

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

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22 **Abstract**

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

43 **Keywords**

44 behavioural variation; cognition; cognitive styles; discrimination; speed–accuracy trade-offs; *Toxotes*
45 *chatareus*

46 **Introduction**

47 To understand the evolution of cognition, it is important to understand both the nature of the variation
48 selection has to work with, and the relationship between individual cognitive performance and fitness
49 (Dukas 2004; Sih and Giudice 2012). Variation in cognitive performance is repeatable at the
50 individual level across a wide array of vertebrate and invertebrate taxa (Cauchoix et al. 2018), and
51 interest in the causes and consequences of this variation has burgeoned (Boogert et al. 2018). Most of
52 the focus on measuring this variation has been devoted to performance or decision outcomes in
53 relation to behavioural traits, but variation can also be expressed in decision time with a link between
54 decision time and outcome (Chittka et al. 2009). Faster decisions are more prone to error than slower
55 decisions, and this relationship between speed and decision accuracy often results in a trade-off that is
56 fundamental to all information pathways and decision making (Standage et al. 2015). This speed
57 accuracy trade-off (SAT) is exhibited across a wide array of organisms (Rival et al. 2003; Latty and
58 Beekman 2011), and is considered to be a major factor underlying differences in cognitive
59 performance (Sih and Giudice 2012; Heitz 2014). Sih and Giudice (2012) proposed that speed–
60 accuracy trade-offs underpin the relationship between cognition and certain behavioural traits where
61 individuals that show consistent and repeatable differences in speed accuracy trade-offs are
62 considered to have different ‘cognitive styles’.

63 Many species have high inter-individual variation in certain behaviours, with individuals exhibiting
64 consistent, repeatable levels of those behaviours (Bell et al. 2009), or suites of correlated behaviours –
65 as per behavioural syndromes (Sih et al. 2004). Many of these behavioural traits or syndromes can be
66 placed on a continuum of fast to slow behavioural types. For example, exploration tendency and
67 activity have been shown to relate to decision speed with more active and more exploratory bank
68 voles, *Myodes glareolus*, make faster decisions (Mazza et al. 2018)) and, similarly, more aggressive
69 spiders, *Portia labiate*, make faster decisions (Chang et al. 2017). Many of these behavioural traits are
70 frequently linked to risk sensitivity (Jones and Godin 2010). According to the cognitive styles
71 hypotheses, individuals with consistently low levels of activity, and higher sensitivity to risk, may be
72 expected to take more time but make more accurate decisions than individuals which are more active

73 and show lower sensitivity to risk (Sih and Giudice 2012). In cognitive tests, as used in
74 psychophysical trials where individuals must discriminate between rewarded and unrewarded cues,
75 slower individuals are expected to achieve greater success than quicker individuals, as shown in
76 bumblebees (*Bombus terrestris*) (Chittka et al. 2003). Conversely, individuals that make quicker
77 decisions are presumed to suffer costs to accuracy, but be less risk-sensitive, more likely to engage
78 with novel objects, and have quicker learning rates in many situations (possibly as a result of being
79 more exploratory and/or less neophobic) (Chittka et al. 2009; Sih and Giudice 2012; Guenther et al.
80 2014). Recent studies of SAT-driven differences in cognitive performance support this hypothesis
81 (Chittka et al. 2003; Chittka et al. 2009; Exnerová et al. 2010; Ducatez et al. 2015; Guillette et al.
82 2015; Moiron et al. 2016). For example, individual great tits (*Parus major*) that tended to make
83 slower decisions were more accurate (Moiron et al. 2016), and Wang *et al.* (2015) showed both that
84 zebrafish (*Danio rerio*) exhibit inter-individual differences in SATs, and that ‘careful’, slow, fish
85 were more accurate than faster individuals in visual discrimination. However, conflicting results have
86 been reported: three-spined sticklebacks (*Gasterosteus aculeatus*) exhibited no speed related cost to
87 accuracy (Mamuneas et al. 2015), with similar results observed in other species including
88 bumblebees, *Bombus terrestris*, (Raine and Chittka 2012), lizards, *Lampropholis delicata*, (Chung et
89 al. 2017), spiders, *Portia labiata*, (Chang et al. 2017), and several other species of fish; *Poecilia*
90 *reticulata* (Lucon-Xiccato and Bisazza 2016), *Gnathonemus petersii* (Kareklas et al. 2017), and
91 *Poecilia mexicana* (Sommer-Trembo and Plath 2018). The link between individual differences in
92 cognition and SAT thus remains inconclusive, with a recent meta-analysis suggesting that measures of
93 individual differences in cognition linked to behavioural traits may be complicated by factors such as
94 sex of individuals, taxa specific differences, but also by methodological issues (Dougherty and
95 Guillette 2018). Several reviews have suggested that the experimental approaches used in this
96 developing field may sometimes impede the exploration of inter-individual differences in cognition
97 and impact the interpretation of results (Carter et al. 2013; Rowe and Healy 2014; Griffin et al. 2015;
98 Boogert et al. 2018).

99 Test difficulty may impact the optimal trade off in SAT strategies, where the relative ease of a task,
100 for example the number of choices in a discrimination test, can be important (Raffa et al. 2002;
101 Chittka et al. 2009). Physiological differences, both within and between individuals, as per the Pace of
102 Life Syndrome (Réale Denis et al. 2010), are also important as metabolic differences and changes
103 may underlie differences in behavioural traits and information use (Biro and Stamps 2010; Mathot
104 and Dall 2013; McKenzie et al. 2015). Motivation in learning assays can be affected by level of
105 satiation (Shettleworth 1972; Ben-Shahar and Robinson 2001), and motivational differences have
106 been shown to override cognitive differences in problem solving tasks (van Horik and Madden 2016).
107 Additionally, coping styles - where individuals show distinct differences in vulnerability and response
108 to stress (Koolhaas et al. 1999) - can drive consistent inter-individual variation in behaviour and can
109 both directly affect learning, for example in reversal learning tests (Bensky et al. 2017), and can also
110 indirectly impact measure of cognition (McEwen and Sapolsky 1995; Mesquita et al. 2015; Raoult et
111 al. 2017). The term coping style is sometimes used interchangeably with behavioural syndromes in
112 the literature and while they may be closely associated and sometimes do correlate with various
113 behavioural syndromes they remain distinct from them, with recent work showing that for some
114 species coping styles do not correlate to behavioural traits and do not form syndromes with
115 behavioural traits (Zidar et al. 2017). One method that has been suggested to reduce the effect of
116 potentially confounding non-cognitive factors is to use repeated, or longitudinal, tests (Thornton and
117 Lukas 2012; Sih et al. 2015; Boogert et al. 2018).

118 We used archerfish (*Toxotes chatareus*) to explore SATs using a repeated discrimination task with a
119 longitudinal design with differentially rewarded cues (targets). Two conditions with different
120 numbers of targets were used to explore the effect of increasing target choice on the ability to reveal
121 interindividual differences in discrimination performance. Archerfish, best known for their specialised
122 foraging ability to shoot down prey by spitting jets of water, are visual predators (Ben-Tov et al.
123 2018) and increasingly used in studies of visual discrimination and other aspects of cognition. They
124 can readily discriminate between targets of different colours, shapes, and complexity (Gabay et al.
125 2013; Newport et al. 2014; Ben-Tov et al. 2015; Newport et al. 2015), use visual search strategies

126 comparable to those of humans and other primates and discriminate between known objects from
127 novel viewing angles (Ben-Tov et al. 2018; Rischawy and Schuster 2013; Newport et al. 2018; Saban
128 et al. 2017; Gabay et al. 2013). They can also learn to associate targets with differential rewards
129 (Karoubi et al. 2017) and exhibit distinct inter-individual differences in latency to shoot (Jones et al.
130 2018), with initial evidence suggesting that individuals may use different decision making strategies
131 (Newport et al. 2013).

132 Our main aim was to examine whether fast–slow cognitive styles exist in archerfish, specifically
133 whether consistent individual decision speeds affected learning and discrimination. We also wanted to
134 test the effect of number of choices, as a proxy for cognitive challenge. We used a discrimination task
135 with differentially rewarded targets (which the fish were trained to shoot), repeated over consecutive
136 days for each individual. We measured decision time (latency to shoot) and decision accuracy as
137 discrimination success (shots at target corresponding to the large reward), hereafter success. We
138 measured success at two levels –daily success, and success in the first trial of the day, where we
139 expected lowest satiation levels. To examine the effect of numbers of choices, we tested fish in a
140 condition with either two or three targets. We expected a trade-off to exist among individuals, with an
141 inverse relationship between speed (latency to shoot) and accuracy (discrimination success).
142 Specifically, that fish with greater latencies to shoot would have increased discrimination success, at
143 least in the first trials of the day.

144 **Methods**

145 **Subjects**

146 We used 20 archerfish, 12 +/- 0.5 cm (total length), from a population of animals housed at the
147 University of St Andrews. All fish were wild caught and sourced as a single order from an accredited
148 ornamental fish retailer. Fish were of unknown sex as archerfish are sexually monomorphic and we
149 cannot be sure of their relatedness either. There is some possibility that the fish were related, however
150 very little of their reproductive biology is known besides the fact that they are broadcast spawners
151 (Simon et al. 2011) which suggests they are unlikely to be kin. The fish had been kept in the

152 laboratory for a year prior to use in the study and had not been trained to shoot in any previous study.
153 At the time of the experiment the fish were estimated to be 20- 24 months old, based on their size and
154 date of arrival from the retailer, however the correlation between age and growth rate in captivity is
155 not well known for this species. Fish were maintained in stock freshwater aquaria in groups of 5-8
156 fish, in large individually filtered tanks (180 × 45 cm and 35 cm deep) with temperatures between 25 -
157 26 °C under a 12:12 h light:dark cycle. Stock tanks had environmental enrichment in the form of 3 cm
158 deep gravel substrate and several plastic plants. Water quality parameters (pH, nitrite, ammonia, and
159 nitrate concentrations) were measured weekly, and levels were kept within a range appropriate for
160 archerfish, as per (Newport et al. 2013), using external canister filters and regular water changes. The
161 fish were fed daily with an alternating mixture of commercial fish food (Tetra Cichlid Sticks) and
162 freeze-dried bloodworms. Fish were measured as they were captured from the stock tank – using a
163 ruler taped to the side of the tank, netted fish were gently pressed against the side of the tank to record
164 their length before being moved to the experimental tank.

165 Experimental set-up

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

175 Experimental procedure

176 The experiment consisted of three phases, two training and one test, and each fish was subjected to the
177 following phases in order. In the first phase, all fish were first trained to shoot a novel target presented

178 on the shooting platform, using two stages – they were first trained to shoot a known food item (a
179 pellet) and then in stage 2 trained to shoot a novel white artificial target. In the second phase the fish
180 were given a set number of trials to familiarise themselves with the experimental targets presented
181 individually. Finally, fish were tested in daily discrimination trials for 30 consecutive days using those
182 targets presented simultaneously in two conditions - two targets or three targets, with differential
183 rewards. The 30-day period was chosen because data from a pilot study suggested some fish required
184 about 20 days to reach criterion, and we wanted to give as much time as possible to slower learners.
185 Each fish was randomly assigned to one of the two conditions before the training phase began.
186 Conditions differed only in the numbers of targets that were presented to the fish to discriminate
187 between in the final phase. In the ‘two targets’ condition fish were presented with two targets - one
188 target which was rewarded with a large reward and one target was rewarded with a small reward; in
189 the ‘three targets’ condition fish were presented with three targets, one target was rewarded with a
190 large reward and two targets with small rewards.

191 The four targets used in this experiment were hand cut plastic squares, (2 cm², 3 - 5 mm thick)
192 differing in colour (green, blue, black or white). Food rewards were pre-cut pieces of 3 mm diameter
193 cylindrical pellets; the large reward was 3 mm long, and the small reward was 0.5 mm long. Of the
194 four targets, white were used only in the training phase and the remainder (green, blue, black) were
195 used in the familiarisation and discrimination testing phases where fish were given either two (blue
196 and green) or three (blue, green and black) targets as per their condition (for more information on the
197 targets we used, see Appendix 2). The target colours were randomly designated to correspond to
198 either a large or small reward for each fish and then remained consistent for each fish for the duration
199 of the study. So, for example, in the two-target condition one fish was trained with a white target, then
200 introduced to and tested with the green (small reward) and blue (large reward) targets. As an example
201 of the three target condition one fish was trained with a white target, and familiarised and tested with
202 the green (large reward), blue (small reward) and black (small reward) targets.

203

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

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

223 *Phase 1: Training*

224 In this phase fish were trained to shoot at an artificial target placed on the target platform to receive a
225 food reward. Training consisted of two stages and was considered complete after a fish had achieved
226 learning criteria in both stages. In the first stage the fish was presented with a pellet (a known food
227 item) as a target, and the first criterion was reached when the fish had completed 10 successful trials
228 in each of two consecutive sessions. Each fish received a single training session per day with up to 50
229 minutes per session with a maximum trial number of ten trials – each trial continued either until the
230 fish shot or the 50 minutes expired. The day after completing the first criterion, the fish entered the

231 second stage of training and was presented with an artificial target, (a white plastic square) and again
232 training sessions continued until the fish hit the target 10 times in a row in two consecutive sessions.
233 In this second stage of training the fish had a maximum trial time of 8 minutes, where the time limit
234 was based on a previous study fish with similar procedure in which all fish shot within 6 minutes
235 (Jones et al. 2018). There was an initial maximum of 45 daily sessions allowed for this part of
236 training, however several fish reached the maximum limit without reaching criterion. These fish were
237 then trained further with three sessions a day until they achieved criterion. The rationale for the
238 training phase was to ensure each fish had reliably learnt to shoot a target to gain a food reward.
239 The training phase also allowed individuals with different sensitivity to risk, and/or stress to habituate
240 to the experimental procedure and potentially reduce the confounding effect of coping styles (Zidar et
241 al. 2017). A related benefit was that estimates of repeatability can be improved with greater
242 acclimatisation time, as shown for other species (O'Neill et al. 2018).

243 *Phase 2: Familiarising with coloured targets*

244 The familiarity phase, beginning the day after achieving the second training criterion, introduced fish
245 to the targets and initial learning opportunity of the corresponding rewards. The rationale for this was
246 to introduce subjects to each cue prior to discrimination trials to ensure similar levels of response
247 across cues (Sturdy and Weisman 2006), and thereby reduce initial target bias.

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

254 *Phase 3: Discrimination testing*

255 The day after the familiarity phase was complete discrimination testing began. Here targets, either two
256 or three according to condition, were presented simultaneously. The order and position of target

257 presentation changed for each trial but targets were never placed in the same position in consecutive
258 trials. The targets were all placed within 4 - 5 cm from each other in either a line, or a triangle
259 configuration, so shot targets could be easily identified, but would not require fish to search different
260 areas of the platform.

261 Discrimination tests were run for 30 consecutive days for each fish, with 12 trials a day, split over two
262 sessions (starting at ~10:00 am and ~16:30 pm), per day. Fish were afforded an 8 minute maximum
263 trial limit. Latency to shoot, colour of the shot target and size of reward were scored from video
264 recordings. A hypothesis-naive secondary observer scored ~20% of the trials. Inter-rater reliability
265 comparing the principal (NJ) and secondary scores of latency to shoot, using the irr package (Gamer
266 et al. 2012), showed high agreement with an inter-class correlation of .992 to .994, and mean of
267 0.993 ; ($F_{1073,1073} = 270, = 141, P < 0.001$).

268 Of the 20 fish we used for this experiment four fish were not used in all the analyses. Two fish were
269 unable to complete training as they consistently failed to hit the targets. Neither fish showed any
270 obvious injury or morphological differences, but they could not hit targets accurately and missed the
271 targets they appeared to aim at (archerfish take a characteristic angle and maintain their orientation
272 towards intended targets before shooting). One fish consistently shot about 20 cm behind the target it
273 aimed at, the other fish shot at least 5 cm to one side of any target. A third fish failed to shoot in
274 sufficient training trials and did not complete the first stage of training even after 9 weeks of training
275 sessions. A fourth fish reached training criterion but shot in less than half of discrimination trials and
276 was excluded from analysis of discrimination success so only 16 fish (8 in each condition) were
277 included in the analyses for speed accuracy trade-offs.

278 Ethics

279 All procedures performed were in accordance with the ethical standards of the University of St
280 Andrews and methods used were approved by the University of St Andrews Animal Welfare and
281 Ethics Committee (AWEC). No procedures required U.K. Home Office licensing. No fish died or
282 suffered ill health during this study, and all individuals were retained in the laboratory for future use.

283 Statistical analysis

284 All analyses were performed in R version 3.5.1., using R Studio version 1.1.456, and where
285 applicable R notation is used to detail the models used. Post hoc pairwise comparisons were
286 conducted using the ‘emmeans’ function in the R emmeans package (Lenth et al. 2018) where
287 appropriate. Data are available at:

288 https://osf.io/6b3v4/?view_only=b49be8debbc5458c99d873fe32da6038

289 *Latency to shoot and training*

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

296 *Speed accuracy trade-off during discrimination phase*

297 Here we tested whether overall latency to shoot (latency) predicted discrimination success, i.e.
298 shooting at the large-rewarded targets. We were also interested in whether the number of targets and
299 satiation (measured by trial number within session) affected latency to shoot. We fitted a generalized
300 linear mixed model (GLMM), using the glmer function in the lme4 package (Bates et al. 2015) with
301 latency to shoot in seconds as our continuous response variable and reward type (large, or small),
302 condition (number of targets) and trial number within session as the fixed factors and day as a
303 covariate to explore change in any of these effects over time. The model included session, and
304 individual fish identity as random factors with random intercepts. We log transformed latency prior to
305 analysis to achieve improved normality of the model residuals. For the final model we included all
306 potential random factors that were significant based on fitting the full model and then tested the
307 significance of each term by dropping them out and doing a likelihood ratio test comparing the
308 reduced with the full model. The model we fitted was the following (in R syntax):

309 $\text{LogLatency} \sim \text{Reward} * \text{Condition} + \text{Reward} * \text{Day} + \text{Condition} * \text{Day} + \text{Trial} + (1|\text{FishID}) + (1|$
310 $\text{Session})$

311 The condition term was a factor with two levels (either two or three targets), and the ‘Reward’ term is
312 a factor with two levels (small or large reward).

313 *Effect of number of targets on success during discrimination phase*

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

317 $\text{Success} \sim \text{Condition} * \text{Day} + (1|\text{FishID}) + (1|\text{Trial}) + (1|\text{Session})$

318 *Consistency of individual differences in latency to shoot*

319 To investigate whether fish exhibited consistent individual differences in latency to shoot we
320 calculated the level of repeatability, R , as per Jones et al. (2018). Repeatability is the fraction of
321 variation that is due to differences between individuals and is used to quantify individual differences
322 (Bell et al. 2009). R was calculated using the rptR package (Stoffel et al. 2017) which builds on the
323 methods developed for mixed-model analysis and uses bootstrapping to provide reliable estimates of
324 R . We estimated R at the level of individual fish, using the same overall latency model, described
325 above, with 1000 parametric bootstraps.

326 *Individual differences in latency and discrimination success*

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

331 $\text{glm}(\text{proportion of success} \sim \text{MeanLatency} * \text{Condition})$

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

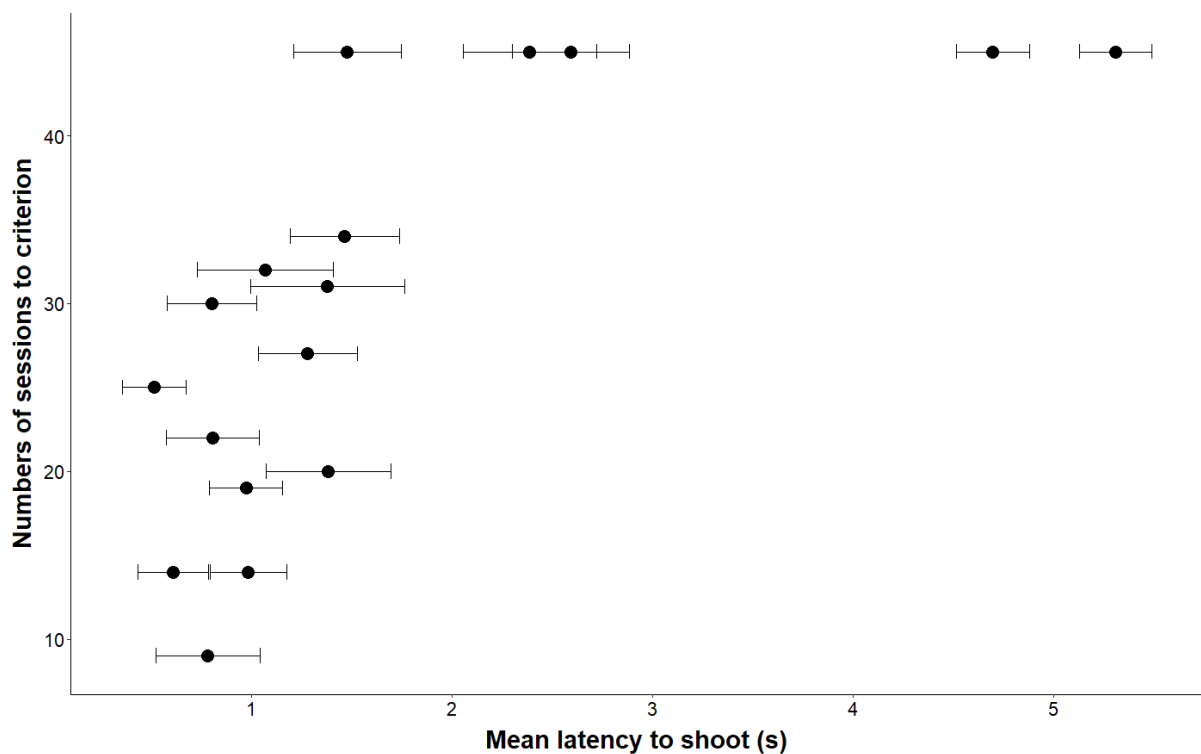
335 `glm(proportion of success ~MeanLatency,)`

336

337 Results

338 Training phase

339 Individual latencies to shoot in the discrimination phase were significantly associated with the
340 numbers of training sessions (combining both stages) required to achieve criterion. Slower shooting
341 fish required more sessions to reach training criteria (LM: $t = 2.395$, $P = 0.030$; Fig 1). A similar
342 effect was found even after removing the two slowest fish (LM: $t = 3.519$, $P = 0.004$).



343

344 Figure 1. Relationship between mean (\pm SEM) latency to shoot and the number of training sessions to
345 achieve both training criteria for 17 fish that completed training. Mean latency was calculated from
346 360 discrimination trials per fish.

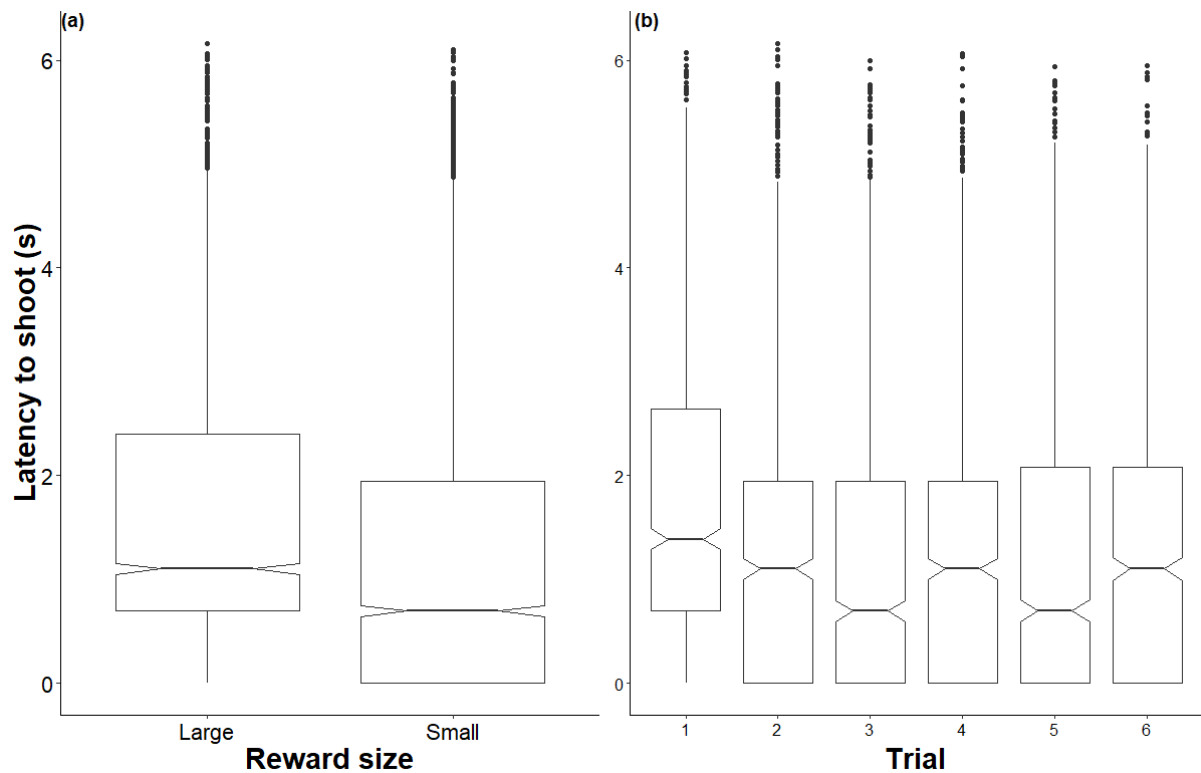
347

348 Discrimination phase

349 *Overall speed accuracy trade-offs*

350 In general, latency increased with accuracy as fish took longer to shoot at the target that corresponded
351 with the larger reward (LRT on 'Reward' predictor : $\chi^2_1 = 84.455$, $P < 0.001$; Table 1). Post hoc
352 contrasts revealed significant differences in latency to shoot depending on the reward associated with
353 the target, and latency to shoot 'large-reward' targets were on average 1.3 seconds greater than 'small-
354 rewarded' targets (emmean: $z_{8,642} = 0.248$, $P < 0.001$; Fig 2a). Trial number was also important, as
355 fish showed higher latency in their first test trial. The first trial lasted significantly longer than all
356 other trials (LRT on 'Trial' predictor: $\chi^2_5 = 136.02$, $P < 0.001$; Fig 2b, Table 1). Latency to shoot was
357 not significantly affected by the number of targets (LRT on 'Condition' predictor: $\chi^2_1 = 1.0884$, $P =$
358 0.297), however there was a significant interaction between time (Day) and condition (LRT (χ^2_1
359 $= 103.4931$, $P < 0.001$)).

360



361

362 Figure 2. Mean latency is significantly ($P < 0.001$) affected by (a) reward size (large or small pellet
 363 reward) and (b) trial number. Box plots show the median, 25th and 75th percentiles, and the notch
 364 indicates the 95% confidence interval around the median. $N = 16$ fish tested for 30 days each.

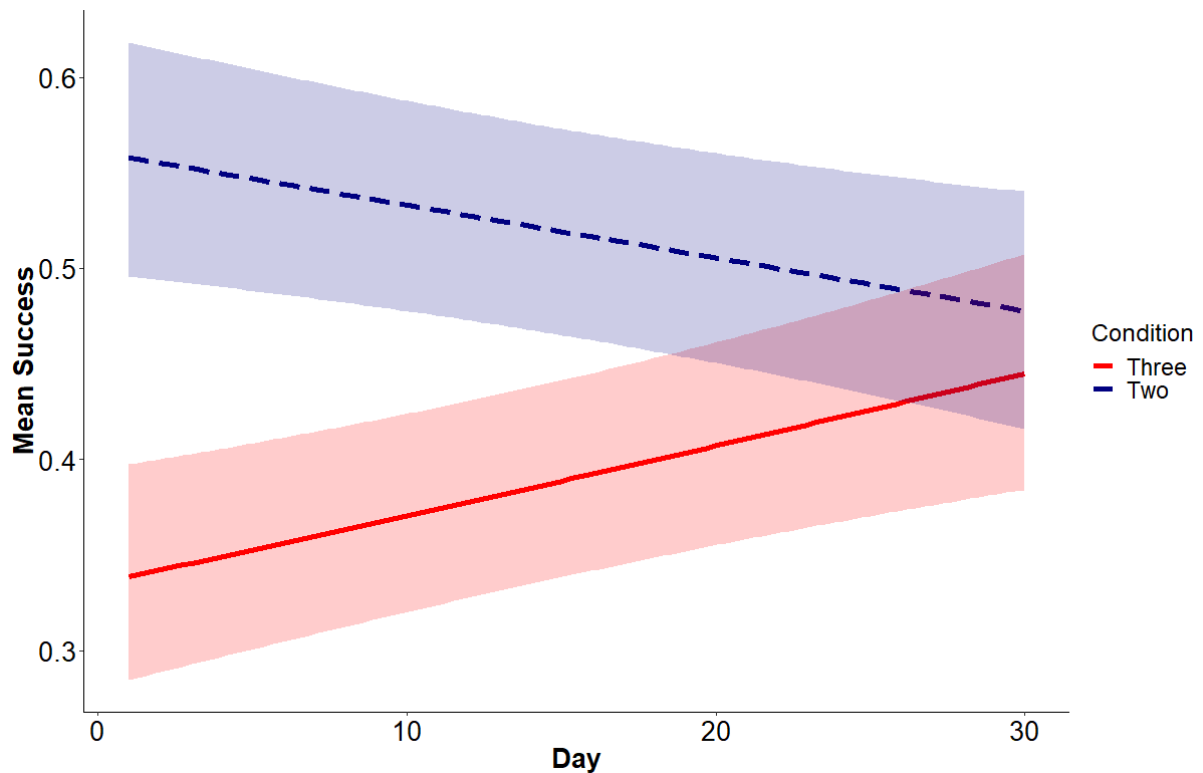
365

366 *Effect of number of targets on success during discrimination phase*

367 Mean success was affected by the number of targets, with fish in the two-target condition shooting at
 368 the large-rewarded target more frequently (LRT on 'Condition': $\chi^2_1 = 10.7317$, $P = 0.001$; Table 2)
 369 supporting our hypothesis that the three-target task was a more challenging discrimination task. This
 370 was reflected in a comparison of success over time, where although individual fish showed high
 371 between-day variation in success (see Fig A2), on average the number of targets was important with a
 372 significant interaction between time (Days) and number of targets (LRT: $\chi^2_1 = 18.0290$, $P < 0.001$; Fig
 373 3; Table 2).

374

375



377

378 Figure 3. Mean, \pm 95% C.I, discrimination success (shots at the target associated with the larger
 379 reward) for all fish in the two conditions over time. Fish had either two (blue line) or three (red line)
 380 targets available to choose from in each condition. $N = 8$ individuals per condition, with 12
 381 discrimination trials each day for 30 days per fish.

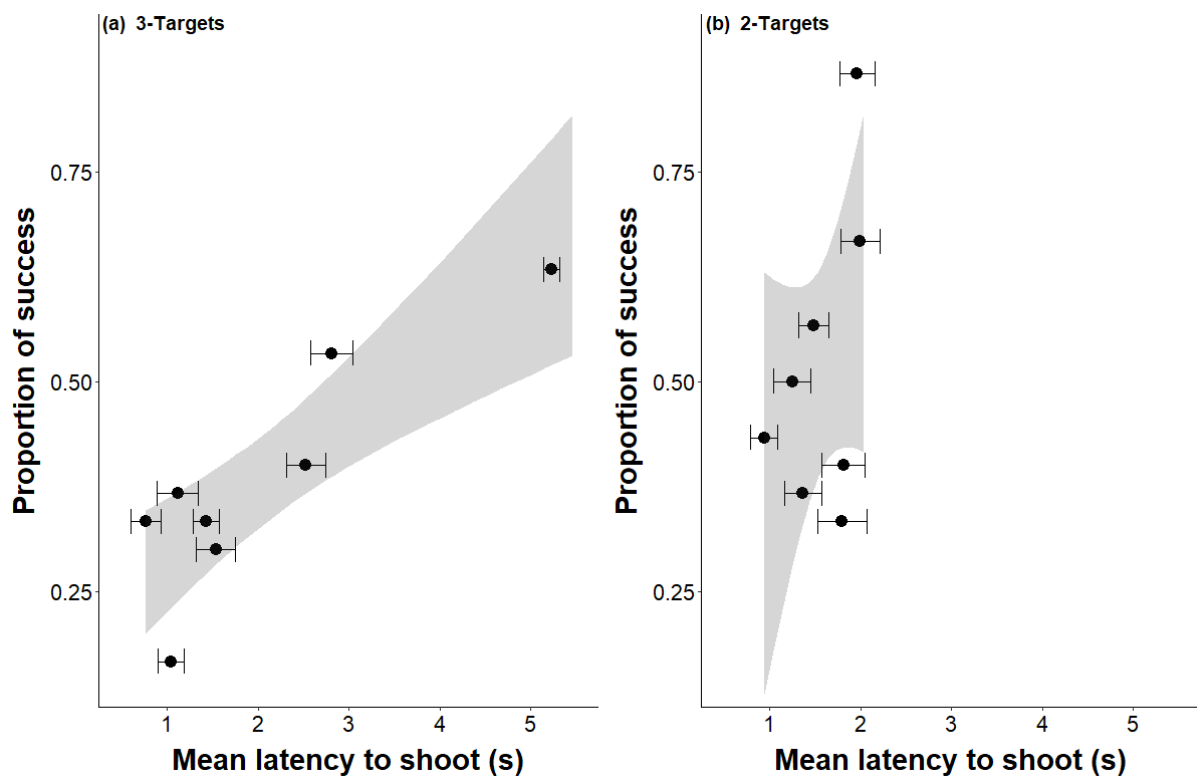
382 *Individual differences in latency to shoot*

383 Bootstrap repeatability estimation showed there was a high individual repeatability in latency to
 384 shoot. The fish identity term within the model accounted for 45% of the variance in latency,
 385 suggesting large inter-individual differences in latency to shoot ($R \pm SE = 0.455 \pm 0.093$) (Table A 1).
 386 It is worth noting that repeatability for overall success was much lower at ($R \pm SE = 0.028 \pm 0.0095$;
 387 Table A 2).

388 *Individual differences in latency and discrimination success*

389 Overall mean daily success (proportion of shots at large rewarded target) was not significantly
 390 affected by individual mean latency (GLM: $t = 2.916$, $P = 0.078$; Table A3), and this held for fish in

391 conditions with both two (GLM: $t = 0.432$, $P = 0.681$; Table A4) and, despite a positive trend between
 392 latency and accuracy, three (GLM: $t = 2.183$, $P = 0.072$; Table A5) targets. Success in the first trial of
 393 the day was affected by individual mean latency: slower fish had greater success in the condition with
 394 three target choice (GLM: $t = 4.374$, $P = 0.005$; Fig 4a), with cumulatively increasing success in first
 395 trials across time for slower fish (Fig A.3a). However, while proportion of success showed a positive
 396 relationship with individual mean latency in the two targets condition but was not statistically
 397 significant (GLM: $t = 1.800$, $P = 0.132$; Fig 4b) and fish speed did not predict cumulative successes
 398 (Fig A.3b).



399

400 Figure 4. Proportion of success (shots at target corresponding to large reward) in initial daily trials
 401 relative to mean latency to shoot in (a) three targets, and (b) two target conditions. The black points
 402 denote the cumulative proportion of successes for all 30 trials for each fish plotted against their
 403 individual mean latency to shoot. The grey band is the estimated 95 % prediction intervals given the
 404 fitted model. $N = 30$ trials (initial trial per day) for 30 days for each of 8 fish per condition.

405 Discussion

406 In line with our primary aim we show that archerfish exhibit consistent individual differences in speed
407 accuracy trade-offs and provide empirical support for the hypothesis that differences in decision speed
408 can explain inter-individual differences in cognitive performance. Archerfish discriminated between
409 differentially rewarded targets, with greater latencies overall for shots at the target associated with the
410 larger food reward. Consistent with the cognitive style hypotheses (Sih and Giudice 2012), archerfish
411 with repeatable differences in latency to shoot showed corresponding differences in learning to shoot
412 a novel target during training and in discrimination success. Individuals with consistently high
413 latencies took longer to train to shoot a novel target, but these slower individuals achieved greater
414 discrimination accuracy during testing, with discrimination success increasing along the fast–slow
415 continuum. These SAT based differences in discrimination accuracy were observed only when
416 comparing the outcomes from the first trial of each day, when motivation is expected to be highest.
417 Our results also suggest that the numbers of targets, or choices, was important for revealing these
418 SAT based inter-individual differences in discrimination success.

419 Mean daily success of individuals within each condition did not significantly differ, consistent with a
420 less frequently explored prediction of Sih and Giudice (2012), namely that individuals along the fast–
421 slow continuum may be expected to achieve similar mean success with different strategies. Our study
422 however had a fixed number of trials per day and so is limited in ability to provide evidence for
423 sustained alternative strategies. It does suggest that slower fish may have begun sampling the targets
424 with smaller rewards after first shooting the more rewarding target in the initial trials of the day.
425 Sampling, the investment in acquiring information, has been proposed as one of the issues in
426 measuring inter-individual variation in cognition (Rowe and Healy 2014) and individuals with
427 different behavioural traits can achieve similar mean rates of food intake while using different
428 sampling strategies (Morand-Ferron et al. 2011). Theory has suggested that individuals with different
429 behavioural traits may have different sampling rates and use sampling information differently
430 especially in foraging contexts (Mathot and Dall 2013). Sampling rate, as related to cognitive styles
431 and SATs, is a major reason to explore inter-individual differences in cognition with ecological and
432 adaptive significance (Chittka et al. 2009; Sih and Giudice 2012). SATs can be associated with

433 environmental differences, for example individual guppies (*Poecilia reticulata*) from populations with
434 high levels of predation tended to make faster decisions, but more errors, in maze tasks than
435 individuals from low predation areas that made slower decisions (Burns and Rodd 2008). The
436 differences may also be linked to foraging roles within a population (Dall et al. 2012): where in a
437 social context individuals can benefit from maintaining consistent behavioural traits (Ioannou and
438 Dall 2016). Archerfish shooting behaviour is open to exploitation by scroungers (Davis and Dill
439 2012), so consistent inter-individual differences in SAT may relate to a producer scrounger dynamic.
440 Repeated testing to investigate inter-individual differences in cognition has been strongly
441 recommended (Thornton et al. 2014; Boogert et al. 2018). Our study underscores this message as
442 detection of aspects of cognitive styles would not have been observed otherwise. Individuals showed
443 large fluctuations in success between days, as expected from previous studies showing metabolic
444 effects on behavioural traits (Careau et al. 2008; Biro 2012; Beckmann and Biro 2013; Auer et al.
445 2018; Montiglio et al. 2018). Satiation level may drive ‘errors’ related to sampling strategies and
446 foraging decisions (Fawcett et al. 2014; Montiglio et al. 2018; Sih et al. 2015; Stephens 2008), and
447 this may be especially pertinent when rapid changes in metabolism after ingesting food can affect
448 behaviour, as shown in the common minnow (*Phoxinus phoxinus*) (McLean et al. 2018). Moreover,
449 relatively minor within-day temperature changes can affect activity and behavioural traits in
450 damselfish *Pomacentrus moluccensis* (Biro et al. 2010). Specifically, for archerfish our study suggests
451 that with a three-target discrimination system, about 15 days of testing is likely to be sufficient to
452 capture differences in learning rates and discrimination success with clear differences in cumulative
453 daily success between fish becoming visible between day 10 and day 15.

454 The numbers of targets was important, as inter-individual differences in discrimination were
455 statistically significant only in the three target condition. In the two-target condition the speed related
456 costs to accuracy may not have been large enough to differentiate between different SATs, fitting
457 theory that suggests choice tests need to be challenging enough to reveal SATs (Chittka et al. 2009).
458 Increasing options in choice tests affects decision making and accuracy, for example in bumblebees
459 (Dukas and Real 1993), and physiological differences at the neural level have been found in

460 comparisons of primate subjects in two and four choice tests (Churchland et al. 2008). We expected
461 differentially rewarded choices would increase the challenge of our discrimination task, as fish had to
462 discern the differences in reward size rather than a simple all or nothing association with the targets.
463 It may well have added a challenge for the fish given a previous study which tested archerfish in a
464 three alternative forced choice test showed faster learning than those in our two-target condition
465 (Newport et al. 2013), however, our results suggest that numbers of targets or visual cues is crucial to
466 making inter-individual differences in SAT. A simple mechanism related to search may drive this:
467 when presented with stationary targets simultaneously archerfish look at each stimulus sequentially,
468 as per serial search (Rischawy and Schuster 2013; Newport et al. 2014), so that search time increases
469 with target number, and although there was no significant difference in latency to shoot in our trials
470 there was a significant interaction effect with day. Archerfish use search strategies similar to other
471 species, including humans (Ben-Tov et al. 2018), and increasing numbers of choices may affect
472 exploration of SATs in other taxa. In addition, the daily mean success in the three-target condition
473 was initially lower than that of the fish in the two-target condition but rose to a similar level over
474 time, suggesting the additional target provided more of a challenge to discrimination. Here we would
475 like to note that the drop in daily success for the two-target condition. We speculate this is linked to
476 satiation effects, especially given the observed peaks and troughs in discrimination success of
477 individual fish across days. Again, we can only speculate, however we would suggest that this may
478 have been a satiation ceiling effect, where fish were less motivated to shoot at the large rewarded
479 target and or more inclined to sample the smaller-rewarded targets on days following high success in
480 combination with the low ‘cost’ for any ‘error’, as fish still received a (small) reward for shooting the
481 ‘non-successful’ targets. Fewer daily trials or smaller rewards may have raised this satiation ‘ceiling’.

482 The differences in time to habituate and train fish with higher latencies corresponds with previous
483 studies which show that individuals with ‘fast’ cognitive styles learn quicker and may be linked to
484 their lower risk sensitivity, exploratory tendencies and or activity levels. This aspect of the cognitive
485 styles hypothesis is well supported, with evidence from multiple studies, for example harvest mice
486 (*Micromys minutus*), with higher activity and exploratory tendencies, learnt quicker than slower

487 individuals (Schuster et al. 2017), and similar findings in other species (Guenther et al. 2014; Guillette
488 et al. 2015; Chung et al. 2017; Kareklas et al. 2017). However, we note that ‘learning’ in cases of
489 training animals to react to novel cues, as in our study, might be a reflection of acclimation and or
490 habituation to testing procedure rather than, or in conjunction with, associative learning. The
491 relationship between training time and cognitive styles also reinforces the cautionary point
492 highlighted by Thornton and Lukas (2012): individuals with positions on one end of the SAT
493 continuum may be overly represented in many cognitive studies resulting in a focus on so-called
494 ‘olympian’ individuals. In archerfish these individuals are likely to be ‘fast’ style fish which learn to
495 shoot in experiments rapidly. Certainly, in our study there were more ‘fast’ style than ‘slow’
496 individuals. And while repeated measures can provide robust estimates from individuals, the
497 downside is fewer individuals may be tested as time is spent on multiple measures per individual. Our
498 study provides a case in point, as slower fish also took much longer to train and habituate to the
499 experimental procedure, and there was one particularly slow individual in the three target condition.
500 While the number of trials for each individual means that we are able to provide very robust estimates
501 of every individual's performance, including that slowest one, removing that individual from the
502 dataset makes the slope non-significant ($p = 0.054$), but with a similar slope estimate (see appendix
503 table A6) showing that our study has only just sufficient sample size to detect the effect of interest.

504 In conjunction with the main aim to test the cognitive styles hypothesis in a longitudinal study one of
505 the focuses in this paper has been attempting to mitigate the methodological issues that may make it
506 hard to reveal inter-individual differences in tests. As such we must note that the influence of sex can
507 be important, and has been shown to explain a significant amount of variation in effect size in studies
508 of inter-individual variation (Dougherty and Guillette 2018). The observed differences in speed
509 related differences in discrimination success may be connected to sex of the individuals. Although we
510 believe this is unlikely given the lack of any morphological or behavioural dimorphism in this species,
511 future studies in this area with archerfish may benefit from investigating the effect of sex.

512 In conclusion, we show that the SATs are an important component in inter-individual differences of
513 discrimination performance in archerfish. Individuals that consistently take more time before shooting

514 are more successful in discriminating between targets with different levels of reward. The behaviour
515 of archerfish in the three-target condition is consistent with the cognitive styles theory as they exhibit
516 consistent individual differences in performance, while maintaining similar mean success. However,
517 as expected from previous theory these SAT effects are only evident across initial trials per day when
518 motivation is expected to be highest, and when more than two choices are presented. Similar
519 longitudinal studies in other taxa may help further disentangle the complexity of cognitive styles and
520 inter-individual differences in cognition.

521 **Declaration of interest**

522 Declarations of interest: none.

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531

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751 **Appendix 1: Additional results**

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

753 **Appendix 2: Results of pilot study exploring the effect of target colour on** 754 **latency and frequency of selection**

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

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

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

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

771 Latency to shoot was not significantly affected by target colour (LRT: $\chi^2_3 = 0.1054$, $P = 0.9912$; Figure
772 A4), however the white target had greater variation in shot latency than the other three targets.
773 Target colour did affect the number of shots made, (LRT: $\chi^2_3 = 18.091$, $P = 0.0004$; Figure A5), fish
774 made fewer shots at white targets compared to green or blue targets (emmean: $t = 3.722$, $P =$
775 0.0036), (emmean: $t = 1.05$, $P = 0.0302$) respectively.

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

779

780 **Data accessibility**

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

783 https://osf.io/6b3v4/?view_only=b49be8debbc5458c99d873fe32da6038

784

785 **Tables**

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

fixed effects	estimate	s.e.	t
intercept	2.504839	0.374106	6.696
	-		
Reward-small	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
ConditionTwo:Day	0.033454	0.003289	10.173
<i>random effects</i>	<i>variance</i>	<i>s.d.</i>	
Fish ID	1.06374	1.03138	
Session	0.00536	0.07321	
Residual	1.07979	1.03913	

787 (*N* = 16 fish, 360 trials each)

788 Table 2: Results of the model fitting target number (condition) on success (shots at large-rewarded

789 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
<i>random effects</i>	<i>variance</i>	<i>s.d.</i>		
Fish ID	8.66E-02	2.94E-01		
Trial	<0.0001	<0.0001		

790 (*N* = 16 fish, 360 trials each)

791 **Appendix tables**

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

Grouping variable	R	SE	Lower CI	Upper CI	Observations
FishID	0.455	0.093	0.234	0.601	5626
Fixed	0.045	0.057	0.016	0.225	

793 Estimates analysed with 1000 bootstraps.

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

Grouping variable	R	SE	Lower CI	Upper CI	Observations
FishID	0.0228	0.0095	0.00727	0.0435	5626
Fixed	0.0158	0.0102	0.00229	0.042	

794 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.

Predictor variable	Estimate	SE	t-value	
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

795 (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.

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

796 (30 trials for each fish).

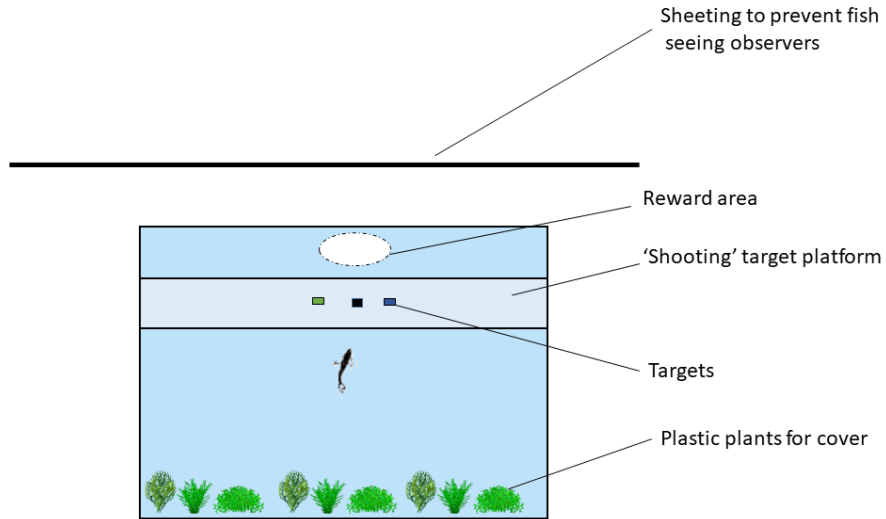
Table A5: Model results of the GLM fitting the influence of individual mean fish speed (latency) on proportion of success in the first trials for ($N = 8$) fish in the three-target condition.

Predictor variable	Estimate	SE	t-value	P
---------------------------	-----------------	-----------	----------------	----------

797	intercept	0.20772	0.04827	4.303	0.00507
	Mean latency of fish (30 trials per fish).	0.08531	0.0195	4.374	0.0047

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.

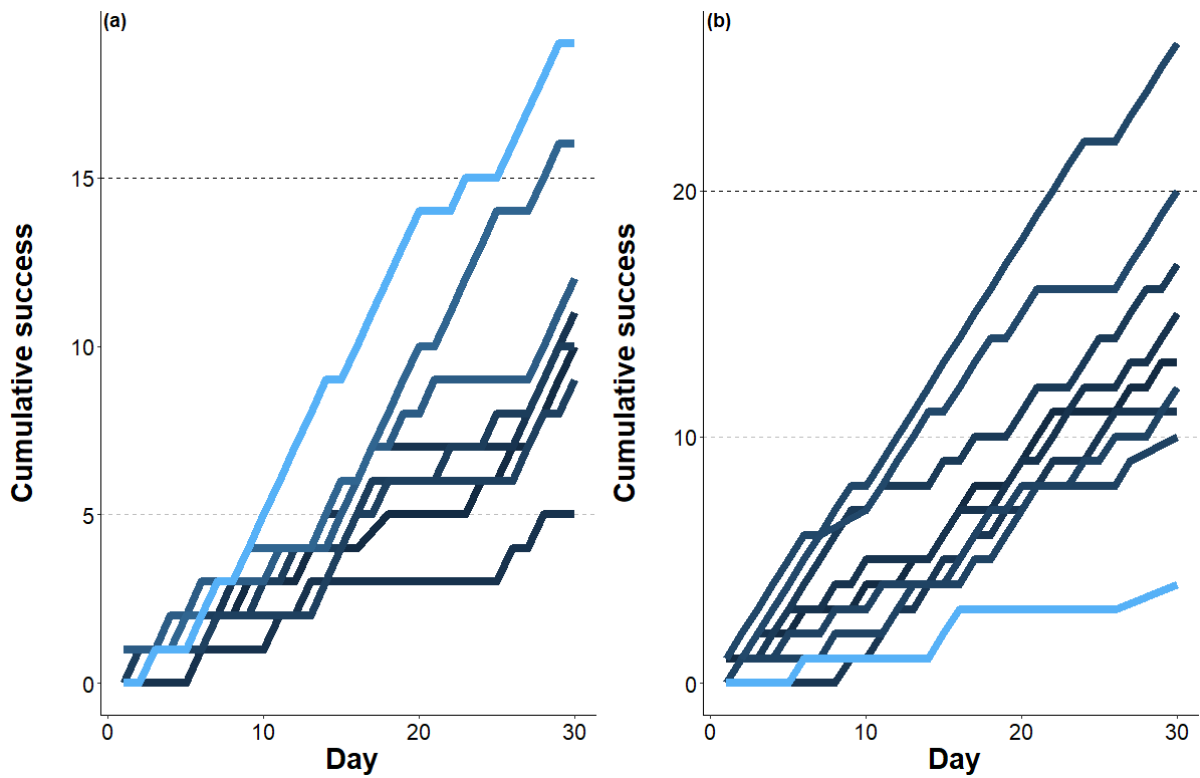
	Predictor variable	Estimate	SE	<i>t-value</i>	<i>P</i>
798	intercept	0.17709	0.07462	2.373	0.0637
	Mean latency of fish	0.10624	0.04245	2.503	0.0543



800

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

803

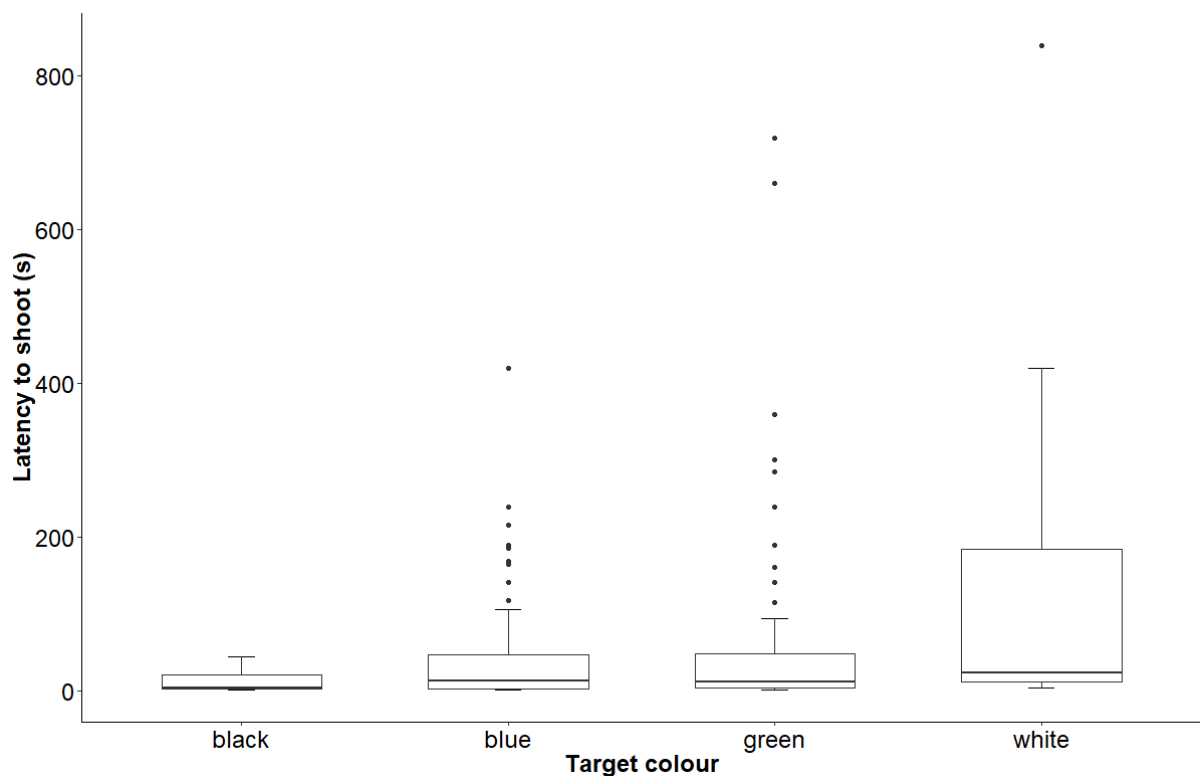


804

805 Figure A2. Success in discrimination over time in both conditions. Bold lines are group means for fish
 806 which had either two (blue) or three (red) targets available to choose from. Pale lines show mean
 807 success of individual fish. Black brackets indicate the periods of time (where we divided the time into
 808 three ten-day periods) during which mean success differed between condition ($P < 0.005$) grey brackets
 809 indicates no significant difference. $N = 8$ individuals per condition, with 12 discrimination trials each
 810 daily for 30 days for each fish.

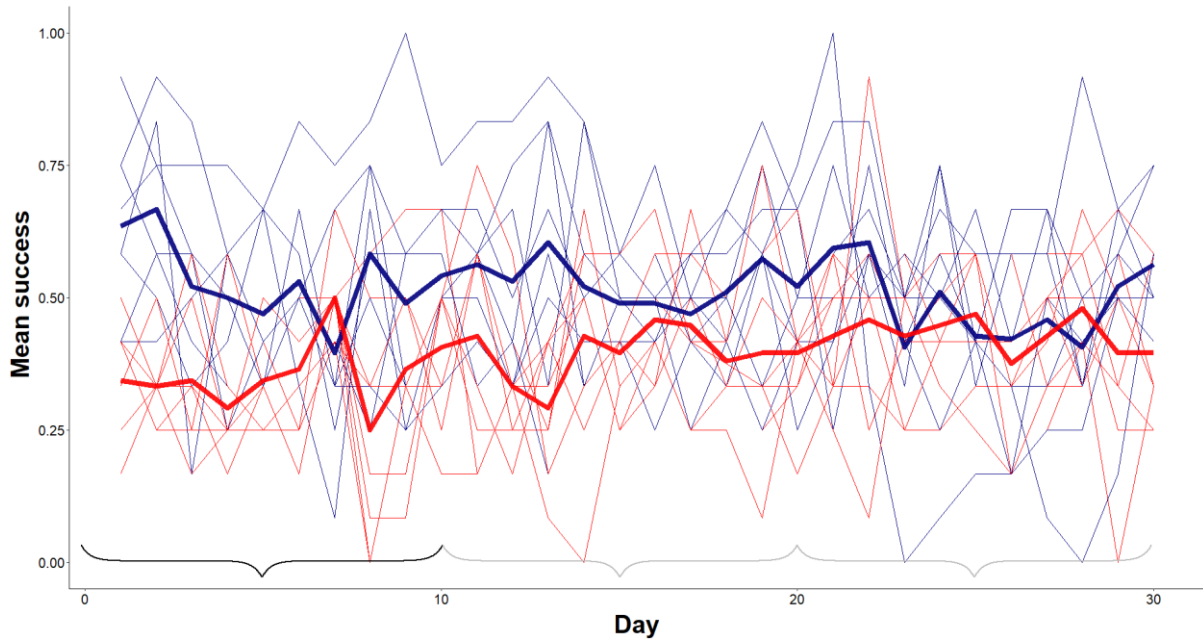
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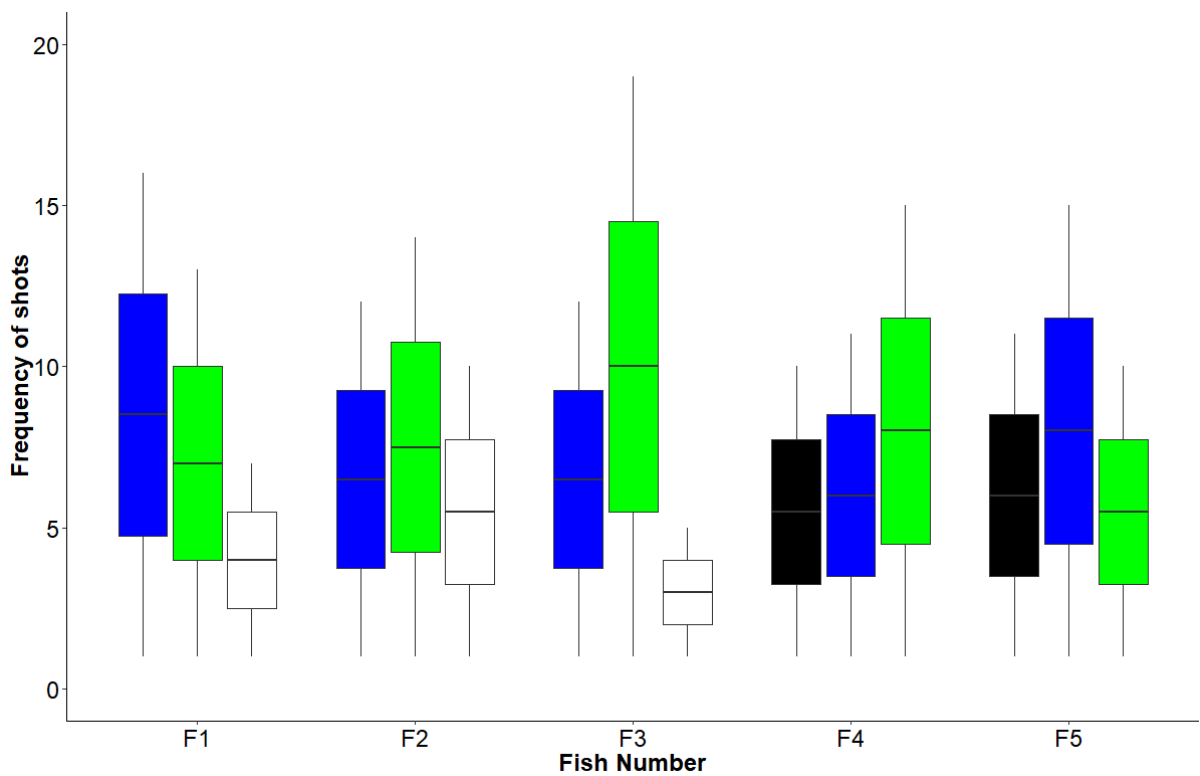
813

814 Figure A3. First trial success (shots taken at target corresponding to large reward) over successive
 815 days for each condition. (a) cumulative success in the first trial for each fish in the three-target
 816 condition and (b) cumulative success in the first trial for each fish in two-target condition. Separate
 817 lines are plotted for each fish with mean speed for each fish indicated by shade of blue (lighter =
 818 slower). Dotted line indicates levels within which cumulative success significantly differs from
 819 chance ($P < 0.05$, Exact binomial test). $N = 8$ fish per condition.



820
821 Figure A4. Latency per target for pilot study. N =5 fish, 36 trials each.

822



823
824 Figure A5. Frequency of shots made per target, by each fish in the pilot study. N =5 fish, 36 trials
825 each. Box plots show the median, 25th and 75th percentiles, the whiskers extend to the data point that
826 is no more than 1.5 times the length of the box as per the Tukey method (R package ggplot2).

827