

# Proprioceptive input to a descending pathway conveying antennal postural information: Terminal organisation of antennal hair field afferents

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## ABSTRACT

Like several other arthropod species, stick insects use their antennae for tactile exploration of the near-range environment and for spatial localisation of touched objects. More specifically, *Carausius morosus* continuously moves its antennae during locomotion and reliably responds to antennal contact events with directed movements of a front leg. Here we investigate the afferent projection patterns of antennal hair fields (aHF), proprioceptors known to encode antennal posture and movement, and to be involved in antennal movement control. We show that afferents of all seven aHF of *C. morosus* have terminal arborisations in the dorsal lobe (DL) of the cerebral (=supraoesophageal) ganglion, and descending collaterals that terminate in a characteristic part of the gnathal (=suboesophageal) ganglion. Despite differences of functional roles among aHF, terminal arborisation patterns show no topological arrangement according to segment specificity or direction of movement. In the DL, antennal motoneuron neurites show arborizations in proximity to aHF afferent terminals. Despite the morphological similarity of single mechanoreceptors of aHF and adjacent tactile hairs on the pedicel and flagellum, we find a clear separation of proprioceptive and exteroceptive mechanosensory neuropils in the cerebral ganglion. Moreover, we also find this functional separation in the gnathal ganglion.

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## 1. Introduction

Many animal species have to walk, run or climb through their environment in the dark, for example because of their burrow-dwelling or nocturnal life style. Such animals often rely on active tactile exploration of their near-range environment during locomotion: burrow-dwelling shrews and rodents use whiskers; nocturnal insects typically use their antennae. An example of the latter is the stick insect *Carausius morosus* (de Sinéty, 1901) which is an important study organism in behavioural and neural physiology of locomotion (e.g., Bässler, 1983; Graham, 1985; Büschges and Gruhn, 2007; Bidaye et al., 2018; Dürr et al., 2018). Stick insects continuously move their antennae during locomotion (Dürr et al., 2001; Krause et al., 2013), and adjust the antennal movement

pattern during visually induced turning (Dürr and Ebeling, 2005) or in response to antennal contacts with obstacles (Schütz and Dürr, 2011; Krause and Dürr, 2012). Antennal contact events were also reported to trigger short-latency adaptation of ongoing front leg swing movements, effectively turning a step into an aimed reach-to-grasp movement (Schütz and Dürr, 2011). Because these targeted reach-to-grasp movements require a computational mapping, i.e., a coordinate transformation from antennal contact position to leg posture, antennal proprioceptors of the two antennal joints must be involved. This is because encoding of antennal contact position requires faithful encoding of antennal pointing direction (Krause and Dürr, 2004). In cockroaches, antennal hair field afferents are known to encode antennal joint angle and angular velocity (Okada and Toh, 2001) and to mediate a tactually-induced turning response (Okada and Toh, 2000). Ablations of antennal hair fields in stick insects affect the antennal joint angle range in multiple ways, too (Krause et al., 2013). Therefore, hair fields are likely candidates for mediating tactually-induced reach-to-grasp responses in stick insects. Moreover, descending interneurons that encode antennal joint angle have been recorded

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(Ache and Dürr, 2013), and two individually identified ones of these were suggested to receive direct input from antennal hair field afferents (Ache et al., 2015). With that background, the main objective of this study is to describe the anatomy of the neural structures involved in encoding of antennal joint angles. With regard to our objectives, this paper addresses the following three questions:

First, we asked to what extent the seven disjunct hair fields of the stick insect antenna (Krause et al., 2013) have distinct projection patterns, particularly because they are located on different antennal segments (scape and pedicel) and on either side of two slanted joint axes (Krause and Dürr, 2004). These attributes could be reflected by a corresponding topology of the afferent terminal arborisation pattern, similar to the topological arrangement of antennal afferents of Johnston's organ in honeybee (Ai et al., 2007), or bimodal (tactile and contact-chemosensory) bristles in cockroaches (Nishino et al., 2005).

Second, we asked whether the hair field afferent terminal arborisations are in vicinity to the dendrites of the antennal motoneurons, as has been found in honeybees (Kloppenborg, 1995) and sphingid moths (Krishnan et al., 2012). In insects, the dendrites of antennal motoneurons are located in the dorsal lobe (DL) of the deutocerebrum (DE), which is synonymous with 'Antennal Mechanosensory and Motor Centre' (AMMC; Rospars, 1988; Homberg et al., 1989).

Third, we asked whether there is a similar divergence of antennal mechanoreceptive afferent projections as has been described for the cricket, where exteroceptive flagellar mechanoreceptors project into the VFA neuropil (VFA: Ventral area of Flagellar Afferents) of the DE, whereas proprioceptive hair field afferents project to the DL of the DE (Staudacher and Schildberger, 1999; reviewed by Staudacher et al., 2005). Whereas afferent projections to the DL have been described in honey bees (Suzuki, 1975; Maronde, 1991; Ai et al., 2007), locusts (Bräunig et al., 1983) and cockroaches (Nishino et al., 2005), the VFA neuropil has not been discerned in these animal groups. In conjunction with this third question, we also wondered to what extent the afferent collaterals descending to the gnathal ganglion (GNG, formerly known as suboesophageal ganglion; Ito et al., 2014) may show divergent projection patterns, too.

These questions were addressed by anterograde and retrograde dye fillings of antennal hair field afferents and antennal nerves which showed that afferents of all seven hair fields and motoneuron neurites project into the dorsal lobe (DL) of the CRG, in proximity to their terminal arborisations. Furthermore, we show

that proprioceptive and exteroceptive mechanosensory neuropils are functionally separated in the CRG and GNG of the stick insect.

## 2. Materials and methods

### 2.1. Animals

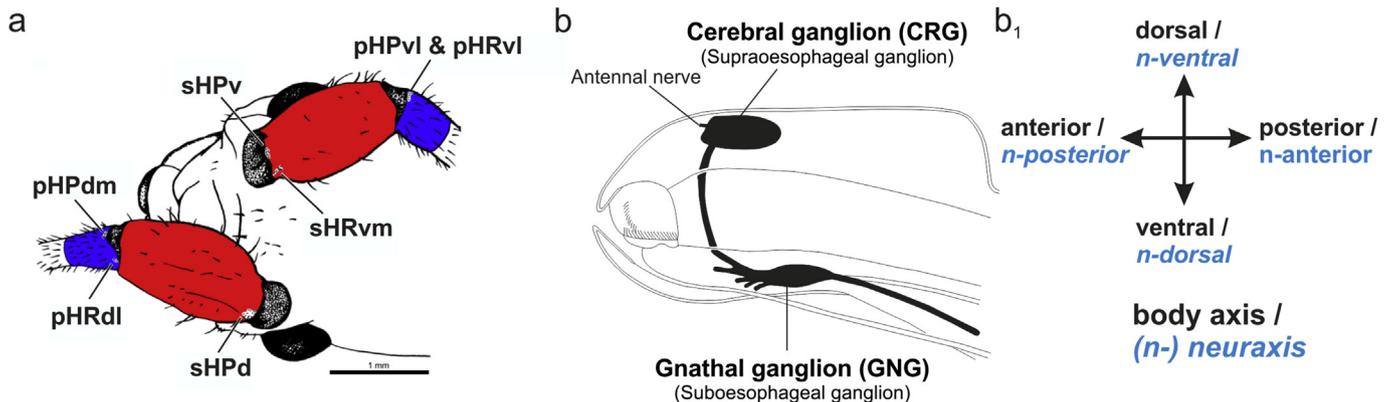
Experiments were performed on adult female stick insects, *C. morosus* (de Sinéty, 1901), taken from a colony maintained at the University of Cologne. Animal colonies were kept at temperatures between 20 °C and 25 °C in an artificial light/dark cycle, and fed *ad libitum* with blackberry leaves (*Rubus fruticosus*).

### 2.2. Terminology of hair fields, muscles, fibre tracts, and neural tissue

*C. morosus* has three hair fields (HF) on the proximal border of the scape, i.e., at the head-scape joint, and four more HFs on the pedicel, at the scape-pedicel joint (see Fig. 1a). A detailed description of the HFs and a proposal for their terminology were given by Krause et al. (2013). Following their terminology, a scapal or pedicellar hair plate (HP) or hair row (HR) is named according to the segment on which it is located on (s: scape, p: pedicel), and the facing direction with regard to the antennal movement (d: dorsal, dl: dorso-lateral, dm: dorso-medial, v: ventral, vl: ventro-lateral, vm: ventro-medial). For example, the dorso-medial hair plate of the pedicel is denoted by pHPdm.

The terminology of antennal nerves and their innervating muscle regions was adapted from Dürr et al. (2001). Hair field fibre tracts in our preparations resemble sensory tracts described for the deutocerebrum of other insect species (reviewed in Staudacher et al., 2005). For a comparison of our findings with detailed anatomical descriptions available in the literature, we therefore adopted the nomenclature proposed by Suzuki (1975) for the honeybee.

Stick insects possess prognathous mouth parts, which is why the supraoesophageal ganglion (recently renamed to cerebral ganglion, CRG; Ito et al., 2014) is tilted backwards in the adult head capsule (Fig. 1b). Irrespective of this situation, all central projections stained and general neuroanatomical descriptions of locations in the cerebral ganglion (CRG) follow the convention of Ito et al. (2014) and are related to the embryonic neuraxis (n-) (Fig. 1b<sub>1</sub>). Thus, the n-



**Fig. 1.** a: Location of four hair plates (HP) and three hair rows (HR) on stick insect scapal (red) and pedicellar (blue) antennal segments. Schematic top view of the head with joints of the right antenna (top) deflected to their dorsal extreme. d: dorsal; dl: dorso-lateral; dm: dorso-medial; v: ventral; vl: ventro-lateral; vm: ventro-medial. Image adopted from Krause et al. (2013). b: Schematic sagittal section with locations of the cerebral ganglion (CRG) and gnathal ganglion (GNG) within the head of the stick insect. Image modified after Bässler (1965). b<sub>1</sub>: Differences of directional terms for body axis (black) and neuraxis (n-; blue). All neuroanatomical descriptions for the cerebral ganglion (CRG) are following the neuraxis (n-). For example the dorsal part of the CRG according to the body axis becomes n-ventral according to the neuraxis.

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