Developmental Biology 420 (2016) 178–185

Contents lists available at ScienceDirect

Developmental Biology

journal homepage: www.elsevier.com/locate/developmentalbiology

Evolution of Developmental Control Mechanisms

Revised lineage of larval photoreceptor cells in *Ciona* reveals archetypal collaboration between neural tube and neural crest in sensory organ formation

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ARTICLE INFO

Keywords:
Photoreceptor cells
Ocellus
Ascidian
Cell lineage
Kaede

ABSTRACT

The *Ciona intestinalis* larva has two distinct photoreceptor organs, a conventional pigmented ocellus and a nonpigmented ocellus, that are asymmetrically situated in the brain. The ciliary photoreceptor cells of these ocelli resemble visual cells of the vertebrate retina. Precise elucidation of the lineage of the photoreceptor cells will be key to understanding the developmental mechanisms of these cells as well as the evolutionary relationships between the photoreceptor organs of ascidians and vertebrates. Photoreceptor cells of the pigmented ocellus have been thought to develop from anterior animal (a-lineage) blastomeres, whereas the developmental origin of the nonpigmented ocellus has not been determined. Here, we show that the photoreceptor cells of both ocelli develop from the right anterior vegetal hemisphere: those of the pigmented ocellus from the right A9.14 cell and those of the nonpigmented ocellus from the right A9.16 cell. The pigmented ocellus is formed by a combination of two lineages of cells with distinct embryonic origins: the photoreceptor cells originate from a medial portion of the A-lineage neural plate, while the pigment cell originates from the lateral edge of the a-lineage neural plate. In light of the recently proposed close evolutionary relationship between the ocellus pigment cell of ascidians and the cephalic neural crest of vertebrates, the ascidian ocellus may represent a prototypic contribution of the neural crest to a cranial sensory organ.

1. Introduction

Well-developed paired eyes are highly conserved in all groups of vertebrates. Some protostomes, such as insects, crustaceans, and cephalopods, also have well-developed paired eyes, yet the development and physiology of these eyes are essentially different from those of vertebrate eyes (Hardie and Raghu, 2001; Fain et al., 2010). Invertebrate deuterostomes, which are closer to vertebrates than are protostomes, have only simple ocelli. Thus the origin and evolution of complex vertebrate eyes have been fascinating topics in evolutionary biology ever since Charles Darwin discussed them in his book (Darwin, 1859; Lamb et al., 2009).

The tadpole-like ascidian larva has a simple eye-spot (ocellus) with a pigment cell and vertebrate-type photoreceptor cells (Kusakabe et al., 2001; Kusakabe and Tsuda, 2007). The latter are ciliary photoreceptor cells that resemble vertebrate cone photoreceptors (Eakin and Kuda, 1971; Gorman et al., 1971), and the opsin used in these cells is a bona fide vertebrate-type ciliary opsin, Ci-opsin1 (Kusakabe et al., 2001). Among invertebrates, this type of opsin has been found only in tunicates. Thus the ocellus of the ascidian larva has the closest evolutionary affinity to vertebrate eyes among all invertebrate photoreceptor organs. Therefore, the elucidation of the developmental mechanism of the ascidian ocellus should provide insights into the origin and early evolution of vertebrate eyes.

In the ascidian *Ciona intestinalis*, the ocellus with a pigment cell is located at the right dorsal side of the brain vesicle (Kusakabe and Tsuda, 2007; Horie et al., 2008). In addition to this pigmented ocellus, the *Ciona* larva has a nonpigmented ocellus at the ventromedial side of the brain vesicle (Horie et al., 2008). The photoreceptor cells of the conventional pigmented ocellus are called group I and group II photoreceptor cells, while the unique photoreceptor cells constituting the nonpigmented ocellus are called group III photoreceptor cells (Fig. 1A; Horie et al., 2008). Group III cells use the same vertebrate-type opsin (Ci-opsin1) that the pigmented ocellus uses. The precise

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http://dx.doi.org/10.1016/j.ydbio.2016.10.014
Received 27 September 2016; Received in revised form 23 October 2016; Accepted 23 October 2016
Available online 24 October 2016
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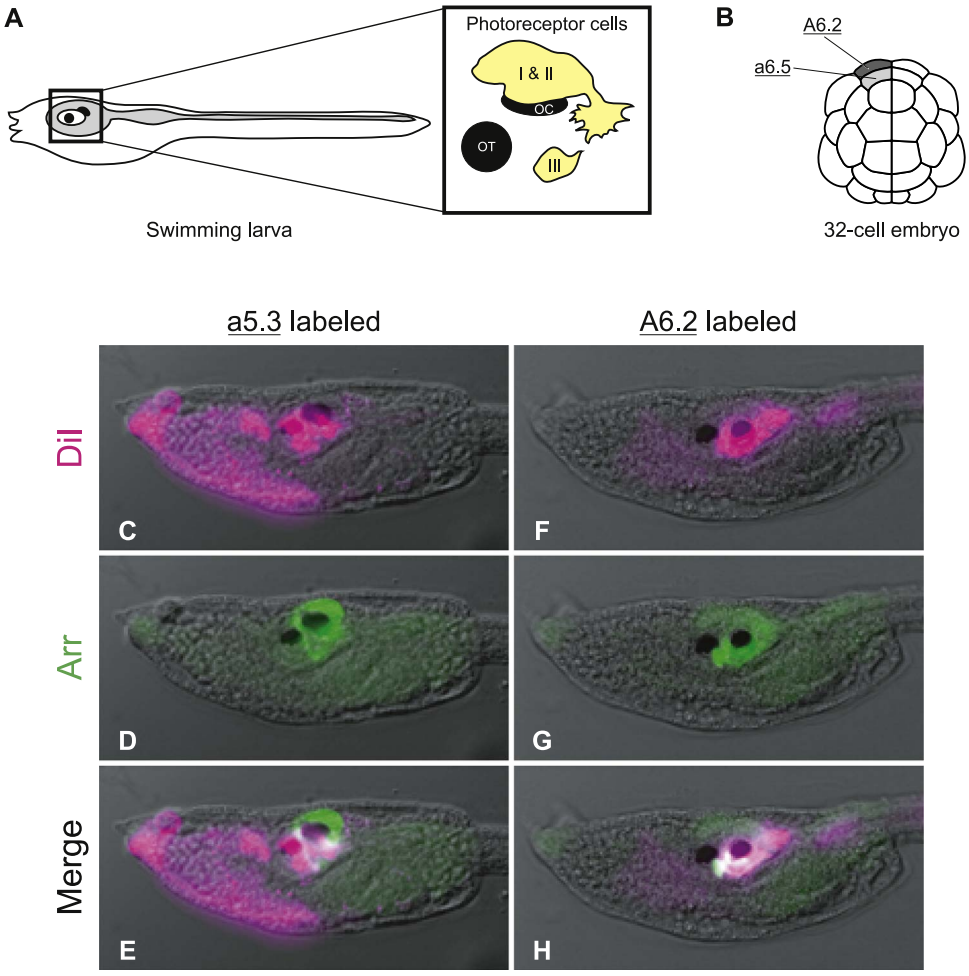

Fig. 1. Cell lineage analysis of the larval photoreceptor cells using DiI. (A) Schematic illustration of the *Ciona intestinalis* larva. Lateral view. Anterior is to the left. The central nervous system is shown in gray. A magnified image of the larval brain vesicle is shown in the right square. Photoreceptor cells are indicated in yellow. OT and OC indicate the pigment cells of the otolith (OT) and the ocellus (OC), respectively. (B) Schematic diagram of the 32-cell embryo. Animal view. Anterior is to the top. The right a6.5 and A6.2 blastomeres (a6.5 and A6.2; left and right blastomeres are distinguished by underlining for right blastomeres; Conklin, 1905) are indicated in light gray and dark gray, respectively. (C-H) Photoreceptor cells were visualized by immunofluorescent staining using anti-Ci-Arr (green), and descendants of a single blastomere were labeled with DiI (magenta). Lateral view. Anterior is to the left. (C-E) A larva in which the right a5.3 cell (progenitor of the right a6.5 cell) was labeled with DiI. (F-H) A larva in which the right A6.2 cell was labeled with DiI. Arrestin-positive photoreceptor cells overlapped with DiI fluorescence in the A6.2-labeled larva (H) but not in the a5.3-labeled larva (E).

identification of the lineage of the photoreceptor cells will be key to understanding both the developmental mechanisms of these cells and the evolutionary relationships between photoreceptor organs of ascidians and vertebrates. To date, however, the exact cell lineage of these photoreceptor cells has not been elucidated. A previous study inferred that the photoreceptor cells of the pigmented ocellus develop from the right a9.33 and a9.37 cells, which are descendants of the a6.5 blastomere (Cole and Meinertzhagen, 2004). The cell lineage was deduced by confocal reconstruction of the positions of nuclei in the embryonic central nervous system from neurulation until hatching. However, the cell lineage is not conclusive because it was the results of speculation based on the observation of different individuals fixed at successive stages without the use of cell differentiation markers. Furthermore, the cell lineage of the group III photoreceptor cells of the nonpigmented ocellus has not been analyzed yet.

In contrast to the ambiguity of the photoreceptor cell lineage, the embryonic origin and developmental mechanism of the pigment cell, another component of the pigmented ocellus, are well documented (Nishida and Satoh, 1989; Squarzoni et al., 2011; Haupaix et al., 2014; Racioppi et al., 2014). The pigment cells of the otolith, a gravity sense organ in the brain vesicle, and ocellus develop from the lateral edges of the a-lineage neural plate (a9.49 cells), and their specification is regulated by the FGF/MEK/ERK and Eph/ephrin signaling pathways (Squarzoni et al., 2011; Haupaix et al., 2014; Racioppi et al., 2014). Recent evidence suggests that these pigment cells are evolutionarily related to the cephalic neural crest of vertebrates (Abitua et al., 2012; Ivashkin and Adameyko, 2013). With this fascinating idea about these pigment cells, elucidation of photoreceptor cell lineage will shed new light on the developmental mechanisms and evolution of a sensory organ comprising distinct cell types.

In this study, we aimed to determine the cell lineage of photoreceptor cells in the *C. intestinalis* larva. In the past decade, technological innovations have enabled us to trace the developmental fates of particular cells in *Ciona* embryos. For example, blastomeres of interest can be labeled by a lipophilic fluorescent dye, such as DiI, and their descendants can be identified by double fluorescence staining with cell- or tissue-specific markers (Imai et al., 2004; Nishitsuji et al., 2012). The photoconvertible fluorescent protein Kaede (Ando et al., 2002) has been used to trace the developmental fates of *Ciona* cells (Horie et al., 2011; Abitua et al., 2012). In these experiments, a kaede transgene placed under the control of *cis*-regulatory regions of genes showing spatially restricted expression patterns was introduced into *Ciona* embryos by electroporation, and fluorescence emitted by Kaede was converted from green to red by irradiation with ultraviolet or violet light. Both DiI labeling and electroporation, however, have been conducted with *Ciona* embryos whose egg envelope (chorion) has been

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