Exploring Octopamine: Immunohistochemical research of a spionid worm *Pygospio elegans* nervous system

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Abstract

Octopamine is a biogenic amine specific for invertebrates distributed in all groups from Cnidaria to Echinodermata. Our study is aimed to investigate the octopamine-positive elements in the nervous system of the spionid worm *Pygospio elegans*. Immunohistochemistry was used to detect octopamine-positive elements in the central and peripheral nervous systems. While the central nervous system exhibited weak staining, the peripheral nervous system showed specifically octopamine-like elements in the palps, peristomium, and body segments. The detected octopamine-like elements were compared with other neurotransmitters in the *P. elegans* nervous system. Our results contribute to the data on annelid octopaminergic nervous system structure.

Keywords: *Pygospio elegans*, nervous system, peripheral nervous system, octopamine, immunohistochemistry, confocal microscopy

Introduction

The biogenic amine octopamine (OA) is a phenolic analog of vertebrate norepinephrine that was first discovered in the octopus by Erspamer and Boretti in 1951 (Roeder, 1999). The presence of octopamine was demonstrated in different invertebrate clades (Pflüger and Stevenson, 2005). Several physiological and biochemical studies in invertebrates offer valuable insights into the significance of OA and its role in animal behavior. OA acts as a modulator of the heart rate, skeletal and smooth muscles in molluscs and annelids (Vehovszky et al., 1998; Barna et al., 2001). A variety of behavior functions have been identified for OA, for example, rhythmic (Sombati and Hoyle, 1984), feeding (Long and Murdock, 1983), swimming (Hashemzadeh-Gargari and Friesen, 1989), and sexual behavior (Gilchrist et al., 1995). The presence of OA was shown in the visual system of *Limulus* (Battelle, Calman, and Hart, 1999). OA is also present in the hemolymph of cockroaches and locusts, where it acts as a neurohormone (Orchard, 1982; Adamo and Baker, 2011). Equally significant are investigations into the nervous system morphology with the objective of examining the distribution of neurotransmitters within cells and their associated structures. OA-containing neurons were found in the central nervous system of leeches (Crisp et al., 2002), molluscs (Elekes, Eckert, and Rapus, 1993; Karhunen, Airaksinen, Tuomisto, and Panula, 1993), lobster (Schneider et al., 1993), and different insects (Stevenson and Pflüger, 1994; Sinakevitch, Niwa, and Strausfeld, 2005; Busch, Selcho, Ito, and Tanimoto, 2009). The study of the invertebrate nervous system entails intricate and labor-intensive methods, therefore the results on structure and physiology are incomplete and fragmentary. Even in the relatively studied groups, such as annelids, data are sparse and are limited to a very

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short list of species. Recently, we have performed a series of studies on the distribution of catecholamine-reactive (CA) (Barmasova, Starunova, Novikova, and Starunov, 2022), histamine- (HA) and gamma-aminobutyric acid-immunoreactive (GABA) elements of the nervous system in the spionid worm *Pygospio elegans* (Starunova, Shunkina, Novikova, and Starunov, 2022). The current study is a continuation of this series and is aimed to describe OA-immunopositive elements of the central and peripheral nervous systems of this animal.

Material and methods

Material

Pygospio elegans Claparède, 1863 were collected from mud and sand flats in the Barents Sea near the Marine Biological Station at Dalnie Zelentsi (69°07' N, 36°05' E). Worms were kept at the laboratory in containers filled with sand and artificial seawater.

Immunohistochemistry

All animals were relaxed using a 7.5 % solution of $MgCl_2 \cdot 6H_2O$ before fixation. Two different fixatives were used: a manufacturer suggested a mixture of a freshly prepared 4 % paraformaldehyde and 0.3 % glutaraldehyde in 0.1M phosphate-buffered saline (PBS) and an alternative fixative solution containing 5 ml 25 % glutaraldehyde, 15 ml saturated picric acid, and 0.2 ml glacial acetic acid (Barna et al., 2001). We used the standardized whole-mount antibody labeling method described in Starunova, Shunkina, Novikova, and Starunov, 2022. Polyclonal rabbit anti-octopamine primary antibody (Millipore, Massachusetts, USA, AB 1799, dilution 1 : 100) was used for the immunostaining process. Since our preliminary observations revealed few cells labeled with this antibody, we applied monoclonal mouse anti-acetylated α-tubulin antibody (Sigma-Aldrich, St. Louis, USA, T-6793, dilution 1 : 1000) to visualize the general topology of the nervous system and ciliary structures in all labeling experiments. Specimens were incubated with secondary antibodies Alexa Fluor 488 Donkey Anti-Rabbit (Molecular probes, Oregon, USA, A-21206) and Alexa Fluor 647 Donkey Anti-Mouse (Molecular probes, Oregon, USA, A-31571) diluted 1 : 800. Additionally, the cell nuclei were counterstained with 1 µg/ml DAPI (Carl Roth, Karlsruhe, Germany, 6335.1).

Microscopy and Image Processing

The stained specimens were mounted in Mowiol 4–88 between two coverslips in dorsoventral orientation and were examined using a laser-scanning microscope Leica TCS SP5 (Leica Microsystems, Wetzlar, Germany). The specimens were scanned in 50–70 coronal optical sections with a thickness of 1 µm. The resulting confocal stacks were processed with Fiji and/or Bitplane Imaris software. The brightness and contrast of the resulting images were adjusted with Krita. The schemes were drawn in Inkscape.

Results

In our research, we used both the manufacturer-recommended fixation method, as well as the alternative one, described in the literature (Barna et al., 2001). Despite employing various approaches, the obtained results were nearly identical. Octopamine antibodies revealed few elements, primarily associated with the peripheral nervous system. A faint signal was registered in the brain region. Within the palps, we identified long pyriform OA-like immunoreactive cells distributed along the entire length of each palp (Fig. 1A, B). Somata of these cells came close to the palp nerves, while their projections were directed towards the food groove. Since the ciliation of the food groove was very dense, it was difficult to determine definitively whether cilia were present at the ends of these processes or not.

The body wall around the mouth and the posterior part of the peristomium contained numerous OA-like cells which can be classified into two different types. The first were bipolar flask-shaped cells with a slight extension at the end, facing the surface (Fig. 1C–G). These cells lacked cilia and were predominantly situated in the upper lip (Fig. 1C–D) and around the mouth, where they were co-localized with the cells of the second type (Fig. 1E–G). The cells of the second type had massive perikaryon and a thin projection (Fig. 1G). They also lacked cilia and were abundant at the posterior part of the peristomium. The wall of the peristomium possessed a thin OA-like immunopositive nerve meshwork which was best seen at the lateral sides (Fig. 1G).

In the body segments, OA-positive elements were found in the ventral nerve cord, segmental nerves, cells at parapodial gills, and nerve fibers in the body wall. At the dorsal side, octopamine antibody labeled several pyriform cells in gills (Fig. 1H, I). Each cell had a rounded nucleus, one tiny projection coming from the tip, and apparently lacked cilia. The OA-like fibers within the longitudinal nerves of the ventral nerve cord were very thin and poorly traced (Fig. 1K). There was also one OA-positive commissure per each segment. In the segmental nerves OA-like fibers were found in three pairs of nerves that supply the parapodia (Fig. 1J). The abdominal segment may contain more than three pairs of OA-like segmental nerves. However, the total number of segmental nerves with OA-like fibers per segment decreased as it approached the posterior end of the animal. No OA-like elements were found in the pygidium. A thin meshwork formed by OA-like immunoreactive nerve fibers was

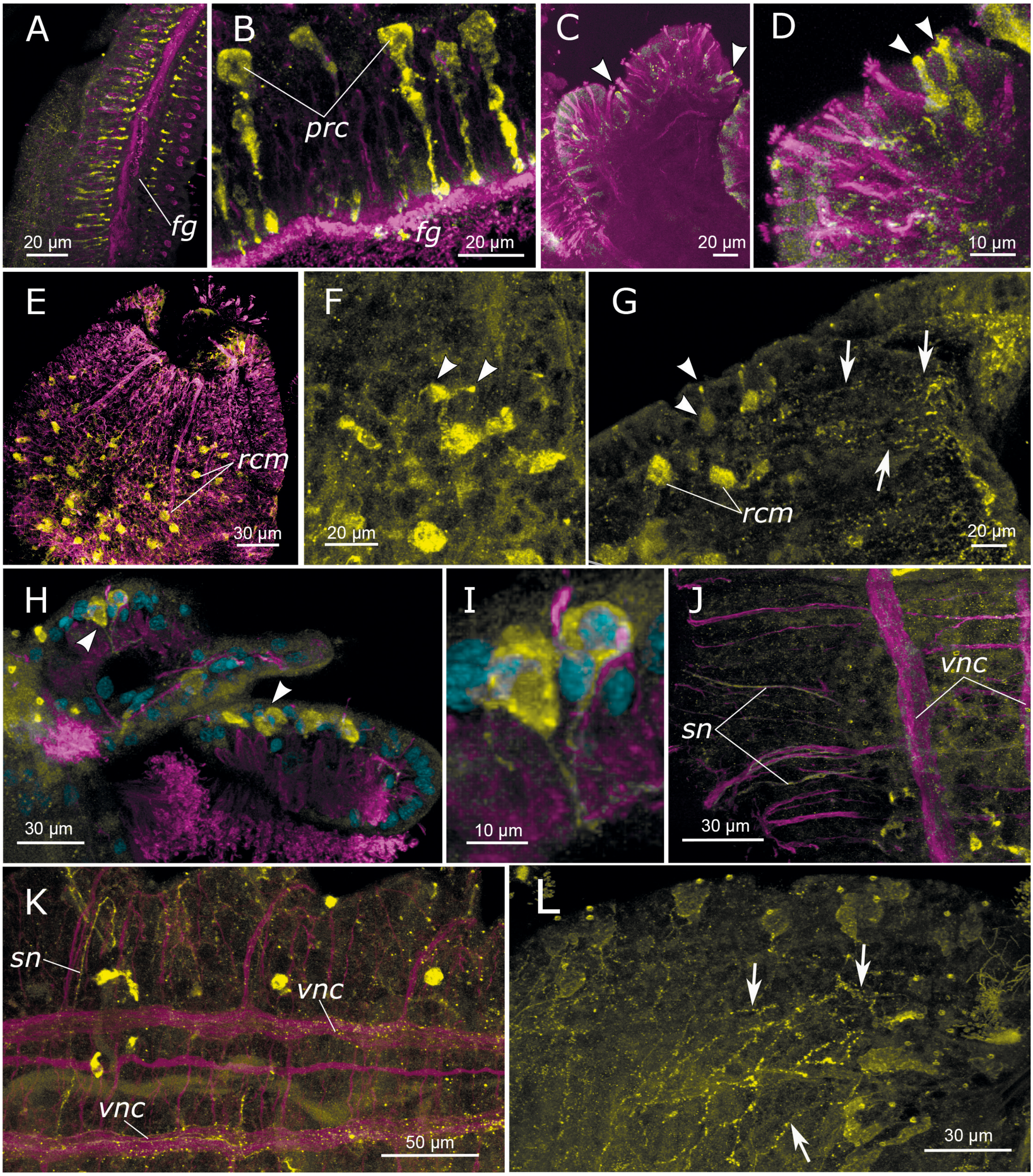

Fig. 1. OA-like elements of *Pygospio elegans*: A, B — OA-like cells of the palps; C, D — OA-like cells at the upper lip of the mouth; E–G — OA-like cells at the posterior part of the peristomium; H — innervation of gills in parapodia; I — nuclei in the receptor cells of gills; J–L — innervation of body segments and body wall.

Abbreviations: *fg* — food groove, *prc* — palp receptor cells, *rcm* — receptor cells of the mouth region, *sn* — segmental nerve, *vnc* — ventral nerve cord.

White arrowheads — receptor cells, white arrows — OA-like nerve meshwork.

OA-like elements are yellow, the general topology of the nervous system and ciliated structures labeled with acetylated α-tubulin antibody are magenta, cell nuclei stained by DAPI are cyan.

found in the body wall (Fig. 1L). The processes were clearly visible, as the cell somata in the body wall were not distinguished.

Discussion

Among the primary groups of invertebrates, octopamine has been well studied in molluscs and arthropods (Pflüger and Stevenson, 2005; Gallo et al., 2016). However, in annelids, the distribution of octopamine has only been studied in a limited number of highly derived groups: leeches *Hirudo medicinalis* and *Macrobella decora*, earthworms *Lumbricus terrestris* and *Eisenia fetida,* and siboglinid *Oligobrachia haakonmosbiensis* (Belanger and Orchard, 1986; Csoknya et al., 1996; Barna et al., 2001; Crisp et al., 2002; Zaitseva et al., 2022). The focus of most of these studies has been on the structure and, in some cases, the physiology of the central nervous system exclusively. Only in 1997 a detailed description of the peripheral nervous system in the digestive tract of the earthworm *E. fetida* was conducted (Csoknya et al., 1997). Some elements of the peripheral nervous system have also been described in the siboglinid *Oligobrachia haakonmosbiensis* (Zaitseva et al., 2022). The lack of comprehensive data on the peripheral nervous system may be attributed to the imperfect and laborious methods used to detect octopamine (Pflüger and Stevenson, 2005).

Our results clearly indicate the presence of OA-like immunoreactive elements in both central (brain and ventral nerve cord) and peripheral (segmental nerves, palp nerves, and nerve plexus of the body wall) parts of the *Pygospio elegans* nervous system. The presence of OA-like immunoreactive elements in the central nervous system corroborates previous data on leeches and oligochaetes, however, the number of detected cells differs significantly. In adult *P. elegans* the brain and ventral nerve cord show only faint immunoreactivity to antibodies against octopamine. This may be due to both differences between groups and differences in the detection techniques used. It is worth noting that in *P. elegans,* another biogenic amine, histamine (HA), has somehow similar distribution in the central nervous system (Starunova, Shunkina, Novikova, and Starunov, 2022). Few HA-immunopositive cells were detected in the brain, while in the ventral nerve cord only HA-immunopositive nerve projections were found. Unfortunately, there are no comprehensive studies of these neurotransmitters in other annelid families made so far. Thus, the obtained

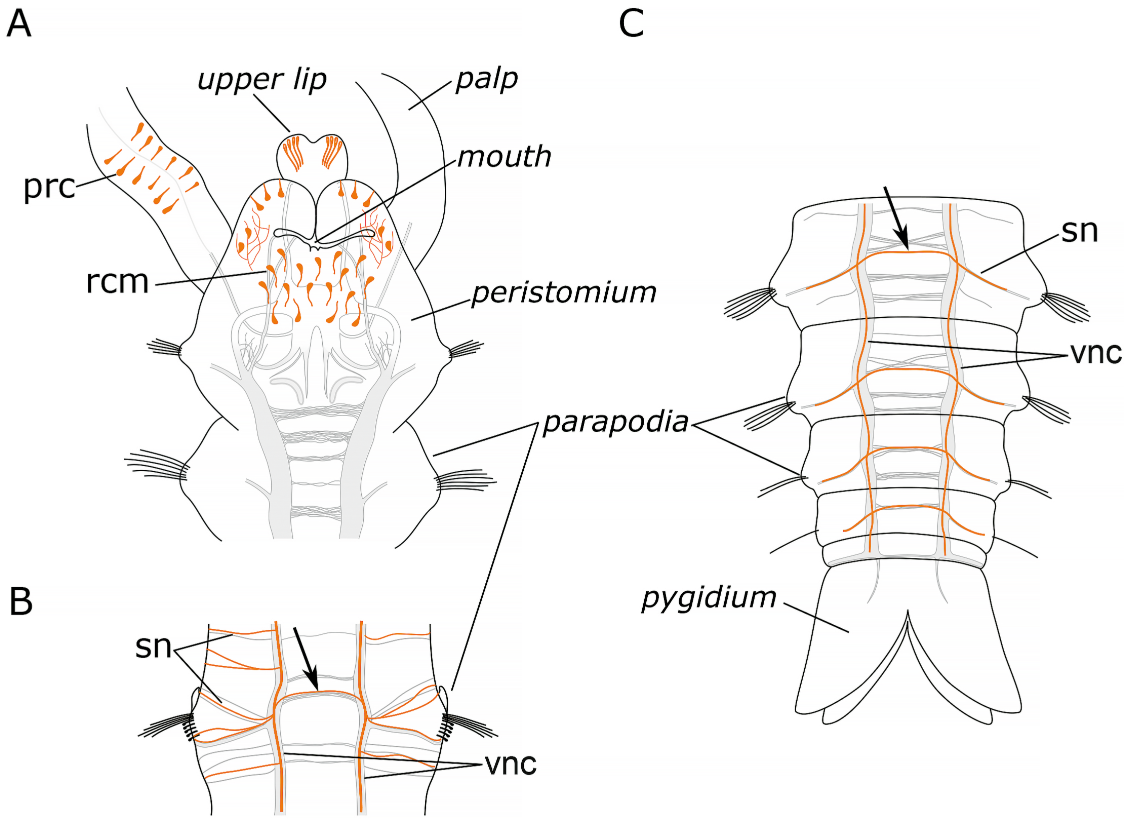

Fig. 2. Schematic representation of OA-like elements (orange) in the anterior part (A) and body segments (B, C) of *Pygospio elegans* from the ventral view. The main nerve tracts of the central nervous system are outlined in grey.

Abbreviations: *prc* — palp receptor cells, *rcm* — receptor cells of the mouth region, *sn* — segmental nerve, *vnc* — ventral nerve cord.

black arrows — commissures of the segmental ganglia.

results indicate the need for further extensive studies in different annelid species to provide new comparative data to understand the functions of these neurotransmitters and the evolution of the annelid nervous system.

All the identified OA-like immunoreactive elements related to the peripheral nervous system are located in the palps, peristomium, gills, and body segments, and are unique in that no other neurotransmitters have been found in them (Starunova, Shunkina, Novikova, and Starunov, 2022; Barmasova, Starunova, Novikova, and Starunov, 2022). Remarkable OA-like immunopositive cells within *P. elegans* palps are densely arranged in rows spanning the entire length (Figs 1, 2A). Some OA-positive cells were also found in the tentacles of *Oligobrachia haakonmosbiensis* (Zaitseva et al., 2022). The cells were monociliary and found in relatively small numbers. Based on their morphology and location, it is plausible that in both *P. elegans* and *O. haakonmosbiensis* OA-like immunopositive cells of the head appendages serve a sensory function.

The octopamine antibody labeled several cells in the gills of *P. elegans*. Data on gill innervation of other neurotransmitter modality in *P. elegans* or other annelids are limited. For instance, in *Alvinella pompejana*, the gill epithelium primarily comprises various secretory cells and only a small number of receptor cells (Storch and Gaill, 1986). Based on their morphology and abundance, the OA-positive cells in the gills of *P. elegans* that we have identified could likely be secretory or neurosecretory.

Most OA-positive cells inside the body wall are found around the mouth where they form a dense plexus. The type 1 receptor cells around the mouth of *P. elegans* are identical in shape to the OA-positive cells from the body wall of *O. haakonmosbiensis* (Zaitseva et al., 2022). Their shape and position suggest that these nerve elements may fulfill sensory functions. Similar results were obtained for the earthworm *E. fetida* in which the OA-containing enteric plexus was found along the alimentary tract and pharynx (Csoknya et al., 1997). The authors suggest the important role of octopamine in the regulation of digestion. The OA-positive cells in this plexus are also considered sensory neurons.

It was shown that the epithelium of the *Lumbricus* exhibits a diverse array of sensory cells with different chemical specificity in both the body wall (serotonin, dopamine, noradrenalin) and gut (GABA, enkephalin, FMRFamide) (Ehinger and Myhrberg, 1971). It is worth noting that the body wall of *P. elegans* showed a reduced diversity of sensory elements (Starunova, Shunkina, Novikova, and Starunov, 2022; Barmasova, Starunova, Novikova, and Starunov, 2022) compared to *O. haakonmosbiensis* (Zaitseva et al., 2022) and earthworms (Ehinger and Myhrberg, 1971; Csoknya et al., 1997), possibly due to the small body size of *P. elegans*. The reduced diversity of sensory elements in the body wall could be a potential reason for the absence of a similar plexus with other studied neurotransmitters (serotonin, FMRFamide, HA, GABA, CA) in *P. elegans* (Starunova, Shunkina, Novikova, and Starunov, 2022; Barmasova, Starunova, Novikova, and Starunov, 2022; Shunkina, Starunova, Novikova, and Starunov, 2023).

OA-positive neurites were found in three segmental nerves supplying the body wall and parapodia. In the wall of body segments, only a neurite meshwork without distinct neuron somata was found. Thus, we can assume, that OA-positive elements of the body segments may contribute to motor innervation. Similarly, motor functions have previously been shown for OA-positive neurons in other invertebrates (Barna et al., 2001).

Conclusion

To summarize, our results indicate a predominant distribution of OA-like elements in the peripheral nervous system of *P. elegans* and suggest their possible sensory and/or secretory function in addition to motor innervation which is common for other studied invertebrates. These findings complement the results obtained with other annelids (Ehinger and Myhrberg, 1971; Csoknya et al., 1997; Zaitseva et al., 2022) concerning octopamine as well as our research exploring other neurotransmitters in the nervous system structure in *P. elegans* (Starunova, Shunkina, Novikova, and Starunov, 2022; Barmasova, Starunova, Novikova, and Starunov, 2022). Nevertheless, the lack of comparative data together with the differences found clearly indicate the need for a broad comparative study of the distribution of this neurotransmitter in other annelid families.

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