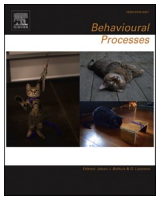
Behavioural Processes 209 (2023) 104885

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Relationship between boldness and exploratory behavior in adult zebrafish

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ARTICLE INFO

Keywords:
Danio rerio
Individual differences
Behavioral profile
Risk-taking
Exploration

ABSTRACT

Behavioral responses vary between individuals and may be repeated in different contexts over time. When a behavioral response set is linked and present regardless of the context, it characterizes a behavioral syndrome. By evaluating how bold and shy (profiles related to risk-taking) individuals perform about exploration and anxiety, we can predict relationships of behavioral syndromes and better understand how different axis of personality is formed. Here we classified the profiles by risk-taking and evaluated their exploration behavior in the open field test. In this context, the two groups showed significant differences in thigmotaxis behavior: bold individuals habituate faster and show decreased thigmotaxis (less anxiety), while shy ones are less prone to leave the security of the side areas of the open tank and present higher anxiety. We emphasized the importance of further investigating the behavior of these profiles in other contexts and the importance of each one for the evolution and fitness of the species, in addition to a better understanding of which behaviors are involved in the behavioral syndromes in zebrafish.

1. Introduction

Throughout life, individuals may suffer the action of several stressors. Depending on the challenges faced, individual behavioral characteristics may be maintained or changed due to phenological plasticity (Dingemanse et al., 2010). Such challenges can be classified as external, such as temperature variation, predation, niche overlap, and pollution, or internal, such as hormonal levels, diseases, genetic factors, etc.) (Koolhaas et al., 2007). While some individuals modify how they deal with stressors and present high plasticity, others are more rigid and present a fixed behavioral pattern that defines their responses. The individual differences within a population result in genetic and behavioral variability (Carere et al., 2010; Carere and Maestripieri, 2013), which may provide benefits in certain situations during the animal's life (Parichy, and Rupia et al., 2009, 2016).

In addition to the individuals' innate characteristics, learning plays an important role in composing the individual personality profile (Parichy, and Rupia et al., 2009, 2016), which presents differences resulting from external factors, such as the environment where they live. Different stimuli, interferent factors and coping situations affect the development and influence the behavioral repertoire one presents. Such individual differences can be observed from the early stages of development (Parichy et al., 2009; Silva et al., 2022), through genetic, metabolic, morphological, anatomical, physiological and behavioral characteristics. However, consistency in behavioral responses between contexts and over time has been receiving attention as researchers have failed to find such robustness (Baker et al., 2018; Thomson, 2017).

Temperament is described by differences in individual behavior that are repeated over time and between situations (Réale et al., 2007). These responses are mainly inherited and appear unaltered throughout the developmental stages (Gosling, 2001). In addition to temperament, other behavioral traits that are shaped by experiences compose the personality and can (or not) persist in different contexts (Gosling and John, 1999; Thomson, 2017). The animals' personalies vary within a continuum, such as boldness, aggressiveness, activity and sociality. The bold-shy dimension is the most studied personality profile, which approaches the individual's propensity to take risks (Wilson et al., 1994).

Bold individuals show a more intense aggressive, exploratory and locomotor behavioral response than shy ones (Roy and Bhat, 2018; Tran and Gerlai, 2013). Together, aligned behavioral responses compose a behavioral syndrome (Sih et al., 2004). In this case, it is expected that an individual with high risk-taking behavior will also show higher levels of activity, aggressive, and exploration responses (Wilson et al., 2010). The syndromes are also correlated to physiological reactions (Koolhaas et al., 1999): thus, bold individuals are characterized by a greater sympathetic and lower HPA (hypothalamus-pituitary-adrenal) responsiveness,

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https://doi.org/10.1016/j.beproc.2023.104885
Received 17 November 2022; Received in revised form 2 May 2023; Accepted 4 May 2023
Available online 5 May 2023

together with being more prone to the routine when compared to shy individuals (Koolhaas et al., 1999; Koolhaas, and Koolhaas et al., 2007, 2010). While the bold and shy profiles described above approach two behavioral extremes, expected to present very consistent features, one of the gaps between these behavioral profiles is how their response correlates in different contexts (Thomson et al., 2020). For profiles to be better understood at the level of individual differences, it is necessary to consider which behaviors relate to different situations, better characterizing bold-shy behavioral profiles (Réale et al., 2007).

The evolutionary continuity between humans and other animals suggests some personality dimensions may be common across species (Carere and Maestripieri, 2013). Characteristics related to the openness of new experiences have been identified in many species, mainly due to their curious behavior, exploration, and interest in new objects and environments (Koolhaas et al., 2007; Carere and Maestripieri, 2013). Thus, the characterization of behavioral profiles based on risk propensity is directly related to impulsiveness in human beings, a potentially risky behavior associated with the use and abuse of psychoactive substances (Evren et al., 2012; Bellot et al., 2022). Thus, this study aims to evaluate the relationship between bold-shy profile and behavioral responses as risk taking and exploration. For translational purposes, we used the zebrafish as an animal model, since it presents high genetic homology with human beings and is suggested as a model for understanding the behavioral and physiological bases of drug effects.

2. Materials and methods

2.1. Ethical statement

The present study was previously submitted to the Ethics Committee of UFRN on the Use of Animals (CEUA) and was approved by evaluation nº 099.002/2018.

2.2. Fish acquisition and housing

We used 60 adult zebrafish (males and females, 6–10 months old) acquired from a local breeding farm (Natal, RN) and transferred to the laboratory. Fish were kept in tanks (80cx25cx40cm; length x width x height; 80 L), at a density of 2 fish/L, with water recirculation and filtration by mechanical, biological, and chemical filters and disinfected by UV light, at a controlled temperature (26–28ºC) and pH (7.1–7.2), and photoperiod of 12 h light, 12 h dark. They were fed twice a day with brine shrimp and commercial feed, half an hour before each experiment. For experimental procedures, the fish were kept in groups of 30 individuals in aquariums measuring 40 × 24 × 20cm for seven days for habituation, under the same initial conditions. After the end of the experiments, all animals were euthanized in a clove oil solution (0.5 ml clove oil/100 ml water), as recommended by the ethics committee.

2.3. Emergence test

The emergence test was performed between 9 am and 12 pm. To separate individuals into two behavioral profiles (bold and shy), a half-white half-black aquarium (40 × 25 × 20 cm) was used. Tank walls were covered with black and white contact paper. A partition covered one side in white and the other in black divided the tank into two parts. The partition contained a guillotined door that allowed fish to move between sides, the door was connected and lifted by a wire, which prevents the fish from seeing the experimenter. For the tests, a group of 15 fish was placed in the black side of the aquarium, where they spent 10 min acclimating. After acclimatization, the door was lifted and fish could access the white side. For each animal that passed from the black side to the white area of the aquarium, the door was closed, and the animal was removed to another aquarium. After 1 min, the door was opened again so that another fish could cross to the white side. This procedure was repeated until 10 fish passed. The first five fish to pass were classified as bold, the next 5 were classified as intermediate and the last five that remained in the black area were classified as shy. The five remaining fish were not used in the further phases (protocol adapted from Tudorache et al., 2013). After the emergence test, the individuals were kept in groups of five of the same profile (bold or shy) in different tanks (30 × 20 × 30 cm) until the open field test, which occurred on the same day. Two fish were lost after the experiments and we ended up with 19 bold and 19 shy individuals, which were used in the analyses.

2.4. Open field test

The open field test was carried out in the afternoon, between 1:30 pm and 5:30 pm, on the same day as the emergence test. For this test, a 50×50×20cm aquarium was filled with water until reached a water column of 10 centimeters. Fish were individually placed in the center of the open field tank and filmed for 10 min. The filming was taken from above, with the camera positioned with a tripod centrally to the aquarium. After filming, individuals were transferred to their home tanks (40 × 20 × 30 cm) in groups of five, according to their behavioral type, under the same initial conditions, until the end of the experiments. For the analysis of behavioral parameters, we used the Zebtrack software (Pinheiro-da-Silva et al., 2017). To evaluate locomotor activity, we analyzed the total distance traveled, and total time stopped (immobility). To evaluate exploration and anxiety-like behavior we analyzed time spent in the central and periphery of the aquarium. To that, the total area of the aquarium was divided into two: the peripheric area was defined as the zone closest to the walls (1 zebrafish body length), and the middle of the aquarium was defined as central zone.

2.5. Statistical analysis

ROUT analysis with a Q value of 1 % was performed to eliminate outliers. The normality of the data was tested with both the Shapiro-Wilk and D'Agostino & Pearson omnibus normality tests. The thigmotaxis data did not pass the normality test so to assess differences between bold and shy we performed a Mann-Whitney test for thigmotaxis analyses of time spent in the central and peripheral areas (non-parametric data). For parametric data in total distance traveled we performed an unpaired *t* test. For total time stopped we performed a Mann-Whitney test. All statistical analyses were performed using PRISM, version 8.0c (GraphPad Software Inc., San Diego, CA, USA). For all tests, $P < 0.05$ was considered statistically significant. Standardised effect sizes (Cohen's d) were calculated.

3. Results

Two shy outliers were identified and eliminated after ROUT analyses. Fig. 1 presents the thigmotaxis response of bold and shy individuals in the open field test. Bold and shy exhibited a statistically significant difference in thigmotaxis response. Bold individuals spent significantly more time in the central zone of the open field than shy ones (Mann-Whitney U=98, $p = 0.0449$, d = 0.85), and shy individuals spent more time in the peripheral zone than bold ones (Mann-Whitney $U = 85$, p = 0.0147, d = 0.88). Fig. 2 presents the locomotor parameters of total distance traveled (Unpaired *t* test, t(36) = 0.7716, $p = 0.4454$, d = −0.25) and total time stopped (Mann-Whitney, $U = 150.5$, $p = 0.9424$, d = 0.02), both analyses were not significative between the profiles bold and shy.

4. Discussion

Our study demonstrated that bold and shy fish differed in exploratory pattern in both tests: emergence test and open field. In the emergency test, bold individuals were the first to explore the new white area, manifesting more risky behavior. In contrast, the high permanence of shy individuals in the dark and known area is related to risk-averse

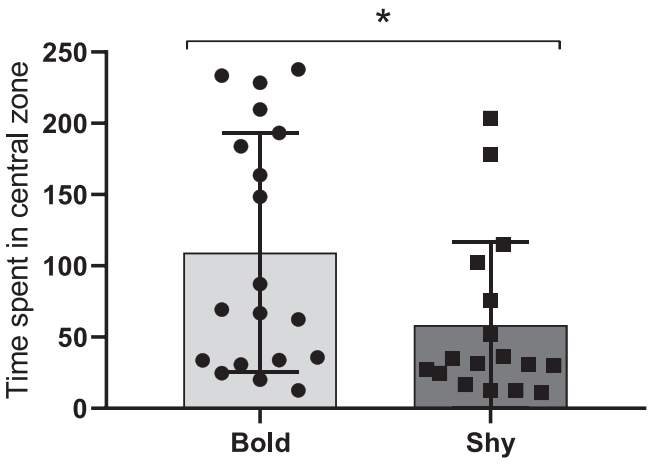

Fig. 1. Thigmotaxis parameter observed for bold and shy zebrafish in the open field test. The graph represents the time spent in the central zone of the open field. Bold and shy profiles were determined by the emergence test. (*) Indicates statistical significance between profiles at $p < 0.05$ (Mann-Whitney test). Bars represent mean values (±SD).

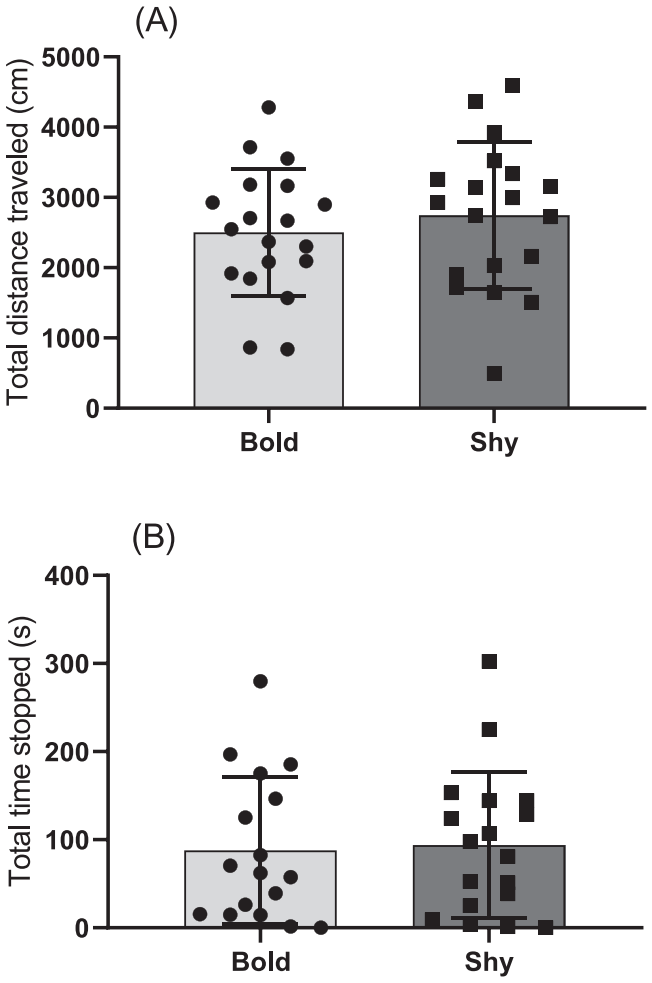

Fig. 2. Locomotor parameters observed for bold and shy zebrafish in the open field test. (A) Total distance traveled and (B) Time stopped. Bold and shy profiles were determined by the emergence test. Bars represent mean values (± SD).

behavior. For the open field, although bold and shy fish showed a great preference for the edges in the open tank, bold animals explored the center of the tank for a longer time, indicating inspection of the environment and typical exploratory behavior in bold profile. In this way, we noticed a behavioral relationship between the two tests. The bold fish exhibited more exploratory behavior and appeared less anxious, as they were the first to venture into a new environment and spent a longer period of time in the central area of the open-field tank. While shy fish showed more avoidant behavior in both environments, they spent more time in the dark area of the aquarium in the emergence test and more time on the edges of the open field. Our results corroborate behavioral differences between boldness and shyness already shown in other research with zebrafish (Alfonso et al., 2020; Baker and Wong, 2019; Baker et al., 2018).

The locomotor parameters (total distance traveled and total time stopped) did not differ between the profiles. Usually, locomotor parameters are measured to evaluate if the stimulus provided would impair the fish's swimming capacity. Some studies have shown that locomotor variables such as increased swimming speed, immobility and erratic movement could indicate anxious-like behavior (Tran et al., 2016). However, Johnson et al. (2023) observed that parameters such as velocity and immobility do not predict anxiety-like behaviors in novel tank dive test, light/dark test and shoaling test. Nevertheless, other studies with open field test relate the pattern of the tank edges' occupation to anxiety parameters, characterizing anxiety behavior in animals exposed to a new environment (Bourin and Hascoët, 2003; Schnörr et al., 2012). In the present study, bold fish showed to be more prone to novelty exploration when seeking the center of the aquarium, while shy fish remained mainly at the edges, which may be related to a higher degree of anxiety during exploration of the new environment.

We observed two important personality traits being expressed in different contexts. When more than one behavior is related and expressed consistently through time or context, it indicates behavioral syndrome (Sih et al., 2004). Our results corroborate other zebrafish studies that show relationship between behaviors in different contexts and over time (Baker et al., 2018; Thomson et al., 2020). Behavioral interactions are essential for understanding the evolution of ecologically important responses (Sih et al., 2003). For example, Ariyomo et al. (2013) found that boldness and aggressiveness have heritable components and so it responds to selection. In another study, with different zebrafish strains (Nadia, TM1 and SH), an activity syndrome was found, with consistent differences between sociability, predator approach and recovery time for the disorder (Moretz et al., 2007). Due to the importance of better understanding the interrelated behaviors between the different profiles, our results emphasize the need to understand better the behavioral syndrome presented in zebrafish, especially in risk-taking tests, which are essential for assessing potential threats for the animal's survival in natural habitat. Both profiles have adaptive advantages since they coexist in nature. When considering exploration and risk-taking, bold individuals would be the first to seek and possibly find new resources, such as food, sex partners, and territory. However, they would be more exposed to the risks of the environment, unlike shy, which remains longer in the known environment, remaining protected and avoiding the risk of exposure.

The aim of this study was to determine whether behaviors related to individual differences in zebrafish are repeatable in different contexts. We found that the risk-taking behavior is repeated by both profiles. Bold is more prone to risk-taking and exploration, and shy is more averse to exploration. Thus, we conclude that zebrafish show a relationship between risk-taking and exploration behavior, characterizing a behavioral syndrome. However, we evaluated only one context, and further studies should be carried out to test other types of behavior between the profiles, and other factors that could differ between them, such as the effect of psychoactive substances. For instance, it is important to know whether the profiles maintain their replicability of behaviors when exposed to psychoactive substances, which can alter their behavior

(Araujo-Silva et al., 2020; Dean et al., 2020; Rosa et al., 2018). Furthermore, behavioral studies are needed to understand better evolutionary mechanisms that guarantee species survival.

5. Conclusions

Adult zebrafish may exhibit a behavioral syndrome between risk-taking and exploration. The findings of this study contribute to the understanding of the individual differences of this species and behaviors that may encompass its behavioral syndrome. Bold and shy individuals show consistency in their behaviors analyzed in two different contexts. Bold has a greater risk propensity and exploration of the aquarium areas, different from shy, that presents less risk-taking and is averse to exploration.

Author contributions

Caroline Peripolli dos Santos and Ana Carolina Luchiari confectioned and designed the study. Data collection was performed by Caroline Peripolli dos Santos and Matheus Neves de Oliveira. Caroline carried out the statistical analysis. The first draft of the manuscript was written by Caroline Peripolli dos Santos. Ana Carolina Luchiari and Priscila Fernandes Silva commented on previous versions of the manuscript. All the authors read and approved the final manuscript.

Funding

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) - Finance Code 001.

Conflict of Interest Statement

The authors have declared that no competing interests exist.

Data availability

Data will be made available on request.

Acknowledgements

The authors are grateful to Maria Clara Galvão for her assistance with video analysis. The experiments carried out in this research as well as the study subjects are part of Caroline Peripolli dos Santos's doctoral thesis.

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