THE STRUCTURAL ELEMENTS OF INSECT NEUROENDOCRINE SYSTEMS

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Instead of the transmission of neural impulses, the primary function of certain neurons is the production of secretory material called neurohormones. These neurons are termed neuroendocrine or neurosecretory cells (NSC) because they have the characteristics of both neurons and endocrine cells, i.e. their products are usually released into the circulatory system, rather than at the interface of target cells. The neurohormones produced by these cells have thus far been found to be peptides. The function of the neuroendocrine system, like that of the nervous and endocrine systems, is to regulate various life processes of animals. While the nervous system initiates rapid, short-term responses, the endocrine system is involved in long term physiological activities such as growth and differentiation. The neuroendocrine system integrates the activities of these two systems and is primarily involved in functions of intermediate duration.

NSC are ubiquitous throughout the animal kingdom, being found in both vertebrates and invertebrates. The neuroendocrine systems of vertebrates and invertebrates appear analogous since in both the products of these cells are synthesized in cell bodies in the brain and then transported via axons to areas outside the brain where they are stored and released. These areas are called neurohemal organs. The major neurohemal organ of insects is the corpus cardiacum-corpus allatum complex (CC-CA complex), that of vertebrates is the posterior pituitary; see diagrams in Figures 1 and 2. These organs have been termed "master glands" since they regulate, either directly or indirectly, most of the physiological activities of these animals. The same histochemical stains are used to locate NSC and trace their tracts in both invertebrates and vertebrates, the most common being aldehyde-fuchsin and alcian blue-performic acid.

The corpus cardiacum (CC) of insects is a ganglion consisting of a neuropile and intrinsic neurons, which are not necessarily neuroendocrine, while the corpus allatum (CA) is an endocrine gland that produces the juvenile hormone. In some insects the CA is also a neurohemal site, with clusters of neurosecretory axons terminating on the surface of this organ, in addition to forming neurosecretomotor synapses with the parenchymal cells of the CA. This relationship of a neurohemal organ such as the CC with an endocrine gland (CA) is analogous to the relationship of the posterior pituitary with the anterior pituitary which is an endocrine gland that also produces hormones that regulate growth, development, differentiation and reproduction. At the ultrastructural level, the neuropeptides produced by these cells appear as spherical granules, enclosed by a unit membrane. These structures are called elementary neurosecretory granules (ENG). The majority of the ENG of vertebrates have an electron dense core surrounded by an electron lucent periphery, and are relatively small (100-200nm) as seen in Figure 3. The ENG of insects are relatively large (150-350nm) with a wide range of electron density from electron lucent to very dense granules (Fig. 4). Thus the ENG of insects have been found to be more morphologically diverse than that of vertebrates. This anatomical diversity may be correlated with the larger variety of neuropeptides found in insects. This, in turn, may be due to the different manner in which the insect and vertebrate neuroendocrine systems perform their regulatory functions. Insect neuroendocrine systems produce a larger number of neuropeptides that act by directly stimulating target organs, as well as indirectly by affecting endocrine glands which in turn regulate a large number of functions. In contrast, vertebrate neuroendocrine systems utilize the latter mode of regulation producing only a few types of neuropeptides that regulate a large wide range of functions by stimulating endocrine glands that produce a large number of hormones.

Due to the similarity in function as well as in structure between vertebrates and insects, the neuroendocrine system of insects can be used as a model system for the general study of neuroendocrine mechanisms. Any new information could be applicable to that of the vertebrate system as well, in addition to supplying information that may result in new methods of controlling pest insects. The advantages of studying the neuroendocrine system of insects is the relatively short life span of insects, their small size, and open circulatory system. The latter permits experiments involving excision and implantation of neuroendocrine elements without the necrosis associated with loss of nutrients, oxygen, and disposal of toxic wastes, in ligation or severance experiments involving the vertebrate pituitary.

There appears to be a greater similarity between the general morphology of the neuroendocrine system of insects and that of vertebrates as seen in Figure 1 and 2, than between that of different orders of insects or even between families of the same order. For example, in two families of Diptera, Culicidae and Muscidae, both have a cephalic neuroendocrine system consisting of paired neurosecretory nerves (nervi corporis cardiaci, NCC) originating in the brain and extending to neurohemal sites in the CC-CA complex. These three structures are associated with dorsal aorta. In Culicidae, the CC-CA complex consists of a fused corpus cardiacum and paired corpora allata, but in the muscid flies both the corpus cardiacum and allatum are fused organs. The cyclorrhaphous dipterans (Muscidae) such as Stomoxys calcitrans have a corpus cardiacum that is both a neurohemal organ and contains intrinsic neuroendocrine cells, whereas the CC of mosquitoes (Culicidae) is a neurohemal organ but the intrinsic neurons of this ganglion are not neurosecretory. The glandular cells of the retrocerebral complex of the latter family appear to be located at the anterior surface of the corpora allata. A comparison of Diptera with another order such as Lepidoptera, shows even more diversity. In the latter order, the CC-CA complex is not associated with the aorta, both the corpus cardiacum and corpus allatum are paired organs, and either or both the cardiacum or allatum can be neurohemal organs depending upon the species.

Therefore it is important for biochemists as well as physiologists to be aware of the neuroendocrine structure of the species they plan to investigate, if they are interested in mixing more than an indigestible soup in their test tubes. Being familiar with the structural composition of an organ, not only aids in locating sites of peptide synthesis and storage, and in determining effects of various agents on these tissues, but just as important, helps in determining the species most suited for a specific research project.

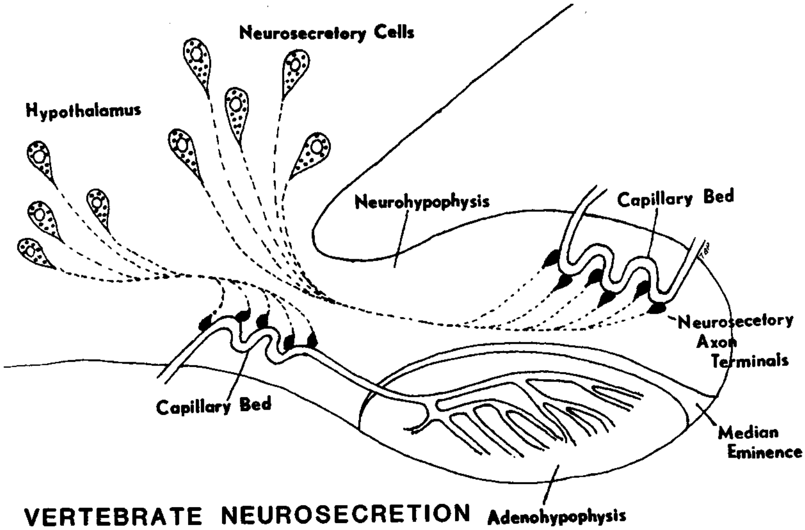

FIG. 1. Schematic diagram of mammalian pituitary. The neurosecretory cell bodies are located in the hypothalamus of the brain, their terminals ending in capillary beds in the posterior neurohypophysis (posterior pituitary). The close proximity of the glandular adenohypophysis (anterior pituitary) and the median eminence to the neural lobe is evident.

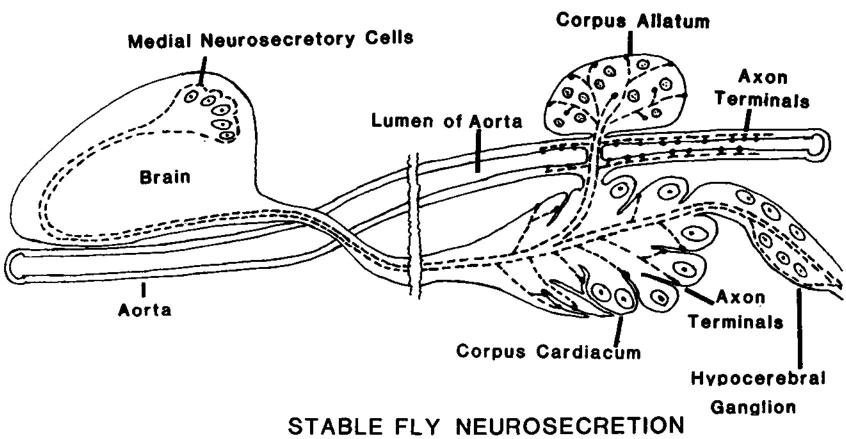

FIG. 2. Schematic diagram of the cephalic neuroendocrine system of a cyclorrhaphous fly showing a cluster of neurosecretory cells (MNC) in the brain have axons terminating in neurohemal sites in the corpus cardiacum and aorta, and forming neurosecretomotor synapses with the endocrine cells of the corpus allatum.

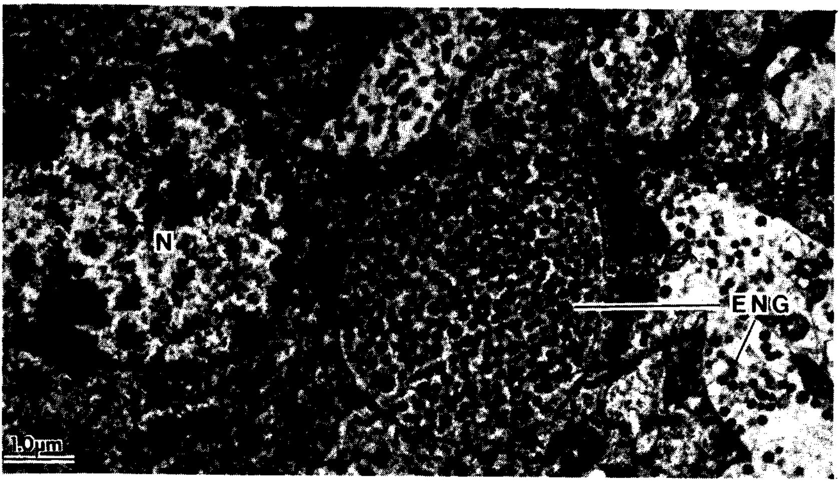

FIG. 3. Ultrastructure of neuroendocrine axons in the posterior pituitary of a rat, showing the uniform size and density of the elementary neurosecretory granules (ENG) of this in the axons terminating in this neurohemal organ.

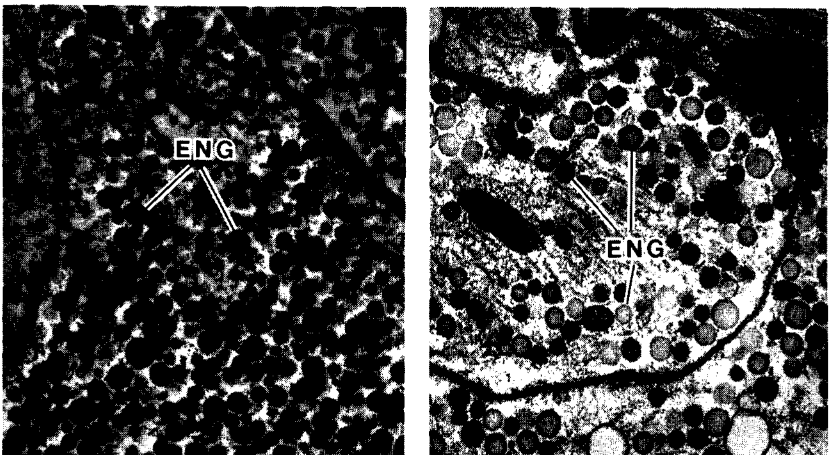

FIG. 4. Two ultrastructural sections of the cephalic neuroendocrine system of the mosquito, Aedes sollicitans illustrate the diversity in size and density of the elementary neurosecretory granules (ENG) in insects. (A) Medial neurosecretory cells of the brain, and (B) Neurosecretory axons in the corpus cardiacum.