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Measuring response inhibition with a continuous inhibitory-control task

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30 **Abstract**

31

32 Inhibitory control enables subjects to quickly react to unexpected changes in external
33 demands. In humans, this kind of behavioural flexibility is often used as an indicator
34 of an individual's executive functions, and more and more research emerges
35 investigating this link in non-human animals as well. Here, we explored the value of a
36 recently developed continuous inhibitory-control task in assessing inhibitory-control
37 capacities in animals. Pigeons completed a response-inhibition task that required them
38 to adjust their movement in space in pursuit of a reward across changing target
39 locations. Inhibition was measured in terms of movement trajectory (path taken
40 towards the correct location for trials in which the target location did and did not
41 change) and velocity (both before and after correcting the trajectory towards the
42 changed location). While the observed velocities did not follow any of our predictions
43 in a clear way, the pigeons' movement trajectories proved to be a good indicator of
44 inhibitory control, showing that pigeons, though limited in their capacities compared to
45 the sophisticated control strategies expressed by humans, are capable of exerting
46 some forms of inhibitory control. These results strengthen the role of this paradigm as
47 a valuable tool in evaluating inhibitory-control abilities across the animal kingdom.

48

49 Introduction

50

51 Humans, and most non-human animals, are able to quickly adapt their behaviour to
52 unexpectedly changing external demands, for example by inhibiting inappropriate or
53 no longer relevant behaviour, or adjusting an action that has already been initiated
54 (e.g., Ardila, 2008; Chan, Shum, Touloupoulou, & Chen, 2008; Jurado & Rosselli, 2007;
55 Suchy, 2009). Such mental flexibility, more specifically referred to as inhibitory control,
56 has long been considered to be an indicator that an individual possesses higher-order
57 cognitive control abilities (e.g., Coutlee & Huettel, 2012; Kabadayi, Bobrowicz, &
58 Osvath, 2018), as it requires a chain of cognitive operations (including detecting the
59 currently relevant response requirements, selecting and implementing the appropriate
60 response and simultaneously inhibiting alternative response options; Verbruggen &
61 Logan, 2015; Verbruggen, McLaren, & Chambers, 2014). This assumption implies that
62 only those species that possess a high level of cognitive control, such as humans,
63 apes, and other big-brained mammals and birds, should be capable of inhibitory
64 control. However, the emergence of studies providing evidence for inhibitory control
65 across a broad range of species (e.g., dogs (*Canis familiaris*): Fagnani, Barrera,
66 Carballo, & Bentosela, 2016; Marshall-Pescini, Virányi, & Range, 2015; Vernouillet,
67 Stiles, Andrew McCausland, & Kelly, 2018; sheep (*Ovis aries*): Knolle, Goncalves,
68 Davies, Duff, Morton, 2019; Knolle, McBride, Stewart, Goncalves, & Morton, 2017; rats
69 (*Rattus norvegicus*): Beuk, Beninger, & Paré, 2014; Eagle & Robbins, 2003;
70 pheasants (*Phasianus colchicus*): Meier, Pant, et al., 2017; guppies (*Poecilia*
71 *reticulata*): Lucon-Xiccato, Gatto, & Bisazza, 2017; Santacà, Busatta, Savaşçı, Lucon-
72 Xiccato, & Bisazza, 2019) is casting doubt on this all-or-nothing approach implied in
73 the earlier work.

74

75 Recently, attention has shifted from merely investigating whether members of a given
76 species possess the ability to inhibit their actions when necessary to establishing a
77 more complete picture of varying degrees of ability in implementing inhibitory control
78 both across and within species. A promising paradigm in this regard is the continuous
79 response-inhibition task, which was first developed by Verbruggen and McLaren
80 (2017) to assess the development of inhibitory control during human childhood and
81 later adapted by Meier, Pant, et al. (2017) for use with animals.

82 In the broadest terms, the paradigm required subjects to leave a start location (in the
83 human computer version, this was the location from which a mouse cursor had to be
84 moved; in the animal version, it was the location from which the subject entered into
85 an experimental arena) and move towards a goal to obtain a reward (see Figure 1 for
86 a two-dimensional schematic of the setup). In the majority of trials, the goal was at a
87 fixed location relative to the start location, and the subject was encouraged to go from
88 the start to the goal as quickly as possible (trials of this nature will henceforth be
89 referred to as "Go trials", and the location that has to be reached to obtain the reward
90 will be called the "Go location"). In a minority of trials, however, shortly after the subject
91 had left the start location and was on the way towards the goal, the location of the goal
92 suddenly changed from its previously designated location to a new location (trials of
93 this type will henceforth be referred to as "Change trials", and the location that has to
94 be reached to obtain the reward will be called the "Change location"). To complete a
95 Change trial and obtain a reward, the subject had to alter the initial course and pursue
96 the goal at its new location (see Figure 1).

97

98 The advantage of this continuous response-inhibition task in investigating individual
99 inhibitory control is the wide variety of dependent variables that can be assessed to
100 obtain a detailed picture of a subject's cognitive abilities and strategies.

101 Verbruggen and McLaren (2017) employed their human version to determine the age
102 at which children begin to show evidence of proactive inhibitory control in performing
103 "mental goal adjustments" between two trials (Bissett & Logan, 2011, 2012;
104 Verbruggen, Schneider, & Logan, 2008): according to this account, on each trial, the
105 subject is faced with a conflict between two mental goals – on the one hand, there is
106 the goal to quickly perform the Go response (i.e., reach the Go location), on the other
107 hand, there is the goal to respond accurately to any sudden change of the response
108 requirements (i.e., an unexpected change of the goal location), which requires the
109 subject to divert attention from the primary goal. In order to respond both quickly and
110 accurately, it is assumed that humans continuously calibrate the balance between
111 focussing mental resources on one goal over the other (cf. Elchlepp, Lavric,
112 Chambers, & Verbruggen, 2016).

113 Adjusting the balance in favour of the mental goal to respond quickly might increase
114 the likelihood of executing the Go response not only when it is appropriate but also
115 when it is inappropriate (i.e., on Change trials), whereas adjustments towards the

116 mental goal to detect a change might facilitate the inhibition of that Go response when
117 necessary but will also lead to slower response execution when the Go response is
118 indeed required. It is assumed that, humans adjust the balance in favour of change
119 detection after experiencing a trial in which the Go response had to be inhibited and
120 vice versa. Consequently, such mental goal adjustments are expressed in the way in
121 which the cognitive control afforded in one trial influences performance on the
122 following trial: in a Go trial following a Change trial, latencies to reach the goal would
123 be slower compared to a Go trial that was preceded by a Go trial. Furthermore,
124 Verbruggen and McLaren (2017) argue that a subject's path towards the Go location
125 would be less direct and more skewed towards the Change location on trials following
126 a Change trial compared to trials following a Go trial. Figure 2 Panel A, left column,
127 shows an illustration of the expected paths for each trial type if the subject performs
128 mental goal adjustments between trials. In addition to trajectories, the logic of
129 Verbruggen and McLaren (2017) implies that such mental processes would also
130 manifest in the speed with which the subject pursues its goal, perhaps speeding up to
131 complete the Go response quickly, or slowing down to be able to respond to the
132 sudden change of location. A subject's velocity during a given trial can thus give further
133 valuable information about its cognitive strategy: it might be expected that subjects
134 enter the arena at a slower pace in Go trials following a Change trial than those
135 following a Go trial, although they might speed up once the change has occurred (or
136 once it becomes unlikely to still occur). The predicted average velocity of subjects from
137 this perspective is shown in Figure 2 Panel A, right column.

138 In their avian version of the continuous response-inhibition task, Meier, Pant, et al.
139 (2017) demonstrated that pheasants were able to adjust their paths flexibly from one
140 goal to another. Their paradigm was not set up, however, to capture the subtle
141 influences of response requirements experienced on previous trials, thus leaving an
142 open question as to whether such inter-trial effects are evidence of mental goal
143 adjustments and the proactive inhibitory control they imply, or whether less cognitively
144 demanding strategies might have similar effects on performance.

145 Firstly, it is important to differentiate the proactive inhibitory process described above
146 from reactive inhibition (cf. Meier, Lea, & McLaren, 2017), which might lead to a quite
147 different pattern of responding. If subjects relied on reactive control, each trial for a
148 given subject would start in much the same way (i.e., there would be no effect of one
149 trial on another). Thus, a subject might begin by rapidly approaching one location

150 (typically the initially indicated Go location), but at some point, this initial trajectory will
151 be brought under control of the information present on that trial. During a Go trial,
152 regardless of the response requirements of the previous trial, as there is no change in
153 the presented information, the subject would continue on its original trajectory. During
154 Change trials, however, the subject would subsequently correct the trajectory in
155 response to the goal change from the Go to the Change location. Figure 2 Panel B,
156 left column, shows an illustration of the expected paths for each trial type if the subject
157 pursues a strategy of response repetition. Contrary to the proactive inhibition
158 approach, subjects would not be expected to alter their velocity based on the previous
159 trial contingencies if relying on response repetition; they might show the same speed
160 upon entering the arena in all trial types. However, they would be expected to gradually
161 slow down when the subject's movements change from an initially fast launch towards
162 the initial target location, akin to a ballistic phase, towards a controlled phase which is
163 slower. The controlled phase involves the use of visual feedback to ensure a
164 continuous reduction of the subject's distance to the goal location - thus, during trials
165 that require greater adjustments to one's trajectory, i.e., Change trials, the decrease
166 in velocity would be expected to be greater than during Go trials. The predicted
167 average velocity of subjects pursuing this strategy is shown in Figure 2 Panel B, right
168 column.

169 Secondly, differences in trajectory patterns could emerge if subjects had a tendency
170 to repeat a previously rewarded response, that is, a tendency to return to the most
171 recently rewarded location, as has been demonstrated to occur early in training
172 (Morgan, 1974). In such a case, in Go trials following a Change trial, the paths taken
173 from the start location to the goal would show an initial approach towards the Change
174 location, just like the trajectories in Change trials following a Go trial would initially be
175 biased towards the Go location, before being adjusted towards the correct location. A
176 straight and direct path towards the Go location would only be observed in Go trials
177 following another Go trial. Figure 2 Panel C, left column, shows an illustration of the
178 expected paths for each trial type if the subject pursues a strategy of response
179 repetition. As for the previous approach, subjects would be expected to show the same
180 speed upon entering the arena in all trial types. Contrary to the reactive inhibition
181 account, however, they might slow down not only in Change trials but also Go trials
182 following a Change trial, as in both trial types it will become necessary to correct their

183 initial trajectory. The predicted average velocity of subjects pursuing this strategy is
184 shown in Figure 2 Panel C, right column.

185 Lastly, subjects might hesitate to approach either the Go or the Change location – or
186 are unable to discriminate between the two – until the change did (or did not) occur
187 and the correct location is unambiguously indicated. In this case, subjects might try to
188 keep an equal distance to both locations as they leave the start location, so that the
189 resulting path leads up in a straight line between the two options before branching off
190 towards the correct location at a sharp angle. Figure 2 Panel D, left column, shows an
191 illustration of the expected paths for each trial type if the subject did not discriminate
192 between the two goal options. The same pattern of average path trajectories would be
193 observed if the subject simply chose a first location at random and approached both
194 locations in succession, regardless of the actual demands of the trial. Regarding
195 predicted velocity, there should be no differences between trials, and subjects might
196 proceed at the same speed from entering the arena to arriving at the correct location,
197 or speed up the closer they get to the see-saw. The predicted average velocity of
198 subjects pursuing this strategy is shown in Figure 2 Panel D, right column.

199

200 In the current study, we assessed which one, if any, of the above mechanisms most
201 accurately describe the response patterns of pigeons (*Columba livia*), which can
202 perform successfully in response-inhibition tasks despite being limited in their
203 cognitive-control capacities (Lea, Chow, Meier, McLaren, & Verbruggen, 2019; Meier,
204 Lea, et al., 2017). In both computerised response-inhibition tasks previously employed
205 with pigeons, subjects showed a pattern of responding that was consistent with a
206 popular model of reactive response inhibition, the independent horse-race model (cf.
207 Verbruggen & Logan, 2009): the pigeons were increasingly unable to correct their
208 behaviour as the time between the initial stimulus and the signal to inhibit an action
209 decreased. We adapted Meier, Pant, et al.'s (2017) paradigm to examine whether the
210 performance of pigeons reflects

- 211 a) proactive inhibitory control (expressed through mental goal adjustments),
- 212 b) reactive inhibitory control,
- 213 c) a bias to approach the previously rewarded location, or
- 214 d) hesitation or inability to commit to one particular location.

215 Each of these mechanisms is expected to result in a distinct pattern of path trajectories
 216 towards the appropriate goal location and different response-time patterns, shown in
 217 Figure 2.

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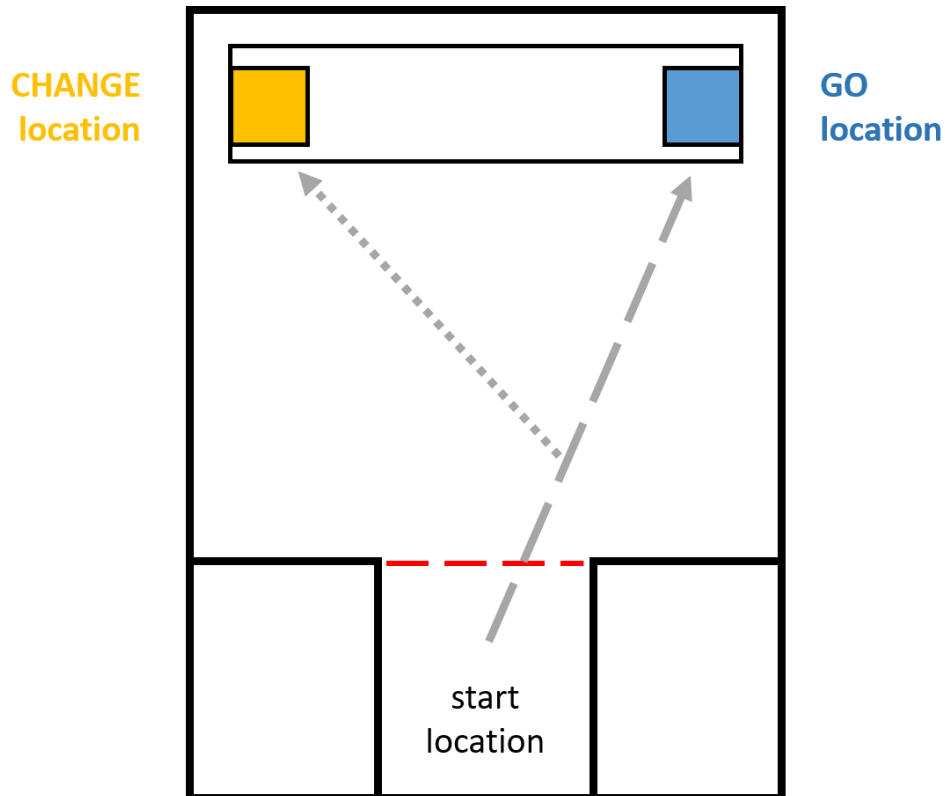


Figure 1. Diagram of the continuous response-inhibition task for animals (adapted from Meier, Pant, et al., 2017). A subject starts a trial by leaving the start location shown at the bottom of the image. In the majority of trials, it has to pursue a path, indicated by the stroked grey arrow, towards the Go location (illustrated in blue on the right) to obtain a reward. On a minority of trials, however, the target location visibly changes from the Go location to the Change location (illustrated in yellow on the left) as the subjects leaves the start location (moment indicated by crossing the imaginary red stroked line); to obtain the reward, the subject has to alter its path towards the Change location, indicated by the dotted grey arrow.

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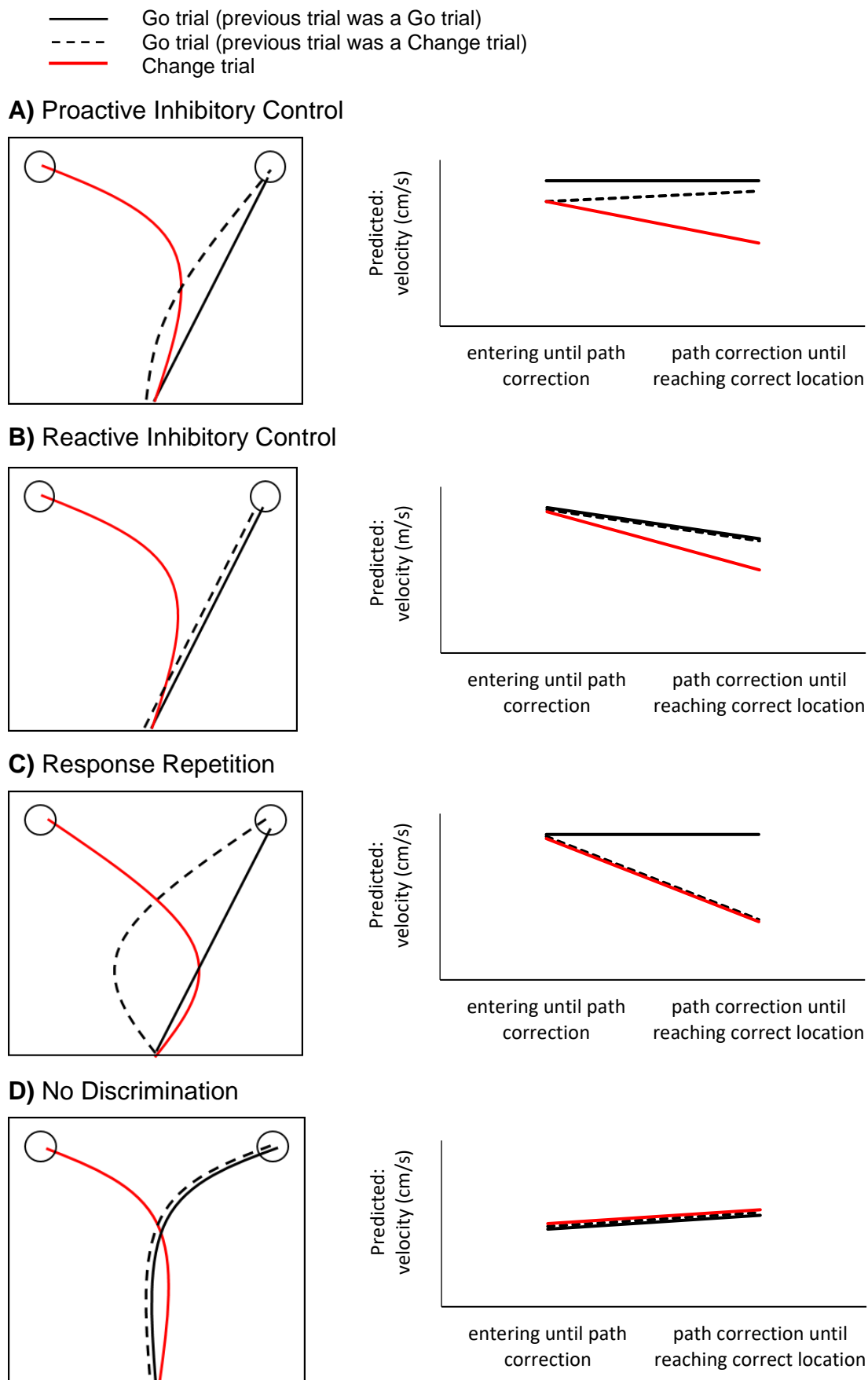


Figure 2. Left column: sketch of expected path trajectories in Go trials (following a Go or following a Change trial) and Change trials if behaviour is governed by A) proactive mental

goal adjustments between trials, *B*) reactive inhibition in response to immediate changes, *C*) a tendency to approach the previously rewarded location, *D*) hesitation or inability to commit to a location, or random choice. *Note:* the target location was on the right in Go trials and on the left in Change trials. Right column: expected corresponding velocities during a trial.

221 **Methods**

222

223 *Subjects*

224 49 adult pigeons entered this experiment; 38 of them completed the entire procedure.
225 They had previous experience with computer-based experiments, in some cases in
226 experiments that tested inhibitory control (Lea et al., 2019; Meier, Lea, et al., 2017),
227 but none in apparatus resembling that used in the present experiment. The pigeons
228 had been obtained as discards from local fanciers, so their ages were not known
229 exactly. Their sexes were not determined. They were kept in the Psychology animal
230 laboratory at the University of Exeter. For the duration of the experiment, they were
231 housed together with other pigeons in two indoor aviaries (each approximately 2m x
232 1m x 2.5m); since most of them had plain white plumage, they were identified by
233 coloured leg rings. They were maintained at or above 80% of their free-feeding weight
234 by controlled feeding after tests. Their weights at time of test ranged from 230 to 400g,
235 corresponding a variation of linear size of about 20% or 5cm, small compared with the
236 dimensions of the apparatus. On conclusion of the experiment, the pigeons were
237 moved to a collective outdoor aviary with unlimited access to food. Each pigeon was
238 tested in isolation. Inside the testing arena, the pigeons had no access to water or grit,
239 but they received water and grit *ad libitum* in all aviaries and holding areas.

240

241 *Apparatus*

242 Figure 3 Panel A is a scale plan of the experimental arena; for a 3D-sketch, see Figure
243 3 Panel D. The arena was mounted onto a sheet of 135x100cm melamine-covered
244 chipboard (Contiboard®) with six pillars of planed softwood, each 10x10x45cm in size.
245 The outer walls of the arena were made of 6mm plywood of 30cm in height; the long
246 walls were 124cm long, the short walls were 80cm long. Because the poles were taller
247 than the walls, a curtain made of blue cloth was drawn between the poles along the
248 long walls (see Figure 3 Panel B) to restrict the pigeons' vision to the inside of the
249 arena. The arena that was accessible to the pigeons measured 82x76cm. The pigeons
250 entered the arena from one of the short walls via a 40cm long and 26cm wide runway
251 corridor (see Figure 3 Panel C). The corridor and the interior walls adjacent to it were
252 made of 6mm plywood and plastic-covered 25mm chicken wire, enabling the pigeons
253 to view the arena from inside the corridor. A see-saw apparatus was mounted along
254 the opposite short wall of the arena. It consisted of a plywood beam of 50cm in length

255 that was hinged on a bolt attached to a block of wood at 10cm off the ground. The
256 block of wood was mounted onto a board of wood 60 cm X 15 cm X 2 cm. A 10 cm X
257 10 cm white Perspex baseplate was screwed flat onto each end of the board to indicate
258 the two food locations, the centres of which were 50 cm apart from each other (see
259 Figure 3 Panel B). A small plastic cup was attached to each end of this axis, cut to
260 size to cover another plastic lid glued in place underneath that served as a food well.
261 The two wells were approximately 35cm apart from each other in the corners of the
262 arena. The see-saw could be operated to cover one of the two food wells. In its default
263 position, the see-saw covered the left (as seen from the corridor entrance) food well,
264 exposing the right well. The beam rested on the armature of a solenoid integrated into
265 the wooden block that held the see-saw hinge. The armature retracted when the
266 solenoid was activated, allowing the see-saw to tip over to cover the right food well
267 and expose the left well. Directly adjacent to the right side of the corridor exit on the
268 inside of the testing area, an IR-LED diode was mounted 7cm from the ground, which
269 continuously generated an infrared beam. The beam was detected by an infrared-
270 sensitive lux meter mounted at the same height on the left side of the corridor exit. The
271 lux meter recorded any changes in lux of the incoming infrared beam and submitted
272 this information to an Arduino[®] One microchip board; if there was an interruption in the
273 light beam, the Arduino[®] One board operated the solenoid attached to the see-saw.
274 The arena was covered by a Plexiglas[®] roof hinging onto one of the long walls. It
275 opened to the top to allow the experimenter to manually remove the pigeon from the
276 arena. The runway corridor was covered by a scrap-board roof. A Kenvo HDV-601S
277 video camera was mounted onto this roof, overlooking the testing arena, to film the
278 trajectories of the participating birds.

279

280 *Procedure*

281 Before testing, all pigeons received a 15-minute habituation session in which the see-
282 saw was fixed in place to expose both food wells, which were both baited. One pigeon
283 at a time was placed into the entrance corridor of the arena and was allowed to freely
284 explore the testing arena and feed from the two food wells. A pigeon received up to
285 three habituation sessions until it fed from both food wells in the same session. If a
286 pigeon had not visited both wells by the third session, it was excluded from any further
287 test sessions. Following a successful visit to both food wells within 15 minutes, the

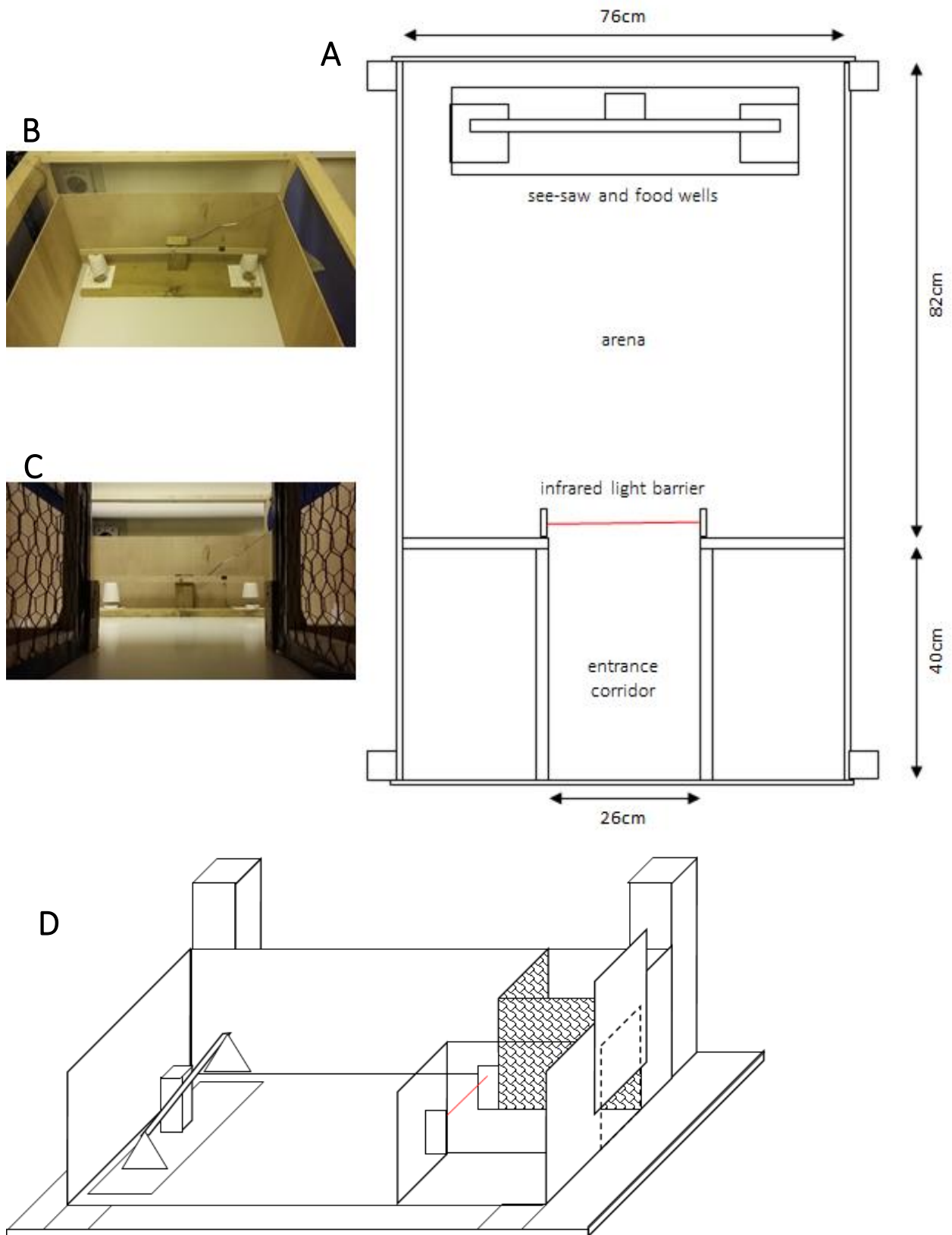
288 pigeon received one 5-minute session in which, again, both food wells were accessible
289 and baited. If the pigeon visited both wells within the 5-minute interval, it was moved
290 on to the test sessions. This 5-minute feeding session was also repeated up to three
291 times, until the pigeon had fed from both wells in the same session. As above, if a
292 pigeon failed to do so within three sessions, it was excluded from any further test
293 sessions. Thirty-eight of the 49 pigeons successfully completed the habituation
294 sessions; the remaining 11 pigeons did not sufficiently explore the arena either during
295 the 15-minute or the 5-minute sessions. We did not observe any visible preference for
296 either location at group level during the habituation phase (Supplementary Table 1,
297 rightmost columns).

298 Test trials were administered in two sessions, presented on two consecutive days,
299 each session consisting of 4 blocks of 3 trials, totalling 24 trials per pigeon. Within a
300 session, the blocks were administered immediately one after the other, with a
301 maximum of five minutes between trials to allow for a reset and cleaning of the arena.
302 The first two trials in each block were 'Go' trials: the see-saw was fixed to expose the
303 right food well (covering the left well) and a pigeon was allowed to feed freely from that
304 well after approaching it. The third trial in a block was a 'Change' trial: at the start of
305 this trial, the see-saw was in the same position as in Go trials but rested loosely on the
306 solenoid armature, so that it tipped to the other side when the pigeon crossed the
307 infrared light beam at the arena entrance and so operated the solenoid. In these trials,
308 the pigeon was allowed to feed from the newly exposed left food well; the right well
309 was covered after the see-saw had tipped over. The sequence of trials was the same
310 for all subjects.

311 A trial ended either once the pigeon had consumed all the food from the available food
312 well or, if the pigeon failed to approach that well, after a maximum of three minutes. In
313 the latter case, the trial was repeated up to two more times until the pigeon approached
314 the exposed food well; if it had not done so by the third trial repetition, the session was
315 aborted. If this was the case, the pigeon repeated the entire block of three trials in its
316 next session.

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Figure 3. A) Scale plan (1:10) of the testing arena. B) View from above at the see-saw. Both food locations are uncovered in this picture. C) The pigeon's view from the inside of the entrance corridor into the arena. Both food locations are uncovered in this picture. D) Design of the testing arena shown from the side (not to scale, for exact proportions see Panel A). See text for details.

327 *Data Collection*

328

329 As the first trial was not preceded by either another Go or a Change trial, it was
330 excluded from analyses. Thus, we analysed responses for seven Go trials preceded
331 by a Change trial, eight Go trials preceded by a Go trial and eight Change trials.

332 We determined the subjects' trajectories as they moved within the arena and towards
333 the correct food location. Using the Open Source Physics Tracker© video tracking
334 software ([Brown, 2009](#)), the coordinates of a pigeon's beak were extracted from the
335 videos of each trial. The axes of coordinates were standardised so that the point of
336 crossing the infrared beam coincided with the point of crossing the x-axis at $(x, 0)$; the
337 available food location in Go trials was located at $(1, 1)$ and the available food location
338 in Change trials was located at $(-1, 1)$. To account for individual differences in the
339 latencies to reach the correct food location, the trajectories of each trial were
340 standardised in a way similar to Vincentization ([Genest, 1992](#); [Ratcliff, 1979](#); [Rouder
341 & Speckman, 2004](#); [Vincent, 1912](#)); that is, the value of the latency for a given trial
342 was split into twenty 0.05-quantile points; the coordinates at each quantile point were
343 connected to create the trajectory for that trial. These were then averaged across the
344 eight (or seven) trials of each trial type for each pigeon.

345 To obtain distinct data points that could be used to compare the trajectories between
346 trials, we extracted an individual's trajectory-correction points for each of the three trial
347 types from the trajectory data. The trajectory-correction point is defined as the
348 inflection point in a pigeon's trajectory. For Change trials, this was the point at which
349 the x-coordinate of the trajectory reached its final local maximum value before it
350 continuously decreased. It indicates the moment at which the subject - potentially after
351 initially approaching the (incorrect) Go location - started approaching the (correct)
352 Change location. For Go trials, it was the point at which the x-coordinate reached its
353 final local minimum value before it continuously increased, indicating the moment at
354 which the subject started to directly approach the Go location.

355 In addition, we recorded the latency from releasing a pigeon into the entrance corridor
356 until it reached the exposed food well in each trial, to get an estimate of the overall
357 time taken to complete the trials that required behavioural adjustments (i.e., Change
358 trials) compared to the time taken to complete the trials in which no such adjustments
359 had to be made (Go trials). However, the conventional measure of response inhibition
360 is the change-signal reaction time ([Verbruggen & Logan, 2009](#); [Verbruggen &](#)

361 McLaren, 2017), that is, the latency between the onset of the signal to withhold the
362 target response and the observable change in behaviour. In our continuous response-
363 inhibition task, this is equivalent to the time to reach the trajectory-correction point
364 measured from the moment of crossing the infrared light beam. However, pure latency
365 measures might be confounded in this task by the simple fact that it might take more
366 time to cover a longer distance (comparing, for example, the assumed straight
367 trajectory during Go trials to the predicted curved path during Change trials). A more
368 accurate measure of inhibition processes might therefore be the speed at which a
369 certain distance was covered. Since our paradigm made it possible to determine a
370 trajectory-correction point both for Change and for Go trials, we analysed the velocities
371 to and from this point for all trial types. It was expected that any differences in velocities
372 between Change and Go trials would primarily be due to different speeds before
373 reaching the trajectory-correction point, followed by completion of the task thereafter.

374

375 *Predictions*

376 Considering the relationships between the trajectory-correction points in Go and
377 Change trials depending on the nature of the previous trial, the following patterns were
378 expected:

- 379 - *Proactive Inhibition* (Figure 2 Panel A): The trajectories for all three trial types
380 should initially be biased towards the Go location. The x-coordinate of the
381 trajectory-correction point should be close to zero (which represents the
382 entrance point into the arena) for Go trials following a Go trial and for Go trials
383 following a Change trial, but positive for Change trials. The y-coordinate should
384 be close to zero (which represents the entrance point into the arena) for Go
385 trials following a Go trial and for Go trials following a Change trial, but greater
386 than zero for Change trials. Average velocities from entering to reaching the
387 trajectory-correction point, and in fact overall velocities for the entire trial, should
388 be the slowest for Change trials, velocities during Go trials following a Change
389 trial should be close to latencies for Change trials, while those for Go trials
390 following a Go trial are expected to be the fastest. Once the correction point
391 has been passed, velocities on Change trials should slow down further, while
392 those for Go trials might become faster, though it is expected that subjects
393 would complete Go trials following a Go trial at a very fast speed throughout the
394 trial.

- 395 - *Reactive Inhibition* (Figure 2 Panel B): The trajectories for all three trial types
396 should initially be biased towards the Go location. The x-coordinate of the
397 trajectory-correction point should be close to zero (which represents the
398 entrance point into the arena) for Go trials following a Go trial and for Go trials
399 following a Change trial, but positive for Change trials. The y-coordinate should
400 be close to zero (which represents the entrance point into the arena) for Go
401 trials following a Go trial and for Go trials following a Change trial, but greater
402 than zero for Change trials. Velocities up to the trajectory-correction point
403 should be equal for Change trials and Go trials. Once the correction point has
404 been passed, velocities should slow down, with a greater decrease from initial
405 velocities observed in Change trials compared to either type of Go trial.
- 406 - *Response Repetition* (Figure 2 Panel C): The trajectories for Go trials following
407 a Change trial and for Change trials should initially be biased towards the
408 incorrect location. The x-coordinate of the trajectory-correction point in Go trials
409 following a Go trial should be close to zero, whereas that of the trajectory-
410 correction point in Go trials following a Change trial should be negative, and
411 that for the Change trial positive. The y-coordinate should be close to zero for
412 Go trials following a Go trial but greater than zero (and of equal magnitude) for
413 Go trials following a Change trial and for Change trials. Velocities up to the
414 trajectory-correction point, just as overall velocities for the entire trial, should be
415 equal for Change trials and Go trials following a Change, and the pigeons might
416 additionally slow down once the correction point has been passed. Go trials
417 following a Go are expected to be completed at a very fast speed throughout
418 the trial.
- 419 - *No Discrimination* (Figure 2 Panel D): The trajectories for all three trial types
420 should initially run straight into the centre of the arena and then converge on
421 the correct location. The x-coordinate of the trajectory-correction point should
422 be close to zero in all trial types, but might be biased towards the Go location
423 in Change trials and vice versa in Go trials due to averaging, because the
424 trajectory-correction point would be close to zero for trials in which the pigeon
425 approached the correct location first, but close to the incorrect location for trials
426 in which that location was approached first. The y-coordinate of the trajectory-
427 correction point should be equal in all three trial types and greater than 0.
428 Velocities up to the trajectory-correction point, like overall velocities for the

429 entire trial, should be equally long for all trial types, and it is expected that the
430 same speed would be maintained throughout a trial (with just a little increase in
431 speed, if any at all, once a goal has been chosen).

432

433 **Results**

434

435 According to the specific predictions stated above, the most informative values for
436 differentiating between the response strategies of interest are the coordinates of the
437 trajectory-correction points on the three types of trial (Go following Go, Go following
438 Change, and Change). There was no observable difference for any individual subjects
439 (see supplementary Table 1) between the correction point for Go trials following a Go
440 trial and the correction point for Go trials following a Change trial that might have
441 indicated that they had pursued a strategy of mere response repetition. The remaining
442 two strategies under investigation could be differentiated by assessing how much the
443 trajectory-correction points of the three trial types differ in terms of their distance from
444 the start location and advancement towards the Go location. For this purpose, each
445 pigeon was ranked according to the average difference of the y-coordinate of its mean
446 Change-trial correction point from the y-coordinates of the mean correction points of
447 the two types of Go trials (the difference in the y-coordinate rather than the absolute
448 distance between points was chosen to preserve the directionality of the distance, i.e.,
449 to be able to determine whether the Change point of the Go points were closer to the
450 start location). In doing so, it emerged that not all subjects showed the anticipated bias
451 to initially approach the Go location before correcting their path if necessary; about an
452 equal number of subjects expressed a reversed bias, approaching the Change
453 location first in all trials and thus having to correct their path on Go trials. It is
454 noteworthy that such a bias during test did not correspond to any observed preference
455 during habituation (Supplementary Table 1), potentially indicating that the pigeons only
456 developed it after at least a few encounters with the arena during habituation and the
457 first test session. For further analyses, the group was therefore split into five subgroups
458 of approximately equal size corresponding to whether the subjects expressed a strong,
459 weak, or no apparent bias to initially approach the Go or the Change location.
460 Individual trajectories and trajectory-correction points including latency information are
461 illustrated in Figure 4.

462 All statistical analyses were performed using jamovi 0.9.5.8 ([jamovi project, 2018](#)).
 463 ANOVAs were subject to Huynh-Feld corrections where applicable, and post-hoc
 464 pairwise comparisons between groups were Tukey-corrected.

465

466 *Trajectory-Correction Points*

467 As shown in Table 1, the x-coordinate of the pigeons' average trajectory-correction
 468 points differed significantly between the five bias groups ($F(4,33)=10.70$, $p<.001$,
 469 $\eta_p^2=.56$). The same was true for the y-coordinate ($F(4,33)=13.40$, $p<.001$, $\eta_p^2=.62$; Table
 470 1). Therefore, all subsequent analyses were carried out separately for each group.

471 *Strong Go bias.* For those subjects having a strong bias to approach the Go location
 472 in all trials (Figure 4, top row), the x-coordinates were comparable for the two types of
 473 Go trials, which both differed significantly from the x-coordinate of Change trials
 474 ($F(2,14)=32.60$, $p<.001$, $\eta_p^2=.82$; pairwise comparison between Go following Go and
 475 Go following Change: $t(14)=1.47$, $p=.33$, comparison of either Go trial type to Change:
 476 $t(14)>4.14$, $p<.001$). The x-coordinates of Go trials following a Go trial and of Change
 477 trials were significantly greater than zero, indicating that the pigeons were closer to
 478 the Go location than to the Change location when they started approaching the correct
 479 location. In contrast, the x-coordinates of Go trials following a Change trial were not
 480 significantly different from zero (Go following Go: $t(7)=2.67$, $p=.032$; Go following
 481 Change: $t(7)=1.06$, $p=.32$; Change: $t(7)=5.98$, $p<.001$). Likewise, y-coordinates
 482 differed significantly between Change trials and either type of Go trial, but were
 483 comparable between the two types of Go trial ($F(2,14)=135.00$, $p<.001$, $\eta_p^2=.95$;
 484 pairwise comparison between Go following Go and Go following Change: $t(14)=0.18$,
 485 $p=.98$, comparison of either Go trial type to Change: $t(14)>14.11$, $p<.001$). The y-
 486 coordinates of Go trials following a Change trial and of Change trials differed
 487 significantly from zero, indicating that the pigeons had moved a considerable distance
 488 from the start location into the arena at the point of correcting their path. In contrast,
 489 the y-coordinates of Go trials following a Go trial did not differ from zero (Go following
 490 Go: $t(7)=1.78$, $p=.12$; Go following Change: $t(7)=3.06$, $p=.018$; Change: $t(7)=18.41$,
 491 $p<.001$). In relation to the above predictions, this pattern suggests mental goal
 492 adjustments evident of proactive response inhibition.

493 *Weak Go bias.* The x-coordinates of those pigeons that showed a weak bias towards
 494 the Go location (Figure 4, second row) were significantly different between Go trials
 495 following a Change trial and Change trials but not between Go trials following a Go

496 and any other trial type ($F(2,12)=5.00$, $p=.030$, $\eta_p^2=.45$; pairwise comparison between
 497 Go following Go and Go following Change: $t(12)=0.61$, $p=.82$, comparison between
 498 Go following Go and Change: $t(12)=2.38$, $p=.083$, comparison between Go following
 499 Change and Change: $t(12)=2.99$, $p=.028$). The x-coordinates of either type of Go trial
 500 did not differ significantly from zero, whereas that of Change trials was significantly
 501 greater than zero, indicating that these pigeons were closer to the Go location than to
 502 the Change location when finally starting to approach the correct Change location (Go
 503 following Go: $t(6)=0.14$, $p=.89$; Go following Change: $t(6)=0.53$, $p=.62$; Change:
 504 $t(6)=3.35$, $p=.016$). y-coordinates differed significantly between Change trials and
 505 either type of Go trial, but were comparable between the two types of Go trial
 506 ($F(2,12)=22.70$, $p<.001$, $\eta_p^2=.79$; pairwise comparison between Go following Go and
 507 Go following Change: $t(12)=0.73$, $p=.75$, comparison of either Go trial type to Change:
 508 $t(12)>5.44$, $p<.001$). The y-coordinates of all three trial types differed significantly from
 509 zero, showing that the pigeons had considerably moved into the arena before
 510 correcting their paths (Go following Go: $t(6)=5.01$, $p=.002$; Go following Change:
 511 $t(6)=8.75$, $p<.001$; Change: $t(6)=18.04$, $p<.001$). Taken together, the observed pattern
 512 provides some evidence for a reactive inhibition account.

513 *No bias.* Regarding those subjects that were labelled as having no distinct bias to
 514 initially approach either location (Figure 4, third row), the x-coordinates of Go trials
 515 following a Change trial and Change trials were significantly different; Go trials
 516 following a Go did not differ from Go trials following a Change but were marginally
 517 different from Change trials ($F(2,14)=6.76$, $p=.017$, $\eta_p^2=.49$; pairwise comparison
 518 between Go following Go and Go following Change: $t(14)=0.96$, $p=.61$, comparison
 519 between Go following Go and Change: $t(14)=2.59$, $p=.052$, comparison between Go
 520 following Change and Change: $t(14)=3.55$, $p=.008$). The x-coordinates of either type
 521 of Go trial did not differ significantly from zero, whereas that of Change trials was
 522 significantly greater, again indicating that the pigeons were closer to the Go location
 523 than to the Change location when they started to correct their path towards the Change
 524 location (Go following Go: $t(7)=0.93$, $p=.38$; Go following Change: $t(7)=1.24$, $p=.25$;
 525 Change: $t(7)=3.68$, $p=.008$). There was no significant difference between the three y-
 526 coordinates ($F(2,14)=2.12$, $p=.18$, $\eta_p^2=.23$). The y-coordinates of all three trial types
 527 were significantly different from zero, indicating that the pigeons had considerably
 528 moved into the arena before correcting their paths (Go following Go: $t(7)=8.31$, $p<.001$;
 529 Go following Change: $t(7)=26.25$, $p<.001$; Change: $t(7)=19.73$, $p<.001$). The overall

530 pattern could point towards a response-repetition or a non-discriminative approach,
531 but evidence for either is weak.

532 *Weak Change bias.* The x-coordinates of those pigeons that showed a weak bias to
533 initially walk towards the Change location (Figure 4, fourth row) were significantly
534 different between Go trials following a Change trial and Change trials but only
535 marginally so between Go trials following a Go and Change trials ($F(2,12)=5.39$,
536 $p=.044$, $\eta^2=.47$; pairwise comparison between Go following Go and Go following
537 Change: $t(12)=0.58$, $p=.84$, comparison between Go following Go and Change:
538 $t(12)=2.51$, $p=.066$, comparison between Go following Change and Change:
539 $t(12)=3.09$, $p=.024$). The x-coordinates of either type of Go trial did not differ from zero,
540 that of Change trials was marginally greater (Go following Go: $t(6)=1.82$, $p=.12$; Go
541 following Change: $t(6)=1.87$, $p=.11$; Change: $t(6)=2.28$, $p=.062$). Y-coordinates
542 differed significantly between Change trials and either type of Go trial, but were
543 comparable between the two types of Go trial ($F(2,12)=8.57$, $p=.012$, $\eta^2=.59$; pairwise
544 comparison between Go following Go and Go following Change: $t(12)=0.92$, $p=.64$,
545 comparison of either Go trial type to Change: $t(12)>3.04$, $p<.026$). The y-coordinates
546 of all three trial types differed significantly from zero, showing that the pigeons had
547 considerably moved into the arena before correcting their paths (Go following Go:
548 $t(6)=19.84$, $p<.001$; Go following Change: $t(6)=9.35$, $p<.001$; Change: $t(6)=4.76$,
549 $p=.003$). Taken together, and considering the initial bias towards the Change location,
550 the observed pattern provides some evidence for a reactive inhibition account.

551 *Strong Change bias.* For those subjects with a strong bias towards the Change
552 location (Figure 4, bottom row), x-coordinates were comparable for the two types of
553 Go trials, which both differed significantly from the x-coordinate of Change trials
554 ($F(2,14)=15.20$, $p<.001$, $\eta^2=.69$; pairwise comparison between Go following Go and
555 Go following Change: $t(14)=0.23$, $p=.97$, comparison of either Go trial type to Change:
556 $t(14)>4.66$, $p<.001$). The x-coordinates of either type of Go trial were significantly
557 smaller than zero – indicating that the pigeons were closer to the Change location than
558 to the Go location when they started approaching the correct Go location –, whereas
559 that of Change trials was not different from zero (Go following Go: $t(7)=4.57$, $p=.003$;
560 Go following Change: $t(7)=4.45$, $p=.003$; Change: $t(7)=0.10$, $p=.93$). Likewise, the y-
561 coordinates differed significantly between Change trials and either type of Go trial, but
562 were comparable between the two types of Go trial ($F(2,14)=55.50$, $p<.001$, $\eta^2=.89$;
563 pairwise comparison between Go following Go and Go following Change: $t(14)=0.25$,

564 $p=.97$, comparison of either Go trial type to Change: $t(14)>8.99$, $p<.001$). The y-
565 coordinates of either type of Go trial differed significantly from zero, whereas that of
566 Change trials did not (Go following Go: $t(7)=15.39$, $p<.001$; Go following Change:
567 $t(7)=20.74$, $p<.001$; Change: $t(7)=1.74$, $p=.13$). Considering the strong initial bias to
568 approach the Change location, this pattern is indicative of reactive inhibition.

569

570 *Velocities*

571 We focussed on median rather than mean latencies when computing velocity, to avoid
572 a misrepresentation of average speed due to often atypically long latencies during the
573 first trial of each session. Figure 4 presents each individual's average trajectories (grey
574 lines) and median latencies (open circles) from which velocities were computed.
575 Overall, velocities (Table 1; Figure 5, right column) did not differ significantly between
576 bias groups ($F(4,33)=1.52$, $p=.22$, $\eta_p^2=.16$). However, to preserve symmetry to the
577 above analyses, the subsequent analyses were carried out for each group separately.
578 *Strong Go bias.* For those subjects having a strong bias to approach the Go location
579 in all trials (Figure 5, top row), velocities did not differ significantly between trial types
580 overall ($F(2,14)=2.63$, $p=.14$, $\eta_p^2=.27$). However, velocities did decrease significantly
581 after subjects reached the trajectory-correction point ($F(1,7)=9.32$, $p=.019$, $\eta_p^2=.57$).
582 Despite the lack of a clear interaction effect between trial type and velocity before or
583 after reaching the correction point, pairwise comparisons show that the only
584 statistically significant decrease occurs in Change trials ($F(2,14)=3.54$, $p=.057$, $\eta_p^2=.34$;
585 comparison of pre- and post-correction velocities for Go following Go: $t(7)=0.92$, $p=.94$,
586 for Go following Change: $t(7)=2.41$, $p=.21$, for Change: $t(7)=3.81$, $p=.017$). This pattern
587 fits our prediction for reactive inhibition, as the subjects seemed to react to a change
588 in contingencies rather than anticipate it, slowing down during Change trials after
589 adjusting their paths. The previous trial did not affect behaviour significantly.

590

Table 1. Average x- and y-coordinates of the trajectory-correction point and average velocity before and after reaching this point for pigeons showing a strong, weak or no bias of approaching either the Go location or the Change location, in Go trials following a Go trial, Go trials following a Change trial and Change trials.

		Trajectory-correction point		Velocity (cm/s)	
		x	y	Entrance to trajectory-correction point	Trajectory-correction point to goal location
Strong Go bias	Go (previous Go)	0.13	0.09	13.49	11.39
	Go (previous Change)	0.04	0.08	18.62	13.13
	Change	0.49	0.77	15.51	6.86
Weak Go bias	Go (previous Go)	-0.01	0.40	20.60	7.74
	Go (previous Change)	-0.05	0.44	23.31	6.90
	Change	0.16	0.75	8.48	5.73
No bias	Go (previous Go)	-0.04	0.66	16.18	4.60
	Go (previous Change)	-0.10	0.64	19.50	5.84
	Change	0.14	0.76	7.97	3.95
Weak Change bias	Go (previous Go)	-0.14	0.82	10.38	5.48
	Go (previous Change)	-0.20	0.74	10.32	5.25
	Change	0.10	0.50	13.60	6.36
Strong Change bias	Go (previous Go)	-0.35	0.77	21.17	7.33
	Go (previous Change)	-0.34	0.78	15.12	5.34
	Change	0.00	0.10	14.89	12.40

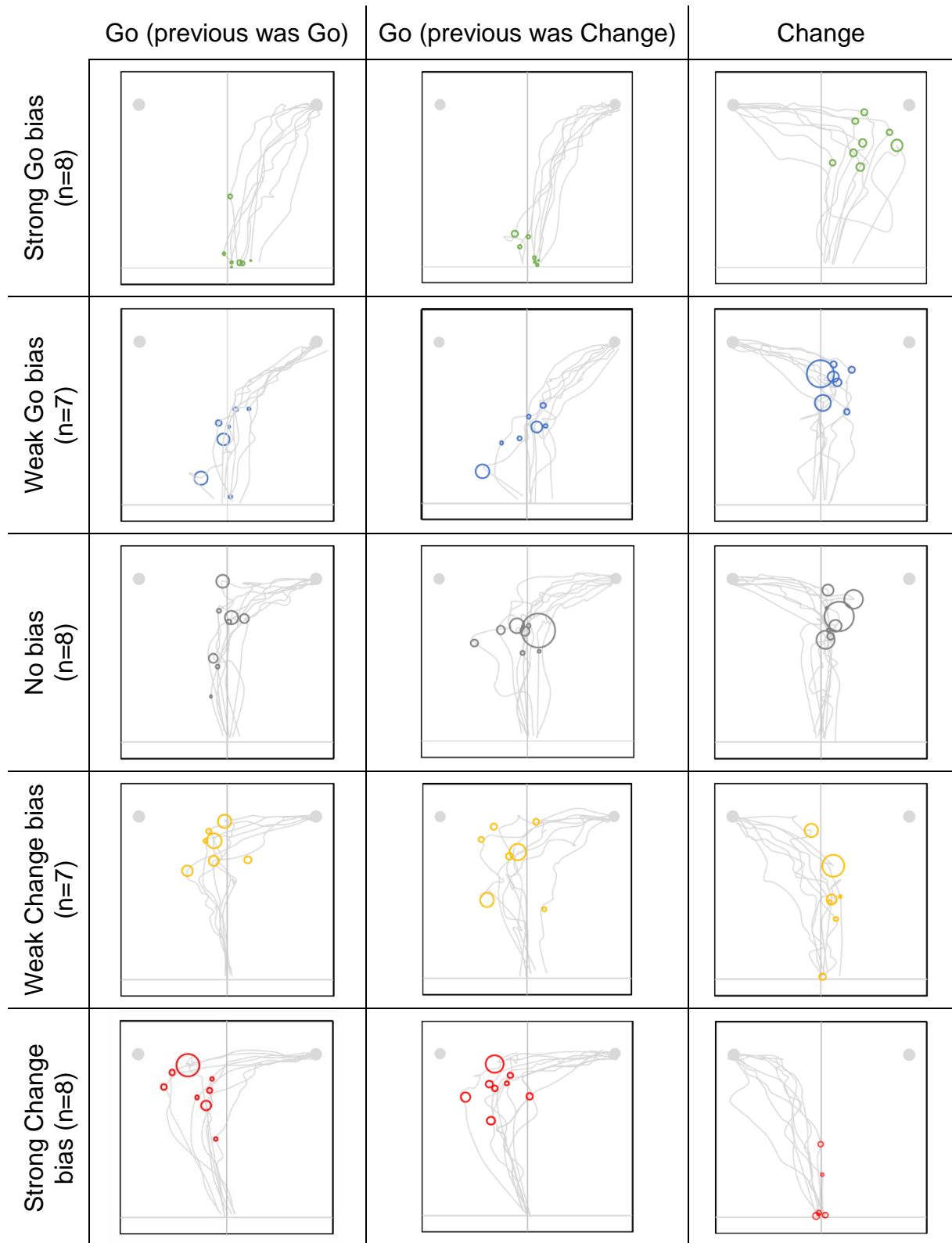


Figure 4. Individual trajectories (grey lines) and trajectory-correction points (open circles) of pigeons showing a strong, weak or no bias of approaching either the Go location or the Change location in Go trials following a Go trial, Go trials following a Change trial and Change trials. The diameter of each circle corresponds to the latency to reach the correction point since entering the arena at (0,0): bigger circles indicate longer latencies. The grey filled circles indicate the locations of the food wells; in Go trials, the reinforced location was at (1,1), in Change trials, it was at (-1,1).

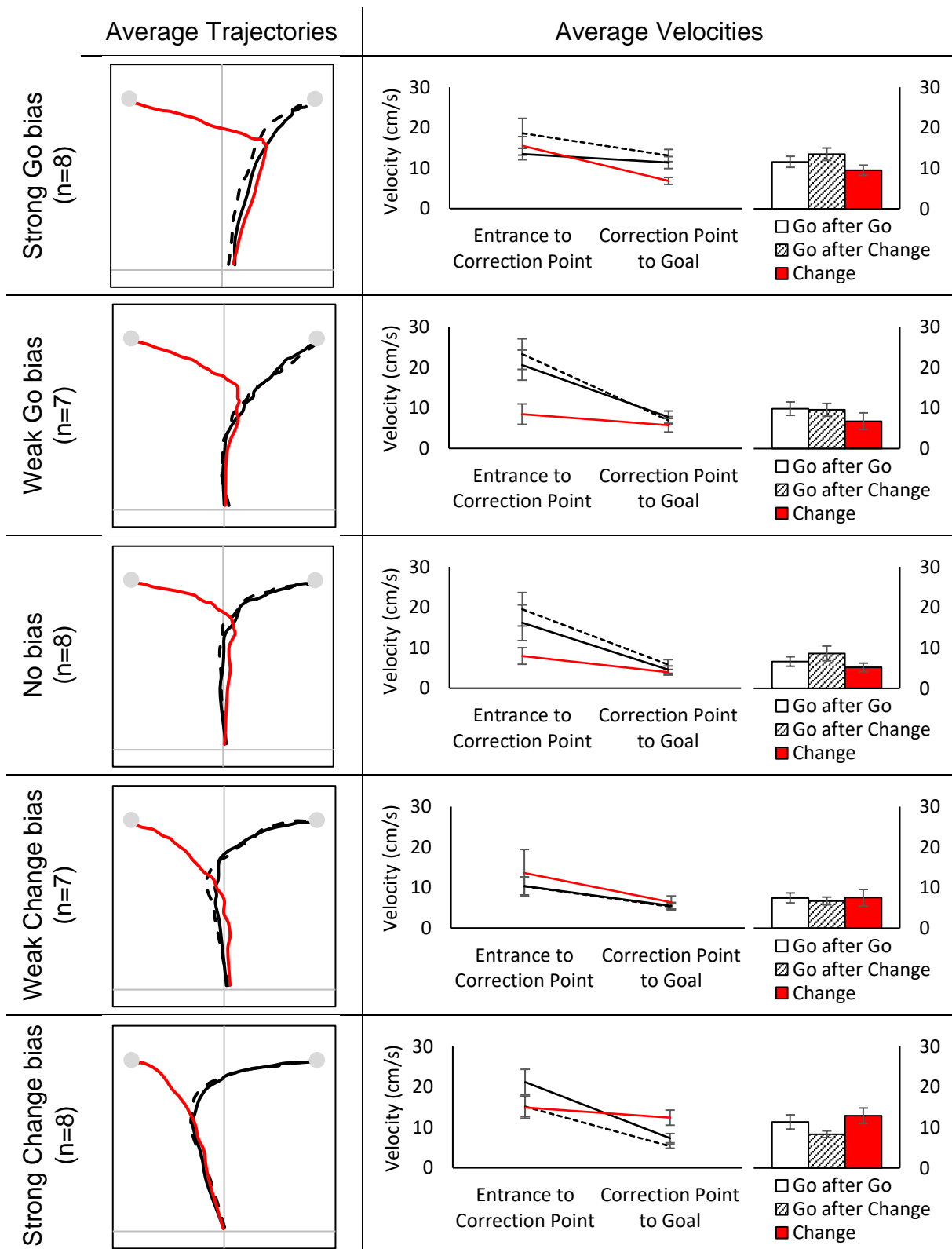


Figure 5. *Left column.* Averaged trajectories per group and trial type. Black solid lines: Go trials following a Go trial, black dotted lines: Go trials following a Change trial, red lines: Change trials. Note that on Go trials, the correct location was on the right; on Change trials, it was on the left. *Right column.* Average velocity to complete a trial, per group and trial type (measured from entering the arena to reaching the trajectory-correction point and from the correction point to reaching the correct location).

593 *Weak Go bias.* Those pigeons that expressed a weaker bias towards the Go location
 594 (Figure 5, second row) showed higher velocities during either type of Go trials
 595 compared to Change trials ($F(2,12)=8.05$, $p=.010$, $\eta_p^2=.57$; pairwise comparison
 596 between Go following Go and Go following Change: $t(12)=0.43$, $p=.91$, comparison
 597 between Go following Go and Change: $t(12)=3.24$, $p=.018$, comparison between Go
 598 following Change and Change: $t(12)=3.67$, $p=.008$). Furthermore, velocities decrease
 599 after subjects reached the trajectory-correction point ($F(1,6)=22.41$, $p=.003$, $\eta_p^2=.79$).
 600 There was a significant interaction effect between the two factors, as the reduction in
 601 velocity was only significant for Go trials, but not for Change trials ($F(2,12)=9.35$,
 602 $p=.004$, $\eta_p^2=.61$; comparison of pre- and post-correction velocities for Go following Go:
 603 $t(6)=4.37$, $p=.007$, for Go following Change: $t(6)=5.57$, $p<.001$, for Change: $t(6)=0.93$,
 604 $p=.93$). Furthermore, Change-trial velocity was only significantly lower compared to
 605 Go trials before the correction point was reached, but not after (pairwise comparison
 606 of pre-correction velocity in Change trials compared to Go trials following a Go or a
 607 Change trial: both $t(12)>4.45$, $p<.002$, comparison of Go following Go and Go following
 608 Change: $t(12)=0.99$, $p=.92$; comparison of post-correction velocity between trials: all
 609 $p>.98$). This pattern does not directly match our predictions for reactive inhibition (as
 610 we assumed that any slowing in velocities during Change trials would occur primarily
 611 once the correction point has been reached), but it shows that these subjects were
 612 already considerably slower during Change compared to Go trials even before
 613 reaching the trajectory-correction point.

614 *No bias.* For subjects without a distinct bias towards either location (Figure 5, third
 615 row), velocities for Change trials were marginally significantly different from those of
 616 Go trials following a Change trial ($F(2,14)=3.92$, $p=.062$, $\eta_p^2=.36$), and velocities
 617 reduced significantly from pre- to post-correction ($F(1,7)=21.89$, $p=.002$, $\eta_p^2=.76$). The
 618 interaction effect was also marginally significant, as the reduction in velocity was only
 619 found in Go trials but not in Change trials ($F(2,14)=3.79$, $p=.066$, $\eta_p^2=.35$; comparison
 620 of pre- and post-correction velocities for Go following Go: $t(7)=3.89$, $p=.011$, for Go
 621 following Change: $t(7)=4.59$, $p=.002$, for Change: $t(7)=1.35$, $p=.76$). Likewise, lower
 622 velocity in Change trials compared to Go trials was only shown in pre-correction
 623 velocity, but not post-correction (pairwise comparison of pre-correction velocity in
 624 Change trials compared to Go trials following a Change trial: $t(14)=3.78$, $p=.010$,
 625 comparisons of Change compared to Go following Go: $t(14)=2.69$, $p=.11$, comparison
 626 of Go following Go and Go following Change: $t(14)=1.09$, $p=.88$; comparison of post-

627 correction velocity between trials: all $p > .99$). As above, this pattern indicates that these
628 pigeons moved slowly primarily during Change trials, suggesting that even though
629 their trajectories did not show an obvious bias towards the Go location, these pigeons
630 nonetheless faced more difficulties pursuing the goal during Change trials.

631 *Weak Change bias.* Subjects expressing a weak bias towards the Change location
632 (Figure 5, fourth row) did not show any significant differences between velocities of
633 different trial types ($F(2,12)=0.44$, $p=.58$, $\eta_p^2=.07$). Velocities decreased marginally
634 after subjects reached the trajectory-correction point ($F(1,6)=4.20$, $p=.086$, $\eta_p^2=.41$).
635 There is no interaction effect between the two factors ($F(2,12)=0.44$, $p=.56$, $\eta_p^2=.07$).
636 This pattern fits the predictions regarding a non-discriminative approach.

637 *Strong Change bias.* Finally, those pigeons that were strongly inclined to approach the
638 Change location first (Figure 5, bottom row) showed marginal differences in overall
639 velocities between trial types ($F(2,14)=3.18$, $p=.072$, $\eta_p^2=.31$). More prominent,
640 however, were the significant decrease in velocity after reaching the correction point
641 ($F(1,7)=44.31$, $p < .001$, $\eta_p^2=.86$) and the significant interaction effect showing that this
642 decrease only occurred in Go trials but not in Change trials ($F(2,14)=9.03$, $p=.003$,
643 $\eta_p^2=.56$; comparison of pre- and post-correction velocities for Go following Go:
644 $t(7)=6.80$, $p < .001$, for Go following Change: $t(7)=4.80$, $p=.001$, for Change: $t(7)=1.23$,
645 $p=.82$). Furthermore, pairwise comparisons showed that velocities only differed
646 marginally between trial types before the correction point was reached, whereas there
647 was a significant difference between Go trials following a Change and Change trials
648 after that point was passed (pairwise comparison of pre-correction velocity in Go trials
649 following a Change trial compared to Go trials following a Change trial: $t(14)=2.77$,
650 $p=.095$, comparisons of Go following Go and Change: $t(14)=2.87$, $p=.076$, comparison
651 of Go following Change and Change: $t(14)=0.10$, $p=1.0$; comparison of post-correction
652 velocity in Go following Go and Go following Change: $t(14)=0.91$, $p=.94$, comparisons
653 of Go following Go and Change: $t(14)=2.32$, $p=.22$, comparison of Go following
654 Change and Change: $t(14)=3.23$, $p=.035$). Taking into account the bias towards
655 Change of these subjects, this pattern fits the predictions of reactive inhibition.
656 Although subjects tended to start Go trial following a Change at a somewhat lower
657 speed than Go trials following a Go, this pattern indicates that they mostly reacted to
658 a change in contingencies rather than anticipating it, slowing down during Go trials
659 after adjusting their paths.

660

661 Discussion

662

663 The ability to inhibit and correct one's actions quickly depending on changes in the
664 environment seems essential to survival. Yet, it has been challenging to assess or
665 even experimentally quantify the mental processes enabling response inhibition. The
666 continuous inhibitory-control task presented in this study was designed to provide
667 observable and measurable variables to achieve this. The paradigm required pigeons
668 to approach a baited food location, a behaviour that is highly prevalent in their natural
669 behavioural repertoire and executed quickly, and would thus require controlled
670 inhibition to be overcome (cf. [Meier, Pant, et al., 2017](#)).

671 Pigeons have shown a good capacity of employing reactive inhibitory control in
672 computerised experiments ([Lea, et al., 2019](#); [Meier, Lea, et al., 2017](#)) and were thus
673 a suitable study species to investigate if this task could suitably identify and contrast
674 inhibitory-control processes from less cognitively demanding strategies. Indeed, we
675 observed a range of different approaches to this paradigm amongst our subjects. In
676 an effort to determine whether the observed response patterns could provide insight
677 into cognitive processes, we specified several potential strategies that might underlie
678 performance in this task and sketched the expected trajectories as well as speed while
679 approaching a location if each of these strategies was pursued.

680

681 Firstly, controlled response inhibition can be characterised not only by a slowing in
682 speed when behaviour has to be adjusted to a sudden change, but also by the paths
683 taken to pursue a goal: an initial movement towards a predisposed location followed
684 by a sharp curve towards an alternative location after the subject realises that the initial
685 location is unavailable (see Figure 2, Panel A). During trials in which no such sudden
686 change occurred and no path correction is necessary, however, trajectories approach
687 the initially chosen location in a straight line from the starting point. Both the human
688 participants in [Verbruggen and McLaren's \(2017\)](#) study and the pheasants tested by
689 [Meier, Pant, et al. \(2017\)](#) showed this pattern of behaviour, as did many pigeons in
690 this study (Figure 5, left column), providing evidence that response inhibition was
691 necessary to correct one's performance. Interestingly, despite the Go location always
692 being the initially available goal (and being reinforced twice as often), we observed an
693 almost even split of our sample between subjects that primarily approached the Go
694 location (Figure 4, top two rows, "strong Go bias" and "weak Go bias") and those that

695 initially steered towards the Change location (Figure 4, bottom two rows, "weak
696 Change bias" and "strong Change bias"). This observation is the first indication that
697 the pigeons' approach to the task might not fit the predicted patterns. The even split
698 between pigeons that approached the Go location first and those that primarily
699 approached the Change location suggests that, instead of the anticipated bias towards
700 Go, at least a portion of the pigeons might have always followed their own internal
701 preference for one of the locations that was independent of the presented information.
702 In such a case, the particular conditions of a trial will have had very little influence on
703 the pigeons' initial behaviour. For those pigeons that preferentially approached the Go
704 location, it is impossible to determine whether their bias was determined by an inherent
705 preference or an attention to the task contingencies. However, either bias can be
706 described by a common response patterns: trajectories towards the preferred location
707 are straight and the trajectory-correction points are very close to the start location from
708 which the pigeons entered the arena, whereas the paths towards the non-preferred
709 location are curved, with a correction point farther into the arena. Taken together, this
710 indicates that the pigeons most likely started their trajectory with an automatic, non-
711 information-driven, response and subsequently had to exert inhibitory control to
712 overcome this bias and approach the correct location.

713

714 As noted above, as this approach begins with a subject's internal preference for one
715 particular location, it is unlikely that the initial trajectory or speed when approaching a
716 goal were influenced by events on previous trials, which as we argue is an important
717 signpost of an individual's ability to perform sophisticated inhibitory-control strategies
718 - in particular its capacity to optimise responses by performing the mental goal
719 adjustments indicative of proactive inhibitory control ([Elchlepp et al., 2016](#); [Verbruggen
& McLaren, 2017](#)) - proposed by the mental goal adjustments account (Figure 2 Panel
721 A). However, the observed response patterns of the majority of our subjects provide
722 coherent evidence for relying on reactive inhibitory control to solve the task (Figure 5,
723 top two rows, "strong Go bias", "weak Go bias" and bottom row, "strong Change bias";
724 the subgroup "weak Change bias", though expressing the predicted pattern in their
725 trajectories, did not show the expected velocities as per the reactive inhibition
726 account). Even though subjects did not show evidence of anticipating a potential
727 change in contingencies, this form of inhibitory control allows subjects to quickly react
728 if the initially approached location is not available by slowing down and altering their

729 path. It has to be noted that, while we predicted that for reactive inhibition velocities
730 would be slower after reaching this trajectory-correction point than before, the
731 observed patterns (which match this prediction) could also reflect a general slowing
732 across the path rather than a change at the correction point. It is therefore possible
733 that the pigeons started fast and progressively slowed down as a result of reactive
734 control being progressively engaged. Only an examination of individual changes in
735 speed across an entire trial would allow inferences about this possibility, and that could
736 not be carried out in the present study.

737 As can be seen in Figure 5, not all pigeons pursued their preferred goal with equal
738 fervour. Those with the strongest bias (Figure 5, top row, "strong Go bias", and bottom
739 row, "strong Change bias") also demonstrated fastest velocities, while those subjects
740 with a less pronounced bias (Figure 5, second row, "weak Go bias", and fourth row,
741 "weak Change bias") were somewhat slower. It might have been the case that strongly
742 biased subjects generally completed the movement towards the Go location until they
743 reached it and only approached the Change location after verifying that the Go location
744 was inaccessible. In fact, any predictions based on latencies or velocities are unable
745 to differentiate between such failed and successful inhibition, as in either case,
746 latencies would be expected to be longer during Change trials compared to Go trials
747 and averaged velocities generally slower on Change trials when subjects need to slow
748 down (or stop entirely) in order to be able to correct their current path. Thus, only an
749 examination of individual trajectories can provide information about whether inhibition
750 was achieved. Trajectory-correction points very close to the incorrect goal location and
751 sharp-angled trajectories on Change trials (or, in the case of a reverse bias, Go trials)
752 speak to the assumption that the more strongly biased subjects among these two
753 subgroups might indeed have faced difficulties inhibiting their preference. That leaves
754 the question as to whether those subjects with a less pronounced bias can be regarded
755 as the truly successful "inhibitors". Some research suggests that human adults might
756 possess a dual-system of impulse control consisting of a "cool" cognitive, self-
757 regulatory system and a "hot" emotional, stimulus-driven system that defies cognitive
758 control, with the balance between the two determined both by the emotional,
759 developmental and cognitive state of the individual (e.g., [Hofmann, Friese, & Strack, 2009](#);
760 [Metcalf & Mischel, 1999](#)). Such a dual system might also exist for pigeons, with
761 more strongly biased subjects being governed more by the hot system than lesser
762 biased subjects. The performance of those pigeons that were grouped into the "weak

763 bias" subgroups during our ranking procedure appear rather varied (see Figure 4),
764 thus this issue should be explored further in future studies.

765

766 Secondly, the pigeons showing no apparent bias towards either location also do not
767 show a convincing pattern of employing inhibitory control to solve the task. An
768 alternative strategy that might have guided behaviour of these subjects could have
769 been a tendency to return to the location that was rewarded in the previous trial. In this
770 case, we would have expected greatly different trajectories for the two different types
771 of Go trials. This was not observed for any subject; most often, subjects took very
772 similar paths towards the Go location, regardless of whether that location had been
773 reinforced in the previous trial (in the case of Go trials following another Go trial) or not
774 (in the case of Go trials following a Change trial). Just as above, we can therefore
775 reasonably conclude that the response requirements of the previous trial had little
776 influence on the pigeons' behaviour.

777

778 Finally, we considered the potential response pattern that would emerge in the case
779 that subjects did not discriminate between the two potential goal locations. Indeed we
780 were able to identify a subgroup of subjects that appeared to fall into this category
781 (Figures 5 and 6, third row, "no bias"). Their average trajectories led straight towards
782 the centre of the arena in all three types of trials before turning towards the correct
783 food location (Figure 5, middle row). Thus, these pigeons moved into the arena without
784 a clear overall preference for one or the other food location, perhaps due to hesitation
785 to approach any location before the correct response requirements are known, or due
786 to a tendency to randomly choose a location at the start of a trial and approach it
787 regardless of the current requirements (which, when averaged out over multiple trials,
788 would result in a straight line). A further point of note is that this subgroup of non-
789 discriminators also showed the lowest overall velocities when completing any trial
790 compared to the other four groups, further highlighting their hesitant approach. Our
791 paradigm relied on the assumption that pigeons would be quick to approach available
792 food, as doing so is a highly prevalent natural behaviour. However, we did not impose
793 any negative consequences for approaching the incorrect location or for responding
794 slowly; therefore, there was no implied demand to quickly readjust any incorrect
795 responses, even though other subjects were clearly able to do so. Nonetheless, there
796 seems to be more than meets the eye for these subjects regarding their ability (or

797 apparent lack) to discriminate between Go and Change trials: they proceed to the
798 trajectory-correction point at the lowest speed during Change trials – perhaps the
799 perceived tipping-over of the see-saw right after entering the arena causes them to
800 slow down further, yet without affecting their previously determined path.

801

802 In conclusion, the continuous response-inhibition paradigm used in this study has
803 proven to be a valuable tool to assess behavioural strategies when faced with a task
804 that can optimally be solved by employing inhibitory control. One of this paradigm's
805 strong advantages in this regard is that it uses a subject's inherent drive to approach
806 a food source, without the necessity to administer a large number of training sessions
807 prior to the test. Although incorporating both trajectories and velocities proved difficult,
808 the paradigm nonetheless provides several options to assess an individual's cognitive
809 capacities in this regard, and the comparison between different measures of inhibitory
810 control highlights that physical movement in space may add additional information
811 about cognitive processes beyond measures based on speed. Pigeons are capable of
812 exerting a variety of cognitive approaches to the problem, including inhibitory control,
813 although their capabilities might not be sufficient to express sophisticated control
814 strategies such as the mental goal adjustments expressed by humans.

815

816 **Open Practices Statement**

817

818 The data and materials for all experiments are available upon request from the first

819 author and will be made available in a data repository prior to publication.

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Supplementary Table 1. Coordinates of individual average trajectory-correction points during Go trials following a Go trial, Go trials following a Change and Change trials. The first location that was approached during habituation is denoted as L (left) or R (right) for the 15-minute and 5-minute habituation session, respectively.

	Subject	Go (previous Go)		Go (previous Change)		Change		Preference during Hab.	
		x	y	x	y	x	y	15'	5'
strong Go bias	Egypt	0.17	0.03	-0.14	0.20	0.44	0.62	L	L
	Chioni	0.03	0.44	0.01	0.18	0.39	0.90	R	R
	Plum	-0.04	0.09	-0.09	0.12	0.37	0.70	L	L
	Sahara	0.05	0.01	0.08	0.03	0.13	0.64	L	L
	Lalibela	0.36	0.04	0.11	0.01	0.86	0.75	R	L
	Toffee	0.04	0.03	0.13	0.04	0.47	0.76	R	R
	Fez	0.26	0.05	0.13	0.02	0.78	0.83	L	R
	Bramble	0.14	0.03	0.08	0.05	0.49	0.95	L	R
weak Go bias	OJ	0.09	0.59	-0.09	0.40	0.19	0.75	L	R
	Tripoli	0.24	0.59	0.18	0.61	0.15	0.86	L	R
	Ross	0.03	0.05	0.21	0.48	0.29	0.57	L	L
	Hery	0.02	0.48	0.02	0.54	0.35	0.83	L	L
	Pekoe	-0.10	0.50	-0.29	0.37	0.14	0.79	R	R
	Kili	-0.04	0.40	0.11	0.47	0.00	0.80	R	R
	Axum	-0.30	0.17	-0.51	0.20	0.02	0.62	L	R
no bias	Oats	0.05	0.76	-0.12	0.71	0.16	0.71	R	R
	Namib	0.19	0.75	0.12	0.68	0.20	0.77	R	R
	Chad	-0.15	0.51	-0.60	0.60	0.05	0.63	R	R
	Satsuma	-0.05	0.98	-0.30	0.68	0.08	0.93	R	L
	Mali	-0.09	0.80	0.13	0.55	0.06	0.82	L	R
	Guy	-0.18	0.28	0.01	0.71	0.11	0.65	L	R
	Sparkle	0.02	0.74	-0.03	0.67	0.37	0.87	L	R
	Boo	-0.11	0.46	-0.06	0.54	0.08	0.68	R	L
weak Change bias	Yuki	-0.21	0.91	-0.38	0.93	0.22	0.51	R	R
	Apple	-0.24	0.85	-0.53	0.86	0.10	0.47	L	R
	Congo	0.23	0.73	0.20	0.43	0.17	0.37	R	L
	Zanzibar	-0.15	0.73	-0.20	0.75	0.02	0.02	L	R
	Seville	-0.15	0.85	-0.11	0.78	0.14	0.70	R	R
	Candy	-0.45	0.67	-0.46	0.48	0.12	0.49	R	R
	Almond	-0.03	0.97	0.10	0.96	-0.11	0.91	R	L
strong Change bias	Navel	-0.43	0.93	-0.37	0.94	-0.06	0.01	L	L
	Pidge	-0.61	0.88	-0.70	0.73	0.04	0.01	L	L
	Walnut	-0.17	0.85	-0.37	0.79	-0.03	0.03	L	L
	Nile	-0.71	0.80	-0.43	0.81	0.01	0.02	R	R
	Rye	-0.34	0.73	-0.23	0.82	-0.03	0.02	R	R
	Gambia	-0.23	0.68	-0.41	0.58	0.00	0.45	L	L
	Luna	-0.12	0.48	0.03	0.74	0.05	0.01	L	L
	Morocco	-0.19	0.78	-0.19	0.87	0.01	0.26	R	R

