Dopamine-like immunoreactivity in sponge larvae

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ABSTRACT: Sponges differ from the majority of multicellular animals by lack of specialized neural cells. Although sponge genomes show the toolkits for metabolism of some neuroactive substances, only few genes of monoamines metabolism were found. We studied larvae of the freshwater sponge *Eunapius fragilis* to analyze the immunoreaction to one of the monoamines – dopamine (DA). We found dopamine-like immunoreactivity in structures located under every flagellum in the larval epithelial cells. Double labeling with anti-DA and anti-58K Golgi protein antibodies, confocal microscopy with improved signal-to-noise ratio and super-resolution (Airyscan), and ultrastructural electron microscopy analysis revealed that the DA-like-immunopositive structures are closely associated with the Golgi apparatus. A similar pattern of immunolabeling was reported in the blastulae of sea urchins, whose ciliary activity is known to be affected by monoamines. Our finding of DA-like immunoreactive structures in sponge ciliated cells provide morphological basis for considering monoamines as potential intracellular regulators of flagellar/ciliary activity.

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Introduction

Monoamines, such as serotonin (5-HT) and dopamine (DA), have a wide range of signal activity in diverse organisms. Besides multicellular animals, monoamines were found in prokaryotes (Hsu et al., 1986; Shahkolahi, Donahue, 1993; Strakhovskaya et al., 1993; Lyte, Ernst, 1992; 1993; Oleskin et al., 1998; Tsavkelova et al., 2000; Clarke et al., 2006; Shishov et al., 2009), protists (McGowan et al., 1985; Csaba 1993), plants (Roshchina, 1991, 2001, 2010; Murch, 2006; Wan et al., 2018), and fungi (Malikina et al., 2010; Roshchina, 2010). Taken together, these data suggest that monoamines are present in most living organisms and apparently underlay regulation of conservative vital functions. This assumption is also supported by the fact that these substances are functionally active from the earliest stages of animal development starting from the oocyte, cleavage, and cell differentiation (Buznikov, 2007). Thus, the function of monoamines is far beyond the participation in signal transmission between specialized cells like differentiated neurons within the nervous system.

In Bilateria, the crucial biological role of monoamines is well-known, while data on other groups of multicellular organisms are scarce. The most evidences for presence of serotonin and catecholamines concerns cnidarian (Mathias et al., 1960; Welsh, 1960, 1968; Wood, Lentz, 1964; Kline, Weissbach, 1965; Carlyle, 1969; Carlberg et al., 1984; Kolber, Martin, 1988; Anctil, 1989; Chung et al., 1989; Chung, Spencer, 1991; Carlberg, 1992; MacCauley, 1997; Dergham, Anctil, 1998; Westfall et al., 2000; Zega et al., 2003; Mayorova, Kosevich, 2013, Moeller et al., 2019). Despite the fact that their genomes lack the genes coding monoamine synthetic enzymes tyrosine hydroxylase and tryptophan hydroxylase (Westfall et al., 2000; Anctil et al., 2002; Anctil, 2009; Moroz, Kohn, 2015; Moroz et al., 2021), monoamines exert various physiological effects in cnidarians. In particular, their role in metamorphosis (Edwards et al., 1987; MacCauley, 1997; Zega et al., 2003; Moeller et al., 2019), rhythmic contraction (Anctil, 1989, Anctil et al., 1991; Tsang et al., 1997), feeding (Hanai and Kitajima, 1984), regeneration (Lenicque and Feral, 1977), and bioluminescence (Anctil et al., 1982; Awad, Anctil, 1993) were shown. Presence in neurons (Kolberg, Martin, 1988; Umbracal et al., 1990; Pani et al., 1995; Anctil et al., 2002; Westfall et al., 2005), biosynthesis and catabolism (Pani, Anctil, 1994), release by exocytosis (Gillis, Anctil, 2001), and inactivation (Kolberg, Martin, 1988) of various monoamines were noted in variety of cnidarians. There are also some data on receptor activity (Hanai, Kitajima, 1984; Awad, Anctil, 1993; Anctil, Bouchard, 2004; Kass-Simon, Pierobon, 2007; Zega et al., 2007; Moeller et al., 2017).

Sponges (phylum Porifera) represent a more basal group than cnidarian and completely lack homologues of monoamine receptors (Riesgo et al., 2014; Moroz, 2021). The other components...
of the classical monoaminergic system (such as synthesis and degradation enzymes, transporters) do not form a coherent group but are rather scattered across the transcriptomes of different sponge species (Riesgo et al., 2014). Nevertheless, it is known that sponges react to the application of serotonin, dopamine, and epinephrine (Ellwanger et al., 2004; Ellwanger, Nickel, 2006). In addition, serotonin was visualized in the larvae of the sponge Tedania ignis (Duchas-saing et Michelotti, 1864) by immunochemical labeling (Weyrer et al., 1999). Histochemical method revealed monoamine oxidase, serotonin, epinephrine in the calcareous sponge Sycon, and the staining was even blocked by inhibitors of their metabolism (Lentz, 1966), while presented histochemical work needs repetition.

In the current work, we present an evidence for the presence of specific DA-like-immunopositive structures in the sponge larvae cells and suggest their correspondence to the intracellular organelles (cilium/flagellum and Golgi apparatus).

Material and methods

Larvae of the freshwater sponge Eunapius fragilis (Leidy, 1851) were collected in the Moscow Canal in 15 June 2018 – 15 July 2021. The presence of larvae in sponges was determined visually, then parts of the sponges were separated from the substrate and placed in a container with fresh water. After a few hours, larvae left the tissues of the mother’s body and were collected using a Pasteur glass pipette.

To fix larvae, we used a 4% paraformaldehyde solution (PFA) prepared in the phosphate buffer (PBS, pH = 7.4). The larvae were fixed for 4 h at room temperature, then washed three times in PBS and immersed for a day in a PBS-based solution with 0.1% Triton X-100 and secondary antibodies (Goat anti-Rabbit Alexa 488 and Goat anti-Mouse Alexa 555, ThermoFisher), and Hoechst nuclear dye (Sigma). If necessary, preparations were stained with phalloidin-Al- exa 488 (1: 600, ThermoFisher) to visualize cell borders. Finally, the samples were washed three times in PBS and transferred to 80% glycerol in PBS. The specific character of antibody binding was checked by the reaction lacking primary antibodies and other rabbit antibodies.

Confocal scanning microscope Zeiss 880 (Carl Zeiss, Germany) was used for the detailed analysis of the preparations. Stacks of optical sections taken with x40 objectives and 0.3 μm intervals were processed by Image J (NIH, USA) to obtain two-dimensional images. The optimal number of stacks was selected to demonstrate the structures of interest. We applied the Airyscan mode of Zeiss 880 scanning microscope to improve signal-to-noise ratio and to get super-resolution images.

Ultrathin sections were gained and processed as described in Sokolova et al., 2019.

Results

The larva of E. fragilis is a free-swimming parenchymella with large cavity in the anterior part (Fig. 1A). It is covered by dense layer of epithelial monolayered cells underlined with amoeboid cells (Fig. 1B). Epithelial cells have pear-shaped nuclei with prominent apical beak (Fig. 1C).

The immunofluorescence revealed a single DA-like immunopositive granule located asymmetrically within the cell body underneath the cilia and adjacent to nuclei (Fig. 1C–E). Confocal images with improved signal-to-noise ratio and super-resolution (Airyscan mode) allowed to visualize DA-like-positive specific structure and position adjacent to each nucleus of epithelial cells (Fig. 2A, B). Note, that each structures contain three-four parts combined in circle (~1 μm in diameter) (Fig. 2C, E), and DA-like positive circles look like thick stick (~1 μm
Fig. 1. Larva of *Eunapius fragilis* and its peripheral cells. A — larva, general view (light microscopy); B — peripheral fragment of larva: larval epithelium underlined with amebocytes (confocal microscopy); C–E — high magnification of the epithelial cells labeled with anti-DA antibodies.

Abbreviations: cav — cavity; le — larval epithelium; lm — larval mesohyl; Phall — phalloidin, Tub — tubulin-positive label, DA — dopamine-positive label. Scale bars: A — 100 µm, B — 10 µm, C–E — 5 µm.

Рис. 1. Личинка *Eunapius fragilis* и ее периферические клетки. A — общий вид личинки (световая микроскопия); B — фрагмент периферического участки личинки: личиночный эпителий из под ним амебоциты (конфокальная микроскопия); C–E — большое увеличение эпителиального слоя личинки, маркирование антителами против ДА.

Обозначения: cav — полость; le — личиночный эпителий; lm — личиночный мезохил; Phall — фаллоидин, Tub — тубулин-позитивная метка, DA — дофамин-позитивная метка. Масштаб: A — 100 µм, B — 10 µм, C–E — 5 µм.
Fig. 2. Immunolabeling of epithelial cells. A–C — Airyscan images of transversal sections, anti-DA labeling (green); D–F — Airyscan images of longitudinal sections, anti-DA labeling (green); G–H — anti-DA (red) and anti-Golgi 58K protein (green) double labeling. Scale bars: A–C — 1 µm; D–F — 1 µm; G — 2 µm; H — 1 µm.

Рис. 2. Иммунохимическое маркирование эпителиальных клеток. A–C — поперечный срез, Airyscan изображение, маркирование антителами к ДА (зеленый); D–F — продольный срез, Airyscan изображение, маркирование антителами к ДА (зеленый); G–H — двойное мечение: против ДА (красный) и 58K протеина комплекса Гольджи (зеленый). Масштаб: A–C — 1 µм; D–F — 1 µм; G — 2 µм; H — 1 µм.
Fig. 3. Ultrastructure of epithelial cells. A — section of the epithelium; B–D — apical parts of the flagellated cells. Structures on B are colored in accordance to the colors of immune labels on Fig. 1: red — flagellum, blue — nucleus, green — Golgi apparatus.

Abbreviations: f — flagellum; Ga — Golgi apparatus; n — nucleus; r — rootlets. Scale bars: A — 1 µm, C–D — 0.2 µm.

The ultrastructural analysis demonstrated characteristic structures of *E. fragilis* larval epithelial cells. Single flagellum emerged from the deep pit at the apical pole of the cell (Fig. 3A, B, D). The kinetid (flagellar apparatus) was connected with the nucleus via rootlets (Fig.
3C). Golgi apparatus demonstrated asymmetrical positioning on one side from the nuclear beak (Fig. 3B–D). Note the size of Golgi apparatus ~1 µm (Fig. 3B, C, D). The described arrangement of the flagellum, nucleus, and Golgi apparatus were observed in every ciliated cell of larval epithelium.

Discussion

The Golgi apparatus located aside the ciliary/flagellar rootlets is an ordinary feature of monociliated cells in diverse taxa (e.g. Nerrevang, Wingstrand, 1970). This organelle is shown to be a site where the flagellar scaffold proteins are produced, maturated and modified (Deane et al., 2001). It also participates in the intraflagellar transport functioning and correct cilia assembly (Follit et al., 2006; Carvalho-Santos et al., 2011). In sponges, the Golgi apparatus often adjoins the flagellar rootlets, even when the nucleus is located away from the kinetid (Pozdnyakov et al., 2018, 2020; Sokolova et al., 2019, 2020).

In larval epithelial cells of Eunapius fragi-
lis, the Golgi apparatus forms a complex with the nucleus and kinetid rootlets. Juxtaposition of immunochemical labeling and ultrastructural analysis demonstrates the spatial correspondence of the DA-like immunoreactive structures and Golgi apparatus, which is confirmed by specific anti-Golgi labeling. Interestingly, some components of monoaminergic system, such as monoamine synthesis enzymes (tryptophane hydroxylase, tyrosine hydroxylase and dopamine-α-hydroxylase) are shown to be associated with the endoplasmic reticulum, microtubules and Golgi apparatus in the 5-HT- and DA-containing central neurons of mammals (Iijima, Awazi, 1973; Pickel et al., 1975, 1976).

A similar pattern of DA- and 5-HT-positive immunolabeling associated with locomotory cilia was observed in the larvae of sea urchins (Katow et al., 2010; Obukhova et al., 2014, 2015). The monoamine-positive structures occurred in association with gamma-tubulin at the base of the cilium at sea urchin blastula stage (Katow et al., 2010). Their correspondence to the Golgi apparatuses was suggested by ultrastructural analysis (Obukhova et al., 2014, 2015). The experimental survey demonstrated that in the sea urchin larvae the Golgi-located monoamines are involved in regulation of cilia growth and regeneration (Obukhova et al., 2014, 2015). It is known that serotonin and dopamine are active molecules affecting ciliary beating frequency in invertebrate larvae (Marinković et al., 2019), including sea urchins (Wada et al., 1997; Katow et al., 2010) and freshwater gastropods (Goldberg et al., 2011). Probably, the monoamine-dependent ciliary regulation is a universal mechanism within invertebrates. We suggested that despite the absence of complete genetic tools for the monoaminergic system, sponge may utilize monoamines for the same purpose. The observed dopamine-like-positive immunoreactivity in sponge larvae supports this suggestion which, of cause, needs to be proved experimentally.

Our work presents the first evidence for intracellular DA-like-immunopositive structures in sponges, the multicellular organisms lacking nerve cells and monoamine receptors. Further studies of monoamines in sponges are very promising to uncover the functions of monoamines as ancient intracellular regulators of cell activity.

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