Cognitive styles: speed−accuracy trade-offs underlie individual differences in archerfish

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Individuals exhibit consistent differences in behaviour and related cognitive performance. 'Cognitive styles'-based hypotheses suggest the trade-off between speed and accuracy is an important factor where an individual's behavioural traits and linked decision speeds may account for its cognitive performance. The expected relationship between accuracy and decision speed, however, is not always clear and some studies have suggested that faster individuals do not suffer the expected cost to accuracy. Contradictory findings may be attributed to taxon-specific differences but may also be due to the difficulty in separating intraindividual from interindividual variation or the use of insufficiently challenging tasks in tests. We trained archerfish, *Toxotes chatareus*, to shoot at artificial targets for food, and then conducted a visual discrimination study to test the cognitive styles hypothesis. To reduce potential confounding effects, we used a longitudinal design, and increased the challenge of the test by using differentially rewarded targets. We also tested fish in one of two conditions with either two or three targets in each test. As expected, archerfish showed repeatable differences in latency to shoot and consistently fast individuals were quicker to achieve initial learning criteria than slower individuals. Repeated tests revealed an inverse relationship between discrimination accuracy and speed, with slower individuals having greater accuracy in initial trials on each day, supporting the cognitive styles hypothesis. However, this relationship was statistically significant only in the three-target condition, underscoring how task design can strongly affect the ability of researchers to detect robust individual variation in cognition. Taken together, our results support the hypothesis that speed−accuracy trade-offs can underlie some observed interindividual differences in cognition.

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To understand the evolution of cognition, it is important to understand both the nature of the variation selection has to work with, and the relationship between individual cognitive performance and fitness (Dukas, 2004; Sih & Giudice, 2012). Variation in cognitive performance is repeatable at the individual level across a wide array of vertebrate and invertebrate taxa (Cauchoix et al., 2018), and interest in the causes and consequences of this variation has burgeoned (Boogert, Madden, Morand-Ferron, & Thornton, 2018). Most of the focus on measuring this variation has been devoted to performance or decision outcomes in relation to behavioural traits, but variation can also be expressed in decision time with a link between decision time and outcome (Chittka, Skorupski, & Raine, 2009). Faster decisions are more prone to error than slower decisions, and this relationship between speed and decision accuracy often results in a trade-off that is fundamental to all information pathways and decision making (Standage, Wang, Heitz, & Simen, 2015). This speed−accuracy trade-off is seen across a wide array of organisms (Latty & Beekman, 2011; Rival, Olivier, & Ceyte, 2003), and is considered to be a major factor underlying differences in cognitive performance (Heitz, 2014; Sih & Giudice, 2012). Sih and Giudice (2012) proposed that speed−accuracy trade-offs underpin the relationship between cognition and certain behavioural traits: individuals that show consistent and repeatable differences in speed−accuracy trade-offs are considered to have different 'cognitive styles'.

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Many species have high interindividual variation in certain behaviours, with individuals exhibiting consistent, repeatable levels of those behaviours (Bell, Hankison, & Laskowski, 2009), or suites of correlated behaviours, as per behavioural syndromes (Sih, Bell, & Johnson, 2004). Many of these behavioural traits or syndromes can be placed on a continuum of fast to slow behavioural types. For example, exploration tendency and activity have been shown to relate to decision speed: more active and more exploratory bank voles, *Myodes glareolus*, make faster decisions (Mazza, Eccard, Zaccaroni, Jacob, & Dammhahn, 2018)) and, similarly, more aggressive spiders, *Portia labiata*, make faster decisions (Chang, Ng, & Li, 2017). Many of these behavioural traits are frequently linked to risk sensitivity (Jones & Godin, 2010). According to the cognitive styles hypothesis, individuals with consistently low levels of activity, and higher sensitivity to risk, may be expected to take more time but make more accurate decisions than individuals that are more active and less sensitive to risk (Sih & Giudice, 2012). In cognitive tests, as used in psychophysical trials where individuals must discriminate between rewarded and unrewarded cues, slower individuals are expected to achieve greater success than quicker individuals, as shown in bumblebees, *Bombus terrestris* (Chittka, Dyer, Bock, & Dornhaus, 2003). Conversely, individuals that make quicker decisions are presumed to suffer costs to accuracy, but be less risk sensitive, more likely to engage with novel objects and learn more quickly in many situations (possibly as a result of being more exploratory and/or less neophobic; Chittka et al., 2009; Sih & Giudice, 2012; Guenther, Brust, Dersen, & Trillmich, 2014). Recent studies of differences in cognitive performance driven by speed—accuracy trade-offs support this hypothesis (Chittka et al. 2003, 2009; Ducatez, Audet, & Lefebvre, 2015; Exnerová, Svádová, Fučíková, Drent, & Štys, 2010; Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2015; Moiron, Mathot, & Dingemanse, 2016). For example, individual great tits, *Parus major*, that tended to make slower decisions were more accurate (Moiron et al., 2016), and Wang, Brennan, Lachlan, and Chittka (2015) showed both that zebrafish, *Danio rerio*, exhibit interindividual differences in speed—accuracy trade-offs and that 'careful', slow, fish were more accurate than faster individuals in visual discrimination. However, conflicting results have been reported: three-spined sticklebacks, *Gasterosteus aculeatus*, exhibited no speed-related cost to accuracy (Mamuneas, Spence, Manica, & King, 2015), with similar results observed in other species including bumblebees (Raine & Chittka, 2012), lizards, *Lampropholis delicata* (Chung et al., 2017), spiders (Chang et al., 2017) and other fish (*Poecilia reticulata*, Lucon-Xiccato & Bisazza, 2016; *Gnathonemus petersii*, Kareklas, Elwood, & Holland, 2017; *Poecilia mexicana*, Sommer-Trembo & Plath, 2018). The link between individual differences in cognition and speed—accuracy trade-offs thus remains inconclusive, with a recent meta-analysis suggesting that measures of individual differences in cognition linked to behavioural traits may be complicated by factors such as the sex of individuals, taxon-specific differences and methodological issues (Dougherty & Guillette, 2018). Several reviews have suggested that the experimental approaches used in this developing field may sometimes impede the exploration of interindividual differences in cognition and impact the interpretation of results (Boogert et al., 2018; Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013; Griffin, Guillette, & Healy, 2015; Rowe & Healy, 2014).

Test difficulty may impact the optimal trade-off in speed—accuracy trade-off strategies, where the relative ease of a task, for example the number of choices in a discrimination test, can be important (Chittka et al., 2009; Raffa, Havill, & Nordheim, 2002). Physiological differences, both within and between individuals, as per the pace of life syndrome (Réale Denis et al., 2010), are also important as metabolic differences and changes may underlie differences in behavioural traits and information use (Biro & Stamps, 2010; Mathot & Dall, 2013; McKenzie, Belão, Killen, & Rantin, 2015). Motivation in learning assays can be affected by level of satiation (Ben-Shahar & Robinson, 2001; Shettleworth, 1972), and motivational differences have been shown to override cognitive differences in problem-solving tasks (van Horik & Madden, 2016). Additionally, coping styles, where individuals show distinct differences in vulnerability and response to stress (Koolhaas et al., 1999), can drive consistent interindividual variation in behaviour and can both directly affect learning, for example in reversal learning tests (Bensky, Paitz, Pereira, & Bell, 2017), and indirectly impact measures of cognition (McEwen & Sapolsky, 1995; Mesquita, Borcato, & Huntingford, 2015; Raoult, Trompf, Williamson, & Brown, 2017). The term coping styles is sometimes used interchangeably with behavioural syndromes in the literature and while coping styles may be closely associated, and sometimes do correlate, with various behavioural syndromes they remain distinct from them, with recent work showing that for some species coping styles do not correlate, or form syndromes, with behavioural traits (Zidar et al., 2017). One method that has been suggested to reduce the effect of potentially confounding noncognitive factors is to use repeated, or longitudinal, tests (Boogert et al., 2018; Sih et al., 2015; Thornton & Lukas, 2012).

We used archerfish, *Toxotes chatareus*, to explore speed—accuracy trade-offs using a repeated discrimination task with a longitudinal design with differentially rewarded cues (targets). Two conditions with different numbers of targets were used to explore the effect of increasing target choice on the ability to reveal interindividual differences in discrimination performance. Archerfish, best known for their specialized ability to shoot down prey by spitting jets of water, are visual predators (Ben-Tov, Ben-Shahar, & Segev, 2018) and increasingly used in studies of visual discrimination and other aspects of cognition. They can readily discriminate between targets of different colours, shapes and complexity (Ben-Tov, Donchin, Ben-Shahar, & Segev, 2015; Gabay, Leibovich, Ben-Simon, Henik, & Segev, 2013; Newport et al. 2014, 2015), use visual search strategies comparable to those of humans and other primates and discriminate between known objects from novel viewing angles (Ben-Tov et al., 2018; Gabay et al., 2013; Newport, Wallis, & Siebeck, 2018; Rischawy & Schuster, 2013; Saban, Sekely, Klein, & Gabay, 2017). They can also learn to associate targets with differential rewards (Karoubi, Leibovich, & Segev, 2017) and exhibit distinct interindividual differences in latency to shoot (Jones, Webster, Templeton, Schuster, & Rendell, 2018), with initial evidence suggesting that individuals may use different decision-making strategies (Newport, Wallis, Temple, & Siebeck, 2013).

Our main aim was to examine whether fast—slow cognitive styles exist in archerfish, specifically whether consistent individual decision speeds affected learning and discrimination. We also wanted to test the effect of number of choices, as a proxy for cognitive challenge. We used a discrimination task with differentially rewarded targets (which the fish were trained to shoot), repeated over consecutive days for each individual. We recorded decision time (latency to shoot) and, as a measure of discrimination success (shots at target corresponding to the large reward, hereafter 'success'), decision accuracy. We measured success at two levels: daily success and success in the first trial of the day, where we expected lowest satiation levels. To examine the effect of numbers of choices, we tested fish with either two or three targets. We expected a trade-off to exist among individuals, with an inverse relationship between speed (latency to shoot) and accuracy (success). Specifically, we expected that fish with longer latencies to shoot would be more successful, at least in the first trials of the day.

METHODS

Subjects

We used 20 archerfish, 12 ± 0.5 cm (total length), from a population of animals housed at the University of St Andrews, U.K. All fish were wild caught and sourced as a single order from an accredited ornamental fish retailer. They were of unknown sex as archerfish are sexually monomorphic and we cannot be sure of their relatedness either. There is some possibility that the fish were related; however, very little of their reproductive biology is known besides the fact that they are broadcast spawners (Simon et al., 2011) which suggests they are unlikely to be kin. The fish had been kept in the laboratory for a year prior to use in the study and had not been trained to shoot in any previous study. At the time of the experiment the fish were estimated to be 20–24 months old, based on their size and date of arrival from the retailer; however, the correlation between age and growth rate in captivity is not well known for this species. Fish were maintained in stock freshwater aquaria in groups of five to eight, in large individually filtered tanks (180×45 cm and 35 cm deep) at 25–26 °C under a 12:12 h light:dark cycle. Stock tanks had environmental enrichment in the form of 3 cm deep gravel substrate and several plastic plants. Water quality parameters (pH, nitrite, ammonia and nitrate concentrations) were measured weekly, and levels were kept within a range appropriate for archerfish (as per Newport et al., 2013), using external canister filters and regular water changes. The fish were fed daily with an alternating mixture of commercial fish food (Tetra Cichlid Sticks) and freeze-dried bloodworms. Fish were measured as they were captured from the stock tank: a ruler was taped to the side of the tank and netted fish were gently pressed against it to record their length before being moved to the experimental tank.

Experimental Set-Up

During trials fish were kept individually in tanks (55×55 cm and 45 cm deep), with a camera above each tank to record trials from a top-down perspective (Appendix 1, Fig. A1). Each tank had an immersion heater (temperatures were kept at 24.5 ± 0.5 °C), a small internal filter (Eheim 305), a 1 cm deep gravel bottom and two plastic plants. The water in the tank was maintained at the same level (± 1 cm) such that a transparent Plexiglas 'target platform' (30 cm wide and 54 cm long) was always 15 ± 1 cm above the water level of the tank. Opaque black plastic sheets were affixed to each side of the tanks to ensure fish were unable to observe fish in other tanks, or the experimenters. A camera (ELP 2 Megapixel USB webcam) was positioned 70 cm above the tank and used to score fish behaviour and shooting events in all trials.

Experimental Procedure

The experiment consisted of three phases, two training and one test, and each fish was subjected to the following phases in order. In the first phase, all fish were trained to shoot a novel target presented on the shooting platform, first a known food item (a pellet) and then a novel white artificial target. In the second phase, the fish were given a set number of trials to familiarize themselves with the experimental targets presented individually. Finally, fish were tested in daily discrimination trials for 30 consecutive days using these targets presented simultaneously in two conditions, two or three targets, with differential rewards. The 30-day period was chosen because data from a pilot study suggested some fish required about 20 days to reach criterion, and we wanted to give as much time as possible to slower learners.

Each fish was randomly assigned to one of the two conditions before the training phase began. Conditions differed only in the number of targets presented to the fish to discriminate between in the final phase. In the 'two-targets' condition, one target was associated with a large reward and the other with a small reward; in the 'three-targets' condition, one target was associated with a large reward and the other two with small rewards.

The four targets used in this experiment were hand cut plastic squares, (2 cm^2, 3–5 mm thick) differing in colour (green, blue, black or white). Food rewards were precut pieces of 3 mm diameter cylindrical pellets; the large reward was 3 mm long, and the small reward was 0.5 mm long. Of the four targets, white ones were used only in the training phase and the remainder (green, blue, black) were used in the familiarization and discrimination testing phases where fish were given either two (blue and green) or three (blue, green and black) targets as per their condition (for more information on the targets we used, see Appendix 2). The target colours were randomly designated to correspond to either a large or a small reward for each fish and then remained consistent for each fish for the duration of the study. So, for example, in the two-target condition one fish was trained with a white target, then introduced to and tested with the green (small reward) and blue (large reward) targets. As an example of the three-target condition one fish was trained with a white target, and familiarized and tested with the green (large reward), blue (small reward) and black (small reward) targets.

In all phases of the experiment a trial was defined as an opportunity to shoot at the presented target(s). A trial began as soon as the target (or last of multiple targets) had been placed on the platform and ended when a shot at any target was made, or after a maximum duration, which differed across the three phases (see below for details). When a shot was made at a target, the corresponding food reward was immediately dropped into the tank, and the target(s) removed. Successive trials within a session were begun ca. 30 s after a previous trial.

As targets were placed by hand, there was a slight delay between placing the first and last ones. In most trials fish shot after all targets had been placed, but if a fish shot at a target prior to all targets being presented it was counted as a trial, an appropriate reward delivered and a latency to shoot of 1 s was recorded. This happened infrequently (27 times out of 5712 trials) as most fish hesitated to shoot while the experimenter was visible, and we included these data as part of the cognitive styles hypothesis which suggests that faster individuals may be more impulsive. On rare occasions, <1% of all trials, fish would make a second shot prior to the reward being dropped. Where this did occur, it was the faster fish that made these shots and, in these cases, only the first choice was rewarded and scored. Some shots were also made while targets were being removed, and these were not rewarded. Shots could easily be seen by the experimenter via the top-down video monitor, as water jets hit the platform and left a water splash. Some archerfish occasionally attempted to jump for food rewards, again <1% of all trials, mostly in the training phase, but the fish were never rewarded for jumping or for shooting at anything except the presented targets.

Phase 1: training

In this phase fish were trained to shoot at an artificial target placed on the target platform to receive a food reward. Training consisted of two stages and was considered complete after a fish had achieved learning criteria in both stages. In the first stage the fish was presented with a pellet (a known food item) as a target, and the first criterion was reached when the fish had completed 10 successful trials in each of two consecutive sessions. Each fish received a single training session per day with up to 50 min per

session and a maximum of 10 trials. Each trial continued either until the fish shot or the 50 min expired. The day after completing the first criterion, the fish entered the second stage of training and was presented with an artificial target (a white plastic square). Again, training sessions continued until the fish hit the target 10 times in a row in two consecutive sessions. In this second stage of training the fish had a maximum trial time of 8 min, which was based on a previous study with a similar procedure in which all fish shot within 6 min (Jones et al., 2018). There was an initial maximum of 45 daily sessions allowed for this part of the training; however, several fish never reached the criterion. These fish were then trained further with three sessions a day until they achieved criterion. The rationale for the training phase was to ensure each fish had reliably learnt to shoot a target to gain a food reward.

The training phase also allowed individuals with different sensitivity to risk and/or stress to habituate to the experimental procedure and potentially reduce the confounding effect of coping styles (Zidar et al., 2017). A related benefit was that estimates of repeatability can be improved with greater acclimatization time, as shown for other species (O'Neill, Williamson, Tosetto, & Brown, 2018).

Phase 2: familiarizing with coloured targets

The familiarity phase, beginning the day after they achieved the second training criterion, introduced fish to the targets and provided an opportunity to learn about the corresponding rewards. The rationale for this was to introduce subjects to each cue prior to discrimination trials to ensure similar levels of response across cues (Sturdy & Weisman, 2006), and thereby reduce initial target bias.

Each fish received six familiarity sessions split over 3 consecutive days to ensure they had been rewarded for shooting each target an equal number of times. Fish in the two-target condition received six trials per session: three with the large-reward target and three with the small-reward target. Fish in the three-target condition received nine trials per session, three trials for each target. In this phase targets were presented individually in random order. All fish that entered this phase shot at the target in all trials.

Phase 3: discrimination testing

The day after the familiarity phase was complete discrimination testing began. Here targets, either two or three according to condition, were presented simultaneously. The order and position of target presentation changed for each trial, but targets were never placed in the same position in consecutive trials. The targets were all placed 4–5 cm apart in either a line or a triangle configuration, so shot targets could be easily identified, but would not require fish to search different areas of the platform.

Discrimination tests were run for 30 consecutive days for each fish, with 12 trials a day, split over two sessions (starting at ca.1000 and ca. 1630 h), per day. Fish had an 8 min maximum trial limit. Latency to shoot, colour of the shot target and size of reward were scored from video recordings. A hypothesis-naïve secondary observer scored ca. 20% of the trials. Interrater reliability comparing the principal (N.J.) and secondary scores of latency to shoot, using the irr package (Gamer, Lemon, Fellows, & Singh, 2012), showed high agreement with an interclass correlation of 0.992–0.994 and a mean of 0.993 ($F_{1073,1073} = 270$, $N = 141$, $P < 0.001$).

Of the 20 fish we used for this experiment four were omitted from the analyses. Two fish were unable to complete training as they consistently failed to hit the targets. Neither fish showed any obvious injury or morphological differences, but they could not hit targets accurately and missed the targets they appeared to aim at (archerfish take a characteristic angle and maintain their orientation towards intended targets before shooting). One fish consistently shot about 20 cm behind the target it aimed at; the other fish

shot at least 5 cm to one side of any target. A third fish failed to shoot in sufficient training trials and did not complete the first stage of training even after 9 weeks of training sessions. A fourth fish reached training criterion but shot in fewer than half of the discrimination trials and was excluded from analysis of success so only 16 fish (eight in each condition) were included in the analyses for speed–accuracy trade-offs.

Ethical Note

All procedures performed were in accordance with the ethical standards of the University of St Andrews and methods used were approved by the University of St Andrews Animal Welfare and Ethics Committee (AWEC). No procedures required U.K. Home Office licensing. All tanks were enriched with gravel and plastic plants for cover. Handling was kept to a minimum, and when fish had to be moved between tanks they were caught using two large hand nets to reduce the likelihood of extended capture periods. In the experimental tanks fish were kept alone in a volume of at least 125 litres. Archerfish are not considered a social species and there are no published studies on the effects or preference for any social context and/or isolation in this species. Multiple previous studies have maintained archerfish in isolation with no reported ill effects or perceived likelihood of stress. During our study we closely monitored each fish, specifically for signs of reduced feeding rate, responsiveness, stereotypic behaviour and colour changes. We observed very few instances of these signs, and they were only temporary and only occurred in the period immediately after fish had been transferred between tanks. No fish died or suffered ill health during this study, and all individuals were retained in the laboratory for future use.

Statistical Analysis

All analyses were performed in R version 3.5.1. (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org), using R Studio version 1.1.456, and where applicable R notation is used to detail the models used. Post hoc pairwise comparisons were conducted using the 'emmeans' function in the R emmeans package (Lenth, Singmann, Love, Buerkner, & Herve, 2018) where appropriate.

Latency to shoot and training

We tested whether individual differences in latency to shoot in the discrimination phase were linked to the training speed, in terms of the number of training sessions needed to reach learning criterion during the training phase by fitting a linear model (LM) with the number of sessions required to reach training criterion as the dependent variable against mean latency of each fish. Mean latency per fish was calculated from all shots made during the discrimination phase (i.e. we only used latencies from fish that had completed training and passed the familiarity phase).

Speed–accuracy trade-off during discrimination phase

Here we tested whether overall latency to shoot (latency) predicted success, that is, shooting at the large-reward targets. We were also interested in whether the number of targets and satiation (measured by trial number within session) affected latency to shoot. We fitted a generalized linear mixed model (GLMM), using the glmer function in the lme4 package (Bates, Mächler, Bolker, & Walker, 2015) with latency to shoot (s) as our continuous response variable and reward type (large, or small), condition (number of targets) and trial number within session as the fixed factors and day as a covariate to explore change in any of these effects over time. The model included session and individual fish

identity as random factors with random intercepts. We log transformed latency prior to analysis to achieve improved normality of the model residuals. For the final model we included all potential random factors that were significant based on fitting the full model and then tested the significance of each term by dropping them out and doing a likelihood ratio test (LRT) comparing the reduced with the full model. The model we fitted was the following (in *R* syntax):

$$\text{LogLatency} \sim \text{Reward} * \text{Condition} + \text{Reward} * \text{Day}$$
$$+ \text{Condition} * \text{Day} + \text{Trial} + (1|\text{FishID})$$
$$+ (1| \text{Session})$$

The condition term was a factor with two levels (either two or three targets), and the reward term was a factor with two levels (small or large reward).

Effect of number of targets on success during discrimination phase

Here we explored whether the number of targets influenced success and the rate of change of success over the duration of the experiment. We fitted models of the binomial family with the binary response variable being success or failure to shoot at the large-reward target. The final model was:

$$\text{Success} \sim \text{Condition} * \text{Day} + (1|\text{FishID}) + (1|\text{Trial})$$
$$+ (1| \text{Session})$$

Consistency of individual differences in latency to shoot

To investigate whether fish exhibited consistent individual differences in latency to shoot we calculated the level of repeatability, *R*, as per Jones et al. (2018). Repeatability is the fraction of variation that is due to differences between individuals and is used to

quantify individual differences (Bell et al., 2009). *R* was calculated using the rptR package (Stoffel, Nakagawa, & Schielzeth, 2017) which builds on the methods developed for mixed-model analysis and uses bootstrapping to provide reliable estimates of *R*. We estimated *R* at the level of individual fish, using the same overall latency model, described above, with 1000 parametric bootstraps.

Individual differences in latency and success

To examine the effect of latency to shoot on overall mean daily success in the discrimination phase we fitted a binomial family generalized linear model (GLM) to the proportion of successful trials from all trials over the 30 days for each fish, with individual mean latency and condition (two or three targets) as the independent variables. The model fitted was:

$$\text{glm(proportion of success} \sim \text{MeanLatency} * \text{Condition)}$$

To explore differences in success in the initial trials of each day when we expected satiation and any effects on motivation to be lowest, we used a similar analysis as above, but only using data from the first trial per day. We fitted the model with data from the two conditions separately, as:

$$\text{glm(proportion of success} \sim \text{MeanLatency)}$$

RESULTS

Training Phase

Individual latencies to shoot in the discrimination phase were significantly associated with the number of training sessions (combining both stages) required to achieve criterion. Slower shooting fish required more sessions to reach training criteria (LM:
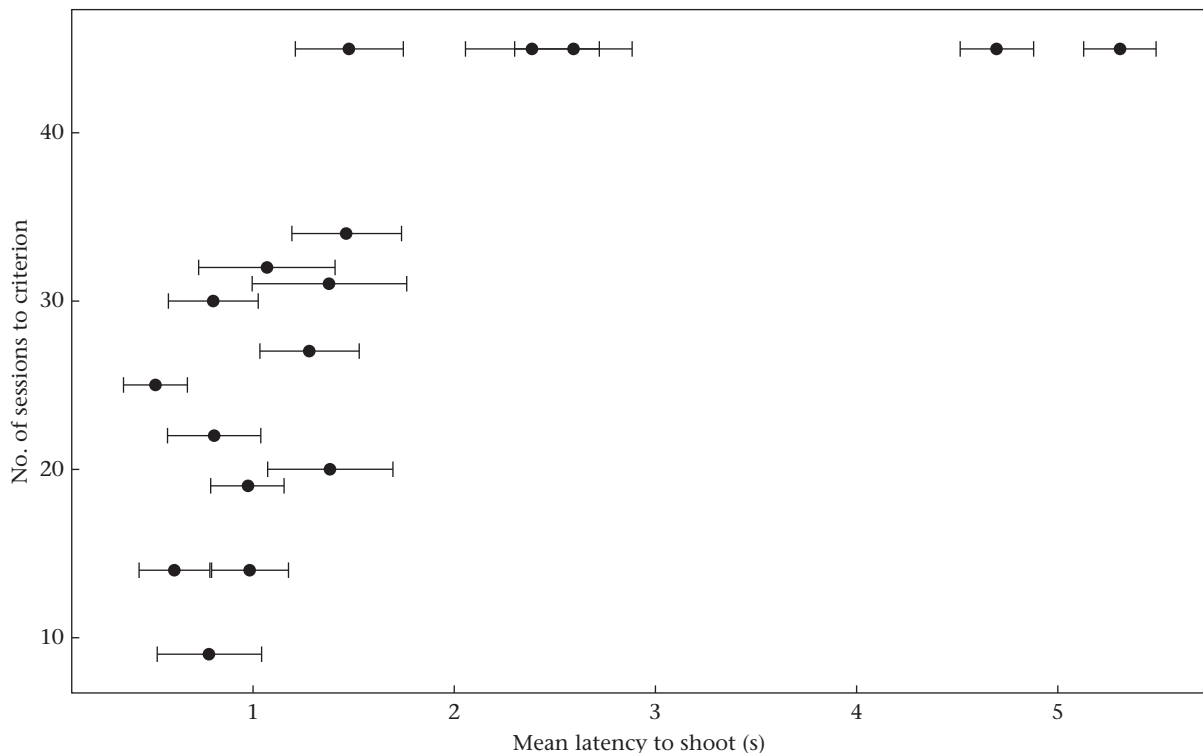

Figure 1. Relationship between mean (± SEM) latency to shoot and the number of training sessions to achieve both training criteria for 17 fish that completed training. Mean latency was calculated from 360 discrimination trials per fish.

$t = 2.395$, $P = 0.030$; Fig. 1). A similar effect was found even after removing the two slowest fish (LM: $t = 3.519$, $P = 0.004$).

Discrimination Phase

Overall speed−accuracy trade-offs

In general, latency increased with accuracy as fish took longer to shoot at the target that corresponded with the larger reward (LRT on 'Reward' predictor : $\chi^2_1 = 84.455$, $P < 0.001$; Table 1). Post hoc contrasts revealed significant differences in latency to shoot depending on the reward associated with the target: latency to shoot large-reward targets averaged 1.3 s longer than that for small-reward targets (emmean: $z_{8.642} = 0.248$, $P < 0.001$; Fig. 2a). Trial number was also important, as fish showed higher latency in their first test trial. The first trial lasted significantly longer than all other trials (LRT on 'Trial' predictor: $\chi^2_5 = 136.02$, $P < 0.001$; Fig. 2b, Table 1). Latency to shoot was not significantly affected by the number of targets (LRT on 'Condition' predictor: $\chi^2_1 = 1.088$, $P = 0.297$); however, there was a significant interaction between time (Day) and number of targets (LRT: $\chi^2_1 = 103.493$, $P < 0.001$).

Effect of number of targets on success during discrimination phase

Mean success was affected by the number of targets, with fish in the two-target condition shooting at the large-reward target more frequently (LRT on 'Condition': $\chi^2_1 = 10.732$, $P = 0.001$; Table 2) supporting our hypothesis that the three-target task was a more challenging discrimination task. This was reflected in a comparison of success over time, where although individual fish showed high between-day variation in success (Appendix 1, Fig. A2), on average the number of targets was important with a significant interaction between time (Day) and number of targets (LRT: $\chi^2_1 = 18.029$, $P < 0.001$; Fig. 3, Table 2).

Individual differences in latency to shoot

Bootstrap repeatability estimation showed there was a high individual repeatability in latency to shoot. The fish identity term within the model accounted for 45% of the variance in latency, suggesting large interindividual differences in latency to shoot (Appendix 1, Table A1). Repeatability for overall success was much lower (Appendix 1, Table A2).

Table 1
Parameter estimates for effects of reward type, condition and trial on latency to shoot

	Estimate/Variance	SE/SD	t
Fixed effects			
Intercept	2.504839	0.374106	6.696
Rewardsmall	−0.225015	0.065541	−3.433
Condition (Two)	−1.042921	0.51992	−2.006
Day	−0.018908	0.003024	−6.252
Trial2	−0.43565	0.047785	−9.089
Trial3	−0.447795	0.047908	−9.347
Trial4	−0.430721	0.047829	−9.005
Trial5	−0.448379	0.047874	−9.366
Trial6	−0.392536	0.048007	−8.177
Rewardsmall*Condition Two	−0.015648	0.057261	−0.273
Condition Two*Day	0.033454	0.003289	10.173
Random effects			
Fish ID	1.06374	1.03138	
Session	0.00536	0.07321	
Residual	1.07979	1.03913	

$N = 16$ fish, 360 trials each. Estimates and SEs are given for fixed effects and variance and SDs for random effects.

Individual differences in latency and success

Overall mean daily success (proportion of shots at large-reward target) was not significantly affected by individual mean latency (GLM: $t = 2.916$, $P = 0.078$; Appendix 1, Table A3), and this held for fish in conditions with both two (GLM: $t = 0.432$, $P = 0.681$; Appendix 1, Table A4) and, despite a positive trend between latency and accuracy, three (GLM: $t = 2.183$, $P = 0.072$; Appendix 1, Table A5) targets. Success on the first trial of the day was affected by individual mean latency: slower fish had greater success in the condition with three targets (GLM: $t = 4.374$, $P = 0.005$; Fig. 4a), with cumulatively increasing success in first trials across time for slower fish (Appendix 1, Fig. A3a). However, while proportion of success showed a positive relationship with individual mean latency in the two-target condition, it was not statistically significant (GLM: $t = 1.800$, $P = 0.132$; Fig. 4b) and fish speed did not predict cumulative successes (Appendix 1, Fig. A3b).

DISCUSSION

In line with our primary aim we have shown that archerfish exhibit consistent individual differences in speed−accuracy trade-offs and have provided empirical support for the hypothesis that differences in decision speed can explain interindividual differences in cognitive performance. Archerfish discriminated between differentially rewarded targets, with greater latencies overall for shots at the target associated with the larger food reward. Consistent with the cognitive styles hypothesis (Sih & Giudice, 2012), archerfish with repeatable differences in latency to shoot showed corresponding differences in learning to shoot a novel target during training and in discrimination trials. Individuals with consistently high latencies took longer to train to shoot a novel target, but these slower individuals achieved greater discrimination accuracy during testing, with success increasing along the fast−slow continuum. These differences in accuracy based on speed−accuracy trade-offs were observed only when comparing the outcomes from the first trial of each day, when motivation was expected to be highest. Our results also suggest that the number of targets, or choices, was important for revealing these interindividual differences in success based on speed−accuracy trade-offs.

Mean daily success of individuals within each condition did not differ significantly, consistent with a less frequently explored prediction of Sih and Giudice (2012), namely that individuals along the fast−slow continuum may be expected to achieve similar mean success with different strategies. Our study, however, had a fixed number of trials per day and so was limited in its ability to provide evidence for sustained alternative strategies. It does suggest that slower fish may have begun sampling the targets with smaller rewards after first shooting the more rewarding target in the initial trials of the day. Sampling, the investment in acquiring information, has been proposed as one of the issues in measuring interindividual variation in cognition (Rowe & Healy, 2014) and individuals with different behavioural traits can achieve similar mean rates of food intake while using different sampling strategies (Morand-Ferron, Varennes, & Giraldeau, 2011). Theory has suggested that individuals with different behavioural traits may have different sampling rates and use sampling information differently especially in foraging contexts (Mathot & Dall, 2013). Sampling rate, as related to cognitive styles and speed−accuracy trade-offs, is a major reason to explore interindividual differences in cognition with ecological and adaptive significance (Chittka et al., 2009; Sih & Giudice, 2012). Speed−accuracy trade-offs can be associated with environmental differences; for example, individual P. reticulata from populations with high levels of predation tended to make faster decisions, but more errors, in maze tasks than individuals from low-predation areas that made slower decisions (Burns & Rodd, 2008). The
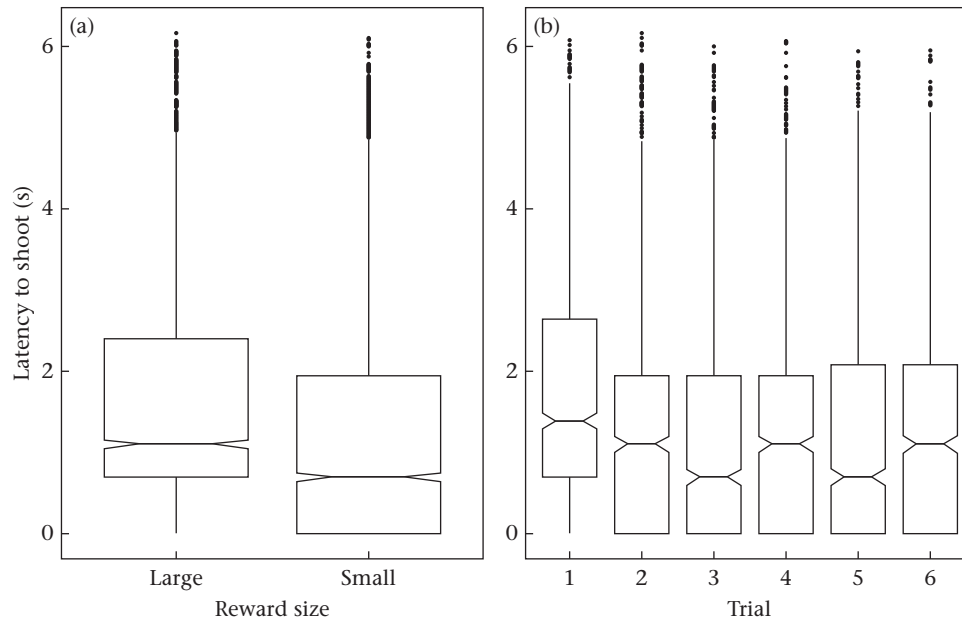
Figure 2. Mean latency to shoot in relation to (a) reward size (large or small pellet reward) and (b) trial number. Box plots show the median and 25th and 75th percentiles; the notch indicates the 95% confidence interval around the median, the whiskers extend to the data point that is no more than 1.5 times the length of the box as per the Tukey method (R package ggplot2) and the circles are outliers. $N = 16$ fish tested for 30 days each.

differences may also be linked to foraging roles within a population (Dall, Bell, Bolnick, & Ratnieks, 2012): in a social context individuals can benefit from maintaining consistent behavioural traits (Ioannou & Dall, 2016). Archerfish shooting behaviour is open to exploitation by scroungers (Davis & Dill, 2012), so consistent interindividual differences in speed−accuracy trade-offs may relate to a producer−scrounger dynamic.

Repeated testing to investigate interindividual differences in cognition has been strongly recommended (Boogert et al., 2018; Thornton, Isden, & Madden, 2014). Our study underscores this message as detection of aspects of cognitive styles would not have been observed otherwise. Individuals showed large fluctuations in success between days, as expected from previous studies showing metabolic effects on behavioural traits (Auer, Dick, Metcalfe, & Reznick, 2018; Beckmann & Biro, 2013; Biro, 2012; Careau, Thomas, Humphries, & Réale, 2008; Montiglio, Dammhahn, Messier, & Réale, 2018). Satiation level may drive 'errors' related to sampling strategies and foraging decisions (Fawcett et al., 2014; Montiglio et al., 2018; Sih et al., 2015; Stephens, 2008), and this may be especially pertinent when rapid changes in metabolism after ingesting food can affect behaviour, as shown in the common minnow, *Phoxinus phoxinus* (McLean, Persson, Norin, & Killen, 2018). Moreover, relatively minor within-day temperature changes can affect activity and behavioural traits in damselfish, *Pomacentrus moluccensis* (Biro, Beckmann, & Stamps, 2010). Specifically, for archerfish our study suggests that with a three-target discrimination system, about 15 days of testing is likely to be sufficient to capture differences in learning rates and success with clear differences in cumulative daily success between fish becoming visible between day 10 and day 15.

The number of targets was important, as interindividual differences in discrimination were statistically significant only in the three-target condition. In the two-target condition the speed-related costs to accuracy may not have been large enough to differentiate between different speed−accuracy trade-offs, fitting theory that suggests choice tests need to be challenging enough to reveal such trade-offs (Chittka et al., 2009). Increasing options in

choice tests affects decision making and accuracy, for example in bumblebees (Dukas & Real, 1993), and physiological differences at the neural level have been found in comparisons of primate subjects in two- and four-choice tests (Churchland, Kiani, & Shadlen, 2008). We expected differentially rewarding the choices would increase the challenge of our discrimination task, as fish had to discern the differences in reward size rather than an all or nothing association with the targets. Differential rewards may well have increased the challenge given that archerfish tested with three targets, but not rewarded for 'incorrect' choices, learnt faster (Newport et al., 2013) than those in our two-target condition. Our results, however, suggest that, despite the differential rewards, the number of targets or visual cues is crucial to determining the extent of interindividual differences in speed−accuracy trade-offs. A simple mechanism related to search may drive the effect of number of targets: when presented with stationary targets simultaneously archerfish look at each stimulus sequentially, as per serial search (Newport et al., 2014; Rischawy & Schuster, 2013), so that search time increases with target number. There was no significant difference in latency to shoot between the two- and three-target conditions in our trials; however, there was a significant interaction effect between condition and day. The daily mean success in

Table 2
Results of the model fitting target number (condition) on success (shots at large-reward target) across time (days of repeated testing)

	Slope/variance	SE/SD	z	Pr(>|z|)
Fixed effects				
Intercept	−0.684902	0.131367	−5.214	1.85E-07
Condition (Two)	0.928385	0.184721	5.026	5.01E-07
Day	0.015447	0.004462	3.462	5.36E-04
Condition Two*Day	−0.026534	0.006249	−4.246	2.18E-05
Random effects				
Fish ID	8.66E-02	2.94E-01		
Trial	<0.0001	<0.0001		

$N = 16$ fish, 360 trials each. Slopes and SEs are given for fixed effects and variance and SDs for random effects.
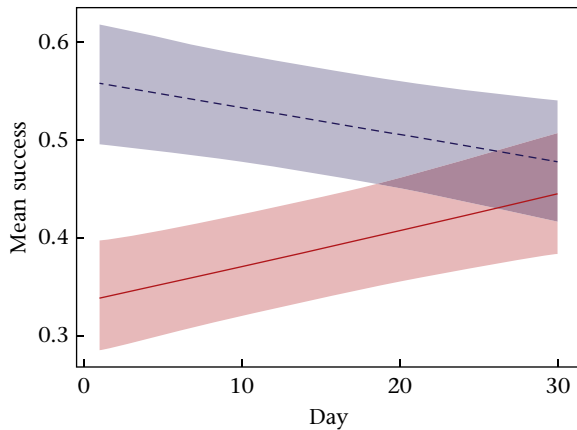
Figure 3. Mean (± 95% confidence interval) success (shots at the target associated with the large reward) for all fish in the two conditions over time. Fish had either two (blue line) or three (red line) targets available to choose from in each condition. N = 8 individuals per condition, with 12 discrimination trials each day for 30 days per fish.

the three-target condition was initially lower than that of the fish in the two-target condition but rose to a similar level over time, suggesting the additional target provided more of a challenge to discrimination.

For fish in the two-target condition there was a decrease in mean success across the 30 days of testing. We speculate that this drop may be linked to satiation effects, especially given the observed peaks and troughs in success of individual fish across days. Again, we can only speculate; however, we would suggest that this variation in success may have been a satiation ceiling effect, where fish were less motivated to shoot at the large-reward target and/or more inclined to sample the small-reward targets on days following high success, in combination with the low 'cost' for any 'error', as fish still received a (small) reward for shooting the 'nonsuccessful' targets. Fewer daily trials or smaller rewards may raise this satiation 'ceiling'.

The difference in time needed to habituate and train fish with long and short latencies corresponds with previous studies which show that individuals with 'fast' cognitive styles learn quicker; this fast learning may be linked to their lower risk sensitivity, greater exploratory tendencies and/or higher activity levels. This aspect of the cognitive styles hypothesis is well supported, with evidence from multiple studies; for example, harvest mice, *Micromys minutus*, with higher activity levels and exploratory tendencies learnt quicker than slower individuals (Schuster, Zimmermann, Hauer, & Foerster, 2017) and there are similar findings in other species (Chung et al., 2017; Guenther et al., 2014; Guillette et al., 2015; Kareklas et al., 2017). However, we note that 'learning' in cases of training animals to react to novel cues, as in our study, might reflect acclimation and/or habituation to the test procedure rather than, or in conjunction with, associative learning. The relationship between training time and cognitive styles also reinforces the cautionary point highlighted by Thornton and Lukas (2012): individuals positioned at one end of the speed–accuracy trade-off continuum may be overly represented in many cognitive studies resulting in a focus on so-called 'Olympian' individuals. In archerfish these individuals are likely to be 'fast' style fish which rapidly learn to shoot in experiments. Certainly, in our study there were more of these 'fast' than 'slow' individuals. While repeated measures can provide robust estimates from individuals, the downside is that fewer individuals may be tested as time is spent on multiple measures per individual. Our study provides a case in point, as slower fish also took much longer to train and habituate to the experimental procedure, and there was one particularly slow individual in the three-target condition. While the number of trials for each individual means that we are able to provide very robust estimates of every individual's performance, including the slowest one, removing that individual from the data set makes the slope nonsignificant (P = 0.054), but with a similar slope estimate (see Appendix Table A6) showing that our study has only just sufficient sample size to detect the effect of interest.

In conjunction with our main aim to test the cognitive styles hypothesis in a longitudinal study, in this paper we have attempted to mitigate the methodological issues that may make it hard to
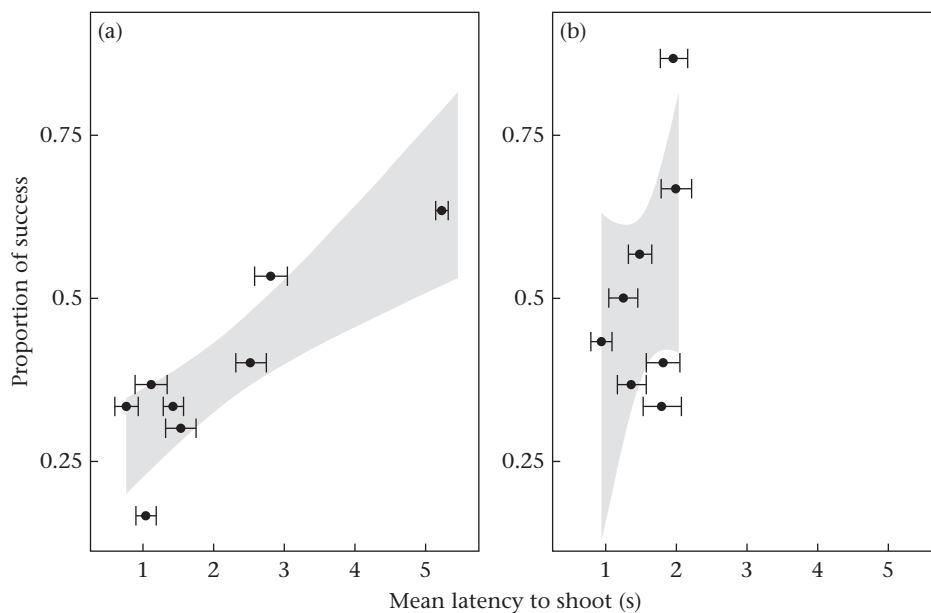

Figure 4. Proportion of success (shots at the target associated with the large reward) in initial daily trials relative to mean latency to shoot in (a) the three-target condition and (b) the two-target condition. The black points denote the cumulative proportion of successes for all 30 trials for each fish plotted against their individual mean latency to shoot. The grey band is the estimated 95% prediction intervals given the fitted model. N = 30 trials (initial trial per day) for 30 days for each of eight fish per condition.

reveal interindividual differences in tests. As such we note that the influence of sex can be important and has been shown to explain a significant amount of variation in effect size in studies of interindividual variation (Dougherty & Guillette, 2018). The speed-related differences in success we observed may be connected to the sex of the individuals. Although we believe this is unlikely given the lack of any morphological or behavioural dimorphism in this species, future studies in this area with archerfish may benefit from investigating the effect of sex.

In conclusion, we have shown that speed–accuracy trade-offs are an important component in interindividual differences in discrimination performance in archerfish. Individuals that consistently took more time before shooting were more successful in discriminating between targets with different levels of reward. The behaviour of archerfish in the three-target condition was consistent with the cognitive styles hypothesis as they exhibited consistent individual differences in performance, while maintaining similar mean success. However, as expected from previous theory, these speed–accuracy trade-off effects were only evident across the initial trials each day when motivation was expected to be highest, and when more than two choices were presented. Similar longitudinal studies in other taxa may help further disentangle the complexity of cognitive styles and interindividual differences in cognition.

Data availability

All data can be provided upon request. They are also available at https://osf.io/6b3v4/?view_only=b49be8debbc5458c99d873fe32da6038.

Declaration of competing interest

We have no conflicts of interest.

Acknowledgments

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APPENDIX 1. ADDITIONAL RESULTS

Table A1
Summary of results for the repeatability *R* in latency to shoot across time

Grouping variable	R	SE	Lower CI	Upper CI	No. of observations
FishID	0.455	0.093	0.234	0.601	5626
Fixed	0.045	0.057	0.016	0.225	

Estimates were analysed with 1000 bootstraps. CI: confidence interval.

Table A2
Summary of results for the repeatability *R* in success

Grouping variable	R	SE	Lower CI	Upper CI	No. of observations
FishID	0.0228	0.0095	0.00727	0.0435	5626
Fixed	0.0158	0.0102	0.00229	0.042	

Estimates were analysed with 1000 bootstraps. CI: confidence interval.

Table A3
Model results of the GLM fitting the influence of individual mean fish speed (latency) on proportion of success in all trials

Predictor variable	Estimate	SE	t
Intercept	0.26677	0.05015	5.32
Mean latency of fish	0.03834	0.02001	1.916
Target number (Two)	0.11155	0.04134	2.698

N = 16 fish, 360 trials each.

Table A4
Model results of the GLM fitting the influence of individual mean fish speed (latency) on proportion of success in the first trials for fish in the two-target condition

Predictor variable	Estimate	SE	P
intercept	0.1101	0.2	0.674
Mean latency of fish	0.2801	0.2	0.132

N = 8 fish, 30 trials each.

Table A5
Model results of the GLM fitting the influence of individual mean fish speed (latency) on proportion of success in the first trials for fish in the three-target condition

Predictor variable	Estimate	SE	t	P
Intercept	0.20772	0.0483	4.303	0.005
Mean latency of fish	0.08531	0.0195	4.374	0.005

N = 8 fish, 30 trials each.

Table A6
Model results of the GLM fitting the influence of individual mean fish speed (latency) on proportion of success in the first trials as above but excluding the slowest fish

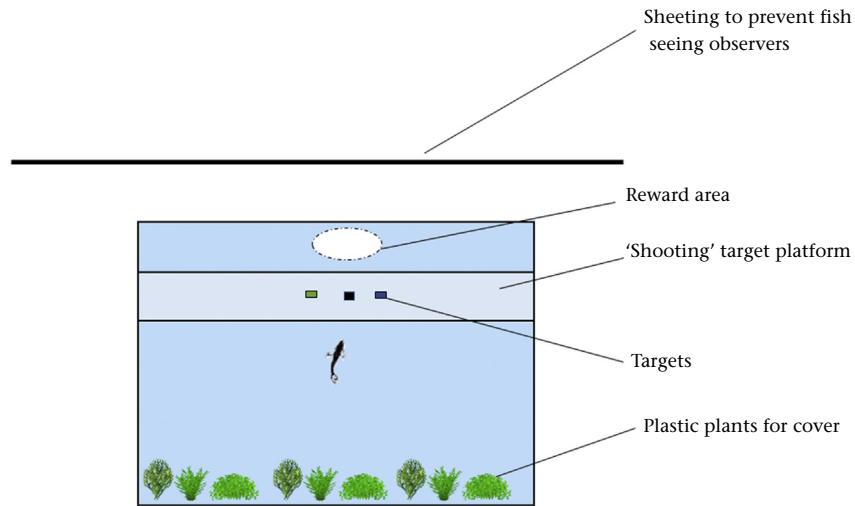| Predictor variable	Estimate	SE	t	P
Intercept	0.17709	0.07462	2.373	0.064
Mean latency of fish	0.10624	0.04245	2.503	0.054

Figure A1. Sketch of the experimental set-up, top-down view, as recorded by the camera above the tank.
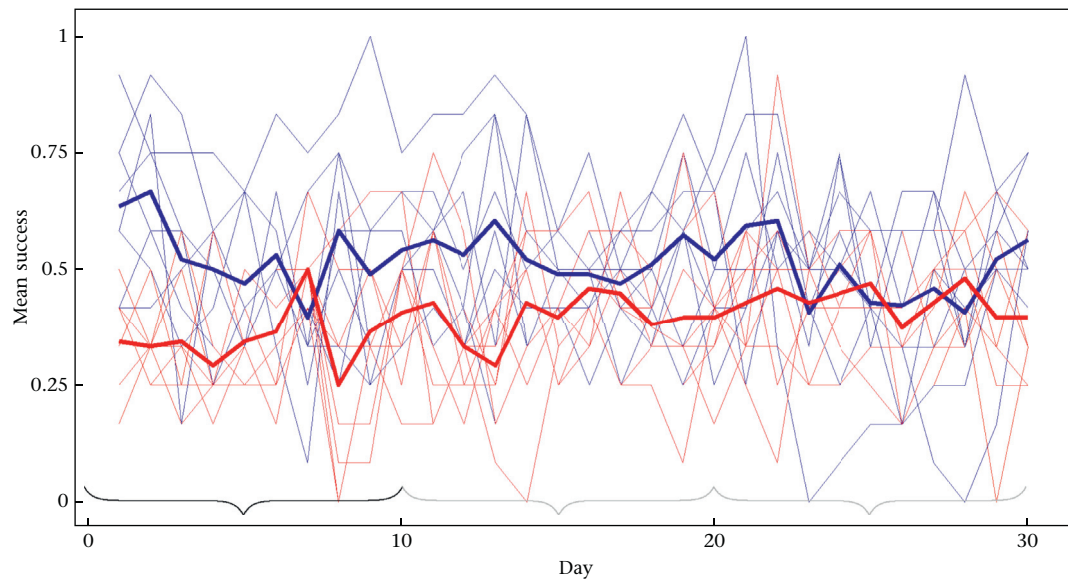

Figure A2. Success in discrimination over time in both conditions. Bold lines are group means for fish that had either two (blue) or three (red) targets available to choose from. Pale lines show mean success of individual fish. Black braces indicate the periods of time (where we divided the time into three 10-day periods) during which mean success differed between conditions ($P < 0.005$); grey braces indicate no significant difference. $N = 8$ individuals per condition, with 12 discrimination trials each daily for 30 days for each fish.
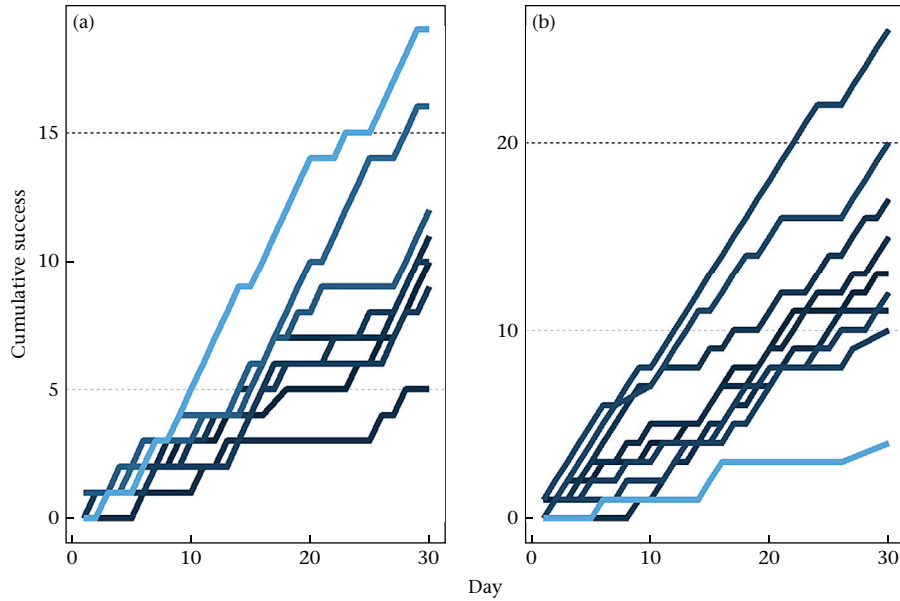
Figure A3. First trial success (shots at the target associated with the large reward) over successive days for each fish in (a) the three-target condition and (b) the two-target condition. Separate lines are plotted for each fish with mean speed for each fish indicated by shade of blue (lighter = slower). Dotted lines indicate levels within which cumulative success differed significantly from chance ($P < 0.05$, exact binomial test). $N = 8$ fish per condition.

APPENDIX 2. PILOT STUDY

To explore whether there were differences in latency to shoot a target and/or preferences across targets we conducted a pilot study with five different fish prior to beginning the main experiment. We presented the same targets with the same colours (black, white, green and blue) as used in the main experiment to each fish that had previously been trained to shoot at a single reward (either black or white). A random selection of three of the four targets were presented simultaneously, and protocols used for these trials were the same as those used for experimental trials, except that we allowed up to 15 min for fish to shoot per trial and all shots at a target were rewarded equally with a small reward.

Fish were presented with three targets at the same time, but position and order of placement of the targets on the shooting platform in each trial were randomized, and each target had the same reward. We recorded which target was shot in each of 18 trials per session and the latency to shoot for each trial.

We analysed effect of target on latency to shoot using a repeated measures ANOVA of latency to shoot according to target, with the fish identity term as a random factor; see below using *R* terminology.

$$\text{modelLatency} = \text{lme}(\text{Latency} \sim \text{Target}, \text{random} = \sim 1|\text{FishID}, \text{data} = \text{PilotColour}, \text{method} = \text{"REML"})$$

Latency to shoot was not significantly affected by target colour (LRT: $\chi^2_3 = 0.105$, $P = 0.991$; Fig. A4); however, the white target had greater variation in shot latency than the other three targets. Target colour did affect the number of shots made (LRT: $\chi^2_3 = 18.091$, $P = 0.0004$; Fig. A5): fish shot white targets less than the other ones (green: emmean: $t = 3.722$, $P = 0.004$; blue: emmean: $t = 1.05$, $P = 0.030$).
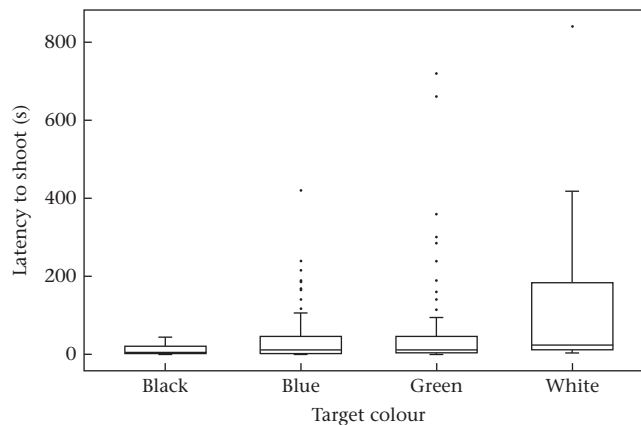

Figure A4. Latency to shoot at targets of different colours in the pilot study. The box plots show the median and 25th and 75th percentiles; the whiskers extend to the data point that is no more than 1.5 times the length of the box as per the Tukey method (R package ggplot2) and the circles are outliers. $N = 5$ fish, 36 trials each.
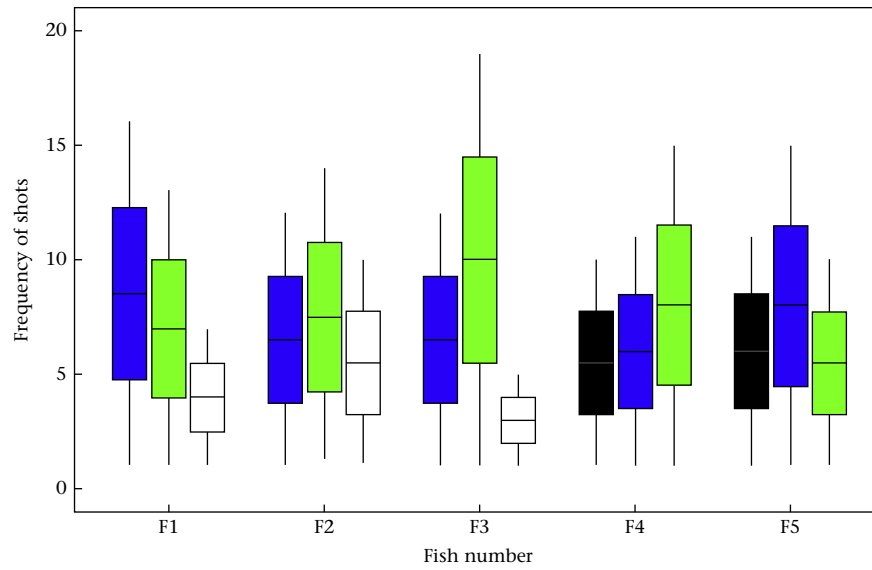
Figure A5. Frequency of shots at blue, green, white and black targets by each fish in the pilot study. Box plots show the median, 25th and 75th percentiles; the whiskers extend to the data point that is no more than 1.5 times the length of the box as per the Tukey method (R package ggplot2). $N = 5$ fish, 36 trials each.

As the blue, green and black targets were all shot with similar frequencies and latencies, they were used as targets in the experimental trials of the main experiment, with white targets reserved for the initial training.