



Contents lists available at ScienceDirect

Arthropod Structure & Development

journal homepage: www.elsevier.com/locate/asd

Effects of force detecting sense organs on muscle synergies are correlated with their response properties

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ARTICLE INFO

Article history:

Received 24 March 2017

Accepted 22 May 2017

Available online xxx

Keywords:

Force

Synergies

Insect

Campaniform

Response

Sensitivity

ABSTRACT

Sense organs that monitor forces in legs can contribute to activation of muscles as synergist groups. Previous studies in cockroaches and stick insects showed that campaniform sensilla, receptors that encode forces via exoskeletal strains, enhance muscle synergies in substrate grip. However synergist activation was mediated by different groups of receptors in cockroaches (trochanteral sensilla) and stick insects (femoral sensilla). The factors underlying the differential effects are unclear as the responses of femoral campaniform sensilla have not previously been characterized. The present study characterized the structure and response properties (via extracellular recording) of the femoral sensilla in both insects. The cockroach trochantero-femoral (TrF) joint is mobile and the joint membrane acts as an elastic antagonist to the reductor muscle. Cockroach femoral campaniform sensilla show weak discharges to forces in the coxo-trochanteral (CTr) joint plane (in which forces are generated by coxal muscles) but instead encode forces directed posteriorly (TrF joint plane). In stick insects, the TrF joint is fused and femoral campaniform sensilla discharge both to forces directed posteriorly and forces in the CTr joint plane. These findings support the idea that receptors that enhance synergies encode forces in the plane of action of leg muscles used in support and propulsion.

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1. Introduction

In standing and walking, leg and body muscles are activated as modular, synergistic groups (Chvatal and Ting, 2013; Safavynia and Ting, 2013). However, the specific mechanisms underlying the organization of muscle synergies are unclear (Gopalakrishnan et al., 2014; Laine et al., 2015). A number of experiments have shown that sense organs that monitor forces have widespread effects in motor neurons to leg muscles (Eccles et al., 1957; Harrison et al., 1983). These effects could function to enhance or reinforce synergies in posture and walking (Duysens et al., 2000, 2013; Hagio and Kouzaki, 2014). However, it is not known if all force detecting sense organs have the same effects on muscle synergies (Nichols, 1999; Nichols and Ross, 2009). Experiments in cats demonstrated that Golgi tendon organs of different leg muscles (ankle or knee extensors) had diverse effects in activation of groups of leg muscles

during treadmill walking (Ross and Nichols, 2009). It was not determined if the effects on muscle synergies were correlated with the specific forces encoded by the receptors.

In insects, grasping the substrate, which is initiated at the start of the stance phase of walking, is achieved by activation of muscle synergies (Bässler et al., 1991). Substrate adhesion is an active process that requires contraction of a number of leg muscles at different intrinsic joints, including muscles acting at the foot (tarsus) and muscles of proximal leg segments (flexor, depressor) (Wile et al., 2008; Zill et al., 2014). The combined action of these muscles ensures that adequate adhesion is rapidly established and maintained after leg contact (Gorb, 2008). Our previous study in cockroaches and stick insects showed that leg campaniform sensilla, that encode forces as cuticular strains, can aid in activation of the synergist muscles that generate substrate grip (Zill et al., 2004, 2015a, b). The receptors of the leg act as an ensemble as campaniform sensilla at different locations reinforce the same muscle synergies with proximally located receptors affecting distal leg muscles. However, the specific groups of sensilla that produced

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effects on muscle synergies were species-specific: in cockroaches, synergist activation was mediated by trochanteral sensilla but this effect was associated with femoral campaniform sensilla in stick insects (Zill et al., 2015a, b).

The factors underlying the difference in effects of specific groups of force receptors upon muscle synergies are not known. Recordings of stick insect trochanteral campaniform sensilla suggested that the motor effects of individual groups of receptors depend upon their sensitivity to forces in the plane of action of the main coxal muscles (coxo-trochanteral (CTr) joint plane) that generate forces in support and propulsion (Cruse and Bartling, 1995; Zill et al., 2012; Dallmann et al., 2016). Although many groups of campaniform sensilla have previously been characterized, the specific structure, responses and directional sensitivities of the femoral groups are poorly understood (Pringle, 1938; Schmitz et al., 1991; Akay et al., 2001). In all insects, the femoral campaniform sensilla are located on the proximal end of the femur, adjacent to the trochanter femur joint (TrF) (Petryszak and Fudalewicz-Niemczyk, 1994). Unlike most leg joints which are similar in structure, the joint between the trochanter and femur is variable and species-specific in the range of movement it allows (Frantsevich and Wang, 2009). In most insects, this joint also represents the point at which autotomy (loss of distal leg segments) occurs (Cardé, 2009). While the TrF joint has been shown to function adaptively in some insects (Watson et al., 2002; Bender et al., 2010), it has also been postulated to function primarily as a spring or shock absorber (Frantsevich and Wang, 2009).

In the present study, we examined the structure of the TrF joint in cockroaches and stick insects. We also characterized the response properties of the femoral campaniform sensilla, which have not previously been determined. These results demonstrate that the femoral groups differ in their directional sensitivity to imposed forces and to forces mimicking muscle contractions. The same group of receptors, therefore, shows different responses in different insect species. Our data also support the hypothesis that receptors that affect muscle synergies encode forces in the plane of action of major intrinsic leg muscles used in support and propulsion. Similar correlation of response specificity in force detection and activation of muscle synergies may occur in other animals, including vertebrates.

2. Methods

Experiments were performed on adult, female stick insects (*Carausius morosus*) raised in animal colonies at the University of Bielefeld or the University of Köln and adult, male cockroaches (*Periplaneta americana*) obtained commercially (Carolina Biological Supply).

2.1. Morphological studies

Legs were removed from animals anesthetized with carbon dioxide. To study the structure of the TrF joint in histological section, the trochanter and femur were isolated and immersed in Karnovsky's fixative, dehydrated in ethanol, embedded in Spur's resin and sectioned using an MT2 microtome (method of Moran et al., 1971). Sections were stained with toluidine blue (an indicator of potential elasticity in cuticular structures; Weis-Fogh, 1960; Wong et al., 2012). For whole mount preparations, the trochanter and femur were bisected, cuticle containing the femoral campaniform was further isolated and treated with 1 M potassium hydroxide for at least 1 h. To image joint membranes, preparations were cleared in Conray (an aqueous clearing agent, iothalamate meglumine, Mallinckrodt), viewed under UV illumination in an Olympus microscope and photographed using a Spot Camera (Diagnostic Imaging,

Inc.; Zill et al., 2011). To view the caps of campaniform sensilla, specimens were fixed in 4% formalin prior to clearing in Conray. For confocal microscopy, specimens were imaged using a Leica TCS SP5 II microscope at the Marshall University Microscopy facility (methods of Zill et al., 2011).

For scanning electron microscopy, middle and hind legs of newly molted stick insects were isolated and partially dissected, then desiccated and sputter coated (Zill et al., 2011). The cuticle was imaged with an Hitachi S450 scanning electron microscope. Digital images of the cuticular caps were measured in ImageJ software (NIH, USA). Data from the middle and hind legs were pooled for analysis as measurements of the sizes and locations of the femoral sensilla indicated no significant difference between the groups in the serially homologous legs.

2.2. Physiological studies

Physiological studies were performed on the left middle legs of stick insects and the left hind legs of cockroaches. These specific legs were utilized to extend findings of previously published studies (Zill et al., 2012; 2015a, b). While the legs are of different body segments, the distribution, number and responses of campaniform sensilla are quite similar in middle and hind legs in both species (Hofmann and Bässler, 1982, 1986; Keller et al., 2007; Zill et al., 2009). Studies of the functions and forces generated by the legs also indicate that they serve similar functions in support and propulsion, although the hind legs are normally the major source of propulsive forces in the cockroach escape reaction (Hughes, 1952; Dallmann et al., 2016). In addition, recordings were found to be most viable in the cockroach hind legs due to their large size.

Animals (intact or after sensory ablation) were first securely restrained and the coxa of the leg was firmly fixed with cyanoacrylate adhesive to small staples placed above and below the segment. The distal leg was amputated in the distal femur, proximal to the femoro-tibial joint and a mixture of Vaseline and paraffin oil placed over the end of the femur to prevent desiccation. The proximal leg segments were not dissected and remained attached to the thorax to insure normal ventilation through the animal's tracheal system.

Recordings of sensory activities were taken, in stick insects, from the main leg nerve using custom oil-hook electrodes (Schmitz et al., 1988) or, in cockroaches, through 50 μ silver wires (Goodfellow Ltd, AG005825) that were insulated to their tip and inserted in the distal coxa (Zill et al., 1999). The tibial flexor muscle was recorded myographically from the femur using a pair of the same type of wires (methods of Zill et al., 2015a, b).

2.3. Ablation of sense organs

To limit recordings to activities of the femoral campaniform sensilla, all groups of trochanteral receptors (Groups 1–4) were ablated with a sharp etched pin (Schmitz, 1993). The cell bodies of the femoral chordotonal organ were ablated by inserting the pin through the cuticle of the anterior side of the proximal femur.

2.4. Mechanical stimulation

The head of a minuten pin (firmly attached to a motor) was inserted into the cuticle distal to the attachment of the depressor muscle tendon. In both stick insects and cockroaches the proximal, ventral part of the trochanter is reinforced by an internal cuticular buttress that creates a small compartment distal to the muscle insertion (described in Zill et al., 2000, 2012). The tip of the pin was inserted through ventral cuticle into this compartment. The pin was also used to resist loads applied to the femur in different directions.

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