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Data Article

ATP4 and ciliation in the neuroectoderm and endoderm of Xenopus embryos and tadpoles

Peter Walentek [a,b,*], Cathrin Hagenlocher [a], Tina Beyer [a,1], Christina Müller [a], Kerstin Feistel [a], Axel Schweickert [a], Richard M. Harland [b], Martin Blum [a]

[a] Institute of Zoology, University of Hohenheim, Garbenstrasse 30, 70593 Stuttgart, Germany
[b] Department of Molecular and Cell Biology, Center for Integrative Genomics, University of California at Berkeley, Berkeley, California 94720, USA

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ABSTRACT

During gastrulation and neurulation, *foxj1* expression requires ATP4a-dependent Wnt/β-catenin signaling for ciliation of the gastrocoel roof plate (Walentek et al. *Cell Rep.* 1 (2012) 516–527.) and the mucociliary epidermis (Walentek et al. *Dev. Biol.* (2015)) of *Xenopus laevis* embryos. These data suggested that ATP4a and Wnt/β-catenin signaling regulate *foxj1* throughout *Xenopus* development. Here we analyzed whether *foxj1* expression was also ATP4a-dependent in other ciliated tissues of the developing *Xenopus* embryo and tadpole. We found that in the floor plate of the neural tube ATP4a-dependent canonical Wnt signaling was required for *foxj1* expression, downstream of or in parallel to Hedgehog signaling. In the developing tadpole brain, ATP4-function was a prerequisite for the establishment of cerebrospinal fluid flow. Furthermore, we describe *foxj1* expression and the presence of multiciliated cells in the developing tadpole gastrointestinal tract. Our work argues for a general requirement of ATP4-dependent Wnt/β-catenin signaling for *foxj1* expression and motile ciliogenesis throughout *Xenopus* development.

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* Corresponding author at: Department of Molecular and Cell Biology, Center for Integrative Genomics, University of California at Berkeley, Berkeley, California 94720, USA.
E-mail address: walentek@berkeley.edu (P. Walentek).
[1] Current address: Medical Proteome Center, Institute for Ophthalmic Research, University of Tübingen, Nägelestrasse 5, 72074 Tübingen, Germany.

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Specification Table

Subject area	Biology
More specific subject area	Cell and developmental biology
Type of data	Text file, figures, movies
How data was acquired	Microscopy (fluorescent, confocal, bright-field)
Data format	Analyzed and annotated figures and movies
Experimental factors	NA
Experimental features	Xenopus embryos were manipulated by morpholino oligonucleotide-mediated knockdown and application of pharmacological inhibitors. Gene expression, morphology and cilia function were analyzed by in situ hybridization, immunofluorescence, and quantification of extracellular fluid flow
Data source location	NA
Data accessibility	The data described here is presented in this article in form of figures and supplemental movies

Value of the data

- Our results indicate that the ATP4/Wnt/β-catenin module is required for neural *foxj1* expression downstream of, or in parallel to, Hedgehog signaling.
- ATP4 function is required for the generation of cerebrospinal fluid flow.
- *atp4a* and *foxj1* are co-expressed in the gastrointestinal tract.
- The tadpole stomach is lined by multiciliated cells, which generate an extracellular fluid flow.

1. Data, experimental design and methods

1.1. Analysis of ATP4a/Wnt-dependent foxj1 expression in floor plate of the neural tube

The floor plate and the brain represent additional sites of vertebrate *foxj1* expression [1,5,6,13]. We tested whether floor plate expression of *foxj1* required ATP4 and Wnt/β-catenin signaling in *Xenopus* by injection of 1 pmol/injection of *atp4a* morpholino oligonucleotide (*atp4a*MO) targeted to dorso-medial regions of developing embryos. Embryos were injected at the two- to four-cell stage using a Harvard Apparatus or Picospritzer setup in 1 × modified Barth's solution (MBSH) with 4% Ficoll (BioChemica) and transferred to 0.1 × MBSH 15 min after injection. Gene expression was analyzed by whole mount in situ hybridization (WMISH). *atp4a* morphants showed a reduction of *foxj1* expression in the floor plate ($p < 0.001$; Fig. 1A,C and G), which was rescued by co-injection of 1 ng/μl *β-catenin* DNA ($p < 0.01$; Fig. 1E and G).

1.2. Monitoring floor plate formation in atp4a morphants

Formation of the floor plate in *atp4a* morphants was analyzed histologically and by analysis of gene expression. Embryos were embedded in gelatin–albumin and sectioned on a vibratome (30 μm). The floor plate was present, as judged by concentration of pigment due to apical constriction of medial neural plate cells, both in *atp4a* morphants and in specimens co-injected with *β-catenin* DNA (Fig. 2A–C, A`–C`). Floor plate-specific *sonic hedgehog* expression (*shh*; [12]) was also present in *atp4a* morphants (Fig. 2D and E).

1.3. Analysis of Hedgehog-dependent foxj1 expression in the floor plate of the neural tube

To analyze if *Xenopus foxj1* expression depended on Hedgehog (HH) signaling, as reported for zebrafish *foxj1* [3,20], embryos were incubated with the HH signaling inhibitor cyclopamine