

1 **Space-use and sociability are not related to public-information use**
2 **in ninespine sticklebacks**

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24 ABSTRACT

25

26 There has been much recent interest in both public information use, and the evolutionary origins
27 and ecological consequences of animal personalities, but surprisingly little integration of these
28 two fields. Personality traits may impact upon the extent to which individuals respond to public
29 information in a number of different ways. As a first step towards addressing some of these
30 questions, in this study we asked whether personality traits predicted public information use in
31 nine-spine sticklebacks (*Pungitius pungitius*). Over a 33-day period, subjects were scored twice
32 for a number of behavioural traits, including measures of activity, exploration and shoaling
33 tendency, and were exposed multiple times to a public information use foraging task, in which
34 they were required to select the richer of two prey patches based upon the foraging success of
35 two demonstrator groups. The repeatable ($r=0.38-0.58$) behavioural traits were reduced to two
36 principle components describing space use and sociability. Neither of these was found to be
37 related to either of two measures of public information use. While the personality traits that we
38 considered did not co-vary with public information use in this species, they may well indirectly
39 affect opportunity for exposure to public information, and this is an obvious avenue for further
40 research.

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42 **KEYWORDS:** Behavioural syndrome; Bold-shy; Innovation; Producer-scrounger; Social
43 learning strategies; Temperament

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46

47 INTRODUCTION

48

49 Animals can acquire public information about their surroundings through observing or
50 interacting with other individuals (Heyes 1994; Hoppitt and Laland 2008). The use of public
51 information, and social learning, has been described in many animal species representing a
52 diverse range of taxa (Avital and Jablonka 2000; Leadbeater and Chittka 2007; Hoppitt and
53 Laland 2013). It is thought that such behaviour may benefit animals by allowing them to
54 minimise the costs associated with sampling the environment, enabling them to acquire
55 information about the distribution and nature of resources, travelling routes, mates, competitors
56 or threats efficiently (Heyes and Galef 1996; Galef and Giraldeau 2001; Valone and Templeton
57 2002; Danchin et al. 2004; Dall et al. 2005; Valone 2007).

58

59 Given the apparent adaptive advantages of social learning, there is currently significant research
60 interest in the costs and benefits of public information use, and the conditions that determine
61 when individuals should copy the behaviour of others (Laland 2004; Laland et al. 2011; Rendell
62 et al. 2011; Rieucan and Giraldeau 2011; Hoppitt and Laland 2013). While the majority of these
63 studies have considered only the effects of external conditions, such as those pertaining to the
64 physical and social environment perceived by the individual, a number of researchers have begun
65 to investigate the role of individual behavioural variation, including personality traits, in
66 determining individual's propensity to use public information (Nomakuchi et al. 2009; David et
67 al. 2011; Webster and Ward 2011; Aplin et al. 2013; Jolles et al. 2013). Personality refers to
68 stability or consistency in the expression of one or more behavioural traits over a given time
69 period. Much as for social learning, personality traits have been described in a diverse range of

70 different species, and their evolutionary origins and their fitness consequences are currently
71 receiving a great deal of interest from researchers (Wilson et al. 1994; Wilson 1998; Gosling and
72 John 1999; Sih et al. 2004a, 2004b; Reale et al. 2007; Sih and Bell 2008; Bell et al. 2009; Conrad
73 et al. 2011).

74
75 Broadly speaking, personality might affect public information use in two ways. First, personality
76 traits might affect the opportunity to acquire public information. Most obviously, more sociable
77 individuals, who spend more time with their group mates, or which interact widely with many
78 individuals, may be more likely to be exposed to public information than individuals which do
79 not frequently spend time near or interacting with others (Sih and Bell 2008). Other personality
80 traits, such as activity levels or tendency to explore might also affect exposure to public
81 information, by influencing the likelihood that individuals will encounter others as they move
82 through the environment. Second, personality traits might predict the use of public information
83 once the animal is exposed to it. Though the mechanisms linking personality traits and tendency
84 to use public information are not clear, such effects have been documented in some species. In
85 great tits (*Parus major*) for example, individuals that were independently categorised as 'faster
86 explorers' were found to be more likely to visit feeders where they saw conspecifics feeding
87 compared to 'slower explorers', suggesting a link between exploration and scrounging behaviour
88 (Marchetti and Drent 2000). In barnacle geese (*Branta leucopsis*) neophobia was seen to be
89 related to scrounging behaviour, with more neophobic individuals being more likely than less
90 neophobic conspecifics to scrounge the food discoveries of others (Kurvers 2010a). Individual
91 neophobia measures were also found to be positively correlated with social-information use
92 under binary choice conditions in this species (Kurvers 2010b).

93

94 In the current study we focused upon the second of these two ideas, that personality traits might
95 be related to the use of public information. Focussing upon ninespine sticklebacks (*Pungitius*
96 *pungitius*), we specifically sought to determine whether public information use about foraging
97 patches, assayed multiple times for each individual, was related to individual behavioural
98 variation in other contexts under conditions in which all individuals had equal exposure to public
99 information cues. We focussed upon four behavioural measures: activity, thigmotaxis (a measure
100 of cover use), a measure of exploration rate and time spent grouping with conspecifics. These
101 behavioural measures were selected because together they allow us to quantify how the animals
102 move through space, and by extension how likely they are to encounter resources and other
103 conspecifics. We used the ninespine stickleback, an emerging model organism in behavioural
104 ecology and evolution (Merilä 2013), because they are facultatively social, and are known to use
105 public information when foraging (Laland et al. 2011; Webster and Laland 2011, 2012, 2013).
106 Furthermore, this species has been used as a study system for exploring inter- and intra-
107 population variation in personality traits (Herczeg et al. 2009; Webster et al. 2009).

108

109 We made no explicit predictions as to how these behaviours might be related to public
110 information use, instead focussing on two broad aims. Our first aim was to identify any
111 correlations between public information use and personality traits that might form the basis for
112 future research into potential social foraging strategies used by animals. Our second aim was to
113 identify relationships between personality traits and the weighting given to different sources of
114 information -here more recently available public information versus earlier-acquired private
115 information- when the two conflict with one another. To achieve this we tested one set of

116 subjects that were naïve to the distribution of resources in the public-information test, and
117 another set of experienced subjects, that had pre-existing information about the distribution of
118 resources that conflicted with the public information that they received in the public-information
119 test. These aims fall within our broader interest in social foraging and the conditions which
120 influence how animals use public information.

121

122 METHODS

123

124 *Subjects*

125

126 Ninespine sticklebacks were collected from Melton Brook, Leicestershire, UK (52°39'43''N,
127 1°06'49''W) in August 2011 (pilot study and the first four of six batches tested in the experiment
128 proper) and again in August 2012 (the final two batches). In the laboratory they were initially
129 held in groups of 30 in 90L aquaria. Each aquarium contained a layer of coarse sand, an external
130 filter, and artificial vegetation for cover. The light: dark regime was held at 12: 12 hours and the
131 temperature was maintained at 8 °C. The fish were fed daily with frozen bloodworms.

132

133 Sixty fish were used as test subjects and around eighty more were used as demonstrators or
134 stimulus fish in the experiments described below. A further forty fish were used in a pilot study,
135 also described below. Testing took place between September 2011 and November 2012. Neither
136 test subjects nor stimulus fish were sexed, and no fish were tested while in reproductive state.
137 Reproductive state can be inferred from the presence of nuptial colouration in males and the
138 presence of an egg mass in females. Previous research has shown that gravid females and

139 reproductive males differ from one another and from non-reproductives in their use of public
140 information, while non-reproductive males and females do not differ in this regard (Webster and
141 Laland 2011). In the closely related threespine stickleback (*Gasterosteus aculeatus*) no sex
142 differences in boldness, sociality or social-exploratory behaviour were detected between non-
143 reproductive males and females (Ward et al. 2004).

144

145 *General Methods*

146

147 For each of sixty ninespine sticklebacks we quantified PI-use on three occasions, and shoaling
148 and (within the same assay) activity, thigmotaxis and exploration on two occasions each. The PI-
149 use, sociability and activity, thigmotaxis and exploration assays are described in detail in the
150 subsections below. Of the sixty test subjects, thirty were given prior experience ('pre-training')
151 of finding food in only one of two artificial feeder units. In the subsequent PI-use assays they
152 were given conflicting public information, in that the feeder to which they had been trained to
153 expect food was manipulated so as to yield less food than it yielded in the PI-use assay, whilst
154 the other (hitherto unproductive) feeder was demonstrated to be the richer of the two. The other
155 thirty fish were fed from both feeders, with one feeder randomly selected to yield food on each
156 day ('sham-training'). Following pre / sham training the two treatment groups are referred to as
157 experienced and naïve. More details of these training procedures are given below.

158

159 Fish were tested according to the schedule in Table 1. Test subjects were selected at random
160 from the housing tanks. They were trained and tested in six batches of ten fish each, with five
161 fish receiving pre-training and five sham-training within each batch. Test subjects were

162 randomly allocated to the pre- and sham-training conditions. Test subjects were first weighed
163 with digital scales to the nearest 0.01g (blotted mass) and measured using callipers to the nearest
164 0.1 mm. We used fish measuring 34.7 to 47.5 mm in standard length. Condition factor
165 ($1000 * (\text{mass} / \text{length}^3)$) was included as covariates in the statistical analyses described below.
166 Weighing and measuring took place 24 hours after feeding. Each fish was then housed alone in a
167 45 l aquarium. Each aquarium contained a gravel substrate, plastic plants and was attached to its
168 own external filter. Two feeder units were also present, in the left and right corners along the
169 longer axis of each aquarium. These were placed opposite the filter inlet, which was located in
170 the centre of the facing wall. The feeder units were used for prey delivery, as described below, in
171 the pre-training / sham training subsection. Each aquarium was visually and chemically isolated
172 from the others. Ninespine sticklebacks are facultatively social, and being housed alone is not
173 likely to be a major stressor. While housed under these conditions they were fed five
174 bloodworms per day each. They were never fed less than 24 hours prior to being tested. On test
175 days they were fed around one hour after testing. On the final day of the testing period they
176 were measured and weighed again (prior to being fed). This allowed us to quantify growth and
177 any change in body condition over the duration of the study period. There were no differences in
178 body mass or condition factor between fish assigned to the naïve and experienced treatment
179 groups at the start of the experiment (One-way ANOVAs: log10 transformed mass, $F_{(1, 59)} = 0.60$,
180 $P = 0.44$; condition factor, $F_{(1, 59)} = 1.79$, $P = 0.19$). Condition factor did not change significantly
181 over the course of the study (paired samples t-test: $t = -1.36$, $df = 59$, $P = 0.83$), and the degree of
182 change did not differ between the two treatment groups (one-way ANOVA: $F_{(1, 59)} = 0.01$,
183 $P = 0.96$).

184

185 The test schedule in table 1 contains some randomisation of testing orders, but is not fully
186 randomised. This is because we wished to standardise the time between pre- or sham-training
187 and the three PI-use tests, so that all the subjects were tested at the same time following training
188 exposure. Similarly, we wished to maintain a two week timespan between the first and second
189 sociability and activity, thigmotaxis and exploration tests. For each individual then, the timing of
190 the first sociability assay was randomly allocated to day 15 or 18 of the testing period, with the
191 first activity, thigmotaxis and exploration assay occurring on the other day. The second of each
192 of these assays took place 14 days later. All assays took place between 10.00 and 16.00 on the
193 day of testing, with randomised individual test ordering.

194

195 *Public-Information Use Assay: pre-training and sham-training*

196

197 As described above, half of the test subjects were given private information about the location of
198 the prey patch, via a period of pre-training. In the test proper, they were then given conflicting
199 public information. The other half of the test subjects were given no consistent private
200 information.

201

202 Test subjects housed in their individual holding aquaria were fed once per day via one of the two
203 feeder units located in the corners of the aquarium. The feeder units consisted of a 4 x 4 cm base,
204 30 cm tall tower, constructed from opaque white plastic. The base of the feeder stopped 1 cm
205 short of the substrate, allowing the fish to eat the prey once it had reached the bottom of the
206 feeder. The fish received a daily food ration of five bloodworms each, as described above. Fish
207 in the pre-training treatment group always received their food via the same feeder unit, left or

208 right. The filter inlet, located centrally on the facing wall provided a reference landmark. The
209 feeder which yielded the food was randomly predetermined for each fish. For those fish in the
210 sham-training treatment group, the feeder unit which yielded the prey was selected at random
211 each day. We used feeder location (left or right) rather than feeder characteristics (such as
212 colour) as the focus of training and public information, because previous research has revealed
213 that it is the location of a feature, and not its physical characteristics that forms the basis of
214 learning via public information and local enhancement in this species (Webster and Laland
215 2013). The pre- and sham-training feeding regimes were continued up until the end of the study,
216 even after the public information trials had been completed.

217

218 In order to determine the efficacy of the pre-training protocol, we first ran a pilot study. Twenty
219 randomly selected fish were subjected to pre-training for 14 days, using the procedure described
220 above, and a further twenty received sham-training. In the pre-training treatment group, 10 fish
221 were trained to expect food from the left feeder only and 10 from the right feeder only.

222 Following this, the fish were tested for feeder preference under binary choice conditions. They
223 were tested in an aquarium identical to the one that they had previously been housed in,
224 including two identical feeder units in the corners and an attached filter unit to provide a landmark
225 reference. The filter was switched off for the duration of the trial. No prey were present in the
226 testing arena at any point during the trial. They were placed within a holding unit, a tower of
227 clear, colourless perforated Perspex measuring 10 x 10 cm x 25 cm tall. It was attached via a
228 monofilament line to a 15 cm long arm clamped to the top of the observer arena, allowing the
229 holding unit to be raised by the experimenter. The holding unit was placed 5 cm from the side
230 wall of the aquarium and half way between the end walls where the feeder units were located.

231 The fish was held for ten minutes in order to acclimatise, before the holding unit was raised
232 10cm, releasing the fish and beginning the trial. The trial lasted for 3 minutes. We point sampled
233 the location of the fish every 6 seconds, noting whether or not it was within 8 cm of either end of
234 the test tank. This pilot experiment, reported in the results section, revealed that fish pre-trained
235 to the left or the right feeder showed a preference for the feeder on that side. In contrast, the fish
236 in the sham-training treatment showed no such preference. The fish used in this pilot experiment
237 played no further part in the remainder of the study.

238

239 **Behavioural assays**

240

241 *Public-Information Use Assay*

242

243 Test arena

244

245 PI-use was tested using a binary choice test tank comprising a main observer arena, set between
246 two demonstrator chambers (Fig. 1a). Each demonstrator chamber contained three conspecific
247 demonstrators and a feeder unit. The feeder units released food at different rates, and were
248 designed so that the observer could see the demonstrators' feeding behaviour, but could not see
249 or otherwise detect the food itself. The observer was therefore able to estimate patch quality only
250 indirectly, by using public information generated by the feeding demonstrators. Following a
251 demonstration period, opaque barriers were placed between the observer arena and the
252 demonstrator chambers, and the observer was released and allowed to move about the observer
253 arena. A goal zone was present at each end of the arena, adjacent to either demonstrator

254 chamber. The amount of time the observer spent in each goal zone was taken as a measure of its
255 preference for that goal zone. A preference for the zone adjacent to the rich patch is taken as a
256 measure of public-information-mediated patch choice.

257

258 We used a glass tank (45 x 30 x 30 cm, water depth 12 cm) as the observer arena. At either end
259 of the observer arena we placed a colourless Perspex demonstrator chamber (27 x 15 x 12 cm,
260 water depth 12 cm). These were placed 0.5 cm from the ends of the observer chamber. Each of
261 the three tanks contained a 1 cm deep layer of coarse sand. Within the observer arena, yellow
262 plastic bars, 1 cm wide and 1 cm deep, secured to the base of the tank and rising to the surface of
263 the sand divided the tank into three zones. These were set eight cm from either end of the
264 observer arena. The two areas between the end of the tank and the bars were designated the prey
265 patch goal zones. An external hanging filter was attached to the wall of the central tank, so as to
266 match the layout of the holding tanks in which the test subjects were housed during their pre- or
267 sham training. The filter was not switched on during the trials, but the filter inlet provided a
268 landmark which may have further aided pre-trained fish to orientate between the left and right
269 feeders.

270

271 Within each of the demonstrator tanks we placed a feeder unit. The feeder unit consisted of a 4 x
272 4 cm base, 30 cm tall tower. The feeder units were placed in the corner of the demonstrator
273 chamber furthest from the observer arena. The front wall of the feeder unit, facing the
274 demonstrators, was transparent so that they could see the prey as it was delivered. The rear wall
275 was white to maximise the visibility of the prey. The side walls were opaque, so that the observer
276 in the central tank could not see the prey. Demonstrators were unable to reach the prey until it

277 sank to the bottom of the feeder, but were able to attack it as it fell. The front wall of the feeder
278 stopped 1 cm short of the floor of the tank, allowing the demonstrators to eat the prey once it had
279 reached the bottom of the feeder. Prey deliveries consisted of two 3 mm long pieces of thawed
280 frozen bloodworm. These were small enough to be consumed with minimal handling by the
281 demonstrators, ensuring that the observing focal fish could see the feeding behaviour of the
282 demonstrators, but not the prey itself. Screening on the outside of the test tank prevented the fish
283 from seeing the experimenter as the prey were added. Housing the demonstrators in watertight
284 chambers ensured that no chemical cues originating from the prey were available to observer,
285 since these may provide direct information about feeder location and prey density (Webster et al.
286 2007a). This ensured that observer could only base their patch choices upon visual cues received
287 during the demonstration phase. No prey were present in the central arena at any point during the
288 trial.

289

290 Within the observer arena, the observer was held within a holding unit for the duration of the
291 settling period and demonstration phase. The holding unit consisted of a tower of clear,
292 colourless perforated Perspex measuring 10 x 10 cm x 15 cm tall. It was attached via a
293 monofilament line to a 15 cm long arm clamped to the top of the observer arena, allowing the
294 holding unit to be raised by the experimenter. The holding unit was placed 5 cm from the side
295 wall of the observer arena, opposite the wall with the filter inlet attached, and half way between
296 the end walls that faced the demonstrator chambers.

297

298 We used two opaque black plastic screens measuring 30 x 30 cm square x 3 mm thick to separate
299 the observer arena from the demonstrator chambers during the choice phase of the trial. These

300 were designed so that they could be simultaneously slid into place between the tanks without
301 causing any vibration that might stress the observer. The exterior walls of both the observer
302 arena and demonstrator chambers were screened in black plastic. Trials were recorded via a
303 webcam fixed 90 cm above the tank.

304

305 The demonstrators measured between 40 and 45 mm in length. Due to limitations in the numbers
306 of available fish of this size range, the demonstrators were drawn from a pool of around 80 fish.
307 No demonstrator was used more than once in any three day period. Observers were only tested
308 once, and no observers were subsequently used as demonstrators, or vice versa. We did not use
309 demonstrators that had previously been housed with the test subjects, in order to remove any
310 potential effects of familiarity (Ward and Hart 2003; Griffiths and Ward 2011).

311

312 Test procedure

313

314 The demonstrators and focal fish were deprived of food for 24 h before testing in order to ensure
315 that they were motivated to feed. Three randomly selected demonstrators were added to each
316 demonstrator chamber and allowed to settle for 10 minutes before the focal fish was added to the
317 central holding unit and allowed to settle for a further 10 minutes. The demonstration phase
318 lasted for 6 minutes and ran as follows. At the beginning of the first, third and fifth minute of the
319 trial, prey suspended in 1 cm³ of tank water were added to the feeder in the designated rich patch,
320 using a pipette. During the first and third minutes of the trial the poor patch received no prey. A
321 'blank' consisting of 1 cm³ of tank water was added to the feeder at the same time that the rich
322 feeder received prey. During the fifth minute the poor feeder also received prey. This ensured

323 that while prey were delivered at a 3:1 ratio, the focal fish was unable to select a prey patch
324 simply on the basis of it being the last place it saw fish feeding. The demonstrators consumed all
325 of the offered prey in each trial.

326

327 For trials involving test subjects held under the pre-training condition, the rich feeder was always
328 located on the opposite side to which they had been trained, providing them with public
329 information that contradicted their previous experience. In trials of subjects held under the sham-
330 training condition, which had no previous experience of one feeder being superior to the other,
331 one side was randomly selected for the location of the rich feeder, and was then used for all three
332 public information trials. This was performed so as to ensure that fish in both the pre- and sham-
333 training treatments received demonstrations that were otherwise identical.

334

335 After the six minute demonstration phase, the opaque black screens were simultaneously slid into
336 place between the observer arena and the two demonstrator chambers. This took approximately
337 10 seconds and did not appear to stress the observer. The observer was allowed to settle for a
338 further 1 minute before being released from the holding unit. The observer was released by
339 raising the holding unit 5 cm from the base of the arena, using the pulley mechanism. The base
340 of the holding unit was left suspended beneath the water surface, so as not to disturb the surface
341 of the water and startle the observer. This commenced the choice phase of the trial, which lasted
342 for five minutes. During the choice phase we recorded the location of the observer every six
343 seconds (whether it was within either goal zone or the central neutral zone, yielding a total of 50
344 data points) and the first goal zone it entered. A fish was deemed to have entered the goal zone if
345 its entire head passed over the delineating yellow goal zone bar.

346

347 *Activity, thigmotaxis and exploration*

348

349 We quantified activity, thigmotaxis and exploration in fish placed within a novel arena. This
350 consisted of an arena within an opaque black plastic container measuring 80cm long x 60cm
351 wide x 35 cm deep and with a water depth of 20cm. A grid consisting of 1 cm wide bars set in
352 the substrate and level with its surface was used to divide the test arena into 18 areas measuring
353 20 x 13 cm each (Fig. 1b). These did not impede the movement of the fish, and were used to
354 quantify exploration, as described below. Two test arena configurations were used. Each test
355 subject was tested once in each, in a randomly determined order. This ensured that each test
356 occurred in a novel arena. The first configuration contained a sand substrate, and the second a
357 coarse gravel substrate, both 1 cm deep. Each contained five landmarks, consisting of a 19 cm
358 tall, 6 cm wide clear plastic cup filled with sand (in the sand substrate configuration) or small
359 rocks (in the gravel substrate configuration). The layout of these varied between the two
360 configurations, as shown in Fig. 1b *i* and *ii*. A holding unit was placed in one corner of the test
361 arena. This consisted of a tower of clear, colourless perforated Perspex measuring 10 x 10 cm x
362 25 cm tall. It was attached via a monofilament line to a 15 cm long arm clamped to the wall of
363 the observer arena, allowing the holding unit to be raised by the experimenter.

364

365 The test subject was added to the holding unit and allowed to acclimate for 10 minutes.

366 Following this, the observer was released by raising the holding unit 10 cm from the base of the
367 arena, using the pulley mechanism. The base of the holding unit was left suspended beneath the
368 water surface, so as not to disturb the surface of the water and startle the test subject. This began

369 the trial, which ran for 15 minutes. We recorded three behaviours; activity, thigmotaxis, and the
370 latency of the test subject to visit half of the zones. Activity was point sampled at 15 second
371 intervals, giving a total of 60 observations. For each sampling instance we noted whether the fish
372 was swimming or whether it was stationary, either in the water column or on the substrate.
373 Thigmotaxis, or wall-following behaviour was also sampled at 15-second intervals. Thigmotaxis
374 was used as a measure of cover use, represented here by the walls and landmarks (Webster and
375 Laland 2011; 2012). For each sampling instance we recorded whether the fish was within 5 cm
376 of either the side wall of the arena or one of the five landmarks within the arena interior. Finally,
377 latency to enter half of the arena zones was recorded as a continuous variable, to the nearest
378 second. Fish failing to enter half of the zones were given a ceiling score of 900 s.

379

380 *Shoaling assay*

381

382 We established a binary choice test arena measuring 80cm long x 60cm wide x 35 cm deep, with
383 a water depth of 20cm in an opaque black plastic container (Fig. 1c). The arena contained a 2 cm
384 deep layer of coarse sand. Ten cm from either end of the arena we placed a 10 cm square, 25 cm
385 tall stimulus chamber. This was constructed from colourless, perforated plastic. A webcam was
386 fixed above the arena, allowing observations to be made. To one of the stimulus chambers we
387 added five unsexed, non-reproductive sticklebacks measuring 40-45 mm in length. Together,
388 these formed the stimulus shoal. The chamber holding the stimulus shoal was selected at random,
389 and other was left empty. The stimulus shoal was allowed to settle for 10 minutes before the test
390 subject was added to the tank, and were changed after every trial. They were drawn from the
391 pool of approximately 80 stimulus fish. No stimulus fish was used twice in the same 48 hour

392 period. As in the PI assay, we did not use demonstrators which had previously been housed with
393 the test subjects, in order to remove any potential effects of familiarity (Ward and Hart 2003;
394 Griffiths and Ward 2011).

395
396 The test subject was placed within a holding unit attached to a pulley mechanism, as described
397 above. The test subject was allowed to acclimatise for a further 10 minutes before the trial began.
398 Following this, the holding unit was raised 10 cm from the base of the arena, also as described
399 above. The trial lasted for a further 20 minutes, during which time we recorded the proportion of
400 time that the test subject spent within 8 cm, approximately two average body lengths, of either
401 stimulus chamber. This distance was selected as it corresponds to the inter-individual shoaling
402 distance seen in free-moving shoals (Webster et al. 2007b).

403

404 *Statistical Analyses*

405

406 In the pilot experiment we used paired-sample t-tests to compare time spent in the goal zone of
407 the target and non-target feeders in the trained-treatment fish and in the left versus the right goal
408 zone in the sham-trained treatment group. Data were normalised using arcsine transformation
409 before analyses were performed.

410

411 We compared the first and second measures of the four behavioural traits -activity, thigmotaxis,
412 latency to enter 50% of the test arena and time spent shoaling- between the naïve and
413 experienced groups using repeated measures ANOVAs. Proportional data (activity, thigmotaxis

414 and shoaling) were normalized with arcsine transformation while count data (latency to explore
415 50% of the arena) were transformed using log10 transformation before analyses were performed.
416 We used Spearman rank correlations to test for consistency of responses between measures for
417 each of these traits, as well as for correlations between all possible combinations of behavioural
418 measure and the three time allocation measures of public information use. These behaviours
419 were then collapsed into two principle components describing ‘space use’ and ‘sociability’ using
420 a principle components analysis, as described below.

421
422 Next we compared public information use between the naïve and experienced groups. We used
423 the first goal zone that each fish entered to determine a first choice score consisting of the
424 number of trials in which it entered the rich patch goal zone first over the three public
425 information tests. We also calculated a time allocation score using the proportion of time spent in
426 the rich goal zone minus the mean proportion of time spent in the poor goal zone in each of the
427 three trials. We used an independent samples t-test and a repeated measures ANOVA
428 respectively to compare these scores between the naïve and experienced treatment groups.

429
430 Finally, we sought to determine the relationship between the space use and sociability measures
431 and the two metrics of PI-use. In order to determine whether either of the two principle
432 components were related to the first goal zone choice of the fish over the three public
433 information assays we performed an ordinal regression using, with first choice score, an ordinal
434 category of 0, 1, 2 or 3, assigned as the dependent variable. Treatment was included as a fixed
435 factor and starting body mass and condition factor, and the space use and sociability principle
436 components were included as covariates, fitted using stepwise backward elimination. In order to

437 test for effects of either of the two principle components upon time allocation we ran two general
438 linear models using gaussian error distributions. These used the mean and median time allocation
439 respectively as the dependent variable. In both cases, treatment was included as a fixed factor
440 and starting body mass and condition factor, and space use and sociability were included as
441 covariates.

442

443 RESULTS

444

445 *Pilot experiment*

446

447 Fish that had been pre-trained to feed from one of two feeders (left or right) spent more time in
448 the goal zone surrounding the feeder to which they had been trained (paired samples t-test: $t=$
449 3.84 , $df= 19$, $P= 0.001$). Naïve fish that had been sham trained, subject to the same training
450 procedure but with food randomly allocated to either feeder on any given day, showed no feeder
451 goal zone preference ($t= -1.17$, $df= 19$, $P= 0.26$, Fig. 2). The results of the pilot experiment
452 demonstrate that the 14 day training period was sufficient to generate a learned bias for one of
453 the two feeders.

454

455 *Behavioural trait measures*

456

457 We saw no differences in the four behaviours (activity, thigmotaxis, latency to enter 50% of the
458 test arena and time spent shoaling) between fish from the naïve and experienced treatment
459 groups (Table 2).

460

461 Because the behavioural trait scores between experienced and naïve treatment groups did not
462 differ, we pooled these data when looking at consistency. The four behaviours were all found to
463 be positively correlated over the two sampling periods (Table 3 and Fig. 3). Moreover, we saw
464 that the two measures of activity were negatively correlated with the measures of latency to
465 explore 50% of the arena and thigmotaxis. These latter two measures were positively correlated
466 with one another (Fig. 3).

467

468 In the shoaling assay, fish spent more time within two body lengths of the chamber holding the
469 stimulus shoal than they did within two body lengths of the empty chamber (naïve and
470 experienced treatment group data pooled, paired samples t-tests on arcsine transformed data,
471 First assay: $t = 12.77$, $df = 59$, $P < 0.001$; Second assay: $t = 9.54$, $df = 59$, $P < 0.001$).

472

473 *Principle components analysis (PCA) of behavioural traits*

474 A PCA was used to reduce the four behaviour measures- activity, thigmotaxis, latency to enter
475 50% of the test arena and time spent shoaling- into a minimal number of components. This
476 yielded two components, describing 54.6% and 25.1% of the variation respectively (Kaiser-
477 Meyer-Olkin Measure: 0.71; Bartlett's Test of Sphericity: $X^2 = 58.12$, $df = 6$, $P < 0.001$). PC1,
478 hereafter 'space use', described negative correlations between activity and thigmotaxis, and
479 between activity and latency to explore half of the arena, and a positive correlation between
480 thigmotaxis and latency. PC2, hereafter 'sociability', contained the measure of time spent
481 shoaling. The loadings of these behavioural measures onto the two PCs is given in Table 4.

482

483 *Public-information use*

484 We saw no differences between naïve and experienced fish in the number of times that they first
485 entered the goal zone demonstrated in the trial to be rich, or in the mean time difference spent in
486 the rich versus the poor goal zone, (Independent samples t-test: first entered rich goal zone, $t = -$
487 0.18 , $df = 58$, $P = 0.85$, Fig. 4a; repeated measures ANOVA: time in goal zone, performance over
488 the three trials, $F(1, 58) = 0.49$, $P = 0.58$, $\eta^2 = 0.008$; performance between training treatments
489 $F(1, 58) = 0.27$, $P = 0.60$, $\eta^2 = 0.005$; performance across trials*training treatments $F(1, 59) =$
490 0.31 , $P = 0.54$, $\eta^2 = 0.06$ Fig. 4b).

491
492 Pooling data from the naïve and experienced treatment groups, we saw that fish entered the rich
493 patch first more often than they entered the poor patch across the three trials (paired samples t-
494 test: $t = 4.41$, $df = 59$, $P < 0.001$). They also spent more time there compared to the poor patch
495 (mean time allocation across the three trials per individual, $t = -7.88$, $df = 59$, $P < 0.001$).

496

497 *Personality and public-information use*

498 An ordinal regression revealed that the number of trials in which fish first entered the rich patch
499 was unrelated to space use or sociability PC scores, nor to their training or body condition (Table
500 5, Fig. 5a and 5b). Confidence intervals for the effect of condition factor were wide, suggesting
501 an effect of condition factor on prey patch first choice may still be possible, but were narrow for
502 mass, treatment and the space use and sociability principal components, suggesting that a large
503 effect of these variables is implausible.

504

505 Similarly, GLMs showed that the mean proportional difference in time spent between the rich
506 and poor patches was not related to space use or sociability, nor to training or body condition.
507 This was true when both mean and median time allocation scores were used as dependent
508 variables (Table 6, Fig. 6a and 6b). Effect sizes were small (0.04 or lower in all cases),
509 suggesting that biologically meaningful effects of prior experience, space use or sociability are
510 unlikely.

511

512 DISCUSSION

513

514 Our study revealed individual consistency in activity, exploration, thigmotaxis and time spent
515 shoaling in nine-spine sticklebacks, measured over a period of several weeks, but found that these
516 traits were unrelated to either of two measures of PI-use. In addition to this, we saw no effect of
517 experience with regards to where to forage in our experiment- while we were able to train fish to
518 prefer one of two feeders, trained fish were just as likely to be influenced by (conflicting) PI as
519 were naïve fish when they were tested. Effect sizes here were seen to be small (Tables 5 and 6)
520 suggesting that this finding reflects a true absence of any substantial effect of these behaviours
521 upon PI-use, rather than being an artefact of insufficient power to detect such a relationship.

522

523 Overall, the majority of fish were net PI-users, being more likely to first enter, and to spend more
524 time in the PI-demonstrated rich patch in most of their successive trials. This is consistent with
525 the findings of earlier work on PI-use in this species carried out in our laboratory (Laland et al.
526 2011). Individual consistency in PI-use over the three trials was low however, with moderate
527 negative correlations in net time allocation to the rich prey patch seen between the first and

528 second and first and third assays (Fig. 3), although no decline in PI-use over successive trials was
529 evident at the treatment group level.

530

531 Our finding that measures of activity, exploration, thigmotaxis and time spent shoaling were
532 consistent across trials within individuals corresponds with the findings of other studies reported
533 in the literature. These and similar behaviours have previously been shown to be correlated
534 across exposures in a wide variety of different species, and are considered to be common sources
535 of personality variation in non-human animals, though potentially with different underlying
536 mechanisms (reviewed by Reale et al. 2007; Sih and Bell 2008; Bell et al. 2009; Conrad et al.
537 2011).

538

539 Our primary finding, that PI-use was unrelated to any of the behavioural traits that we looked at,
540 contrasts with those of some previous studies, such as Marchetti and Drent (2000), Kurvers et al.
541 (2010a, 2010b) and David et al. (2011), where similar behavioural traits were seen to be linked
542 to scrounging behaviour and PI-use respectively. We note of course that these studies were
543 carried out in different species and using differently designed assays. On the other hand, our
544 findings are consistent with those from studies investigating different forms of social information
545 use in the threespine stickleback (Webster et al. 2007c; Harcourt et al 2010). In these studies,
546 attraction to feeding conspecifics alone (Webster et al. 2007c), and attraction to feeding
547 conspecifics and response to other social cues (Harcourt et al. 2010) were not seen to be related
548 to measures of boldness or exploratory behaviour. This suggests that such relationships between
549 public learning and foraging and other behavioural traits are probably species, and context,
550 specific, and that attempts to generalise across species may sometimes be misleading.

551

552 The absence of a relationship between PI-use and the behavioural traits considered in this study
553 could be due to a number of factors. For example, theoretical analyses have shown that
554 discriminatory use of public information is generally adaptive (Rendell et al. 2010). While
555 ninespine sticklebacks are not an obligatorily shoaling species, and were seen in this study to
556 vary in their sociability, they are nevertheless generally social. All individuals are therefore
557 likely to be exposed to PI at different times throughout their lives, and may all therefore have had
558 ample opportunity to learn to associate conspecific feeding behaviour with the presence of food
559 prior to being used in our experiments. If conspecific feeding behaviour is a reliable indicator of
560 prey availability then we might expect all individuals to respond to such cues, irrespective of any
561 variation between them in other behaviours.

562

563 Finally, it remains plausible that variation in space use or sociability or other behavioural traits
564 might indirectly affect how individuals use PI, by affecting their exposure to it. This possibility
565 was deliberately excluded by our experimental design, as we sought to determine whether PI-use
566 co-varied with these personality traits when opportunity for exposure was standardised. It seems
567 intuitive that, for example, individuals that spend more time interacting with others, or which are
568 more strongly attracted to large groups of conspecifics, might be exposed to PI more frequently
569 or from a greater variety of different sources. Individuals that are more active or exploratory, or
570 which interact more frequently with novel elements in their environment, might themselves be
571 more likely to encounter other individuals, and thus be exposed to PI more frequently too. At the
572 same time those individuals might also be more likely to privately acquire information about the
573 nature and distribution of resources in the environment. Given this it seems clear that personality

574 traits that affect how individuals move through their environment and encounter and interact
575 with others might affect how they acquire information from both private and social sources. In
576 principle, such effects can be quantified via information-diffusion experiments, in which groups
577 of freely moving individuals are monitored as they interact and uncover hidden resources. Social
578 network analysis can be used to quantify the structure of social interactions (Croft et al. 2008;
579 Wilson et al. 2013), which in turn can be used to inform network-based diffusion analysis
580 (NBDA) models which attempt to identify the effects of social structure and other variables upon
581 the rate and order at which individuals acquire information about resources such as food patches
582 (Franz and Nunn 2009; Hoppitt et al. 2010). This approach has recently been used to quantify
583 social effects on information acquisition in fish (Atton et al. 2012, 2014; Webster et al. 2013).
584 Useful further research could account for individual level variation in a range of different
585 behavioural traits that might conceivably affect how likely individuals are to encounter resources
586 and interact with others. Such work could prove useful in revealing the importance of the
587 behavioural traits which comprise personalities in the acquisition and spread of information.

588

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590

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597 ETHICAL STANDARDS

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599 The experiments described in the article were performed in accordance with the current laws of
600 the UK.

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780 **Table 1** Test schedule

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Day	Treatment
1	First weighing and measuring, assigned to individual housing aquarium
1-14	Pre-training / sham training
15	Sociability assay I / space use assay I
18	Sociability assay I / space use assay I
22	PI-use assay I
24	PI-use assay II
26	PI-use assay III
29	Sociability assay II / space use assay II
32	Sociability assay II / space use assay II
33	Final weighing and measuring

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796 **Table 2** Comparing behavioural trait scores between experienced and naïve treatment groups
 797 (repeated measures GLM). Measure describes within-subjects comparisons between the first and
 798 second trial. Treatment describes conditions where fish either had or had not received feeder
 799 preference training. Refer to main text for further details
 800

	F _(1, 58)	P	ηp²
Activity			
Measure	0.01	0.91	<0.01
Treatment	0.29	0.58	0.01
Measure * Treatment	0.05	0.82	0.01
Latency to enter 50% of arena			
Measure	1.09	0.30	0.02
Treatment	0.19	0.65	0.01
Measure * Treatment	0.28	0.59	0.01
Thigmotaxis			
Measure	0.01	0.97	<0.01
Treatment	0.64	0.43	0.01
Measure * Treatment	0.58	0.49	0.01
Shoaling			
Measure	0.01	0.92	<0.01
Treatment	0.01	0.91	<0.01
Measure * Treatment	0.01	0.93	<0.01

801

802 **Table 3** Consistency of behavioural measures (Spearman's rank correlation)

803

Behaviour	N	<i>r</i>	P	95% CI
Activity	60	0.58	<0.001	0.41, 0.71
Thigmotaxis	60	0.42	<0.001	0.25, 0.58
Latency to enter 50% of arena	60	0.38	<0.001	0.14, 0.58
Time shoaling	60	0.44	<0.001	0.21, 0.62

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822 **Table 4** PCA loadings of behavioural measures

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Behavioural measure	PC1 'space use' (54.6% of variance)	PC2 'sociability' (25.1 % of variance)
Activity measure	-0.86	-0.12
Latency to enter 50% of arena measure	0.86	0.06
Thigmotaxis measure	0.83	-0.06
Shoaling measure	-0.10	0.99

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842 **Table 5** Summary of an ordinal regression investigating the effects of condition factor and
843 behavioural trait variables, and naïve / experienced treatment upon the number of times entered
844 the rich goal zone first in PI-use trials

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Variable	X²	df	P	Parameter estimate	95% CI
Condition factor	2.21	1	0.17	90.43	-10.80, 241.52
PC 'space use'	1.71	1	0.15	0.34	-0.01, 1.04
PC 'sociability'	2.14	1	0.12	-0.07	-0.98, 0.14
Treatment	1.50	1	0.22	-0.13	-1.81, 0.42

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862 **Table 6** Summary of a GLM investigating the effects of condition factor and behavioural trait
 863 variables, and naïve / experienced treatment upon (a) mean and (b) median time allocation to the
 864 rich goal zone in PI-use trials (time in rich goal zone – time in poor goal zone)
 865

(a)							
Variable	DF	Mean square	F	P	B	95% CI	η^2
Model	4	28.63	0.58	0.67			0.04
Intercept	1	113.53	2.32	0.13	4.64	-2.16, 7.46	0.04
Condition factor	1	12.39	0.25	0.62	191.11	-252.40, 634.63	0.01
PC 'space use'	1	19.05	0.39	0.53	0.59	-1.24, 2.44	0.01
PC 'sociability'	1	63.25	1.29	0.26	1.07	-0.77, 2.92	0.02
Treatment	1	55.58	1.14	0.29	-1.08	-4.83, 2.66	0.02
Total	60						
Corrected total	59						
(b)							
Model	4	22.72	0.27	0.89			0.02
Intercept	1	186.99	2.22	0.14	6.85	-2.09, 9.80	0.04
Condition factor	1	3.71	0.04	0.83	121.75	-460.47, 703.98	0.01
PC 'space use'	1	6.31	0.07	0.78	0.36	-2.06, 2.78	0.01
PC 'sociability'	1	27.89	0.33	0.57	0.93	-1.49, 3.35	0.01
Treatment	1	81.98	0.97	0.33	-1.90	-6.82, 3.02	0.02
Total	60						
Corrected total	59						

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874 FIG. LEGENDS

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876 **Fig. 1** Plan views of the experimental arenas used to quantify (a) public information use, (b)
877 measures of space use and (c) shoaling behaviour. Solid black lines represent opaque surfaces
878 and broken black lines represent colourless transparent surfaces. The solid grey lines in (a) and
879 (b) represent the public information use goal zones and the different zones of the arena used to
880 quantify movement respectively. These were level with the substrate surface and did not impede
881 fish movement. The grey squares in (a) represent the feeder units and the large grey rectangle
882 represents the filter unit. The circles in (b) represent landmark features. (b *i* and *ii*) represent the
883 two landmark configurations used in the successive space use assays. The hatched areas in (c)
884 represent the zones in which fish were deemed to be shoaling. See main text for full details and
885 procedures

886

887 **Fig. 2** A pilot experiment run to test the efficacy of pre-training fish to expecting food from one
888 of two feeders (left or right). The white points show the amount of time (mean +/- 95% CI) spent
889 in the left and right feeder goal zones by sham-trained fish, where food had been randomly
890 assigned to the left or right feeder on each day of testing. The black points show amount of time
891 spent in the target (i.e. the side to which they were trained) or non-target feeder goal zones by
892 pre-trained fish, where food had been consistently delivered to the left or right feeder only on
893 each day of testing. * indicates $P < 0.05$, ns indicates no significant difference. The grey points
894 show a breakdown of the pre-training data into fish trained to the left feeder and fish trained to
895 the right feeder.

896

897 **Fig. 3** A heatmap showing correlation coefficients obtained from Spearman rank correlations for
898 all combinations of the behaviours measured in the study. *PI 1-3* refers to the time allocation
899 scores (time in rich patch – time in poor patch) in the three public information use trials. *Move*
900 refers to the amount of time spent moving in the two novel arena assays. *Exp* refers to the latency
901 to enter 50% of the zones of the arena floor in the two novel arena assays. *Thig* refers to the
902 measures of thigmotaxis, the proportion of time the fish remained within 5cm of the walls and
903 landmarks in the two novel arena assays. *Shoal* refers to the proportion of time that the fish spent
904 shoaling in the two shoaling assays. Red and blue cells indicate positive and negative
905 correlations respectively

906
907 **Fig. 4** (a) The number of times out of three trials in which each fish first entered the rich patch
908 goal zone. The grey and white sections show first entries into the rich patch by fish in the
909 experienced and naïve treatments respectively. The hatched section of the bar shows first entries
910 into the poor patch goal zone. Black sections indicate trials in which the fish failed to enter either
911 goal zone. Each bar represents one fish. These are arranged in order of most to fewest first
912 entries into the rich patch goal zone. There was no difference in rich patch goal zone entries by
913 fish in the experienced and naïve treatment groups. (b) The time allocation scores to the rich
914 patch (time in rich patch goal zone minus time in poor patch goal zone) for each of three trials
915 per fish. The points show the time allocation for the median ranked trial, and the error bars show
916 the highest and lowest time allocation scores for each individual. The red cross symbols show the
917 mean time allocation score for each individual. Where error bars are absent, the median and
918 highest / lowest scores were identical. Grey and white points represent fish from the experienced
919 and naïve treatments respectively. Data are arranged in order of highest to lowest median time

920 allocation to the rich patch goal zone. Analyses were performed for both median and mean time
921 allocation scores. There was no difference in rich patch goal zone entries by fish in the
922 experienced and naïve treatment groups

923

924 **Fig. 5** (a) Scatterplot showing the number of first entries into the rich patch goal zone plotted
925 against the principle component scores describing space use. (b) The number of first entries into
926 the rich patch goal zone plotted against the principle component scores describing sociability.
927 Grey and white points represent fish from the experienced and naïve treatments respectively. No
928 relationship was seen between these variables

929

930 **Fig. 6** (a) Scatterplot showing the mean time allocation to the rich patch goal zone (time in rich
931 patch goal zone minus time in poor patch goal zone) plotted against the principle component
932 scores describing space use. (b) Mean time allocation to the rich patch goal zone plotted against
933 the principle component scores describing sociability. Grey and white points represent fish from
934 the experienced and naïve treatments respectively. No relationship was seen between these
935 variables

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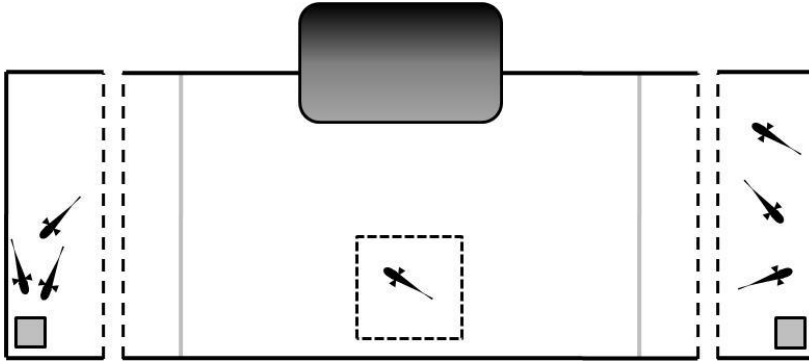
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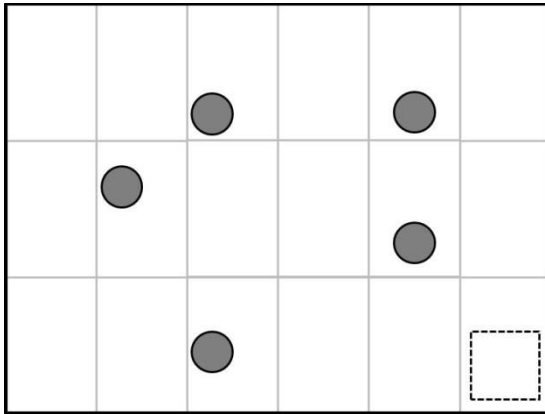
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947 **Figure 1.**
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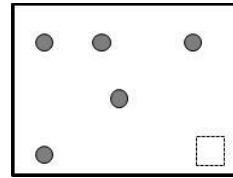
(a)



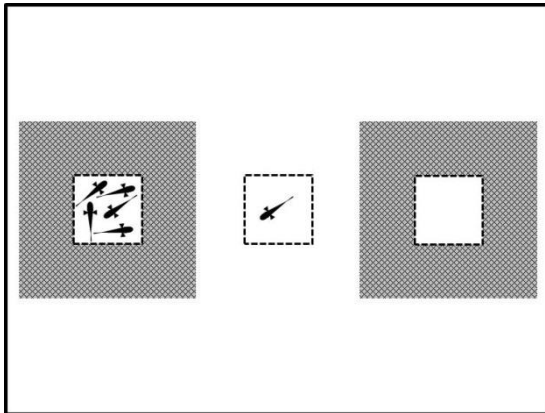
(b) (i)



(ii)

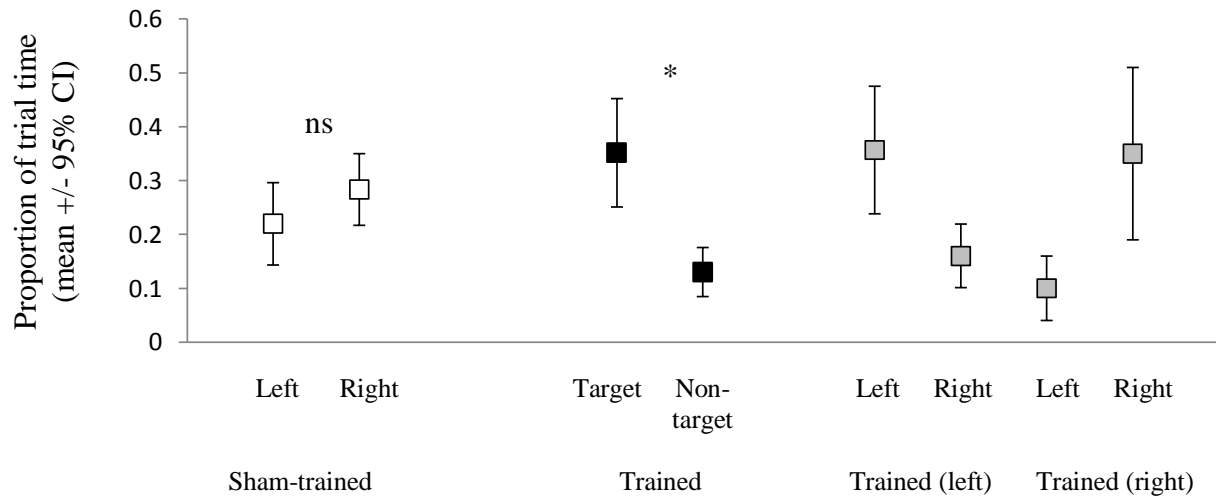


(c)



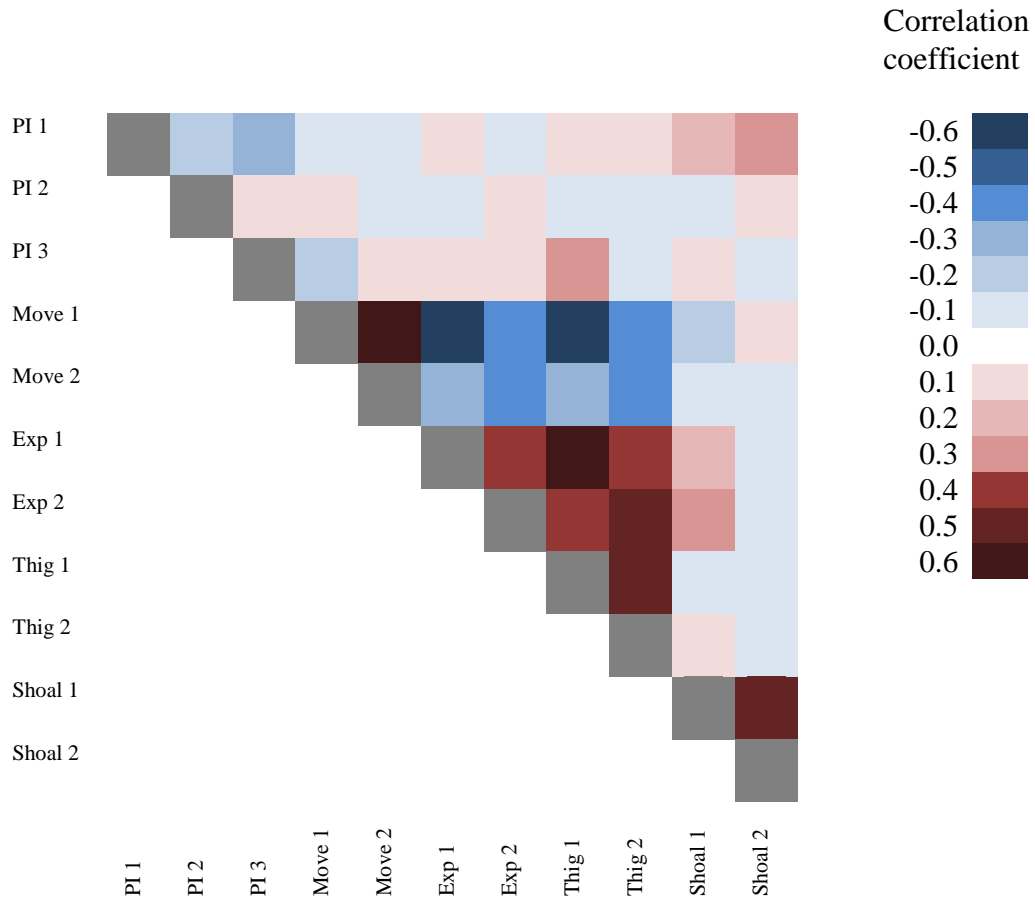
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957 **Figure 2.**
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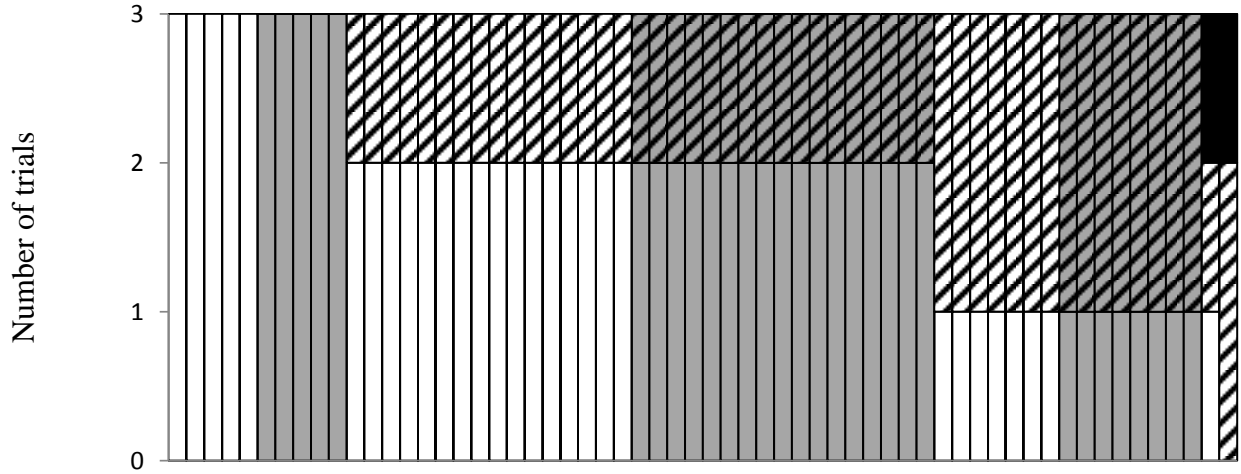
990 **Figure 3.**
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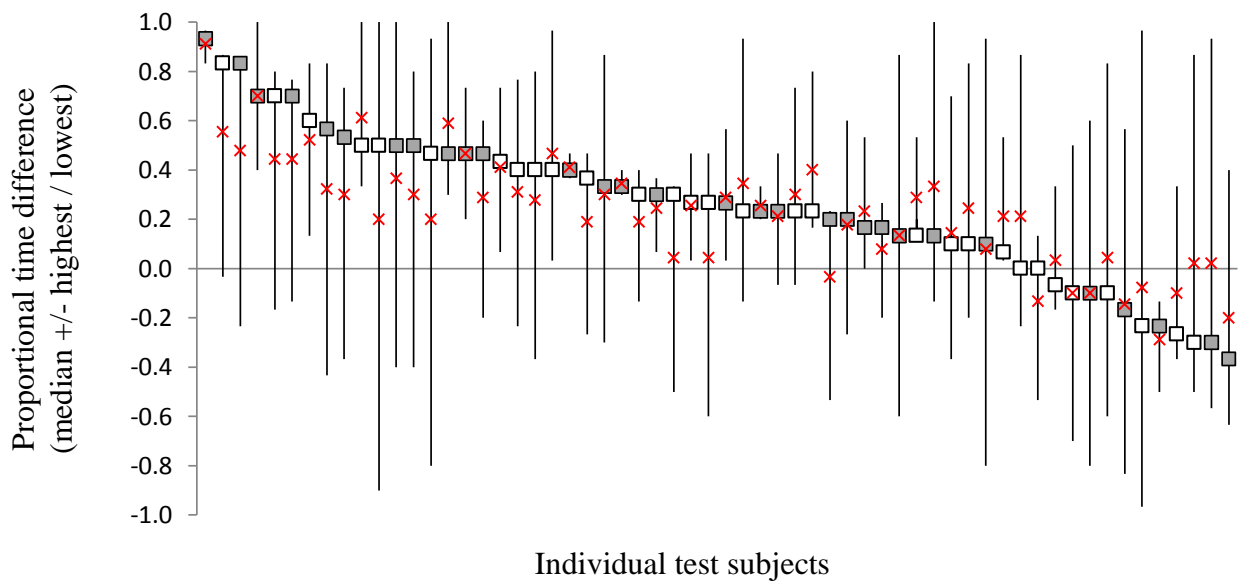
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1011 **Figure 4.**
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(a)



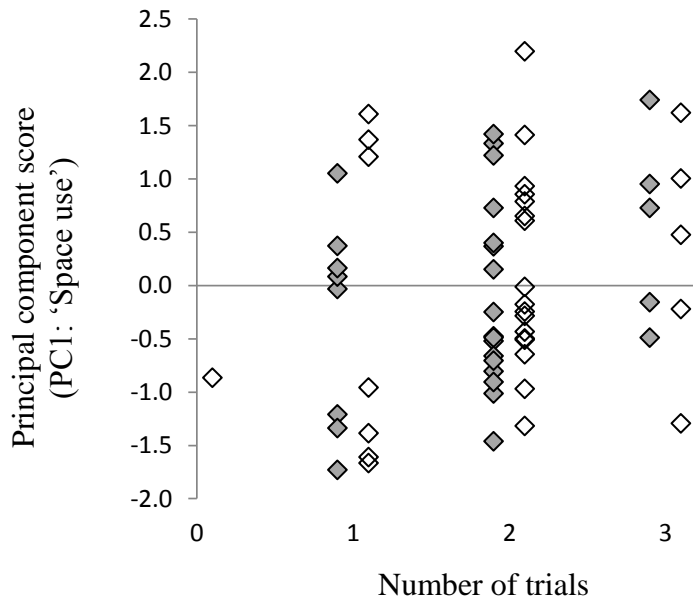
(b)



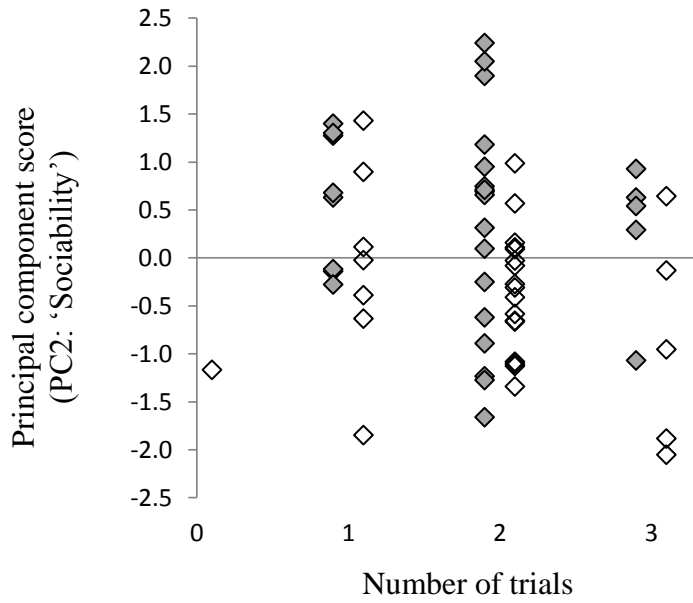
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1023 **Figure 5.**
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(a)



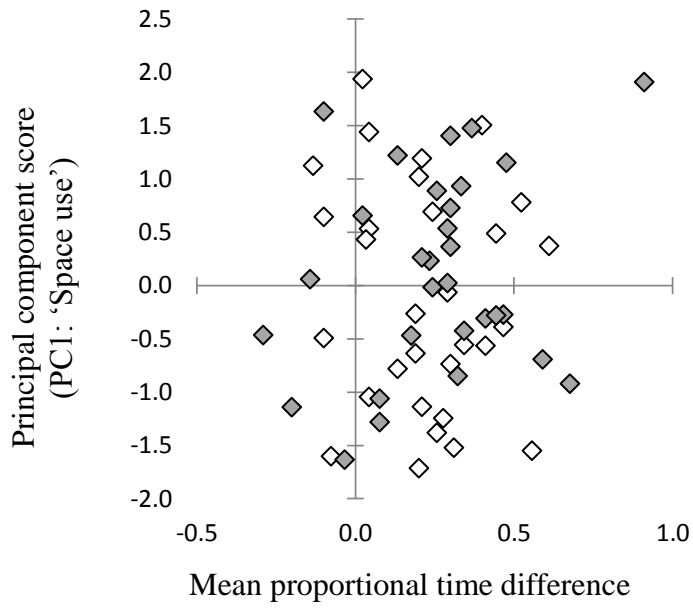
(b)



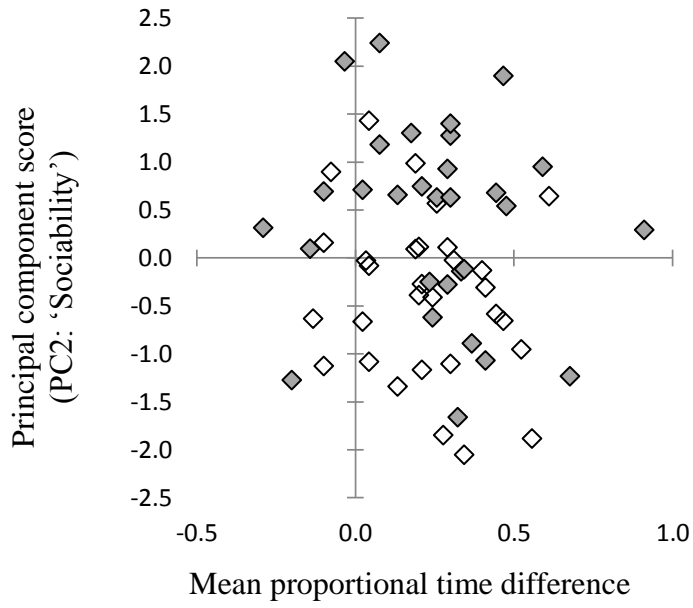
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1033 **Figure 6.**
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(a)



(b)



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