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ORIGINAL PAPER

Exploring visual categorical learning in teleost fish *Danio rerio* and *Xenotoca eiseni*

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Abstract

Categorization skills enable animal species to sort entities based on their similarities, providing significant advantages in terms of learning efficiency. The extent of these skills and the mechanisms involved vary across taxa, making it critical to explore categorization in as many lineages as possible. From an evolutionary standpoint, fish are valuable models for studying categorization processes; however, until recently, this group of vertebrates has been neglected in visual categorization research. To address this gap, we conducted three experiments to investigate, for the first time, the visual categorical learning skills of the redtail splitfin (*Xenotoca eiseni*) and the zebrafish (*Danio rerio*), two teleost species studied in other contexts of animal cognition. Using a two-alternative forced-choice task, we first trained the fish to discriminate between several pairs of stimuli. Then, we tested their ability to generalize to pairs of new stimuli of the same categories. The stimulus categories varied across the experiments (Experiments 1 and 2: alphanumeric characters; Experiment 3: fish silhouettes) and were consistent with those used in past studies involving different taxa. Both fish species met the learning criterion in the training phase across all three experiments, but their ability to generalize to novel stimuli differed based on stimulus features. Moreover, both species presented interindividual differences in their ability to generalize what they learnt. Our results validate the use of *X. eiseni* and *D. rerio* as models for research on categorical learning. They also encourage further investigation into how experimental methods and stimuli could affect learning-based generalization abilities in these species.

Keywords Fish · Visual discrimination · Categorization · Learning · Cognition · Stimuli

Introduction

Categorizing similar stimuli into classes may enhance discriminating useful (e.g., food stuff vs. non-food stuff) and dangerous elements (e.g., threatening vs. harmless species), allowing to emit the appropriate behavioral responses (Shettleworth 2010). This ability is not an exclusively human trait. Of the three modalities for category formation (Anderson 1991), one, based on linguistic labelling, has been described only in humans (Xu 2002; Lupyan et al. 2007), but the other two, relying on visual (e.g., Job et al. 1992; Lotto et al. 1999; Mash 2006; Rosch et al. 1976) and functional (e.g., Träuble and Pauen 2007) similarities, can be present in other animals as well. Indeed, there has been a plethora of studies showing category learning in nonhuman animals (see Aust 2017; Greggor and Hackett 2018; Lazareva and Wasserman 2017 for reviews). Consistent and adaptive responses to ecologically similar stimuli are expected to offer significant advantages in terms of learning

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efficiency. Understanding the degree to which this occurs and the mechanisms involved across various taxa is a key area of research, especially in visual science.

Different theories explain how categories are represented and processed. The classical view defined categories by necessary and sufficient features (e.g., a square has four equal sides and angles), but this fails for fuzzy categories with overlapping traits (Smith and Sloman 1994).

Prototype theory (Rosch and Mervis 1975) proposes that categories center around a typical exemplar, and categorization depends on similarity to this prototype. Exemplar theory (Medin and Shaeffer 1978; Nosofsky 1988) instead posits that categorization is based on similarity to stored individual examples. Findings suggest people may use both prototype and exemplar strategies, even within a single task (Malt 1989). Evidence of visual categorization at different levels of complexity and abstractness has been reported in numerous vertebrates - especially mammals and birds - and some invertebrates, with learning and generalization abilities that may vary across species and tasks (see Aust 2017; Greggor and Hackett 2018; Lazareva and Wasserman 2017 for reviews). Many taxa have shown the ability to sort stimuli in perceptual categories characterized by items that have physical properties in common (e.g., insects: Bernard et al. 2006; fish: Schluessel et al. 2012; birds: Huber and Aust 2017; mammals: Roberts and Mazmanian 1988). Some species have proven to be able to form associative categories represented by items considered equivalent due to a shared functional association (e.g., different edible items, Bovet and Vauclair 1998) or to an experimentally induced arbitrary association (see Zentall et al. 2014 for a review). Several species have also demonstrated the ability to manage relational categories defined by logical relationships among multiple items rather than by the characteristics of individual items (e.g., classifying groups of stimuli on the basis of whether all the items in the group are the same or differ from one another; see Lazareva and Wasserman 2017 for a review). Unfortunately, assigning a categorization task to a specific level can be challenging in practice, as the boundaries between category types may be unclear, and the mechanisms by which animals achieve a task are not always obvious (e.g., Xu and Plowright 2022; Smith et al. 2016).

Teleosts represent a derived clade of ray-finned fishes that originated approximately 250 million years ago. Their brain is fundamentally different from that of tetrapods, but data on brain function indicate that wide pallial regions in the telencephalon of teleost fish present homologies with the neocortex of mammals (Portavella and Vargas 2005; Wullimann and Mueller 2004). Thus, from an evolutionary perspective, fish could represent good models for studying categorization processes, especially considering that different neural architectures can lead to similar categorizations (Greggor and Hackett 2018). Research on categorical learning abilities in fish is still limited, and evidence to support this is sparse. Archerfish (*Toxotes chatareus*) can learn to distinguish between different object categories by generalizing from examples (Volotsky et al. 2022), an ability mediated in this species by a small population of neurons in the optic tectum (Volotsky and Segev 2025). The teleost African cichlid *Pseudotropheus* sp. (Schluessel et al. 2012) and the gray bamboo shark *Chiloscyllium griseum* (Schluessel and Düngen 2015) can be trained to distinguish between 2-D object categories, ‘‘fish’’ versus ‘‘snail’’ and generalize to unknown stimuli. The rainbow trout (*Oncorhynchus mykiss*) is able to discriminate recurrent photographs of conspecifics from abstract shapes or objects but not between photographs of conspecifics and blue shapes or images of other fish species (Kleiber et al. 2021). Overall, studying visual categorization in fish is a promising research area. Further in-depth studies are essential to fully grasp the extent of variation in how various species expand and generalize what they learn.

The current study contributes to filling this gap by investigating for the first time the categorical learning skills of the redtail splitfin (*Xenotoca eiseni*; family *Goodeidae*) and the zebrafish (*Danio rerio*; family *Cyprinidae*), two teleost species widely recognized in animal cognition studies for their visual discrimination abilities. *X. eiseni* and *D. rerio* are established teleost models in behavioral and neurobiological research (e.g., Baratti et al. 2022; Kalueff et al. 2014; Rosa Salva et al. 2016 for reviews; Gatto et al. 2021) and their differing ecological and biological traits - including geographic distributions, morphologies, reproductive and foraging behaviors, as well as social and locomotor patterns - may shape distinct cognitive strategies (e.g., Healy and Braithwaite 2000; Shettleworth 2010; Sovrano et al. 2020). Moreover, from their comparison, it is possible to learn more about the diversity of fish cognition. Zebrafish and redtail splitfins are believed to have diverged around 220 million years ago (timetree.org), providing ample time for cognitive divergence. Past research on their ability to perceive and discriminate visual stimuli has shown that they are capable of amodal completion (*X. eiseni*: Sovrano and Bisazza 2008; *D. rerio*: Sovrano et al. 2022b) and sensitive to visual illusions (*X. eiseni*: Sovrano and Bisazza 2009; Sovrano et al. 2015, 2016; *D. rerio*: Agrillo et al. 2020; Gori et al. 2014; Santancà et al. 2020). Moreover, the first evidence of the “classifying-together” phenomenon, also known as the “Bateson effect”, was recently reported in *X. eiseni.* This finding indicates that simultaneous exposure to visual stimuli impairs the subsequent ability of the fish to discriminate between those stimuli (Sovrano et al. 2022a).

In three experiments with a two-alternative forced-choice task, fish were trained to discriminate between pairs of 2D visual stimuli from two categories, and then tested on their ability to generalize this learning to novel exemplars. We examined categorization across different types of stimuli: letters and numbers in various fonts (Experiments 1 and 2); and black-and-white silhouettes of two teleost species (Experiment 3). The stimuli in Experiment 1 resembled those used in prior discrimination studies with redtail splitfin and zebrafish (Sovrano and Bisazza 2008; Sovrano et al. 2022a, 2022b), while those in Experiment 2 mirrored those used with humans and nonhuman primates in categorization tasks (Schrier et al. 1984). The silhouettes in Experiment 3 served as more ecologically valid and visually complex stimuli, in line with prior fish categorization studies (e.g., Schluessel et al. 2012). We hypothesized that both species would form visual categories, but with potentially different performance profiles (accuracy and learning) depending on stimulus complexity - simple abstract symbols versus complex, ecologically relevant shapes - and the species' ecological traits.

Methods

Experiment 1. Categorical discriminative learning of letters and numbers, "G" versus "0"

The aim of this first experiment was to assess the ability to learn, discriminate, and generalize stimuli belonging to the "letter G" category from stimuli belonging to the "number 0" category in the redtail splitfin fish (X*enotoca eiseni*) and zebrafish (*Danio rerio*), using different fonts (typefaces) for each category. The choice to use these two categories of stimuli comes from the encouraging results obtained in a previous study on the phenomenon of amodal completion in redtail splitfin and zebrafish, where, during training, the fish learned to discriminate a full disk from an amputated disk (in its upper-right portion; cf., Guthrie 1983), which is quite similar to a G vs. 0 comparison (Sovrano and Bisazza 2008; Sovrano et al. 2022a, b).

Experimental subjects

The experimental subjects used in Experiment 1 were a total of 27, consisting of 12 naïve adult male *X. eiseni* specimens, with an average length ranging from 5 to 7 cm, and 13 naïve adult male *D. rerio* specimens, with an average length ranging from 4 to 5 cm, all from the animal facility of the Animal Cognition and Neuroscience Laboratory (ACN Lab) at the Center for Mind/Brain Sciences (CIMeC, University of Trento). To ensure consistency with previous research conducted on the same species, only male subjects were considered, in order to reduce biological variability, thereby facilitating data interpretation.

Six *X. eiseni* and seven *D. rerio* were trained with the letter G as the positive stimulus, while six *X. eiseni* and six *D. rerio* were trained with the number 0 as the positive stimulus. Eleven out of 13 *D. rerio* completed the learning phase, and all except 1 completed the test phase. All the *X. eiseni* specimens completed the two phases.

In the acclimatization phase, prior to the experiment, the fishes were fed twice a day with dry flake food (Sera®, GVG-Mix). During the experiment, however, the fishes were fed exclusively within the experimental apparatus, as an incentive for learning. Additionally, at the end of each daily experimental session, before returning to their home tank, fish received a food reward. In this phase, the fishes were kept in 25-L glass tanks, complete with vegetation and multicolored gravel as enrichments (e.g., Arechavala-Lopez et al. 2022; Gatto et al. 2025). They were housed in groups of four per tank, separated by partitions made of plastic borders with a central mesh section, allowing for visual and olfactory contact between individuals. This arrangement optimized the use of space while still enabling social interaction, thus preventing isolation. Water quality was ensured by the use of a filter (Aquarium Systems Duetto®, NEWA), and the temperature was maintained at 26 ± 1 °C using a heater (NEWA Therm®, NEWA). In addition to the subjects undergoing the procedures, two conspecific female fish were used as sexual and social reinforcement, housed within the experimental apparatus for both species.

Experimental apparatus and stimuli

The experimental apparatus consisted of an octagonal arena (diagonal segments: 4×15 cm; straight segments: 9×15 cm), made of white polypropylene (Poliplak®), inserted into a square arena ($15 \times 15 \times 15$ cm); see Fig. 1a, b. The apparatus was placed inside a large rectangular tank (length × height × width = $57 \times 18 \times 38$ cm), forming a comfortable external space, providing a rest area (where reinforcement, in the form of food and conspecific females, was released), complete with vegetation and gravel. The tank was located in a dark room, and the apparatus was illuminated centrally by white light (18 W), at a distance of 30 cm. Finally, the tank was placed on a rotating platform, allowing easy rotation of the apparatus (90° clockwise for each trial) and preventing the fish from using any potential external visual cues.

On two sides of the octagonal arena, along the diagonal, small corridors were placed (3×4.5 cm, 2.5 cm in depth, 2.5 cm in height), made of white plastic material (Poliplak®) and ending in two "doors" (3×4.5 cm), constructed from a colored flexible plastic upper portion (2.5×4.5 cm) and a lower portion made of transparent acetate (0.5×4.5 cm); see Fig. 1c. The two doors were visually identical, but only one of them could be opened, while the second was blocked

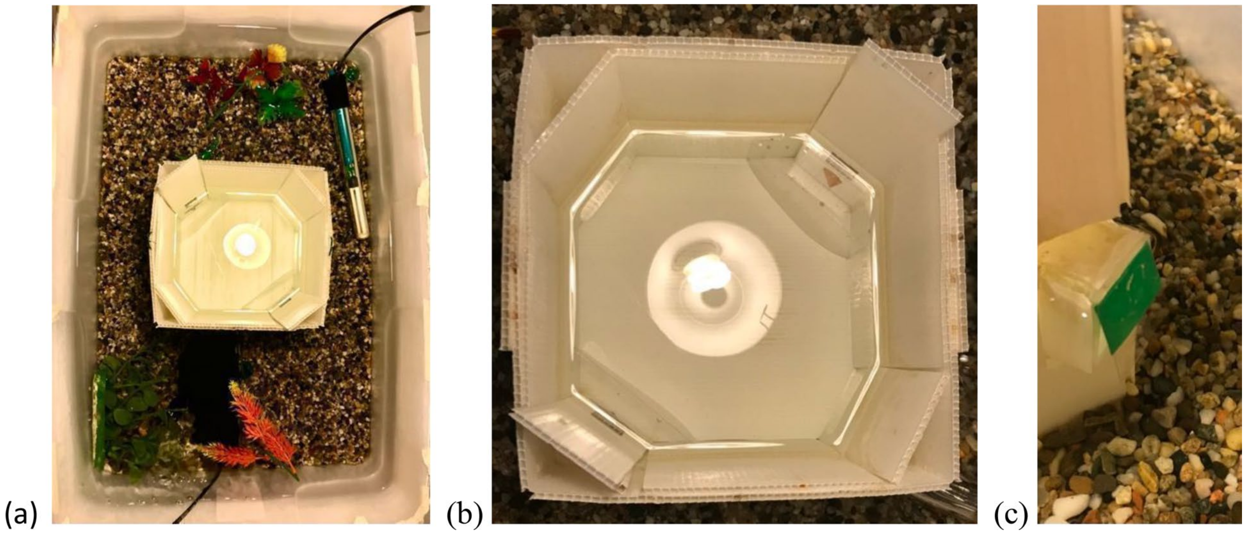

Fig. 1 Photographs of the apparatus. (**a**) Top view of the experimental apparatus, consisting of the white plastic (Poliplak®) arena and the external reinforcement release area, (**b**) top view of the arena, and (**c**) in detail, the opening at the end of the corridor, which allowed the animal to exit the arena

by a metal clip from the outside. The experimental subject could open the unblocked door by applying light pressure on it. Moreover, the closed doors allowed regular water flow through lateral openings, to avoid any potential non-visual cues that could be detected by extra-visual sensory modalities (touch and/or lateral line; Sovrano et al. 2018; Sovrano et al. 2020). In front of each corridor, a white plastic (Poliplak®) panel (length × height = 4 × 15 cm) was placed, to which a laminated stimulus was attached; a transparent acetate barrier (9 × 4 cm) was positioned 2 cm in front of it, ensuring a global visual perception of the stimulus for the experimental subject. The water level was maintained at the upper edge of the corridors. Above and centrally with respect to the apparatus, a webcam (LifeCam Studio, Microsoft, USA) was positioned to video-record each experimental trial.

For this first experiment, 30 numbered pairs of laminated stimuli in black on a white background (side = 3.5 cm) were used, placed on white plastic (Poliplak®) panels (length × height = 4 × 15 cm). Each pair consisted of a reproduction of the letter "G" and the number "0," each differing from the others in terms of font type, including both Serif fonts ("with serifs") and Sans-Serif fonts ("without serifs"), as shown in Fig. 2. The typefaces were selected from those available in the Microsoft Word and Google Docs word processing programs. During the training phase, each experimental subject was trained using 20 of these stimuli (randomized into three different combinations); for the generalization test, the remaining 10 stimuli were used, with which the subject had never interacted before and for which no reinforcement had been given.

Experimental procedure

A procedure widely validated in the literature on fish, particularly in *X. eiseni* and *D. rerio*, was adopted to investigate discriminative learning and perceptual illusions (Albertazzi et al. 2017; Sovrano and Bisazza 2008, 2009; Sovrano et al. 2015, 2016, 2022a, b; Truppa et al. 2010). The procedure was divided into two phases: a training phase over repeated sessions and a generalization test phase. The training phase involved the fish learning to discriminate the positive, reinforced stimulus, from the negative, non-reinforced stimulus, until reaching the learning criterion. Full attainment of the learning criterion was defined as achieving a performance equal to or greater than 70% in two consecutive daily training sessions (learning and confirmation sessions). The test phase required the fish to generalize the learning to stimuli never seen before (with further different fonts), but belonging to the same training category, i.e., letter G or number 0.

In the first phase, the training phase, an operant conditioning procedure was employed (Skinner 1938; Thorndike 1898). In this context, the reinforced behavior consisted of exiting the corridor marked by the correct stimulus. The same types of reinforcement, validated in previous studies (Albertazzi et al. 2017; Baratti et al. 2022; Daggett et al. 2019; Potrich et al. 2019; Sovrano and Bisazza 2008, 2009; Sovrano et al. 2015, 2016, 2022a, b; Truppa et al. 2010) were used for both species: dry food and female conspecifics, which provided additional social and sexual incentives.

During the training phase, the animal was asked to discriminate between the letter category "G" and the number category "0". This phase required the experimental subjects to undergo a daily session of 10 trials, with a maximum of

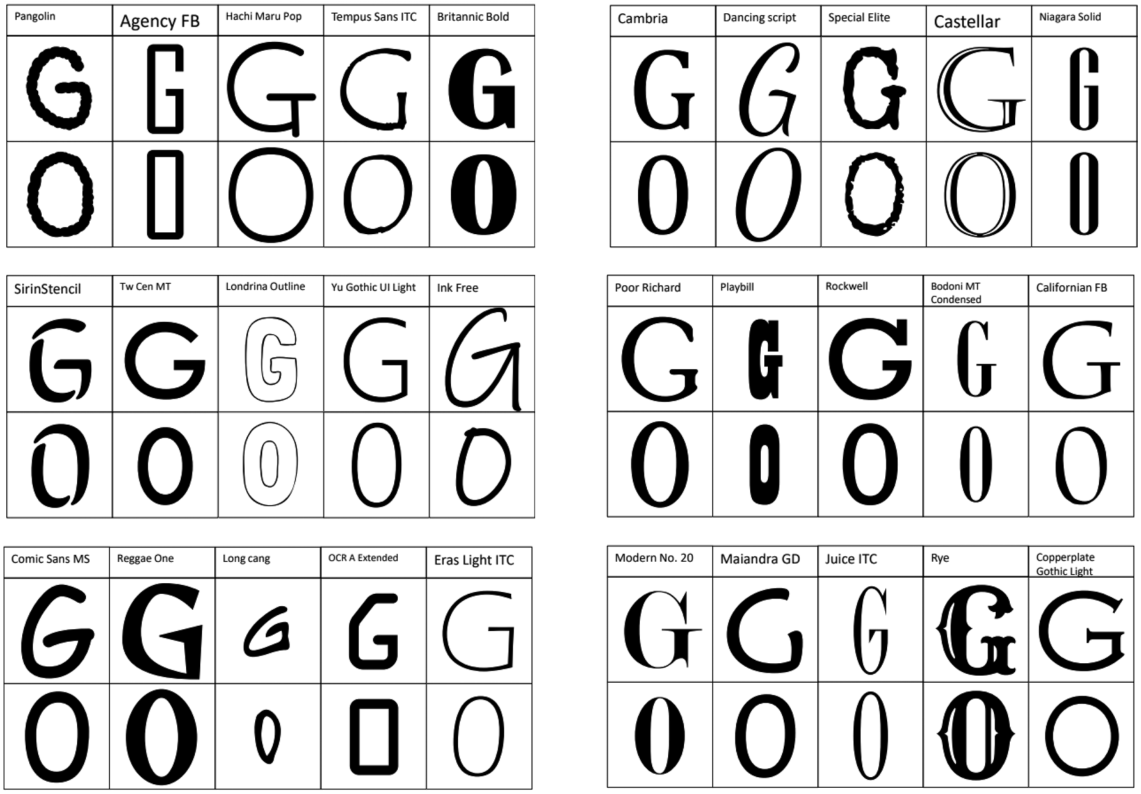

Fig. 2 Experimental stimuli used for Experiment 1, "G versus 0". Each column lists the pairs of stimuli consisting of the letter "G" and the number "0" along with their respective font. The typefaces were selected from Microsoft Word and Google Doc

30 sessions. Before starting the daily session, the fish was transferred from the holding tank to the experimental apparatus, where it was allowed to acclimate for 5 min. Fish, accustomed to human handling, were transferred from the home tank using a net, which was then placed in a container filled with the same tank water during transport to the experimental apparatus. Each fish remained in the annular zone of the apparatus for the entire working session and was gently moved into the central area at the beginning of each trial, in full compliance with ethical standards for animal care and use. At the center of the apparatus a glass cylinder (diameter = 6 cm; height = 8 cm) allowed the fish to observe both stimuli for approximately 30 s. After this observation period, the cylinder was slowly raised vertically, and the animal was free to move within the apparatus to approach the corridors corresponding to the stimuli.

The choice for a stimulus was recorded when the animal completely entered the chosen corridor, displaying tail movements as if to force an exit. Multiple correct choices could be made if the fish explored the correct door without exiting or if, when attempting to exit, it did not exert enough force to pass through the door. The maximum time allowed to exit the arena was 10 min. Every two trials, the entire apparatus was rotated by 90° clockwise to prevent the fish from using any external visual cues to identify the correct stimulus.

Inter-trial intervals depended on the animal's performance, with the following amounts: 6 min (full reinforcement) in the case of the first correct choice, during which the animal spent time in the external comfortable zone with food and female conspecifics; 2 min (partial reinforcement) in the case of incorrect choices, during which the animal spent time outside but without food reinforcement; and 5 min without reinforcement, in the case of a null trial, where the animal did not provide any choice within the maximum time allowed (10 min). A corrective method (Caro et al. 1979) was used, which allowed the fish to correct its first or initial choices directed toward the wrong stimulus. If the subject failed to exit the arena within 10 min, the trial was considered null; if this occurred consecutively for two trials, the experiment would be interrupted, and the subject would be returned to the holding tank until the following day.

After reaching the learning criterion and learning to discriminate between the letter category and the number category, the fish underwent a generalization test phase, during which new, non-reinforced stimuli belonging to the same category as the stimuli used during the training phase were used. The test phase consisted of a session of 10 trials, with a total duration of 120 s for *X. eiseni* and 60 s for *D.*

rerio, using a procedure known as "response extinction". Both doors were blocked from the outside to prevent any differential reinforcement, thus preventing the animal from moving from the arena to the reinforcement zone, and the subject could make multiple choices. The target stimulus was alternately placed on the door that had been open during the training trials. This measure helped control the use of any alternative cues to the stimuli in solving the task during the test phase. Observation times during the test phase differed between the two species (120' vs. 60') due to species-specific movement patterns, with the total number of choices more than doubled in the zebrafish compared to the red-tail splitfin fish (Sovrano et al. 2020), aiming to match the amount of behavioral observations. For each test trial, the first choice, the total number of choices for each stimulus, and the movement strategies (perimeter swimming, clinging to the walls, vs. direct swimming, from the center to the corner with the stimulus) were recorded and coded.

Test trials were conducted over several consecutive days, with each daily session comprising 10 trials overall. To counteract the loss of motivation in the absence of reinforcement, recall trials with the stimuli and reinforcements used during training were inserted between each test trial in each session. During the recall trials, if the subject successfully completed two consecutive trials (i.e., without errors), they proceeded to the subsequent test trial. In the event of an error in either of the two trials, the subject continued to perform additional recall trials until a performance level of 70% or higher correct responses across the total number of recall trials performed (e.g., 3 correct out of 4 recall trials, 5 correct out of 7 recall trials, etc.).

Each trial was videorecorded with the help of a webcam (LifeCam Studio, Microsoft, USA) positioned centrally above the apparatus. The experimenter started the camera when the fish was positioned in the center of the apparatus, inside the transparent glass cylinder, and, during the training phase, stopped it after the fish exited through the corridor with the open door, marked by an exemplar of the reinforced stimulus category. During the generalization test phase, however, since both corridors led to closed doors (extinction procedure), the experimenter stopped the camera after 2 min of observation or, if this time had elapsed, until the first entry into one of the two corridors.

Ethical statement

This research was conducted at the FISH Group, within the Animal Cognition and Neuroscience Laboratory (A.C.N. Lab.) of the Center for Mind/Brain Sciences (CIMeC) at the University of Trento (Italy). The conditions for housing and breeding the fish, along with the experimental procedures, comply with European Legislation on the Protection of Animals Used for Scientific Purposes (Directive 2010/63/EU) and were previously authorized by the Animal Welfare Body (OPBA) of the University of Trento and the Italian Ministry of Health (authorizations number: 1111/2015-PR and 848/2020-PR).

Statistical analysis

The performance of the fish, both in training and in the generalization test, was calculated based on the choices made at the corridors marked by different stimuli, and estimated as an index of success (IoS), calculated as the ratio between the correct choices and all choices (correct plus incorrect) performed by the animal, using the formula: Success Index = (Correct Choices)/(Correct Choices + Incorrect Choices). Similarly, the index of choices of the local corner was calculated as the ratio between the choices of the local corner and the choices toward both the local and the opposite corner performed by the animal.

ANOVAs were applied to evaluate whether species, as a between-subjects factor, had a significant effect on each of the dependent variables, namely: criterion trials and time in seconds until the learning criterion was reached (time till learning); first choices and total choices (as a success index) in the learning session (day 1, above the 70% threshold) and in the validation session (day 2, consecutive to day 1, above the 70% threshold); generalization test (total seconds; analyses for 60 s and 30 s are reported in the Supplementary Materials); and strategy use (local angle, perimeter movement vs. direct movement from the center to the angle).

ANOVAs were applied to assess possible differences between the two species in the frequency of stimulus approach, cumulatively considering correct and incorrect responses, based on the total time (120 s for *X. eiseni* and 60 s for *D. rerio*; see Supplementary Materials for the same analysis, but on a period of 60 s and 30 s).

A one-sample Student's t-test was applied to compare the fish performance with the level of chance (= 0.5) and determine a significant preference for visual stimuli, concerning training, generalization test, and movement strategies use. Partial eta-squared, η_p^2, was used as an index for the ANOVA, and Cohen's d as an index for the Student's t-test to estimate the effect size of the significant data analyses.

Data were analyzed using the R software (R Core Team 2015), version 4.2.2. Plots were realized with the *ggplot2* package (version 3.5.1; Wickham 2016), effect sizes were calculated with the *effectsize* package (version 0.8.6; Ben-Shachar et al. 2020).

Results

Training

Descriptive data are reported in Fig. 3a. The two-way ANOVA with Species (*X. eiseni* vs. *D. rerio*) and Type of Rewarded Stimulus (G vs. 0) (both as between-subjects factors) on the number of trials needed for learning showed a main effect of Species (F (1, 19) = 6.287, p = .02, η^2_p = 0.25), with *D. rerio* requiring more than twice the trials required by *X. eiseni* to learn (M = 117.18 (SE = 24.17) vs. M = 50.25 (SE = 10.79)). No further effect reached significance (Type of Rewarded Stimulus: F = 0.10, p = .74; interaction: F = 0.37, p = .54).

The same ANOVA as above on time till learning showed no significant effect (Species: F = 1.87, p = .18; Type of Rewarded Stimulus: F = 0.61, p = .44; interaction: F = 0.07, p = .93).

A two-way ANOVA as above was also run by considering the index of success on the first choice and on the total amount of choices (Fig. 3b). For the first choice, the analysis showed no main effects (Species: F = 0.65, p = .42; Type of Rewarded Stimulus: F = 1.81, p = .19), but a significant interaction (F (1, 19) = 4.44, p = .04, η^2_p = 0.19), indicating that while *X. eiseni* tended to perform better when 0 was rewarded (M = .85, SE = .03) than when G was rewarded (M = .73, SE = .05), *D. rerio* did the opposite (M_0 = .78, SE = .01; M_G:.75, SE = .08). None of the two differences, however, reached significance when tested by means of a post-hoc t-test comparison (*X. eiseni*: t = −2.15, p = .14; *D. rerio*: t = .75, p = .47; p-values were fdr corrected). When the total amount of choices was considered, the ANOVA did not show any significant effect (Species: F = 1.15, p = .29; Type of Rewarded Stimulus: F = 3.59, p = .07; interaction: F = 1.21, p = .28). As a final analysis, to test whether the overall performance was better than chance, a one-sample t-test against the chance level was run considering all the data together. Both species significantly chose the correct door more often than the incorrect one, whether their first choice or the total of their choices was considered (respectively: t (22) = 14.78, p < .001, d' = 3.08; (t (22) = 14.80, p < .001, d' = 3.09).

A final analysis was conducted on the index of success for the confirmation session – needed to ascertain learning effectiveness. The ANOVA showed no difference between species either on the first choice (Species: F = 0.94, p = .34; Type of Rewarded Stimulus: F = 0.33, p = .56; interaction: F = 0.37, p = .54) or on the total amount of choices (Species: F = 0.76, p = .39; Type of Stimulus Rewarded: F = 0.005, p = .94; interaction: F = 1.44, p = .24). The follow-up one-sample t-test (against chance) considering all the data together showed a significant effect for both the first choice (M = 0.77, SE = 0.02; t (23) = 13.57, p < .001, d' = 2.83) and the total amount of choices (M = 0.81, SE = 0.01; t (22) = 17.11, p < .001, d' = 3.57).

Generalization test

All fishes that reached learning underwent the generalization test. Of these, all subjects except one *D. rerio* did not

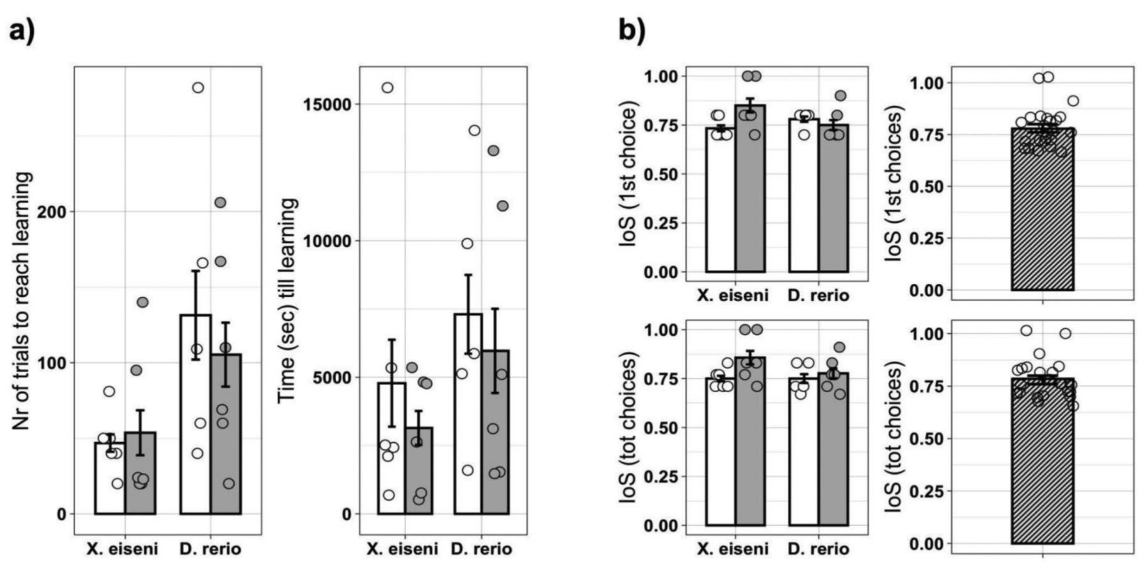

Fig. 3 Data of the training. (**a**) Fish performance in reaching learning for G (white) and 0 (gray) as a rewarded stimulus. Points represent individuals' performance; bars represent mean standard errors; (**b**) Index of success both as a function of rewarded stimulus (G = white, 0 = gray) and species (left column) and as overall performance (right column). IoS = index of success. Points represent individuals' performance; bars represent mean standard errors. The upper row reports the data for the first choice, whereas the lower row the data for the total amount of choices

complete it. To evaluate animals' performance, choices obtained during the test under response extinction were divided according to observation time as first choice and total amount of time (i.e., 120 s for *X. eiseni*, 60 s for *D. rerio*; analyses for 30 s and 60 s period are reported in the Supplementary Materials). Both the index of success and motor behaviors were analyzed.

Frequency of choices

The one-way ANOVA showed no significant effect ($M_{\text{X. esieni}}$= 55.08 (SE = 6.78) vs. $M_{\text{D. rerio}}$ = 38.20 (SE = 6.40), F = 3.06, p = .09).

Index of success

Descriptive statistics are reported in Fig. 4a. Considering the total amount of time, the one-way ANOVA showed no significant effect either on the first choice (F = .04, p = .88) or on the total amount of choices (F = .73, p = . 40). Thus, data from the two species were jointly considered in a further analysis to test whether the overall performance was better than chance. Notably, the average of the total amount of correct choices was significantly higher than the chance level (one-sample t-test, t (21) = 2.40, p = .025, d' = 0.51), however, this effect did not prove to be significant when only the first choice was considered (t = 0.70, p = .48).

Motor behavior

An ANOVA considering the index of local corner choice (rewarded during the recall trials prior to each test) as dependent variable and the species (*X. eiseni* vs *D. rerio*) as between-subjects factor, and the full time showed differences between species (F (1, 19) = 5.071, p = .03, η^2_p = 0.20). A one-sample t-test against chance showed that while *D. rerio* chose the local corner more often than chance ($M_{\text{index of choices of the local corner}}$ = .67 (SE = .06), t (9) = 2.60, p = .02, d' = 0.82), *X. eiseni* did not ($M_{\text{index of choices of the local corner}}$ = 0.52 (SE = 0.02), t = 1.18, p = .25). Further analyses on motor behavior (for this and the following experiments) are reported in the Supplementary Materials.

Performance of the best and the worst subjects

To evaluate possible inter-individual variability in the subjects' performance, we considered the best and the worst subjects on the basis of a subjective criterion of an index of success ≥ 0.55 and ≤ 0.45, respectively, during the generalization test. We considered the 30-seconds period, in which first choices and total choices were consistent and possibly not penalized by a motivational drop induced by the extinction procedure. The best subjects were 2 *X. eiseni* (fish 3, 12) and 4 *D. rerio* (fish 7, 10, 11, 12). Because of the small numerosity, non-parametric analyses were adopted. The Kruskal-Wallis test with the index of success as dependent

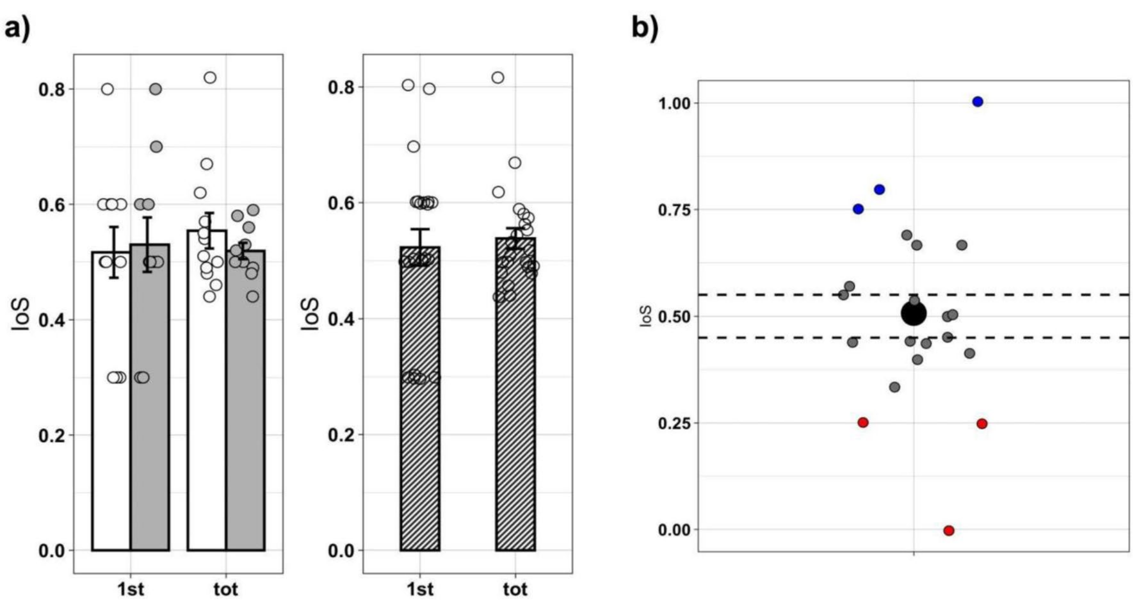

Fig. 4 Data for the Generalization. (**a**) Index of success as a function of the time considered, both separately for species (left panel, white = *X. eiseni*, gray = *D. rerio*) and as overall performance (right panel). IoS = Index of Success; 1 st = first choice in the total amount of time; tot = total amount of choices in the total amount of time. Points represent individuals' performance; bars represent mean standard errors; (**b**) Index of success for single subjects highlighting the best and worst individuals. The dashed lines represent the 0.45 and the 0.55 thresholds; the big black point represents the overall mean; the small points represent subjects' performance; the blue and the red points represent the best and worst subjects with respect to the z-score criterion

variable and the species as between-subject factor showed no significant effect (first choice: χ^2 (1) = 0.05, p = .81; total amount of choices: χ^2 (1) = 0.85, p = .35). When data from the two species were jointly considered, the Wilcoxon test showed that the overall performance (first choices: $M_{\text{index of choice}}$ = 0.80, SE = 0.04; total amount of choices: $M_{\text{index of choice}}$ = 0.74, SE = 0.05) was better than chance (first choice: V = 21, p = .03; total amount of choices: V = 21, p = .03).

The worst subjects were 5 *X. eiseni* (fish 5, 7, 8, 9, 10) and 2 *D. rerio* (fish 5, 8)). The Kruskal-Wallis test showed no significant effect (first choice: χ^2 (1) = 0.18, p = .66; total amount of choices: χ^2 (1) = 0.15, p = .69). The follow-up analysis jointly considering data from the two species showed that the performance (first choices: $M_{\text{index of choice}}$ = 0.28, SE = 0.04; total amount of choices: $M_{\text{index of choice}}$ = 0.30, SE = 0.05) was worse than chance (first choice: V = 0, p = .02; total amount of choices: V = 0, p = .02).

To evaluate possible inter-individual variability in a more objective way, we transformed the index of success for the total choices in the 30-seconds period into z-scores and identified the best and worst subjects, those with a score ≥ 0.1 and ≤ −0.1, respectively. One *X. eiseni* (fish 3) and 2 *D. rerio* (fish 10, 12) were classified as best, and 2 *X. eiseni* (fish 8, 10) and 1 *D. rerio* (fish 8) as worst. Because of the small numerosity, no statistical analysis was conducted. Data are represented in Fig. 4b.

The results are summarized in Tables 1 and 2. Taken together, the results of the training showed categorical learning with some differences between species. Specifically, *D. rerio* required more trials than *X. eiseni* to learn. Moreover, when considering the first choice, *X. eiseni* tended to perform better with 0, whereas *D. rerio* did the opposite. About the performance in the test, the Index of Success was higher than chance without differences between species. This was true only when the total amount of time and choices were considered. Finally, with regard to motor behaviors, *D. rerio* chose the local corner more often than chance, and opted always for a movement directed toward the corner. The analysis of the best and worst subjects' performance highlights possible individual differences, with the limitation of not determining whether the solution to the task was actually understood.

Experiment 2: categorical discriminative learning of letters and numbers, "A" versus "2"

The goal of the second experiment was to expand the samples within the letter vs. number categories, evaluating also the ability of *X. eiseni* and *D. rerio* to learn, discriminate, and generalize between the letter category "A" and the number category "2," the same categorical discrimination

Table 1 Summary of the results of the training session

Variable	Experiment 1				Experiment 2				Experiment 3			
	ANOVA			t-test	ANOVA			t-test	ANOVA			t-test
	Species	Rew. Stim.	Interac.	Overall	Species	Rew. Stim.	Interac.	Overall	Species	Rew. Stim.	Interac.	Overall
N trials	p = .02	ns	ns	--	ns	ns	ns	--	ns	ns	ns	--
Time till learning	ns	ns		--	ns	ns	ns	--	ns	ns	ns	--
IoS 1st	ns	ns	p = .04	p < .001	ns	ns	ns	p < .001	ns	ns	ns	p < .001
IoS tot	ns	ns	ns	p < .001	ns	ns	ns	p < .001	ns	ns	ns	p < .001
IoS 1 st – confirm.	ns	ns	ns	p < .001	ns	ns	ns	p < .001	ns	ns	p = .01	--
IoS tot –confirm.	ns	ns	ns	p < .001	ns	ns	ns	p < .001	ns	ns	p = .05	--

N trials = Number of trials; IoS 1 st = Index of Success considering the first choice; IoS tot = Index of Success considering the total amount of choices; IoS 1 st – confirm = Index of Success considering the first choice in the confirmation session; IoS tot – confirm = Index of Success considering the total amount of choices in the confirmation session; Rew. Stim. = Rewarded Stimulus; Interac = Species x Rewarded Stimulus interaction; Overall = one-sample t-test on the overall performance of both species against the chance level; ns = not significant; -- = test not applied

Table 2 Summary of the results of the generalization session

Variable	Experiment 1		Experiment 2		Experiment 3	
	ANOVA - Species	Overall	ANOVA - Species	Overall	ANOVA - Species	Overall
Freq. Choices	ns	--	p=.04	--	ns	--
IoS 1st	ns	ns	ns	ns	ns	ns
IoS tot	ns	p=.04	ns	ns	ns	ns
Local Corner	p=.03	--	ns	p=.02	ns	ns

Freq. Choices = Frequency of choices; IoS 1 st = Index of Success considering the first choice; IoS tot = Index of Success considering the total amount of choices; Overall = one-sample t-test on the overall performance of both species against the chance level; ns = not significant; -- = test not applied

that has been investigated in non-human primates such as *Macaca arctoides* (Schrier et al. 1984).

Experimental subjects

The experimental subjects used in the study were 27 naïve fish, 12 adult male *X. eiseni* and 15 adult male *D. rerio* (two of which did not reach the established learning criterion of 70% correct choices in two consecutive daily sessions) from the same facility of Experiment 1. Six *X. eiseni* and eight *D. rerio* were trained with the letter as the positive stimulus; in contrast, six *X. eiseni* and seven *D. rerio* were trained with the number as the positive stimulus. Twelve out of 15 *D. rerio* specimens reached the learning criterion, and 10 of them also completed all the generalization tests. One specimen died of natural causes during the training. The reduction in the number of animals reaching the test phase was due to the lack of response during the test trials, conducted under extinction conditions (with the doors closed), On the other hand, all the *X. eiseni* specimens reached the learning criterion.

Apparatus, stimuli, and procedure

The apparatus used was the same as that described for *Experiment 1*. The stimuli were 30 numbered pairs each consisting of a reproduction of the letter “A” and the number “2”, and differing by the font type, i.e., the typeface, including both Serif fonts (“with serifs”) and Sans-Serif fonts (“without serifs”), as shown in Fig. 5. Each experimental subject was trained using 20 of these stimuli (randomized into three different combinations); for the generalization test, the remaining 10 stimuli were used, which had never been reinforced before during the testing phase. The same experimental procedure as in *Experiment 1* was adopted.

Results

Training

Descriptive statistics are reported in Fig. 6a. The two-way ANOVA with Species (*X. eiseni* vs. *D. rerio*) and Type of Rewarded Stimulus (A vs. 2) (both as between-subjects factors) on the number of trials needed for learning showed no significant effect (Species: F=1.43, p=.24, Type of Rewarded Stimulus: F=0.01, p=.89; Species x Type of Rewarded Stimulus: F=2.28, p=.08). Also the two-way ANOVA on time till learning showed no significant effect either (Species: F=0.82, p=.37; Type of Rewarded Stimulus: F=0.68, p=.41; interaction: F=0.05, p=.81).

The same two-wayANOVA was also run by considering the index of success on the first choice and on the total amount of choices (Fig. 6b). No significant effect emerged in either analysis (First choice: Species F=0, p=1, Type of Rewarded Stimulus F=0.70, p=0.41, interaction F=0.17, p=.67; Total amount of choices: Species F=0.01, p=.89, Type of Rewarded Stimulus F=0.96, p=.33, interaction F=0.31, p=.58). All data were thus considered together in a further analysis to test whether the overall performance was better than chance. A one-sample t-test against the chance level showed significance for both the first choice (t (23)=16.26, p<.001, d' = 3.32) and the total amount of choices (t (23)=18.24, p<.001, d' = 3.73).

The ANOVA to ascertain learning effectiveness with Species (*X. eiseni* vs *D. rerio*) and Type of Rewarded Stimulus (A vs 2) showed no difference between species either on the first choice (Species: F=0.30, p=.84; Type of Stimulus Rewarded: F=0.03, p=.84; interaction: F=1.81, p=.19) or on the total amount of choices (Species: F=0.09, p=.76; Type of Stimulus Rewarded: F=1.38, p=.25; interaction: F=0.76, p=.39). The follow-up one-sample t-test (against chance) considering all the data together showed a significant effect for both the first choice (M=0.77, SE=0.02; t (23)=13.61, p<.001, d' = 2.78) and the total amount of choices (M=0.78, SE=0.02; t (23)=12.89, p<.001, d' = 2.63).

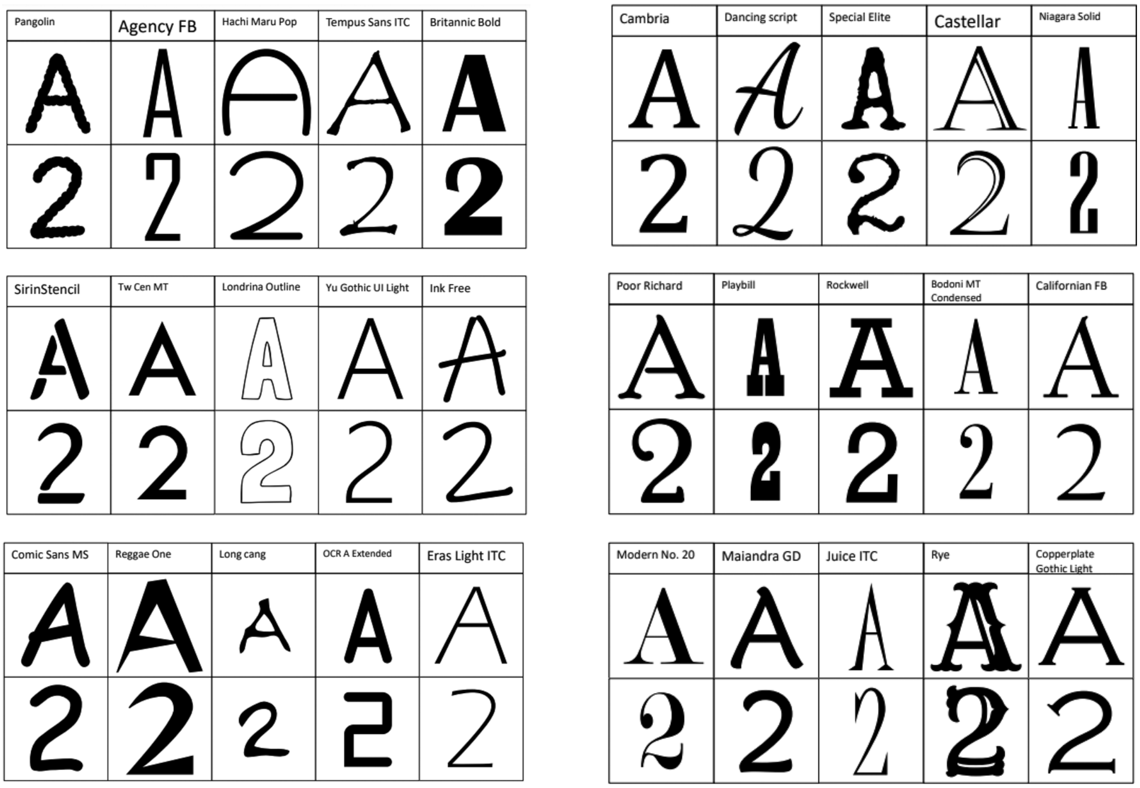

Fig. 5 Experimental stimuli used for Experiment 2, "A versus 2". Each column lists the pairs of stimuli consisting of the letter "A" and the number "2," along with the corresponding font. The typefaces were selected from those available in the word processing programs Microsoft Word and Google Docs

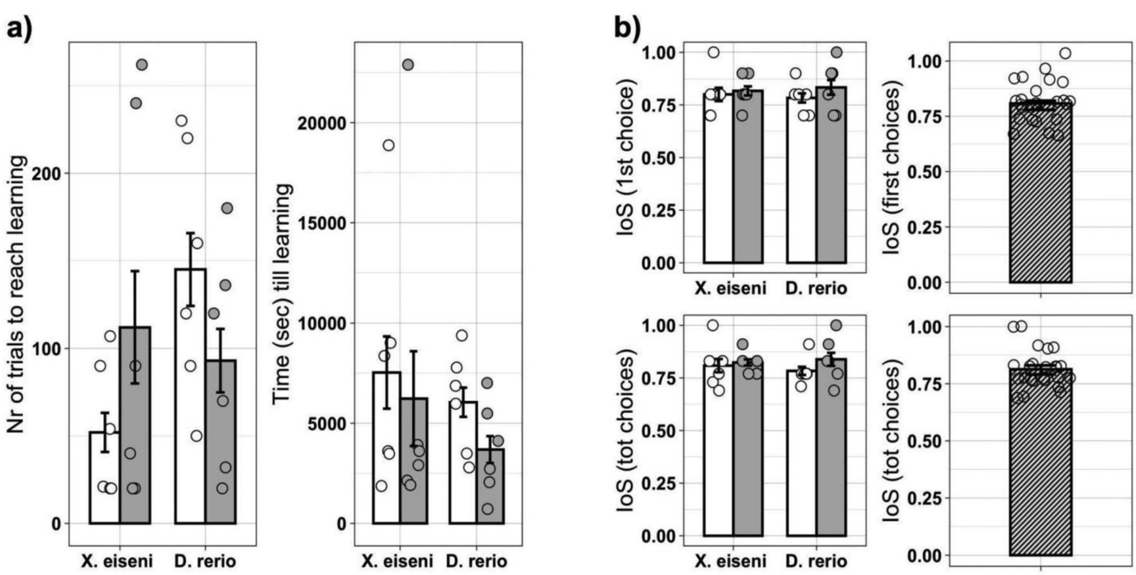

Fig. 6 Data for the Training. (**a**) Fish performance in reaching learning for A (white) and 2 (gray) as a rewarded stimulus. Points represent individuals' performance; bars represent mean standard errors; (**b**) Index of success both as a function of rewarded stimulus (A = white, 2 = gray) and species (left column) and as overall performance (right column). IoS = index of success. Points represent individuals' performance; bars represent mean standard errors. The upper row reports the data for the first choice, whereas the lower row the data for the total amount of choices

Generalization test

All fishes that reached the learning criterion (i.e., 12 *X. eiseni* and 12 *D. rerio*) underwent the generalization test. Of these, all subjects except two *D. rerio* completed it. The analytic approach was identical to Experiment 1.

Frequency of choices

The one-way ANOVA showed a significant effect ($M_{X.\ esieni}$= 41.25 (SE = 4.11) vs. $M_{D.\ rerio}$ = 55.30 (SE = 4.95), F = 4.40, p=.04).

Index of success

Descriptive statistics are reported in Fig. 7a. The one-way ANOVA showed no significant effect either on the first choice (F = 0.22, p=.64) or on the total amount of choices (F = 0.22, p=.64). Thus, data from the two species were jointly considered in a further analysis to test whether the overall performance was better than chance. A one-sample t-test against the chance level showed no significant effect for either the first choice (t = −0.23, p=.81), or the total amount of choices (t = −1.17, p=.25), indicating no generalization to the test.

Motor behavior

The ANOVA considered the index of choices of the local corner (for the full time) as dependent variable and the species (*X. eiseni* vs. *D. rerio*) as between-subjects factor. The analysis showed no significant effect (F=.25, p=.61). A one-sample t-test against chance jointly considering the data for the two species showed a significant effect (M=.56, SE=.02, t (21) = 2.36, p=.02, d' = 0.50), indicating a preference for the local corner.

Performance of the best and the worst subjects

Considered together, the subjects with the highest level of performance (i.e., index of success ≥ 0.55 during the generalization test; 5 *X. eiseni* (fish 4, 6, 7, 8, 9) and 2 *D. rerio* (fish 6, 9) showed an overall performance better than chance (first choices: $M_{index\ of\ choice}$ = 0.74, SE = 0.07; total amount of choices: $M_{index\ of\ choice}$ = 0.70, SE = 0.06) (first choice: V = 28, p=.02; total amount of choices: V = 28, p=.02), with no significant differences between species (first choice: χ^2 (1) = 0.03, p=.84; total amount of choices: χ^2 (1) = 0.15, p=.69). The same analysis run on the subjects with the worst performance (i.e., index of success ≤ 0.45 during the generalization test; 4 *X. eiseni* (fish 1, 2, 10, 12) and 2 *D. rerio* (fish 2, 7)) revealed a performance below chance (first choices: $M_{index\ of\ choice}$ = 0.27, SE = 0.05; total amount of choices: $M_{index\ of\ choice}$ = 0.31, SE = 0.06) (first choice: V = 0,

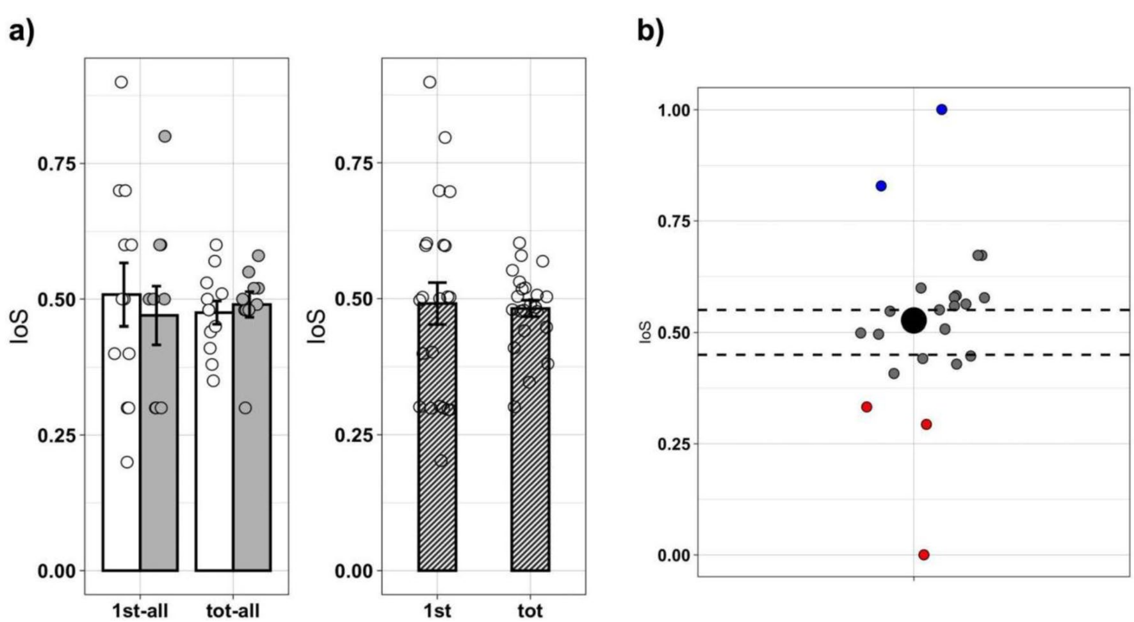

Fig. 7 Data for the Generalization. (**a**) Index of success as a function of the time considered, both separately for species (left panel, white = *X. eiseni*, gray = *D. rerio*) and as overall performance (right panel). IoS = Index of Success; 1 st = first choice in the total amount of time; tot = total amount of choices in the total amount of time. Points represent individuals' performance; bars represent mean standard errors; (**b**) Index of success for single subjects highlighting the best and worst individuals. The dashed lines represent the 0.45 and the 0.55 thresholds; the big black point represents the overall mean; the small points represent subjects' performance; the blue and the red points represent the best and worst subjects with respect to the z-score criterion

p=.03; total amount of choices: V = 0, p=.03) and no species differences (first choice: χ^2 (1) = 1.37, p=.24; total amount of choices (χ^2 (1) = 1.92, p=.16)).

Possible inter-individual variability was further evaluated by transforming the index of success for the total choices in the 30-seconds period into z-scores. Subjects with a score ≥ 0.1 and ≤ −0.1 were identified as the best and the worst, respectively. One *X. eiseni* (fish 7) and 1 *D. rerio* (fish 6) were classified as best and 3 *X. eiseni* (fish 1, 10, 12) as worst. Because of the small numerosity, no statistical analysis was conducted. Data are represented in Fig. 7b.

The results are summarized in Tables 1 and 2. Together, the results of the training showed no difference between species in the number of trials and the time needed to learn. Considering the data from the two species together, fish did better than chance at the level of both the first and the total amount of choices. Considering the performance in the test phase, frequency of choices was higher for *D. rerio* than for *X. eiseni*. Differently, the Index of Success did not show any significant effect except for when the performance of the best subjects was considered, in which case the performance was better than chance at the level of both the first and the total amount of choices. Finally, with regard to motor behaviors, irrespectively of the species, the fish preferred to choose the local corner, and opted always for a movement directed toward the corner.

Experiment 3: categorical inter-species discriminative learning, *Xiphophorus maculatus* (Platy) vs. *Barbus barbus* (Barbel)

The objective of this experiment was to assess the ability to learn, discriminate, and generalize between the silhouettes of two species of teleost fish (Platy vs. Barbel), in *X. eiseni* and *D. rerio*, regardless of variation in prominent morphological characteristics such as dorsal fin size and body orientation. These categorical learning and discrimination were inspired by the comparative work of Roberts and Mazmanian (1988), conducted with pigeons, non-human primates *Saimiri sciureus*, and humans, particularly regarding the simpler discrimination between two different species within the same class of experimental subjects (concrete categorical level). However, in Experiment 3, animal photographs were not used, but silhouettes were computer-generated from realistic images.

Experimental subjects

The experimental subjects were 24 naïve fish, 12 adult male *X. eiseni* and 12 adult male *D. rerio*. Six *X. eiseni* and six *D. rerio* were trained with the Platy (*X. maculatus*) as the positive stimulus, while the other six *X. eiseni* and six *D. rerio* were trained with the Barbel (*B. barbus*) as the positive stimulus. Ten out of 12 *X. eiseni* completed the experiments, while two specimens died of natural causes during the training. Seven out of 12 *D. rerio* successfully completed the experiments, reaching the learning criterion. The fish used were from the same population as described in *Experiment 1*.

Apparatus, stimuli and procedure

The apparatus and the general procedure were the same as in *Experiments* 1 and 2. Regarding the stimuli, 4 numbered pairs of laminated stimuli (side = 3.5 cm) were used for the training phase, and one pair for the testing phase. Each pair consisted of one stimulus depicting the silhouette of an *X. maculatus* individual (distinguishable by its more rounded caudal fin) and one depicting the silhouette of a *B. barbus* individual (Fig. 8, training). Pairs of stimuli differed in the size of the dorsal fin and the orientation angle of the body (0°, 50°) as shown in Fig. 8. The pair of silhouettes used during the test phase, on the other hand, had intermediate dorsal fin size and a body orientation (25°) (see Fig. 8, test). The stimuli were created using Blender (version 2.8), a cross-platform 3D graphics software.

Under a preliminary experimental setup, the silhouettes used were black and fully filled. Three individuals of *X. eiseni* were trained with these stimuli, with the ‘Platy’ stimulus specifically reinforced. None of the subjects were able to complete the training, exhibiting signs of stress (e.g., freezing behavior), which led to the experiment being interrupted and the stimuli being replaced with an outline-only version.

Results

Training

Descriptive statistics are reported in Fig. 9a. The two-way ANOVA with Species (*X. eiseni* vs. *D. rerio*) and Type of Rewarded Stimulus (Platy vs. Barbel) (both as between-subjects factors) on the number of trials needed for learning showed no significant effect (Species: F = 3.82, p=.07, Type of Rewarded Stimulus: F = 0.07, p=.78; Species x Type of Rewarded Stimulus: F = 0.12, p=.72). Similarly, the two-way ANOVA on time till learning showed no significant effect either (Species: F = 3.07, p=.10; Type of Rewarded Stimulus: F = 1.06, p=.32; interaction: F = 1.76, p=.20) (Fig. 9a).

The same two-way ANOVA was run also by considering the index of success on the first choice and on the total amount of choices (Fig. 9b). No significant effect emerged

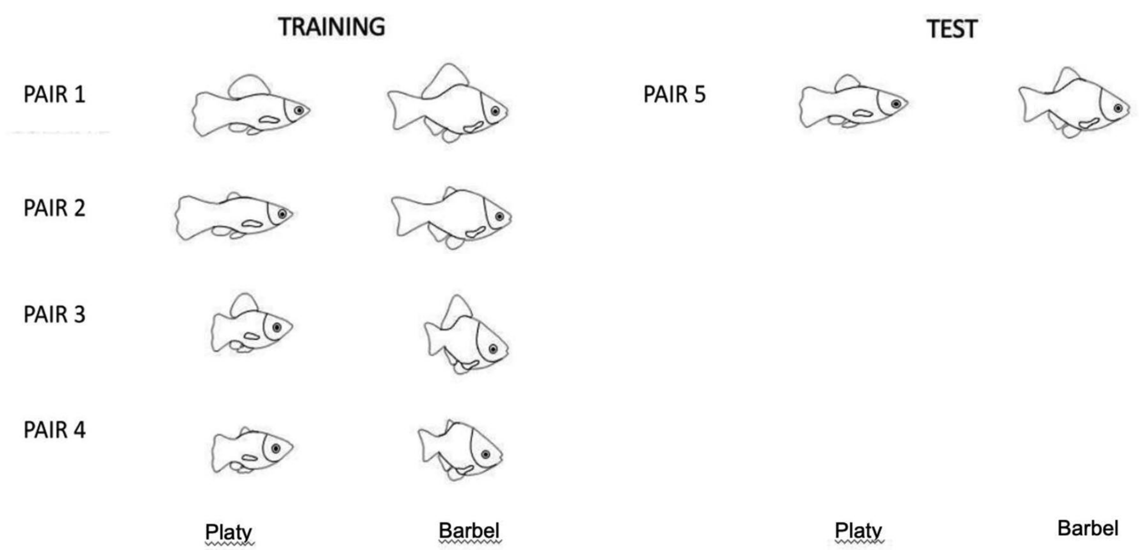

Fig. 8 Representation of the stimulus pairs used in Experiment 3, "Platy versus Barbel". Pairs 1 and 2 differ from each other in the size of the dorsal fin (large or small) but both are presented with a lateral body orientation (0°). Pairs 3 and 4 differ from each other in the size of the dorsal fin (large or small) but both are presented with a transverse body orientation (50°). The pair 5, used during the test, represents an intermediate variant of the characteristics of the four pairs used in the training phase (medium dorsal fin, transverse body orientation of 25°)

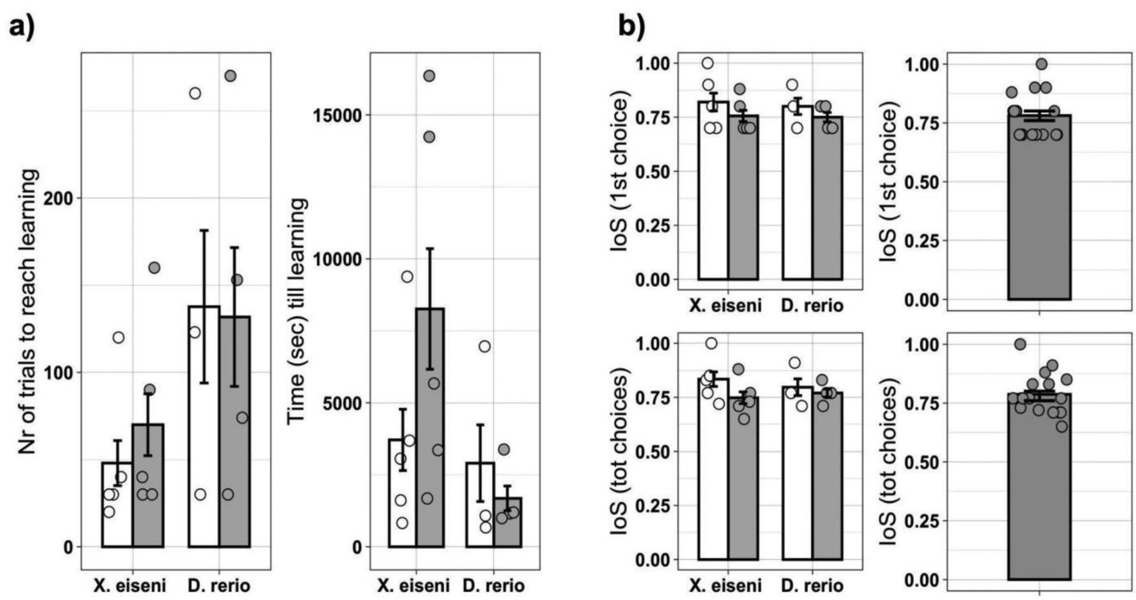

Fig. 9 Data for the training. (**a**) Fish performance in reaching learning for Platy (white) and Barbel (gray) as a rewarded stimulus. Points represent individuals' performance; bars represent mean standard errors; (**b**) Index of success both as a function of rewarded stimulus (Platy = white, Barbel = gray) and species (left column) and as overall performance (right column). IoS = index of success. Points represent individuals' performance; bars represent mean standard errors. The upper row reports the data for the first choice, whereas the lower row the data for the total amount of choices

in either analysis (First choice: Species $F = 0.11$, $p = .73$, Type of Rewarded Stimulus $F = 1.49$, $p = 0.24$, interaction $F = 0.02$, $p = .88$; Total amount of choices: Species $F = 0.04$, $p = .83$, Type of Rewarded Stimulus $F = 2.04$, $p = .17$, interaction $F = 0.45$, $p = .51$). All data were thus considered together in a further analysis to test whether the overall performance was better than chance. A one-sample t-test against the chance level showed significance for both the first choice ($t\ (16) = 12.37$, $p < .001$, $d' = 3.00$) and the total amount of choices ($t\ (16) = 13.52$, $p < .001$, $d' = 3.28$).

The ANOVA to ascertain learning effectiveness showed a significant Species by Type of Stimulus Reward interaction ($F\ (1, 13) = 7.09$, $p = .01$, $\eta^2_p = 0.35$). Post-hoc t-test comparisons (p-values fdr corrected) showed that the differences between the two rewarded stimuli was significant for *D. rerio* ($M_{\text{Platy}} = 0.93$, $SE = 0.05$ vs. $M_{\text{Barbel}} = 0.72$, $SE = 0.05$,

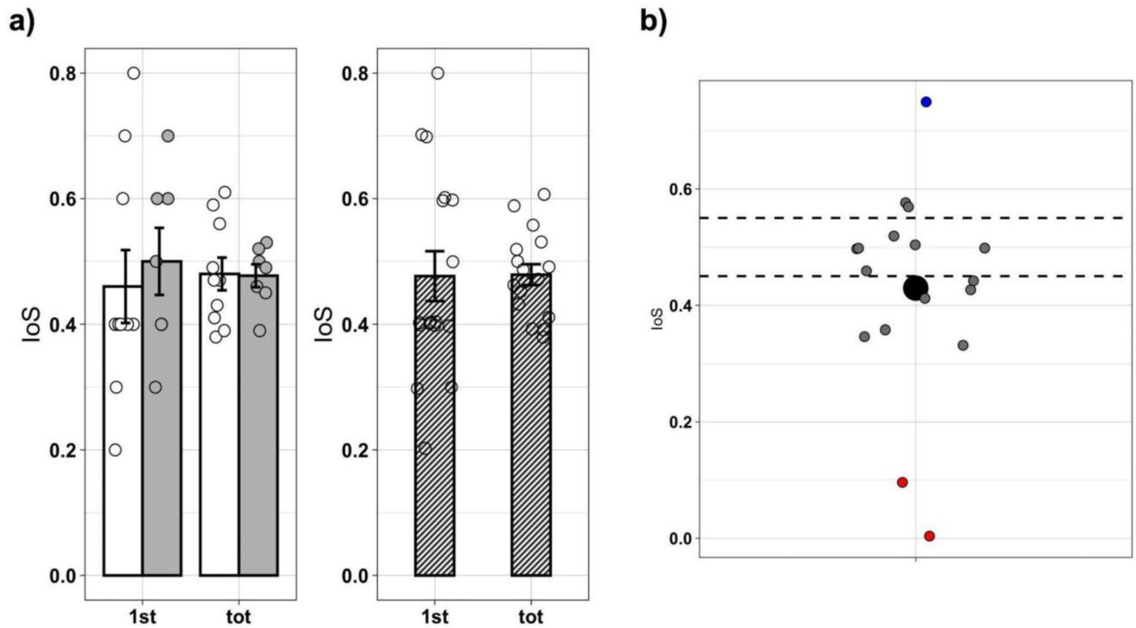

Fig. 10 Data for generalization. (**a**) Index of success as a function of the time considered, both separately for species (left panel, white = *X. eiseni*, gray = *D. rerio*) and as overall performance (right panel). IoS = Index of Success; 1 st = first choice in the total amount of time; tot = total amount of choices in the total amount of time. Points represent individuals' performance; bars represent mean standard errors; (**b**) Index of success for single subjects highlighting the best and worst individuals. The dashed lines represent the 0.45 and the 0.55 thresholds; the big black point represents the overall mean; the small points represent subjects' performance; the blue and the red points represent the best and worst subjects with respect to the z-score criterion

p=.01), but not for *X. eiseni* (M_{Platy} = 0.78, SE=0.13 vs. M_{Barbel} = 0.84, SE=0.11, p=.46). The same ANOVA on the total amount of choices showed that the interaction was on the boarder of significance (F (1, 13)=4.66, p=.050, η^2_p=0.26). Post-hoc t-test comparisons failed to show significant differences (*X. eiseni*: M_{Platy} = 0.79, SE=0.13 vs. M_{Barbel} = 0.84, SE=0.09, p=.50; *D. rerio*: M_{Platy} = 0.91, SE=0.08 vs. M_{Barbel} = 0.74, SE=0.07, p=.10).

Generalization test

All fishes that reached the learning criterion (i.e., 10 *X. eiseni* and 7 *D. rerio*) underwent the generalization test. The same statistical approach used in Experiment 1 was adopted.

Frequency of choices

The one-way ANOVA showed no significant effect ($M_{X.\ eiseni}$= 46.00 (SE = 6.23) vs. $M_{D.\ rerio}$ = 47.57 (SE = 5.63), F=0.03, p=.86).

Index of success

Descriptive statistics are reported in Fig. 10. The one-way ANOVA showed no significant effect either on the first choice (F=0.23, p=.63) or on the total amount of choices (F=0.006, p=.93), indicating no generalization to the test. Thus, data from the two species were jointly considered in a further analysis to test whether the overall performance was better than chance. A one-sample t-test against the chance level showed no significant effect for either the first choice (t=−0.59, p=.56), or the total amount of choices (t = −1.27, p=.22).

Motor behavior

The ANOVA considered the index of choices of the local corner (for the full time) as dependent variable and the species (*X. eiseni* vs *D. rerio*) as between-subjects factor. The analysis showed no significant effect (F=0.03, p=.85). A one-sample t-test against chance jointly considering the data for the two species showed a significant effect (M=.58, SE=.02, t (16)=3.22, p=.005, d' = 0.78).

Performance of the best and the worst subjects

The subjects with the highest level of performance (i.e., index of success≥0.55 during the generalization test; 2 *X. eiseni* (fish 1, 6) and 1 *D. rerio* (fish 7)) showed no significant effect either for the first choice ($M_{\text{index of choice}}$ = 0.77, SE = 0.03, V=6, p=.25) or the total amount of choices ($M_{\text{index of choice}}$ = 0.63, SE=0.05, V=6, p=.25), but this result might be also due to the low numerosity. As it was also taken into account in the previous two experiments, the same analysis run on the worst subjects (i.e., index of success ≤ 0.45 during the generalization test; 6 *X. eiseni* (fish 2, 3, 4, 6, 8, 10) and 2 *D. rerio* (fish 2, 6)) showed a performance below chance (first choices: $M_{\text{index of choice}} = 0.25$, $SE = 0.05$; total amount of choices: $M_{\text{index of choice}} = 0.30$, $SE = 0.05$; first choice: $V = 0$, $p = .007$; total amount of choices: $V = 0$, $p = .007$) and no species differences (first choice: χ^2 (1) = 1.77, $p = .18$; total amount of choices: χ^2 (1) = 0.44, $p = .50$).

Possible inter-individual variability was evaluated by transforming the index of success for the total choices in the 30-seconds period into z-scores. The best and worst subjects were identified as those with a score ≥ 0.1 and ≤ −1, respectively. One *X. eiseni* (fish 7) was classified as best and 2 *X. eiseni* (fish 2, 3) as worst. Because of the small numerosity, no statistical analysis was conducted. Data are represented in Fig. 17.

The results are summarized in Tables 1 and 2. Taken together, the results of the training showed no difference between species in the number of trials and the time needed to learn. Considering the data from the two species together, fishes did better than chance at the level of both the first and the total amount of choices. Of note, in the confirmation session, *D. rerio* did better with the Platy than with the Barbel stimulus, whereas *X. eiseni* performed equally with the two types of stimuli. When considering the performance in the test, neither frequency of choices nor the Index of Success did not show any significant effect. Finally, with respect to motor behaviors, irrespectively of the species, fish preferred to choose the local corner, and opted always for a movement directed toward the corner. The analysis of best and worst subjects' performance suggested possible individual differences.

Discussion

Across the three experiments, the ability of *Xenotoca eiseni* and *Danio rerio* to learn and generalize discriminations between pairs of visual stimuli belonging to distinct symbolic or naturalistic categories - G vs. 0, A vs. 2, and Platy vs. Barbel silhouettes - was evaluated. The alphanumeric characters (G/0, A/2) were informed by previous findings on figural discrimination and amodal completion (Guthrie 1983; Sovrano and Bisazza 2008; Sovrano et al. 2022a, b), while the naturalistic stimuli in Experiment 3 allowed testing of figural processing.

Learning performance across experiments

In all three experiments, the majority of subjects reached the learning criterion (≥ 70% correct choices). Notably, *X. eiseni* consistently showed strong learning performance, reaching the criterion in all tasks, while *D. rerio* showed greater variability - particularly in Experiment 3, where fewer individuals succeeded. In Experiment 1, but not in Experiment 2 and 3, *X. eiseni* required significantly fewer training trials than *D. rerio*, suggesting a task-specific advantage. This difference aligns with prior findings on species-specific motor strategies and sensory cue prioritization (Sovrano and Bisazza 2008; Sovrano et al. 2020; Baratti and Sovrano 2023; Santacà et al. 2019, 2021b). Across all experiments, response latencies and accuracy during training and confirmation phases did not differ significantly between species.

Generalization performance and motor patterns

The generalization results diverged across experiments. Only in Experiment 1 (G vs. 0) did both species, particularly *X. eiseni*, shows clear evidence of generalization to novel stimuli of the same category, but only when analyzing the full test duration (120s for *X. eiseni*, 60 s for *D. rerio*). In Experiments 2 and 3, generalization performance was at chance level for most subjects, with only a few individuals exhibiting categorical abstraction (5 *X. eiseni* and 2 *D. rerio* in Experiment 2; 2 *X. eiseni* and 1 *D. rerio* in Experiment 3). This suggests that the ability to generalize categories is both task- and species-dependent, possibly linked to the discriminability of the stimuli and the species' visual processing traits (cf., Sovrano et al. 2020). The G vs. 0 discrimination appears more accessible to *X. eiseni*, while A vs. 2 and naturalistic shapes presented greater challenges for both species. A recurring pattern across all experiments was the increased motor activity of *D. rerio*, especially evident in Experiments 2 and 3. While this did not impair learning, it may have affected generalization performance by reducing deliberate, goal-directed attempts - suggesting a potential link between hyper-arousal and diminished features-linked transfer in contrast to the more measured behavior of *X. eiseni* (cf., Sovrano et al. 2020). Both species consistently exhibited a center-to-corner movement strategy during testing. While this strategy was associated with successful learning during training, it appeared to limit generalization. This seems consistent with prior spatial cognition studies showing that perimeter-based strategies are more effective in geometric tasks (Baratti and Sovrano 2023; Baratti et al. 2023). Another recurring strategy was the use of the previously rewarded "local corner", particularly evident in Experiments 2 and 3, toward which both species showed a significant bias. In contrast, in Experiment 1, this was observed only in *D. rerio*. Importantly, the use of this spatial strategy did not seem to interfere with generalization in Experiment 1, but may reflect a fallback behavior when perceptual cues are less salient.

Considerations on learning and generalization across species and experiments

The G vs. 0 discrimination may be particularly salient or cognitively accessible, being the only condition where both learning and generalization were achieved by both species. Interestingly, with our design, the stimulus pairs changed across trials but remained within the same category, and both species reached the learning criterion in most cases, suggesting reinforcement-driven abstraction of common perceptual features. The main exception came from *D. rerio*, with 10 individuals failing to learn, possibly due to their lesser reliance on vision compared to other modalities (Lazzari et al. 2014; Santacà et al. 2019, 2021a). Generalization failure could stem from multiple factors, including high visual variability of training stimuli, which might have made abstraction difficult — especially for non-ecological and monochromatic stimuli —as well as reliance on exemplar-based rather than prototype-based representations (Smith et al. 2016) or photographic learning of individual stimuli (Mackintosh 1983).

Stimulus features and perceptual salience

Compared to prior studies using ecologically relevant stimuli (Shluessel et al. 2012; Volotosky et al. 2022), our use of abstract, non-natural categories may have raised task difficulty. Even in Experiment 3, the use of black-and-white fish silhouettes instead of full-color or realistic images may have reduced salience, particularly for *D. rerio*, which is sensitive to color cues (Gatto et al. 2020). The success in Experiment 1 may be linked to the particular perceptual salience of the stimuli used: the closed vs. open shape distinction (0 vs. G) resembles conditions in previous amodal completion studies (Sovrano and Bisazza 2008; Sovrano et al. 2022a, b) and may have provided a simple yet effective cue for categorization. Still, even if success in G vs. 0 was based on the presence/absence of an opening in the upper portion rather than abstract category formation, perceptual cues and abstract processing are not mutually exclusive. A perceptual "trigger" may support categorization by enhancing salience (cf., Guthrie 1983).

Individual variation and decision-making strategies

Individual-level data revealed that some fish could generalize learning to new exemplars, suggesting the presence of categorical abstraction in at least a subset of individuals. Differences between "exploration" (novelty-seeking) and "exploitation" (choosing familiar stimuli) strategies were evident, aligning with known individual personality differences in fish cognition and behavior (e.g., Braga Goncalves et al. 2023; Luchiari and Maximino 2023; Lucon-Xiccato 2024). In the figurative task (Platy vs. Barbel), more animals selected novel stimuli over same-category ones (3 vs. 8), suggesting a stronger tendency toward exploration, potentially due to the social relevance of the silhouettes. These patterns imply that while some individuals may form category-based representations, others rely on exploratory behaviors, affecting overall population-level performance.

Alternative strategies

Across experiments, during generalization fish showed a strong tendency to choose the previously reinforced corner in recall trails, especially in Experiments 2 and 3. This "local corner" strategy might perhaps suggest reliance on spatial or procedural memory rather than visual discrimination when stimuli became less salient or more complex. In *D. rerio*, olfactory cues may have contributed to this strategy (Madeira and Oliveira 2017; Namekawa et al. 2018), possibly helping fish identify the previously rewarded door through water flow gradients or scent traces, though this remains speculative. Notably, Experiment 1 saw successful generalization despite partial use of this strategy, suggesting that perceptual salience still plays a key role.

Motor patterns

Both species showed a consistent preference for direct center-to-corner movements across all phases, deviating from the perimeter-based strategies observed in spatial geometry tasks with rectangular arenas (Baratti et al. 2023). This may reflect an adaptation to the square testing environment, which lacks the directional and metric cues present in rectangular settings (Baratti et al. 2022; Sovrano et al. 2018, 2020). While this movement strategy may have supported task performance during learning, it did not predict success during generalization.

Conclusions and future directions

These findings show that both species can discriminate complex visual stimuli, though consistent generalization was rare. Categorical discrimination and generalization abilities in teleost fish are modulated by the properties of the stimuli, species-specific perceptual and behavioral traits, and possibly the cognitive load of the task. While *X. eiseni* showed more consistent generalization abilities, *D. rerio* displayed higher motor activity that may interfere with deliberate categorization. Future research might perhaps explore: Enhancing stimulus salience (e.g., size, color, Gatto et al. 2020), modifying environmental geometry (e.g., square vs. rectangular setups; Baratti et al. 2021, 2023), investigating the role of multi-sensory integration, the potential sex-related cognitive differences and individual personality traits in learning and categorization strategies, also in light of the growing interest in sexual and individual differences in fish cognition within the international scientific community.

Overall, these results contribute to a growing body of evidence on conceptual processing in non-mammalian vertebrates, supporting the use of teleost models in comparative cognition research.

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Data availability Research data are available in submitted Supplementary Excel files.

Declarations

Competing interests The authors declare no competing interests.

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