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

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Abstract

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 taxa specific differences but may also be due to the difficulty in separating intra-individual from inter-individual 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. In an attempt 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 where we presented 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 of every day, supporting the cognitive styles hypothesis. However, this relationship was only statistically significant 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 inter-individual differences in cognition.

Keywords

behavioural variation; cognition; cognitive styles; discrimination; speed–accuracy trade-offs; Toxotes chatareus
Introduction

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 and Giudice 2012). Variation in cognitive performance is repeatable at the individual level across a wide array of vertebrate and invertebrate taxa (Cauchoirx et al. 2018), and interest in the causes and consequences of this variation has burgeoned (Boogert et al. 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 et al. 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 et al. 2015). This speed accuracy trade-off (SAT) is exhibited across a wide array of organisms (Rival et al. 2003; Latty and Beekman 2011), and is considered to be a major factor underlying differences in cognitive performance (Sih and Giudice 2012; Heitz 2014). Sih and Giudice (2012) proposed that speed–accuracy trade-offs underpin the relationship between cognition and certain behavioural traits where individuals that show consistent and repeatable differences in speed accuracy trade-offs are considered to have different ‘cognitive styles’.

Many species have high inter-individual variation in certain behaviours, with individuals exhibiting consistent, repeatable levels of those behaviours (Bell et al. 2009), or suites of correlated behaviours – as per behavioural syndromes (Sih et al. 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 with more active and more exploratory bank voles, *Myodes glareolus*, make faster decisions (Mazza et al. 2018)) and, similarly, more aggressive spiders, *Portia labiate*, make faster decisions (Chang et al. 2017). Many of these behavioural traits are frequently linked to risk sensitivity (Jones and Godin 2010). According to the cognitive styles hypotheses, 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 which are more active...
and show lower sensitivity to risk (Sih and 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 et al. 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 have quicker learning rates in many situations (possibly as a result of being more exploratory and/or less neophobic) (Chittka et al. 2009; Sih and Giudice 2012; Guenther et al. 2014). Recent studies of SAT-driven differences in cognitive performance support this hypothesis (Chittka et al. 2003; Chittka et al. 2009; Exnerová et al. 2010; Ducatez et al. 2015; Guillette et al. 2015; Moiron et al. 2016). For example, individual great tits (*Parus major*) that tended to make slower decisions were more accurate (Moiron et al. 2016), and Wang et al. (2015) showed both that zebrafish (*Danio rerio*) exhibit inter-individual differences in SATs, 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 et al. 2015), with similar results observed in other species including bumblebees, *Bombus terrestris*, (Raine and Chittka 2012), lizards, *Lampropholis delicata*, (Chung et al. 2017), spiders, *Portia labiata*, (Chang et al. 2017), and several other species of fish; *Poecilia reticulata* (Lucon-Xiccato and Bisazza 2016), *Gnathonemus petersii* (Kareklas et al. 2017), and *Poecilia mexicana* (Sommer-Trembo and Plath 2018). The link between individual differences in cognition and SAT 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 sex of individuals, taxa specific differences, but also by methodological issues (Dougherty and Guillette 2018). Several reviews have suggested that the experimental approaches used in this developing field may sometimes impede the exploration of inter-individual differences in cognition and impact the interpretation of results (Carter et al. 2013; Rowe and Healy 2014; Griffin et al. 2015; Boogert et al. 2018).
Test difficulty may impact the optimal trade off in SAT strategies, where the relative ease of a task, for example the number of choices in a discrimination test, can be important (Raffa et al. 2002; Chittka et al. 2009). 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 and Stamps 2010; Mathot and Dall 2013; McKenzie et al. 2015). Motivation in learning assays can be affected by level of satiation (Shettleworth 1972; Ben-Shahar and Robinson 2001), and motivational differences have been shown to override cognitive differences in problem solving tasks (van Horik and Madden 2016).

Additionally, coping styles - where individuals show distinct differences in vulnerability and response to stress (Koolhaas et al. 1999) - can drive consistent inter-individual variation in behaviour and can both directly affect learning, for example in reversal learning tests (Bensky et al. 2017), and can also indirectly impact measure of cognition (McEwen and Sapolsky 1995; Mesquita et al. 2015; Raoult et al. 2017). The term coping style is sometimes used interchangeably with behavioural syndromes in the literature and while they 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 to behavioural traits and do not form syndromes with behavioural traits (Zidar et al. 2017). One method that has been suggested to reduce the effect of potentially confounding non-cognitive factors is to use repeated, or longitudinal, tests (Thornton and Lukas 2012; Sih et al. 2015; Boogert et al. 2018).

We used archerfish (Toxotes chatareus) to explore SATs 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 specialised foraging ability to shoot down prey by spitting jets of water, are visual predators (Ben-Tov et al. 2018) and increasingly used in studies of spitting jets of water, are visual predators (Ben-Tov et al. 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 (Gabay et al. 2013; Newport et al. 2014; Ben-Tov et al. 2015; Newport et al. 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; Rischawy and Schuster 2013; Newport et al. 2018; Saban et al. 2017; Gabay et al. 2013). They can also learn to associate targets with differential rewards (Karoubi et al. 2017) and exhibit distinct inter-individual differences in latency to shoot (Jones et al. 2018), with initial evidence suggesting that individuals may use different decision making strategies (Newport et al. 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 measured decision time (latency to shoot) and decision accuracy as discrimination success (shots at target corresponding to the large reward), hereafter success. 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 in a condition 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 (discrimination success).

Specifically, that fish with greater latencies to shoot would have increased discrimination success, 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. All fish were wild caught and sourced as a single order from an accredited ornamental fish retailer. Fish 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 5-8 fish, in large individually filtered tanks (180 × 45 cm and 35 cm deep) with temperatures between 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 – using a ruler taped to the side of the tank, netted fish were gently pressed against the side of the tank to record their length before being moved to the experimental tank.

Experimental set-up

During trials fish were kept individually in tanks of equal dimensions (55 x 55 cm and 45 cm deep), with a camera above each tank to record trials from a top-down perspective, see 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 observe and record for later scoring of 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 first trained to shoot a novel target presented
on the shooting platform, using two stages – they were first trained to shoot a known food item (a pellet) and then in stage 2 trained to shoot a novel white artificial target. In the second phase the fish were given a set number of trials to familiarise themselves with the experimental targets presented individually. Finally, fish were tested in daily discrimination trials for 30 consecutive days using those targets presented simultaneously in two conditions - two targets 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 numbers of targets that were presented to the fish to discriminate between in the final phase. In the ‘two targets’ condition fish were presented with two targets - one target which was rewarded with a large reward and one target was rewarded with a small reward; in the ‘three targets’ condition fish were presented with three targets, one target was rewarded with a large reward and two targets with small rewards.

The four targets used in this experiment were hand cut plastic squares, (2 cm², 3 - 5 mm thick) differing in colour (green, blue, black or white). Food rewards were pre-cut 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 were used only in the training phase and the remainder (green, blue, black) were used in the familiarisation 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 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 familiarised 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 ~30 seconds after a previous trial.

Targets were placed by hand, such that in the trials there was a slight delay between placing the first and last targets. 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 second 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 attempted to jump for food rewards occasionally, again <1% of all trials, and mostly these jumps were made 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 minutes per session with a maximum trial number of ten trials – each trial continued either until the fish shot or the 50 minutes 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) and 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 minutes, where the time limit
was based on a previous study fish with similar procedure in which all fish shot within 6 minutes
(Jones et al. 2018). There was an initial maximum of 45 daily sessions allowed for this part of
training, however several fish reached the maximum limit without reaching 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
acclimatisation time, as shown for other species (O’Neill et al. 2018).

Phase 2: Familiarising with coloured targets

The familiarity phase, beginning the day after achieving the second training criterion, introduced fish
to the targets and initial learning opportunity of 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 and Weisman 2006), and thereby reduce initial target bias.

Each fish was subjected to six familiarity sessions split over three 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 within 4 - 5 cm from each other 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 ~10:00 am and ~16:30 pm), per day. Fish were afforded an 8 minute maximum trial limit. Latency to shoot, colour of the shot target and size of reward were scored from video recordings. A hypothesis-naive secondary observer scored ~20% of the trials. Inter-rater reliability comparing the principal (NJ) and secondary scores of latency to shoot, using the irr package (Gamer et al. 2012), showed high agreement with an inter-class correlation of .992 to .994, and mean of 0.993 ; \( F_{1073,1073} = 270, \ = 141 , P <0.001 \).

Of the 20 fish we used for this experiment four fish were not used in all 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 less than half of discrimination trials and was excluded from analysis of discrimination success so only 16 fish (8 in each condition) were included in the analyses for speed accuracy trade-offs.

Ethics

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. 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., 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 et al. 2018) where appropriate. Data are available at:

https://osf.io/6b3v4/?view_only=b49be8debbec5458c99d873fe32da6038

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 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 discrimination success, i.e. shooting at the large-rewarded 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 et al. 2015) with latency to shoot in seconds 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 comparing the reduced with the full model. The model we fitted was the following (in R syntax):
LogLatency ~ Reward * Condition + Reward * Day + Condition * Day + Trial + (1|FishID) + (1|Session)

The condition term was a factor with two levels (either two or three targets), and the ‘Reward’ term is 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-rewarded target. The final model was:

Success ~ Condition * Day + (1|FishID) + (1|Trial) + (1|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 et al. 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 discrimination success**

To examine the effect of latency to shoot on overall mean daily success in the discrimination phase we fitted a binomial family GLM to the proportion of successful trials from all trials over the thirty days for each fish, with individual mean latency and condition (2 or 3 targets) as the independent variables. The model fitted was:

glm(proportion of success ~ MeanLatency * 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 numbers of training sessions (combining both stages) required to achieve criterion. Slower shooting fish required more sessions to reach training criteria (LM: \( t = 2.395, P = 0.030 \); Fig 1). A similar effect was found even after removing the two slowest fish (LM: \( t = 3.519, P = 0.004 \)).

**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.
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, and latency to shoot ‘large-reward’ targets were on average 1.3 seconds greater than ‘small-rewarded’ targets (emmean: $\bar{z}_{8.642} = 0.248, P < 0.001$; 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: $\chi^2_1 = 1.0884, P = 0.297$), however there was a significant interaction between time (Day) and condition (LRT ($\chi^2_1 = 103.4931, P < 0.001$).
Figure 2. Mean latency is significantly ($P<0.001$) affected by (a) reward size (large or small pellet reward) and (b) trial number. Box plots show the median, 25th and 75th percentiles, and the notch indicates the 95% confidence interval around the median. $N = 16$ fish tested for 30 days each.

**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-rewarded target more frequently (LRT on ‘Condition’: $\chi^2_{1} = 10.7317$, $P = 0.001$; 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 (see Fig A2), on average the number of targets was important with a significant interaction between time (Days) and number of targets (LRT: $\chi^2_{1} = 18.0290$, $P < 0.001$; Fig 3; Table 2).
Figure 3. Mean, ± 95% C.I, discrimination success (shots at the target associated with the larger 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.

**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 inter-individual differences in latency to shoot (*R* ± SE =0.455 ± 0.093) (Table A 1). It is worth noting that repeatability for overall success was much lower at (*R* ± SE =0.028 ± 0.0095; Table A 2).

**Individual differences in latency and discrimination success**

Overall mean daily success (proportion of shots at large rewarded target) was not significantly affected by individual mean latency (GLM: *t* =2. 916, *P* = 0.078; Table A3), and this held for fish in
conditions with both two (GLM: $t = 0.432, P = 0.681$; Table A4) and, despite a positive trend between latency and accuracy, three (GLM: $t = 2.183, P = 0.072$; Table A5) targets. Success in the first trial of the day was affected by individual mean latency: slower fish had greater success in the condition with three target choice (GLM: $t = 4.374, P = 0.005$; Fig 4a), with cumulatively increasing success in first trials across time for slower fish (Fig A.3a). However, while proportion of success showed a positive relationship with individual mean latency in the two targets condition but was not statistically significant (GLM: $t = 1.800, P = 0.132$; Fig 4b) and fish speed did not predict cumulative successes (Fig A.3b).

Figure 4. Proportion of success (shots at target corresponding to large reward) in initial daily trials relative to mean latency to shoot in (a) three targets, and (b) two target conditions. 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 8 fish per condition.

**Discussion**
In line with our primary aim we show that archerfish exhibit consistent individual differences in speed accuracy trade-offs and provide empirical support for the hypothesis that differences in decision speed can explain inter-individual 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 style hypotheses (Sih and 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 success. 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 discrimination success increasing along the fast–slow continuum. These SAT based differences in discrimination accuracy were observed only when comparing the outcomes from the first trial of each day, when motivation is expected to be highest. Our results also suggest that the numbers of targets, or choices, was important for revealing these SAT based inter-individual differences in discrimination success. Mean daily success of individuals within each condition did not significantly differ, 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 is limited in 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 inter-individual variation in cognition (Rowe and Healy 2014) and individuals with different behavioural traits can achieve similar mean rates of food intake while using different sampling strategies (Morand-Ferron et al. 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 and Dall 2013). Sampling rate, as related to cognitive styles and SATs, is a major reason to explore inter-individual differences in cognition with ecological and adaptive significance (Chittka et al. 2009; Sih and Giudice 2012). SATs can be associated with
environmental differences, for example individual guppies (*Poecilia 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 and Rodd 2008). The differences may also be linked to foraging roles within a population (Dall et al. 2012): where in a social context individuals can benefit from maintaining consistent behavioural traits (Ioannou and Dall 2016). Archerfish shooting behaviour is open to exploitation by scroungers (Davis and Dill 2012), so consistent inter-individual differences in SAT may relate to a producer scrounger dynamic.

Repeated testing to investigate inter-individual differences in cognition has been strongly recommended (Thornton et al. 2014; Boogert et al. 2018). 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 (Careau et al. 2008; Biro 2012; Beckmann and Biro 2013; Auer et al. 2018; Montiglio et al. 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 et al. 2018). Moreover, relatively minor within-day temperature changes can affect activity and behavioural traits in damselfish *Pomacentrus moluccensis* (Biro et al. 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 discrimination success with clear differences in cumulative daily success between fish becoming visible between day 10 and day 15.

The numbers of targets was important, as inter-individual 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 SATs, fitting theory that suggests choice tests need to be challenging enough to reveal SATs (Chittka et al. 2009). Increasing options in choice tests affects decision making and accuracy, for example in bumblebees (Dukas and Real 1993), and physiological differences at the neural level have been found in
comparisons of primate subjects in two and four choice tests (Churchland et al. 2008). We expected differentially rewarded choices would increase the challenge of our discrimination task, as fish had to discern the differences in reward size rather than a simple all or nothing association with the targets. It may well have added a challenge for the fish given a previous study which tested archerfish in a three alternative forced choice test showed faster learning than those in our two-target condition (Newport et al. 2013), however, our results suggest that numbers of targets or visual cues is crucial to making inter-individual differences in SAT. A simple mechanism related to search may drive this: when presented with stationary targets simultaneously archerfish look at each stimulus sequentially, as per serial search (Rischawy and Schuster 2013; Newport et al. 2014), so that search time increases with target number, and although there was no significant difference in latency to shoot in our trials there was a significant interaction effect with day. Archerfish use search strategies similar to other species, including humans (Ben-Tov et al. 2018), and increasing numbers of choices may affect exploration of SATs in other taxa. In addition, the daily mean success in 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. Here we would like to note that the drop in daily success for the two-target condition. We speculate this is linked to satiation effects, especially given the observed peaks and troughs in discrimination success of individual fish across days. Again, we can only speculate, however we would suggest that this may have been a satiation ceiling effect, where fish were less motivated to shoot at the large rewarded target and or more inclined to sample the smaller-rewarded 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 ‘non-successful’ targets. Fewer daily trials or smaller rewards may have raised this satiation ‘ceiling’.

The differences in time to habituate and train fish with higher latencies corresponds with previous studies which show that individuals with ‘fast’ cognitive styles learn quicker and may be linked to their lower risk sensitivity, exploratory tendencies and or 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 and exploratory tendencies, learnt quicker than slower
individuals (Schuster et al. 2017), and similar findings in other species (Guenther et al. 2014; Guillette et al. 2015; Chung et al. 2017; Kareklas et al. 2017). However, we note that ‘learning’ in cases of training animals to react to novel cues, as in our study, might be a reflection of acclimation and or habituation to testing 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 with positions on one end of the SAT 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 learn to shoot in experiments rapidly. Certainly, in our study there were more ‘fast’ style than ‘slow’ individuals. And while repeated measures can provide robust estimates from individuals, the downside is 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 that slowest one, removing that individual from the dataset makes the slope non-significant (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 the main aim to test the cognitive styles hypothesis in a longitudinal study one of the focuses in this paper has been attempting to mitigate the methodological issues that may make it hard to reveal inter-individual differences in tests. As such we must 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 inter-individual variation (Dougherty and Guillette 2018). The observed differences in speed related differences in discrimination success may be connected to 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 show that the SATs are an important component in inter-individual differences of discrimination performance in archerfish. Individuals that consistently take more time before shooting
are more successful in discriminating between targets with different levels of reward. The behaviour of archerfish in the three-target condition is consistent with the cognitive styles theory as they exhibit consistent individual differences in performance, while maintaining similar mean success. However, as expected from previous theory these SAT effects are only evident across initial trials per day when motivation is expected to be highest, and when more than two choices are presented. Similar longitudinal studies in other taxa may help further disentangle the complexity of cognitive styles and inter-individual differences in cognition.

**Declaration of interest**

Declarations of interest: none.

**Acknowledgements**

We thank Helen Spence-Jones for acting as a secondary video scorer. Thanks to Tania Mendo for support and advice throughout the study. Barbara Klump and Samuel Walmsley provided useful comments and Maria Joao Janeiro for statistical advice. A special thank you to Rory Malcolm.

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References


Ioannou CC, Dall SRX. 2016. Individuals that are consistent in risk-taking benefit during collective foraging. *Scientific Reports*. 6:33991. doi:10.1038/srep33991.


**Appendix 1: Additional results**

Supporting tables and graphs are presented here as mentioned in the main text.

**Appendix 2: Results of pilot study exploring the effect of target colour on latency and frequency of selection**

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 we allowed up to 15 minutes 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 was randomised, and each target was rewarded with 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.

```
modelLatency = lme(Latency ~ Target, random = ~1|FishID,data=PilotColour, method="REML")
```

Latency to shoot was not significantly affected by target colour (LRT: $\chi^2_3 = 0.1054$, $P = 0.9912$; Figure 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: $\chi^2_3 = 18.091$, $P = 0.0004$; Figure A5), fish made fewer shots at white targets compared to green or blue targets (emmean: $t = 3.722$, $P = 0.0036$), (emmean: $t = 1.05$, $P = 0.0302$) respectively.
As the blue, green, and black targets were all targeted 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.

**Data accessibility**

All data can be provided upon request. Data has also been uploaded to the OSF, please use the link below to view the data. This link has been anonymised for the double-blind review process:

https://osf.io/6b3v4/?view_only=b49be8debb6c5458c99d873fe32da6038
### Table 1: Parameter estimates for effects of reward type, condition, and trial, on latency to shoot.

<table>
<thead>
<tr>
<th>fixed effects</th>
<th>estimate</th>
<th>s.e.</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept</td>
<td>2.504839</td>
<td>0.374106</td>
<td>6.696</td>
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<tr>
<td>Reward-small</td>
<td>0.225015</td>
<td>0.065541</td>
<td>-3.433</td>
</tr>
<tr>
<td>Condition (Two)</td>
<td>1.042921</td>
<td>0.51992</td>
<td>-2.006</td>
</tr>
<tr>
<td>Day</td>
<td>0.018908</td>
<td>0.003024</td>
<td>-6.252</td>
</tr>
<tr>
<td>Trial2</td>
<td>-0.43565</td>
<td>0.047785</td>
<td>-9.089</td>
</tr>
<tr>
<td>Trial3</td>
<td>0.447795</td>
<td>0.047908</td>
<td>-9.347</td>
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<tr>
<td>Trial4</td>
<td>0.430721</td>
<td>0.047829</td>
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<tr>
<td>Trial5</td>
<td>0.448379</td>
<td>0.047874</td>
<td>-9.366</td>
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<tr>
<td>Trial6</td>
<td>0.392536</td>
<td>0.048007</td>
<td>-8.177</td>
</tr>
<tr>
<td>Reward-small:Condition Two</td>
<td>-0.015648</td>
<td>0.057261</td>
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<tr>
<td>ConditionTwo:Day</td>
<td>0.033454</td>
<td>0.003289</td>
<td>10.173</td>
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**random effects**

<table>
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<th>variance</th>
<th>s.d.</th>
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<td>Fish ID</td>
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<tr>
<td>Session</td>
<td>0.00536</td>
</tr>
<tr>
<td>Residual</td>
<td>1.07979</td>
</tr>
</tbody>
</table>

(N = 16 fish, 360 trials each)

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

| fixed effects                  | slope    | s.e.  | z    | Pr(|z|) |
|-------------------------------|----------|-------|------|-------|
| 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 |
| ConditionTwo:Day              | -0.026534 | 0.006249 | -4.246 | 2.18E-05 |

**random effects**

<table>
<thead>
<tr>
<th>variance</th>
<th>s.d.</th>
</tr>
</thead>
<tbody>
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<td>Fish ID</td>
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<tr>
<td>Trial</td>
<td>&lt;0.0001</td>
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</tbody>
</table>

(N = 16 fish, 360 trials each)
Appendix tables

Table A1. Summary of results for the repeatability ‘R’ in latency to shoot across time.

<table>
<thead>
<tr>
<th>Grouping variable</th>
<th>R</th>
<th>SE</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>FishID</td>
<td>0.455</td>
<td>0.093</td>
<td>0.234</td>
<td>0.601</td>
<td>5626</td>
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<tr>
<td>Fixed</td>
<td>0.045</td>
<td>0.057</td>
<td>0.016</td>
<td>0.225</td>
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</tr>
</tbody>
</table>

Estimates analysed with 1000 bootstraps.

Table A2. Summary of results for the repeatability ‘R’ in success.

<table>
<thead>
<tr>
<th>Grouping variable</th>
<th>R</th>
<th>SE</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>FishID</td>
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<td>0.0095</td>
<td>0.00727</td>
<td>0.0435</td>
<td>5626</td>
</tr>
<tr>
<td>Fixed</td>
<td>0.0158</td>
<td>0.0102</td>
<td>0.00229</td>
<td>0.042</td>
<td></td>
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</tbody>
</table>

Estimates analysed with 1000 bootstraps.

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

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept</td>
<td>0.26677</td>
<td>0.05015</td>
<td>5.32</td>
</tr>
<tr>
<td>Mean latency of fish</td>
<td>0.03834</td>
<td>0.02001</td>
<td>1.916</td>
</tr>
<tr>
<td>Target Number (Two)</td>
<td>0.11155</td>
<td>0.04134</td>
<td>2.698</td>
</tr>
</tbody>
</table>

(360 trials for each fish $N = 16$).

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 $N = 8$ fish in the two-target condition.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Estimate</th>
<th>SE</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept</td>
<td>0.1101</td>
<td>0.2</td>
<td>0.674</td>
</tr>
<tr>
<td>Mean latency of fish</td>
<td>0.2801</td>
<td>0.2</td>
<td>0.132</td>
</tr>
</tbody>
</table>

(30 trials for each fish).

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 $N = 8$ fish in the three-target condition.
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.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept</td>
<td>0.20772</td>
<td>0.04827</td>
<td>4.303</td>
<td>0.00507</td>
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<tr>
<td>Mean latency of fish</td>
<td>0.08531</td>
<td>0.0195</td>
<td>4.374</td>
<td>0.0047</td>
</tr>
</tbody>
</table>

(30 trials per fish).
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 which had either two (blue) or three (red) targets available to choose from. Pale lines show mean success of individual fish. Black brackets indicate the periods of time (where we divided the time into three ten-day periods) during which mean success differed between condition ($P<0.005$) grey brackets indicates 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 taken at target corresponding to large reward) over successive days for each condition. (a) cumulative success in the first trial for each fish in the three-target condition and (b) cumulative success in the first trial for each fish in two-target condition. Separate lines are plotted for each fish with mean speed for each fish indicated by shade of blue (lighter = slower). Dotted line indicates levels within which cumulative success significantly differs from chance ($P < 0.05$, Exact binomial test). $N = 8$ fish per condition.
Figure A4. Latency per target for pilot study. N = 5 fish, 36 trials each.

Figure A5. Frequency of shots made per target, by each fish in the pilot study. N = 5 fish, 36 trials each. 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).