



## The subesophageal ganglion modulates locust inter-leg sensory-motor interactions via contralateral pathways

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### ABSTRACT

The neural control of insect locomotion is distributed among various body segments. Local pattern-generating circuits at the thoracic ganglia interact with incoming sensory signals and central descending commands from the head ganglia. The evidence from different insect preparations suggests that the subesophageal ganglion (SEG) may play an important role in locomotion-related tasks. In a previous study, we demonstrated that the locust SEG modulates the coupling pattern between segmental leg CPGs in the absence of sensory feedback. Here, we investigated its role in processing and transmitting sensory information to the leg motor centers and mapped the major related neural pathways. Specifically, the intra- and inter-segmental transfer of leg-feedback were studied by simultaneously monitoring motor responses and descending signals from the SEG. Our findings reveal a crucial role of the SEG in the transfer of intersegmental, but not intrasegmental, signals. Additional lesion experiments, in which the intersegmental connectives were cut at different locations, together with double nerve staining, indicated that sensory signals are mainly transferred to the SEG via the connective contralateral to the stimulated leg. We therefore suggest that, similar to data reported for vertebrates, insect leg sensory-motor loops comprise contralateral ascending pathways to the head and ipsilateral descending ones.

### 1. Introduction

Animal locomotion is based on multidirectional, dynamic interactions within and between several control levels: central pattern-generating neuronal circuits, sensory inputs that modulate these circuits, and higher neuronal centers residing in the brain or head ganglia.

Ample research across several decades has focused on the central pattern generators (CPGs), demonstrating that these neuronal oscillators constitute the basis of practically all rhythmic behaviors, including locomotion (Marder and Bucher 2001; Mulloney and Smarandache 2010; Ayali and Lange 2010; Rybak et al. 2015). Similarly, extensive research has been dedicated to the role of sensory feedback in shaping the CPG-induced behavior in different animals. In legged-locomotion specifically, sensory inputs have been attributed a role in the functional adaptability of leg motor patterns to the changing environment (e.g., Altman 1982; Burrows 1987; Pearson 1993, 2004; Education et al., 2004; Pearson et al., 2006; Ayali et al. 2015b). Leg proprioception during walking has been shown to be instrumental for inter-leg

coordination in the stick insect (e.g. Cruse 1990; Büschges et al. 2008; Borgmann et al. 2009) and, similarly, mechano-sensory feedback was reported to mediate intersegmental information transfer and adjust locomotion patterns in cockroaches (Zill et al. 2009; Fuchs et al. 2012; Ayali et al. 2015a; Couzin-Fuchs et al. 2015a,b). The effect of local sensory input is context- and task-dependent, influenced by the activity of neighboring legs (Knop et al. 2001; Hellekes et al. 2012) and descending information (Ridgel et al. 2007; Mu and Ritzmann 2008).

The higher motor centers provide additional control of locomotion. The insect central complex, for example, was shown both to process environmental cues and to execute appropriate commands for walking, such as speed change and turning (for review: Pfeiffer and Homberg 2014). The subesophageal ganglion (SEG), one of the insect head ganglia, which is located below the esophagus (Ito et al. 2014). Beyond its role in local control of the mouthparts (Rand et al. 2008, 2012), the SEG was shown to play an important role in insect locomotion. Ablating the SEG in cockroaches was demonstrated to affect walking and initiation and duration of escape (Gal and Libersat 2006; Kaiser and

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Libersat 2015). Recordings from locust SEG descending interneurons (DINs) demonstrated elevated activity during and after the preparatory phase of walking (Kien 1990a). These DINs typically fire throughout the walking bout, as temporally-structured patterns that are not directly correlated with the stepping cycles (Kien 1990b). It has recently been shown in *Drosophila* larvae that a small group of neurons in the subesophageal zone contribute to the control of larval chemotaxis (Tastekin et al. 2015). Inhibiting these neurons compromised the timing and coordination of reorientation maneuvers while activation of these neurons through optogenetic and thermogenetic techniques were sufficient to initiate reorientation maneuvers. In *in-vitro* preparations, removal of the subesophageal zone affected the degree of asymmetry of fictive crawling motor patterns (Pulver et al. 2015). However, the intricate interactions among CPGs, sensory information, and higher motor centers, which together generate coordinated walking behavior, are still far from fully understood.

In an attempt to characterize the interplay among the different neuronal elements that control walking in the desert locust, *Schistocerca gregaria*, we previously mapped the central basis of inter-leg coordination in the thoracic ganglia (Knebel et al. 2017). Following that, we demonstrated the role of the SEG in modulating the coupling between segmental leg CPGs (Knebel et al. 2018). These findings are supported by anatomical descriptions showing that the SEG contains both descending and ascending interneurons and modulatory projections that reach all thoracic ganglia and the brain (Kien and Altman 1984; Bräunig 1991; Roth et al. 1994), and thus may be important in translating higher motor commands into direct execution signals.

In the current study, we revealed the role of the SEG in integrating proprioceptive information from the legs and generating intersegmental responses. To this end, we investigated the interactions between descending signals from the SEG and walking-related thoracic sensory-motor responses by means of extracellular recordings from nerves containing leg depressor and levator motoneurons during stimulation of sensory nerves, before and after lesioning the connections between the SEG and the thoracic ganglia. Our findings indicate a contribution of the SEG in intersegmental sensory-motor interactions.

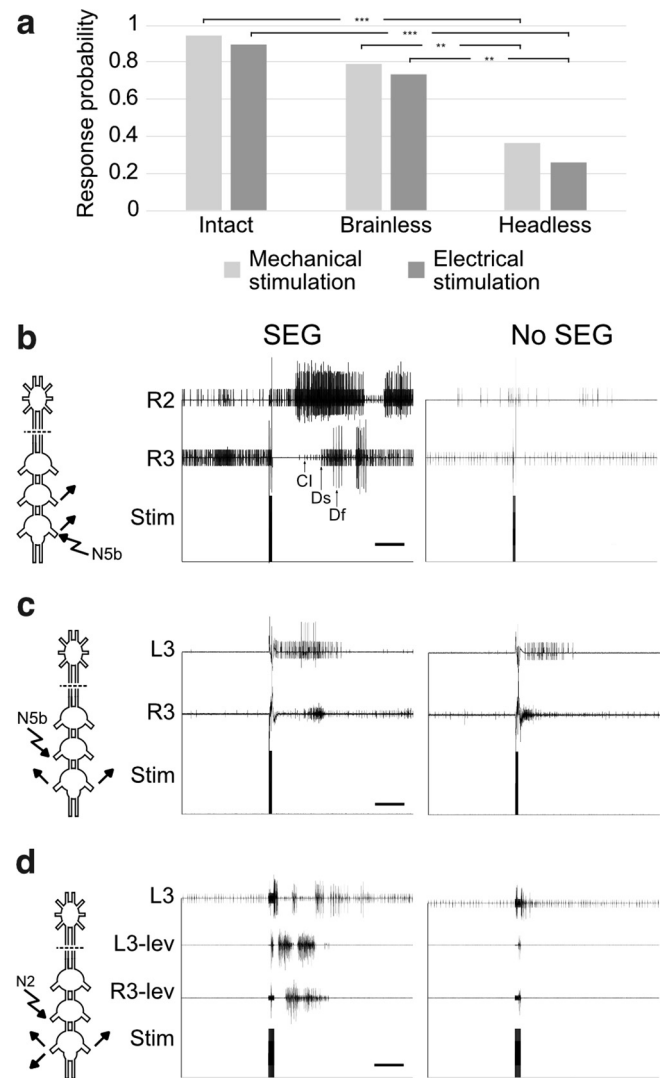
## 2. Materials and methods

### 2.1. Animals and preparation

All experiments were performed on adult desert locusts, *Schistocerca gregaria*, from our breeding colonies. Extracellular recordings were performed on *in-vitro* preparations of the thoracic ganglia and the SEG as follows: locusts were anesthetized with CO<sub>2</sub>, legs and wings were cut and the dorsal part of the head, including the supraesophageal ganglion (brain), was removed by a horizontal cut ventral to the compound eyes. After excising the abdomen, the thorax was opened along the dorsal midline. Gut, fat tissue, air sacs, and cuticular parts, including the tentorium from the head cuticle, were carefully removed, exposing the ventral nerve cord. All peripheral nerves were cut close to the ganglia, except for the meso- and metathoracic leg nerves 5 (numbered after Campbell, 1961), which were cut as distally as possible. Finally, the circumoesophageal connectives and the connectives between the last thoracic- and the first abdominal ganglia were cut, and the thoracic-SEG ganglia chain with its surrounding tracheal supply was dissected out of the body cavity, pinned in a clean Sylgard dish (Sylgard 182 silicon Elastomer, Dow Corning Corp., Midland, MI, USA), dorsal side up, and bathed in locust saline (in mM: 150 NaCl, 5 KCl, 5 CaCl<sub>2</sub>, 2 MgCl<sub>2</sub>, 10 Hepes, 25 sucrose at pH 7.4). The two main tracheae were opened and floated on the saline surface.

### 2.2. Electrophysiological recordings

Electrophysiological experiments were carried out at both Konstanz and Tel Aviv Universities. We used custom-made suction electrodes: (a)



**Fig. 1.** Responses to sensory stimulations, with and without the SEG. (A) Response probabilities of the middle leg to mechanical and nerve stimulation of the hind leg in intact, brainless and head less animals.  $**p < .01$   $***p < .001$ . (B) *In vitro* recordings from the ipsilateral meta- and mesothoracic depressors during stimulation of the metathoracic N5b, with and without the SEG intact (left and right panels, respectively). The different units in the depressor nerves are tagged (Df – fast depressor, Ds – slow depressor, CI – common inhibitor). Scale bar is 1 sec. (C) As in (B), but for stimulating the mesothoracic N5b and recording from the ipsi- and contralateral metathoracic depressors. (D) As in (B) but for recordings of the meta-thoracic levator and depressor nerves during stimulation of the mesothoracic nerve 2. In all examples, responses decreased either in intensity and duration, or disappeared completely after SEG removal.

to record extracellularly the activity of the 5A nerves, which contain three depressor motor axons (the slow and fast trochanteral depressors and a common inhibitor; Fig. 1b), and (b) to stimulate nerve 5B, which contains the majority of the leg sensory branches. Activity seen in the hemi-segmental depressor motor neurons reflect the motor output produced by the depressor-levator CPG of each leg, in which each part act in alternation with the other (e.g. Knebel et al. 2017). Stimulation of the 5B branch, the main leg sensory nerve, was chosen as a mean for generating a general, unspecific, leg sensory stimulation. Thus, although this did not allow investigating very specific sensory modulations, it enabled us to trace general sensory-motor routes within the nervous system. To monitor activity from the connectives, we used silver wire hook electrodes. After dissection, and after every cut of the connectives, we left the preparation to recover for 15 min before

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