



Sensory basis for detection of benthic prey in two Lake Malawi cichlids



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ABSTRACT

The adaptive radiations of African cichlids resulted in a diversity of feeding morphologies and strategies, but the role of sensory biology in prey detection and feeding ecology remains largely unexplored. Two endemic Lake Malawi cichlid genera, *Tramitichromis* and *Aulonocara*, feed on benthic invertebrates, but differ in lateral line morphology (narrow and widened lateral line canals, respectively) and foraging strategy. The hypothesis that they use their lateral line systems differently was tested by looking at the relative contribution of the lateral line system and vision in prey detection by *Tramitichromis* sp. and comparing results to those from a complementary study using *Aulonocara stuartgranti* (Schwalbe et al., 2012). First, behavioral trials were used to assess the ability of *Tramitichromis* sp. to detect live (mobile) and dead (immobile) benthic prey under light and dark conditions. Second, trials were run before, immediately after, and several weeks after chemical ablation of the lateral line system to determine its role in feeding behavior. Results show that *Tramitichromis* sp. is a visual predator that neither locates prey in the dark nor depends on lateral line input for prey detection and is thus distinct from *A. stuartgranti*, which uses its lateral line or a combination of vision and lateral line to detect prey depending on light condition. Investigating how functionally distinctive differences in sensory morphology are correlated with feeding behavior in the laboratory and determining the role of sensory systems in feeding ecology will provide insights into how sensory capabilities may contribute to trophic niche segregation.

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1. Introduction

The mechanosensory lateral line system of fishes plays critical roles in prey detection, predator avoidance, communication, rheotaxis, and navigation around obstacles (reviewed in Webb et al., 2008; Bleckmann and Zelick, 2009). The system demonstrates a considerable degree of morphological variation among bony fishes (Webb, 1989b), but understanding the relationship between structure and function in the lateral line system and lateral line-mediated behavior continues to be a particularly challenging task because of the multiple levels at which both structure and function may vary.

The physiological response of the lateral line system (and ultimately the fish's behavior) depends on the properties of the different morphological components that define the system. Variation in the morphology of the neuromasts (hair cell morphology, density, and orientation; neuromast shape; shape and length of the cupula into which the apical ciliary bundles of the hair cells are embedded; and patterns of neuromast innervation and cen-

tral projections), in the morphology of the lateral line canals in which canal neuromasts are found (canal diameter, pore size, presence of canal constrictions), and in the hydrodynamic context (biotic, abiotic, and self-generated flows) in which the system functions may all contribute to physiological, and thus behavioral, responses (reviewed in Webb, 2014). Ecological correlates of lateral line morphology have been proposed (Dijkgraaf, 1963; reviewed by Webb, 1989b), but there are notable exceptions. For instance, fishes in hydrodynamically active environments tend to have narrow canals and fewer superficial neuromasts, but this relationship does not always hold in light of different sets of selection pressures (Carton and Montgomery, 2004). In addition, some types of morphological variation (differences in canal diameter in the vicinity of canal neuromasts) do not result in differences in physiological responses by neuromasts (e.g., Antarctic notothenioids: Coombs and Montgomery, 1992; Montgomery et al., 1994).

Testing hypotheses concerning the functional evolution of the lateral line system requires that experiments be carried out in a well-defined comparative context using closely related species pairs with divergent morphology and the presentation of ecologically relevant stimuli. Narrow and widened cranial lateral line canals, two of the four types of lateral line canals defined among teleosts (Webb, 1989a), are of particular interest because of their distinctive morphologies and contrasting functional properties (theoretical and experimental work of Denton and Gray, 1988,

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1989). Narrow canals are well ossified with small canal pores and widened canals are typically weakly ossified with partial ossification of the canal roof over the canal neuromasts leaving large canal pores between neuromast positions that are covered by a tympanum-like epithelium typically pierced by very small pores. Narrow canals are widespread among teleosts, while widened canals have evolved convergently in just a dozen or so teleost families suggesting that the evolution of widened canals is adaptive, and further, that it represents an adaptation for prey detection.

The ability to determine the functional distinctions between narrow and widened canals has been hampered by the inability to identify appropriate species pairs that are accessible for experimental study. The percid fishes are a useful model system for illustrating the relationship between the functional morphology of the lateral line system and feeding ecology of fishes. European perch (*Perca fluviatilis*) and yellow perch (*Perca flavescens*) have narrow canals and Eurasian ruffe (*Gymnocephalus cernuus*) has widened canals. The sensitivity of the large neuromasts in the widened canals of ruffe (van Netten, 2006) generally supports behavioral and ecological findings. European perch and ruffe have some seasonal and life stage-dependent diet overlap in their native habitat where they co-occur (Rezsu and Specziar, 2006; Schleuter and Eckmann, 2008), but ruffe occupy a greater depth range than perch and spend more time close to the substrate (Bergman, 1987, 1991). In addition, ruffe are able to feed more successfully in visually compromised habitats when compared to *Perca* spp. (Disler and Smirnov, 1977; Bergman, 1988; Janssen, 1997; Schleuter and Eckmann, 2006) and increase in abundance and replace perch in turbid water and/or low light conditions (Bergman, 1991). Interestingly, the accidental introduction of ruffe in the North American Great Lakes has generated concern over potential for competition with native yellow perch (*P. flavescens*, Ogle et al., 1995).

The speciose cichlids of the African Rift Lakes provide new opportunities for comparative studies of sensory biology, feeding behavior, and ecology. There has been intense study of the functional morphology of the cichlid feeding apparatus and the diverse trophic niches that they occupy (Fryer and Iles, 1972; Liem, 1973, 1980; Albertson et al., 2005; Hulsey et al., 2010), but only a few studies have addressed the sensory basis for prey detection (Hofmann et al., 2009; O'Quin et al., 2010; Mogdans and Nauroth, 2011; Schwalbe et al., 2012). The vast majority of cichlid species have narrow cranial lateral line canals (e.g., Branson, 1961; Peters, 1973; Webb, 1989b). However, a few genera in Lake Tanganyika (*Aulonocranus* and *Trematocara*) and in Lake Malawi (*Aulonocara*, *Alticorpus*, and *Trematocranus*) have widened canals (Konings, 2007).

One of these genera, *Aulonocara* (16–20 spp.), and a genus with narrow canals, *Tramitichromis* (~6 spp.), are found at either the rock–sand interface or over sand, and feed on invertebrates buried in the sand (Fryer and Iles, 1972; Konings, 2007), but use different prey search strategies. *Tramitichromis* plunge into the substrate filling their mouths with sand, and sift out invertebrate prey using their gill rakers (“sand sifting”; Fryer, 1959). How they choose to direct their plunges, and thus the sensory basis for the detection of their benthic prey, is still unknown. In contrast, *Aulonocara stuartgranti* swims just above the substrate, detect water flows generated by prey with their lateral line system (as confirmed with cobalt chloride ablations), and strike at individual prey in the sand (Konings, 2007; Schwalbe et al., 2012). With respect to lateral line morphology, the narrow canals of *Tramitichromis* spp. are well ossified with small pores while the widened canals of *Aulonocara* spp. have large canal pores covered by an epithelium pierced by small perforations. A recent analysis of neuromast morphology in juvenile *Tramitichromis* sp. and *A. stuartgranti* (Becker, 2013) has shown that these fishes have the same number of canal neuromasts and canal pores, despite distinct differences in canal and pore

morphology (Fig. 1). They also have the same number of linear series or clusters of very small superficial neuromasts on the head, but late-stage juvenile (and presumably adult) *A. stuartgranti* tend to have more superficial neuromasts within some of these series. The canal neuromasts are diamond-shaped in both species, but those in *A. stuartgranti* are a bit larger (Fig. 1B) and tend to sit in slight constrictions in the canal, which is a characteristic of many species with widened canals.

Thus, *Tramitichromis* sp. and *A. stuartgranti* present an excellent model system in which to ask questions about the relationship of lateral line morphology to its role in prey detection. These fish differ with respect to only some aspects of the morphology of the lateral line system (narrow vs. widened canals, minor differences in canal neuromast size, and the number of superficial neuromasts). Experimental work has already determined that the lateral line system is critical for prey detection in *A. stuartgranti* (Schwalbe et al., 2012) and it is hypothesized that the role of the lateral line system in prey detection in *Tramitichromis* sp. would be different from that in *A. stuartgranti*. In order to test this, behavioral trials (as described in Schwalbe et al., 2012) were conducted in which *Tramitichromis* sp. was presented with live (mobile) and dead (immobile) tethered adult brine shrimp under light and dark conditions (Experiment I). Then, the role of the lateral line system in prey detection was directly addressed by temporarily inactivating the lateral line system with cobalt chloride (Experiment II). Data on number of prey strikes, prey detection distance and angle and preference for live or dead prey were then compared with that for *A. stuartgranti* (data from Schwalbe et al., 2012) to contrast the roles of the lateral line system and vision in prey detection behavior in these two species.

2. Materials and methods

2.1. Study species

Adult *Tramitichromis* sp. (= *Tramitichromis* hereafter, unless otherwise noted) were acquired from a commercial supplier (Old World Exotic Fish, Inc., Homestead, FL, USA) and housed in small groups in 190 l aquaria with mechanical and biological filtration. For housing and experimental procedures, fish were maintained at 1 ppt salt (Cichlid Lake Salt; Seachem Laboratories, Inc., Madison, GA, USA) at 26 ± 1 °C with a 12:12 h light:dark cycle. Fish were fed daily with cichlid pellets (New Life Spectrum Cichlid Formula; New Life International, Inc., Homestead, FL, USA) and supplemented with live adult brine shrimp. Animal care and all experimental procedures followed an approved University of Rhode Island IACUC protocol.

2.2. Behavioral trials

Two experiments were conducted to determine the ability of *Tramitichromis* to detect live and dead prey in light and dark trials (Experiment I) and to determine the contribution of the lateral line system to prey detection in light trials (Experiment II).

2.2.1. Experiment I – light and dark trials

Light and dark trials were conducted using *Tramitichromis* following Schwalbe et al. (2012). Briefly, trials were performed in a large experimental tank (375 l) lined with sand. Adult brine shrimp (*Artemia* sp.) were tethered with elastic thread in pairs (1 live; 1 dead, freshly frozen) onto each one of six mesh platforms (a total of 6 live prey + 6 dead prey = 12 total prey) to serve as a proxy for naturally occurring benthic prey. Platforms were placed on the bottom of the tank in a 2 × 3 grid so that their top surfaces were flush with that of the sand. All filters in the experimental tank were turned off to eliminate hydrodynamic noise during all behavioral trials.

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