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Impact of social rearing-environment on performance in a complex maze in females of a cichlid fish

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ABSTRACT

Spatial orientation is an important skill as it improves, for example, foraging, localisation of recourses, predator avoidance or navigation. Habitat complexity positively affects spatial abilities in various fish species with a more complex environment promoting learning ability. However, to what extent a complex social environment affects cognitive abilities in fishes has received less attention. Here, we investigated differences in maze performance of adult females of the West African cichlid fish *Pelvicachromis taeniatus*, which had been reared and maintained either in a group or in isolation from an early age on. Fish had to master the route through a maze in order to gain a food reward. Our results indicate marked differences in performance contingent upon social rearing-environment: isolation fish ran successful trials (i.e. locating the food reward) significantly more often than group fish and were faster during trials, also in a reversed maze. However, the number of mistakes did not differ between isolation and group fish and the time needed to relocate the food reward did not diminish with elapsed training days. In a second experiment, the activity of group and isolation fish was analysed in an open field test. Here, isolation fish were less active than group fish. We discuss different possibilities for performance differences of group and isolation fish including enhanced cognitive abilities of isolation fish, motivational/emotional differences and hyperactivity.

1. Introduction

Spatial orientation plays an important role in foraging, localisation, predator avoidance and navigation in many animal species (Shettleworth, 2001; Brown and Krause, 2006), since it allows to relocate objects efficiently, e.g. a food source, territory or mate (e.g. Spritzer et al., 2005; Cheng et al., 2006; Batty et al., 2009). It is a crucial fitness-relevant cognitive trait, because it enables individuals to adapt to a changing environment and modify behaviour to changing circumstances (for a review see Odling-Smee and Braithwaite, 2003; Sherry, 2006). Habitat complexity positively influences cognitive abilities such as learning and memory (e.g., Odling-Smee et al., 2008). Furthermore, social experience also influences social and non-social behaviour (for a review see Taborsky, 2016). In mammals, which serve as models for the study of human mental diseases, the social environment crucially affects development and (social) behaviour. For example, early social deprivation causes abnormal aggressive behaviour (Toth et al., 2008, 2011), increased anxiety (Ros-Simo and Valverde, 2012), hyperactivity (Zhao et al., 2009; Ros-Simo and Valverde, 2012), impairs learning (Bshary et al., 2002; Bianchi et al., 2006; Pritchard et al., 2013; but see Levy et al., 2003) and affects brain development (e.g., Veenema, 2009). Furthermore, early stressors such as malnutrition and maternal separation impair spatial learning in adult humans (Bedi, 2003). The effects of social environment on behaviour and development have also been well studied in birds (e.g. Adkins-Regan and Krakauer, 2000; Gersick et al., 2012) and fishes (Ichihashi et al., 2004; Moretz et al., 2007). For instance, the social environment experienced by individuals was suggested to affect cognitive behaviour and (brain) development in fishes (Gonda et al., 2009; Taborsky et al., 2012). Moreover, social isolation may impair kin recognition (Olsen and Winberg, 1996; Hesse et al., 2012) and result in abnormal social behaviour and reduced growth (for a review see Gómez-Laplaza and Morgan, 2000b, a; Hesse and Thünken, 2014). In addition, fish reared in isolation were more susceptible to stress (Earley et al., 2006) and showed less shoaling behaviour (Paxton, 1996; Hesse and Thünken, 2014).

Fishes are a major group in animal cognition research (e.g., Mackintosh and Sutherland, 1963; Warburton, 1990; Rodriguez et al., 1994; López et al., 1999; Cheng, 2004; Portavella et al., 2004; Vargas et al., 2004; Brown and Krause, 2006; Saito and Watanabe, 2006; Walton and Moller, 2010; Patton and Braithwaite, 2015; Uceda et al., 2015). They have been shown to master complex visual discrimination

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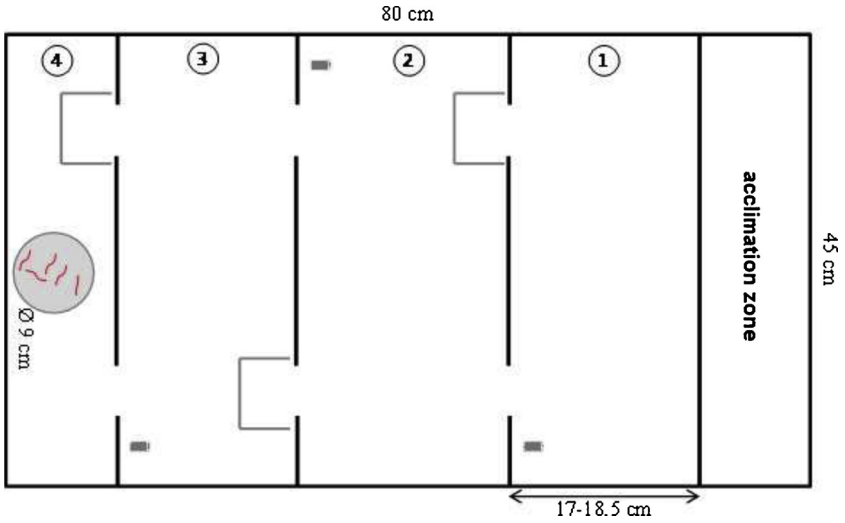

Fig. 1. Experimental tank in stage 2 from above. "Dead-ends" are placed behind one door of each compartment (1–4); open doors are marked with grey filter stones. The last compartment contains the food reward.

tasks, e.g. image/mirror-image discriminations (Gierszewski et al., 2013) and form constancy (i.e., recognising objects from different angles, Schluessel et al., 2014). Furthermore, fishes are able to categorise and recognise objects (von der Emde and Fetz, 2007; von der Emde et al., 2010; Schluessel et al., 2012, 2014; Schluessel et al., 2018). Moreover, quantity discrimination could be demonstrated in several fish species (e.g., Agrillo et al., 2008; Gómez-Laplaza and Gerlai, 2011; Thünken et al., 2014; Mehlis et al., 2015). In fishes, spatial learning abilities differ between river and lake populations (Girvan and Braithwaite, 1998, 2000; Sheenaja and Thomas, 2011), populations from clear and turbid waters habitats (Burt de Perera and Garcia, 2003) and limnetic and benthic species of the threespine sticklebacks (*Gasterosteus aculeatus* complex) (Odling-Smee et al., 2008) since habitat complexity influences cognitive abilities. Shumway (2008) showed that brain size is positively correlated with habitat complexity in cichlid fishes from the Ectodine clade and that spatial memory is enhanced in species originating from a more complex environment. Furthermore, conditions experienced during development may affect cognition and memory (Brown et al., 2003; Kotrschal and Taborsky, 2010). A less complex social environment has been shown to negatively affect brain size in nine-spined sticklebacks (*Pungitius pungitius*, Gonda et al., 2009) and brain size in turn correlates with cognitive abilities in fishes (e.g., Lefebvre and Sol, 2008; Shumway, 2008; Buechel et al., 2018).

In our study, we aimed to investigate the impact of the social rearing environment on cognitive abilities of female cichlid fish *Pelvicachromis taeniatus*. Experimental fish that were reared and maintained either in isolation or in a group from an early age on were trained to solve a maze task and their performance was compared. Maze tasks are a well-established method to investigate cognitive abilities in animals including fishes (e.g., Warburton, 1990; Cain and Malwal, 2002; Sheenaja and Thomas, 2011). Additionally, in an open field test activity was measured in group and isolation fish since isolation has been shown to cause hyperactivity in mammals (Zhao et al., 2009; Ros-Simo and Valverde, 2012). In fishes, effects are ambiguous depending on the species and duration of social isolation (Gómez-Laplaza and Morgan, 1991; Shams et al., 2017). Hyperactivity may affect exploration behaviour and thus confound results of a maze task.

2. Material and methods

2.1. Study animals

P. taeniatus is a small, cave-breeding cichlid from Western Africa (Lamboj, 2006). Our study population originates from the Moliwe River in Cameroon. The bed of the stream contains rocks of volcanic origin and terrestrial plants from the shore grow over the water and create the habitat where *P. taeniatus* is usually found (TT, personal observation). *P. taeniatus* is a socially monogamous species with biparental brood care (Thünken et al., 2010) and mutual mate choice (Thünken et al., 2012). Juveniles live in groups until they reach sexual maturity (Lamboj, 2006).

2.1.1. Experimental fish

All experimental fish were F_2 offspring from wild-caught fish and bred under standardised conditions between April and October 2011 in the laboratory of the Institute for Evolutionary Biology and Ecology at the University of Bonn. Fish were housed in family groups in tanks (50 cm × 30 cm × 30 cm) equipped with an air-driven filter ("gully filter" by HOBBY), gravel and java moss (*Taxiphyllum barbieri*). The water temperature was kept at 24 ± 1 °C and the experimental fish were held under a light/dark regime of 12:12 h. Additionally, up to 6 fish of each family were kept in isolation from an early age on (14 ± 1 days after hatching) and thus housed individually (tank size: 30 cm × 20 cm × 20 cm) under the same environmental conditions. Fish were fed daily *ad libitum* with a mixture of defrosted *Chironomus* larvae, *Artemia* and black mosquito larvae. All tanks were surrounded by opaque plastic sheets to prevent visual contact between inhabitants of different tanks. A grey filter stone was placed in each tank to familiarise test fish with the landmarks used in the experiment. The experiment was performed between May and October 2014.

2.2. Maze task

2.2.1. Experimental set-up

Trials took place in experimental tanks (three were observed simultaneously, length x width x height: 80 cm × 45 cm × 45 cm or 80 cm × 45 cm × 40 cm, respectively, Fig. 1), which were separated into 5 compartments by opaque grey plastic sheets. The first compartment was the acclimation zone and separated from the rest of the tank by a removable plastic barrier. The last compartment contained a food reward (5 red defrosted mosquito larvae placed on a sand-filled plastic Petri dish, Ø 9 cm). Compartments 1–3 were approximately equally sized in all 3 experimental tanks (17–18.5 cm). Plastic sheets separating the different compartments had two doors each (5 cm × 6 cm) allowing the test fish to swim from one compartment to the other. The doors could be closed and converted into "dead-ends" by inserting rectangular boxes made of transparent plastic (Fig. 1). Filter stones (made of grey clay, cylindrical, height approx. 2 cm, diameter approx. 1.2 cm)

were placed as landmarks next to open doors (Fig. 1). Tanks were filled up to a water level of 10 cm with equal parts of tap water and substrate-treated water (see Meuthen et al., 2011). Water temperature was 24 ± 1 °C. Inner surfaces of the tanks were covered with grey plastic to minimise reflections. Tanks were illuminated from above by fluorescent tubes (Osram Lumilux L 58 W). Trials were recorded from above by a webcam (Logitech QuickCam Pro 9000) attached to a tripod.

2.2.2. Experimental protocol

Only adult females of *P. taeniatus* were used in this experiment since females are less prone to stress (SH, personal observation) and tend to be more active (see below). Fish within a group were identified by individual patterns of black dots on dorsal and anal fins. The test fish was netted carefully and introduced into the acclimation zone. After an acclimation period of 15 min, the partition separating the start zone from the rest of the tank was removed by hand allowing the test fish to explore the maze. Behaviour of the test fish was recorded for 45 min. Afterwards, the test fish were netted and put back to their home tanks. Test fish were not fed during the experimental period; their only food source was the food reward offered during trials. Test fish that entered the last compartment usually ate all provided food items. Each test fish was tested daily with approx. 24 h between trials. Tank mates of group fish were fed to satiation when the test fish participated in the trial; leftover food was removed. After each trial, experimental tanks were rinsed and cleaned with tap water and refilled.

All test fish were measured (standard length (cm): from the tip of the snout to the beginning of the caudal fin) and weighed (g) (balance Sartorius LC221S) 4–5 days before the trials started and 1–2 days after they had finished the trials. All test fish were food deprived for 4 days prior to the experiment to increase their motivation to explore the maze.

2.2.2.1. Stage 1: "acclimation stage". During the acclimation stage, all doors were open and had a filter stone placed next to them. The acclimation stage lasted 5 consecutive days and allowed the test fish to habituate to the new environment (days 1–5). Food was offered as a reward in the last compartment to encourage test fish to swim through the maze. Test fish that did not feed during stage 1 were excluded from the following trials and replaced (excluded group fish N = 13, isolation fish N = 4).

2.2.2.2. Stage 2: "training stage". After two days of food deprivation, test fish entered the training stage. In the training stage, "dead-ends" were placed behind one door of each compartment (see Fig. 1). Grey filter stones were placed next to open doors only. The route through the maze ("left-right-left" or "right-left-right", respectively) was constant for each test fish but alternated between individual fish to correct for possible side effects. Filter stones reliably indicated the correct route through the maze. Stage 2 lasted for 12 days (5 consecutive days (Monday to Friday) followed by a 2 day break (Saturday and Sunday) and 5 consecutive days (Monday to Thursday with Friday being the day of the laterally reversed trial)) or until the test fish reached the criterion of optimal performance. A test fish reached the criterion of optimal performance when it needed 200 s or less to find the food reward in four trials (this represented a direct swim through the maze with little or no mistakes). The criterion of optimal performance was based on the results of preliminary tests in which the set-up and time-frame were established. It was similar to the optimal performance criterion in Girvan and Braithwaite (1998), who used a similar set-up for learning experiments in three-spined sticklebacks.

2.2.2.3. Stage 3:"laterally reversed trial". In the laterally reversed trial, "dead-ends" were placed mirror-inverted (i.e., the test fish had now to swim left-right-left instead of right-left-right) but landmarks were still reliable cues and marked the correct route through the maze. The laterally reversed trials took either place on test day 12 or when the test fish had reached the criterion of optimal performance.

2.2.3. Data acquisition

Film recordings were watched blindly with regard to the identity of test fish. Trials began when the test fish left the acclimation compartment (marked by a black line on the bottom of the tank). We recorded whether the test fish entered the last compartment (yes/no, fish entering the last compartment usually fed) and how long they needed after the start of the trial to enter it (s). For test fish entering the last compartment (successful trial = yes), the number of errors was noted. Furthermore, it was noted when a test fish reached the criterion of optimal performance.

2.3. Activity

2.3.1. Experimental set-up

Activity trials were performed independently from the maze task in an open field activity test to control for general differences in activity levels. Male as well as female fish took part in the experiment. Test fish were carefully netted and individually transferred into an experimental tank (30 cm x 20 cm x 20 cm, water level: 10 cm, water temperature 24 °C ± 1.0), which was surrounded by white Styrofoam on all 4 sides to minimise disturbance. Behaviour of test fish was recorded from above using a webcam. Test fish were allowed to acclimatise for 15 min and activity was recorded for 60 min.

After the activity trial, test fish were measured and returned to their home tanks. Activity trials were analysed using the tracking software (Biobserve Viewer^2, St. Augustin, Germany). We defined activity as total track length (cm) of test fish.

2.4. Data analysis

Calculations were performed with the R. 2.9.1 statistical software-package (R Core Team, 2013). Binomial and counting data were analysed using a generalized linear mixed effect model (GLMM; no over-dispersion was detected). Linear mixed effect models (LME) were used when original or transformed data were normally distributed according to Kolmogorov-Smirnov-Lilliefors-tests and showed homogeneous variances according to Bartlett tests. Non-significant factors were removed from the models. Tests of statistical significance were based on likelihood ratio tests (LRT), which follow a χ^2-distribution. Reported p-values of models refer to the increase in deviance when the respective variable was removed.

Body mass and size (standard length) were used to calculate condition factors (CF) for test fish before and after they successfully completed the experiment (Bolger and Connolly, 1989, condition factor = body mass (g) x 100/standard length (cm) ^3) and to calculate the difference (CF after trials – CF before trials). Change in condition index was calculated since group fish ran less successful trials (see results) and lost significantly more body mass in the later stages (LME, LRT: N_{group} = 20, $N_{isolation}$ = 9, χ^2 = 5.000, df = 1, p = 0.025). Additionally, a Pearson's chi-squared test was done to compare differences between treatment groups. P-values are two-tailed throughout.

2.4.1. General analysis and pre-tests for performance in the maze

Overall, 46 test fish took part in the first stage (N_{group} = 33, $N_{isolation}$ = 13). A LME was used to analyse differences in body size between treatments: size (standard length, cm) was the dependent variable and social rearing-environment the explanatory variable, family was entered as random factor. Since isolation and group fish significantly differed in size (LME, LRT: N_{group} = 33, $N_{isolation}$ = 13, χ^2 = 8.715, p = 0.003; mean size ± SD: group fish 4.307 cm ± 0.214, isolation fish 4.131 cm ± 0.175), size was always included in the models. Furthermore, all models listed below were also run with split data sets for isolation and group fish. Size never explained any variation in the dependent variable in either social rearing-environment (p-values

always > 0.1). Additionally, a LME was used to analyse differences in initial CF between treatments, condition factor was the dependent variable and social rearing-environment the explanatory variable, family was entered as random factor. There were no significant differences in initial CF were found (LME, LRT: N_{group} = 33, $N_{isolation}$ = 13, χ^2 = 1.300, df = 1, p = 0.205). Furthermore, we investigated whether the probability that test fish ran a successful trial in stage 2 (fish reached the last compartment yes/no) increases with consecutive trial number. In addition, the interaction between trial number and social rearing-environment was examined. Test fish that had achieved the criterion of optimal performance were excluded from the following analysis (N = 4, all isolation fish) as they differed from the rest of the test fish in the duration of stage 2 (N_{group} = 20, $N_{isolation}$ = 5). A GLMM with binomial distribution was run with trial success (fish reached the last compartment yes/no) as dependent variable, social rearing-environment (GLMM, LRT: N_{group} = 20, $N_{isolation}$ = 5, χ^2 = 6.129, df = 1, p = 0.013), trial number, difference in CF (GLMM, LRT: N_{group} = 20, $N_{isolation}$ = 5, χ^2 = 0.432, df = 1, p = 0.511) and body size (GLMM, LRT: N_{group} = 20, $N_{isolation}$ = 5, χ^2 = 0.049, df = 1, p = 0.825) as explanatory variables. Family and individual were added as random factors. This analysis was done to examine general learning abilities in group and isolation fish. However, neither did the trial number explain a successful trial (GLMM, LRT: N_{group} = 20, $N_{isolation}$ = 5, χ^2 = 0.694, df = 1, p = 0.405) nor was there an interaction between trial number and social rearing-environment (GLMM, LRT: N_{group} = 20, $N_{isolation}$ = 5, χ^2 = 2.556, df = 1, p = 0.111).

2.4.2. Analyses of performance in stage 1, 2, 3 and of activity

For the analyses of performance in stage 1 (acclimation stage), 2 (training phase), 3 (reversed maze) and of activity we run various multivariate linear models (details in Table 1). For analyzing whether performance speed in stage 2 was above or below average, the average performance level of all test fish independent of treatment was calculated by averaging the time needed to enter the last compartment across all test days of stage 2 (N_{group} = 17, $N_{isolation}$ = 9; three group fish explored the maze but did not enter the last compartment during stage 2). Then, we calculated the mean for each individual test fish across test days and compared it to the average performance level. A similar procedure was done for the analysis of latency for leaving the acclimation zone in stage 1 and 2. The average time test fish needed to leave the acclimation zone independent of treatment was calculated by averaging the time needed to leave the acclimation zone across all test days of stage 1 (N_{group} = 32, $N_{isolation}$ = 13; one group fish did not leave the acclimatisation zone and was excluded from analysis) and stage 2 (N_{group} = 20, $N_{isolation}$ = 5). Then, we calculated the mean for each individual test fish across test days for stage 1 and stage 2 and compared it to the average latency. Due to overdispersion, we could not run a GLMM with criterion of optimal performance as dependent variable so a chi-square test was done.

3. Results

3.1. Stage 1: "acclimation stage"

Test fish reared in isolation were more likely to perform a successful trial than group fish (Fig. 2a, Table 2). Size of the test fish did not significantly explain probability to perform a successful trial (Table 2). Reaching stage 2 (test fish progressed successfully from stage 1 to stage 2 (yes/no)) was not significantly influenced by social rearing-environment or body size (Table 3).

3.2. Stage 2: "training stage"

Test fish reared in isolation were more likely to perform a successful trial than group fish (Fig. 2b, Table 2). Neither difference in condition factor nor body size did significantly explain probability to perform a successful trial (Table 2).

Table 1
Multivariate linear statistical models applied to analyse the data.

Model	dependent variable	explanatory variables	random factors	sample size
Question:				
	Stage 1 - Is there a difference in reaching the food compartment between treatments?			
GLMM	trial success?	treatment, body size	family, individual	N_{group} = 33, $N_{isolation}$ = 13
Question:				
	Stage 2 - Is there a difference in reaching the food compartment between treatments?			
GLMM	trial success?	treatment, body size, diff. CF	family, individual	N_{group} = 20, $N_{isolation}$ = 5
Question:				
	Stage 1 - Is there is a difference in reaching stage 2 between treatments?			
GLMM	reaching stage 2?	treatment, body size	family, individual	N_{group} = 33, $N_{isolation}$ = 13
Question:				
	Stage 3 - Is there a difference in reaching the food compartment between treatments?			
GLMM	trial success?	treatment, body size, diff. CF	family, individual	N_{group} = 20, $N_{isolation}$ = 9
Question:				
	Stege 2 - Is there a difference in the average speed in reaching the food compartment between treatments?			
GLMM	performance above average?	treatment, body size, diff. CF	family, individual	N_{group} = 17, $N_{isolation}$ = 9
Question:				
	Stage 2 - Is there a difference in latency leaving the acclimation zone between treatments?			
GLMM	performance above average?	treatment, body size, diff. CF	family, individual	N_{group} = 20, $N_{isolation}$ = 5
Question:				
	Stage 1 - Is there a difference in latency leaving the acclimation zone between treatments?			
GLMM	performance above average?	treatment, body size, diff. CF	family, individual	N_{group} = 32, $N_{isolation}$ = 13
Question:				
	Stage 2 - Is there a difference in the number of mistakes between treatments?			
LME*	number of mistakes	treatment, body size, diff. CF, day of trial, time to reach food	family, individual	N_{group} = 17, $N_{isolation}$ = 9
Question:				
	Stage 2 - Is there a difference in reaching the 200 s criterion between treatments?			
GLMM	200 s criterion?	treatment, body size, diff. CF	family, individual	N_{group} = 20, $N_{isolation}$ = 9
Question:				
	Stage 2 - Is there a difference in CF between treatments?			
LME	CF	treatment	family	N_{group} = 20, $N_{isolation}$ = 9
Question:				
	Is there a difference in activity between treatments?			
LME	track length covered	treatment, sex, body size	family	N_{group} = 60, $N_{isolation}$ = 36

treatment = social rearing-environment; CF = condition factor; diff. = difference in; stage 1 = acclimation stage; stage 2: training stage; stage 3: reversed maze; * boxcox transformed data.

3.3. Stage 3: "laterally reversed trial"

Social rearing-environment significantly explained the probability of successful trials in stage 3 (Fig. 2c, Table 2) but difference in condition factor and body size did not (Table 2).

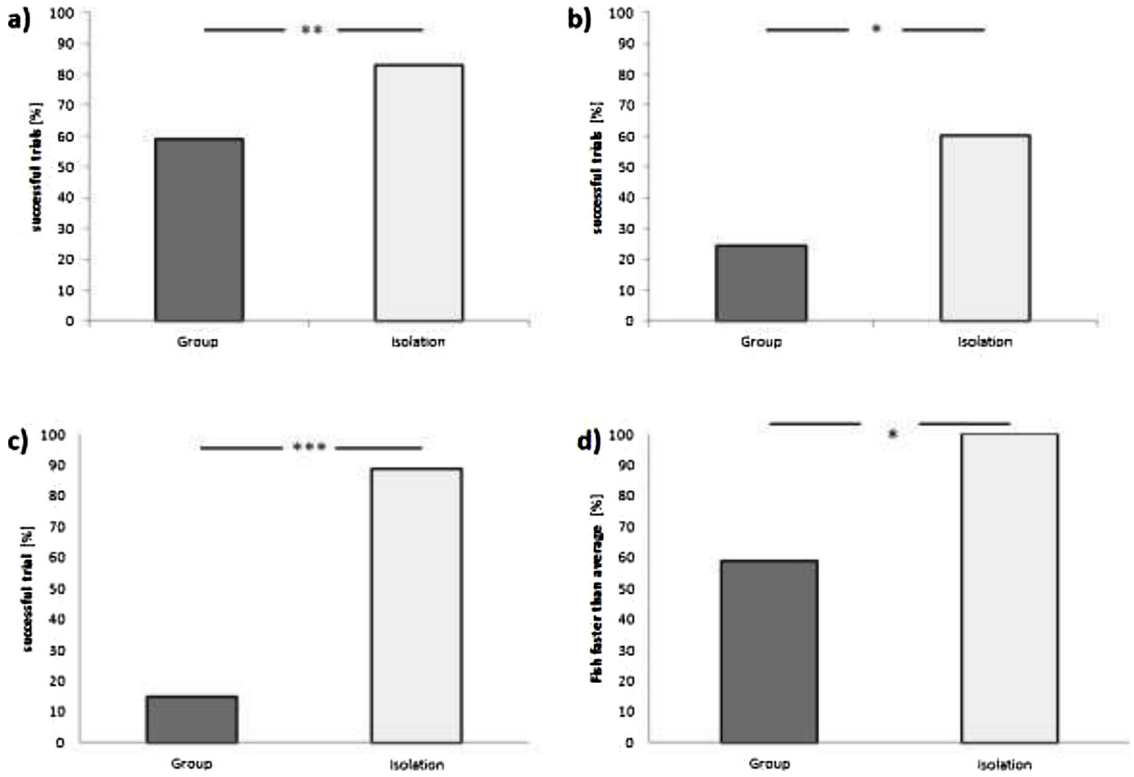

Fig. 2. Proportion of successful trials (%) of group and isolation fish in a) stage 1 (acclimation stage), b) stage 2 (training stage), c) stage 3 (reversed maze), and d) proportion of test fish (%) that were faster than average in locating the food reward in stage 2. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

3.4. Performance differences

Social rearing-environment significantly explained whether test fish were faster than average (mean ± SD = 1476.72 s ± 2591.49) in locating the food reward in stage 2 (Fig. 2d, Table 3) but difference in condition factor (Table 3) and body size did not (Table 3). Neither social rearing-environment (Table 4), difference in condition factor (Table 4) nor body size (Table 4) significantly explained whether test fish left the acclimatisation zone faster than average in stage 1 (mean ± SD = 423.85 s ± 559.89) and stage 2 (mean ± SD = 427.37 s ± 619.56). Number of mistakes a test fish made was neither significantly explained by social rearing-environment difference in condition factor body size, day of trial nor time to reach reward (Table 5).

3.5. Achievement of criterion and optimal performance level

Achievement of the 200 s criterion at least once was significantly explained by difference in condition factor (Table 3, negative correlation). Differences in condition factor were not significantly explained by social environment (LME, LRT: $N_{group} = 20$, $N_{isolation} = 9$, $\chi^2 = 2.836$, df = 1, p = 0.092). Neither social rearing-environment nor body size significantly explained achievement of 200 s criterion (Table 3). Achievement of optimal performance level was explained by social rearing-environment. Isolation fish achieved the optimal level of performance more often than group fish (Pearson's chi-squared test: $\chi^2 = 13.426$, df = 1, $p < 0.001$).

3.6. Activity

Social rearing-environment influenced activity (mean track length: group fish: 3380.123 cm ± SD 2782.91, isolation fish: 2018.575 cm ± 1801.001; LME, LRT: $N_{group} = 60$, $N_{isolation} = 36$, $\chi^2 = 8.948$, df = 1; p = 0.003) whereas sex of test fish (LME: LRT: $N_{group} = 60$, $N_{isolation} = 36$, $\chi^2 = 3.452$, df = 1, p = 0.063) and body size of the test fish (LME, LRT: $N_{group} = 60$, $N_{isolation} = 36$, $\chi^2 = 0.011$, df = 1, p = 0.917) did not. All interactions between explaining variables were not significant ($p > 0.05$).

4. Discussion

We found significant differences regarding spatial orientation and activity between group-reared fish and fish reared in isolation. Isolation fish were more likely to perform a successful trial, i.e. locate the food reward, in all three stages (acclimation stage, training stage, reversed maze stage). Furthermore, the overall performance was better in

Table 2
Results of a binomial GLMM analysing the occurrence of a successful trial of test fish in relation to social rearing-environment, difference in condition factor (CF) and body size in stage 1, 2 and 3; family and individual are included as random factors. Significant effects ($p < 0.05$) are in bold font. Stage 1: $N_{group} = 33$, $N_{isolation} = 13$, stage 2: $N_{group} = 20$, $N_{isolation} = 5$, stage 3: $N_{group} = 20$, $N_{isolation} = 9$.

succesful trial									
		stage 1			stage 2			stage 3	
variable	χ^2	df	p	χ^2	df	p	χ^2	df	p
social environment	9.896	1	**0.002**	5.672	1	**0.017**	4.229	1	**0.039**
difference in CF	n/a	n/a	n/a	0.063	1	0.849	0.226	1	0.635
body size	0.692	1	0.406	0.031	1	0.861	0.168	1	0.682

Table 3
Results of a binomial GLMM analyzing the occurrence of reaching stage 2 (N_{group} = 33, $N_{isolation}$ = 13), whether test fish were faster than average (N_{group} = 17, $N_{isolation}$ = 9) and whether test fish achieved the 200 s criterion at least once (N_{group} = 20, $N_{isolation}$ = 9) in relation to social rearing-environment, difference in condition factor (CF) and body size; family and individual are included as random factors. Significant effects ($p < 0.05$) are in bold font.

	dependent variable								
	reaching stage 2			faster than average			achievement of criterion		
variable	χ^2	df	p	χ^2	df	p	χ^2	df	p
social environment	1.847	1	0.174	6.016	1	**0.014**	2.975	1	0.085
difference in CF	n/a	n/a	n/a	1.044	1	0.307	12.250	1	**< 0.001**
body size	2.610	1	0.106	2.931	1	0.087	0.280	1	0.597

Table 4
Results of a binomial GLMM analyzing whether test fish left the acclimatisation zone (AZ) faster than average (stage 1: N_{group} = 32, $N_{isolation}$ = 13; stage 2: N_{group} = 20, $N_{isolation}$ = 5) in relation to social rearing-environment, difference in condition factor (CF, only stage 2) and body size; family and individual are included as random factors.

	dependent variable					
	left AZ faster than average (stage 1)			left AZ faster than average (stage 2)		
variable	χ^2	df	p	χ^2	df	p
social environment	1.877	1	0.171	0.723	1	0.395
difference in CF	n/a	n/a	n/a	0.192	1	0.665
body size	0.741	1	0.389	2.541	1	0.111

Table 5
Results of a LME analyzing whether number of mistakes in stage 2 (N_{group} = 17, $N_{isolation}$ = 9) was dependent on social environment, difference in condition factor (CF), time to reach reward (s), day of trial and body size; individual nested in family was included as random factor.

	dependent variable Number of mistakes (stage 2)		
variable	χ^2	df	p
social environment	1.765	1	0.184
difference in CF	0.027	1	0.869
time to reach reward	1.639	1	0.200
day of trial	0.132	1	0.717
body size	2.442	1	0.118

isolation fish; they were faster and tended to achieve the 200 s criterion significantly more often than group fish. Only isolation fish achieved the level of optimal performance (four trials under 200 s; cf. Girvan and Braithwaite, 1998). Nevertheless, the number of mistakes in stage 2 did not differ between isolation and group fish nor did they perform better over time. Isolation fish did not more often progress from stage 1 to stage 2 (if they consumed food in stage 1) and did not leave the acclimation zone faster indicating that stress and anxiety levels were similar for both treatment groups. Furthermore, contrary to expectations from mammalian literature (e.g., Zhao et al., 2009; Ros-Simo and Valverde, 2012), isolation fish were less active than group-reared fish in an open field test.

Spatial orientation plays an important role for individual fitness since it allows relocating important resources such as food or mates (Brown et al. 2006). The complexity of the rearing environment affects spatial orientation (Huber et al., 1997; Kotrschal et al., 1998; Roy and Bhat, 2016) but results are ambiguous especially where social deprivation is involved (e.g., Branchi, 2009; Levy et al., 2003; Sterlemann et al., 2010). Here, we investigated whether fish differed in their ability to relocate food in a maze contingent upon their social rearing-environment (isolation vs. group). Our results indicate marked differences already in the acclimation stage (stage 1) between isolation and group fish. Even with all doors open, isolation fish were more likely to run a successful trial than group fish. However, isolation and group fish did not differ in their probability to enter stage 2 (i.e., whether they fed in stage 1 or not) of the experiment implicating that both experienced similar stress levels. Thus, a fearful emotional state preventing group fish from solving the maze task, for example due to unfamiliarity of being alone in a new environment or being separated from their tank mates, can most likely be ruled out. This assumption is supported further by the elapsed time until test fish left the (safe) acclimation zone, which did not significantly differ between isolation and group fish indicating that group fish were equally willing to explore the maze on their own as isolation fish. It has been shown that general stress levels can be negatively influenced by isolation in fishes (Earley et al., 2006), thus isolation fish would be expected to be more stressed than group fish but our results do not support this assumption. Food was used as a ubiquitous reward to ensure isolation and group fish were likewise motivated to solve the maze task. There was no initial difference in condition factor between treatment groups, so hunger levels should have been similar. Taken together, our results strongly indicate equal motivational and stress levels in group- and isolation-reared test fish.

In stage 2, isolation fish were again more likely to run a successful trial. However, trial number, i.e. the number of days fish took part in the trial, did not affect probability for a successful trial and neither did the number of mistakes decrease with a test fish's advancement in the experiment indicating that elapsed time did not improve performance of test fish. A negative correlation between day of trial and number of mistakes was only found in one individual, a group fish. These results are in contrast with other studies in fishes, which report a steady decrease in time needed to solve a maze task and also a decreasing number of mistakes with elapsed training days (e.g. Girvan and Braithwaite, 1998; Sheenaja and Thomas, 2011). Thus, in the present study, fish did not seem to learn the correct route through the maze. The difference in performance between group fish and isolation fish existed right from the beginning. As there were differences in the number of successful trials as well as the time needed to relocate the reward it can be assumed that isolation fish memorised the food location more accurately. In addition, the level of optimal performance, i.e. four trials in less than 200 s, was achieved by isolation fish only. No group fish ran the maze in less than 200 s in four trials and they were also less likely to achieve the 200 s criterion. As hyperactivity of isolation fish might explain the difference in performance and as results from mammalian studies suggested hyperactivity in isolated individuals (e.g., Ros-Simo and Valverde, 2012) and studies in fishes produced conflicting results (Gómez-Laplaza and Morgan, 1991; Shams et al., 2017), we performed an experiment on activity in isolation and group fish. In contrast to results from mammalian studies, isolation did not cause hyperactivity in *P. taeniatus* but decreased activity in test fish. Consequently, faster trials and the achievement of 200 s criterion are likely not the result of hyperactivity in isolation fish.

Studies on the effect of long-term isolation on zebrafish (*Danio rerio*) have found either no influence of social deprivation on locomotor activity (Shams et al., 2015, 2017) or an increased activity (Shams et al., 2018) while short-term isolation decreased activity in angelfish

(*Pterophyllum scalare*, Gómez-Laplaza and Morgan, 1991). It has been suggested that seeking the company of conspecifics is an important motivation to explore a novel environment (Gallup and Suarez, 1980; Gómez-Laplaza and Morgan, 1991). Isolation fish might lack the incentive to locate conspecifics as they are not used to living in a group. It has been demonstrated that both male and female isolation fish spent significantly less time with a potential mate or opponent than group fish indicating a general lack of interest in social interactions (Hesse et al., 2016). Thus, the decreased activity might be a byproduct of their impaired social behavior.

The number of mistakes in stage 2 did not differ between group and isolation fish. Though a difference in the number of mistakes per successful trial would endorse performance differences even further, other studies investigating for example population differences in spatial learning in fishes, also failed to report differences in (mean) number of mistakes depending on population (Girvan and Braithwaite, 1998; Sheenaja and Thomas, 2011). This could indicate that the number of mistakes might not be a sensitive indicator for performance differences. Furthermore, isolation fish tended to achieve the 200 s criterion (i.e. at least one successful trial under 200 s) more likely than group fish. But achievement of the 200 s criterion was significantly explained by difference in condition factor suggesting that hunger seriously affected this variable. Hunger has been shown to affect several aspects of behaviour in fishes for example shoal choice (Hensor et al., 2003; Frommen et al., 2007), foraging (Priyadarshana et al., 2006) and predator response (McCormick and Larson, 2008). However, no other variable we investigated was significantly affected by condition factor and thus, hunger.

In the laterally reversed maze trial (stage 3), dead-ends were placed mirror-inverted but landmarks were reliable cues and marked open doors. Here, isolation fish were again significantly more likely to perform a successful trial than group fish. A successful trial in this mirror-inverted maze indicates that fish used landmarks to navigate through the maze (Girvan and Braithwaite, 1998, 2000). Nevertheless, given the inconsistent learning performance of test fish in stage 2, it is difficult to say whether a successful trial was due to memorised landmarks or not.

Taken together, our results clearly indicate marked differences in spatial orientation ability of isolation and group fish. Isolation fish were more likely to run a successful trial, they were faster, and achieved the 200 s criterion more often than group fish. In short, isolation fish performed better than group fish probably indicating enhanced spatial ability in isolation fish. In mammals, results of the effects of social isolation (e.g. maternal and/or peer deprivation) on spatial learning are ambiguous. Some studies found a decreased performance of isolated animals in spatial learning tasks (e.g., Bshary et al., 2002; Pritchard et al., 2013; Modlinska et al., 2018) while others found no difference (e.g., Levy et al., 2003). However, there is evidence that isolation affects brain development in mammals (e.g., Champagne and Curley, 2005; Veenema, 2009). Since there are to the best of our knowledge no studies on fishes investigating the effects of long-term social isolation on spatial learning, our results elucidate how the social environment shapes cognitive skills. An enhanced performance of isolation fish may be due to differences in brain development. Since we did not compare brain regions between individuals from different environments, assumptions are only hypothetical. Nonetheless, habitat complexity and social interactions can influence brain regions (Hofmann and Fernald, 2001; Pollen et al., 2007). Taborsky et al. (2013) showed that the early social environment affects brain transcription profiles in the cooperatively breeding cichlid *Neolamprologus pulcher*. Furthermore, social environment affected general brain size as well as size of different brain parts in nine-spined sticklebacks (*Pungitius pungitius*, Gonda et al., 2009) with brain parts, which were more important for the individual in question being larger than those of less importance. For example, fish that were reared in isolation could only smell but not see their conspecifics which led to an increased size of the bulbus olfactorius compared to group-reared fish. Kotrschal et al. (1998) also demonstrated that the size of brain parts is dependent on the importance of the part in question for the specific individual. In *P. taeniatus* social skills are negatively affected by social isolation; fish reared in a group perform better in various social tasks, they are less aggressive (Hesse and Thünken, 2014), more willing to cooperate (Hesse et al., 2015) and more interested in potential mates (Hesse et al., 2016). Thus, isolation impairs social competence in our study species. Since in isolation fish no social stimuli were present, cognitive abilities linked to non-social tasks might have become more important compared to group fish, resulting in an enhanced performance of isolation fish in a non-social task. However, further experiments, for example confronting test fish with a simpler plus maze, recording more reliable indicators of stress and comparison of brain parts, are required to clarify this assumption. Furthermore, cognitive abilities of male isolation fish should be investigated since there are differences between male and female cichlids for example in cerebral lateralization (e.g. Reddon and Hurd, 2009).

In summary, our results clearly demonstrate marked differences in performance of group-reared and isolation fish probably due to different cognitive abilities. Isolation fish performed better in the maze task than group fish. Possible explanations for performance differences might be a higher anxiety level in group fish, motivational differences, hyperactivity caused by isolation or enhanced spatial abilities of isolation fish. Our results largely excluded the afore-mentioned possibilities other than differences of spatial ability but further experiments are necessary to determine the exact cause for the enhanced performance of isolation fish.

Compliance with ethical standards

The experiment complies with current laws of the country in which it was performed. Holding and rearing conditions were approved by the City of Bonn Amt für Umwelt, Verbraucherschutz und Lokale Agenda, § 11 Abs. 1 TierSchG. No further permissions were needed. All applicable international, national, and/or institutional guidelines for the use of animals were followed.

Declaration of Competing Interest

The authors state that they have no conflict of interest.

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