

# The comparative investigation of the stick insect and cockroach models in the study of insect locomotion

Amir Ayali<sup>1,2</sup>, Anke Borgmann<sup>3,7</sup>, Ansgar Büschges<sup>3</sup>, Einat Couzin-Fuchs<sup>1,4,8</sup>, Silvia Daun-Gruhn<sup>3,6</sup> and Philip Holmes<sup>4,5</sup>



Evolution has perfected very different six-legged walking machines from common neural and biomechanical components in an ancestral insect, as exemplified by the American cockroach and the stick insect. Comparative experimental investigations of both intact animals and reduced neural preparations, integrated with mathematical modeling, have been instrumental in advancing our understanding of insect locomotion. Locomotion in stick insects and cockroaches can be described by a related series of mathematical models that describe and quantify the effects of central coupling and feedback, and help explore the role of descending inputs (from higher neuronal centers) and neuromodulation. Insights into sensory-motor interactions and adaptive motor control in insects are useful in designing more responsive, robust, and adaptable bio-robots, which, in turn, can contribute to hypothesis-testing in biology.

## Addresses

<sup>1</sup> Department of Zoology, Tel Aviv University, Tel Aviv 6997801, Israel

<sup>2</sup> Sagol School of Neuroscience, Tel Aviv University, Tel Aviv 6997801, Israel

<sup>3</sup> Zoological Institute, Biocenter Cologne, University of Cologne, Zülpicher Straße 47b, 50674 Cologne, Germany

<sup>4</sup> Department of Mechanical and Aerospace Engineering, Princeton University, Princeton, NJ 08544, USA

<sup>5</sup> Program in Applied and Computational Mathematics and Princeton Neuroscience Institute, Princeton University, Princeton, NJ 08544, USA

<sup>6</sup> Institute for Neuroscience and Medicine, Cognitive Neuroscience, Research Center Juelich, Juelich 52428, Germany

Corresponding author: Ayali, Amir ([ayali@post.tau.ac.il](mailto:ayali@post.tau.ac.il))

<sup>7</sup> Authors appear in alphabetical order.

<sup>8</sup> Current address: Department of Biology, Neurobiology, University of Konstanz, Universitätsstraße 10, 78457 Konstanz, Germany.

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and ecosystems distribution). One reason for this preeminence is their remarkable capacity to rapidly generate adaptable movement in terrestrial, airborne, and aquatic environments. Six-legged locomotion, in particular, is exceptionally effective, having the advantage of static stability during much of walking, and dynamic stability as speed increases [1–3]. To generate different behaviors in changing environments (on both physiological and evolutionary time-scales), insects employ multi-level adaptations in anatomical structures of body, legs and joints, as well as in control mechanisms [4,5]. They can therefore provide invaluable information for understanding adaptive control of animal behavior.

Drawing common neural and biomechanical components from early terrestrial ancestors of insects, evolution has perfected very different walking machines. The American cockroach, *Periplaneta americana*, is adept at rapid running on planar surfaces (the floor of the tropical rainforest or that of your kitchen), regardless of details of the terrain; in contrast, the stick insect, *Carausius morosus*, has adapted for walking in complex, unpredictable environments, with emphasis on precise leg placement rather than speed. Figure 1a presents the rather close phylogenetic relations of these two very different insects.

Our understanding of legged locomotion in general, and specifically in insects, has been greatly facilitated by acknowledging the importance of interactions among neural commands, muscle and body mechanics, and the environment. Employing comparative approaches and combining experiments and theory have been instrumental. As we argue here, this is very well exemplified in studies of stick insects and cockroaches.

## The stick insect model

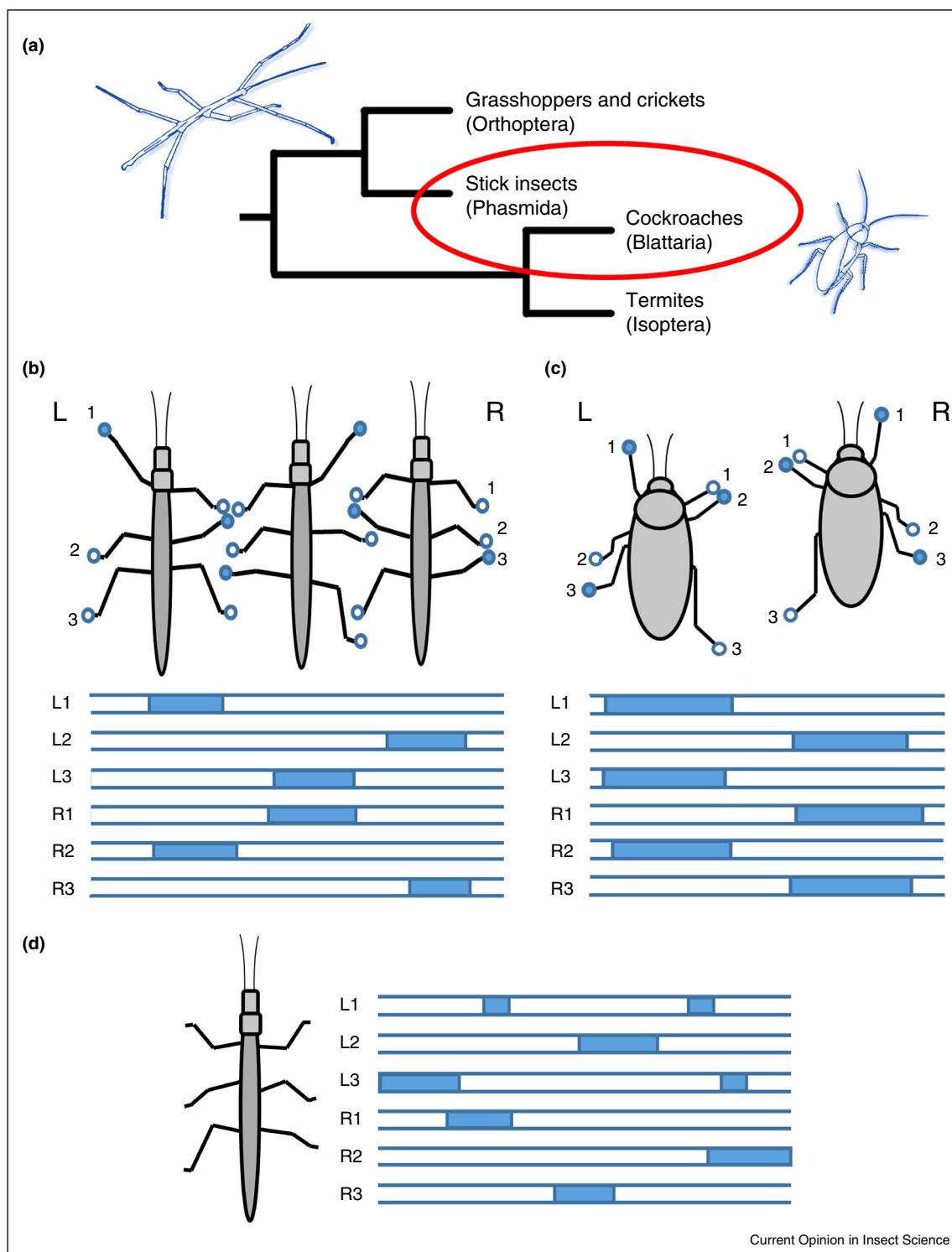
Stick insects are nocturnal animals that inhabit bushes and trees. Their locomotor system is optimized for climbing and propulsion in unpredictable environments, while avoiding predation by means of twig mimesis. Their relatively slow movements, and the easy access to their neuro-muscular machinery for walking, make them ideal for studying the neural basis of motor behavior.

One important characteristic of the stick insect locomotor system is the prominent modular structure of the thoracic neural circuits. Central pattern generators (CPGs), neuronal

## Introduction

Insects are among the most evolutionary successful groups of organisms (in terms of biomass, dispersion

Figure 1



**(a)** A reduced phylogenetic tree demonstrating the close relations between stick insects and cockroaches. **(b)-(d)** Leg coordination patterns. At high speed with little or no load, stick insects usually utilize the *tetrapod* coordination (b). The *tripod* or *double-tripod* gait, predominantly used by cockroaches (c), is seen in larval stages of the stick insect but much less so in adults; adult stick insects also utilize other non-distinct, less regular, coordination patterns (d). Blue bars represent swing phases of the left (L) and right (R) front (1), middle (2) and hind legs (3).

circuits capable of generating rhythmic motor output in the absence of descending or sensory inputs, have been identified for individual joints and legs. Mechano-sensory feedback pathways have been shown to sculpt CPGs output to produce functional stepping (see review [6]). Current knowledge on stick insect motor control is among the most complete in the animal kingdom, spanning the identification of component neurons within CPGs [7] to the biomechanical properties of leg muscles (e.g. [8–10]), and has enabled studies of modifications in sensorimotor processing for motor flexibility [11•,12].

Three different consistent coordination patterns have been described for stick insects walking on level ground. At very low speeds or carrying loads, the legs coordinate in a *metachronal* wave that propagates from back to front on one and then the other body side, leaving five legs on the ground (in stance) at all times. At higher speeds with little or no load, four legs are typically in stance and a diagonally opposite pair in swing in *tetrapod* coordination (Figure 1b). A third coordination pattern, the *tripod* or *double tripod*, with three legs in stance and three in swing (Figure 1c), is observed in larval stages but rarely in adults [4,13•,14]. It should be noted, however, that these three gaits represent ideal forms of coordination; walking animals do not typically produce such distinct gaits, but rather non-discrete, intermediate versions of them ([14]; Figure 1d).

A set of six *coordination rules*, describing inter-leg coordination, have been identified by studying the influence of perturbations of the stepping movements of one leg on itself and on the movements of other legs [13•,15]. This strongly suggests that sensory feedback is required to create proper inter-leg coordination [13•], a notion supported by recent studies, e.g. on the influence of front-leg sensory feedback on motor activity in adjacent caudal segments (e.g. [16,17]). Experiments on *in vitro* thoracic preparations, isolated from all descending and sensory inputs, generating fictive locomotion (i.e. rhythmic motor output resembling that recorded during normal intact walking), indicate that no strong central couplings exist among the segmental networks that generate rhythmic motor activity in the stick insect [18]. Hence, it can be concluded that the control of stick insect locomotion is largely based on a feedback control scheme.

### The cockroach model

Renowned for their fast and stable locomotion, cockroaches are important in the study of all aspects of legged locomotion: performance, maneuverability and dynamic stability (e.g. [19,20]), neural control (e.g. [21–23]), and biomechanics (e.g. [3,24–26]). Work has focused to date mainly on the American cockroach (*P. americana*) and on the slower-walking discoid cockroaches (*Blaberus discoidalis*), which offer larger size and durability.

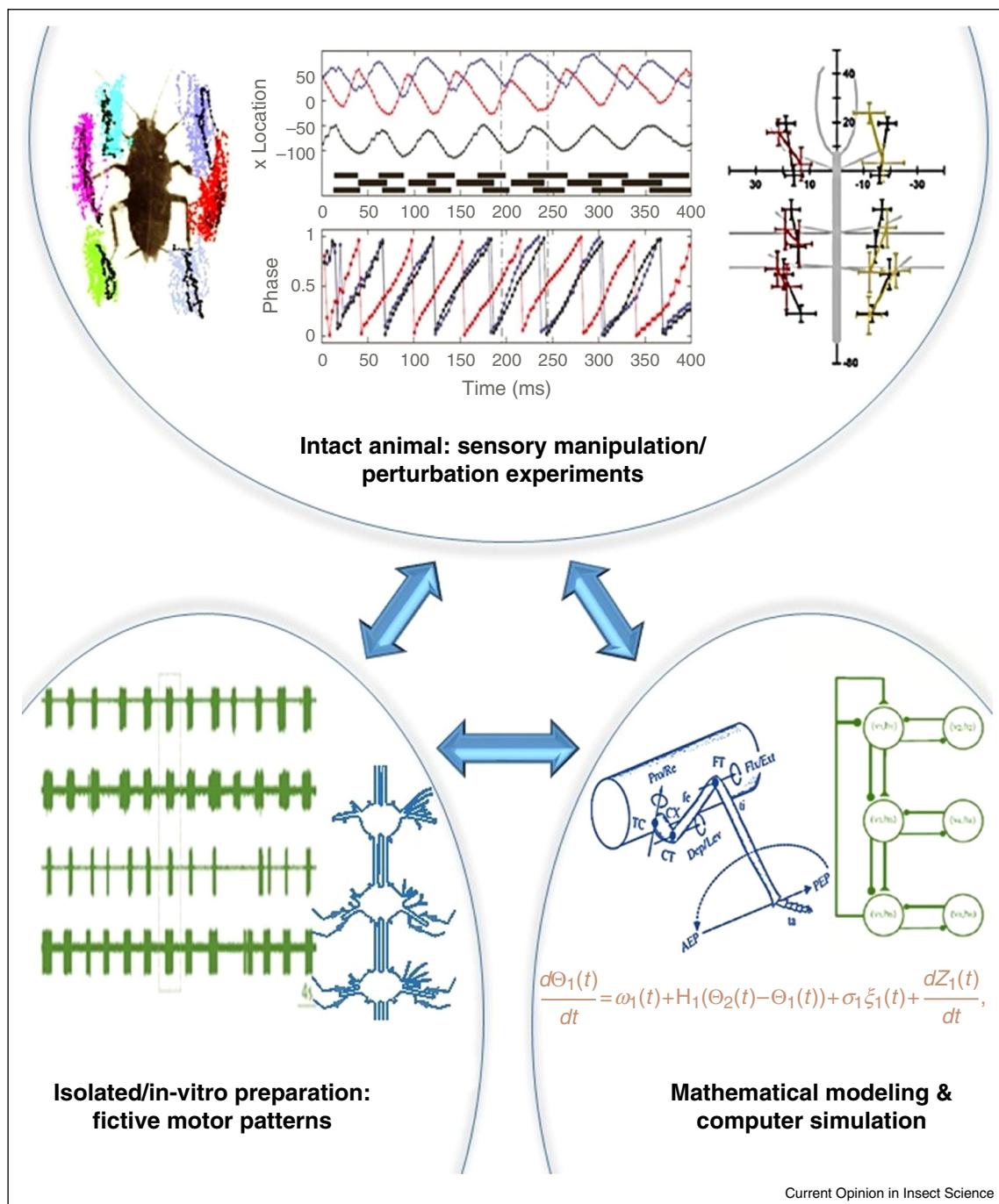
Stability in cockroach locomotion is partly due to the use of the double-tripod gait over most of the insect's speed range, from 2 cm/s to 1.5 m/s (for *P. americana*), Figure 1c [1,27]. Cockroaches also have the ability to sustain speed and gait patterns while seemingly ignoring features of the terrain and minor obstacles [28,29]. Furthermore, a coordinated fictive walking gait with consistent double-tripod-like phase relationships can be generated by the thoracic ganglia of the cockroach without sensory feedback from leg proprioceptors (e.g. [23]). These findings have led to a general view that inter-limb coordination in the cockroach is based primarily on feed-forward motor control [21]. As discussed below, this view has also prevailed in modeling cockroach locomotion [30,31].

However, as recently reviewed by Ayali *et al.* [32], sensory feedback is also instrumental for generating adaptive locomotion in cockroaches (see also [33]). Signals from leg mechanoreceptors detecting muscle stretch, load, joint angles, and position adjust the magnitude of muscle contractions, both through reflex activation of motor-neurons (MNs) and via pattern-generating inter-neurons (INs) (see [34] and references therein). Such signals not only contribute to coordination of the joints actuating each leg, but also help establish inter-leg coordination, as demonstrated by providing controlled sensory inputs to reduced, deafferented preparations during pharmacologically induced fictive walking-like motor patterns (e.g. [35]), or by manipulating specific sensory inputs in intact, walking preparations (e.g. [33,36•]). Mechanisms for inter-segmental transfer of joint angle information and inter-leg mechanical coupling mediated through local reflexes have been suggested [37].

While cockroach locomotion has been well-studied, our knowledge is still far from complete. Detailed descriptions of thoracic CPGs, muscle properties, body mechanics, and their interactions are lacking (to a somewhat lesser extent this also applies to the stick insect). This review aims partly to draw attention to these limitations and to call for further research. Such gaps in our knowledge can also be bridged by means of mathematical models, and computer simulations (Figure 2). As we illustrate below, models ranging from rigid bodies with passively sprung legs to biophysically based neural circuits actuating muscles in realistic body and limb geometries, have already advanced our overall understanding.

### Mathematical models of insect locomotion

Theoretical neuroscience provides a quantitative basis for describing what nervous systems do, determining how they function, and uncovering the general principles by which they operate. Mathematical models and their computational realizations are key tools in this theory. In the present case, such models are based on data acquired by both observation and experimental manipulation of

**Figure 2**

Comparative experimental investigation, including studies of intact behaving insects and reduced, *in vitro*, neural preparations, together with mathematical modeling, offer an integrated approach to extending our understanding of legged locomotion in insects.

intact animals and on fictive motor patterns recorded *in vitro* (Figure 2). Early models of insect CPGs used coupled oscillators [38]; more detailed descriptions of feedback and stepping rules were subsequently developed [13°,39°]. These models predicted leg kinematics and intra-leg and inter-leg timing relations, but did not include muscle

mechanics or address dynamical stability. Locomotion requires that neural circuits conspire with muscles and limbs to generate reaction forces that propel the body. Mathematical models can likewise integrate neural substrates with biomechanics [40,41°], as we indicate in the following.

## Current modeling efforts for stick insects

Stick insect functional stepping motor outputs rely heavily on proprioceptive feedback modifying the activity of rhythmic CPGs (cf. [6,42]). Their variable walking patterns [14] suggest independent control of leg joints, and subgroups of INs and MNs that can achieve this have been identified [7,18,43]. Current models therefore contain three joint CPGs for each leg [44–46,47•], and such leg CPGs can be connected to produce inter-leg coordination. These models use biophysically based ion-channel (Hodgkin–Huxley-type) models of INs and MNs (see Box 1) to describe cellular mechanisms that generate rhythmic motor activity and neural circuits responsible for adaptive behaviors like backward and sideward stepping.

Sensory feedback of motions and forces in leg segments has been included in recent models [48], although these utilize thus far only behavioral descriptions relating to anterior and posterior extreme positions of individual legs during walking (cf. the rules of Cruse [13•]). The identification of neural substrates for inter-leg coordination will require models that describe specific feedback pathways on the cellular level. First steps in this direction were made by [49,50,51•].

## Current modeling efforts for cockroaches

Passive machines and models (based on passive dynamics only) show that stable walking is possible without sensory

### Box 1 Mathematical models and phase reduction.

Differential equations first developed by Hodgkin and Huxley [83] are key components of CPG models:

$$\begin{aligned} C \frac{dv}{dt} &= -\sum_k g_k(\mathbf{w})(v - V_j) - I_{syn} + I_{ext}, \quad \tau_k(v) \frac{dw_k}{dt} \\ &= w_{k,\infty}(v) - w_k. \end{aligned}$$

The state variable  $v(t)$  is the neuron's transmembrane voltage and components  $w_k(t)$  of the vector  $\mathbf{w}(t)$  track opening and closing of channels transporting ions across the cell membrane. Parameters  $C$ ,  $V_j$  denote membrane capacitance and reversal potentials. Nonlinear functions  $w_{k,\infty}(v)$ ,  $\tau_k(v)$  containing more parameters, characterize channel states and response time dependence on voltage; currents  $I_{syn}$ ,  $I_{ext}$  describe synaptic inputs from other cells in the thoracic network and from mechanoreceptors, SOG and brain.

In CPGs voltages typically oscillate in limit cycles and the state of each neuron or of a local network can be described by its phase  $\theta_i$ . For the model of Couzin-Fuchs *et al.* [36•] this phase reduction is

$$\frac{d\theta_i}{dt} = \omega_i + \sum_{j=1, j \neq i}^6 \alpha_{ij} H_{ij}(\theta_j - \theta_i), \quad i = 1, \dots, 6$$

Interdependence of the frequencies  $\omega_i$ , coupling strengths  $\alpha_{ij}$  and other parameters characterizing the inter-leg coupling functions  $H_{ij}$  reveal how gaits change with speed.

feedback [52]. Models of cockroach walking [24] began with a passive platform similar to the spring-loaded inverted pendulum [53], to which a CPG, muscles, and simplified leg geometries were added to create an integrated neuro-mechanical model [30,31,54]. Although only translation motions and yaw rotations in the ground plane were considered, over 270 differential equations were needed to describe CPG INs, MNs, muscles, and rudimentary proprioceptive feedback.

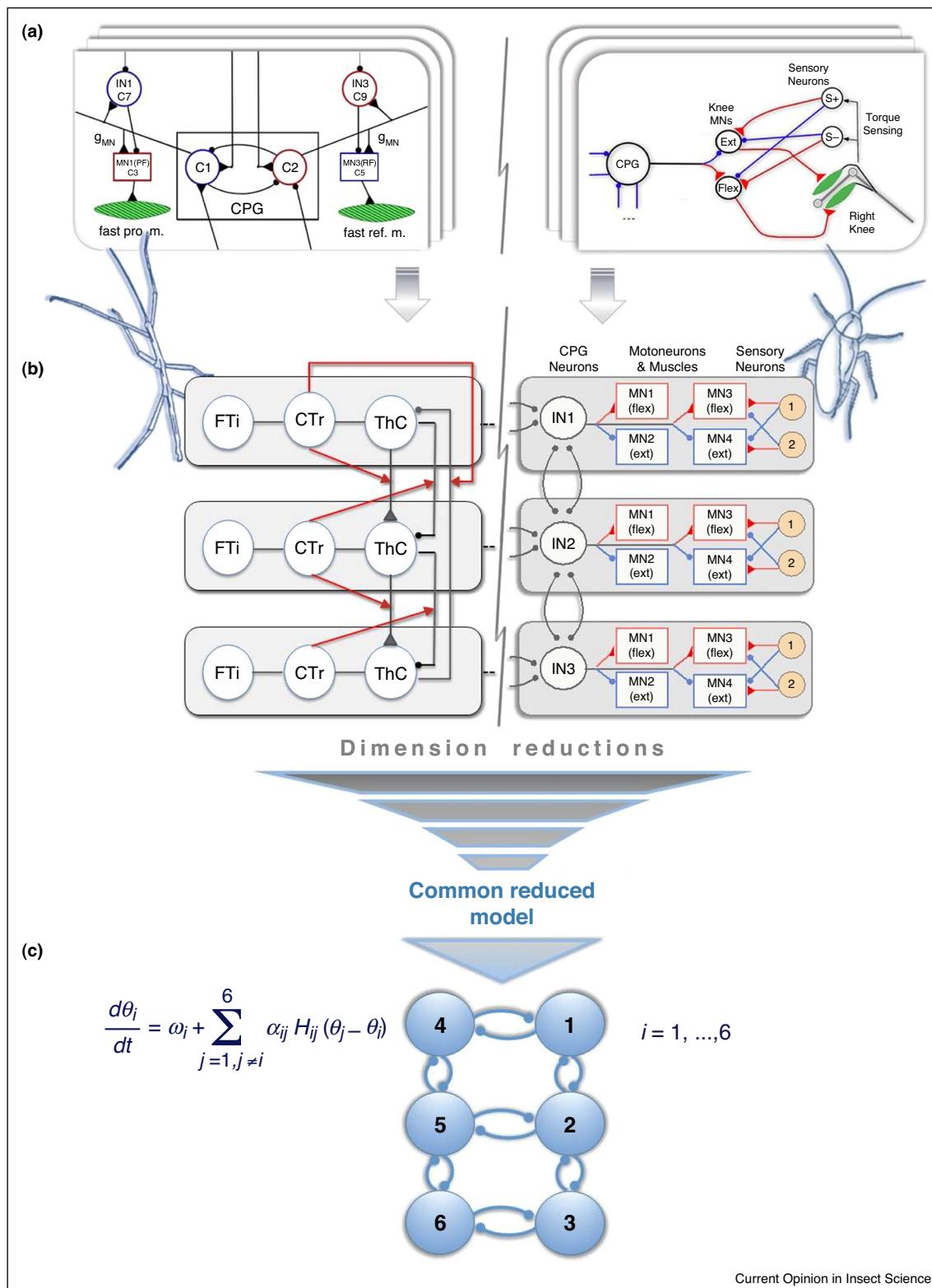
Fortunately, mathematical analysis can simplify such a model, running in an idealized periodic rhythm, by reducing it to an interconnected set of *phase oscillators* depicting subunits of the CPG-MN-muscle system [55]. The degree of reduction depends on the question addressed: from a single joint [56] to 24 oscillators representing MNs driven by the CPGs and subject to feedback from leg forces [57]. Recently, Couzin-Fuchs *et al.* [36•] modeled the network coordinating each leg as a single oscillator (see Box 1), in which inter-dependence of oscillator frequencies, preferred phase differences, and coupling strengths between oscillators characterized how gaits change with speed. This reduction, however, lumps the effects of central, sensory, and mechanical coupling together, and so cannot distinguish among them.

## Toward unified models

Models such as those of Kukillaya *et al.* [31] and Tóth *et al.* [46,47•] span the space of central-decentralized and feedforward-feedback control (cf. [58]), but their complexity makes analyses of such models difficult. A ‘complete’ stick insect model, with 18 joint CPGs, muscles, and sensory pathways would contain over 500 differential equations. However, as in [56], phase reduction could simplify each leg network and thus help determine the contributions to inter-limb coordination from different joint CPGs and mechanosensors, facilitating studies of dynamic stability under varying conditions (Figure 3). Such reductions combine or blur biophysical details, but their efficacy can be tested. Specifically, phase-response-curves, which quantify the receptivity of oscillators to inputs [16,35,51•] and are used in computing coupling functions [30,55], can be estimated experimentally. Thus, phase reduced models can be compared directly with data.

More generally, because their neural architectures and mechanosensory pathways are practically similar, stick insects and cockroaches can be described by a common set of mathematical models with suitably differing parameters (Figure 3). Models ranging in detail from 6 leg units to 18 joint oscillators plus associated MNs and muscles would enable direct comparisons of the effects of central coupling and feedback, as well as exploration of the role of descending inputs and neuromodulation. We now briefly address the latter two important concepts in locomotor behavior.

Figure 3



A unified modeling framework. **(a)** Neuromuscular models of a single joint in a stick insect leg (left; following Tóth *et al.* [51\*]) and in a cockroach leg (right; following Kukillaya *et al.* [31]). **(b)** Reduced models of ipsilateral locomotion networks in the stick insect, including three joints per leg (left; following Daun-Gruhn [50]), and in the cockroach (right; following Kukillaya *et al.* [31]). In both (a) and (b) inhibitory

## Motor pattern selection in insect locomotion

Based on their phylogenetic relations, and on shared principles of their legged locomotion, one can posit a common motor control scheme for stick insects and cockroaches, and for insect locomotion in general. Under this scheme, specific motor behaviors are initiated and different adaptations are mediated via two major mechanisms: descending control and neuromodulation. While much of the neural architecture for generating and coordinating rhythmic leg movements resides in local circuits of the thoracic ganglia, neural circuits mediating initiation, maintenance, and modification of locomotion are found in the insect head ganglia. It is well accepted that removing the brain and leaving the suboesophageal ganglion (SOG) connected to the thoracic ganglia uncovers an inhibitory influence of the brain. This increases the tendency for locomotion, albeit with specific deficits in postural adjustments (e.g. [59,60]). Recent work has provided further insights into the interplay among head ganglia and their role in motivation and decision to engage in locomotion. One particular insect brain region has drawn considerable attention: the midline neuropils of the protocerebrum forming the *central complex* (CC) are currently thought to be physiologically genetically homologous to the basal ganglia of vertebrates [61<sup>••</sup>]. The CC has been implicated in locomotion-related sensory processing, in initiation and maintenance of walking, and in turning and obstacle crossing behaviors (recent reviews in [62,63]). Studying the effects of wasp venom on cockroach locomotion, Kaiser and Libersat [64] recently suggested that the CC is predominantly permissive for the initiation of spontaneous walking, with a role antagonistic to that of the mushroom bodies (brain neuropils important in olfactory information processing, learning, and memory). Under this scheme the SOG is also instrumental in spontaneous walking initiation, in leg coordination, and in sensory–motor integration [60,64–66]. The insect head ganglia may also include descending interneurons, acting as command neurons [67] responsible for executing specific locomotor patterns (e.g. forward or backward walking in the fly [68]), as also reported for other invertebrates (e.g. worms [69]).

Neuromodulation plays an important role in the selection of motor outputs (e.g. [70,71]). Neuromodulatory neurons can activate and organize, and thus modify, sensory–motor networks, allowing a wide repertoire of variations on single motor patterns (e.g. [72]). Insect neuromodulators (primarily bio-amines and peptides) are involved at different levels, from central neural circuits to the periphery (e.g. [73<sup>••</sup>,74,75]). They can thus dynamically adjust coupling strengths among joint and leg CPGs to generate different coordination patterns, and modulate context-dependent shifts from feedforward-dominated to

feedback-dominated control for different walking speeds and environments, or at successive developmental stages.

Insect-specific locomotor behavior can thus be realized through the complex combination and interaction among distinct descending control and neuromodulatory states.

## Concluding remarks

The comparative experimental investigation of different leading models, including studies of both intact behaving animals and reduced neural preparations, aided by mathematical modeling (Figures 2 and 3), remains the best way to facilitate our understanding of legged locomotion in general, and specifically in insects. There is also much interest in insect locomotion in the rapidly growing field of bio-inspired robotics. Drawing inspiration from insects' compact and efficient designs and robustness coupled with plasticity, engineers have created successful models and machines (e.g. [39<sup>••</sup>,76–78]). The present review has provided insights into interactions between sensory and motor control pathways in general, and highlighted concepts in adaptive motor control that may be useful in designing more responsive, robust, and flexible robots. Such bio-robots, in turn, can greatly contribute to hypothesis-testing in biological studies [79,80].

As noted above, a major question in insect locomotion regards the role of the head ganglia and, moreover, the interaction of descending inputs and neuromodulation in the control of locomotion circuits. This is where a comparative approach will be most effective. While much knowledge has been and will be drawn from the genetically tractable fly model (e.g. [68,81<sup>••</sup>,82<sup>•</sup>]), such data can gain substantial merit when compared to findings from the well-established stick insect and cockroach models.

Finally, data from insect models must always be considered within the broader perspective of legged locomotion in general. Insects offer evolutionarily perfected solutions to challenges in all aspects of locomotion, from neural and muscle mechanisms to body form and kinematics. Evolution tends to preserve successful principles, if not details, and knowledge gained from insects can and should be applied elsewhere.

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