Student's Name:
Date:
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**Background**

Larval features such as the apical organ, apical ciliary tuft, and ciliated bands often complicate the evaluation of hypotheses regarding the origin of the adult bilaterian nervous system. Understanding how neurogenic domains form within the bilaterian head and larval apical organ requires expression data from animals that exhibit aspects of both centralized and diffuse nervous systems at different life history stages. Here, we describe the expression of eight neural-related genes during the larval development of the brachiopod, *Terebratalia transversa*.

**Results**

Radially symmetric gastrulae broadly express *Tt-Six3/6* and *Tt-hbn* in the animal cap ectoderm. *Tt-NK2.1* and *Tt- otp* are restricted to a central subset of these cells, and *Tt-fez* and *Tt-FoxQ2* expression domains are already asymmetric at this stage. As gastrulation proceeds, the spatial expression of these genes is split between two anterior ectodermal domains, a more dorsal region comprised of *Tt-Six3/6, Tt-fez, Tt-FoxQ2*, and *Tt-otp*expression domains, and an anterior ventral domain demarcated by *Tt-hbn* and *Tt-NK2.1* expression. More posteriorly, the latter domains are bordered by *Tt-FoxG* expression in the region of the transverse ciliated band. *Tt-synaptotagmin 1* is expressed throughout the anterior neural ectoderm. All genes are expressed late into larval development. The basiepithelial larval nervous system includes three neurogenic domains comprised of the more dorsal apical organ and a ventral cell cluster in the apical lobe as well as a mid-ventral band of neurons in the mantle lobe. *Tt-otp* is the only gene expressed in numerous flask-shaped cells of the apical organ and in a subset of neurons in the mantle lobe.

**Conclusions**

Our expression data for *Tt-Six3/6, Tt-FoxQ2*, and *Tt-otp* confirm some aspects of bilaterian-wide conservation of spatial partitioning within anterior neurogenic domains and also suggest a common origin for central *otp*-positive cell types within the larval apical organs of spiralians. However, the field of sensory neurons within the larval apical organ of *Terebratalia* is broader and composed of more cells relative to those of other spiralian larvae. These cellular differences are mirrored in the broader spatial and temporal expression patterns of *Tt-FoxQ2* and *Tt-otp*. Corresponding differences in the expression of *Tt-hbn, Tt-NK2.1*, and *Tt-FoxG* are also observed relative to their respective domains within the cerebral ganglia of spiralians. Based on these data we argue that the anterior region of the bilaterian stem species included *Six3/6, NK2.1, otp, hbn, fez*, and *FoxQ2*expression domains that were subsequently modified within larval and adult neural tissues of protostome and deuterostome animals.

**References**

(*The following two styles should be used for articles in a journal*)

Dunn CW, Hejnol A, Matus DQ, PANG K, Browne WE, Smith SA, Seaver E, Rouse GW, Obst M, Edgecombe GD, Sørensen MV, Haddock SHD, Schmidt-Rhaesa A, Okusu A, Kristensen RM, Wheeler WC, Martindale MQ, Giribet G. 2008. Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* 452: 4261-4270

Halanych KM, Bacheller JD, Aguinaldo AMA, Liva SM, Hillis DM, Lake JA. 1995. Evidence from 18S ribosomal DNA that the lophophorates are protostome animals. *Science* 267:1641-1643.

(*The following style should be used for chapters in a book or a thesis*)

Reed CG. 1987. Phylum Brachiopoda. In: Strathmann MF editor. Reproduction and development of the marine invertebrates of the northern Pacific coast Seattle and London: University of Washington Press. pp. 486-493.

**Reference Tips**

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