ScienceDirect

Developmental Biology
Volume 514, October 2024, Pages 66-77

Tadpoles rely on mechanosensory stimuli for communication when visual capabilities are poor

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https://doi.org/10.1016/j.ydbio.2024.05.006

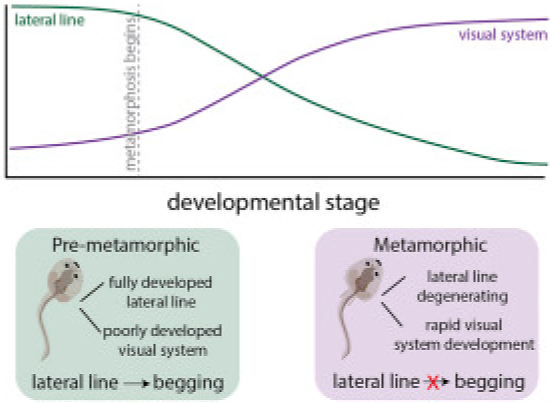
Highlights

- *Ranitomeya imitator* tadpoles hatch with fully developed lateral line systems.
- Use of mechanosensory stimuli for begging is dependent on developmental stage.
- The visual system of *R. imitator* tadpoles continues to develop through metamorphosis.
- When visual capabilities are poor, tadpoles rely more on mechanosensory inputs.

Abstract

The ways in which animals sense the world changes throughout development. For example, young of many species have limited visual capabilities, but still make social decisions, likely based on information gathered through other sensory modalities. Poison frog tadpoles display complex social behaviors that have been suggested to rely on vision despite a century of research indicating tadpoles have poorly-developed visual systems relative to adults. Alternatively, other sensory modalities, such as the lateral line system, are functional at hatching in frogs and may guide social decisions while other sensory systems mature. Here, we examined development of the mechanosensory lateral line and visual systems in tadpoles of the mimic poison frog (Ranitomeya *imitator*) that use vibrational begging displays to stimulate egg feeding from their mothers. We found that tadpoles hatch with a fully developed lateral line system. While begging behavior increases with development, ablating the lateral line system inhibited begging in pre-metamorphic tadpoles, but not in metamorphic tadpoles. We also found that the increase in begging and decrease in reliance on the lateral line co-occurs with increased retinal neural activity and gene expression associated with eye development. Using the neural tracer neurobiotin, we found that axonal innervations from the eye to the brain proliferate during metamorphosis, with few retinotectal connections in recently-hatched tadpoles. We then tested visual function in a phototaxis assay and found tadpoles prefer darker environments. The strength of this preference increased with developmental stage, but eyes were not required for this behavior, possibly indicating a role for the pineal gland. Together, these data suggest that tadpoles rely on different sensory modalities for social interactions across development and that the development of sensory systems in socially complex poison frog tadpoles is similar to that of other frog species.

Graphical abstract



Introduction

Animals use a variety of sensory modalities to detect the environment around them. For species with parental care, the ability to detect and respond to a potential caregiver can be a matter of life-and-death. Caregiver recognition can be complicated by the fact that some sensory modalities continue to change throughout development, where young animals may need to make complex social decisions with limited or varying sensory capabilities. Investigating how animals recognize potential caregivers at an early developmental age and how this might change throughout development is critical for our broader understanding of how sensory systems develop and evolve for communication.

Many aquatic animals possess a mechanosensory lateral line system that allows them to detect near-by water movements (Dykgraaf, 1933). The lateral line system is composed of neuromasts, or bundles of hair cells, similar to those in the mammalian inner ear. Nearby water movements create a shear force on the hair cells that opens mechanically gated ion channels, permitting the detection of hydrodynamic stimuli. In fishes, the lateral line system is important for rheotaxis (Montgomery et al., 1997), schooling (Partridge and Pitcher, 1980), prey detection (Schwalbe et al., 2012), predator avoidance (Stewart et al., 2014; Canfield and Rose, 1996), and social communication (Butler and Maruska, 2016). While less is known about the role of the lateral line in tadpoles, it has been implicated in responding to water currents (Brown and Simmons, 2016; Simmons et al., 2004) and predator avoidance (Jung et al., 2020). In many species of frogs, the lateral line system is nearly or fully developed at hatching (Lannoo, 1987; Zelena, 1964; Saccomanno et al., 2021; Jung et al., 2020; Roberts et al., 2009) but degrades during metamorphosis (Wright, 1951; Zelena, 1964; Brown and Simmons, 2016). As such, mechanosensation via the lateral line system is a potential communication channel during early-life stages that could play a role in detecting and recognizing social stimuli.

Although the adults of many species use vision for detecting social stimuli, the young of many species have limited or absent visual capabilities. For example, cats and dogs are born with their eyes closed and are functionally blind, whereas mouse pups do not open their eyes until they are 11–12 days old (UCSF Lab Animal Resource Center). Although open or shut eyes are often used as a proxy for whether mammalian neonates can see or not, this assumption is less clear in young animals of other taxa, whose eyes remain visible throughout development. Since as early as the mid 1800s, frogs and toads have been fundamental in visual neuroscience research (for review, see Donner and Yovanovich, 2020), as adults have a fully developed and complex retina similar to other vertebrates. Tadpoles of some species, however, hatch with externally visible, partially developed eyes, but their visual capabilities are not well-developed (Hoff et al., 1999). Grant et al. (1980) divided early development of the tadpole retina into four stages, with visual function being present at the end of the first stage shortly after hatching, but noted that a mature retina was not present until there is significant hindlimb development. In addition, retinal projections to brain regions important for visual processing, such as the optic tectum, are still forming throughout metamorphosis (Fujisawa, 1987). Despite poor or absent vision, these young animals likely make complex social decisions by relying on information from other sensory modalities. However, it is unclear how retinal development coincides with the development of other sensory modalities and the complex visual behaviors observed in tadpole behavioral ecology.

Poison frogs (Family Dendrobatidae) are an emblematic amphibian taxa known for their bright coloration, which advertises their chemical defenses to predators. These taxa display a wide range of parental care strategies, notably tadpole transport and egg provisioning (Summers and Earn, 1999; Summers and Tumulty, 2014; Weygoldt, 2009). Tadpoles of these species also show an impressive diversity of complex behaviors, such as aggression and begging for egg meals from their parents by vigorously vibrating their bodies. Recently, it was hypothesized that poison frog tadpoles are dependent on visual cues for many of these social behaviors (Stynoski and Noble, 2012; Fouilloux et al., 2022; Fouilloux et al., 2023). Indeed, research in the Strawberry poison frog (*Oophaga pumilio*), suggests that tadpoles use visual cues to recognize parents apart from heterospecifics (Stynoski and Noble, 2012; Fouilloux et al., 2022) and sexually imprint on the color morph of their caregiver (Yang et al., 2019). In dendrobatid frogs with extended parental care, parents dive into the small aquatic nursery during visits, which could generate water movements that stimulate the tadpole lateral line. Their movements on nearby fronds above the nursery might also create vibrations that are transmitted to the water and detectable by the lateral line. Despite the growing utility of poison frogs as a model system for neuroethology research, sensory system development in poison frog tadpoles has not been well studied.

Here we examined the development of the lateral line and visual systems in tadpoles of the mimic poison frog (*Ranitomeya imitator*). In this species, fathers transport hatched tadpoles to individual pools in bromeliad leaves. Every few days, the parents will visit the tadpole, and the tadpole will beg for food by rapidly vibrating its body (Yoshioka et al., 2016). Tadpoles must also attempt to avoid predation from spiders and other tadpoles, as sympatric *Ranitomeya variabilis* tadpoles cannibalize *R. imitator* tadpoles (Brown et al., 2008). In *Oophaga pumilio* tadpoles, predation accounts for as much as 67% of tadpole mortality, emphasizing the importance of detecting and avoiding potential predators (Maple, 2002). As such, *R. imitator* tadpoles may make complex decisions about the identity of pool visitors. Here, using anatomical, experimental, and transcriptomic approaches, we tested two hypotheses: (1) that tadpoles, independent of developmental stage, use mechanosensory stimuli detected via the lateral line system for decisions about begging, and (2) that vision facilitates begging behavior, but that young tadpoles have overall poor visual capabilities. Answers to these questions will help clarify the mechanisms by which *R. imitator* tadpoles process the diverse sensory inputs they receive during development and therefore better inform our understanding of behavioral mechanisms in tropical tadpoles.

Section snippets

Experimental animals

All *Ranitomeya imitator* tadpoles were captive bred in our poison frog colony from adult breeding pairs using standard animal procedures in our laboratory. Briefly, reproductive male and female *R. imitator* were housed in a glass terrarium (12×12×18 inch) containing several water pools, greenery, and a moss-substrate floor. Water pools were checked regularly for deposited tadpoles. Transported tadpoles were housed individually in circular containers (5cm diameter) in a large aquarium…

Older tadpoles are more likely to beg

To lay a foundation for understanding the sensory contributions to begging behavior, we conducted begging behavior assays with randomly selected tadpoles and reproductive females. We initially classified tadpoles as begging or non-begging independent of stage. In general, ~70% of tadpoles begged during behavior trials (Fig. 1A), with an average begging duration of 85.652s (Fig. 1B). However, when we accounted for tadpole stage, there was uneven distribution of stage within each group (Fig. 1…

Discussion

Animals rely on sensory information to carry out vital life processes, even at a young age. Visual capabilities are well documented to vary throughout life, where the young of several taxa have absent or reduced vision. However, even young animals have to make complex decisions about their environment and may rely on other sensory modalities that are more developed. Here, we examined development of the lateral line and visual systems in *Ranitomeya imitator*, a species of dendrobatid poison frog…

Conclusions

We show that poison frog tadpole sensory systems change throughout development, with a decreasing reliance on mechanosensory stimuli during social interactions coinciding with an increase in visual capabilities. Full visual capabilities likely do not emerge until metamorphosis, as suggested by the presence of development genes in phosphoTRAP data, changes in retina morphology, and retinotectal connections. Despite an underdeveloped visual system, even young tadpoles display begging behaviors…

Funding

This work was supported by a Bauer Fellowship from Harvard University to LAO, the Rita Allen Foundation to LAO, the National Institutes of Health (DP2HD102042) to LAO, a National Science Foundation Postdoctoral Research Fellowship in Biology (NSF-2109376) to JMB, and a L'Oreal For Women in Science Postdoctoral Fellowship to JMB. SCL and JM were supported by a Stanford University Biology Summer Undergraduate Research Program Fellowship and by a Stanford University Major Grant. MM was supported…

Data statement

PhosphoTRAP sequence data has been uploaded to NCBI (Accession PRJNA1124168). Results from the phosphoTRAP analysis, the *R. imitator* tadpole transcriptome, R analysis code, and an example behavior video are available on Dryad (https://doi.org/10.5061/dryad.h9w0vt4s2 ↗). The western blot, tadpole ethogram, and tadpole staging guide has been uploaded as supplemental information. The phototaxis assay protocol is available on protocols.io at dx.doi.org/10.17504/protocols.io.x54v9p294g3e/v1.…

CRediT authorship contribution statement

Julie M. Butler: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jordan E. McKinney:** Writing – review & editing, Methodology, Investigation, Data curation. **Sarah C. Ludington:** Writing – review & editing, Methodology, Investigation, Data curation. **Moremi Mabogunje:** Investigation, Data curation. **Penelope Baker:** Writing – review & editing, Methodology,…

Acknowledgements

We thank members of the O'Connell and Edwards labs, especially Madison Lacey, David Ramirez, Mesi Fisher, and Billie Goolsby, for their assistance with animal care and discussions about this research. We thank the Harvard University FAS Bauer Core for facilitating the transcriptomic work. We also thank Dr. Eva Fischer for discussions about analyzing phosphoTRAP data.…

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