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Bolder stickleback fish make faster decisions, but they are not less accurate

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There have been many investigations into consistent, individual differences in behavior (animal personalities), but rather less attention has been given to the possibility that individuals might differ consistently in their "cognitive style," which refers to the way information is acquired, processed, stored, or acted on. Both personality and cognition have important fitness consequences, and it has been proposed that variation in cognition could be functionally related to variation in personality. Here, we test this hypothesis using three-spined sticklebacks (*Gasterosteus aculeatus*) as a model and adopt a classic T-maze with food reward experimental paradigm. We first confirmed that fish choose the correct arm of the maze significantly more than would be expected by chance and that this improves with trial number. We then explored predictors of individual differences in the speed (time to making a decision) and accuracy (whether the first decision is correct) in decision making. We find bolder behavioral types (who tend to be male) arrive at the correct decision sooner than their shyer conspecifics. However, boldness was not related to decision accuracy. Moreover, we did not find any significant difference in fish's improvement in decision accuracy over successive trials according to boldness or sex. This suggests that although bolder fish may acquire information more quickly because they make decisions faster, they do not differ from shyer conspecifics in their decision-making accuracy. The absence of such a trade-off might offer a functional explanation for why, in stickleback fish and many other species, bolder individuals tend to initiate movement and shyer individuals to follow—bold leaders may result in faster group decisions without compromising accuracy.

Key words: behavioral syndromes, decisions, Gasterosteus aculeatus, learning, maze, personality

INTRODUCTION

In the past 10 years, there has been significant development in the field of animal personality research, that is, the study of consistent individual differences in behavior within a species. Research on a broad range of taxa has shown that individuals of the same species exhibit consistent differences over time in boldness, aggressiveness, sociability, activity, and exploratory tendency (Dingemanse et al. 2003; Dall et al. 2004), and these individual differences may correlate across contexts (Dingemanse and Réale 2005; Cote et al. 2011; Rodríguez-Prieto et al. 2011). Such consistent, individual differences in boldness, aggressiveness, activity, and/or exploratory behavior have been referred to as variation in "fast–slow" behavioral types (BTs), and they have been the focus of many investigations (Sih and Del Giudice 2012). In a foraging context, for example, fast BT individuals may experience benefits with respect to resource acquisition if they show greater exploratory tendencies (Nannini et al. 2012) but suffer a higher predation risk because this often leaves them exposed to predator attacks (Huntingford 1976; Ward et al. 2004). Such trade-offs make consistent, cross-context correlations in behavior particularly interesting from an evolutionary perspective.

Rather less attention has been given to the possibility that individuals might differ consistently in "cognitive style," which refers to the way individuals acquire, process, store, or act on information (Sih and Del Giudice 2012). Both personality and cognition have important fitness consequences, and it has been proposed that variation in cognition could be functionally related to variation in personality. Specifically, it is assumed that fast BTs are primarily guided by internal cues, causing them to explore more quickly but less thoroughly, whereas slow BTs predominantly rely on external cues and so take longer to travel through their environment but may pay more attention to external cues. Sih and Del Giudice (2012) recently formalized this general hypothesis suggesting that fast BTs might often be associated with speed over accuracy as a cognitive style. For example, in black-capped chickadees (*Poecile atricapillus*), fast BTs appear to be better at learning discrimination tasks but perform worse when the task is changed compared with slow BTs (Guillette et al. 2009, 2011), and fast exploring guppies (*Poecilia reticulata*) are known to make rapid but less accurate decisions in a spatial memory task compared with slower exploring guppies (Burns and Rodd 2008).

Three-spined sticklebacks (*Gasterosteus aculeatus*) have been used extensively in personality studies where they demonstrate consistency in behavior over time and across contexts (e.g., behavior interpreted as boldness, aggression, activity, or exploration: Bell 2005; Dingemanse et al. 2007; Harcourt, Sweetman, et al. 2009) and learn and respond to environmental features (e.g., water flow direction, or landmarks: Braithwaite and Girvan 2003; Odling-Smee and Braithwaite 2003; Braithwaite and De Perera 2006). This makes the stickleback model ideal for exploring the potential for a link between cognitive decision-making styles and variation in BTs. Here, we test the general hypothesis that bolder three-spined sticklebacks show speed as opposed to accuracy in their cognitive styles (Sih and Del Giudice 2012). We consider three-spined stickleback individual differences along a shy–bold axis that considers an individual's tendency to explore an open environment in search of food and be caught by an experimenter in a net; behaviors that are repeatable over time, and correlated (King et al. 2013).

Using a T-maze with food reward experimental paradigm that has previously been used in a variety of species and contexts (Tolman and Gleitman 1949; Collett et al. 2001; Odling-Smee and Braithwaite 2003; Nørgaard et al. 2007; Sutherland et al. 2009), we first confirm that fish learn to choose the correct arm of the maze. We then go on to explore interindividual differences in task performance, and specifically, whether boldness predicts differences in the speed and/or accuracy of fish decision making. We expected that bolder fish would be quicker to choose an arm of the maze (Prediction 1), but less accurate in their decisions (Prediction 2), in line with the speed–accuracy trade-off proposed by Sih and Del Giudice (2012). Consequently, we expected bolder fish to show poorer learning across trials compared with shyer fish (Prediction 3).

Research has also shown interrelationships among sex, personality, and learning. For instance, males are found to be bolder than females in some instances (e.g., guppies: Croft et al. 2003; Harris et al.

2010; three-spined sticklebacks: King et al. 2013; great tits: van Oers et al. 2005) but not others (e.g., three-spined sticklebacks: Ward et al. 2004; Harcourt 2010), and although male great tits with faster BTs show more flexibility in learning compared with males with slower BTs, females show exactly the opposite relationship (Titulaer et al. 2012). Thus, although the literature does not appear to offer a consensus on the precise nature of the relationships between sex, personality, and learning, these can be predicted in accordance with life-history trade-offs (King et al. 2013), and we have found that bolder BTs tend to be male in the population used in this study (King et al. 2013). Therefore, in all of our analyses, we tested for and controlled for the effect of sex, under the expectation that (bolder) male fish would tend to show faster, but less accurate decision making.

METHODS

Study subjects and housing

We used a laboratory population (N = 48 fish) of three-spined sticklebacks, G. aculeatus, net-caught from Histon and Swaffham Bulbeck areas of the River Cam, Cambridgeshire, UK, in April 2011. Fish were housed together in an aerated and filtered gravel-lined "holding aquarium" (120×40×30 cm) with plastic plants. Temperature was kept at 16°C, and lights were set to 8:16 h dawn–dusk cycle regime, with a 20-min light-change up/down period. Fish were fed defrosted bloodworms (Chironomid larvae) daily. During the experimental period (see below), fish were housed in 48 individual, transparent gravel-lined 2.8-L selfcleaning polycarbonate tanks within a ZAD Series Aquaneering (Aquaneering Incorporated) rack system. Housing in these tanks (which were in 4 rows of 12 tanks, with positions rotated weekly) allowed fish to see each other and ensured all fish were subject to the same water conditions and feeding regime. When the experiments were over, the fish were kept in their holding aquarium and were not used for any further experiments.

Boldness assessment

Prior to taking part in the decision-making task (see below), fish underwent behavioral tests for assessing the proportion of time an individual spent out of cover in search of food (foraging context, e.g., Harcourt, Sweetman, et al. 2009) and the order in which they were net-caught by an experimenter from their aquarium (predation context, e.g., Sneddon 2003). These tests revealed that the time individuals spent out of cover was correlated over 2 test days and that scores for males were significantly higher than females. Also, catch order was negatively correlated with the proportion of time fish spent out of cover, was repeatable 9 months later, and males tended to be caught sooner than females. Full details of these experiments and results are published in King et al. (2013). Using these data, we created a "boldness index" based on these 2 correlated measures (proportion of time out of cover, and catch order). We started by ranking the fish for each of the 2 measures, in reverse order (such that the individual that spent most time out of cover/ was first to be caught was given rank 48, and the fish that spent least time out of cover/was last to be caught was given rank 1); we then computed the sum of these 2 ranks and scaled it by dividing it by 96, giving an index between 0 and 1, where 1 was the boldest fish in our sample (mean ± standard error [SE]: 0.48±0.03; median = 0.51).

Decision-making task

Three-spined sticklebacks are able to learn to follow both egocentric and landmark cues when navigating a simple maze (Odling-Smee and Braithwaite 2003). A T-maze was constructed out of opaque gray plastic with dimensions as indicated in Figure 1. Each of the 3 arms had a removable panel insert with a smaller round entrance that prevented the fish from seeing the contents of the end chambers without entering, as well as providing a clear way to identify fish' choices. Two Panasonic HDC-SD60 high-definition video cameras, each mounted directly above 2 of the mazes, were used to record the movement of the fish. Two experiments were run simultaneously to improve data yield, and all fish were allowed time to acclimatize to the maze in groups (n = 5) for 3h, 3 days prior to the start of the trials. One fish died at the start of the decision making trials, and so, our sample size was reduced to 47 for further analyses.

Before each trial, a bloodworm reward was consistently located in either the left or right arm for each fish, in accordance with the experimental condition to which the fish in question was allocated (left, n = 24; right, n = 23; alternating by fishID number). The order that fish undertook trials within a day was randomized. During a trial, a fish was placed in the "start box" in the central arm of the T-maze and then left in the maze for 10 min. After each trial, the maze was swilled out and refilled with aerated water that had no contact with fish or experimenters. Every fish did 2 trials per day for 2 weeks, with a break in testing lasting over the weekend. We tested for any effect of this weekend break on our measures of interest but did not find any significant results and so all results presented are for the full experiment. By the end of the study, each fish had completed a total of 18 trials. On occasions where fish did not find and consume the food reward in the maze experiments, they were additionally fed in their individual tanks at the end of the experimental day.
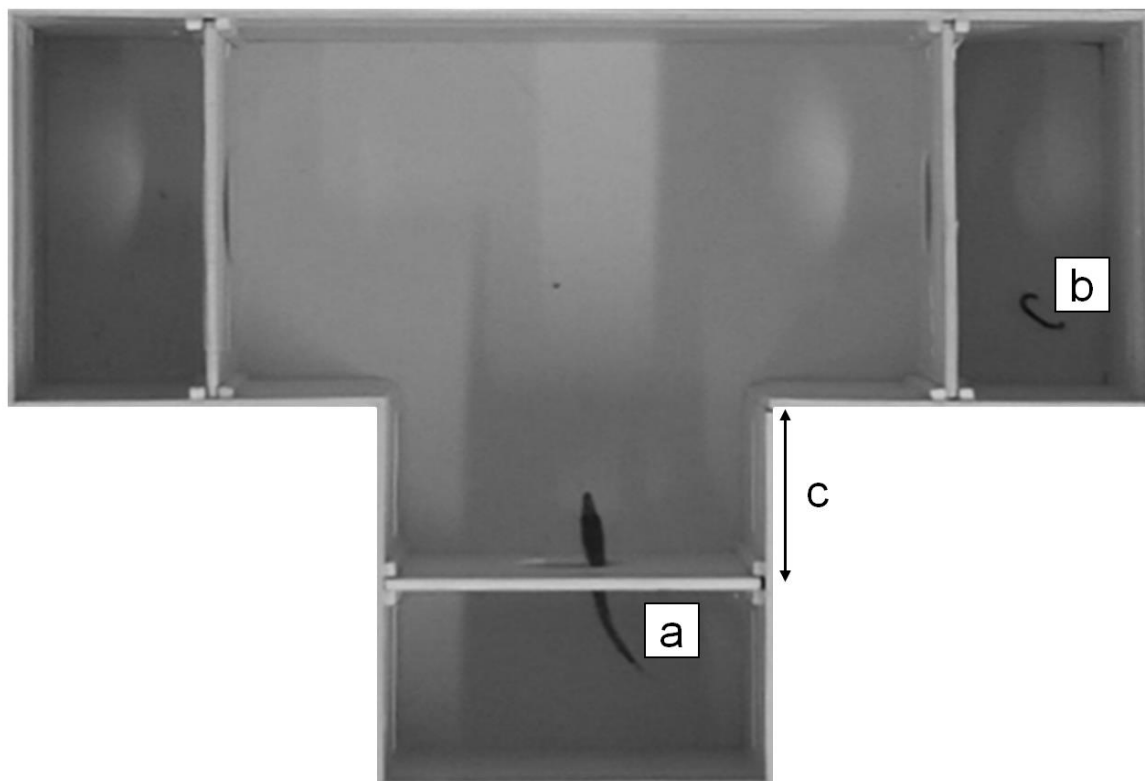

Figure 1. T-maze constructed out of opaque gray plastic. Each of the 3 arms has a removable panel insert with a smaller round entrance that prevented the fish from seeing the contents of the end chambers without entering, as well as providing a clear way to identify fish's choices. (a) The "start box" where fish began the trial. (b) A bloodworm reward was placed in 1 of the 2 arms consistently. (c) The maze had 50 mm wide arms with each box being 25 mm across the short side (scale bar); entry–exit holes were 20 mm in diameter.

Measures of decision speed and accuracy

We were interested in the activity of the fish only once they exited this start box. Therefore, we computed the time to first decision as the time that elapsed between the fish fully leaving the starting box and fully entering either chamber. The time to correct decision was the time taken for a fish to fully enter the correct chamber after exiting the starting box. The fish exited the starting box in every trial but did not make a decision in a median of 3 trials out of 18. We, therefore, define the number of times a fish made a decision as "task engagement," and if a fish engaged with the maze task on every occasion (i.e., made a decision), then this measure is equal to trial number. Accuracy of decision

making was simply whether the fish made the correct decision with its first choice. We further calculated a measure of fish learning: over consecutive trials, fish scored +1 if they their first decision was correct and −1 if their first decision was incorrect. Therefore, positive scores represent learning to move toward the food, a score of 0 suggests no evidence for learning about the food (i.e., chance), and a negative score would suggest that a fish was repeatedly choosing the empty chamber of the maze over successive trials.

Statistical analyses

Simple bivariate statistics and correlation tests were used to explore general patterns of fish decision speed, decision accuracy, and learning. Linear mixed models (LMMs) or generalized linear mixed models (GLMMs) using Markov Chain Monte Carlo estimations were used to assess the predictive capacity of BTs and sex for speed of decisions, accuracy of decisions, and learning. For our analyses of decision speed and accuracy, we ran 2 models, one where our response variable was decision speed (time to first decision: LMM) and another in which our response was decision accuracy (correct or incorrect first choice; GLMM with binomial error structure). We evaluated the effect of boldness (see above), sex (male, female), hiatus in training (pre and post weekend break), and trial number (continuous), which were fitted as fixed effects. Day of trial, trial order, and Fish ID were included as random effects to control for the potential non-independence of individual's choices within and across days. For our analyses of learning, we ran a model with learning score as our response variable (LMM) with trial number as a covariate and the following fixed effects: sex, boldness, trial number (as described above), and task engagement (continuous). Fish ID was included as a random effect. All models were run in MLwiN version 2.28. All tests were 2 tailed, and α was set at 0.05.

RESULTS

General patterns of fish decision-making

Overall, fish chose the correct arm of the maze significantly more than would be expected by chance (one-sample T-test: n = 47, mean proportion of correct decisions = 0.71, SE = 0.030, T = 6.97, P = <0.001; Figure 2a). Over consecutive trials, fish took less time to move towards one arm of the maze after exiting the start box (LMM: Effect [SE] = -0.012 [0.004], Wald = 7.58, P <0.001; Figure 2b), as well as to choose the correct arm of the maze (LMM: Effect [SE] = -0.021 [0.004], Wald = 22.67, P <0.001; Figure 2b). The time elapsed between a first decision to move to an arm, and the decision to move to the correct arm was seen to decline with trial number (Pearson's r = -0.54, n = 18, P = 0.022; Figure 2c) as a consequence of learning over successive trials (LMM: Effect [SE] = 0.288 [0.020], Wald = 209.30, P <0.001; Fig 2d).

Inter-individual differences in decision-making

When controlling for the effects of trial number (above), we found that neither boldness (LMM: Effect [SE] = -0.318 [0.194], Wald = 2.68, P = 0.10) or sex (LMM: Effect [SE] = -0.178 [0.095], Wald = 3.52, P = 0.060) predicted the speed with which fish made their first decision. Similarly, neither boldness (GLMM: Effect [SE] = +0.463 [0.658], Wald = 0.49, P = 0.48) or sex (GLMM: Effect [SE] = -0.179 [0.264], Wald = 0.458, P = 0.500) predicted the accuracy of this decision. However, we did find that bolder fish were faster to arrive at a correct decision (LMM: Effect [SE] = -0.384 [0.194], Wald = 3.910, P = 0.047), and independent of boldness, males were also significantly faster than females in arriving at the correct decision (LMM: Effect [SE] = -0.260 [0.095], Wald = 7.48, P <0.001).

We also investigated the improvement in fish's decision making over successive trials. After considering the effect of trial number (Figure 1), we found that neither boldness (LMM: Effect[SE] = 0.455 [0.490], Wald = 0.861, P = 0.355) or sex (LMM: Effect [SE] = 0.152 [0.243], Wald = 0.391, P = 0.531) were related to the fish learning scores and only 'task engagement', i.e., how often the fish made a decision, positively influenced learning (LMM: Effect [SE] = 0.266 [0.025], Wald = 115.93, P

< 0.001). Also note that boldness and task engagement were not correlated (Pearson's r = 0.13, n = 18, P = 0.404).
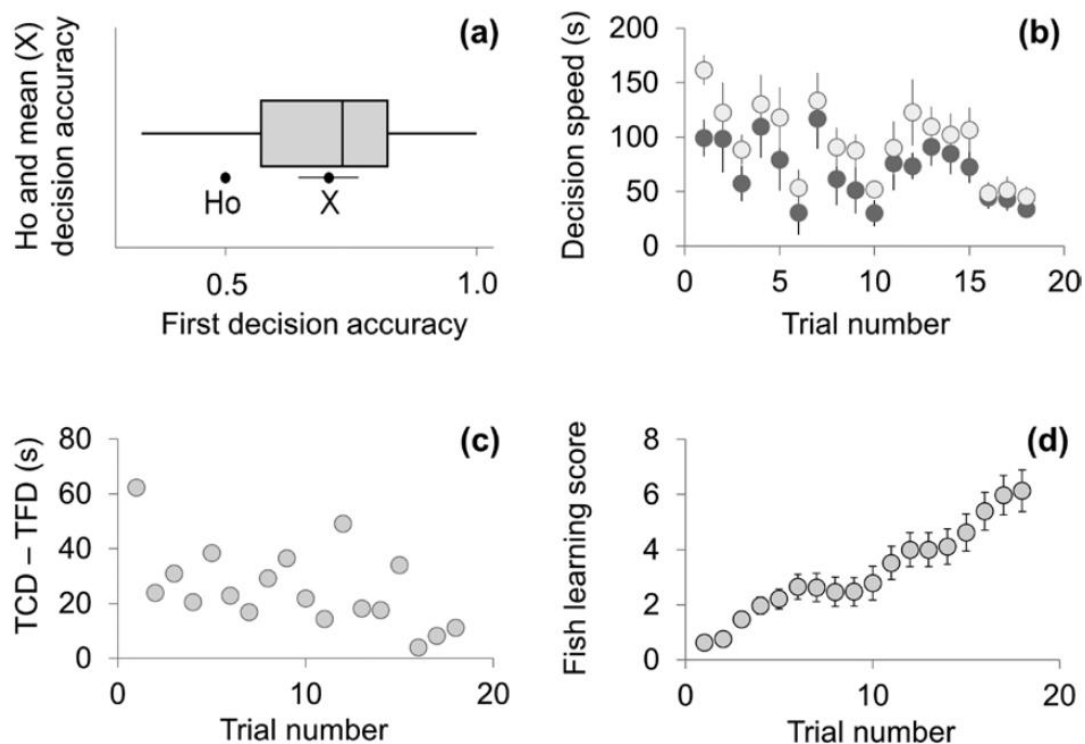

Figure 2 General patterns of fish decision making for n = 47 fish over 18 trials. (a) Box plot illustrating first decision accuracy, showing Ho and 95% confidence interval for the mean. (b) Mean ± SE time taken (s) to make the first decision (TFD, light filled points) and correct decision (TCD, dark filled points) as a function of trial number. (c) The time difference (s) between the TCD and TFD and as a function of trial number. (d) Mean ± SE "fish learning score," which is a cumulative score, where fish score +1 for correct decision and −1 for incorrect first decision over trials.

DISCUSSION

A recent theoretical framework (Sih and Del Giudice, 2012) suggests that faster BTs (bolder, more aggressive, or more exploratory individuals) might differ consistently in 'cognitive style'; exploring their environment more quickly, but less thoroughly, than slower BTs. As a consequence, faster BTs are predicted to make faster, but less accurate decisions (Sih and Del Giudice, 2012). Here, we tested this hypothesis and investigated how three-spined stickleback fish act on information during a simple activity based task – a T-maze experiment with food reward. We found that fish chose the correct arm of the maze significantly more than would be expected by chance, and that the accuracy of their choices was predicted by how many trials they had completed. Controlling for this trial effect, we found no significant differences in the accuracy with which bolder fish made decisions. However, bolder fish did consistently arrive at the correct decision more quickly. Therefore, whilst we find support for our prediction that bolder fish should make faster decisions (Prediction 1), we did not find that they were less accurate (Prediction 2). We also failed to find support for Prediction 3: that shyer fish would show a greater improvement in learning over trials and better retention of information, as we found no significant effect of boldness upon fish learning scores. Together, our findings offer only partial support for the predictions of the cognitive style-behavioural type framework (Sih and Del Giudice, 2012). Bolder individuals do appear to acquire information more quickly, since they made faster decisions, but they were no less accurate in their decision making – at least for our simple activity-based task.

Our findings may have implications for understanding the emergence of leaders and followers as a solution to coordination problems in stickleback fish and other group-living species. These kinds of social roles (i.e. leaders and followers) might be advantageous (Johnstone and Manica, 2011) and leadership roles have been linked to measures of boldness in three-spined stickleback fish, with bolder fish tending to emerge as leaders and shyer fish as followers (Harcourt et al., 2009a; Nakayama et al., 2012a). This leader-follower dynamic also appears to be robust, with the same individuals emerging as leaders repeatedly, a reflection of the consistency of traits over time and across contexts in this species (Nakayama et al., 2012b). In addition, regardless of individual boldness, three-spined stickleback fish associate preferentially with shoals composed of bold fish (Croft et al., 2009; Harcourt et al., 2009b) and we know across different species and contexts, few leaders are required to initiate group movement (Dyer et al., 2009; King et al., 2009; Reebs, 2000). Our results might therefore offer a functional explanation for why bolder fish tend to lead movement decisions in shoals: they can have higher exploratory tendencies, yet do not suffer from the predicted cost to their decision-making accuracy.

Sex was previously shown to be a factor in predicting BTs in this study population of sticklebacks (King et al., 2013) and we did find that male fish (which tend to be bolder), arrived at the correct decisions more quickly, though with no greater or lesser accuracy than females. This result is predicted by life-history trade-offs (i.e. males are predicted to show high risk but potentially high return behaviours: King et al., 2013), but it may also indicate a different way of gathering information in the environment; a notion supported by work with humans showing males tend to focus more on global information, compared to a preference for local, detailed information by females (Bos et al., 2013). This might point toward a more general difference in the regulation of emotion between different sexes or BTs, as shown in experiments with fish (Reddon and Hurd, 2008, 2009) and by both direct and indirect testosterone manipulations at an early age in rats, with higher testosterone being associated with the faster, more global based BT (de Visser et al., 2011).

It is possible that some of our observations were limited by the relative simplicity of the task and that further work could reveal a speed-accuracy trade-off suffered by the male/bold BT. Indeed, a meta-analysis of radial and water maze studies using rats and mice by Jonasson (2004) suggests an advantage for males in spatial tasks and memory in both species. It also appears that there is a difference between rats and mice with females of the latter displaying a slight advantage in some water maze experiments. However, the radial maze tasks are generally more complex and performance of test subjects is influenced by a number of additional factors, including age, strain, training and possibly the conditions in which the animals were raised (Bos et al., 2013). Future work may therefore increase the complexity of the task and alter the salience of cues, and consider the use of social information by testing individuals in a social context. Sticklebacks provide an interesting opportunity for comparative work on this issue: three-spined sticklebacks have been shown to fail to use public information irrespective of their personality type (Harcourt et al., 2010), but nine-spined sticklebacks readily use such social cues (Kendal et al., 2005). Finally, we recognise that we might observe different responses to the maze task depending on what types of cues the fish are using (olfactory versus visual for instance). We did not limit/control bloodworm chemical cues within each trial because we were not concerned with the specific cues fish were using to navigate and make decisions. Rather, we wanted to see how quickly and accurately they would do so. However, it is possible that there are also differences in the types of cue used/prioritised by different personalities and this would be an interesting further avenue to pursue.

Overall, our findings demonstrate that whilst bolder fish may acquire information more quickly, they do not differ from shyer conspecifics in their decision-making accuracy, contrary to the general hypothesis that fast BTs might often be associated with speed over accuracy as a cognitive style (Sih and Del Giudice, 2012). This may offer a functional explanation for why for stickleback fish (and many other species) bolder individuals are more likely to initiate movement and shyer individuals to follow – since it may result in faster group decisions without compromising accuracy. We confirm the finding that bolder BTs sample their environment more quickly, and thus arrive at correct decisions

faster than slower BTs. This adds to the body of empirical data that will enable us to understand the adaptive value in individual differences in the way animals behave and make decisions.

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