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

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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.

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 (Mamuneas 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)

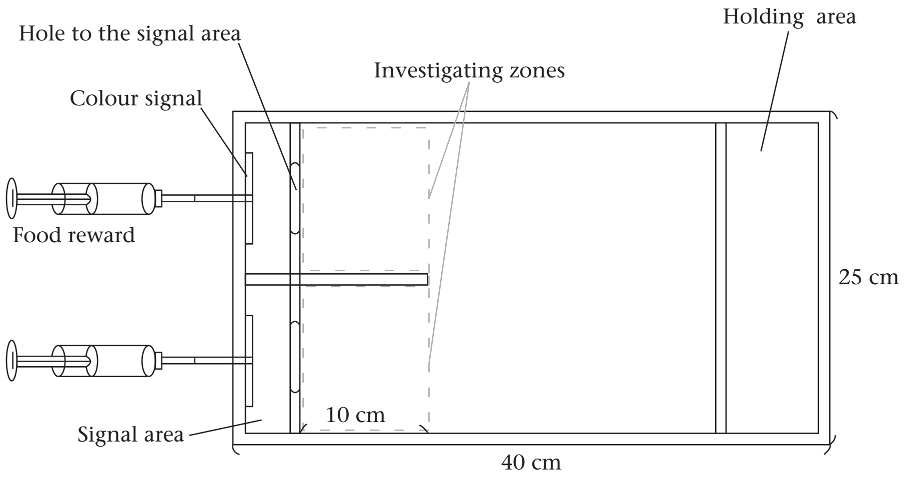

Figure 1. Experimental apparatus for the pilot study, pre-training and all three sets of experiments. Zebrafish were habituated to the holding area for 3 min, and subsequently the barrier was lifted to allow the fish to explore the main space of the tank. When the fish passed through the hole to the signal area, this was considered as a decision. Fish were held in the signal area and given food reward when making correct choices, while punishment (stirring the water) was applied when fish chose the wrong colour. Investigating time was considered as the time spent by fish in the investigating zones and when fish were facing the colour signals.

and the hole to the signal area was blocked with a barrier), the fish chose the rewarded colour significantly more (green = rewarded, brown = punishment; mean = 63.3 + 5.7% correct choices; one-sample t test: $t_4 = 5.099$, $P = 0.007$). This parallels findings from other animal species (e.g. bees), where the method of reinforcement substantially influences colour discrimination performance (Chittka et al., 2003; Wang, Ings, Proulx, & Chittka, 2013). Thus we used both reward and punishment for the following experiments.

Experiment 1: Speed–Accuracy Trade-offs between Individuals in Colour Discrimination

To test for SATs in a colour discrimination test in zebrafish, individuals were trained to associate the colour green with reward and to distinguish a similar hue, turquoise, from the rewarding target. Colour targets were set at RGB values of R120 G255 B150 (green) and R120 G255 B200 (turquoise). We chose similar colours because an easy discrimination task that can be solved 'at a glance' is not likely to be affected by SATs (Dyer & Chittka, 2004). Thirty fish were tested for 20 discrete trials with the same procedure as during pre-training. In addition to receiving a food reward for a correct choice, fish received punishment for an incorrect choice (see above). The positions of the colour signals were randomized in each trial. The choices and decision times of the fish were recorded.

Experiment 2: Test for Individually Consistent Performance

To investigate whether fish showed a stable strategy over time, we tested 15 naïve fish with the same methods as experiment 1 for 20 discrete trials, and repeated the same procedure after 24 and 48 h. The fish received 20 trials per day for three consecutive days, resulting in a total of 60 trials per individual. In this experiment, fish were kept individually between experiments (tanks 22 × 20 × 12 cm). Tank walls were transparent and fish could see other individuals in neighbouring tanks. Since tanks were on a recirculating system, fish could also have had exchanged chemosensory information.

Experiment 3: Decision Making in Pairs

Following the previous experiments, we aimed to determine how fish made decisions in a pair, where members of the pair had different individual strategies. Thirty-six naïve fish were first tested individually with the same procedures as in experiment 1 for 20 trials to quantify their individual strategies when tested alone. The fish were classified as 'careful' or 'fast-and-inaccurate' by comparing their performance with the average decision time and accuracy of all 20 trials for fish tested in experiment 1. Identical results were produced by classifying by decision time or by accuracy.

Fish were then paired randomly into three categories based on their strategies: (1) one careful and one fast-and-inaccurate fish (16 individuals/eight pairs); (2) two careful fish (10 individuals/five pairs); and (3) two fast-and-inaccurate fish (10 individuals/five pairs). Paired fish were housed in separate areas of the same tank with a transparent barrier in the middle. Twenty-four hours after being tested individually, fish were tested in pairs for 20 discrete trials using the same paradigm as before. We avoided the first 2 h after the lights were switched on in order to avoid possible courtship behaviour or male–male competition (Darrow & Harris, 2004; Spence, Gerlach, Lawrence, & Smith, 2008). Because zebrafish are not obviously sexually dimorphic, our pairs were a combination of same-sex and mixed-sex pairs. A previous study found no shoaling preference between wild-type male and female zebrafish (Snekser, Ruhl, Bauer, & McRobert, 2010), but the influence of sex on group foraging would be an interesting area for future study.

Data Recording and Analysis

In the pilot study and in all three experiments, the positions of the fish were recorded with three-dimensional coordinates calculated 50 times/s using two video cameras (SciTrackS, Pfaffhausen, Switzerland) connected to a computer running Trackit 3D software (BIOBSERVE GmbH, Bonn, Germany). In dyad experiments, the tracking software provided live-time tracking, which allowed us to identify the two fish during the experiment. As a backup, for rare cases when fish were temporarily lost by the 3D tracking system, the experiments were also recorded by video camera (JVC GZ-MC200) and were analysed by Move-tr/2D (Library Co. Ltd, Tokyo). If fish crossed paths and the software was unable to distinguish them, we compared the video and tracking data to identify the fish manually. For all the pairs of fish we used, individuals could be unambiguously identified by morphology and striping pattern. The video recordings ensured that the decisions of fish were not misclassified due to experimenter bias. In addition, the two observers performing the experiments were not informed with respect to the hypotheses behind the tests until after the termination of data evaluation.

Based on the time and position data recorded by the Trackit 3D software, we calculated the investigating time that fish spent in front of the colours. Investigating zones were 12 cm (length) by 10 cm (width) by 7 cm (height) in front of the colour signals. We discarded data when fish swam away from the colour signals (when the distance from the target in the previous second was higher than the present one), since in such cases the fish were unlikely to view the colour targets.

To explore whether individuals behaved in a consistent manner over time, repeatability was calculated following Lessells and Boag (1987), which calculates whether the proportion of variance within individuals is greater than the between-individual variance. Data were analysed using R (v.2.15.1; repeatability calculated from the ‘rptR’ package) and SPSS (v.22, IBM). All statistical tests were two tailed.

RESULTS

It is useful to evaluate individual strategies in SATs only once training has been completed, because there may be a variety of fluctuations in speed and accuracy while fish are learning the task. Since fish in all three experiments were initially trained under identical conditions, we first plotted the average learning curve for all 81 individuals that completed training (Fig. 2b). Performance in terms of accuracy was insignificantly different from chance during the first five trials (one-sample Wilcoxon test: $Z = 0.167$, $P = 0.86$), showing there was no pre-existing bias for either colour. As a result of learning, accuracy was significantly different from chance in all later trials (6–20 trials, $P < 0.05$) and reached saturation at an average level of ~60% correct choices after 10 learning trials, confirming that the discrimination task was challenging but manageable. Times for making choices, likewise, improved progressively over the first 10 trials, but levelled out in the second ten (Fig. 2a). Therefore, for all subsequent evaluations of the SAT, we limited the analyses to the last 10 trials during which performance had stabilized for experiment 1. Decision speed for each individual was the mean of decision time for the last 10 trials, and accuracy was the number of correct choices divided by 10 (last 10 trials). Since we tested the fish repeatedly in experiments 2 and 3, and the fish performed stably on days 2 and 3, we analysed the entirety of the data for these days.

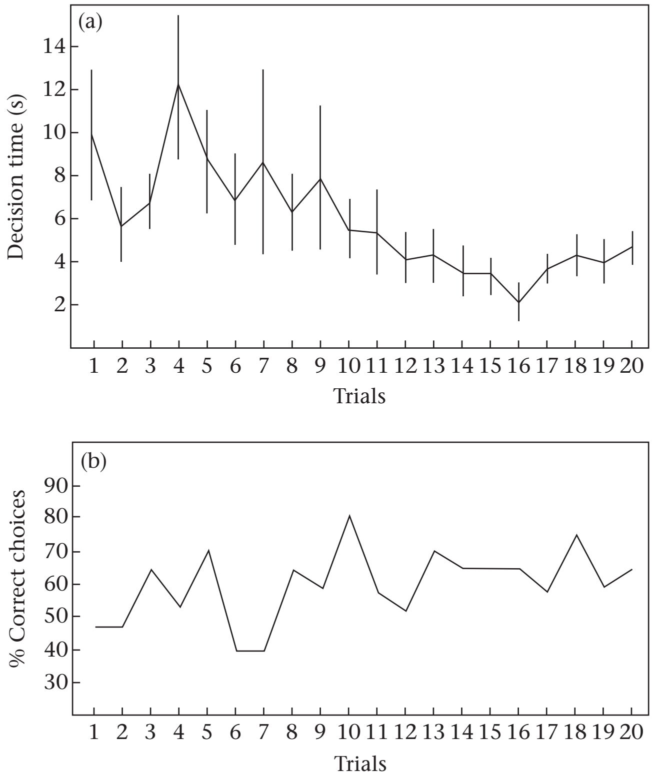

Figure 2. Change in performance of zebrafish with experience in terms of (a) mean ± SE decision time for all fish in each trial and (b) percentage of correct (rewarded) choices (number of correct choices/total number of fish) per trial. Lines show average performance of 81 fish tested in the course of the study.

Experiment 1: Fish Showed Speed–Accuracy Trade-offs in Discrimination of Similar Colours

There was a significant positive correlation between individuals' decision time and accuracy (Spearman rank-order correlation: $r_S = 0.41$, $N = 30$, $P = 0.023$; Fig. 3, Table 1). On average, the more time an individual fish spent in front of the colour signals, the more accurate was the decision made.

Experiment 2: Individual Fish Showed a Consistent Strategy over 3 Days

The previous experiment showed that individual fish displayed a between-individual speed–accuracy trade-off, where some fish, within a single set of trials, were more careful and others were fast and inaccurate. We further tested whether this strategy was constant over time using the same pair of similar colours in experiment 1. The fish presented significant repeatability within 48 h in investigating time and accuracy (repeatability test, decision time: $R = 0.64$, $N = 15$, $P = 0.001$; accuracy: $R = 0.79$, $N = 15$, $P < 0.0001$; Fig. 4, Table 1). In all 3 days, there was significant correlation between decision time and accuracy of fish (Spearman rank-order correlation: day 1: $r_S = 0.53$, $N = 15$, $P = 0.04$; day 2: $r_S = 0.59$, $N = 15$, $P = 0.02$; day 3: $r_S = 0.60$, $N = 15$, $P = 0.02$).

Experiment 3: When Paired with Careful Fish, the Fast-and-inaccurate Fish Increased Decision Time and Accuracy

In the previous experiments, we found a between-individual SAT in zebrafish, and the strategy was consistent over 3 days for each individual. We therefore tested how pairs of fish with various

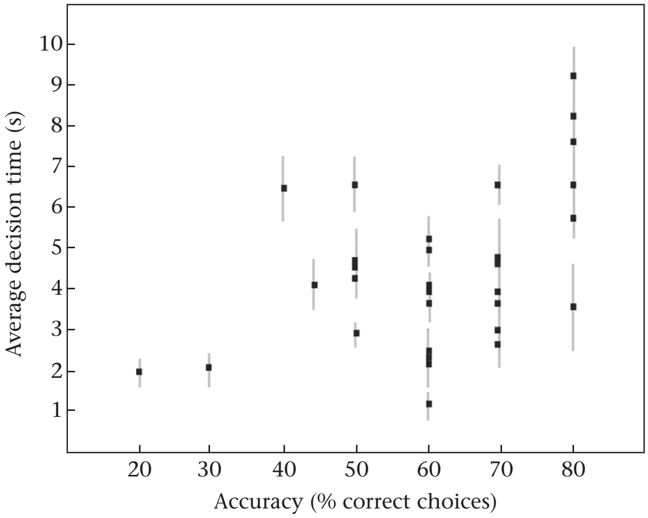

Figure 3. Relation between decision speed and accuracy in the colour discrimination task in experiment 1. Points represent individual zebrafish, and error bars show means ± SE.

Table 1
Mean decision time and accuracy of zebrafish for the three sets of experiments

	Mean±SE decision time (s)	Mean±SE accuracy (proportion correct)
Experiment 1 (N=30 individuals)		
Day 1 (last 10 trials from total 20 trials)	4.4±0.4	61.7±2.7
Experiment 2 (N=15 individuals)		
Day 1 (20 trials)	5.2±0.5	59.3±2.2
Day 2 (20 trials)	5.0±0.5	61.3±2.4
Day 3 (20 trials)	4.9±0.4	63.7±2.6
Experiment 3 (N=36 individuals)		
Day 1: individual test (20 trials)	6.5±0.9	58.6±1.6
Day 2: pair test (20 trials)		
Careful+fast-inaccurate pairs (N=16 individuals, 8 groups)		
Performance in a pair	10.9±1.3	63.4±4.2
Differences between behaviour types	1.2±0.3	1.9±0.9
Careful+careful pairs (N=10 individuals, 5 groups)		
Performance in a pair	12.1±1.6	65.5±3.0
Differences between behaviour types	0.9±0.2	1.0±1.0
Fast-inaccurate+fast-inaccurate pairs (N=10 individuals, 5 groups)		
Performance in a pair	7.3±2.3	55.0±5.2
Differences between behaviour types	0.8±0.2	3.0±2.0

strategies (careful versus fast and inaccurate) made decisions together. When tested in pairs, the fish tended to forage together (which we defined as swimming at a distance less than the sum of their body lengths; mean ± SE percentage of time spent foraging together = 84.5 ± 2.3%). The mean ± SE time difference between the two fish entering the signal area was 1.0 ± 0.2 s. In most cases (97%, by the above criterion) the two fish were swimming together and made decisions at almost the same time. When foraging in pairs, both careful and fast-and-inaccurate dyads showed significant correlation between speed and accuracy (Spearman rank-order correlation: careful fish: $r_S = 0.69$, $N = 16$, $P = 0.0016$; fast-and-inaccurate fish: $r_S = 0.72$, $N = 16$, $P = 0.0007$).

When careful fish were paired with fast-and-inaccurate fish, the behaviour of the pair converged (entering the same signal area at the same time), but this was due to changes made by just one member of the pair. The fast-and-inaccurate individual significantly increased decision time (paired t test: $t_{14} = 4.35$, $P = 0.0007$; Fig. 5a) and accuracy (Wilcoxon test: $Z = 2.31$, $P = 0.02$; Fig. 5b), while there was no significant difference in decision time (paired t test: $t_{14} = 1.90$, $P = 0.08$; Fig. 5a) or accuracy (Wilcoxon test: $Z = -0.06$, $P = 0.95$; Fig. 5b) for the careful individual before or after pairing. In fact there was a trend for decision time to increase (i.e. diverging from the fast-and-inaccurate behaviour) after pairing. In line with this, the magnitude of the change in both decision time and accuracy after being placed in a pair was significantly larger for the fast-and-inaccurate fish than for the careful individual (time: t test: $t_{14} = 2.52$, $P = 0.03$; accuracy: Wilcoxon test: $Z = 2.35$, $P = 0.02$). There was no significant difference between the numbers of cases where the careful or the fast-and-inaccurate fish chose first (mean ± SE number of careful fish leading = 11.3 ± 1.1, mean number of fast-and-inaccurate fish leading = 8.8 ± 1.3; t test: $t_{14} = -1.56$, $P = 0.14$), which indicates that neither the careful nor the fast-and-inaccurate fish consistently led when making joint choices.

When both fish were careful or both were fast-and-inaccurate, the strategy of individuals tested jointly was not significantly different from those of the individuals when tested singly (careful pairs: mean ± SE decision time of more careful fish foraging individually = 5.1 ± 0.4 s; paired t test: $t_8 = 1.32$, $P = 0.22$; mean decision time of the less careful fish tested individually = 4.8 ± 0.4 s; paired t test: $t_8 = 1.55$, $P = 0.16$). The mean ± SE accuracy of the more careful fish when foraging individually was 76.0 ± 2.5% correct choices. This was not significantly different from accuracy when foraging in pairs (Wilcoxon test: $Z = -1.45$, $P = 0.15$). The less careful fish also did not change its accuracy (when tested individually = 72.0 ± 2.0% correct choices; Wilcoxon test: $Z = -0.83$, $P = 0.41$; Table 1).

For fast-and-inaccurate pairs, the mean decision time of less fast-and-inaccurate fish foraging individually was 3.7 ± 0.2 s, statistically indistinguishable from the same fish tested in pairs (paired t test: $t_8 = -0.54$, $P = 0.60$). The mean ± SE decision time of the relatively more fast-and-inaccurate fish of the pair when tested

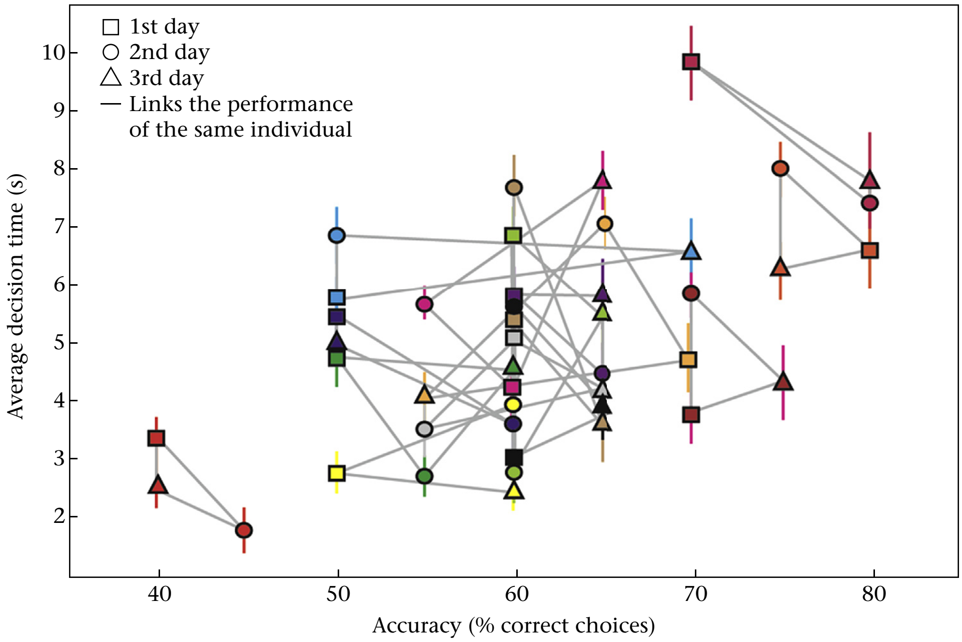

Figure 4. Relation between decision speed and accuracy in a colour discrimination task over 3 days in experiment 2. Each colour represents the same zebrafish individual, and error bars show means ± SE.

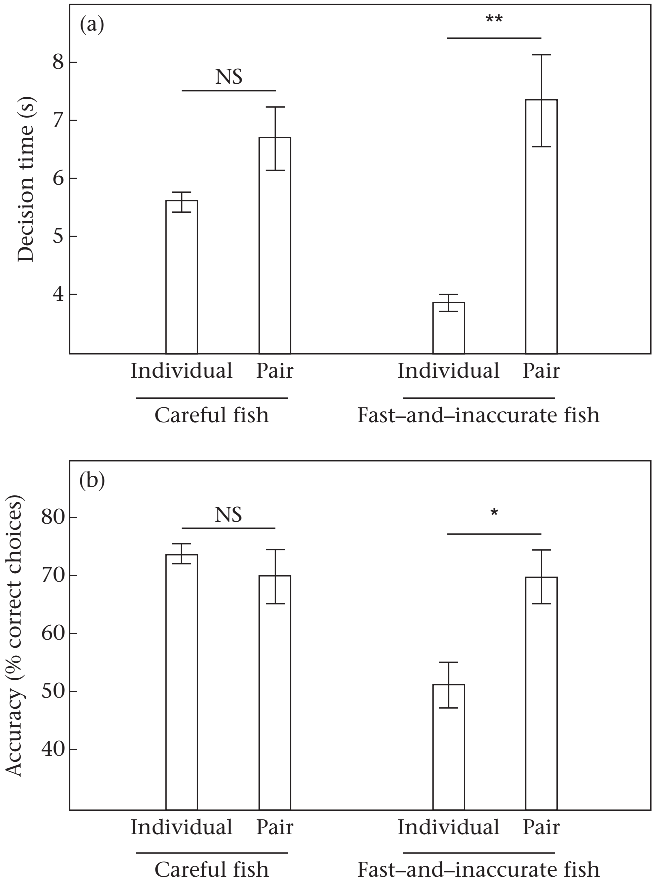

Figure 5. Mean ± SE (a) decision time and (b) accuracy of careful and fast-and-inaccurate zebrafish individuals when foraging individually and in pairs in experiment 3. $^{*}P < 0.05$; $^{**}P < 0.001$.

individually was 3.4 ± 0.4 s, not significantly different from when they were tested in pairs (paired t test: $t_8 = 0.66$, $P = 0.53$; Table 1). The mean ± SE accuracy of the relatively less fast-and-inaccurate individual when tested singly was 58.0 ± 2.0% not significantly different from accuracy in pairs (Wilcoxon test: $Z = -1.81$, $P = 0.07$). The mean accuracy for the more fast-and-inaccurate fish when tested singly was 46.0 ± 7.5%, again, not significantly different from pairs (Wilcoxon test: $Z = -0.11$, $P = 0.91$). In conclusion, when we paired a careful and a fast-and-inaccurate fish, only the fast-and-inaccurate one increased the decision time and accuracy, while the strategy of the careful fish remained the same. When we paired two careful or two fast-and-inaccurate fish, the strategy of either fish did not change, nor was their joint performance superior to how they performed individually.

DISCUSSION

We find that some individual fish consistently make rapid choices but with low accuracy, whereas other fish are slower but more accurate. This observation cannot simply be explained by individual differences in sensory discrimination ability, since in that case individuals' accuracy and speed would be positively correlated or uncorrelated. In previous studies of fish, in which speed–accuracy trade-offs were not observed (Mamuneas et al., 2015; Proulx et al., 2014), the ease of the task might either not require appreciable sampling times (Dyer & Chittka, 2004), or simple differences in sensory ability, motor behaviour or motivational levels might explain individual differences that do not display a SAT. We also found that the individual SAT strategy is consistent over time in zebrafish, which fulfils a key criterion of animal personality (Gosling, 2001; Sih et al., 2004).

In other species, the movement of fish shoals can be determined by collective decisions, or certain individuals may take the lead as a result of their positions in the shoal, as well as other individual factors. Studies in roach, threespine stickleback (Bumann & Krause, 1993) and medaka (Ochiai, Suehiro, Nishinari, Kubo, & Takeuchi, 2013) show that individuals in the front or the ones who make more decisive movements are more dominant in the direction of the shoal. Recent studies show individual personality and physical status can also influence the leadership in a group (Harcourt et al., 2009; Nakayama, Johnstone, & Manica, 2012).

We observed that when zebrafish were put in pairs during the colour discrimination task, the mean dyad decision was closer to that of the careful individual, which made more accurate choices but took longer to solve the problem. In a related, but somewhat contrasting finding on sticklebacks, shy individuals tend to behave in a bolder manner when paired with a bold individual (Harcourt et al., 2009). In our case, we often observed that the fast-and-inaccurate individual initiated a rapid movement, but returned to the proximity of the careful individual when this individual declined to follow. Overall, this resulted in higher decision accuracy for the fast-and-inaccurate individual than if this individual decided singly. Indeed, average accuracy for fast-and-inaccurate–careful pairs was higher than for both individuals, although accuracy did not exceed that of the careful individual in a manner that was statistically significant.

A key difference between this study and earlier studies on SAT in fish was the existence of a negative 'punishment' stimulus, which may have changed the salience of the task. This difference may also partly explain the behaviour of zebrafish in pairs, which resembled that of the 'cautious, accurate' partner more than the 'fast-and-inaccurate' individual. Suboski et al. (1990) demonstrated that zebrafish could socially learn information about simulated predators from visual observation of the alarm behaviour of group members. Similar transmission of information about the potential negative stimulus may underlie the switch of behavioural strategies to a cautious, accurate approach.

Accurate estimations and decisions are essential for animals, and group-living species are able to balance personal and social information received from other group members (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Leadbeater & Chittka, 2007). Individual variation can affect social interactions and benefit the group's decision making (Krause, James, & Croft, 2010; Pike, Samanta, Lindström, & Royle, 2008), and average judgements of the social group can be higher in accuracy compared with individual opinions (Bisazza et al., 2014; Galton, 1907; Surowiecki, 2005). In the present study, zebrafish in pairs did not exhibit superior average performance compared to average individual foraging (for example, decreased investigating time with equal or higher accuracy), although fast-and-inaccurate fish gained an advantage from following the more careful individual by gaining quicker access to the food reward. Another explanation may be that the fast-and-inaccurate individual hesitated to make a rapid decision in exchange for remaining in the pair. Either way, it appears that the decision strategy of the careful individual was unaffected by that of the fast-and-inaccurate individual. Our results add the zebrafish, an important model of developmental biology and neuroscience, to the list of animals whose decision making can be affected by SATs, and for the first time, explore such trade-offs in dyads of fish.

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