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Chemosensory Mediation of Food Searching in the Buenos Aires Tetra *Hyphessobrycon anisitsi* (Characidae)

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Abstract—Food searching behavior of the Buenos Aires tetra *Hyphessobrycon anisitsi* has been investigated before and after experimentally induced anosmia combined with visual deprivation. The threshold concentration of a water extract of familiar food (chironomid larvae) for fish with intact olfaction was 10^{-6} g/L. Induced anosmia led to complete loss of the search reaction to food odor. The chemosensory behavioral response to the water extract of food used at high concentrations (10^{-1}–10^{-2} g/L) was not restored in fish after 1.5, 5, or 13.5 months of anosmia. The obtained results show that the external sense of taste is absent or extremely poorly developed in the Buenos Aires tetra.

Keywords: Buenos Aires tetra *Hyphessobrycon anisitsi*, feeding behavior, chemoreception, olfaction, anosmia
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INTRODUCTION

Characiformes are among the most numerous orders of modern fishes. However, the behavior of these fish, including the feeding behavior, remains extremely poorly investigated, in contrast to that of the closely related Cypriniformes and Siluriformes. Mexican cave fish *Astyanax fasciatus* (= *A. mexicanus*) is the only exception, since the blind (cave) form of this fish is often used as a convenient model object for research on various compensatory transformations affecting the behavior and sensory systems of animals (Wilkens, 1988; Romero and Green, 2005; Kasumyan and Marusov, 2015).

Olfaction plays an important role in the food searching behavior of most fish (Malyukina et al., 1974, 1980). Olfaction disorders caused by injuries, infections, parasite invasions, and other deleterious factors, as well as experimentally induced acute anosmia, lead to a complete loss of the searching response to food odors in fish. This ability can be partially restored in fish that have external taste buds (Cyprinidae and Acipenseridae), although the development of the compensatory processes is slow, taking up to several months. Chronic visual deprivation (enucleation) does not induce compensatory processes, in contrast to anosmia, and has no effect on the development of these processes when combined with anosmia (Kasumyan and Marusov, 2007). The blind form of *A. fasciatus* is the only representative of Characidae in which the effects of sensory deprivation were thoroughly studied. These fish lost vision completely during phylogeny, but they have a more advanced morphology of the external gustatory system and lateral line providing for successful survival in complete darkness and with limited food resources available (Wilkens, 1988; Franz-Odendaal and Hall, 2006; Varatharasan et al., 2009; Bibliowicz et al., 2013). However, the recovery of chemoorientation towards food stimuli in blind cave fish subjected to chronic anosmia is incomplete (Kasumyan and Marusov, 2015), this being indicative of the scarcity of external taste buds in these fish. The existence of differences between the organization of the central interactions of sensory systems in Characidae and other fish studied previously (cyprinids and acipenserids) (Devitsina and Marusov, 2007) cannot be ruled out either.

The aims of the present work were to characterize sensitivity to the natural food odor and to test for the presence of a compensatory response to chronic olfactory deprivation in Buenos Aires tetra *Hyphessobrycon anisitsi* (=*Hemigrammus caudovittatus*), a characid fish used in experimental research on the behavior and sensory systems of fish (Glaser, 1968; Campos, 1969; Mikheev and Pakul'skaya, 1988; Mikheev et al., 1992).

MATERIALS AND METHODS

The experiments involved 12 sexually mature aquarium-reared Buenos Aires tetra individuals (full length 50–61 mm, weight 3.0–4.1 g) purchased from the Akva Logo company. Anosmia was induced by cauterization of the olfactory organ, and vision was destroyed by cauterization of the cornea, lens, and vitreous body. All surgery was performed under cold-induced anesthesia. The fish were divided into two groups of six individuals. Anosmia was induced 2.5 months after vision loss in the first group of fish and 1.5 months before vision loss in the second group of fish. No deaths were observed among the operated fish.

The experiment was performed on fish maintained in individual tanks (30.5 × 20.5 × 14.5 cm, water level 12 cm) with a slow water flow; the chemical stimuli were administered at a single site, and water circulated in a closed system including a charcoal and gravel biofilter. The water purified by the biofilter was fed into each aquarium through a silicone tube (internal diameter 4 mm) with the tube outlet directed downwards and located at the height of 5 cm from the bottom in the front part of the aquarium. The water flowed along the longer axis of the aquarium and was directed into the biofilter again by an airlift. The time of complete water exchange was approximately 1.5 h. The bottom in the aquaria was bare. The fish were acclimated to the experimental conditions for at least 2–3 weeks.

The stimulus solutions and pure water (sampled at the outlet of the biofilter) were injected at a rate of 0.025 L/min for 3 min into the total constant water flow entering the tank from the biofilter; this flow was maintained at 0.075 L/min before and during the experiment. Pure water (control) was presented to each fish at the beginning of the experiment, and a water extract of larvae (Chironomidae) at concentrations ranging from 10^{-1} to 10^{-7} g/L was injected after 7–10 min. The number of such series during one day did not exceed two, and the interval between them was at least 3 h. The stimulus solutions were used within 3 h after preparation. Aquarium water was partly replaced by fresh water after the experiments. Water temperature was maintained at 24°C by electric heaters. The fish were fed with live chironomid larvae once a day until satiation, with the feeding performed after the end of the experiments on the days of experiments.

The reaction of the fish was evaluated qualitatively (according to changes of behavior) and quantitatively (according to the total time of searching for food, that is, exploratory swimming in a tilted position, touching the aquarium bottom with the head, and test biting) in the 1/3 part of the aquarium bottom surface adjacent to the outlet of the tube used to injection the stimulus solutions or fresh water. Reaction time was recorded using a JS-6618 handheld stop-watch (JUNSO) during the entire period of solution administration (3 min). The total number of the experiments performed was 516. Wilcoxon's matched pairs test (T) was used for statistical processing of the data.

RESULTS

Intact tetras form a dynamic shoal moving over all the volume of the aquarium with a preference to the distant part. The food administrated near the front wall of the aquarium is grasped in a quick visually controlled movement as the food is sinking, and then the fish return to the distant part of the aquarium before a new grasping movement. The fish are reluctant to collect the sunken food from the aquarium bottom and usually start doing this after several minutes waiting.

The fish recovered well after anosmia, with complete normalization of behavior taking not more than 2 weeks at most (and usually even less). The recovery period was longer in blinded fish with intact olfaction. These fish were swimming slowly near the bottom or in the water column during the first days after the surgery; difficulties in orientation during feeding and swimming subsided over time. The fish started swimming routinely over the entire aquarium, usually along the lower part of the walls and sometimes performing searching movements with the body tilted at approximately 45° and the lower jaw and the gular surface sliding along the bottom. The fish swimming in this position performed infrequent bites on the bottom or debris particles. If a fish was at a distance of 3–5 cm from the live chironomid larvae added to the aquarium during feeding, it started swimming more quickly, descended to the bottom and slid along it in small circles or eight-shaped trajectories, making sharp turns. The search area was gradually narrowed. The food was grasped after an occasional touch by the lips only, while the food touching by other parts of the head, trunk, or fins did not evoke a grasping response. Successful grasping of the food enhanced the activity of searching in the area, with the body of the fish sometimes assuming a nearly vertical position.

The background behavior of fish that lost the sense of smell 2.5 months after losing vision was restored after two weeks at most, becoming similar to the respective behavior of blinded fish. However, living chironomid larvae added to the aquarium during feeding neither attracted the fish nor caused active searching for food; the latter behavior was only stimulated if the fish accidentally touched the food by the lips during the sporadic short searching swim bursts in a tilted position. The fish that touched the food with the lips grasped it immediately and started searching for food actively at the site. The search area was expanded gradually if other larvae were not found. A similar food capture behavior was observed in a group of double-operated fish in which olfaction was destroyed 1.5 months before the destruction of vision.

Water extracts of chironomid larvae caused a distinct food-searching behavior in fish with an intact olfactory system and no vision (blinded 2 months before the experiment). The fish that swam over the entire aquarium prior to the injection of the stimulus solution lingered in the zone of olfactory stimulus injection to the aquarium, started swimming at a much higher speed, and moved in zigzag-shaped or circular patterns with a small turning radius. Fish were tilted forward at angles ranging from 45° to 90°, so that the lips and lower jaw touched the bottom, and frequent spontaneous seizing movements of the mouth were observed. The response of the fish to the chironomids extract injected at high concentrations (10^{-3}–10^{-4} g/L) was evoked immediately after the entry of the fish to the zone of diffusion of the stimulus solution. The reaction was pronounced and prolonged; it was manifested as multiple repeated entries to the zone of odor distribution. Intensity of the reaction and duration of the food-searching behavior decreased as the concentration of the solution decreased. Solutions with concentrations of 10^{-3}–10^{-6} g/L (table) caused a significant ($p < 0.001$) increase of the duration of the reaction period of the fish relatively to the duration observed under control conditions (pure water).

Induced anosmia completely abolished the ability of tetra to react to chironomid extract, so that the stimulus solutions did not evoke a response in fish tested 1.5, 5.0, and 13.5 months after olfaction loss (that is, 4.0, 3.5, and 12.0 months after vision loss) even when high concentrations (10^{-1}–10^{-2} g/L) were used. The fish involved in the experiment retained the background food searching behavior completely: searching for food was spontaneous and of short duration, and the total duration of searching for food during the experiment did not show a significant differences from the value for pure water in most cases (table).

DISCUSSION

The experiments performed revealed high olfactory sensitivity of Buenos Aires tetra to food odor. The threshold concentration of the water extract of chironomid larvae (familiar food of the experimental fish) was 10^{-6} g/L. This is an order of magnitude lower than the threshold concentration of food extract in the blind form of *A. fasciatus* and the benthivorous carp *Cyprinus carpio*, and several orders of magnitude lower than in many other cyprinid, salmonid, balitorid, and acipenserid fish (Kasumyan et al., 2010; Kasumyan and Marusov, 2015).

High olfactory sensitivity of the tetra to food odor may be related to the specific habitat features of these fish. Tetras mostly inhabit small freshwater water bodies with rich vegetation in the monsoon zone of South America (Cordiviola de Yuan and Pignalberi de Hassan, 1985). The water level is rather low during the dry period, whereas the onset of the rainy season is followed by a significant rise of the water level and a considerable increase in water turbidity imposing severe restrictions on the use of visual system for orientation and food search by the fish. High olfactory sensitivity may facilitate the search for prey considerably under the conditions described above, similarly to the situation observed in the case of nocturnal or bottom-dwelling fish (Wunder, 1927; Teichmann, 1959; Pavlov, 1962; Kasumyan et al., 2010).

Interestingly, olfactory sensitivity to food odor in Buenos Aires tetra is higher than in the cave form of blind cave fish . This may be indicative of the absence of a marked enhancement of olfactory reception upon the loss of vision in blind cave fish that inhabit underground waters (Kasumyan and Marusov, 2015) in contrast to compensatory changes in the gustatory system and the lateral line (Wilkens, 1988; Franz-Odendaal and Hall, 2006; Varatharasan et al., 2009).

The food odor presented to vision-deprived tetras elicits a food searching behavior typical for fish devoid of vision. Such behavioral patterns as swimming in circles and S-shapes with the head tilted, sliding the head along the bottom in the odor distribution zone, frequent test bites, and an almost vertical position at the moments of maximal food-related arousal, are characteristic of both blinded tetras and other fish deprived of vision in the course of experiments. Enucleation was followed by similar behavior in brown trout *Salmo trutta*, rainbow trout *Oncorhynchus* (=*Parasalmo*) *mykiss*, bitterling *Rhodeus sericeus amarus*, and minnow *Phoxinus phoxinus* (Marusov, 1997; Kasumyan and Marusov, 2002, 2008; Marusov and Kasumyan, 2010). The blind form of *A. fasciatus* and the blinded specimens of this species captured in over-the-ground water bodies demonstrate similar food-searching behavior (Schemmel, 1967, 1980; Glaser, 1968; Hüppop, 1987; Kasumyan and Marusov, 2015). These fish grasp the object of search after preliminary assessment of its sensory properties. The gustatory system, including the taste buds located on the head, body, and fins in fish with external gustatory reception and/or intraoral taste buds present on the lips of all fish plays the leading role in the assessment.

The behavior of Buenos Aires tetra allows for the assumption of the absence of external taste buds in this species, since blinded fish grasp food only after accidental touches by the lips. Food touching by any other parts of the head, body, or fins does not stimulate grasping. Neither the presence nor the localization of taste buds on the external surface of the head and body were reported in Buenos Aires tetra, although scarce taste buds were found on the lips of the fish (Campos, 1969). External taste buds are reportedly quite scarce outside of oral cavity and mostly localized near the mouth opening of seeing form of *A. fasciatus* inhabiting over-the-ground water bodies (Schemmel, 1974; Bensonilah and Denizot, 1991).

Our data demonstrating the absence of any signs of compensatory recovery of the ability to respond to chemical food stimuli after prolonged olfactory deprivation in Buenos Aires tetra are in complete agreement with the assumption of the absence of external taste buds in this species. Tetras failed to respond to high concentrations of food extract even after 13.5 months of anosmia. The recovery of reaction to food odor was reported to occur only in fish that have external taste buds, although the number of such taste buds may be relatively low: for instance, the density of taste buds on the head surface of the bitterling is several times lower

Duration of searching for food ($M \pm m$) in vision-deprived singly Buenos Aires tetra *Hyphessobrycon anisitsi* with intact olfaction or after chronic anosmia in response to pure water (control) or the extract of chironomid larvae during 3 min of stimulation

Stimulus	Concentration, g/L	Intact olfaction, 2.0 months of blindness		1.5 months of anosmia, 4.0 months of blindness		5.0 months of anosmia, 3.5 months of blindness		13.5 months of anosmia, 12.0 months of blindness	
		searching for food, s	n	searching for food, s	n	searching for food, s	n	searching for food, s	n
Control	–	–		0.79 ± 0.23	24	1.58 ± 0.81	24	1.25 ± 0.30	24
Extract	10^{-1}	–		0.67 ± 0.17	24	0.75 ± 0.33	24	0.53 ± 0.18**	24
Control	–	–		1.00 ± 0.32	24	1.17 ± 0.40	24	0.92 ± 0.33	24
Extract	10^{-2}	–		0.58 ± 0.17	24	0.88 ± 0.36	24	0.77 ± 0.25	24
Control	–	1.11 ± 0.43	18	–		–		–	
Extract	10^{-3}	44.61 ± 5.64***	18	–		–		–	
Control	–	3.54 ± 2.17	24	–		–		–	
Extract	10^{-4}	25.71 ± 4.45***	24	–		–		–	
Control	–	1.25 ± 0.43	24	–		–		–	
Extract	10^{-5}	19.38 ± 3.52***	24	–		–		–	
Control	–	0.38 ± 0.16	24	–		–		–	
Extract	10^{-6}	5.17 ± 1.03***	24	–		–		–	
Control	–	0.38 ± 0.19	24	–		–		–	
Extract	10^{-7}	0.25 ± 0.11	24	–		–		–	

$M \pm m$—mean value and error of the mean; n—trial number; significant difference from the control values at p: ** < 0.01, *** < 0.001.

than in the closely related carp and minnow, whereas other body parts of the bitterling are completely devoid of taste buds (Gomahr et al., 1992). However, the bitterling exhibits complete compensatory recovery of the reaction to food odor after prolonged anosmia (Marusov and Kasumyan, 2010). The compensatory processes do not occur in fish that do not have external taste buds, such as salmonids. This was demonstrated previously in experiments with rainbow trout after chronic anosmia (Kasumyan and Marusov, 2008). The absence of compensation in Buenos Aires tetra and the relatively poor recovery of the ability to react to food odor in blind form of *A. fasciatus* after chronic anosmia (Kasumyan and Marusov, 2015) may be indicative of poorly developed central interactions of the olfactory and the gustatory systems in characid fishes as compared to apparently more complex and varied intersystem interactions of various chemoreception channels occurring in cyprinids and acipenserids.

Olfaction-deprived tetra individuals presented with the control stimulus searched for food over a longer time than in case of injection of a stimulus solution. The difference was observed in all series of experiments and even reached the level of significance in one of the series. These differences persisting in the different series may be due to the specific features of the experimental setup. The vision-deprived fish kept under the same conditions for a long time may have developed a conditional reflex to the sounds and manipulations performed by the experimenter during the daily feedings, so that the searching activity was enhanced in response to these cues. The actions of the experimenter related to switching of the water flow during the injection of a stimulus solution or pure water may have been reminiscent of food introducing. The control solution (pure water) was injected first in all experiments, with the stimulus solution injection shortly afterwards, and the effect of the repeated imitation of feeding was presumably less pronounced.

Thus, the behavior, feeding patterns, fish size, and other biological features vary greatly within the large Characidae family. Comparison of two species of this family (Buenos Aires tetra and blind cave fish) revealed that despite of a comparably high olfactory sensitivity these species are different in threshold concentrations of the food chemical stimulus and the ability of taste reception to undergo compensatory development in response to prolonged anosmia. Further research is needed to identify the effects of diverse biological features of characid fish on feeding behavior and olfactory sensitivity, as well as on functional interactions of the chemosensory systems.

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