Fine Structure of the Ventral Organ of the House Fly Larva, *Musca domestica* L.*

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Summary. The ventral organs of the cephalic lobes of the house fly larvae, *Musca domestica* L., were studied by scanning and transmission electron microscopy. Four sensilla were found. Three of them are each innervated by a single dendrite whose ending possesses a tubular body and communicates to the exterior through an opening. These sensilla are assumed to be mechanoreceptors. The 4th sensillum is supplied by 2 bipolar neurons with the unbranched dendritic tips (without tubular bodies) exposed to the exterior through a single opening and is probably a contact chemoreceptor.

Key words: Sensilla — Insecta — Diptera — *Musca domestica* L. — Ultrastructure.

Introduction

The cephalic lobes of the house fly larvae, *Musca domestica* L. (Diptera: Muscidae), have 3 pairs of sensory organs. Bolwig (1946) named these the dorsal, terminal and ventral organs. The fine structure of the dorsal and terminal organs has been described (Chu and Axtell, 1971; Chu-Wang and Axtell, 1972). The fine structural analysis of the ventral organ (also named "maxillary sense organ" by Ludwig, 1949) is presented in this paper.

Materials and Methods

Cephalic lobes of house fly larva (*Musca domestica* L., third-instar) were fixed in cold 5% glutaraldehyde with sodium-cacodylate buffer for 20 hours and post-fixed in 1% OsO₄ with veronal-acetate buffer (Palade, 1952) for 2 hours. The tissues were dehydrated in ethanol and embedded in hard Epon 812 over propylene oxide. Sections, cut on a Reichert Om U2 ultramicrotome with a diamond knife, were picked up with formvar-coated slot grids. After double-staining with uranyl acetate (in 50% ethanol) and lead citrate (Venable and Coggeshall, 1965), grids were examined in a Siemens Elmiskop 1A.

The whole larva, killed in hot water and coated with gold, was examined in a JEOL JSM-2 scanning electron microscope (SEM) for studying the external morphology.

Observations

The paired ventral organs are anterior to the mouth opening and are the simplest of the 3 cephalic sensory organs (Fig. 1). Externally the ventral organ is a lobe with 4 small pores (0.16 μ in diameter) in the center which can be detected with SEM (Fig. 2). These pores are the separate routes of communication of

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Fig. 1. Diagram of a longitudinal section of the cephalic lobe showing the dorsal, terminal and ventral organ. *Ax* axon; *BM* basement membrane; *BN* bipolar neuron; *C* cuticle; *CR* ciliary region; *Ep* epidermis; *Gl* glial cell; *Hc* haemocoel

the dendrites of 4 sensilla whose structure was studied by transmission electron microscopy. These sensilla are medially to laterally designated V_1 , V_2 , V_3 and V_4 .

V_1 , V_3 and V_4 are structurally the same. Each sensillum is innervated by one bipolar neuron concentrically ensheathed by an inner (trichogen) and an outer (tormogen) enveloping cell (Fig. 3). The conspicuous feature of this type of sensillum is that the dendritic tip possesses a tubular body (Thurm, 1964) and is exposed to the exterior environment through an opening (Fig. 4). The tubular body, a prominent characteristic of most mechanoreceptors, has the same regularly arranged microtubules and microfilaments as described in the terminal organ (Chu-Wang and Axtell, 1972). As usual in sensillar dendrites, a constricted ciliary region, about 25μ below the pore, divides the dendrite into an inner (proximal) and an outer (distal) segment. As in the terminal organ, there are 2 basal bodies in tandem in close proximity to the ciliary region, ciliary microtubules arise from the distal ends of the 2 basal bodies and rootlets extend from the proximal ends of both basal bodies (Figs. 5 and 6). In the constricted ciliary region there is a so-called "fibrillar body". This term is adopted from Smith (1969), who studied the haltere sensilla of a blowfly. A similar structure,

Fig. 2. Frontal view of the ventral organ showing 4 pore openings. The V_1 opening (arrow) is difficult to see in this photograph. SEM. $\times 1000$

referred to as an abnormal or modified ciliary structure, is also found in the mechanoreceptors of other flies (Uga and Kubawara, 1967; Thurm, 1970; Hansen and Heumann, 1971). Distal to the constricted ciliary region the dendrite is encased by an electron-dense dendritic sheath (cuticular sheath, scolopale).

The V_2 sensillum is supplied by 2 bipolar neurons (Fig. 3). The dendrites are bathed in an electron-transparent fluid secreted by the surrounding inner enveloping (trichogen) cell. The inner enveloping cell is again encircled by an outer enveloping (tormogen) cell. Both unbranched dendritic tips do not have tubular bodies and are exposed to the outside by means of the pore opening. About $30\ \mu$ below the opening, the dendrites are divided into 2 dendritic segments by a constricted ciliary region. The ultrastructure of the ciliary region is essentially the same as that in the V_1 , V_3 and V_4 sensilla.

The ganglion of the ventral organ is inside the cephalic lobe (Fig. 1) and ventral to the ganglia of the dorsal and terminal organs which have been previously described (Chu and Axtell, 1971; Chu-Wang and Axtell, 1972). The ganglion is composed of bipolar neurons, glial cells, trichogen cells, tormogen cells and epidermal cells. The nerve from the ventral organ unites proximally with that from the terminal organ and connects to the central nervous system below the oesophagus (Bolwig, 1946; Ludwig, 1949). The fine structural details of neuron cell bodies, glial cells and nerves are the same as in the dorsal and terminal organs. Cross sections through the distal part of the ganglion show 5 dendrites which innervate the 4 sensilla in the ventral organ. However, 7 axons are seen in cross sections of the nerve of the ventral organ. The innervation of the other 2 neurons was not determined.

Fig. 3. Cross section of the distal portion of the ganglion of the ventral organ showing the dendrites and their enveloping cells for sensilla V_1 , V_2 , V_3 and V_4 . V_2 contains 2 dendrites and the others 1 dendrite each. F fluid-filled vacuole; Ep epidermal cell. $\times 7700$

Fig. 4. Longitudinal section through the tip of the V_1 sensillum showing the dendritic ending containing a tubular body (TB) and exposed to the exterior through an opening (arrow). C cuticle; DS dendritic sheath. $\times 19000$

Discussion

Bolwig (1946) stated: "The whole structure of the terminal and ventral organs of the cephalic lobes as well as the fact that their nerves extend to the central nervous system below the oesophagus gives good reason to believe that the organs have a gustatory function". Unfortunately he was unable to prove his postulation from behavioral experiments. We found the ventral organ possesses 4 sensilla.

Fig. 5. Diagram of the dendritic ciliary region

Sensillum V_2 has the dendritic tips externally exposed through a single pore, and therefore probably is a contact chemoreceptor similar to those found in certain other insects (Dethier, 1955; Dethier *et al.*, 1963; Adams *et al.*, 1965). In sensilla V_1 , V_3 and V_4 , the dendritic tip has a tubular body, a characteristic of mechanoreceptors (Thurm, 1964), and communicates to the outside by means of a pore. It has been reported in a number of papers that the dendritic endings of mechanoreceptors are exposed to the outside environment through a pore (Moeck, 1968; Blaney and Chapman, 1969; Kendall, 1970; Corbière-Tichané, 1971; Chu-Wang and Axtell, 1972). This pore is formed by deposition of the cuticular material around the dendritic sheath during the moulting process (Gnatzy and Schmidt, 1971; Schmidt and Gnatzy, 1971) and is not involved in sensory reception. Therefore, sensilla V_1 , V_3 and V_4 probably are mechanoreceptors.

All 4 sensilla in the ventral organ have 2 basal bodies arranged in tandem proximal to the ciliary region. Ciliary microtubules as well as rootlets arise from these 2 basal bodies. This unique feature is observed in the dorsal, terminal and ventral organs of the house fly larvae but has not been reported in other arthropods (Steinbrecht, 1969; Slifer, 1970). The distal basal body sends 9-double microtubules distally and 9 rootlets proximally. From the proximal basal body we found single and double ciliary microtubules, the number varying from 3 to 14 and the number of rootlets seemed to vary from 4 to 8. An explanation

Fig. 6a—g. Corresponding to Fig. 5. a, Longitudinal section through the ciliary region. $\times 42000$. b and c, Cross sections at level 1 (Fig. 5) showing 9 outer double-ciliary tubules from the distal basal body and 10(b) or 14(c) inner tubules (single and double) from the proximal basal body. Note the fibrillar body (arrow) in between. $\times 90000$. d, Cross section at level 2 showing the distal basal body encircling the inner ciliary tubules from the proximal basal body. $\times 44000$. e, Cross section at level 3 demonstrating the proximal basal body (long arrow) surrounded by the 9 rootlets (short arrow) from the distal basal body. $\times 57000$. f and g, Cross sections at level 4 presenting 2 sets of rootlets. The 9 outer rootlets (short arrow) are extended from the distal basal body and the 6 (f) or 8 (g) inner rootlets (long arrow) from the proximal basal body. $\times 48000$; $\times 57000$

for the different number of tubules and rootlets in the distal and the proximal basal body is not known. Perhaps only certain triple-tubules in the proximal basal body could form the ciliary microtubules and rootlets.

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