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# Force feedback reinforces muscle synergies in insect legs

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ABSTRACT

The nervous system solves complex biomechanical problems by activating muscles in modular, synergist groups. We have studied how force feedback in substrate grip is integrated with effects of sense organs that monitor support and propulsion in insects. Campaniform sensilla are mechanoreceptors that encode forces as cuticular strains. We tested the hypothesis that integration of force feedback from receptors of different leg segments during grip occurs through activation of specific muscle synergies. We characterized the effects of campaniform sensilla of the feet (tarsi) and proximal segments (trochanter and femur) on activities of leg muscles in stick insects and cockroaches. In both species, mechanical stimulation of tarsal sensilla activated the leg muscle that generates substrate grip (retractor unguis), as well as proximal leg muscles that produce inward pull (tibial flexor) and support/propulsion (trochanteral depressor). Stimulation of campaniform sensilla on proximal leg segments activated the same synergistic group of muscles. In stick insects, the effects of proximal receptors on distal leg muscles changed and were greatly enhanced when animals made active searching movements. In insects, the task-specific reinforcement of muscle synergies can ensure that substrate adhesion is rapidly established after substrate contact to provide a stable point for force generation.



## 1. Introduction

Activation of muscles in modular groups with similar biomechanical actions (synergists) is viewed as a basic mechanism in motor control (Ting and Macpherson, 2005; De Groote et al., 2013). The use of muscles in synergist groups simplifies the regulation of limbs with multiple degrees of freedom (Bernstein, 1967) and may be reflected in the organization of pre-motor elements in the nervous system (Hart and Giszter, 2010). Similar synergies can be utilized in diverse behaviors, such as standing and walking, but the magnitude and timing of muscle activation is adaptable and depends upon the behavior and context, i.e. it is task specific (Chvatal and Ting, 2013).

Sensory receptors of the limbs that monitor forces and movements could readily contribute to the generation and adaptation of muscle synergies (Safavynia and Ting, 2013; Duysens et al., 2013). Some types of sense organs, such as receptors that monitor muscle forces and loads, have been shown to have widespread effects on motor neurons to leg muscles (Eccles et al., 1957; Harrison et al., 1983). However, the specific contribution of force feedback to use of muscles as synergists is poorly understood.

The present experiments have studied how force feedback in insects contributes to activation of muscle synergies in substrate grip, a behavior that involves the coordinated activation of muscles at different leg joints. In all insects, substrate contact occurs through adhesive and frictional structures on the feet (tarsi) (reviews Gorb, 2001, 2008; Labonte et al., 2014) but it is established and actively maintained by a discrete pattern of activation of leg muscles at different leg joints as synergists (Wile et al., 2008; Zill et al., 2014). Previous studies have shown that forces exerted in substrate grip are detected by campaniform sensilla, sense organs that detect strains in the exoskeleton (Zill et al., 2010). Experiments in stick insects have demonstrated that campaniform sensilla of the tarsus (foot) can provide positive feedback to the muscle that directly generates substrate grip (Zill et al., 2014). However, it has been not clear how these effects are integrated with force signals from campaniform sensilla of other leg segments and how they contribute to the requisite muscle synergies.

In the present study, we characterized the effects of campaniform sensilla of the feet (tarsi) and proximal segments (trochanter and femur) on activities of leg muscles in stick insects and

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cockroaches. These experiments were designed to test the hypothesis that the effects of force detecting sense organs of the feet are integrated with force generation for support of body load through activation of the same muscle synergies. The tarsal campaniform sensilla in both species have been identified and characterized but their motor effects were only studied in stick insects (Zill et al., 2014). Many groups of campaniform sensilla are found on the proximal leg segments, the trochanter and femur (Schmitz, 1993). Previous studies in cockroaches have suggested that the sensilla of proximal segments can strongly activate distal leg muscles: in 'pegleg' experiments, the leg is severed or denervated in the mid femur (Noah et al., 2004). Animals still use the leg stump in walking and show 'phantom' bursting in the tibial flexor and extensor muscles if the stump is pressed against the substrate, even though the distal muscles produce no tensions or movements. Those results suggested that the proximal sense organs can contribute to the activation of distal leg muscles, as was shown in earlier studies of stick insects (Akay et al., 2001). In addition, stick insects are advantageous in that extensive previous research has shown that the effects of leg sense organs are not constant but can be experimentally changed according to the behavior of the animal (Bässler and Büschges, 1998; Hellekes et al., 2012). Overall, our results support the idea that inputs of sense organs that detect forces in different leg segments are integrated, in part, through the activation of common muscle synergies.

## 2. Methods

Adult male cockroaches (Fig. 1A, *Periplaneta americana*) were obtained from Carolina Biological Supply and fed puppy chow (Purina). Adult female stick insects (Fig. 1B, *Carausius morosus*) were obtained from breeding colonies at the Universities of Bielefeld and Cologne.

### 2.1. Preparations for recording and mechanical stimulation

The methods of mechanical stimulation of tarsal campaniform sensilla have been previously described (Zill et al., 2010, 2014). Animals were restrained and all proximal segments (up to the second or third tarsal segment) of the left middle leg (stick insects) or right hind leg (cockroaches) were supported and constrained by staples (Fig. 2A, B). The distal tarsal segment and pretarsus were free to move. Myographic activities were recorded with pairs of 50 micron silver wires. The wires were placed in the proximal coxa to record the depressor, mid femur to monitor the flexor and proximal tibia to record the retractor unguis muscle (recordings of the femoral part of the retractor were complicated by cross talk). Forces were imposed on the tarsus using a probe with strain gauges mounted on a piezoelectric crystal (Fig. 2A, B; Zill et al., 2010). Voltage waveforms were generated from pre-recorded sequences using a Cambridge Electronics laboratory interface (power 1401mkII, CED Ltd., Cambridge, UK).

### 2.2. Forces applied to the depressor muscle insertion

Forces were applied to the insertion of the Trochanteral Depressor muscle using a computer-controlled motor (as previously described, Zill et al., 2012) The shaft of a minuten pin was attached to the armature of the motor and the sharp end was inserted into the cuticle distal to the attachment of the depressor muscle tendon (Fig. 4A). In both cockroaches and stick insects, the proximal, ventral part of the trochanter is reinforced by an internal cuticular buttress (Zill et al., 2000, 2012), creating a small compartment distal to the muscle insertion. The tip of the pin was inserted through ventral cuticle into this compartment. Forces were applied to the pin and insertion point to mimic depressor

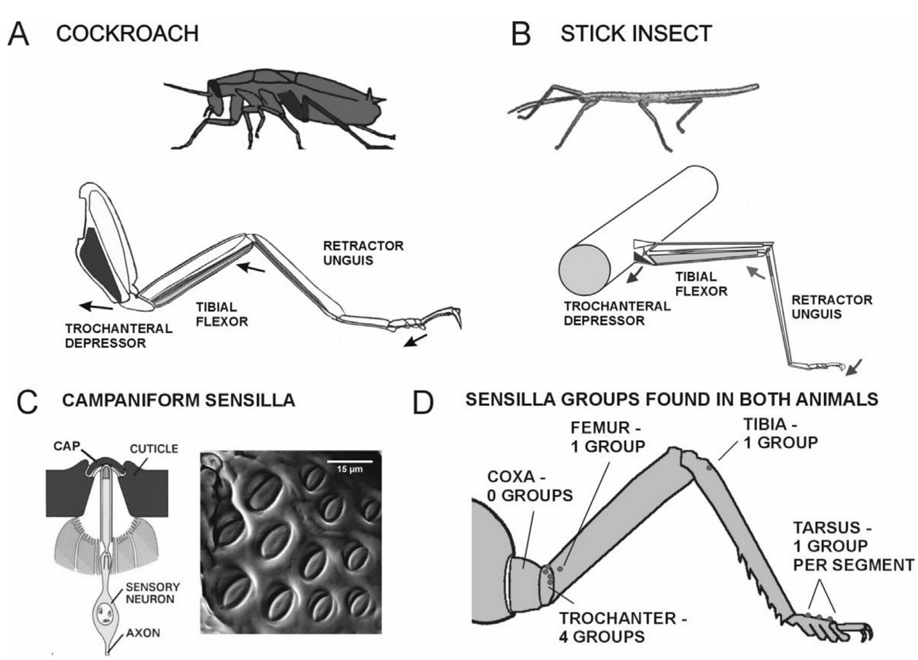


**Fig. 1.** Homologous leg muscles used in substrate grip and force detecting sense organs in cockroaches and stick insects – A. Cockroach leg muscles used in substrate grip – Diagram of cockroach hind leg. The tarsus is pressed against the substrate by the action of the retractor unguis muscle. Adhesion is enhanced and maintained by the tibial flexor and trochanteral depressor muscles. B. Homologous muscles in stick insect (middle leg) – The same muscles (retractor, flexor and depressor) are activated in substrate contact and adhesion in stick insects. C. Campaniform sensilla – Forces in the exoskeleton are detected by campaniform sensilla through attachments to cuticular caps in the exoskeleton. The sensilla are arranged in groups with consistent orientations of the oval shaped caps (scanning electron micrograph – stick insect trochanteral campaniform sensilla imaged by Annelie Exter, University of Bielefeld). D. Distribution of groups of campaniform sensilla – Diagram showing groups campaniform sensilla on the legs. A similar (common) arrangement of sensilla is found in both stick insects and cockroaches.