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A review on neurosecretory cells in Lepidoptera

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Abstract
Neurosecretory cells in Lepidoptera, a broad order of insects comprising moths and butterflies, grant the physiological regulation. These special neurons synthesize, store, and secrete neurohormones that regulate development, molting, maturation, and transformation. Neurosecretory cells are most numerous in the pars intercerebralis, where they are mainly located in the brain and subesophageal ganglion. They are associated with the corpora cardiaca, which are reservoirs and distribution sites for various neurohormones, including juvenile hormone (JH) and prothoracicotropic hormone (PTTH). JH controls development in the larval stage and reproductive cycles, whereas PTTH stimulates metamorphosis by initiating the production of ecdysone. The review discusses the taxonomy, morphology, and functional dynamics of neurosecretory cells in Lepidoptera, particularly emphasizing their crucial roles in the regulation of intricate physiological processes. It will also discuss recent research that can enlighten researchers about the natural phenomena how these neurosecretory cells interact with their surroundings and explains how these insects have evolved into adapting to such a phenomenon. Understanding the neurosecretory system in Lepidoptera advances our knowledge of their developmental biology and contributes to a general discussion on the functions of neuroendocrine in other mammalian kingdoms.

Keywords: Neurosecretory cells, lepidoptera, moths, scaly wings, neuroendocrinology, insect physiology

Introduction

Lepidoptera is a very large order of insects, including moths and butterflies. Neurosecretory cells play a crucial role in the physiological control of Lepidoptera. These specialized neurons produce, store, and release neurohormones, which subsequently regulate many important processes, such as development, molting, reproduction, and metamorphosis [1]. Neurosecretory cells produce and secretes hormone chemicals in the insect blood known as hemolymph that acts on distant organs and tissues, which is different from the normal neurons that transmit electrical impulses.

In Lepidoptera, neurosecretory cells are predominantly found in the brain and in the subesophageal ganglion, even though they also occur in other ganglia along the ventral nerve cord. The highest population of neurosecretory cells is found in the pars intercerebralis of the brain. Such cells are connected to the corpora cardiaca, a pair of neurohemal organs, that store and release neurohormones [2]. There are two types of Lepidopteran neurosecretory cells that can be grouped depending on how they stain and the hormones they produce, like prothoracicotropic hormone (PTTH), allatotropins, and allatostatins.

PTTH is a neurohormone that has been quite intensively studied in Lepidoptera and is needed for transformation to start. The neurosecretory cells of the brain produce PTTH that is transported to the corpora cardiaca and released into the hemolymph [3]. Once it enters the circulation, PTTH stimulates ecdysone production, which is the hormone responsible for triggering molting and all metamorphic changes from prothoracic glands. The initiation of developmental changes must occur during the most favourable times and thus, the regulation of PTTH discharge is rather very sensitive towards environmental factors such as temperature, light, and diet.

Among the many roles performed by neurosecretory cells in Lepidoptera, control of juvenile hormone (JH) is one of the very important roles it plays. It inhibits precocious metamorphosis and keeps the organism in a larval state. Allatostatins and allatotropins, mediated through neurosecretory cells in the brain, modulate corpora allata, which produce JH. Allatostatins inhibit, and allatotropins are reported to stimulate, the synthesis of JH, thus making very much necessary regulation of development and reproduction [4].

Apart from the function they have in development and metamorphosis, neurosecretory cells in Lepidoptera have a very significant role in reproductive processes. For instance, ovary-stimulating hormone, which is critical for oocyte maturation and regulation of sexual behaviours that include mating and laying of eggs, is produced by neurosecretory cells present in female moths [5]. Neurosecretory cells present in male Lepidoptera produce factors controlling spermatogenesis and other reproductive process involved in the development of the species.

Elaborate physiological activities like metamorphosis and molting, as well as reproduction in Lepidoptera are controlled by neurosecretory cells. This allows these insects to adapt to changes in the environment throughout their lifecycle since their capacity for integrating mechanisms of hormonal regulation with environmental information [6]. Information on Lepidopteran neurosecretory cells have broader implications in relation to the neuroendocrine systems of other animals, although it only provides crucial leads for understanding the developmental biology of these insects themselves.

Lepidoptera

The directive Moths and butterflies are members of the order Lepidoptera. has about 1,80,000 species, one of the largest families. It is the world's most widely distributed and well-known insect order. The Greek term "Scaly Wings," which refers to the presence of scale on the wings, is where the word Lepidoptera originates. The mouth is nocturnal, and the butterflies that dwell it are stunning insects with a variety of colors and designs on their wings [7]. Lepidopteran species make up 10% of all described species of living organisms and are categorized into 46 super families, which are further subdivided into 126 families. Butterflies are vital to the ecosystem since they are both a pollinator and a food source. There are four phases in the life cycle: eggs, larvae, pupae, and adults. It takes 21 to 28 days to complete the life cycle.

The brain is a bilobed organ located in the middle of the insect's brain. The three areas of the brain are as follows: 1) Forebrain, also known as the protocerebrum 2) Two lateral antennal nerves emerge from the deutocerebrum. Deutocerebrum or midbrain 3) The tritocerebrum or hindbrain. Optic nerves from optic lobes and ocellary nerves from median and lateral innervating the antennae are received by the protocerebrum [8]. A pair of later frontal neurons that innervate the labrum are supplied by the tritocerebrum. Authors including Bretschneide, Henstrom, Power, Bullock, and Horridge provided a thorough analysis of the morphology and anatomy of an insect's brain.

Neurosecretory Cells

The brain and ventral nerve cord contain multiple groups of neurosecretory cells that make up the neurosecretory system [9]. Neurosecretory cells (NSCs) are separated into three pairs:

- Medial neurosecretory cells (MNC)
- Lateral neurosecretory cells (LNC)
- Ventral neurosecretory cells (VNC).

Three types of neurosecretory cells are distinguished: A cells, B cells, and C cells. In the pars inter cerebralis area of the protocerebrum, the MNC are located mid-dorsally. Each protocerebrum's lateral area contains the LNC [10]. The inner edge of each of the brain's tritocerebral lobes is home to VNC cells. The form and size of the neurosecretory cells allow to recognize them based on their histomorphological characteristics.

Neurosecretory cells in lepidoptera

Nayar (1958) was the first to classify insect neurosecretory cells [11]. The endocrinology of insects is becoming more and more understood, but little is known about how the neurosecretory cells in their target organ function. In insects, the brain and ventral nerve cord have multiple sets of neurosecretory cells that make up the neurosecretory system. For most orders, there is ample evidence of neurosecretory cells in the insect brain. Neurosecretory cells in the brains of various Lepidoptcra species are fundamentally composed of the same cells. Herman and Gilbert's (1996) research reveal that the brains of lepidopteran species contain a variety of cell types and neurosecretory cells [12].

The neurosecretory cells found in the brains of Lepidopteran larvae are primarily divided into two categories: A and B.

There are three different types of neurosecretory cells found in the brains of Lepidopteran larvae: A, B, and C.

There are four different types of neurosecretory cells found in the brains of Lepidopteran larvae: A, B, C, and D.

Panov and Kind (1980) separated A cells into smaller groups and added new classifications for cells that were consistently different [13]. The following are them:

A Cells

- **A1 Cells**: Only take place in the medial group. The axon is where neurosecretory material frequently appears.
- **A2 Cells:** Only appear in the medial group, scattered across the AI cells. The axon is where neurosecretory material frequently appears.
- **A3 Cells: -** consist of extremely tiny granules and are found in the medial group of most species, posterior to the AI and A2 cells. Sometimes visible in the axons is neurosecretory material.
- **A4 Cells: -** consist of the lateral groups' A cells. Occasionally apparent neurosecretory substances in the axons

B Cells

B1 Cells: Cells that are situated between and below the A cells in the medial group. Neurosecretory material is less clearly distinguished in the axons but frequently apparent in the axon hillocks.

B2 Cells: Include the B cell on the side. Neurosecretory substance is hardly present in their axons.

C Cells

C1 Cells: In the medial group of each hemisphere, there is a solitary, larger-than-B cell cell that lies between the A cells.

C2 Cells: Each lateral group has one or two cells that are linked to B2 cells.

D Cells: Axons are exceedingly fine and have a limited trace length, however neurosecretory material is occasionally evident in the axon hillocks.

The D cells are the largest neurosecretory cells in the brains of *O. fasciatus* and *Sagregaria*, but they are always smaller than the A1 cells in Lepidoptera [14].

Table 1: Summary of Research Studies on Insect Development and Physiology.

Author Name	Topic Covered	Research Study
Kh and Keshan (2021) [19]	Larval feeding status and gene expression	Explores the relationship between larval feeding status and the expression of genes encoding prothoracicotropic hormone (PTTH) and allatoregulatory peptides, highlighting the impact of larval nutrition on hormonal regulation affecting growth and development in *Bombyx mori.*
Klöcklerová *et al*. (2023) [20]	Insulin-like peptides in silkworms	Investigates the expression of insulin-like peptides (ITP) and their analogs (ITPL), suggesting their involvement in various physiological processes, including reproductive maturation and environmental stress responses, emphasizing the complexity of the insulin signalling pathway in silkworms.
Krishnan *et al.* (2021) [21]	Impact of agricultural chemicals on Lepidopteran development	Addresses the impact of neonicotinoids on Lepidopteran development, demonstrating that exposure leads to arrested pupal ecdysis, highlighting ecological implications and the need for further research on molecular mechanisms and long-term effects on silkworm populations.
Li *et al.* (2020) [22]	Identification and expression profiling of neuropeptides	Presents a study on the identification and expression profiling of neuropeptides and their receptors in *Atrijuglans hetaohei*, revealing distinct expression patterns across developmental stages and contributing to the understanding of neuropeptide function in insects.
Liu *et al.* (2023) [23]	Glial cell expansion in *Bombyx mori*	Utilizes single-cell transcriptomics to investigate glial cell expansion in *Bombyx mori*, highlighting heterogeneity and dynamic changes throughout development, uncovering novel glial subtypes and their roles in the nervous system, especially during metamorphosis.
Makarova *et al.* (2021) [24]	Metamorphosis of the CNS in *Trichogramma telengai*	Focuses on structural and functional changes during the metamorphosis of the CNS in *Trichogramma telengai*, documenting alterations in neural architecture, including neuronal apoptosis, proliferation, and differentiation, enhancing understanding of insect neurobiology.

Because they provided models for the identification and characterization of the neurosecretion process, insects were crucial in the development of neuroendocrinology. As to Novak's (2007) definition, neurosecretion is the endogenous product of nerve cells that exhibit physiological activity [15]. Specialized neurons known as neurosecretory cells have acquired secondary endocrine structure and activity. nerve cell that possesses both typical neural properties and those linked to glandular action. The neurosecretory neuron in these terms.

Diverse definitions of neurosecretion have been given by different people. Van der Kloot (1994) defines neurosecretory cells as nerve cells that exhibit secretory characteristics under a microscope [16]. Hormones are released by some of these cells, whereas chemicals with transient effects are released by others. Moths intended for dissection were deprived for a minimum of two to three days, during which they had a significant reduction in body fat.

Most investigations have concluded that rapid evolutionary changes are occurring. Villanes (2017) claims that the three sections of a lepidopteran insect's brain are the protocerebrum, which is the first brain, the deutocerebrum, which is the second brain, and the tritocerebrum, which is the third and smallest brain of the three [17]. Local effects on muscles may be seen from the neurohormone produced from the nerve. Yosuhiro and Sholchi reported that removing folic acid from artificial die reduced the growth of silkworms.

The evidence presented by Wigglesworth points to the pars intercerebralis of the supra oesophageal ganglion of Rhodnius as the site of the moulting hormone synthesis [18]. The adult silk moth's lack of leptin in its brain suggests that the hormone is purely peripheral in origin and may function as a peripheral signal molecule to control endocrine and other physiological processes in the brain.

Neurosecretory cells

The protocerebrum's anterodorsally and middorsal pars intercerebralis regions are on either side of the median fissure, while the posterior region of the protocerebrum is situated below the neuropile in the brain and the anterolateral region is situated above the corpora pedunculata [25].

Ultrastructure of neurosecretory cells

The morphology of the medial neurosecretory cells is oval or spherical. There are certain canaliculi that are connected to the well-differentiated plasma membrane. Studies using electron microscopy demonstrate that cells have a nucleus at their core. Concentric long granular endoplasmic reticulum (GER), mitochondria (MT), and Golgi complexes (GC) in close proximity to NSG occupy the majority of the perikaryon [26]. The mitochondria have a rod-like form. The cytoplasm and axonal terminals are common locations for the accumulation of NSG.

Golgi complexes, endoplasmic reticulum, and ribosomes are examples of cell organelles [27]. The production of granules known as neurosecretory material (NSM) occurs in all organelles.

❖ Nucleus (N)

The nucleus, which is spherical or oval in shape and has conspicuous nucleoli of irregular shape and scattered chromatin material, is located in the center of the cell [28]. The nuclear membrane (NM) is shown to be composed of two layers: the outside thin layer and the inside thick layer, according to the electron micrographic analysis. At times, the endoplasmic reticulum is linked to the outer layer. Numerous dense granules that are uniformly dispersed or grouped into tiny colloids can be found in the nucleus. The nucleolus is visible as an amorphous, black patch.

❖ Mitochondria (MT)

Numerous filamentous, rod-like, or even beaded-like mitochondria can be seen in the cytoplasm of MNC [29]. They leave a lot of stain. The mitochondria are dispersed randomly or occasionally congregate in clumps. Cristae and double membranes make up mitochondria.

❖ Endoplasmic reticulum (ER)

The cytoplasm of the neurosecretory cells has sporadic distributions of the endoplasmic reticulum (ER). A small number of smooth-surfaced (SER) reticulate alternate with the majority of the rough-surfaced ER membranes [30]. The rough endoplasmic reticulum is connected to the ribosomes (RER).

❖ Golgi complex (GC)

Vesicles and smooth membrane stacks make up the Golgi complex. NSG can occasionally be found at the terminal ends of Golgi lamellae, and the vesicles and tubules have been observed to contain an electron-dense substance, suggesting that the Golgi complex is involved in the synthesis of NSG [31]. The NSG exhibit a progressive enlargement after their separation from the Golgi complex. There is a membrane surrounding the fully developed NSG.

❖ Neurosecretory Granules (NSG)

The cytoplasmic perikarya of NSC include neurosecretory granules, which are fine, spherical, or ellipsoidal, electron-dense elementary granules (EG). The granules measured between 500 and 2500 Å (1500 Å in diameter), and their electron density was comparatively homogeneous. The neurosecretory cells' axonal terminals are frequently home to the NSG [32].

❖ Synthesis of the NSM

The MNC exhibits the synthesis of electron-dense, fine, spherical, or ellipsoidal NSG. The Golgi zone, rough endoplasmic reticulum, and mitochondria are all in close proximity to where the NSG are generated. The Golgi zone is often in close proximity to the NSG [33]. There are few NSG, and they are covered in membranes. The NSG are dispersed equally throughout the NSC perikarya.

❖ Release and transport of NSM

Neurosecretory routes allow the NSG to move to the corpora cardiaca along the axons of the brain's neurosecretory cells. The perikarya of neurosecretory cells directly discharge neurosecretory material into the canaliculi, which is then sent to the blood sinus. The NSC plasma membrane and the canaliculi are intimately related [34]. The exocytosis step releases the NSM straight from the cell into the hemolymph.

Types of neurosecretory cells in lepidoptera

Neurosecretory cells in Lepidoptera, or butterflies and moths, are essential in the endocrine system, with the hormones secreted that control some of the physiological processes. There are three main types: peripheral neurosecretory cells, neurosecretory cells in the brain, and hypothalamic neurosecretory cells, all holding different characteristics and functioning for different purposes [35].

Hypothalamic Neurosecretory Cells

These special neurons of the brain's hypothalamus are known as hypothalamic neurosecretory cells and have proven necessary to Lepidoptera's endocrine regulation [36]. Their axons are long enough to extend to neurohemal organs, and the cells are usually aggregated into distinct clusters or nuclei. This structure permits them to deposit their neurohormones directly into the hemolymph, or the insect equivalent of blood. These cells are mainly concerned with the synthesis of a few quite crucial hormones, such as the prothoracicotropic hormone (PTTH), which stimulates the prothoracic glands to produce ecdysteroids necessary for initiating the molting and metamorphosis process. Neurosecretory cells of the hypothalamus influence the larva-to-pupa change by governing these hormonal processes [37]. Additionally, these cells respond to most of the environmental stimuli such as temperature and photoperiod, and because of these reasons, they get involved in timing reproductive reproduction and seasonal adaptation in Lepidoptera. In this regard, their role to fruitful development as well as reproduction gets more highlighted through the interaction of environmental stimuli with the hormones' release.

Neurosecretory Cells in the Brain

Neurons in the brain also have a significant role in controlling Lepidopteran hormones, though sometimes augmented by the hypothalamus [38]. These neurons are found dispersedly in the brain though highly concentrated in the corpora cardiaca and the corpora allata control centers. Corpus allatum secretes vital hormones, of which juvenile hormone (JH) comes from neurosecretory cells in such areas and controls growth, metamorphosis, and reproductive development. Neurosecretory cells from corpora allata are able to have their complex physiological processes integrated and are life cycle-related for the insect because of their production and release of such hormones. They also master the use of combined sensory information in order to coordinate hormone reactions with changes in the environment or the state of the insect [39]. The capability of physiological events to be linked to particular behavioral expressions, such as feeding, mating, and migration highlights the manner in which neurosecretory cells in specific areas of the brain determine the adaptability of the Lepidoptera.

Peripheral Neurosecretory Cells

In Lepidoptera, peripheral neurosecretory cells play a very important role in local control of hormones and quick responses. These cells are outside the central nervous system [40]. The cell is placed strategically near the target tissues to allow easy administration of hormones. They are found in several tissues and organs. Fat body and reproductive organs are examples. Their primary function is the secretion of hormones that affect peripheral tissues and change parameters such as metabolic activity and immunological function. To control energy homeostasis at different stages of an insect's life cycle, for example, hormones released from neurosecretory cells of the periphery can play a crucial role in regulating the storage and mobilization of nutrients in the fat body. Furthermore, these cells play crucial functions in sexual processes, such as gamete and reproductive organ maturation, that would consequently regulate reproduction at the most appropriate time of favourable conditions in the environment [41]. Consequently, the peripheral neurosecretory cells' role in producing their respective hormones is critical to Lepidopteran homeostasis and successful reproduction.

Given the various neurosecretory cells of these organisms, the complex hormonal regulation of growth, metabolism, reproduction, and behavior in Lepidoptera could be elucidated [42]. Hence, these cells make it possible for Lepidoptera to adapt to their environment and ensure the success of their life cycles, a critical function that underlines the significance of their study in the domain of insect physiology and ecology.

Conclusion

Neurosecretory cells play an important role in the physiological control of Lepidoptera, as these cells correspond to growth, development, metamorphosis, and reproduction. These are mainly specialized neurons that are found in the ventral nerve cord and in the brain. They synthesize, store, and release neurohormones, which are necessary in regulating molting and metamorphosis like prothoracicotropic hormone or PTTH and juvenile hormone or JH. They are medial, lateral, and ventral, with unique roles and hormonal outputs. There are three types, thanks to this research that relates neurosecretory cells with their target organs to give a coherent view of the complex regulation involved in both physiological and ecological dynamics. The mechanism that regulates such species as *Atrijuglans hetaohei* and *Bombyx mori* spells much about the evolutionary importance of neurosecretory systems in insects and how it affects neuroendocrinology. More studies on the neurosecretory cells of Lepidoptera can help control pest as well as conserve species.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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