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REVIEW ARTICLE

Neuroendocrine System and Neurosecretory Cells in Hymenoptera

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ABSTRACT

The neuroendocrine system in insects plays a vital role in regulating essential physiological processes such as development, reproduction, and metabolism. This system comprises neurosecretory cells in various anatomical regions across the insect body, including brain, ventral and sympathetic ganglia, corpora cardiaca, corpora allata, midgut, and gonads. The order Hymenoptera which includes ants, bees, wasps, and other related species serves as a key focus of study, providing insight into the functional integration of neuroendocrine signals in insect life. These signals coordinate various biological activities, influencing individual and colony-wide behaviors, reproductive cycles, and metabolic homeostasis. The review focuses on understanding the structure and function of the neuroendocrine system in order Hymenoptera, which can offer broader insights into the regulatory mechanisms underlying insect physiology and behavior, with potential implications for pest control, pollination ecology, and the evolution of complex social systems in insects.

KEY WORDS: Hymenoptera,Insects,Neuroendocrine system, Neurosecretory cells

INTRODUCTION

The processes in an insect's life cycle that require precisely coordinated control are embryonic and post-embryonic development, reproductive activity, and changing metabolic and behavioral patterns (Scharrer, 1987). Neuroendocrine system regulates different homeostatic mechanisms in insects, including reproduction, stress, growth and development, and diapause. Endocrine glands are themselves an integrated system where hormone production and release are controlled through feedback loops and the release of a hormone is controlled by negative feedback of endocrine system (Ewer *et al*., 1997).

Neuroendocrine system of insects includes

i) Neurosecretory cells in the brain, ventral and sympathetic ganglion,
ii) Corpora cardiaca and other neurohaemal organs,
iii) Corpora allata (CA) and
iv) Ecdysial gland.

Some neurosecretory activities are found in the midgut as well as gonads (Tembhare, 2012). Neuroendocrine systems in insects had been described anatomically based on several complementary investigative approaches. Rowell (1976) explained neurosecretory cells (NSCs) and neurohemal organs located throughout insect central and peripheral nervous systems by the histochemical, physiological, and ultrastructural detection of neurosecretory material in the insect body.

Numerous homeostatic processes are regulated by endocrine glands. These consist of the following: the control of major metabolic pathways (carbohydrate synthesis, storage, and release), the control of the ionic milieu through absorption and excretion, development and maturation of gametes, growth and regeneration of the body, and the activity of neurons, muscles, and pigment cells during specific behaviors (food intake, fight, and flight, and reproduction) (Hartenstein, 2006). Biogenic amines are important neuromodulators, neurohormones, and neurotransmitters in the honeybee (Blenau *et al.*, 1998).

Brain

Brain is organized bilaterally, and the protocerebrum, deutocerebrum and tritocerebrum are three segments of the brain that are fused into one cerebral ganglion

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(CRG) with less distinct borders (Dettner & Peters, 2011). Ozluk (1991) observed the brain of *Pimpala turionellae* consists of these three segments. There are two large optic lobes formed by combined eyes at both sides of the protocerebrum. Deutocerebrum is easily distinguishable and has two big lobes closely located to each other where antennal nerves come. Tritocerebrum and suboesophageal ganglion surround the esophagus completely hence, the nerve between these parts is very short. Thus, the suboesophageal ganglion also appears as part of the brain. No difference is observed in the brain anatomy of males and females (Ozluk, 1991).

The anterior midline of the brain is called pars intercerebralis which contains the largest collection of neurosecretory cells in the insect body (Raabe, 1989). The mini brain (smaller than one cubic millimeter) of honey bees contains 950,000 neurons. It could be indeed considered as having limited cognitive abilities (Giurfa, 2007).

The brain and ventral nerve cord are the two areas of the *Tetraponera rufonigra* body that have ganglions. The head capsule, which is attached to the compound eyes, contains the brain implanted in it. Two areas of the brain's structure are identified as (i) the outer cortex, which contains a variety of cell types such as neuroglia, neurosecretory cells, and neuronal cells, and (ii) the inner medulla, which is made up of a layer of nerve fiber without neuronal cells. These ganglia differed in location, but their fundamental elements are strikingly similar. There is an inner medulla and an outer cortex in every ganglion. Perhaps because of ganglia merging throughout insect evolution, the second and fourth ganglia are larger than the first thoracic ganglion (Somala *et al.,* 2020).

Most of the immune localized neuropeptide F (NPF) receptor cells in the fire ant queen brain are foundnear the mushroom body which is the primary hub for sensory processing, memory retention and the integration of other complex actions in insects (Seid *et al.,* 2005). In fire ant, *Solenopsis invicta* the role of the brain is in oocyte maturation in addition to regulation of juvenile hormone (Barker, 1978). Mushroom bodies of the ant brain are the centers of learning and memory and have been shown to increase in size and synaptic complexity during adult ant maturation (Stieb *et al.,* 2010). In Hymenoptera, especially ants, the mushroom bodies are particularly developed and may occupy ~40% of the brain volume (Gronenberg, 1999). The brain anatomy of the honey bee is the most comparable to that of a fire ant. Each of the two calyces (lateral and medial calyces) in both species' huge mushroom bodies has a peduncle that gives birth to the median and vertical lobes. Input to the calyx comes from the optical and olfactory systems, whose neuron synapses with the intrinsic neurons of the mushroom body, called Kenyon cells. Within the brain, information is successively integrated and sent by the Kenyon cells (Seid *et al.,* 2005).

The brain architecture of paper-wasp castes differed greatly. Workers invested more in visual processing compared to brain tissues used for antennal processing than queens. The differences in caste are observed in central and peripheral brain regions. The worker optic lobe/antennal lobe ratios in the peripheral sensory lobes are higher than the queen ratios. The castes do not differ significantly in antennal lobe volume but the peripheral visual/antennal ratio variations are mostly caused by smaller optic lobes in queens. The peripheral visual/antennal ratio caste differences are not significantly different between polymorphic and monomorphic animals. The size of peripheral visual/antennal ratio caste differences do not differ substantially between independent- and swarm-founding species (O'Donnell *et al.,* 2014).

Neurosecretory cells

Bargmann & Scharrer (1951) defined neurosecretory cells or neuroendocrine cells. The cell can secrete hormones directly into either the bloodstream or the local extracellular space in an activity-dependent manner. Using histological techniques, the earlier work revealed different neurosecretory cells in different organisms. The neurosecretory cells (NSCs) of insects are first described in the pars intercerebralis of honeybee *A. mellifera* (Weyer, 1935). Firstly, the single group of neurosecretory cells found i.e., MNC after Ritcey and Dixon (1969) reported three groups of neurosecretory cells (NSCs), medial (MNC), lateral (LNC)groups in protocerebrum and ventral (VNC) group in tritocerebrum in the brain of *A. mellifera*.

Ozluk (1991) classified the NSCs in *P. turionellae* and divided them into three different groups according to their colors and granules. These cells are called Type-I, Type-II, and Type-III neurosecretory cells. Type I: These are 12-16 cells and they are observed in the pars inter-cerebralis of the protocerebrum. Type II: These types of cells are observed in median, lateral, and ventral sections of the protocerebrum and in the suboesophageal ganglion. Type III: They are in both lateral parts of the protocerebrum. The emergence of the two pairs of nervi corporis cardiaci(NCC), i.e., NCC-I and NCC-II reported from the brain of ants and *A. mellifera* respectively (Gawande, 1968 and Breed, 1983). Neurosecretory material amount in median neurosecretory cells of *P. turionellae* changes during the reproductive activity. It is also estimated that the egg-laying and egg maturation phases of *P. turionellae* are controlled by the median neurosecretory cells hormone (Nursel & Ozluk, 2010).

Larvae of *Neodiprion lecontei, N. swainei,* and *Diprion hercyniae* show cephalic neuroendocrine organs in brain sections stained with paraldehyde fuchsin (PAF), and four distinct grouping of neurosecretory cells were visible. Thoracic neuroendocrine organs: -A distinct group of neurosecretory cells visible on either side of the thoracic ganglia in stained sections. Four or five cells that have been highly purple-stained with PAF make up each group. Neuroendocrine organs of the abdomen: - A dilated portion of an auxiliary nerve lies over the base of each lateral segmental nerve. The lateral neurohaemal organs, which are made up of the dilated portions of these nerves, resemble the thoracic neurohaemal organs in structure (Hinks, 1973).

The presence of abundant nerve processes in the middle ileum of the ant (*Formica nigricans*) containing neurosecretory granules indicate a neural involvement in the control of the ileum wall. Some nerve processes are related to muscle cells, suggesting a regulatory role over both gut motility and the draining of the absorbed fluid from the sub-epithelial space to the haemolymph (Villarao *et al.,* 1999).

During metamorphosis, brain and retrocerebral complex of red eye pupa of *A. cerana indica* worker was studied histologically. Four neurosecretory cell groups with different types of neurosecretory cells are observed in various regions of the pupal brain of worker honeybees. Retrocerebral complex constituting corpora cardiaca and corpora allata loaded with neurosecretory materials. The structure of neurosecretory cells and their number in various regions of brain are unique with different staining properties by using Chrome alum Haematoxylin-Phloxine (CHP) stain (Barsagade & Jiwatode, 2020).

The median neurosecretory cells (MNCs) in the honeybee constitute a compact group of 120-130 cells in the dorsal pars inter-cerebralis, frontal to the central body and ventral to the median calyces (Weyer, 1935; Formigoni, 1956). The neurosecretory cells from workers show an almost constant amount of secretion granules until the first 15 days of age and a decrease in the month 20th, 30th and 40th days (Hofling-Da-Cruz & Da-Cruz-Landin, 1977). During the early larval period, the neurosecretory complex is built up. This complex becomes active in the 4th larval instar. In the first and second larval instar, single group of cells develops in the pars inter-cerebralis which is distinctly separated from the motor neurons (Dogra *et al.,* 1977).

Axons of the big inter-neurons in the *Paravespula vulgaris* ocellar nerve cross sections are entirely isolated from one another by glial cells, whereas the thin axons, which are primarily located in the outer portion of the tract, are primarily bare. There are features in some of the thin axons that could be up to 160 nm-diameter neurosecretory granules. These axons may meet other brain components synaptically (Kral, 1983).

The Corpora Cardiaca (CC)

Insect corpora cardiaca are recognized as neurohaemal organs that store and produce neurosecretory material. The CC of some insect species also includes intrinsic neurosecretory cell bodies that produce and secrete neurohormones, even though axons, with cell bodies that lie as nervi corporis cardiaci (NCC) in the brain, make up most of the glands. The two neuroglandular structures known as the corpora cardiaca are located behind the brain and on either side of the aorta and they function as an endocrine center. Prothoracotropic hormone (PTTH), which stimulates the secretory activity of the prothoracic glands essential for moulting, is one of the neurohormones that they not only produce but also store and release. Neurohormones are released by the neurosecretory cells of CC to regulate several metabolic processes (Smith *et al.,* 1966). A single pair of fused NCC-I and NCC-II nerves innervating the CC in the honeybee. Only a single pair of nerve NCC is found in red eye pupa of *A. cerana indica* (Laere, 1970).

P. turionellae CC cells possess cytoplasm and organelles that are characteristic of secretion cells. Large nuclei packed with euchromatin and distinct chromosentrum bodies are seen in CC cells. Numerous large and tiny granules were observed in these cells. Microtubules present in the axons of NCC. Connective tissue-based thick capsules encased these glands. A further region of the CC in adult female *P. turionellae* specimens revealed that the intrinsic neurosecretory cell exhibited an expanded nucleus containing chromosomes and small-large mixed vacuoles within the cytoplasm. Numerous neurosecretory endings surrounded this cell, and the cytoplasm of these ends packed with material that was electron-dense. Many mitochondria and microtubules are present in the cytoplasm of the NCC axons in CC (Nursel *et al.,* 2013).

Corpora Allata (CA)

The CA are endocrine glands located in the head, lateral to the oesophagus, and posterior to the brain. Embryologically, the CA is ectodermal in origin, consisting of modified epithelial cells arranged in small, spherical organs delimited by an amorphous outer membrane. The CA is innervated by nerve endings from the brain and the CC and ventilated by tracheal branches present in the organ intercellular spaces (Bonetti *et al.,* 2006). The CA produces juvenile hormones, which have been implicated in regulating caste development in the social Hymenopterans. CA is connected to CC through the nervicarporisallati I (NCA-I) and their connection and entry into the brain to different neurosecretory cells (Breed, 1983).

In the third instar larvae of *Melipona quadrifasciata*, CA cells had large, regular-shaped nuclei with multiple nucleoli and loosely dispersed chromatin, filled with numerous mitochondria in the cytoplasm. The intercellular space is narrow and contained tracheal tubes and nerve terminals from neurosecretory neurons (Bonetti *et al.,* 2006). In larva of *Polistes gallicus*, the CA is wrapped in basal lamina and is 150 nm thick, only rarely separated from the haemolymph by ellipsoid cells. The nuclei are often found in the periphery of the gland and contain finely dispersed chromatin and a single large nucleolus. Contiguous secretary cells frequently show cytoplasmic areas of varying transparency, due to either cell's indifferent metabolic phases or due to the cells in the same phase but with hyaloplasmic fields of different density (Delfino *et al.,* 1981).

In *Rhytidoponera metallica*, the CA is variable in size, and always ellipsoidal, rather narrow measuring 36μ × 19 μ and broad measuring 39 μ × 27 μ. Each contains about 18 spherical nuclei 6 μ- 10 μ in diameter (Whelden, 1960). In *A. mellifera*, CA seems more active in 20-day-old workers than in others ones, which is following the possible stimulatory functions of the brain hormone (Hofling-Da-Cruz & Da-Cruz-Landin, 1977).

Corpora allata cells of *P. turionellae* possess typical secretion cell-like organelles and cytoplasm. Nuclei of cells are generally oval shapes and homogeneous or peripherally located chromatin material (Ozluk, 2011).

Subesophageal Ganglion (SOG)

The suboesophageal ganglion (SOG) of honeybee is contiguous with the deuto-cerebral and tritocerebral parts of the brain. The SOG is composed of fused mandibular, maxillary, and labial neuromeres. These neuromeres receive sensory projections from the receptors located on the respective mouthparts through the corresponding mandibular, maxillary, and labial nerves and give rise to motor neurons that supply the muscles of the mouthparts (Rehder, 1988). In the suboesophageal ganglion of *A. mellifera,* three types of immunoreactive neurosecretory cells were identified (Eichmuller *et al.,* 1991). In *Odontomachus*, the suboesophageal ganglions' giant sensory axons contact equally with the thick motor axons. The entire system consists of eight giant cells, two sensory and two motor neurons on either side (Gronenberg, 1996).

In *Solenopsis invicta*, the somata in the SOG and in the ganglia of the central nervous system appeared to project axons to various neurohaemal organs. One such neurohaemal organ was the pair of CC, which releases neurohormones into the haemolymph (Choi *et al.,* 2009).

Ecdysial Glands (Prothoracic Glands)

The Ecdysial glands play a key role in metamorphosis. These glands secrete moultinghormones during juvenile stages and reduce after the full development of insects (Tembhare, 2012).

In *A. mellifera*, the ecdysial glands are composed of loose cords of large cells, possessing characteristic oval nuclei,that are diffusely arranged throughout the lateral thorax (Schaller, 1955). The glands of queen and worker larvae are much more diffused than soldier larvae, and the planimetry determined surface area of the queen glands is 2½ times larger than that of the glands of both workers and soldiers (Schaller, 1955). The nuclei of queen larvae gland cells are ten times the size of workers when compared in the prepupal period (Lukoschus, 1952). Soldier gland cells attain maximal diameters of 20-25 μ and the workers 15-18 μ. The queens have the gland size of about 30-35μ (Formigoni, 1956). Gland size in castes of honeybee larvae is inversely proportional to the length of the pupal stage. The glands of *Myrmica rubra* are elongated cords, 2-3 cells wide and 150-200 μ long, lying between the two main tracheae in the head and neck (Weir, 1959).

CONCLUSION

The brain architecture among hymenopterans exhibits remarkable variations, with features such as the cerebral ganglion, optic lobes, and mushroom bodies playing crucial roles in sensory processing, learning, and memory. Neurosecretory cells, integral to hormonal regulation, are distributed across different regions of the hymenopteran brain. Researchers have classified these cells into different types based on their locations and functions. Moreover, studies on species like *P. turionellae* and fire ants shed light on the neurosecretory control of reproductive activities and oocyte maturation. The corpora cardiaca (CC) and corpora allata (CA) serve as neurohaemal organs, releasing neurohormones for various physiological functions. Additionally, the SOG and ecdysial gland (prothoracic gland) have been investigated, revealing their roles in sensory processing, motor functions, and the secretion of moulting hormones.

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