



Contents lists available at ScienceDirect

## Animal Behaviour

journal homepage: [www.elsevier.com/locate/anbehav](http://www.elsevier.com/locate/anbehav)

Special Issue: Social Evolution

## Speed–accuracy trade-offs and individually consistent decision making by individuals and dyads of zebrafish in a colour discrimination task

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## ARTICLE INFO

## Article history:

Available online xxx

MS. number: SI-14-00880

## Keywords:

behavioural variation

*Danio rerio*

decision making

foraging

repeatability

social experience

Speed–accuracy trade-offs are well studied in human decision making, but we are only beginning to understand how such trade-offs affect other animals. Similarly, it is poorly understood how consistent individual differences in decision making are influenced by their social context. Here we investigated whether zebrafish, *Danio rerio*, show individual consistency ('personality') in speed–accuracy trade-offs based on a colour discrimination task, and how pairs of fish with distinct personalities make consensus choices. The results showed that zebrafish exhibit between-individual speed–accuracy trade-offs: some fish made 'careful', slow but accurate decisions, while others made swift but less accurate choices. We also found that these decision-making strategies were constant over time: fish retained the same strategy for 3 days. When testing pairs of careful and fast-and-inaccurate individuals, the combined choice strategy was intermediate in speed, but statistically indistinguishable from the careful individual, whereas accuracy of the dyad decision was moderately higher than that of each individual when tested singly, although this was again not significantly different from the more careful individual. For the first time, our study thus demonstrates that two individuals influence one another's speed–accuracy trade-off in decision making.

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When animals are given longer time to gather information, their choices are often more accurate, whereas fast judgments can be more error-prone (Chittka, Skorupski, & Raine, 2009). This correlation, called the speed–accuracy trade-off (SAT), has been studied in human experimental psychology since the 1960s and has been found to affect a wide range of cognitive tasks (Chittka et al., 2009; Pachella, Fisher, & Karsh, 1968; Schouten & Bekker, 1967; Shadlen & Kiani, 2013). Neural mechanisms have been explored in a variety of recent studies (Bogacz, Wagenmakers, Forstmann, & Nieuwenhuis, 2010; DasGupta, Ferreira, & Miesenböck, 2014). In the field of animal perception, there are far fewer studies on SATs, despite their obvious ecological relevance in natural settings. Nevertheless, SATs have been demonstrated in animal decision-making contexts such as visual discrimination (Chittka, Dyer, Bock, & Dornhaus, 2003), scent detection and identification (Uchida & Mainen, 2003), visual predator–prey interactions (Burns & Rodd, 2008; Ings & Chittka,

2008) and nest site selection (Franks, Dornhaus, Fitzsimmons, & Stevens, 2003). However, some other tasks are not affected by SATs, for example, relatively easy perceptual or orientation tasks (Dyer & Chittka, 2004; Mamuneas, Spence, Manica, & King, 2015) or those that can be solved by parallel visual search (Proulx, Parker, Tahir, & Brennan, 2014), and therefore such trade-offs must be explored on a case-by-case basis.

Here we explore SATs in a colour discrimination task of the zebrafish *Danio rerio*, an important model organism in genetics, developmental biology and neuroscience (Grunwald & Eisen, 2002; Lele & Krone, 1996; Mathur & Guo, 2010). Speed–accuracy trade-offs in animals are often explored using visual discrimination tasks (Chittka et al., 2009). Zebrafish have fine visual discrimination abilities and good colour vision (Bilotta & Saszik, 2001; Colwill, Raymond, Ferreira, & Escudero, 2005; Risner, Lemerise, Vukmanic, & Moore, 2006; Spence & Smith, 2008). Here we used two colour signals, one associated with food reward and another with punishment, to test for between-individual SATs in zebrafish.

The exploration of reproducible individual behavioural differences has a century-long and venerable history in the study of social insects (see Jandt et al., 2014; Thomson & Chittka, 2001), and

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more recently, has become a popular topic in vertebrate behavioural ecology, where it is variously referred to as animal personality (Gosling, 2001), behavioural syndromes (Sih, Bell, Johnson, & Ziemba, 2004), animal temperament (Réale, Reader, Sol, McDougall, & Dingemanse, 2007) or coping style (Koolhaas et al., 1999). Interindividual differences have been found for a range of different behaviours in zebrafish (Moretz, Martins, & Robison, 2007; Norton & Bally-Cuif, 2012; Wisenden, Sailer, Radenic, & Sutrisno, 2011). Individual differences in SATs, where some individuals show a 'careful' strategy with, on average, more accurate choices, and others with faster but less accurate choices, were first demonstrated in bumblebees (Chittka et al., 2003); more recently, individual differences in SATs were also explored in studies of fish, but in the tasks employed, trade-offs were not found (Mamuneau et al., 2015; Proulx et al., 2014).

Despite widespread interest in animal personalities, the question of how individuals with different behavioural strategies interact with each other is still relatively poorly understood. Previous studies have examined social interactions in the context of exploration, aggression and dominance (Dingemanse & de Goede, 2004; Verbeek, Boon, & Drent, 1996), investigating how different strategies influence social behaviour. The reverse question: how social context might influence behavioural strategies has been only rarely addressed. Even when animals show consistent personality, social information can influence individuals' strategies (Marchetti & Drent, 2000; van Oers, Klunder, & Drent, 2005). When a group is formed, individual differences may be reduced (Krause & Ruxton, 2002). Certain personality types can be more dominant and change the performance of the group. For example, when travelling with a 'bolder' individual, a 'shy' animal can be more explorative and follow the lead of the bold one (Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009; Schuett & Dall, 2009). 'Safety in numbers' (Hamilton, 1971) can encourage the group to engage in higher exploratory activity compared with single individuals, and such examples can be found in diverse animal groups (Magurran & Pitcher, 1983). The experience of foraging in a group can also alter the animal's strategy even when subsequently tested individually (Weiss, Segev, & Eilam, 2014).

Zebrafish are a shoaling species that often swim in groups, whether in natural habitats or in captivity, and this makes them an excellent model for studying group behaviour (Bisazza et al., 2014; Engeszer, Ryan, & Parichy, 2004; Miller & Gerlai, 2007). Zebrafish in particular have been demonstrated to learn social preferences early in life (Engeszer et al., 2004) and to socially learn alarm reactions to novel stimuli (Suboski et al., 1990). More generally, shoaling fish have demonstrated widespread abilities to socially learn visual foraging tasks (reviewed in Brown & Laland, 2003). Fish shoals, in species such as zebrafish, therefore provide an ideal situation in which to investigate how social context influences individually consistent behaviour.

Here, we tested the consistency in SAT decisions to address the questions of whether consistent individual differences exist in zebrafish, and how they compromise with each other when foraging in pairs. We aimed to answer the following three questions. (1) Is there interindividual variation in the speed and accuracy with which zebrafish solve a colour discrimination task? (2) To what extent is the strategy of individuals consistent over time? (3) How do fish in a minimal group (a dyad) influence each other when they have different strategies?

## METHODS

### Ethical Note

All animal work was carried out following approval from the Queen Mary Research Ethics Committee, and under licence (PPL 70/

7345) from the Animals (Scientific Procedures) Act 1986. All the fish had been bred and reared in the aquarium facility at Queen Mary University of London, licensed by the U.K. Home Office. Care was taken to minimize the numbers of animals used in this experiment in accordance with the ARRIVE guidelines (<http://www.nc3rs.org.uk/page.asp?id=1357>). Specifically, we examined data from pilot studies and studies with other species to carry out a power calculation and assess the minimum number of animals necessary for the expected effect size with power of 0.8.

### Study Animals and Pre-training

A total of 98 adult AB wild-type zebrafish (aged between 6 and 18 months) were tested in one pilot study and three sets of experiments. Prior to the experiment, fish were housed in glass tanks (25 × 20 × 12 cm) in a recirculating system (Aquatic Habitats, Apopka, FL, U.S.A.) at 28 °C (room temperature) with a 14:10 h light:dark cycle. Fish were fed with brine shrimp twice per day or during experiments and pre-training. Two or three days before the experiment, fish were pre-trained in an apparatus that was identical to the actual experimental set-up (Fig. 1) but without colour signals for 20 discrete trials. The purpose of the pre-training was to get the fish accustomed to the signal area and to collect food rewards there. Each fish was first allowed to explore and get used to the holding area of the tank for 3 min. After habituation, the barrier between the holding area and the main space of the tank was lifted and fish were able to investigate the set-up and make decisions. A fish crossing the hole to the signal area (radius of 3 cm) was considered as having made a decision. The mean ± SE body length of the fish was 2.73 ± 0.03 cm ( $N = 98$ ). Thus, the fish were able to pass through the hole without difficulty. The hole was closed with a second barrier when the fish entered either chamber, and a small amount of brine shrimp reward was given (a volume of 0.5 ml of 1-day-old brine shrimp larvae solution containing 112 ± 16 brine shrimp). When fish stopped consuming the food, the hole was opened by lifting the barrier and fish were gradually moved back into the holding area by dipping the barrier into the water in front of the fish and very gently moving it towards the holding zone. Any leftover brine shrimp in the signal area were removed with a pipette. The fish were able to keep the motivation for at least 20 discrete trials. The choices and the investigating time of the fish were recorded. The mean ± SE decision time for a single trial was 34.1 ± 6.6 s, and fish took around 90 min to finish all 20 trials. When a fish showed a persistent bias for a certain position (visited the same chamber for more than seven consecutive trials, which would be significantly different from random choice), or did not enter the chamber for more than 2 h, it was removed from the experiment (seven fish were removed in total; two had a persistent preference for a certain chamber and five stopped foraging during the pre-training).

In a pilot experiment, we tested whether punishment for incorrect choices, in addition to reward for correct choices, was necessary for the fish to solve a colour discrimination test in a single 20-trial training session (10 fish). We used two distinct colours (green and brown) to decrease the difficulty of discrimination. These were set at RGB values of R120 G255 B150 (green) and R200 G150 B100 (brown) using Adobe Photoshop CS2 and printed with an Epson PX-9500 printer and laminated. When choosing between one rewarding colour (green) and one nonrewarding colour (brown, without punishment for incorrect choices), fish chose the colours at random (50% correct choices; mean ± SD = 51.0 ± 6.6% correct choices; one-sample  $t$  test:  $t_4 = 0.343$ ,  $P = 0.749$ ). Only when punishment was introduced (stirring the water in the signal area for 3 s with a net (frame: 2 × 3 cm, depth of net: 2 cm), without actually touching the fish (Reader, Kendal, & Laland, 2003)

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