



orthodenticle/otx ortholog expression in the anterior brain and eyes of *Sepia officinalis* (Mollusca, Cephalopoda)

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ABSTRACT

The origin of cerebral structures is a major issue in both developmental and evolutionary biology. Among Lophotrochozoans, cephalopods present both a derived nervous system and an original body plan, therefore they constitute a key model to study the evolution of nervous system and molecular processes that control the neural organization. We characterized a partial sequence of an ortholog of *otx2* in *Sepia officinalis* embryos, a gene specific to the anterior nervous system and eye development. By *in situ* hybridization, we assessed the expression pattern of *otx2* during *S. officinalis* organogenesis and we showed that *otx* is expressed (1) in the eyes, from early to late developmental stages as observed in other species (2) in the nervous system during late developmental stages. The *otx* ortholog does not appear to be required for the precocious emergence of the nervous ganglia in cephalopods and is later expressed only in the most anterior ganglia of the future brain. Finally, *otx* expression becomes restricted to localized part of the brain, where it could be involved in the functional specification of the central nervous system of *S. officinalis*. These results suggest a conserved involvement of *otx* in eye maturation and development of the anterior neural structures in *S. officinalis*.

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Most metazoan bilaterian groups present a central condensed nervous system. This kind of organization selected during evolution remains a major point in developmental studies, dealing with the origin of cerebral structures. The study of homeobox genes superfamily has considerably increased the understanding of the nervous system evolution since it has revealed that homologous molecular processes control similar steps of brain development in vertebrates and Ecdysozoa (Holland and Takahashi, 2005).

Among those genes, *otx2/otd* homologs encode transcription factors that play a key role in the brain and eye development. In vertebrates, where three *otx* paralogs are known, *otx2* is involved in the early anterior neural plate specification (Acampora and Simeone, 1999; Simeone, 1998), in the maintenance of the anterior neural pattern (Acampora et al., 2001; Simeone et al., 1993), in the anterior positioning of the fore- and midbrain, delimitating the midbrain–hindbrain boundary, and in the development and terminal differentiation of photoreceptors (Martinez-Morales et al., 2001; Plouhinec et al., 2005). Similarly, in Ecdysozoa, *orthodenticle*

(*otd*) plays a major role in patterning the rostral brain in *Drosophila* (Acampora et al., 2000; Cohen and Jürgens, 1990), and is also involved in the development and terminal differentiation of photoreceptors (Finkelstein et al., 1990; McDonald et al., 2010; Vandendries et al., 1996). In the nematode *Caenorhabditis elegans*, *otx/otd* paralogs are involved in the generation step of the various subcategories of sensory neurons (Satterlee et al., 2001) and in the implementation of the right/left normal asymmetry of the brain (Lanjuin et al., 2003; Nakano et al., 2010).

In Lophotrochozoa, *otx* homologs and their paralogs have been studied in annelids, platyhelminthes and in mollusks. In all these taxa, expression is observed in some anterior nervous structures and eyes. In annelid larva, *otd/otx* orthologs are expressed in the precursors of adult eyes and cerebral ganglia (*Hydroides elegans*, Arenas-Mena and Wong, 2007; *Platynereis dumerilii*, Steinmetz et al., 2011; *Helobdella triserialis*, Bruce and Shankland, 1998). In platyhelminthes (*Dugesia japonica*, Umeson et al., 1999), *otd/otx* orthologs are expressed in the cephalic part of the adult and in photosensitive cells, and in the head during the regeneration processes (*Dugesia tigrina*, Stornaiuolo et al., 1998). In mollusks, *otd/otx* orthologs have only been studied in the gastropod *Patella vulgata*, at the trochophore larvae stage. It is expressed in sensorial

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head parts: stomodaeum region, prototroche, and in some precursor neural cells (Nederbragt et al., 2002). Until now the expression of *otx* orthologs has been studied in Lophotrochozoa species with an indirect development, showing trochophore larvae with a simple and transient nervous system different than that of the adult one.

Cephalopods (Mollusca) belong to Lophotrochozoa but develop directly: the adult morphology and the adult nervous system are reached at hatching without any metamorphosis (Boletzsky et al., 2006), and no trochophore or veliger larval stage can be observed within the egg. As a consequence, the development of cephalopods provides intriguing issues regarding both its evolution and its mechanisms: the embryonic morphology and orientation are unique among mollusks and the complex brain they possess, even if analogous to that of vertebrates, shows very few bauplan similarities with that of vertebrates. The neural induction in cephalopods first gives rise to a set of distant ganglia, unlike in vertebrates in which the nervous system derives from a unique anlage (Yamamoto et al., 2003). The brain forms from the condensation and fusion of some of the typical mollusk ganglia (cerebroid, pedal and visceral ganglia, Budelmann, 1995), which later differentiate into the highly hierarchized lobes of the brain. The molecular mechanisms at the basis of this organization stay largely unknown and very few data about embryonic polarity are available. Therefore, as a “marker” of anteriority and as a key gene in metazoan brain formation, *otx2* homolog could turn out to be a key gene whose expression study can enlighten the understanding of cephalopod development and of cephalopod brain formation in particular. Here we report for the first time the expression pattern of an *otx2* ortholog in a cephalopod, *Sepia officinalis*, during organogenesis by whole mount *in situ* hybridization. Our results show that *so-otx* is specific to photosensitive structures and brain. *so-otx* is expressed in the retina during all organogeneses, suggesting that it could have conserved an ancestral function in the early setting up and maturation of cephalopod’s eyes. Its expression in the nervous system begins at late developmental stages and is restricted to some ganglia that later constitute the most anterior part of the adult brain. These results reveal that *so-otx* also constitutes a “marker” of anteriority in *S. officinalis* embryos.

1. Results

1.1. *S. officinalis* development

S. officinalis develops directly (i.e. without metamorphosis). The discoidal segmentation of the egg until stage 9 gives rise to a disk-shaped embryo at the animal pole of the egg, which lies on the yolk mass. The gastrulation stretches from stage 10 to 15 and the organogenesis proceeds until stage 30 for 1 month at 20 °C ending in the hatching of the juvenile (Boletzsky et al., 2006). From stage 16 to stage 30, three morphological phases can be described (Fig. 1). During the first period, from stage 15 to 20, the embryo has a disk shape with arms, mouth and eyes primordia located at the periphery, and mantle, gills and funnel primordially located in the center (Fig. 1A and B). At this phase, ganglia emerge in numerous distant regions of the embryo, probably stemming from neurogenic placodes, similar to what is described in the pygmy squid *Idiosepius paradoxus* (Yamamoto et al., 2003) (see colored area in Fig. 1A). In a subsequent phase, from stage 20 to 22, the embryo goes through drastic morphological changes and then acquires the adult orientation (straightening phase of the embryo, Fig. 1C and D). Some ganglia start to contact each other: the cerebroid ganglia develop toward the eyes and form a morphological unit with the future optic ganglia at stage 20, and the visceral ganglia and pedal ganglia get closer (see arrows Fig. 1C). In a third phase, the adult arrangement is reached at stage 22: eye, mouth and arms are located at the yolk side (cephalopodium), and the visceral mass and surrounding mantle (visceropalium) at the opposite side (Fig. 1E–J). This is the last phase of the final brain formation, where ganglia condense and differentiate into lobes. The cerebroid ganglia give rise to the supraesophageal mass (SPM) mostly involved in integrative function, and includes the vertical lobes, the frontal lobes and the basal lobes (Fig. 1G and I). A subesophageal mass (SBM), essentially composed of motor centers is made from two pedal ganglia and two visceral ganglia. The two pedal ganglia form the ASM (anterior subesophageal mass) and the MSM (median subesophageal mass). The two visceral ganglia form the PSM (posterior subesophageal mass) (Fig. 1E and G). The two optic lobes develop on both sides of the brain between the eyes (Fig. 1E and I).

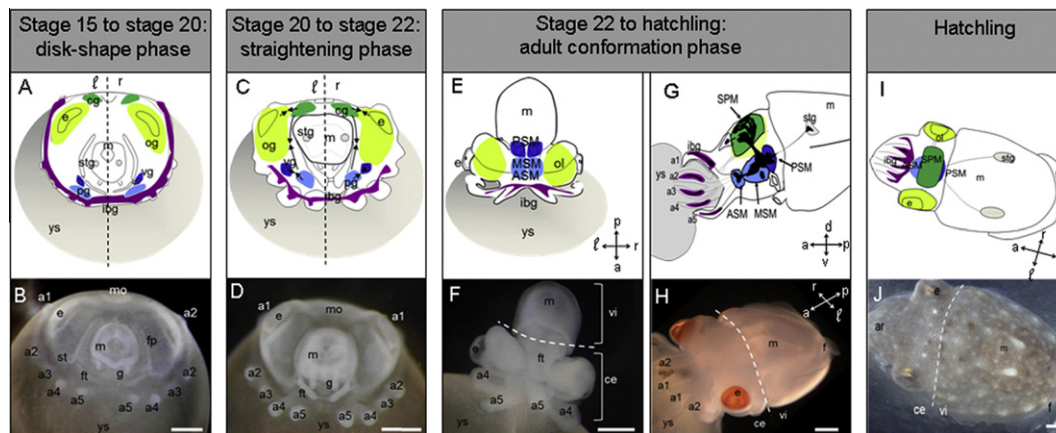


Fig. 1. Up: Embryonic neural territories during *S. officinalis* development, down: corresponding embryos' photographs. *S. officinalis* organogenesis is divided into three phases visually based on the embryo shape. (A and B) Stage 18 representing the disk-shaped phase, apical views. (C and D) Stage 21 representing the straightening phase, apical views. The black arrowheads illustrate the connections of ganglia between them. (E and F) Stage 24 corresponding to the adult conformation phase, ventral views. The cephalopodium and visceropalium are clearly distinguishable (see white dotted line). (G and H) Stage 26, adult conformation phase, lateral views. (I) Longitudinal section showing the nervous interactions between the nervous masses in the brain and with the periphery. (J and K) Embryo at hatching stage, dorsal views. a, anterior; a1–a5, arms; ar, arms; ASM, anterior subesophageal mass; bg, brachial ganglia; ce, cephalopodium; cg, cerebroid ganglia; d, dorsal; e, eye; fp, funnel pouch; ft, funnel tube; g, gill; ibg, interbrachial ganglia; l, left; m, mantle; mo, mouth; MSM, middle subesophageal mass; og, optic ganglia; ol, optic lobe; p, posterior; pg, pedal ganglia; PSM, posterior subesophageal mass; r, right; SPM, supraesophageal mass; st, statocyst; stg, stellate ganglia; v, ventral; vg, visceral ganglia; vi, visceropalium; y, yolk; ys, yolk sack. Scale bars correspond to 1 mm.

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