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CENTRAL PROJECTIONS OF CUTICULAR MECHANORECEPTORS IN SPIDERS: THE SPECIFICITY OF PROXIMAL LEG SENSILLA

INTRODUCTION

In the wandering spider, *Cupiennius salei* Keys. (Ctenidae), stimulation of tactile hairs located on the ventral aspects of proximal leg parts elicits tactile reflexes in prosomal muscles and evokes "body raising" in freely moving animals (Eckweiler and Seyfarth 1988; Milde and Seyfarth 1988). The ventral "coat" of tactile hairs can be as dense as 400 hairs/mm^2 of leg surface. To provide a framework for an investigation of specific synaptic connections of hair afferents in the leg ganglia, we have selectively cobalt-filled the axons of particular (i.e. identifiable) mechanosensory hairs and compound ("lyriform") slit sense organs on the proximal leg segments and the sternum. Our results show that the projection pattern of each sensillum type in the fused subesophageal ganglia is specific and surprisingly constant from preparation to preparation.

METHODS

Nerve branches, single axons and sensory cell somata and dendrites were traced by retrograde cobalt impregnations of the leg-nerve in *Cupiennius* as described previously (Seyfarth et al. 1985). To trace the afferent projections within the subesophageal ganglion complex, selective anterograde cobalt fillings of 1 to 5 sensilla in a given leg area were carried out in vivo (2.5 % cobalt chloride solution; overnight diffusion) similar to methods described by Altman and Tyrer (1980) . The preparations were silver-intensified (Bacon and Altman 1977); drawings of afferent projections in the leg ganglia were reconstructed from serial sections using a light-microscope with a drawing-tube attachment. We used selective cobalt-staining of serrated tactile hairs (Fig. 1) located near the sensilla in question to confirm the specificity of each new projection pattern and to control against misinterpretation resulting from accidental parallel fillings.

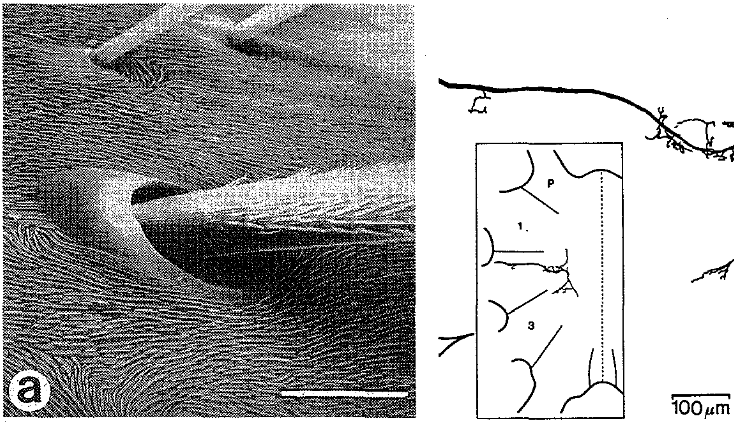

Fig. 1 a, b. Serrated tactile hairs on the leg femur. **a** Stereoscan micrograph (SEM) of hair socket and proximal hair shaft; scale bar: 20 μm . **b** Anterograde cobalt-fill of sensory ending entering second leg-neuromere on left body side (L2) ; dorsal view. Inset: position of sensory ending in left half of fused subesophageal ganglia drawn on reduced scale: outlines of leg neuromeres (1-4), pedipalpal ganglion (P), and their septal partitions; longitudinal midline is dotted

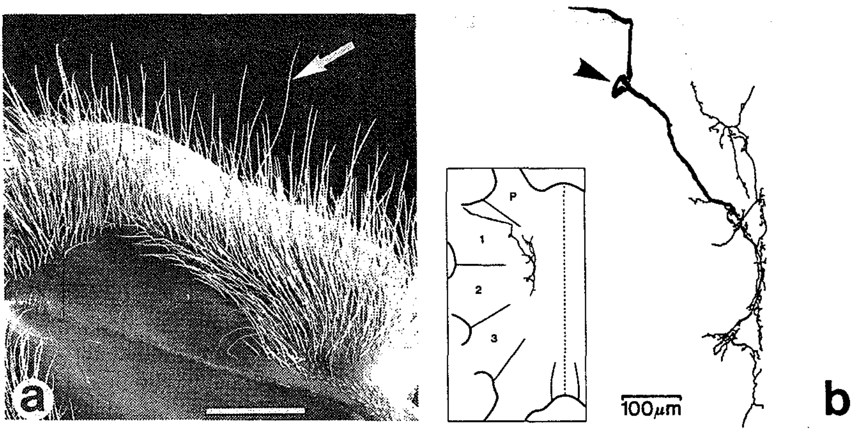

Fig. 2 a, b. "Whip-shaped" hair on ventral leg coxa. **a** SEM; anterior view of coxa, ventral side up; scale bar : 1 mm . Hair differs from other neighboring tactile hairs by the particular shape and length of its shaft (white arrow). **b** Axon enters neuromere (L1 in this example) via anterior sensory nerve and ascends in a loop (arrowhead) before it branches extensively into longitudinal central tracts (inset and abbreviations as in Fig. 1)

RESULTS AND DISCUSSION

Figures 1 to 4 show representative examples for mechanoreceptive hairs and slit sensilla located on the ventro-lateral coxa, trochanter, and femur of walking legs. Each reconstruction of the specific projection pattern in the leg ganglia is shown in dorsal view.

(i) The vast majority of tactile hairs are serrated bristles (Fig. 1a) which are innervated by 3 mechanosensitive cells. Typically, part of the terminations are confined to the very ventral region of the ipsilateral neuromere, while one of the axons ascends gradually and arborizes in mid-ventral neuropil (Fig. 1b). Some of these latter terminals reach into the neighboring, ipsilateral neuromeres and merge into plurisegmental, longitudinal tracts previously described by Babu and Barth (1984).

(ii) Single, especially long serrated hairs are located on the sternum and the ventral coxa (Fig. 2a). In addition to their exceptional length (ca. 2 mm), they are easily identified by the particular "whip-shape" of their hair shafts (Fig. 1a). One of the 3 sensory cells supplying these hairs enters the ganglion ventrally and ascends steeply in a loop (Fig. 2b) before it projects into the neighboring posterior neuromere; the central terminals merge into plurisegmental, longitudinal tracts. Projections of the 2 remaining sensory cells appear to be confined to the ventral part of the ipsilateral leg neuromere.

(iii) The afferents of coxal hair plate sensilla (Fig. 3 a ; each hair is innervated by only a single, bipolar mechanosensitive cell) enter the ganglion via separate, small sensory nerves and terminate within the ipsilateral neuromere. The axons of sensilla from both the anterior and the posterior hair plate arborize in a characteristic, 3-pronged fork and are confined to a ca. 100 µm-thick horizontal neuropil layer (Fig. 3b). It is interesting to note here that the central projections of long "smooth" hairs , which are also located on the coxa (singly innervated: Eckweiler et al. 1988), branch in a somewhat similar fork-like pattern but have a typical long , central prong.

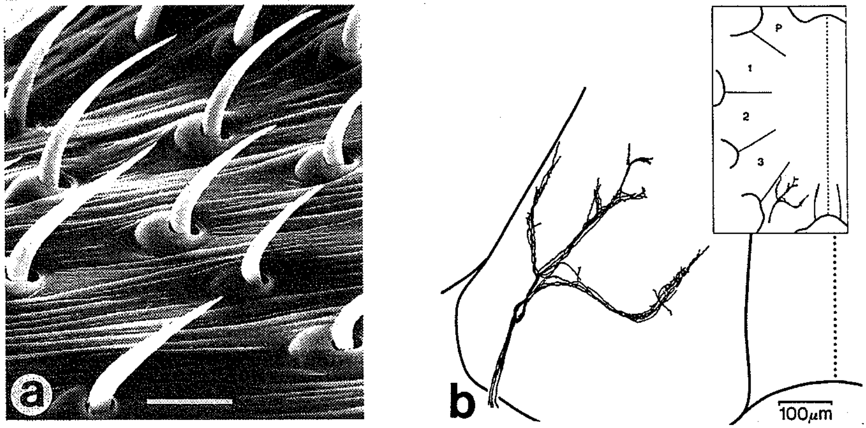

Fig. 3 a, b. Coxal hair plate sensilla. **a** SEM of several hairs and their sockets within the anterior plate; scale bar: 20 μm . **b** Central projection pattern of 4 axons in left hindleg neuromere; typical arborization (shape resembles 3-pronged fork) is confined to ipsilateral neuromere (inset and abbreviations as in Fig. 1)

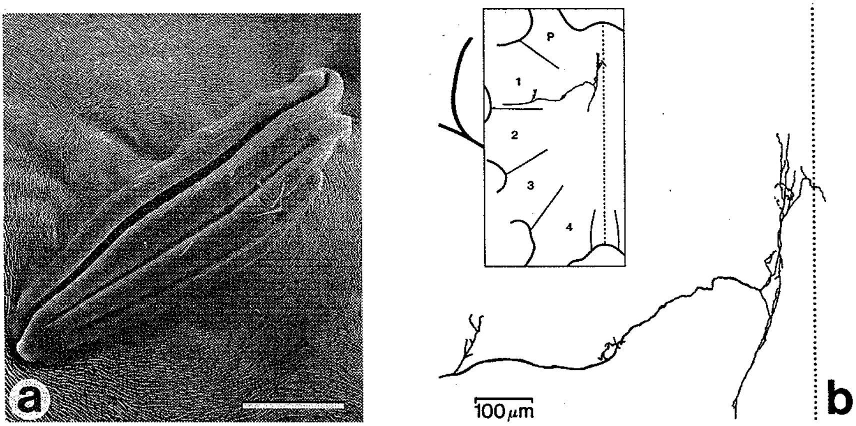

Fig. 4 a, b. Lyriform slit sense organ (HS-1) located on the posterior side of leg coxa. **a** SEM of cuticular slit structures; scale bar: 25 μm. **b** Axon enters leg neuromere (L1) via posterior coxal nerve and, after ascending, branches in dorsal-most central sensory tract near longitudinal midline of subesophageal ganglion complex (inset and abbreviations as in Fig. 1)

(iv) Axons from lyriform organ HS-1 on the posterior coxa (Fig. 4a ; 3 slits, each dually innervated) enter the leg ganglion dorsal to the hair afferents mentioned above. They ascend gradually. Typically, one of the axons gives off a small anterio-ventral branch after entering the leg neuromere; it arborizes extensively in the central part of the neuropil (Fig. 4b). The central terminals merge into the innermost dorsal, longitudinal tract near the longitudinal midline of the ganglionic complex. As yet it is unclear whether the 2 cells innervating each slit have similar projection patterns.

Somatotopically, cuticular sense organs on the proximal leg segments (such as coxa and trochanter) tend to project into mid-ventral neuropil, while those on more distal leg parts (i.e. the femur) project into more dorsal areas.

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Jocqué: Could you indicate how the knowledge of the innervation patterns of sensilla and sensory organs can help to explain behaviour?

Seyfarth: It is one of the basic data we need, together with data from other fields, e.g. electrophysiology, to understand simple behaviour such as body raising.

Schmidt: Findet man die gleichen Haartypen, die Sie uns bei Cupiennius gezeigt haben, auch bei Jagd- und Netzspinnen anderer Familien von Labidognathen und Orthognathen?

Seyfarth: Ja, wir haben z.B. die coxalen Borstenfelder bei mehreren, ganz verschiedenen Spinnenfamilien gefunden, bei Pisauridae, Araneidae, Ctenidae und Sparassidae. Auch die gefiederten Tasthaare sind für viele Familien beschrieben (s. Arbeiten von Foelix et al.).

Platen: Does the loop in some of the efferent neurons has a special function?

Seyfarth: It may be a loop around a blood vessel or a construction necessity of the steep ascendence of the neurons to give more elasticity.