

Sensory projections of identified coxal hair sensilla of the scorpion *Heterometrus fulvipes* (Scorpionidae)

K SASIRA BABU, K SREENIVASULU and V SEKHAR
Department of Zoology, S V University P G Centre, Kavali 524 201, India

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Abstract. The topography of long hair sensilla on the coxae of walking legs and pedipalps of the scorpion *Heterometrus fulvipes* is described. Identified long hair sensilla are cobalt filled, and central projections of sensory fibres are reported for the first time in the suboesophageal ganglion of this scorpion. The afferent fibres arising from each long hair sensilla segregate into ventral, dorsomedial and dorsal tracts upon their entry into the suboesophageal ganglion. These transverse tracts bifurcate towards the middle of the leg neuromere and form three ipsilateral, plurisegmental, longitudinal sensory pathways. Filling a pair of bilaterally distributed long hair sensilla shows bilaterally arranged longitudinal afferent tracts interconnected by distinct transverse commissures. Similar patterns of sensory projections are observed when filling homologous hairs on other legs and pedipalps. Numerous fine collaterals arise from the longitudinal sensory tracts that subdivide and end in small blebs presumed to be presynaptic endings. The dorsal and dorsomedial longitudinal tracts and their respective commissures are in close association with the dendritic arborisations of pedipalpal and leg motor neurons, suggesting direct contact between them. The probable functions of these multisegmental hair afferent pathways are discussed.

Keywords. Long hair sensilla; central projections; cobalt staining; scorpions.

1. Introduction

Although recent studies on central projections of cuticular receptors in spiders have been described (Eckweiler and Seyfarth 1988; Babu and Barth 1989; Eckweiler *et al* 1989; Seyfarth *et al* 1990; Anton and Barth 1991), similar studies for comparative evaluation are lacking in other important arachnids like the scorpions. Of the various types of cuticular receptors described in scorpions (Kasaiah *et al* 1989; Babu *et al* 1993), the long hair sensilla (LHS) are the most conspicuous and ubiquitously distributed tactile sensilla. Earlier histological (Venkateswara Rao 1963; Foelix and Schabronath 1983), physiological (Babu and Sanjeeva Reddy 1967; Sanjeeva Reddy 1971) and behavioural (Palka and Babu 1967; Kasaiah 1989) studies indicate a mechanoreceptive function for LHS.

Our studies have shown that each LHS is innervated by seven bipolar sensory

Abbreviations used: LHS, Long hair sensillum; SOG, suboesophageal ganglion; VTT, ventral transverse tract; DMT, dorsal median tract; DT, dorsal tract; VLST, ventral longitudinal sensory tract; AVT, anterior ventral transverse tract; CVT, central ventral transverse tract; PVT, posterior ventral transverse tract; VDC, ventrodorsal connective; DMLST, dorsomedial longitudinal sensory tract; ADC, anterior dorsal commissures; M DC, medial dorsal commissure; DLST, dorsal longitudinal sensory tract; PDT, posterior dorsal transverse tract; AVC, anterior ventral commissure; CVC, central ventral commissure; PVC, posterior ventral commissure; ADT, anterior dorsal transverse tract; PDC, posterior dorsal commissure; PDN, pedipalpal nerve; VNC, ventral nerve cord.

cells (Kasaiah *et al* 1989), and the axons arising from it project ipsilaterally into four successive ganglia of the ventral nerve cord (Babu *et al* 1993). Such long through-conducting sensory systems are unique among invertebrates, and it would be interesting also to know the organizational pattern of these hair sensilla in the anterior fused suboesophageal ganglionic mass of the scorpion. A detailed study on the projection patterns could be an anatomical basis for understanding the defensive behaviour of the scorpions (Palka and Babu 1967; Kasaiah 1989). It may also serve as a guide for future physiological studies.

Accordingly we report here for the first time, an analysis of the afferent sensory projections from identified single, as well as homologous pairs of hairs located on coxal segments of the pedipalpal and walking legs of the scorpion, *Heterometrus fulvipes* (C L Koch 1838).

2. Materials and methods

The scorpions, *H. fulvipes* were obtained from shrub jungles nearby our campus and maintained under the laboratory conditions.

2.1 Mapping of the hair sensilla

Adult scorpions were fixed ventral side up to a dissection board and the number and distribution of LHS on the coxal segments of the pedipalps and walking legs were examined under a binocular stereomicroscope.

Drawings were made with the help of a camera lucida. Representative hairs were pulled out and the length and diameter of the hairs were measured with an ocular micrometer.

2.2 Cobalt fillings

Anterograde cobalt fillings were done as described earlier (Babu and Barth 1989; Babu *et al* 1993). The cuticular surface at the base of selected LHS was scraped till the subcutaneous membrane was exposed. A small vaseline cup was made around the sensillum and filled with distilled water. After 10 min the distilled water was replaced with a mixture of 4% cobalt chloride in scorpion ringer (Padmanabha Naidu 1967) containing Triton-X (1 drop in 100 ml of CoCl_2) and sealed with vaseline.

The preparation was kept at 4° C for 24–36 h and the cephalothoracic nerve mass was quickly isolated and transferred for 10 min to 10 ml ringer solution containing two drops of concentrated ammonium sulphide. Later the tissue was washed in fresh ringer and fixed in Bouins for 6–10 h. Excess picric acid in the ganglion was removed by washing the nerve mass overnight in 70% alcohol. Cobalt precipitated in the neurons of the suboesophageal ganglion (SOG) was silver intensified as per Bacon and Altman (1977) with slight modifications (Babu and Barth 1989). After dehydration and clearing in methyl salicylate, observations were made from either whole-mounts or hand sectioned materials (about 200 μm thick).

3. Results

3.1 Topography of long hair sensilla

The distribution of LHS on coxal segments of adult scorpions is shown in table 1. The location of each hair sensillum on the coxal segments is remarkably constant. The hairs are arranged bilaterally in homologous pairs (figure 1). The LHS are mostly distributed on the edges of each segment while the middle portion is almost devoid of hairs. Each LHS is suspended in low rimmed sockets on the cuticular surface permitting a wide range of hair movements. The tactile hairs are inserted into the cuticle either straight or at an angle, depending upon their location on the coxal segments. The shaft lengths ranging from 2100–3000 μm decrease gradually in diameter from base (40–50 μm) towards the distal end (10 μm).

Table 1. Distribution of long straight hair sensilla on the coxae of the pedipalps and walking legs of the adult scorpion, *H. fulvipes*.

Appendage	Number of LHS on coxal segments	Standard deviation	Coefficient of variation	Maximum length of the hair (μm)
Pair of pedipalps	54	0.083	0.15	3000
1st pair of walking legs	12	0.083	0.72	2600
2nd pair of walking legs	32	0.160	0.51	2500
3rd pair of walking legs	28	0.160	0.58	2500
4th pair of walking legs	24	0.083	0.35	2100

Each number is the average of twelve animals

3.2 Central projections

The sensory projections were observed from wholemounts or from hand sectioned materials. A total of fifty good cobalt filled preparations were used in the present study. The following criteria were used for identification of the sensory fibres: (i) they enter the leg neuromere *via* the leg nerve, (ii) they are not connected to cell somata in the CNS and (iii) they branch extensively and form small blebs which are presumably presynaptic.

3.2a Single hair projections: The afferent fibres arising from the seven bipolar cells of a single LHS located on the left second coxal segment, enter the SOG through the ipsilateral ambulatory leg nerve (figure 2). On entering the leg neuromere the sensory axons divide into a dorsal and a ventral bundle of fibres. The ventral bundle consisting of three sensory axons runs further midcentrally as ventral transverse tract (VTT), whereas the dorsal bundle consisting of four axons divide into a dorsal median (DMT) and a dorsal tract (DT).

(i) *Ventral longitudinal sensory tract:* Towards the middle of the leg neuromere the

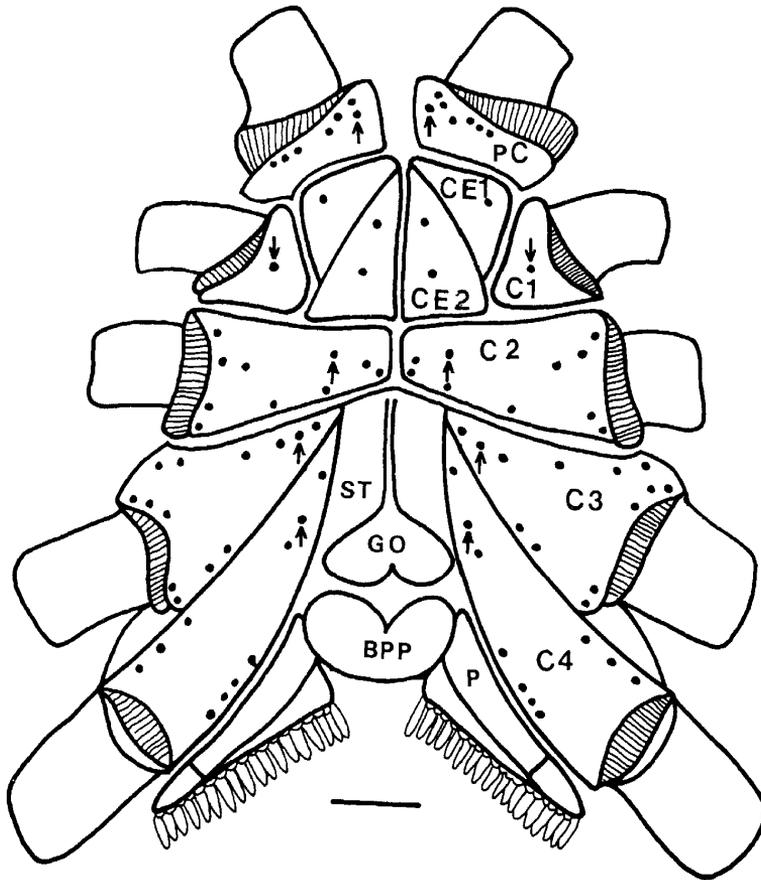


Figure 1. Ventral view of the cephalothorax of the scorpion, *H. fulvipes* showing positions of LHS (●) on the coxal leg and pedipalpal segments. Cobalt filled sensilla are shown by an arrow (↑) mark. BPP, Basal piece for pectines; C 1-4; coxae of 1st to 4th pair of walking legs; CE 1, coxal endite 1; CE 2, coxal endite 2; GO, genital operculum; P, pectines; PC, coxa of pedipalps; ST, Sternum. Scale Bar: 1.5 mm.

VTT bifurcates, sending fibres anteriorly and posteriorly, forming an ipsilateral ventral longitudinal sensory tract (VLST, figure 2). This tract is 1000 μm long and 30 μm thick. It extends anteriorly up to the pedipalpal ganglion and descends posteriorly up to the abdominal ganglion of the suboesophageal mass. Along its course numerous short lateral collateral branches arise that subdivide to form a fine mesh ending in small blebs. Such blebs in insects are considered as presynaptic endings (Tyrer and Altaian 1974). At the anterior, middle and posterior region of VLST, longer collateral fibres arise that cross the midcentral region of SOG and form three transverse tracts. Of these, the anterior ventral transverse tract (AVT) is located anterior to the first leg neuromere. The second tract, viz., central ventral transverse tract (CVT) is located at the second leg neuromere. The third viz., posterior ventral transverse tract (PVT) is located at the fourth leg neuromere.

(ii) *Dorsomedial longitudinal sensory tract*: The DMT (figures 2 and 4C), ascends

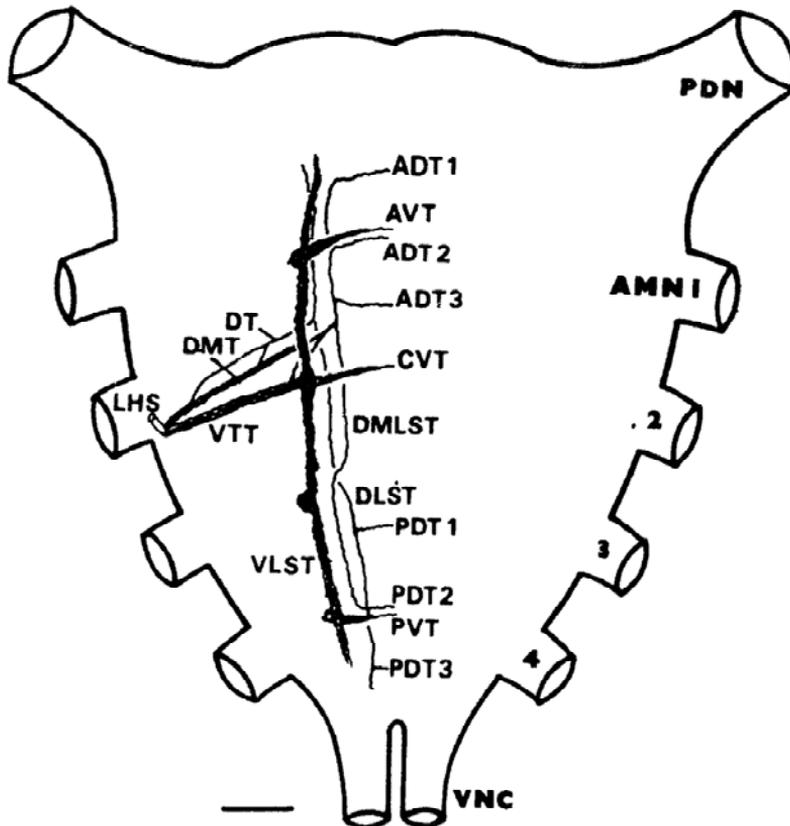


Figure 2. Central projections from a single LHS located on the second left coxal leg segment of the scorpion. View from the ventral side of a wholemount cobalt preparation of the SOG. Sensory fibres enter the leg neuromere and divide into three transverse tracts (VTT, DMT and DT). Each tract towards the midcentral region of the leg neuromere bifurcates into an anterior and posterior pathway. Thus three ipsilateral longitudinal sensory tracts (VLST, DMLST and DLST) are formed. Longer collateral fibres from these multisegmental pathways form transverse tracts, like AVT, CVT and PVT from VLST; ADT 1–3 from DMLST; PDT 1–3 from DLST. Scale Bar: 0.5 mm.

and extends transversely towards the middle region of the leg neuromere. One or two axons from VTT join DMT through the ventrodorsal connective (VDC, figure 3). DMT extends further into the dorsal ganglionic neuropil and bifurcates anteriorly and posteriorly forming an ipsilateral dorsomedial longitudinal sensory tract (DMLST, figure 2). The posterior segment of DMLST consisting of about two fibres extends up to the 4th leg neuromere. Along its posterior course numerous fine collaterals arise that subdivide and end in small blebs in the surrounding neuropil.

The anterior segment of DMLST extends up to the pedipalpal neuromere. Numerous short fine fibres arise along its course, branch extensively and terminate in the surrounding neuropil in small blebs. Longer collateral fibres crossing the mid-central region of the SOG form three transverse tracts [anterior dorsal commissures (ADC) 1–3] anteriorly.

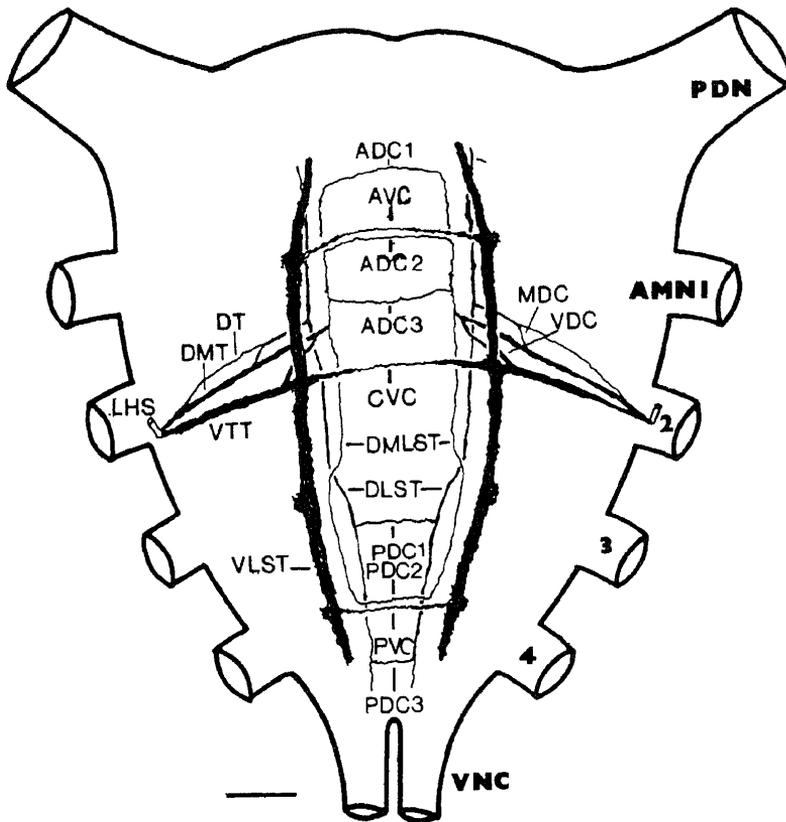


Figure 3. Projections from a pair of bilaterally distributed homologous LHS (ventral view of SOG). A mirror image of transverse tracts and longitudinal pathways obtained for left LHS, were also obtained for the right LHS. Consequently the two VLSTs are interconnected by three commissures (AVC, CVC and PVC); the two DMLSTs are joined by three anterior commissures (ADC 1–3) and the two DLSTs are interlinked by three posterior commissures (PDC 1–3). Scale Bar: 0.5 mm.

(iii) *Dorsal longitudinal sensory tract:* The dorsal transverse tract (DT, figures 2 and 4C) consisting of only one sensory axon ascends into the dorsal neuropil of the leg neuromere. A few branches from DMT join DT, through the medial dorsal connective (MDC, figure 3). The DT extends further towards the middle region of the leg neuromere where it divides into an anterior and posterior tract forming an ipsilateral dorsal longitudinal sensory tract (DLST, figures 2 and 4C) that passes through the dorsal most neuropil region of the SOG. The anterior segment of DLST, extends up to the pedipalpal ganglion and gives off on its way to numerous small collateral branches that subdivide into finer branches and end in small blebs. In contrast to this, the posterior branch of DLST receives one or two fibres from DMLST and extends posteriorly up to the abdominal ganglionic neuropil. On its way longer collaterals crossing the mid central region of SOG form three posterior dorsal transverse tract (PDT). The pattern of single hair projections described is typical of coxal hairs in the two pedipalpal and four pairs of walking leg ganglion in the suboesophageal mass.

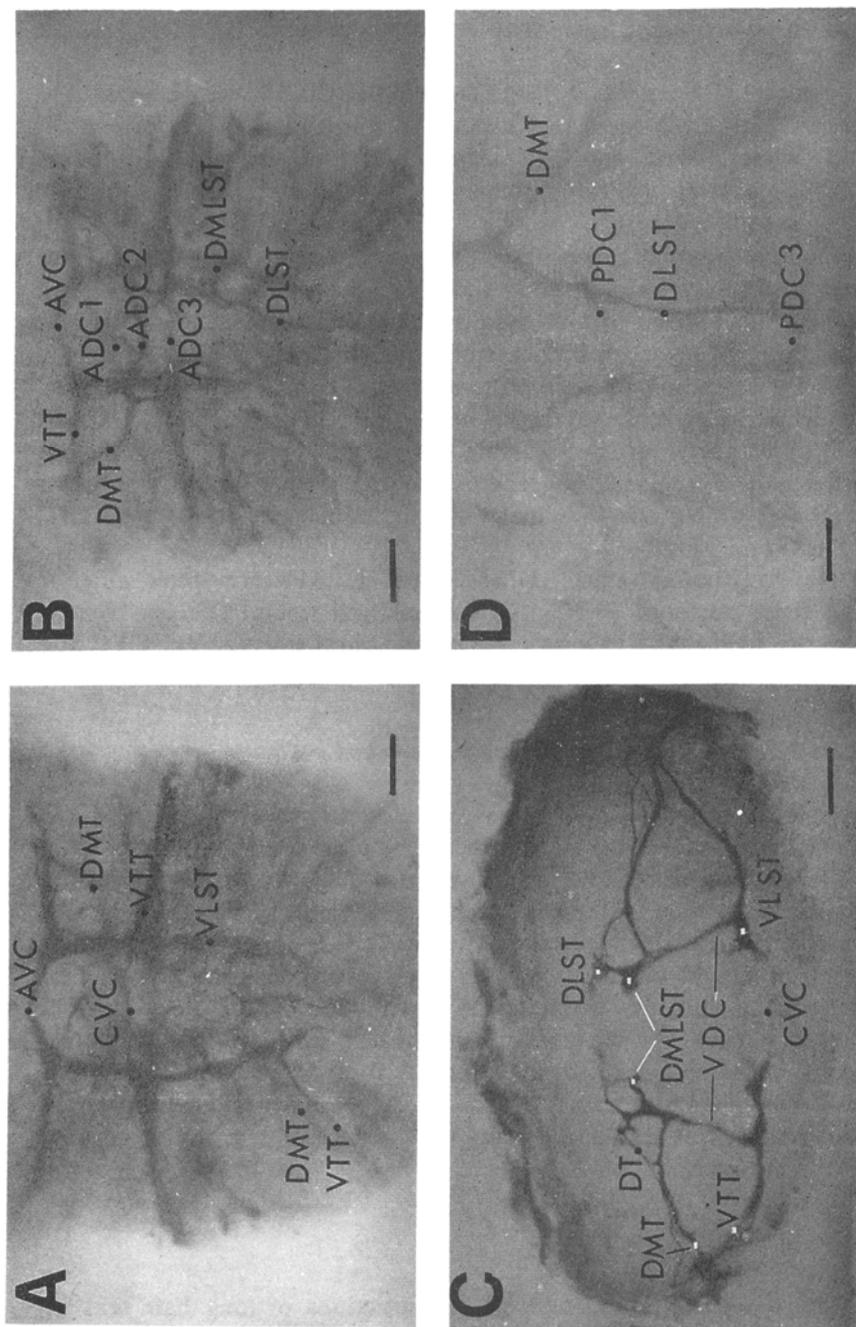


Figure 4. Cobalt filled hair afferents from wholmount preparations of SOG after silver intensification. (A) Distribution pattern of primary sensory fibres arising from homologous pair of LHS located on 1st, 2nd and 4th pair of walking legs. Note the bilaterally distributed transverse (VTT, DMT) and VLST. Ventral view. Scale Bar: 50 μ m. (B) Same as (A) when viewed from the dorsal side, shows DMLST and DLST, along with transverse commissures (AVC, ADC 1-3). Scale Bar: 50 μ m. (C) Transverse section of the SOG (200 μ m). Cobalt filling of a pair of bilaterally situated LHS shows spatial distribution of the three pairs of transverse (VTT, DMT and DLST), sensory tracts, VLSTs run along the ventral region of the neuropil. Whereas DMLSTs and DLSTs are located at the dorsal region of the neuropil, where dendritic arborizations of motor neurons are located. Top side is the dorsal region of SOG. Scale Bar: 100 μ m. (D) Bilateral arrangement of DLST along with transverse commissures (PDC 1 and 3). Scale Bar: 200 μ m.

3.2b *Projections from one pair of hair sensilla*

Filling a pair of identical hairs on left and right side of a segment shows, apart from the transverse (VTT, DMT and DT) and longitudinal (VLST, DMLST and DLST) tracts, fully formed commissural tracts that cannot be obtained by filling a single hair.

When two bilateral hairs are cobalt filled (figure 3) two VLSTs are obtained. The longer collaterals arising from these two sensory tracts on both sides, form AVT, CVT and PVT, whose fibres cross the midline and form the anterior ventral commissure (AVC), central ventral commissure (CVC), and posterior ventral commissure (PVC).

Similar commissural tracts are also observed to form from DMLST. The three ipsilateral anterior dorsal transverse tracts (ADT 1-3) arising from DMLST of both sides form three distinct anterior commissural tracts (ADC 1-3). Such commissural tracts are absent from the posterior branches of DMLST. Cobalt filling of a pair of hairs also shows the formation of three posterior dorsal commissural tracts (PDC 1-3) arising from the longer collateral branches of the left and right sides of the DLST. Figure 3 shows tracts formed by filling homologous pair of hair sensilla on the coxae of 2nd pair of walking legs. There are three pairs of transverse tracts (VTT, DMT and DT) which form three pairs of longitudinal sensory tracts (VLST, DMLST and DLST).

The two dorsal longitudinal tracts (DMLST and DLST) form three anterior (ADC 1-3) and three posterior (PDC 1-3) commissural tracts. The two ventral longitudinal sensory tracts (VLST) form three commissural tracts (AVC, CVC and PVC).

3.2c *Projections from hair sensilla on all walking legs and pedipalps*

Identified bilaterally distributed pairs of hairs on coxal segments of pedipalps and of four pairs of walking legs are also cobalt filled. The basic central organization of afferent fibre tracts described earlier for a pair of hairs is found for paired homologous hairs located on other coxal segments (figure 5). The longitudinal tracts (VLST, DMLST and DLST) and the anterior (ADC 1-3) and posterior (PDC 1-3) commissural tracts however are thicker and contained more fibres. This increase in fibre content obviously is due to the contribution of sensory axons from all ipsilateral sensory hairs. The sensory axons from hair sensilla of the pedipalpal and of four pairs of walking legs together join to form the ventral and dorsal longitudinal and commissural tracts. Thus a specific pattern of arrangement in SOG is noticed in formation of central tracts by afferent fibres arising from long hair sensilla of the scorpion.

4. Discussion

The foregoing morphological study on central projections of long hair sensilla, demonstrates for the first time complex distribution pattern of primary afferent fibres in the suboesophageal ganglion of the scorpion *H. fulvipes*. A remarkable feature of the central projections of hair afferents is their extensive distribution in SOG, forming conspicuous longitudinal and commissural tracts which may relay

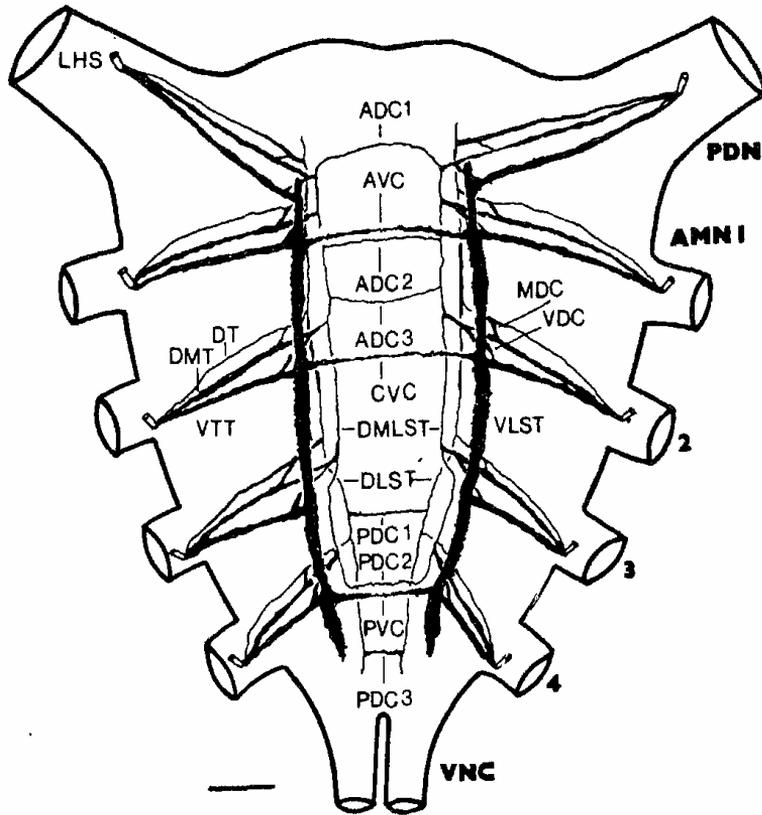


Figure 5. Projections of single hair afferents from the coxal segments of eight walking legs and the two pedipalps. The pattern of arrangement of transverse and longitudinal tracts obtained by filling a pair of bilateral hairs, is repeated for other bilateral hairs located on other coxal segments. Fibres from all five ipsilateral VTTs converge to form one ipsilateral VLST. And the two VLSTs from each half of the SOG are interconnected by three commissures (AVC, CVC and PVC). Fibres from the other two transverse tracts (DMT and DT) from each of the five ganglia, like wise join to form the respective ipsilateral longitudinal tracts (DMLST and DLST) which are inturn connected by three anterior (ADC 1-3) and three posterior (PDC 1-3) commissures. Scale Bar: 0.5 mm.

tactile information directly to all ipsilateral and also to contralateral leg and pedipalpal ganglia for eliciting quick and coordinated activity of the cephalo-thoracic appendages.

4.1 Comparison with other cuticular sensilla in arthropods

The earliest neuroanatomical studies on the CNS of scorpion by Hanström (1921, 1928) were based on Golgi and silver impregnation studies. Yellamma (1980) using cobalt sulphide method reported that the sensory neurons terminate as simple endings in the respective segmental ganglion. Babu (1965) first described dorsal and ventral transverse sensory tracts in the SOG but did not discriminate between different species of sensory neurons. Filling targeted hair sensilla, we have now

shown that these sensory tracts arise from the LHS located on the coxal segments of the pedipalpal and walking legs of the scorpion. LHS located on other segments of these appendages also contribute their afferents to the tracts described in the present study (unpublished observations). Thus these sensory pathways seems to provide plurisegmental ipsilateral afferent input to integrating centres of the SOG.

Among arthropods, the majority of the sense organs are innervated by a single neuron and sensory endings are restricted to the homolateral region of a single ganglion (Bullock and Horridge 1965). In spiders the central endings of long smooth hairs (Eckweiler *et al* 1989) and coxal plates (Seyfarth *et al* 1990) are limited to the ipsilateral leg neuromere. The cobalt method also reveals that afferents from cereal hairs in crickets (Murphey 1985) are restricted to the ipsilateral half of the last abdominal ganglion. Similarly in locusts the multipolar sensory cells (Bräunig *et al* 1981), strand receptors (Bräunig and Hustert 1980), chordotonal organs (Bräunig and Hustert 1980), companiform sensilla (Hustert 1978; Hustert *et al* 1981) and single hairs (Altman and Kien 1979; Pflüger 1980) are restricted to the ipsilateral half of the ganglion.

However, in some arthropods anatomically and physiologically identified first order sensory neurons having multisegmental distribution were reported. In locusts the mechano-receptors like companiform sensilla on head (Gewecke 1979; Tyrer *et al* 1979), chordotonal organs on thorax and abdomen (Hustert 1978; Bräunig and Hustert 1980; Pflüger *et al* 1988) and wing stretch receptors on thorax (Altman and Tyrer 1974) are plurisegmental. In *Manduca* larvae hair sensory neurons on abdominal segments extend their processes to both anterior and posterior ganglia (Levine *et al* 1985). In lobsters (Alexandrowicz 1951) and crayfish (Wiersma and Hughes 1961; Fields and Kennedy 1965) the afferent fibres from muscle receptor organs enter the cord and divide into anterior and posterior branches extending from brain to the last abdominal ganglion. In the spider, *Cupiennius salei*, the afferents of silt sensilla (Babu and Barth 1989) and trichobothria (Anton and Barth 1991) enter the leg ganglion and divide to form multisegmental longitudinal sensory tracts.

The fact that a single LHS in scorpions is innervated by as many as seven sensory cells suggests its probable functional diversity (Sanjeeva Reddy 1971; Babu *et al* 1993). The central projections of afferent fibres from each hair sensillum in scorpions are characteristically different from that of other arthropods as they form extensive and complex transverse and longitudinal tracts providing direct sensory input to each pedipalpal and four walking leg ganglia.

In the scorpion hair afferents do not branch on entering the leg neuromere but give off extensive small collateral fibres along the course of the three longitudinal tracts with some fibres crossing over to the opposite half of the ganglion. In spiders (Babu and Barth 1989; Eckweiler and Seyfarth 1988), however the afferents on entering the leg neuromere first give off numerous large collateral branches, while the formation of longitudinal tracts is not as extensive as in the scorpions. The fast turning responses elicited by deflecting a hair (Palka and Babu 1967; Kasaiah 1989) are thus attributable to the multi-segmental sensory pathways in the scorpion.

4.2 Synaptic contacts

The available data points to particular areas which are likely to have input-output contacts if one considers the branching pattern and the presence of bleb-like

structures as indications of synaptic contacts as is usually done in Insects (Tyner and Altman 1974). The anatomical studies of Babu (1965) and Bowerman and Burrows (1980) have reported two groups of motor neurons located for each leg ventrally in the SOG near the entrance of each leg nerve. Injecting cobalt sulphide into single motor neurons, Bowerman and Burrows (1980) showed numerous dendritic branches that profusely ramified in the dorsal neuropil of each leg ganglion.

In the present study the formation of a tactile sensory field is noticed in the midcentral and dorsal region of leg ganglia as a result of extensive branching of the three transverse sensory tracts (VTT, MDC and DT). Moreover the dorsomedial and dorsal longitudinal sensory tracts, also pass through the dorsal neuropil of the four ipsilateral leg and pedipalpal ganglia. Collateral branches forming commissural tracts also terminate in the dorsal neuropil of the contralateral leg ganglia. The finer branches terminate as small blebs. Thus the primary afferents may form monosynaptic contacts with ipsi- and contralateral motor neurons as judged from the available anatomical evidences.

4.3 Importance of long hair sensilla

The LHS serve as mechanical antennae protruding conspicuously on the body of the scorpion. Regarding their number they are second only to short white hairs and are arranged along the longitudinal axis of the appendages on prominent ridges. The LHS are distributed at constant locations and are arranged bilaterally in homologous pairs (Kasaiah 1989; Jacob Doss 1990). Moreover the density of LHS increases from proximal to distal segments on legs, pedipalps and metasoma (Foelix and Schabronath 1983; Moro and Geethabali 1985, 1986; Kasaiah 1989). These important morphological features of LHS indicate that they constitute an important category of cuticular receptors of the scorpion.

4.4 Sensory hairs as mechanoreceptors

On the basis of histological studies Venkateswara Rao (1963) and Kasaiah *et al* (1989) have classified LHS as mechano-receptors. Foelix and Schabronath (1983) through EM studies also reported them as mechanoreceptors. The electrophysiological studies of Babu and Sanjeeva Reddy (1967), Sanjeeva Reddy (1971), Brownell and Farley (1979a, b) and the recent studies of Babu *et al* (1993) have also considered these hair sensilla as tactile receptors. Removal of LHS on various body segments results in general flaccidity and the absence of withdrawal response in scorpions (Sanjeeva Reddy 1969; Kasaiah 1989).

According to Palka and Babu (1967) and Kasaiah (1989), deflecting hair sensilla on the leg segments of an agitated scorpion, immediately produces a turning response with raised pedipalps towards the source of stimulus. This fast coordinated leg and pedipalpal reflex activity is suggested to be mediated by the long plurisegmental sensory pathways arising from the long hair mechanoreceptors of the scorpion. This presumably is the functional significance of LHS.

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