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THE CEPHALIC NEUROENDOCRINE SYSTEM OF THE DRAGONFLY *ORTHETRUM CHRYSIS* (SELYS) (ANISOPTERA: *LIBELLULIDAE*)

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In *O. chrysis* 8 groups of neurosecretory cells are present in the brain: 2 medial and 2 lateral groups in the protocerebrum, 2 ventral groups in the tritocerebral lobes and 2 optic groups in the optic lobes. The cerebral neurosecretory cells are classified as A1-, A2-, B- and C cells. A1 cells are present in the medial groups of the ultimate instar larva and in the adult, while A2 cells are confined to the medial and lateral groups of the larval stage. The B- and C cells occur in all groups of the larval and adult dragonflies. The axons of neurosecretory cells of all the groups form distinct neurosecretory pathways inside the brain. Only a single pair of nerves, the nervi corporis cardiaci, emerges out of the brain and each of them enters the corpus cardiacum on its own side. In the larva as well as in the adult the corpora cardiaca mainly function as storage organs for cerebral neurosecretory material and, secondarily, may also produce their own hormone. The corpora allata are composed of a large number of cells and sometimes they appear as syncytial structures. Cerebral neurosecretory material is never found in the corpora allata or along with any of the nerves of these glands.

INTRODUCTION

A perusal of the ever growing literature on the neuroendocrine system in insects (for reviews cf. VAN DER KLOOT, 1960; DE WILDE, 1964; GILBERT, 1964; BERN & HAGADORN, 1965; GABE, 1966; NOVÁK, 1966; HIGHNAM & HILL, 1969; ENGELMANN, 1968; WIGGLESWORTH, 1970) reveals that little work has been done on Odonata in comparison to other orders. The present investigation has, therefore, been undertaken to study the structure and physiological activities of the neuroendocrine system in the dragonfly *Orthetrum chrysis*; this paper deals with the histomorphology of the cephalic neuroendocrine system in the ultimate instar larva and the adult.

MATERIAL AND METHODS

Ultimate instar larvae and adults of both sexes were collected from local ponds and tanks. The cephalic neuroendocrine organs were dissected in Ringer's solution, fixed in 10% formalin-saline and wholemount preparations were made after staining with performic acid victoria-blue (PAVB) or with Cameron and Steel's aldehyde fuchsin (AF) according to DOGRA & TANDAN (1964).

The head capsules were punctured and directly fixed in aqueous Bouin's fluid for 15-18 hours. The cephalic neuroendocrine organs were dissected out in 70% ethyl alcohol, dehydrated and embedded in paraffin wax in the usual way. Serial sections were cut at 4μ and stained with the following techniques: (1) Bargmann's chromalum-haematoxylin phloxine: CHP (PEARSE, 1968); – (2) Ewen's aldehyde-fuchsin: AF (EWEN, 1962a); – (3) Delphin's alcian-blue phloxine: ABP (DELPHIN, 1965); – (4) Paget's aldehyde-thionin: ATH (PAGET, 1959) and – (5) Heidenhain's Azan (GURR, 1962).

ABBREVIATIONS USED

A1, A2	Neurosecretory cells	MNC	Medial neurosecretory cells
AO	Aorta	MNSP	Medial neurosecretory pathways
AX	Axons	NCA1, NCA2	Nervi corporis allati 1 and 2
B	Neurosecretory cells	NCC	Nervi corporis cardiaci
BR	Brain	NCON	Nervus connectivus
C	Neurosecretory cells	NCS	Nervi cardiostomatogastrici
CA	Corpus allatum	NL	Labral nerve
CC	Corpus cardiacum	NO	Ocellar nerve
CCC	Commissura corporis cardiaci	NOM	Medial ocellar nerve
CCO	Circum oesophageal connective	NR	Recurrent nerve
CF	Frontal connective	NSM	Neurosecretory material
CP	Corpora pedunculata	OES	Oesophagus
GF	Frontal ganglion	ONC	Optic neurosecretory cells
GH	Hypocerebral ganglion	ONSP	Optic neurosecretory pathways
GSO	Suboesophageal ganglion	VNC	Ventral neurosecretory cells
LNC	Lateral neurosecretory cells	VNSP	Ventral neurosecretory pathways
LNSP	Lateral neurosecretory pathways	X	Chiasma

OBSERVATIONS

The cephalic neuroendocrine system in *Orthetrum chrysis* consists of the neurosecretory cells in the brain, the corpora cardiaca, the corpora allata and the aorta. The topographical inter-relationships of these structures are shown in Figure 1.

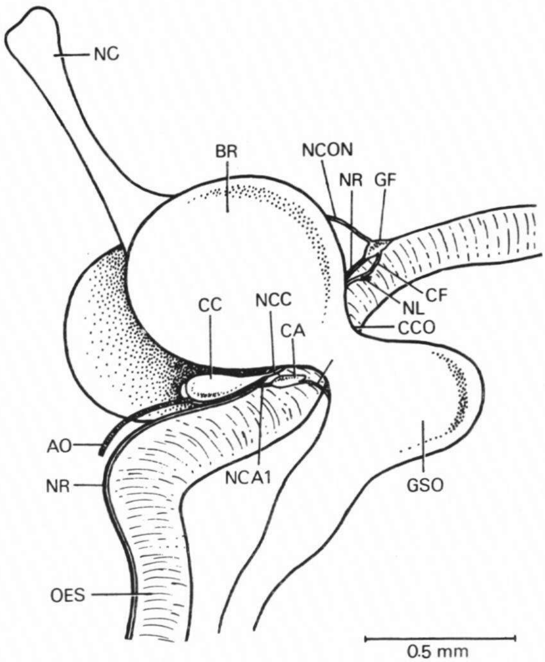


Fig. 1. Lateral view of cephalic neuroendocrine complex of *Orthetrum chrysis*.

THE CEREBRAL NEUROSECRETORY CELLS

In the ultimate instar larva and the adult dragonfly, eight groups of neurosecretory cells (four in each hemisphere) are present in the brain and from their location they can be recognised as medial, lateral, ventral and optic neurosecretory cells (Figs. 2-3).

The neurosecretory cells of these groups are classified as A, B and C cells according to the staining affinities and other cytological details (Table I). The A cells are further classified into A1 and A2 cells on the basis of their size.

The medial neurosecretory cells (MNC) form conspicuous groups and are situated in the antero-dorsal part of the pars intercerebralis (Figs. 4-10). Two medial groups lie close to each other on either side of the root of the median ocellar nerve. Each medial group is composed of about 30-32 A1, 6 A2, 18-21 B and 6 C cells in the ultimate instar larva and 42-44 A1, 27-30 B and 6 C cells in the adult dragonfly. The A2 cells are totally lacking in the medial groups of the adult.

The lateral neurosecretory cells (LNC) form two small groups outside the pars intercerebralis and lateral to the corpora pedunculata (Figs. 11-14). There are

Table I

Histomorphological characteristics of the cerebral neurosecretory cells of the adult and larval *Orthetrum chrysis* (Selys)

Cell type	Staining reaction						Shape	Size (in μ)			
	PAVB	CHP	AF	ATH	ABP	AZAN		Adult		Ultimate instar larva	
								Cell	*Nuclei*	*Cell*	*Nuclei*
A1	dark blue inclusions	blue black inclusions	dark purple inclusions	purple inclusions	blue inclusions	bright red droplets	pyriform	10.54 ± 0.54	5.80 ± 0.23	8.60 ± 1.30	4.68 ± 0.07
A2	dark blue inclusions	blue black inclusions	dark purple inclusions	purple inclusions	blue inclusions	bright red droplets	pyriform	–	–	22.34 ± 1.44	10.22 ± 0.08
B	–	red inclusions	greenish cytoplasm	greenish cytoplasm	red inclusions	faintly bluish cytoplasm	spheroidal	8.08 ± 0.78	4.38 ± 0.33	15.04 ± 1.64	8.93 ± 1.38
C	–	bluish inclusions	faint purple or brown inclusions	faint purple or brown inclusions	bluish inclusions	pinkish inclusions	ellipsoid	16.92 ± 1.21	7.73 ± 0.56	27.77 ± 0.06	14.70 ± 1.78

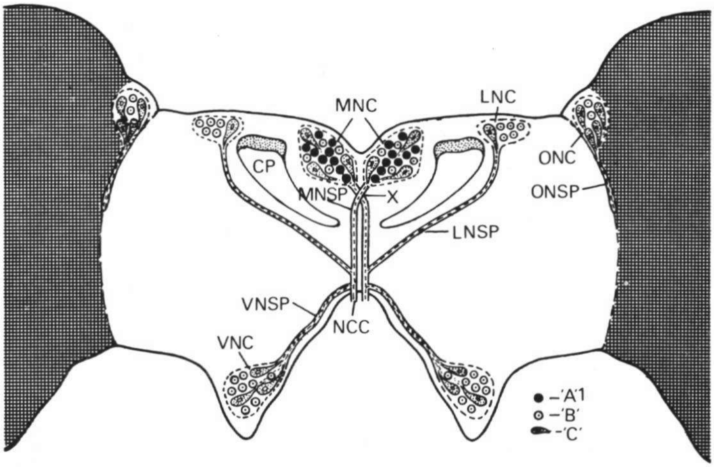


Fig. 2. Diagrammatic representation of the topography of neurosecretory cells and pathways in the brain of adult *Orthetrum chrysis*.

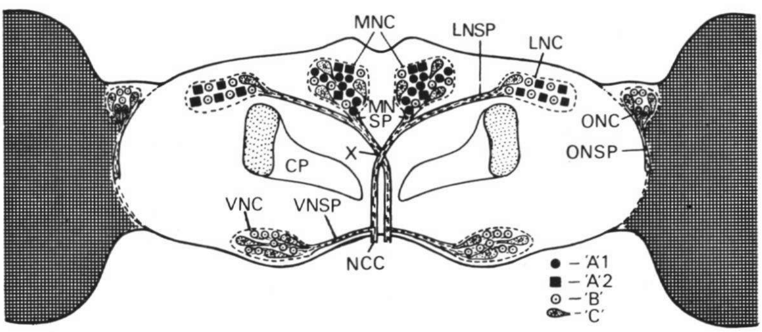
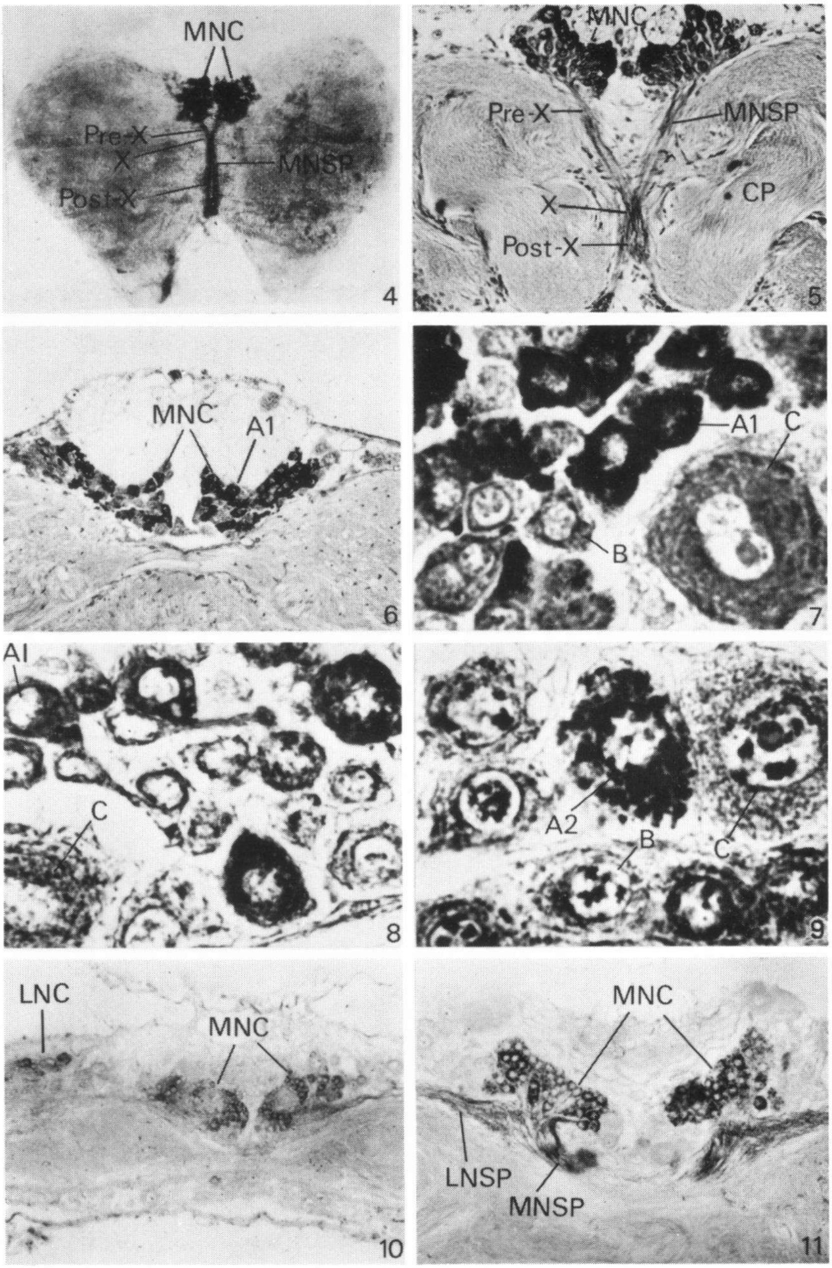


Fig. 3. Diagrammatic representation of the topography of neurosecretory cells and path ways in the brain of the ultimate instar larva of *Orthetrum chrysis*.

about 10-12 A2, 14-16 B and 2 C cells in each lateral group in the larva and 14-16 B and 2 C cells in the adult, suggesting that the A2 cells are present in the larval lateral groups only while they are altogether absent in the adult stage.

The ventral neurosecretory cells (VNC) are situated on either side of the median line in the ventral part of the tritocerebral lobes of the brain (Fig. 15). They lie just above the root of the circum-oesophageal commissures. Each ventral group contains about 12-15 B and 8-9 C cells in the ultimate instar larva and 10-12 B and 6-8 C cells in the adult.

The optic neurosecretory cells (ONC) are located in the antero-dorsal region of the root of the optic lobes (Figs. 16-19). They are scattered among the small


MNC
Pre-X
X
MNSP
Post-X
4
MNC
Pre-X
MNSP
CP
X
Post-X
5
MNC
A1
6
A1
C
B
7
AI
C
8
A2
B
C
9
LNC
MNC
10
MNC
LNSP
MNSP
11

nerve cells. Each group bears about 8-10 B and 10-12 C cells in the larval, and 5-6 B and 10-12 C cells in the adult stage.

THE NEUROSECRETORY PATHWAYS

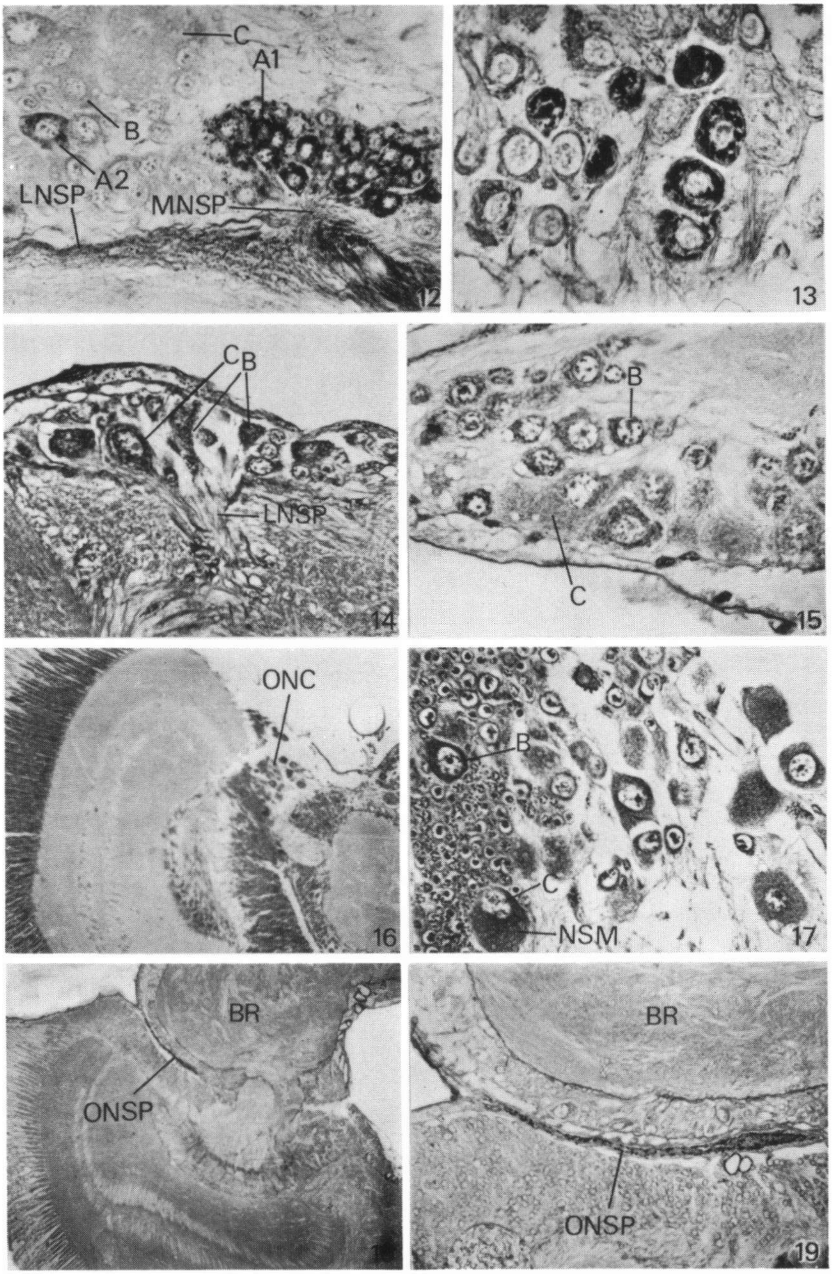
The axons of MNC, LNC, VNC and ONC form distinct medial, lateral, ventral and optic neurosecretory pathways inside the brain (Figs. 2-3). Both medial neurosecretory pathways (MNSP) take a sort of oblique path and run towards the middle of the brain and in between the mushroom bodies they decussate so that the MNSP of the right side of MNC comes to the left side and vice-versa. After the chiasma, both the MNSP run parallel to each other towards the ventero-posterior side of the brain. The prechiasmatic (pre-x), chiasmatic (x) and postchiasmatic (post-x) portions of the MNSP are clearly visible in the sections as well as in the bulk preparations (Figs. 4-5). The lateral neurosecretory pathways (LNSP) run anterior to the mushroom bodies and join the MNSP at the prechiasmatic portion in the larva (Figs. 11-12) while in the adult dragonfly, each LNSP runs obliquely towards the posterior side and after encircling the mushroom bodies from outside, joins the postchiasmatic region of the MNSP. The ventral neurosecretory pathways (VNSP) run for a short distance along the ventral border of the brain and finally merge into the combined MNSP and LNSP on their own side just before the emergence of the NCC from the brain. The optic neurosecretory pathways (ONSP) run posteriorly towards the medulla interna where they release the NSM in the close vicinity of the inner chiasma (Figs. 18-19).

Due to the fusion of MNSP, LNSP and VNSP a pair of thick nerves, the nervi corporis cardiaci (NCC) emerges out of the brain. Both the NCC run parallel to each other on either side of the aorta, dorsal to the oesophagus and each of them ultimately enters the corpus cardiacum on its own side.

THE CORPORA CARDIACA

The corpora cardiaca (CC) are paired elongated fusiform glistering white bodies, lying just behind the brain, dorsal to the oesophagus. They are connected ventrally with the hypocerebral ganglion by two lateral nerves, the nervi cardio-stomatogastrici (NCS) (Fig. 21). The CC are intimately associated with the dorsal aorta. Two corpora cardiaca are free from one another anteriorly, but

Figs. 4-11. In situ preparation (4) and sections (5-11) through the brain of *Orthetrum chrysis*: (4) adult, PAVB, X35; – (5) PI, last instar larva, CHP, X135; – (6) PI, adult, CHP, X215; – (7) PI, adult, CHP, X865; – (8) PI, adult, ABP, X1000; – (9) PI, last instar larva, CHP, X900; – (10) last instar larva, AF, X65; – (11) last instar larva, AF, X135. – PI, pars intercerebralis.


C
A1
B
A2
LNSP
MNSP
12
13
C
B
LNSP
14
B
C
15
ONC
16
B
C
NSM
17
BR
ONSP
BR
ONSP
19

posteriorly they are fused and form a single lobe (Figs. 20, 22), and in the middle region both the CC are connected with each other by a dorsal commissure, the commissura corporis cardiaci (CCC) (Fig. 21).

In the corpora cardiaca, two types of cells, the chromophilic and chromophobic are observed (Figs. 22-23). The chromophilic cells stain blue with PAVB, black with CHP, purple with AF, blue with ABP and red with Azan. They lie in the middle region of the anterior lobe of the CC and are pear shaped with centrally placed nuclei. The chromophobic cells stain with counterstains and are totally devoid of stainable material. They are scattered throughout the substance of CC but are abundant in the posterior lobe of the CC.

The CC are innervated by the NCC from the brain. The axons of the NCC after entering the CC at its anterior end divide into two bundles, each running towards the periphery of the CC, where they ramify.

THE AORTA

Some axons of the NCC, loaded with cerebral NSM, come out of the posterior end of the CC and innervate the aorta (Fig. 24). The NSM does not accumulate in the aorta wall though it lies in varying quantities in the innervating axons.

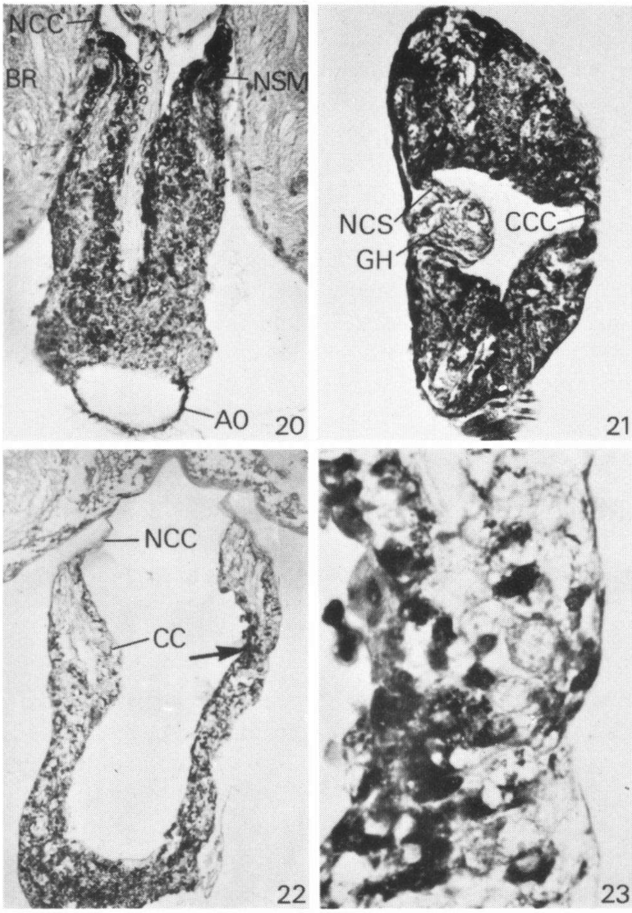
THE CORPORA ALLATA

The corpora allata (CA) are elongated cylindrical bodies, situated anterolaterally to the corpora cardiaca and lateral to the oesophagus just near the suboesophageal commissures. Some of the axonal fibres of the NCC emerge out of the CC, and proceed towards the CA as the nervus corporis allati 1 (NCA1). Each NCA1 bifurcates at the anterior end of a corpus allatum (Figs. 25, 26). Both branches superficially innervate the CA from either side and again reunite at the other side forming the NCA2. The NCA2 terminates in the suboesophageal ganglion. The axons of the NCA1 are not seen in the CA body. The cerebral NSM is not found in the CA, NCA1 and NCA2 of the larva nor in those of the adult dragonfly.

The corpora allata are composed of a large number of small spherical cells and some giant cells (Figs. 27-28). The external wall of the CA is made up of connective tissue.

In the ultimate instar larva as well as in the adult, the CA, though primarily cellular structures, sometimes do show a syncytial condition (Fig. 29).

Figs. 12-19. Sections through the brain of *Orthetrum chrysis* LNC: (12) last instar larva, AF, X265; – (13) last instar larva, CHP, X400; – (14) adult, CHP, X335; – (15) tritocerebrum, last instar larva, AF, X165; – (16-19) optic lobe, last instar larva, AF, (16) X35; – (17) X335; – (18) X40; – (19) X135.

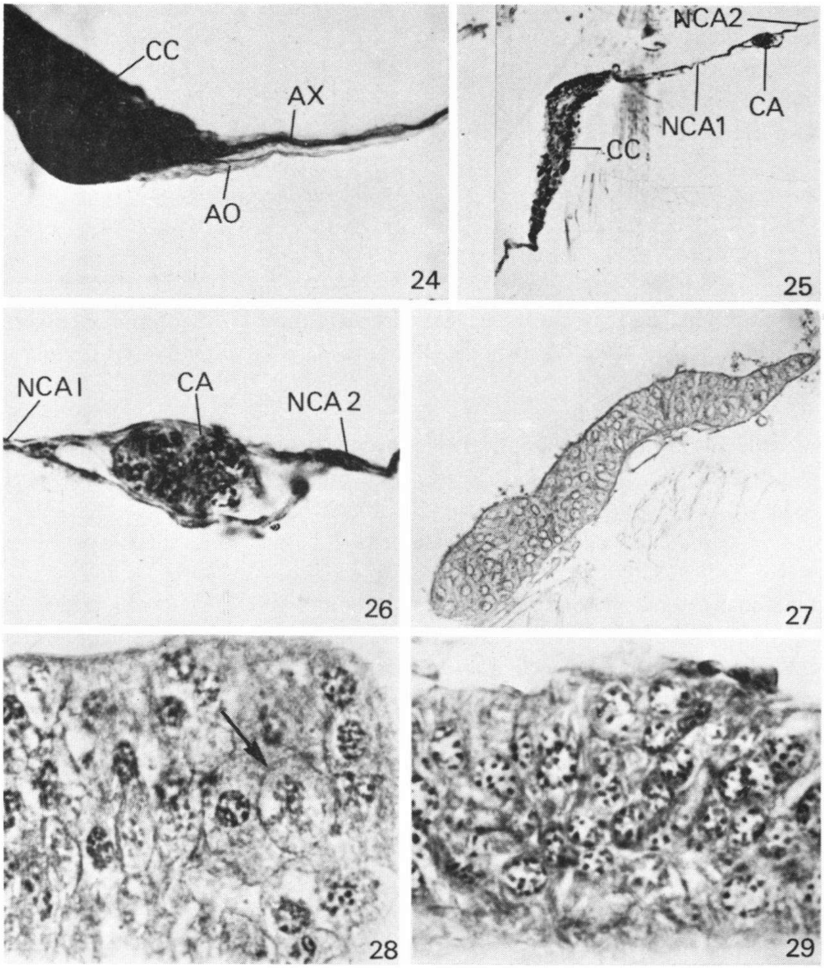


Figs. 20-23. Sections through brain and CC of *Orthetrum chrysis*: (20) adult, CHP, X135; – (21) adult, CHP, X285; – (22) last instar larva, AF, X105; – (23) anterior lobe, AF, X735.

DISCUSSION

The cephalic neuroendocrine system of the dragonfly *Orthetrum chrysis*, while displaying the general feature of the cephalic neuroendocrine system described in other insects, including dragonflies, presents a number of peculiarities.

Although it is well known that the proteinaceous active substances (neurohumors and neurohormones) are synthesized and released by the ordinary neurons (BERN, 1962; SCHARRER, 1969; WIGGLESWORTH, 1970; SMITH,



Figs. 24-29. In situ preparation (24) and sections (25-29), *Orthetrum chrysis*: (24) CC and AO, AF, X135; – (25-26) last instar larva, retro-cerebral complex, CHP, (25) X85, (26) X500; – (27) last instar larva, CA, AF, X265; – (28) adult female, CA, arrow: giant nuclei during vitellogenesis, CHP, X900; – (29) syncytium in CA of one day old adult, CHP, X900.

1971), the neurosecretory cells are clearly differentiated from the former by the use of selective histological techniques. In the present study the neurosecretory cells are identified on the basis of three criteria: (1) the presence of stainable granules, (2) the presence of neurosecretory material in their axons and terminals, and (3) their cyclic activity manifesting itself by changes in quantity of neurosecretory material in relation to changes in physiological activities.

While a large amount of information is accumulated on the MNC groups in other dragonfly species (HANSTRÖM, 1940: *Aeshna juncea, Calopteryx virgo, Lestes sponsa, Coenagrion* sp.; – CAZAL, 1947, 1948: *Aeshna grandis, A. cyanea, Sympetrum flaveolum, Crocothemis erythraea, Libellula depressa, Lestes virens, Platycnemis pennipes, Calopteryx virgo*; – DEROUX-STRALLA, 1948a: *Aeshna grandis*; – ARVY & GABE, 1952, 1953: *Sympetrum vulgatum, Aeshna cyanea, Calopteryx splendens, Coenagrion pulchellum*, – SCHALLER & MEUNIER, 1968: *Aeshna cyanea, A. isosceles, A. mixta, Anax imperator*; – GILLOTT, 1969: *Coenagrion angulatum*; – CHARLET, 1972: *Aeshna cyanea*), the neurosecretory cells present in other regions of the brain have received but little attention. Besides the MNC, the neurosecretory cells of other localities (LNC, VNC, ONC) have been thoroughly studied in larval and adult *Orthetrum chrysis*.

BEATTIE (1971) perhaps was the first to report the presence of neurosecretory cells in the optic lobes of the cockroach, *Periplaneta americana*. In the present study also, neurosecretory cells were observed in the optic lobes of the dragonfly, *O. chrysis* along with the ONSP having a considerable quantity of stainable NSM. The release of NSM at the internal optic chiasmatic region, however, indicates its functional relationship with the physiology of the eye.

On the basis of tinctorial affinities, only A and B cells were reported in the MNC groups of the Odonata. CHARLET (1972, 1974) has demonstrated the presence of C cells in the medial and other groups of the larval *Aeshna cyanea*. There is, however, no other report on the occurrence of C cells in dragonflies. In the present study, these have been observed in all eight groups of *Orthetrum chrysis*.

The A cells are divisible into A1 and A2 in the ultimate instar larva. The A1 cells lie predominantly in the medial groups and the A2 cells in the medial and lateral groups. In the adult, on the other hand, medial groups contain only A1, while A2 cells are totally lacking. The presence of A2 cells in the larval stage suggests a specific function of these which might be related to metamorphosis and moulting.

In the adult *O. chrysis* the LNSP joins the MNSP after crossing over the MNSP. In its larva, however, LNSP joins the prechiasmatic region of the MNSP before the chiasmata formation. Thus, while in the adult only the axons of the MNC groups decussate, in the larva the axons of MNC and LNC decussate. To our knowledge no such situation has ever been reported in any insect.

CAZAL (1947, 1948) and ARVY & GABE (1952), however, recorded two NCC pairs, i.e. NCCI and NCCII. Recently VARMA (1972) has erroneously reported three pairs of NCC. Our present study, based on the same species as that of the latter worker, reveals that the CC are innervated in the ultimate larval as well as in the adult stage by a single pair of nerves (NCC). Our observations are thus in agreement with the evidence produced by HANSTRÖM (1940, 1942), DEROUX-STRALLA (1948a), GILLOTT (1969) and Schaller (personal communication).

The corpora cardiaca of *Orthetrum chrysis*, in their histomorphology, resemble other dragonflies (HANSTRÖM, 1940, 1942; CAZAL, 1947, 1948; ARVY & GABE, 1952, 1953).

The arrangement of chromophilic and chromophobic CC cells in *O. chrysis* presents a situation similar to that found in other dragonfly species. In the orthopteran *Schistocerca gregaria* the NCC breaks into the substance of CC and emerges as NCA going to CA. In the CA also the nerve NCA splits into fine branches (HIGHNAM, 1961). AWASTHI (1968), on the contrary, describes that in *Gryllodes sigillatus* the nerve NCC does not break into the CC but passes superficially to it and continues at the other side as NCA1 which further lies superficially to CA and continues as NCA2 going to the suboesophageal ganglion. On its way to the suboesophageal ganglion, it presents a swelling which is supposed to be a second storage organ of cerebral NSM. In *O. chrysis*, the NCC splits into branches in the substance of CC. Some axons of the NCC terminate inside the CC, some run along with the aorta and the rest of them emerge out as NCA1. Each NCA1 does not enter the CA but bifurcates near the anterior end of CA and innervates the gland superficially. GILLOTT (1969) reported that in the damselfly *Coenagrion angulatum* the NCA1 lies just near the CA and turns as NCA2. He does not make any reference to the further course of this nerve. In *O. chrysis* NCA does not present any swelling. Further neurosecretory material has been observed neither in the NCA1 nor in the NCA2, suggesting that all the neurosecretory material of the brain accumulates in the CC. Here the NCA2 terminates into the suboesophageal ganglion.

Although the axons, loaded with stained material, pass from the CC into the aorta, the cerebral NSM does not accumulate in the aorta wall, which suggests that the aorta is, in *O. chrysis*, only a releasing site and not a secondary storage organ for the cerebral NSM (THAKARE & TEMBHARE, 1975).

The CA of the ultimate larval instar and of the adult *O. chrysis* show similarities in their position and structure with those of other dragonflies described by CAZAL (1947, 1948), DEROUX-STRALLA (1948) and ARVY & GABE (1952, 1953). The histological details of the CA sustain the objection of GILLOTT (1969) against these workers that "the French authors may have mistaken a part of the salivary glands for the corpora allata". Recently, however, VARMA (1972) has wrongly described the salivary reservoirs as CA.

MENDES (1948) found four types of cells and EWEN (1962b) two types of cells in the CA of *Melanoplus differentialis* and *Adelphocoris lineolatus* respectively. In *O. chrysis* the CA are composed of only a single kind of cells in larval and adult stages. DE LERMA (1932), PALM (1947), KAISER (1949), SCHARRER & VON HARNACK (1958), SIEW (1965) and KRISHNANDAM & RAMAMURTY (1971) have reported the presence of some giant cells at the periphery of the glands. The same type of giant cells are also observed at the periphery of CA in the adult female during the vitellogenic stages. The syncytial and the cellular nature of the CA in adult and larva seem to be related to the secretory and non-secretory stages of the glands. The syncytial condition may be due to the obliteration of cell membranes for the release of internal secretory products during the secretory phase of the glands.

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