibial motor neurons (locust [22]; stick insect, D. Hess, unpublished results). (3) The non-spiking interneurons provide excitatory (eight of these neurons) or inhibitory (three of these neurons) synaptic drive onto the excitatory extensor motor neurons, the slow extensor tibiae (SETi) and the fast extensor tibiae (FETi) [28,110]. Interneurons that excite extensor motor neurons are named with the prefix E (E1–E8), interneurons that inhibit extensor motor neurons are termed I (I1, I2, I4).

The second digit gives a specific number for each type of identified neuron. (4) Excitatory (FETi, SETi) and inhibitory (C1i) motor neurons determine the force produced by the muscle fibers of the extensor tibiae muscle [16,17]. (5) Both antagonistic muscles (extensor and flexor tibiae) influence tibial movements by the forces generated [16]. The neuronal network governing the femur–tibia joint thus acts in a distributed manner (see also Ref. [89]). The actual motor output and the joint movements are always the difference between supporting and opposing influences interacting on each of the five different levels. As an anthropomorphic comparison Büssler [11] has called this kind of information processing ‘parliamentary’ due to its analogies with the actions of a governmental parliament.

During active leg movements this neuronal network is involved in generating the active reaction upon chordotonal organ information signalling joint flexion (Fig. 10B, see above). At present, the following alterations in network action (compared to the resting animal) have been de-
present during the active reaction but now much weaker synaptic inputs known from the inactive animal are still resistance reflex. This indicates that the depolarizing with the same latency as the depolarization during a beginning of the active reaction Fig. 11C, arrow. 

ion, thus mediating a disinhibition of extensor motor neuron during resistance reflexes of the inactive animal by interneuron contributes to extensor motor neuron activation change in synaptic inputs of I1 is most obvious from the recording the net-membrane currents in both situations under voltage clamp conditions (Fig. 11D) [59]. All the other non-spiking interneurons of this network also change their responses during an active reaction and all these changes appear to result from a different weighting of excitatory and delayed inhibitory inputs. The detailed mechanisms mediating these changes in weighting of synaptic inputs are not known yet.

There is indication that the active reaction is also generated in a distributed way, thus paralleling results on the generation of the resistance reflex in the inactive animal. Only for 3 out of the 11 identified interneurons (E2, I2, E3; Fig. 11E) the time course in membrane potential closely mirrors the activity of SETi during an active reaction, while the time course in membrane potential of most of the other interneurons does not (e.g., E1, E4, E5, E6, I1, I4). From the latter fraction only E6 performs the transition from the first to the second part of the active reaction but it is not hyperpolarized during the first part (Fig. 11F).

The above conclusions on the role of the premotor interneurons in the generation of the active reaction are supported by simulation studies [14,107]. By introducing the experimentally described responses of nonspiking interneurons into a simulation, the network of Fig. 10A executed an active reaction in extensor motor neurons. Therefore, changes in the responses of the nonspiking interneurons are a sufficient explanation for the switch from the resistance reflex to the active reaction (Fig. 11).

However, the present results do not provide a sufficient explanation for the position dependent transition from part 1 to part 2 of the active reaction. This switch could only be simulated, when (i) position information was weighted considerably higher than in the inactive animal and when (ii) a bistable system (e.g., mutual inhibition like in Fig. 9) was introduced for all those non-spiking interneurons that performed such a transition, i.e., interneurons of type E2, E3, E6, I2. To explain the transition from the first to the second part of the active reaction, three questions have to be answered:

(a) How is the weighting of position information increased in the active animal? There are several candidate mechanisms that could contribute to a change in relative weighting of position- and velocity information in the FT-control network. It is, for example, quite conceivable that presynaptic inhibition of afferents from the femoral chordotonal organ is involved. Presynaptic inhibition of fCO afferents is known to contribute to the tuning of sensorimotor pathways to the movement parameters velocity and position [108].

(b) How is the transition from part 1 to part 2 of the active reaction synchronized in individual premotor neurons? Several nonspiking neurons (E2, E3, E6, I2) perform the transition from part 1 to part 2 of the active reaction (Fig. 11E,F) [59]. Interestingly three of these neurons receive position information in the inactive animal. However, at the moment it remains unknown, how the transition in these interneurons is synchronized.

(c) How is this bistable system realized and is it the same as the central rhythm generator generating the alternating pattern of flexor and extensor activity in the deaf-ferented preparation? At present some information is already available regarding this question. Firstly, the network of Fig. 10A does not contain such a bistable system. But one of its members, interneuron E6, is able to influence the transition from part 1 to part 2 of the active reaction, when it is depolarized by current injection (Fig. 11G). Thus, it is most likely a member of the network.
generating the transition. Then, however, there have to be other additional neurons and/or connections not known yet and not included in Fig. 10A that together generate the transition as a network action.

Secondly, in deafferented isolated thoracic ganglia with pharmacologically-induced rhythmic motor activity, all non-spiking premotor interneurons known from the femur–tibia control network, as well as the majority (70%) of newly identified premotor interneurons driving motor neurons of the coxa–trochanter and/or the thoraco–coxal joints exhibit strong rhythmic oscillations in membrane potential and membrane conductance (Fig. 12A–C) [30]. For some interneurons these changes can be attributed to rhythmic changes in the net-membrane currents initiated by synaptic signals in the interneurons (Fig. 12B). Since there are no sensory influences left these oscillations must originate from central networks within the same ganglion e.g., from relaxation oscillators or bistable systems. Most of the tested neurons were unable to reset one of the rhythms. But individual interneurons could reset rhythmic

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**Fig. 12. Role of local nonspiking interneurons in central rhythm generation as revealed from experiments with pharmacologically induced rhythms in isolated deafferented mesothoracic ganglia.** (A) Oscillations in membrane potential of interneuron E5/6 in parallel with the extensor motor neurons (SETi and FETi), recorded extracellularly in nerve n3. In a deafferented preparation the interneurons type E5 and E6 cannot be distinguished, and were therefore named E5/6. (B) Oscillation in membrane potential is mediated by changes in the net-membrane currents in the interneurons. This is shown in a DCC and SEVC recording from an interneuron of type E5/6. Please note that during rhythmic depolarization in phase with extensor burst a net-inward current is present and during hyperpolarization (pauses of extensor motor neuron activity) a net-outward current is present. (C) Alteration in membrane conductance of nonspiking interneuron NSI2 during rhythmic modulation in membrane potential. Current steps of 2 nA amplitude were injected into the interneuron in DCC mode from different holding currents (+2 nA and 0 nA). During bursts in both depressor motor neurons (SDTr and FDTr) voltage deflections induced by the current steps were markedly decreased. This indicates the influence of an additional conductance during this phase of the cycle. (D) Injecting depolarizing current pulses into interneuron I4 resets rhythmic motor activity of depressor motor neurons. All figures taken from Ref. [30].
motor activity when depolarized by current injection (Fig. 12D) indicating that they are either part of these bistable system or that they at least feedback onto them. Resetting the rhythmic activity means that activity of motor neurons is not only affected during the time the current was injected (as one would expect from a pure premotor neuron) but the stimulus additionally changes the time of occurrence of the following bursts in the rhythm (e.g.,...
the loop from the chordotonal organ to the extensor motor neurons, namely E4 and I4. Current injection into E4 is able to reset the pilocarpine induced rhythms in the extensor as well as in the levator/depressor motor neurons and I4 is able to reset the levator/depressor rhythm (Fig. 12D). Perhaps, interneurons common to two modules are the basis for the weak coupling between motor neuron pools of different joints in the deafferented pilocarpine-treated preparation during the SRPs.

7. Synopsis and test of the experimental strategy

The investigation of the origin of walking movements in the stick insect led first to the result that there are six pattern generators (one for each leg) and that the leg coordination results from the interaction between them (Fig. 3). It was then found that in each of these pattern generators the switch from one phase of the step cycle to the other is determined by several equivalent influences (sense organs of the ‘own’ leg and coordinating influences from other legs). The more detailed investigation of the general structure of the walking pattern generator revealed that it again consists of several modules. The common action of these modules again gives the impression of a unique system but this common action results from the interaction between the modules. The final investigation of the neural basis of one of these modules (the active reaction) again demonstrated a distributed structure of the underlying neuronal network. In such a system, ‘decisions’ (e.g., to switch from stance to swing) cannot be attributed to a certain module; they must be attributed to a certain combination of the action of all modules. The modular nature of walking pattern generation is certainly an important reason for the flexibility of walking movements.

The strategy used enables to incorporate findings on the neuronal level (e.g., measurement of membrane potential and membrane conductance of an identified neuron) into the functional context of the whole pattern generating network. However, such a strategy is affected by two facts that need attention. (1) Most of the conclusions summarized in the preceding paragraphs are only sufficient but not necessary and therefore need further verification. (2) One has to assure that results obtained in a restrained or reduced preparation can be applied to free walking as well. To test whether the top–down analysis led to results that are appropriate for the walking animal, identified premotor

Fig. 13. (A,B) Schematic top view and side view of a stick insect in the semi-intact walking preparation (taken from Ref. [112]). (C) Simultaneous intracellular recording from interneuron E4 in the mesothoracic ganglion and the motor neuron pools supplying the retractro coxae (Ret), the protractor coxae (Pro), as well as the extensor tibiae (Ext) during walking. The phase of the three ipsilateral legs in their walking cycle is given in addition (R1–R3). Please note that injection of pulses of depolarising current (+ DC) is able to stop an ongoing stance phase and induces leg swing. This is obvious from the alteration in motoneuronal activity and leg movement (taken from Ref. [33]). (D) Correlation between motoneuronal activity in protractor coxae and extensor tibiae motor neurons and the actual membrane potential in E4 during walking (taken from Ref. [33]). (E) Recording from a nonspiking interneuron physiologically characterized as I1 in the walking stick insect. Please note that injection of depolarising current pulses into I1 inhibits release of leg swing which is obvious from the activity in the extensor nerve recording (Büschges, Kittmann, Schmitz, unpublished).
interneurons were investigated in almost intact walking animals.

The first intracellular records from central neurons in semi-intact animals walking on a treadwheel were performed by Godden and Graham [66] (see also Fig. 13A,B). One of the questions that should be resolved with this experimental approach on identified interneurons [112,33] was: Is the role of identified non-spiking interneurons congruent to that one would expect from results obtained by the top–down analysis? At present, due to the lack of detailed data for other interneurons the answer to this question is restricted to interneurons of type E4 and I1.

During walking (Fig. 13C,D) the membrane potential of E4 is correlated with the activity of the extensor motor neurons, which receive synaptic drive from this interneuron. No correlation, however, was detected between membrane potential of E4 and other motor neuron pools that receive synaptic drive from E4, e.g., protractor and retractor motor neurons [33]. Interestingly, the maximum depolarization of E4 in the walking cycle is correlated with the switch from retractor to protractor activity. Injection of depolarizing current into E4 stops retractor activity and induces a premature leg swing. Thus, E4 exhibits properties of a neuron that was a member of the protractor–retractor oscillator and a premotor element of the extensor system. This is very similar to its functioning in reduced preparations (see Section 5). Interestingly, particular in case of interneurons of type E4 it could be shown that homologous interneurons in different insect species play a similar role in the generation of leg walking movements [123].

A similar congruence of the results is present for interneurons of type I1. Interneurons I1 do provide inhibitory synaptic drive onto extensor motor neurons, but not to protractor and retractor motor neurons [30]. From its role during the generation of the active reaction one would expect interneuron I1 to show a pronounced depolarization at the transition from extensor to flexor activity [59]. Moreover interneuron I1 should show some negative correlation with extensor activity in the step cycle [31]. Recordings from interneuron I1 in the walking preparation verified these assumptions (Fig. 13E). The membrane potential of interneuron I1 is relatively depolarized during leg stance and relatively hyperpolarized during leg swing, with a sharp depolarization occurring during the transition from extensor to flexor activity, a situation sharing similarities to the time course in membrane potential at the begin of part I of the active reaction. Similar data are reported for potentially homologue interneurons I1 in the locust walking system [123]. Injection of depolarizing current terminates extensor activity, thus verifying the hypothesis on its role in the control of extensor motor activity (Fig. 13E).

In summary, the recordings from interneurons in semi-intact walking animals were found to be in agreement with results and conclusions drawn from more reduced preparations so far used.

8. Discussion

Three aspects arise from the investigations on walking pattern generation in the stick insect that seem to be interesting for studies on this kind of locomotion conducted in other vertebrate and invertebrate systems.

8.1. Distinction between central, peripheral and coordinating influences

Applying the terms generally used for the description of the generation of rhythmic motor patterns we can state: In the stick insect, the motor output driving the muscles of an individual leg during walking is generated by the interaction of (i) central, (ii) peripheral and (iii) coordinating influences. (i) According to these terms central actions would mainly concern the bistable systems (relaxation oscillators) each driving an individual leg joint. (ii) Peripheral actions would appear to have three different functions. They either trigger distinct phases in a bistable system, or they coordinate different oscillators or they modulate the strength of the actual motor output. (iii) Coordinating influences from other legs induce or inhibit phase transitions and/or modulate the strength of the motor output.

Our results demonstrate that these terms are not clear in all cases. At first there is possibly no exact distinction between central and peripheral elements. There is some probability that the same bistable system is involved in the generation of the transition from the first to the second part of the active reaction (a peripheral mechanism according to the generally used definition) as well as in the generation of the flexor–extensor rhythm in deafferented or isolated thoracic ganglia (a central mechanism according to the above definition). The fact that relaxation oscillators or bistable systems may appear, depending on the experimental context, as a central or as a peripheral mechanism was also deduced from theoretical considerations [6]. It is particularly the construction and action of the bistable system, i.e., central rhythm generators, that will need attention in order to better understand the action of the neural machinery generating walking movements of legged organisms.

The delimitation of coordinating influences from influences on the same leg is also not very sound. On one hand coordinating influences on another leg involve not only influences on the timing of that leg, but on the other hand also influences on the walking direction (i.e., influences on the way the different leg joints are coordinated) and influences on the way a step is performed (e.g., targeting response). Whether there are differences to coordinating influences between the different joints of a leg remains open until we know the neural basis of both kinds of influences (see also Ref. [43]).

Results on mechanisms in walking pattern generation in the stick insect accord with findings on other animals on the operational level. These similarities involve the influ-
ence and role of position and load sensitive sensory information on stance–swing transition in cat, crayfish, human and cockroach, active-reaction-like reflex reversals in humans, cat, crayfish and locust (For references see Section 8.3) and the fact that there are partially independent pattern generators for each leg in all investigated mammals, crustaceans and insects (e.g., Refs. [38, 58, 75, 105, 95, 96, 116]).

Differences between the walking pattern generation in different species are present in the completeness in which an isolated CNS is able to generate a relatively ‘normal’ walking motor output (‘fictive locomotion’). They are based on differences in centrally pre-programmed couplings between activities in adjacent leg joints. The one extreme is the mostly independent centrally generated activity in individual leg joints (stick insect [34]), the other extreme is the very rigid coupling between motoneuronal activities in different leg joints that resembles walking so closely (crayfish [36, 37]; locust [106]) that it was called ‘fictive locomotion’. However, also in the latter cases, similarities of the neuronal mechanisms acting have to be shown to be similar to the ones underlying locomotion ‘in vivo’.

The fact that interneurons E4 and I4 are part of several modules indicates that task-specific reorganization of given neuronal elements, that share some of their neurons, contributes to the generation of the motor output during walking. In this case the walking system would show similarities to other pattern generating systems, in which reorganization and reconfiguration takes part in the generation of different motor outputs, e.g., pattern generation in the stomatogastric nervous system of lobster [57], withdrawal and swimming of Tritonia [65, 85] or feeding, regurgitation and rejection in Pleurobranchia [88].

8.2. Generation of reflex reversal by a distributed network

Beside the stick insect walking system (see above) numerous examples of reflex reversals contributing to the generation of walking movements have been added (reviewed in Ref. [95]), for example, in cat [62, 97], human [60], crayfish [56, 115] and the locust [122, 9]. The detailed nature of the neuronal networks responsible remains mostly unknown at present, but besides data from the stick insect, evidence on other systems indicates as well that interneuronal pathways are primarily involved in the generation of reflex reversals: (i) In crustaceans rhythmic presynaptic inhibitory drive, most likely via intercalated interneurons, was recorded in the central terminals of sensory afferents that project onto motor neurons exhibiting reversed reflex actions [61]. (ii) In the cat, interneuronal pathways from group I afferents onto motor neurons mediate the generation of motor activity in the locomotor state in which reflex reversals are exhibited upon sensory stimulation [67, 68].

The current results in the stick insect on the generation of both resistance reflexes in standing and reflex reversals in walking appear to extend the common notion on the generation of reflex reversals. At present it is often reported or inferred that reflex reversals are controlled by the additional opening (or closing) of specific neuronal pathways (e.g., Ref. [67]). In the stick insect, however, evidence suggests that a reflex reversal is rather generated by a change in weighting of antagonistic pathways that are always open (summary in Ref. [31]). This is possible only when the underlying neural network is acting in a distributed or ‘parliamentary’ manner [11], i.e., when it includes not only parallel, but partly antagonistic information processing, with respect to the actual motor output generated.

8.3. Decisions in modular systems

The coordinated movements of all legs during walking as well as the coordinated movements of the joints of a leg give the impression as if they were generated by a strictly determined, hierarchical system. It is perhaps this impression that in former times led to the idea of a single central walking-pattern generator (see also Ref. [54]). The detailed investigation of the structure of the walking pattern generator of the stick insect has revealed that it consists of several modules (see also Ref. [10]), thus paralleling to some extend the ‘unit-burst generator’ concept formulated by Grillner [74]. The common action of these modules supports the impression of one unique system but this common action results from the interaction between the modules. The investigation of the neural basis of one of these modules again demonstrated a distributed interaction of the relevant neurons. Except for an unknown system that has to induce walking, we did not find a hierarchical organization on any level. Instead, we found an interaction between modules of more or less equal importance. The interaction was only partly co-operative, antagonistic interactions also occurred on all levels.

In such a system, a certain decision, i.e., the generation of a specific motor output or movement, cannot be addressed to a unique neuronal structure, it can only be addressed to a certain balance between all instances with influence on this decision. As the same balance may be obtained in different ways, a certain decision (e.g., to switch from stance to swing phase) may result from different combinations of factors. The walking-pattern generator is therefore a typical example for a network with highly distributed information processing.

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