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1 **Route-following ants respond to alterations of the view sequence**

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19 **Keywords:** *Cataglyphis*, desert ants, homing, navigation, route-following, view sequence

20

21 **ABSTRACT**

22 Ants can navigate by comparing the currently perceived view with memorised views along a  
23 familiar foraging route. Models regarding route-following suggest the views are stored and  
24 recalled independently of the sequence in which they occur. Hence, the ant only needs to  
25 evaluate the instantaneous familiarity of the current view to obtain a heading direction. This  
26 study investigates whether ant homing behaviour is influenced by alterations in the  
27 sequence of views experienced along a familiar route, using the frequency of stop-and-scan  
28 behaviour as an indicator of the ant's navigational uncertainty. Ants were trained to forage  
29 between their nest and a feeder which they exited through a short channel before  
30 proceeding along the homeward route. In tests, ants were collected before entering the nest  
31 and released again in the channel, which was placed either in its original location or halfway  
32 along the route. Ants exiting the familiar channel in the middle of the route would thus  
33 experience familiar views in a novel sequence. Results show that ants exiting the channel  
34 scan significantly more when they find themselves in the middle of the route, compared to  
35 when emerging at the expected location near the feeder. This behaviour suggests that  
36 previously encountered views influence the recognition of current views, even when these  
37 views are highly familiar, revealing a sequence component to route memory. How  
38 information about view sequences could be implemented in the insect brain as well as  
39 potential alternative explanations to our results are discussed.

40

41

42 **INTRODUCTION**

43 Solitary foraging desert ants are expert navigators that seek and retrieve food morsels under  
44 extreme heat conditions. When foragers locate a bountiful food source they will shuttle  
45 rapidly back and forth along idiosyncratic visually-guided routes (Kohler and Wehner, 2005;  
46 Mangan and Webb, 2012; Wystrach et al., 2011b). That is, each ant will follow a fixed path  
47 to the feeder before returning home by a similarly fixed but different path. These paths are  
48 unique to each ant despite their journeys sharing the same start and end points,  
49 demonstrating a lack of pheromone guidance. Instead visual information provided by the  
50 ants' surroundings is sufficient for route following and individuals can even recover their  
51 normal route direction following a displacement either by an experimenter (Kohler and  
52 Wehner, 2005; Mangan and Webb, 2012; Sommer et al., 2008) or a wind gust (Wystrach and

53 Schwarz, 2013), suggesting that visual memories (here termed ‘views’) can be accessed  
54 independently of the animal’s recent experience.

55 This memory feature is embedded in recently developed computational models of  
56 visual route following. A key insight was that if retinotopy is maintained in the view encoding  
57 (Baddeley et al., 2012; Baddeley et al., 2011; Collett et al., 2017; Möller, 2012; Wystrach et  
58 al., 2013; Zeil et al., 2003), the correct direction to move at any point along a route can be  
59 recovered by finding the viewing direction that produces the best match, or least novelty,  
60 when compared to the complete set of views stored in a previous traversal of the route. By  
61 simply moving along the direction with the least novelty the animal would repeatedly align  
62 with the direction it previously travelled and retrace its path. Ardin and colleagues (Ardin et  
63 al., 2016a) demonstrated that the circuitry of the insect mushroom body (MB) is ideally  
64 suited to measure the novelty of the current ‘view’ against those previously experienced.  
65 Each view is assumed to create a unique sparse activation pattern in the MB Kenyon cells  
66 and can be stored as ‘familiar’ by reducing the output weights of those cells. Views from  
67 novel locations or from familiar locations when facing the wrong direction will produce novel  
68 activation patterns and thus still activate the network’s output, to trigger steering  
69 corrections. Computational models using such novelty-driven MB networks have produced  
70 realistic route following behaviours in simulated environments (ants: (Ardin et al., 2016a);  
71 bees: (Müller et al., 2018)) and on a mobile robot in a real ant habitat (Kodzhabashev and  
72 Mangan, 2015). Both experimental- (Freas et al., 2018; Narendra et al., 2013; Wehner and  
73 Räber, 1979; Wystrach et al., 2011a) and neurobiological data (Ardin et al., 2016b; Webb  
74 and Wystrach, 2016) in ants accommodate the mentioned models although some other  
75 processes may also be at work (Cartwright and Collett, 1983; Mangan and Webb, 2009;  
76 Möller, 2012; Wystrach et al., 2012).

77 As noted, a key feature of these models is that ‘memory of a route’ does not include  
78 any information about the sequence in which views are encountered. The agent can tell  
79 whether a given view is familiar or not, but cannot tell whether it corresponds to the  
80 beginning, the end or any other location along the route. Consequently, the agent has no  
81 information about whether two views should be experienced in succession nor any  
82 expectation that any particular view will occur after another. In theory, one could present all  
83 the views from a familiar route in a random order with no difference in the agents’  
84 behaviour.

85           This simple scene-action control hypothesis is parsimonious , however, data from  
86 behavioural studies suggest that the picture may not be so simple (Wehner et al., 1996).  
87 Specifically, (Wystrach et al., 2013) showed that ants displaced from their nest to an  
88 unfamiliar location do not immediately engage in a systematic search but instead backtrack  
89 along their just travelled route bearing. This effect is only present in ants that have been  
90 captured at the nest indicative of ants possessing some memory of recent visual  
91 experiences. Furthermore, (Collett, 2014; Wystrach et al. 2019) demonstrated that ants  
92 forced to retrace their homeward routes twice in succession (moved from the feeder back to  
93 the start of their inward route) display a period of confusion where they do not seem to  
94 recognise their familiar path. Graham and Mangan (Graham and Mangan, 2015) postulate a  
95 series of possible explanations for such behaviours including the use of temporal  
96 information about their routes such as the sequence in which views were experienced. This  
97 study aims to address this possibility directly by assessing whether ants have knowledge  
98 about the sequence of views encountered along their familiar foraging route. It is already  
99 known that ants and bees can be trained to learn sequences of patterns (Schwarz and  
100 Cheng, 2011) and motor actions (Collett et al., 1993; Macquart et al., 2008) or to act  
101 accordingly to the cue they have just previously encountered (Giurfa et al., 2001; Zhang et  
102 al., 2005). However, these feats requires many trials of experimental conditioning, and  
103 although some can be parsimoniously explained (Cope et al., 2018), it remains unknown  
104 whether these insects spontaneously learn information about the sequence of views  
105 experienced along their familiar foraging routes (Riabinina et al., 2011).

106           In our study, ants were trained to home along a route through semi-natural terrain.  
107 The route started with a short section through a channel providing a unique visual  
108 experience as ants begin their homeward journey. During tests, the familiar channel was  
109 moved to a different location at the middle of the route so that ants exiting the channel  
110 were exposed to a familiar view that is not the one they usually experience immediately  
111 after the channel. To assess whether breaking the normal sequence of views in such a way  
112 impacted the ants, the number of scanning behaviours that ants displayed after exiting the  
113 channel in several tests and control conditions was quantified. Scanning behaviour typically  
114 provides a proxy for assessing the ants' current navigational uncertainty (Wystrach et al.,  
115 2014). The results showed a strong effect of changing the sequence, which we discuss in the  
116 light of insect behaviour and neurobiology.

117

## 118 **MATERIALS AND METHODS**

### 119 **Species and study site**

120 All experiments were carried out on the desert ant *Cataglyphis velox* at a field site in the  
121 periphery of Seville, Spain. *Cataglyphis velox* is a thermophilic ant species common in the  
122 area that exhibits behavioural traits typical for desert ants (Cerda, 2001). Instead of  
123 following pheromone trails, *C. velox* foragers venture out solitarily to search for food during  
124 the heat of the day and develop idiosyncratic routes relying on visual terrestrial and celestial  
125 navigational cues (Mangan and Webb, 2012, Schwarz et al. 2017).

126

### 127 **General experimental set-up**

128 Two experiments were conducted over two field seasons in June 2016 and June 2017. In  
129 both experiments ants were trained to run along a defined route to collect food items at a  
130 feeder location (Figs. 1A, C; 2A, B). The routes were enclosed by slippery white plastic planks  
131 (approx. 5 cm high) submerged in a 5 cm ditch. This enabled the ants to perceive the  
132 surrounding natural scenery during route-following while preventing them to forage  
133 elsewhere (Wystrach et al., 2012). The foraging routes were cleared of clutter and  
134 vegetation to ease the movements of the foragers on the ground. Small plastic bowls  
135 (15×15×15 cm) sunk into the ground so that their top edges aligned with the ground surface  
136 served as feeders. The upper rim of the feeder walls was covered with transparent tape to  
137 prevent the ants from escaping. Foraging ants eventually jumped or fell into the feeder and  
138 picked up a biscuit crumb or meal worm piece and were then individually marked with  
139 acrylic or enamel modelling paint. In both experiments, foragers that had picked up a food  
140 item started their homing journeys by travelling through an open-topped, 50×5×10 cm white  
141 plastic channel that directly connected the feeder to the start of the homeward route. Thus,  
142 the visual route memories of all ants across conditions for the first 50 cm of their route was  
143 inside of the white channel. Only well-trained individuals with high familiarity of the visual  
144 surroundings were tested (see detail for each experiment below). For tests, homing ants  
145 were captured just before entering their nest so that their current path integration  
146 homeward vector (accumulated during the outbound trip) had returned to zero; hence  
147 termed zero-vector ants (ZV). For proper homing motivation, only ants holding a food item  
148 were tested. Once captured, the ant was transferred in a darkened plastic vial and released

149 at one of the test locations along the route, either within a ‘test channel’ or directly on the  
150 ground (see details below). The transition between the capture point at the nest and the  
151 release at either the feeder or mid-route location caused an additional alteration of the view  
152 sequence and hence could trigger scanning behaviour. In all conditions, ZV ants were likely  
153 to scan a few times upon release from the carrying tube. However, ZV ants were always  
154 released 50 cm before the actual test areas, giving the foragers enough time and space to  
155 recover their bearings and resume visual homing before data recording started at the  
156 designated test areas (Figs. 1A, B; 2A). Furthermore, the test channel was always placed at  
157 the exact location where the ant homed during her previously displayed homing path. This  
158 procedure helped minimise changes in visual familiarity during tests. To avoid differences in  
159 the ground substrate across the different test locations the immediate area after the  
160 channel exit (50×50 cm) was covered with a layer of sand (Figs. 1, 2; grey areas). In all tests,  
161 a GoPro Hero3+ camera was mounted on the top end of the test channel and the behaviour  
162 of the tested ant was recorded on the 50x50 cm area after the channel exit. Panoramic  
163 images shown in figures were taken with a Sony™ Bloggie camera and unwarped with  
164 PhotoWarp2™.

165

## 166 **Experiment 1**

167 In June 2016 ants were trained to follow a curved outbound route to a feeder located  
168 approx. 8 m away from the nest and then a zigzagged shaped inbound route back to the  
169 nest (Fig. 1A). The homeward paths of ants started inside the plastic channel which had an  
170 approximate slope of 30° linking the entrance at the dug-in feeder to the channel exit at  
171 ground level (Fig. 1B). Hence the channel pointed up towards the sky and ants could see no  
172 terrestrial cues from inside. For each individually marked forager, training continued at least  
173 until they were able to negotiate a straight homebound route without colliding into the  
174 baffles or the surrounding planks enclosing the zigzag route (Fig. 1A). ZV ants were tested in  
175 one of the following conditions:

- 176 1. Test channel to feeder (start of the route). Ants were transferred into a test  
177 channel that was identical to the training channel and placed alongside the  
178 training channel (Fig. 1A) at the feeder. Thus, in the *Feeder Test*, the sequence of  
179 visual memories experienced was unaltered from training.

- 180 2. Test channel to mid-route. Ants were transferred into the same test channel as at  
181 the feeder but this time the channel was placed in the middle of the third leg of  
182 the zigzag route with the same compass orientation as at the Feeder (Fig. 1A).  
183 The visual surrounding of the *Mid-Route Test* differed greatly from the one of the  
184 Feeder test as it contained several big, nearby artificial objects (Fig. 1A, C). Thus,  
185 this is the crucial experimental condition in which the sequence of familiar visual  
186 memories was altered as compared to a normal homing journey.
- 187 3. Novel channel to start or mid-route. A control for the potential difference in  
188 visual familiarity between the feeder- and mid-route release was the *Novel*  
189 *Channel Test*. Ants were transferred into an unfamiliar channel and released at  
190 either the feeder or the mid-route location (Fig. 1A). The novel channel was a  
191 modified version of the normal test channel. The walls and the ground were  
192 covered with thin beige cardboard and hence provided a different substrate  
193 material and colour.
- 194 4. Mid-route no channel (control). To control for the possibility that ants might  
195 always scan when released at the mid-route location, irrespective of the  
196 sequence alteration, a *Mid-Route Control* was conducted. The test channel was  
197 placed as for the Mid-Route Test location but the ants were released on the  
198 ground, right beside the beginning of the test channel (Fig. 1A).
- 199 5. Channel to unfamiliar location (control). To verify that scanning behaviour is  
200 evoked by visual unfamiliarity, ants were released in the familiar test channel  
201 after it had been placed so that they would emerge in completely unfamiliar  
202 visual surroundings approx. 25 m away (Fig. S1).

203 Each ant was tested only once, in one of the test conditions.

204

## 205 **Experiment 2**

206 To account for individual variance in Experiment 1, a second experiment was conducted in  
207 June 2017 in which the same ant was tested in all conditions and therefore provided paired  
208 data across trials. Ants were trained to follow a straight foraging route (approx. 8 m long and  
209 1.2 m wide; Fig. 2A) and similar training procedures to Experiment 1 were followed, whereby  
210 foragers always returned from the feeder via a 50 cm long channel before continuing their  
211 homebound trip. The training and test channels were augmented with black stripes attached



212 to the walls to enhance visual contrast and optic flow as well as to lower potential  
213 reflections from the sun. An additional channel at the middle of the route (Mid-Route Test  
214 location) was present during all training trials (approx. 6 m in feeder-nest direction; Fig. 2A,  
215 B) to diminish differences of the views due to the test channel during Mid-Route Test and  
216 Mid-Route Control. Ants were individually marked and considered trained after performing  
217 at least five straight homing bounds. Trained ZV ants were subjected to the following test  
218 conditions.

- 219 1. Test channel to feeder (start of the route). In the *Feeder Test*, ants were released in a  
220 test channel (identical to the training channel) and placed alongside the training  
221 channel (Fig. 2A, B). As in the equivalent condition of Experiment 1, the sequence of  
222 views experienced by the ant was unaltered from training.
- 223 2. Test channel to mid-route. In the *Mid-Route Test*, ants were transferred to the same  
224 test channel as for Feeder Tests, but this time the channel was placed exactly on the  
225 location of the mid-route channel, thus replacing it (Fig. 2A, B). Here too, visual  
226 differences between Mid-Route- and Feeder Test location were emphasised by the  
227 additional visual objects (Fig. 2B). As in the equivalent condition of Experiment 1, the  
228 usual sequence of views experienced by the ant was thus altered.
- 229 3. Mid-route no channel (control). As in Experiment 1, for the *Mid-Route Control* ants  
230 were released on the ground, right beside the beginning of the mid-route channel  
231 (Fig. 2A, B) to test whether this location might appear less familiar than the Feeder  
232 location irrespective of the sequence.
- 233 4. Familiarity Control with altered visual surrounding at the Feeder Test was  
234 additionally conducted to test whether the increase of scans during Mid-Route tests  
235 could have been caused by a drop of familiarity just as the ant is exiting the test  
236 channel (Fig. S2). This exact view (at the border between the channel exit and the  
237 Mid-Route test surrounding) has never been encountered by the ants and might have  
238 triggered the scan increase in Experiment 1 and 2 instead of the altered sequence of  
239 views.

240 In Experiment 2, each ant was tested once in each condition, with at least two uninterrupted  
241 training trips between test. This provided individually paired data across the three tests. The  
242 order of tests varied across individuals in a systematic fashion.

243

## 244 **Data recording and analysis**

245 The number of scans performed by the ants on the 50×50 cm test areas was assessed in two  
246 ways. Firstly, scans were observed and recorded directly in the field by two experimenters.  
247 Scans were defined by the following criteria: the ant stops forward motion and rotates at  
248 least in one direction on the spot before resuming forward motion. Given the rotational  
249 component, such a behaviour is usually obvious and hence unambiguous. Experimenters  
250 agreed upon the number of scans on each test and the data-point was recorded. This was  
251 supported by video recording of all tests using a GoPro Hero3+ (1920×1080 pixel; 60 fps) and  
252 a Panasonic Lumix camera (DMC FZ200) for Fig. S2. Some video files were corrupted  
253 (Experiment 1: 17 out of 76; Experiment 2: 2 out of 66; Fig. S2: 12 out of 44) and the number  
254 of scans were solely based on live observations of two experimenters.

255 Differences between the number of scans across tests were analysed with a General-  
256 linear-model (GLM) for count data (quasipoisson distribution). For Experiment 2 with paired  
257 data, we used the GLM for mixed effects with conditions as fixed effect and individual ants  
258 as random effect. In both experiments, the key Mid-Route Test condition – where the  
259 sequence of view is altered – was compared to both other conditions (Feeder Test and Mid-  
260 Route Control) simultaneously in the model.

261

## 262 **RESULTS**

263 To investigate whether recently experienced views affect the route following behaviour of  
264 ants, ZV ants were tested at the feeder (unaltered sequence of views) or at the middle of  
265 their familiar route (altered sequence of views) and the number of scans displayed in the  
266 area following the channel exit was analysed. The occurrence of scans is a suitable indicator  
267 of navigational uncertainty in this experimental context: ants exiting the test channel in  
268 totally unfamiliar surroundings showed systematic scanning behaviours (90%, 9/10) and the  
269 highest numbers of scans (up to 6) across all test conditions (Fig. S1).

270

### 271 **Experiment 1**

272 In Feeder Tests, that is without altered visual sequence, not a single ant (0%, 0/14) scanned  
273 in the test area (Fig. 1D). In contrast, in the Mid-Route Test, where ants experienced an  
274 altered visual sequence, 50% of ants (7/14) scanned at least once in the test area (Fig. 1D),  
275 indicating some degree of navigational uncertainty. There is a significant increase of scans in

276 the Mid-Route Test when compared to the Feeder Test (GLM:  $P=0.026$ ,  $Z=-2.357$ ). In the  
277 Mid-Route Control, with the ants released beside of the mid-route-channel, only two out of  
278 twelve ants (16%) scanned (Fig. 1D) suggesting that the increased scanning number in the  
279 Mid-Route Test is not due to unfamiliarity of the absolute position, although this difference  
280 did not reach significance (GLM:  $P=0.215$ ,  $Z=-1.272$ ; Fig. 1D). An additional control confirmed  
281 that the increase of scans was due to the altered sequence of views from test channel to the  
282 visual surrounding at the exit of the test channel and not caused by a lack of visual route  
283 knowledge. Ants from the Novel Channel Tests showed no significant difference between  
284 the feeder and mid-route release points (GLM:  $P=0.932$ ,  $Z=0.097$ ; Fig. 1E). Both tests bore  
285 unfamiliarity due to the novel test channel and produced scans in 50% (7/14) and 42% (6/12)  
286 of ants respectively.

287

## 288 **Experiment 2**

289 In Experiment 2, each ant was tested in all three conditions (Feeder Test, Mid-Route Test  
290 and Mid-Route Control), providing paired data accounting for individual differences. As  
291 before, in the Feeder Test few ants (14%, 3/22) scanned in comparison to 77% (17/22) of  
292 ants in the Mid-Route Test condition (Fig. 2C). Also, in accordance with data from  
293 Experiment 1, only 9% (2/22) of ants in the Mid-Route Control scanned, which is in line with  
294 data observed in the Feeder Test (Fig. 2C). We observed a significant increase in scans during  
295 the Mid-Route Test as compared to the Feeder Test (GLM:  $P=0.001$ ,  $Z=-3.502$ ) and Mid-  
296 Route Control (GLM:  $P=0.002$ ,  $Z=-3.166$ ). This effect was not due to a few ants scanning  
297 many times as most of the ants (31/44) displayed a higher number of scans in the Mid-Route  
298 Test (Fig. 2D) and only one single ant decreased her number of scans between the Feeder-  
299 and Mid-Route Test. The sequence across test conditions was balanced across individual and  
300 had no detectable effect on the results (GLM:  $P=0.463$ ,  $Z=-0.734$ ).

301

## 302 **DISCUSSION**

303 A reliable sign of navigational uncertainty in ants is the occurrence of scanning behaviour  
304 (Wystrach et al., 2019; Wystrach et al., 2014). In the current study, 90% of ants leaving a  
305 familiar channel from a feeder and finding themselves in a completely novel location  
306 exhibited repeated scanning (Fig. S1). This behaviour was used as an assay to investigate  
307 whether experiencing familiar views in an altered, novel sequence also produces uncertainty

308 in ants, indicating that their memory of routes includes some information about the  
309 sequence of views experienced. If so it would challenge, or require augmentation of the  
310 current prevailing models of ant route memory. The main finding of this study is that an  
311 alteration of the sequence of views along a familiar route reliably increases the probability of  
312 a scanning response in ants.

313         Specifically, in experiments conducted across two field seasons and with different  
314 nests, ants were trained along a homing route that started with a 50 cm channel, providing a  
315 unique and well-controlled visual experience, before exiting into the open route  
316 surroundings which they followed home. During tests, trained ants were captured close to  
317 their nest (to prevent the use of PI) and released in an identical-looking test channel. Upon  
318 release, these foragers dashed along the correct homing direction and out of the channel  
319 showing that they recognised the familiar channel scenery. If they then found themselves  
320 close to the unaltered (training) Feeder Test location they scanned rarely if at all (0% and  
321 14% of ants scanned). However, if the channel had been relocated to the middle of the  
322 route, creating an altered visual sequence, foragers emerging from the channel typically  
323 stopped and displayed one or two scans (Mid-Route Test, 50% and 77% of ants scanned)  
324 before resuming their normal motion and completing the route at their usual pace (Figs. 1D,  
325 2C). Mid-Route Control ants, released 50 cm before the test area beside the beginning of the  
326 test channel showed little scanning behaviour in the actual test area (Mid-Route Control,  
327 16% and 9%; Figs. 1D, 2C). On the other hand, using a novel channel tended to equally  
328 induce scans in both the feeder and mid-route locations (Novel Channel Test, 50% and 42%;  
329 Fig. 1E). Overall, results suggest that it is the change in sequence, rather than anything about  
330 the mid-route location or the displacement from the nest back to the route, that causes  
331 navigational uncertainty.

332         Interestingly, ants exiting an unfamiliar looking channel (Novel Channel Tests) also  
333 displayed a high number of scan. This suggest that the novelty component of the channel  
334 (new wall colour and substrate) extended from inside to outside the channel, putting  
335 forward the idea that the unfamiliarity experienced at a given moment may have a sustained  
336 impact on behaviour.

337

338 **Alternative explanations to sequence encoding**

339           The overall experimental designed aimed to contrast the hypothesis of sequence of  
340 views vs. previous models of ant navigation. Results in all conditions validate the a priori  
341 predictions of the use of view sequence, and thus favour this novel hypothesis. However,  
342 alternative explanations may also explain the results.

343           The channel may exert a motor constraint by forcing the ants to keep to a fixed  
344 straight path and perhaps stereotyped movements on exiting it. It could be argued that it is  
345 these motor components rather than the scene in the channel that contributes to  
346 generating the unmet expectation that leads the ants to scan when exiting the Mid-Route  
347 channel during tests. Several papers have shown sequential links between vision and motor  
348 behaviour (Chittka, 1998; Collett et al., 1993; Macquart et al., 2008; Vowles, 1965; Zhang et  
349 al., 1996). However, all these studies examine whether seeing a particular visual pattern can  
350 prime a turn in one direction, rather than the reverse. Motor constraints should have been  
351 minimal in our case because the straight and fast paths of *C. velox* held no apparent  
352 differences within the channel or not, at least to the naked eye, but this idea may still be  
353 worth investigating in other contexts.

354           It should be also noted that both the ants from the Mid-Route Test and the Mid-  
355 Route Control walked 50 cm before testing occurred (Fig. 1A, 2A). In both conditions, tested  
356 ants typically scanned upon release, that is, 50 cm before the test area. Scans before the test  
357 area were not recorded which in hindsight would have allowed further scrutiny about  
358 potential differences between test and control. Yet, in the actual test area most scans  
359 occurred during Mid-Route Tests and hardly ever during Mid-Route Controls (Fig. 1D, 2C).

360           When ants emerge from the (familiar) channel into (familiar) mid-route  
361 surroundings, they must experience for a very brief moment a composite view (channel in  
362 the rear-view and mid-route scene in the frontal visual field) which must be unfamiliar. It  
363 may be argued that this short moment where the overall scene must appear unfamiliar  
364 induced the scanning response observed in the Mid-Route Tests. In a follow-up control  
365 experiment (Fig. S2), we altered the rear-ward portion of the view as ants emerged from the  
366 channel into the (expected) start of the route (Feeder Test) and found that ants indeed  
367 would scan at a similar rate to those exiting the channel in the (unexpected) middle of the  
368 route (Mid-Route Test). However, this alternative explanation remains uncertain for several  
369 reasons. First, the artificial change created in this follow-up experiment exerted a much  
370 longer-lasting visual unfamiliarity than the one experienced at the exit line of the test route

371 channel (Fig. S2). Second, Feeder tests and Mid-Route Controls also contained elements of  
372 unfamiliarity because ants were released on a location slightly offset compared to their  
373 usual route, but this did not trigger scans. Finally, the test channels were lopsidedly dug into  
374 the ground so that ants could not see the visual surroundings before exiting the channel (Fig.  
375 1B), and hence the unfamiliar composite view would be experienced for no more than a  
376 split-second when passing the exit line (Fig. S2). Short moments of unfamiliarity must be  
377 experienced regularly when ants navigate through grassy environments or new fallen debris  
378 (not to mention bystander experimenters). Yet ants do not trigger scans in these cases  
379 (pers. observ. SS, MM, BW, AW). Visual recognition in grassy environments must be noisy  
380 and responding to brief drops in the familiarity signal would lead to regular stops and scans,  
381 which seem counterproductive in these rapid runners.

382         The possibility of learning sequences in ants has been explored before in several  
383 experimental contexts but the results were not clear-cut (Macquart et al., Riabinia et al.,  
384 2011; 2008; Schwarz and Cheng, 2011;). Bulletproof evidence for learning a sequence of  
385 views would probably require experiments in virtual reality, where the tested ants can be  
386 easily and instantaneously 'transferred' from one part of the route to another.

387

### 388 **How could sequences of views be encoded in the insect brain?**

389 A most 'peripheral' explanation to the encoding of information about the visual sequence  
390 would be that ants do not store static but dynamic views, that is, how the visual input is  
391 actually changing as they move forward. Altering the sequence of familiar views as we did  
392 here would produce a novel – and thus unfamiliar – dynamical visual input, hence triggering  
393 scanning behaviours. Past observations in ants cast doubt upon this hypothesis. First, during  
394 scanning behaviours, ants actually stop and pause, exposing the visual system to a static  
395 view of the world during a tenth of a second or so before resuming motion in a correct  
396 direction. This behaviour is particularly apparent in fast walking desert ants such as  
397 *Melophorus bagoti* (Wystrach et al., 2014). During learning walks ants display numerous  
398 scan-like pauses while leaving the nest (Fleischmann et al., 2016; Fleischmann et al., 2017;  
399 Müller and Wehner, 2010; Wystrach et al., 2014) or the feeder (Judd and Collett, 1998;  
400 Nicholson et al., 1999), suggesting that they do learn static views of the world. Moreover,  
401 dynamic views of the world would intrinsically encode information about absolute distances  
402 of object, but experiments altering object configuration show that ant searches are based on

403 retinal overlap rather than absolute distance (Graham et al., 2003; Judd and Collett, 1998;  
404 Wehner and R aber, 1979), suggesting that the stored views are static rather than dynamic.  
405 Third, recent experiments in *C. velox* (work in preparation) and other species (Murray et al.,  
406 2020) show that ants easily recognise familiar views when tethered to run on the spot on a  
407 spherical air treadmill (Dahmen et al., 2017), thus proving that views can be recognised  
408 without the change produced by forward motion.

409         Alternatively, information about view sequence could be encoded in the mushroom  
410 bodies, which are thought to be the sieve of visual memories for navigation (Webb and  
411 Wystrach, 2016). There are several hypotheses for how a succession of views could be  
412 encoded in the mushroom bodies. One is that recurrency in this circuit could be exploited for  
413 learning temporal sequences (Arena et al., 2013; Cognigni et al., 2018; Gr unewald, 1999; Li  
414 and Strausfeld, 1999). Another is that connections between Kenyon cells (KC) could adapt  
415 through Hebbian mechanisms to alter the responsiveness to repeated pattern sequences  
416 (Nowotny et al., 2003). Further, it is known that KCs possess several gap junctions between  
417 each other (Wu et al., 2011), suggesting that each active KC could increase the activation  
418 probability of other KCs, given a small delay. Under this assumption, the pattern of KCs  
419 activity at a given time is not only dependant of the current stimulus but also the previously  
420 active pattern of KCs, that is, the stimulus previously experienced (Nowotny et al., 2003).

421

## 422 **Ultimate considerations**

423 The current study suggests that the disturbance of one transition along the sequence affects  
424 the behaviour. This can be accounted by the storage of a short-sequence and does not  
425 necessarily imply that the complete sequence of experienced views is stored. From a  
426 computational perspective there are potential advantages in storing even short sequences  
427 of view memories, as it can reduce the risk of aliasing errors (Graham and Mangan, 2015).  
428 Matching of short sequence images has been shown to be very robust in robot localisation  
429 algorithms, even with drastic changes in the lighting such as sunny days vs. stormy nights  
430 (Milford and Wyeth, 2012), using very low resolution images (Milford, 2013), or with  
431 substantial tilt and pitch variation (Stone et al., 2016). Robustness to visual change and  
432 reduction of memory load would obviously be beneficial for ants that need to memorise and  
433 recognise long visual routes across their lifetime.

434           Lastly, it is worth mentioning that mechanisms for visual navigation and the neural  
435   underpinning of visual memories seem to be shared across insects or at least across central  
436   place foraging hymenoptera (Cheng, 2012; Warrant and Dacke, 2016; Webb and Wystrach,  
437   2016; Wehner et al., 1996; Zeil and Fleischmann, 2019). Hence, it is likely that the influence  
438   of the sequences of views during route-following is not only limited to *C. velox* but also  
439   present in other ants and visually guided insects.

440

#### 441 **CONCLUSION**

442   This study shows that altering the usual sequence of views triggers a transient resurgence of  
443   scanning behaviours even though the ants are still in their familiar environment.

444   Functionally, learning sequences of views might improve the robustness of visual recognition  
445   to environmental change. The experimental manipulations required to altered the sequence  
446   of views in the real world will always enable alternative explanations to be put forward.

447   Hence, future experiments using virtual reality could provide the means to a definite proof  
448   and the way to explore the mechanisms underlying visual sequence learning, which is likely  
449   to be widespread among insect navigators.

450

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458

459   **Ethics.** This work did not require any ethical approval. Ants were free to forage and return to  
460   the nest at will in our set-up. Only self-motivated foragers (holding their cookie crumbs)  
461   were tested. No ants were killed.

462

463   **Competing interests.** The authors declare no competing interest.

464



465 **Author contributions.** Conceptualisation: S.S., M.M., B.W., A.W.; Methodology: S.S., M.M.,  
466 B.W., A.W; Formal analysis: S.S., A.W.; Investigation: S.S., A.W.; Writing - original draft: S.S.,  
467 A.W.; Writing - review & editing: S.S., M.M., B.W., A.W.

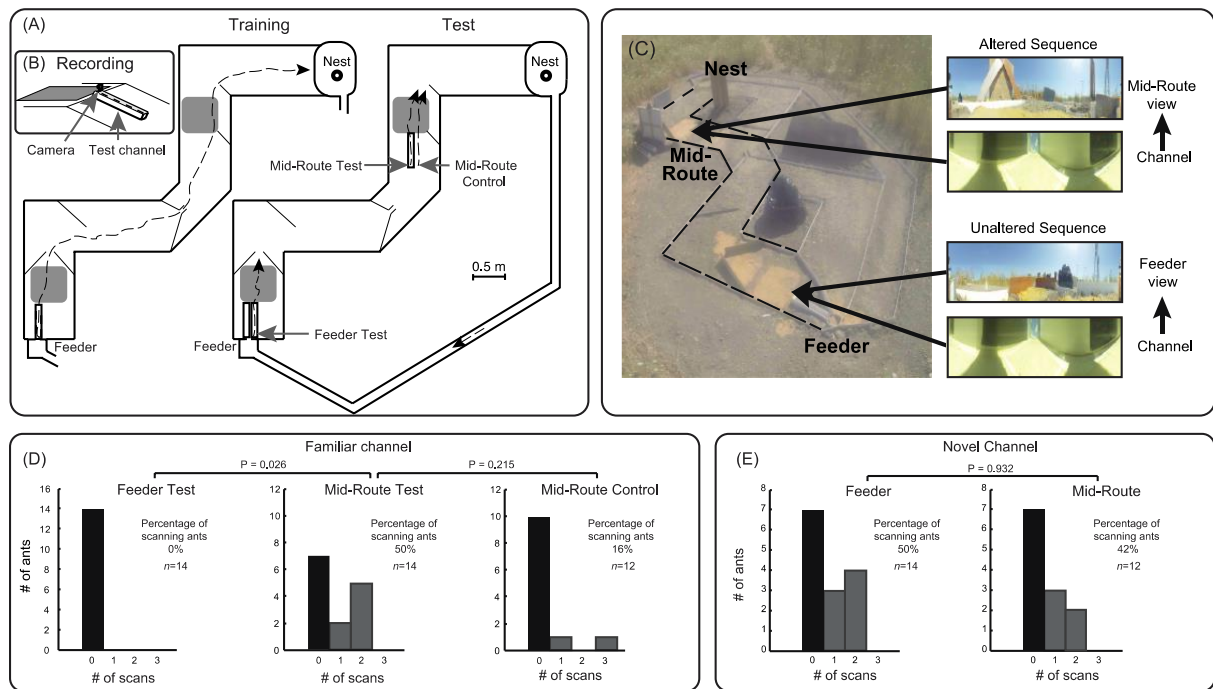
468

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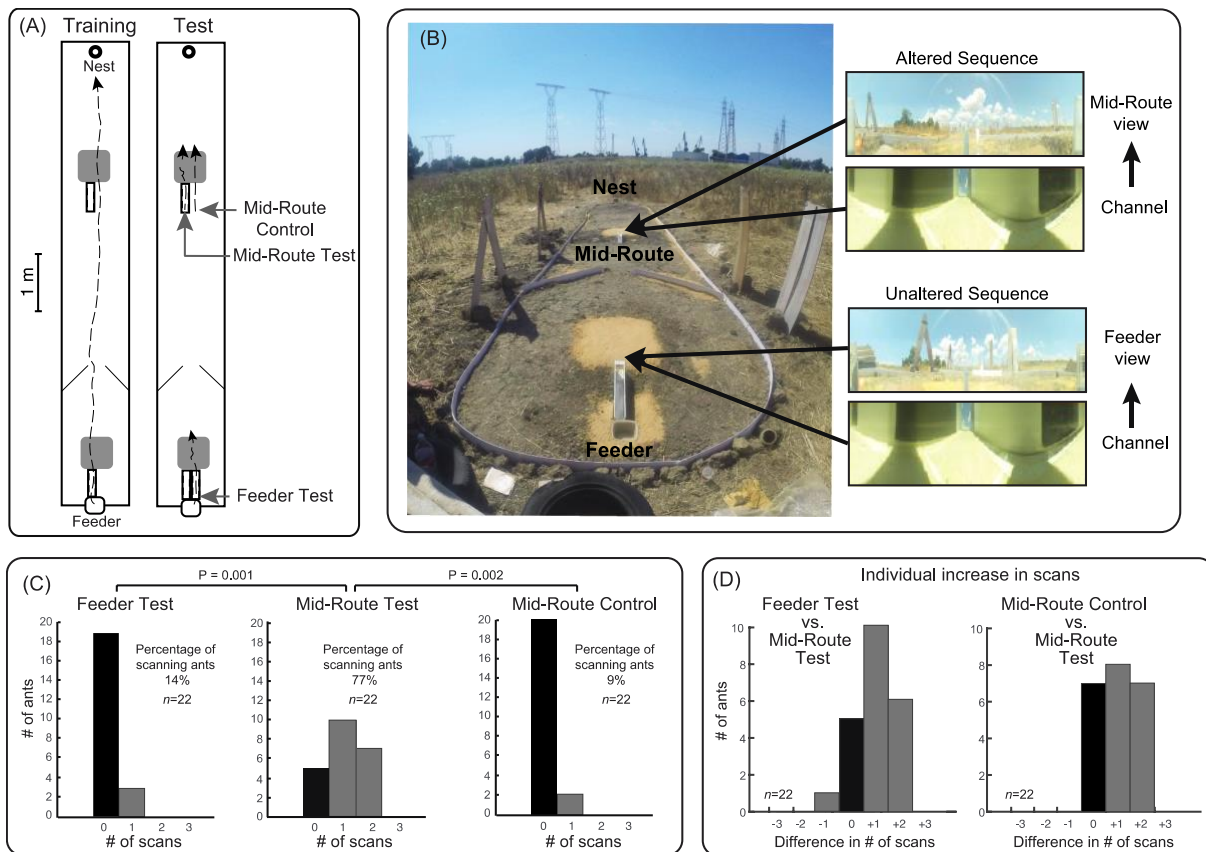
473 **Data availability.** All data generated or analysed during this study are included in this  
474 published article (and its Supplementary information).

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476

477 **Fig. 1. Experiment 1.** (A) Schematic aerial view of the experimental set-up with training and  
 478 testing conditions. Ants were limited to follow a one-way foraging route between the nest  
 479 and feeder. The feeder was connected to a channel that all ants had to pass to before they  
 480 could return back to the nest along a zigzag-shaped inbound route. During tests zero-vector  
 481 ants were transferred to one of three release points (Feeder Test, Mid-Route Test, Mid-  
 482 Route Control) and their scanning behaviour was recorded in the designated test areas (grey  
 483 quadrants). Dashed arrows indicate example paths of training and testing and black lines  
 484 within the route depict baffles. (B) Schematic of test channel and data recording. All  
 485 channels in training and testing were lopsidedly placed onto the ground with an approx. 30°  
 486 slope. Tested ants were released in the channel and their subsequent scanning behaviour in  
 487 the test area (grey quadrant) was recorded with a small camera at the top end of the  
 488 channel. (C) Photographs of the experimental set-up with panoramic images from within the  
 489 test channel, the Feeder- (unaltered view sequence) and the Mid-Route view (altered view  
 490 sequence). Dashed line framing the set-up indicates the part of the route used in the  
 491 experiment. (D) Results of the Feeder Test, Mid-Route Test and Mid-Route Control. Ants  
 492 scanned significantly more at the Mid-Route Test as compared to the Feeder Test (GLM:  
 493  $P=0.026$ ,  $Z=-2.357$ ) but did not reach a significant difference when compared to Mid-Route  
 494 Control (GLM:  $P=0.215$ ,  $Z=-1.272$ ). (E) Results of the Novel Channel Test. Ants showed no  
 495 difference in scanning behaviour between Feeder and Mid-Route release points (GLM:  
 496  $P=0.932$ ,  $Z=0.097$ ).



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**Fig. 2. Experiment 2.** (A) Schematic aerial view of the experimental set-up with training and testing conditions. Ants were trained to forage on a route between the nest and feeder. The feeder was connected to a channel that all ants had to pass to before they could return back to the nest. During tests zero-vector ants were transferred to one of three release points (Feeder Test, Mid-Route Test, Mid-Route Control) and their scanning behaviour was recorded in the designated test areas (grey quadrants). Dashed arrows indicate example paths of training and testing and black lines within the route depict baffles. (B) Photographs of the experimental set-up with panoramic images from within the test channel, the Feeder (unaltered view sequence) and the Mid-Route view (altered view sequence). (C) Results of the Feeder test, Route test and Route Control. Each ant was tested at all three release points. Ants scanned significantly more at the Mid-Route release as compared to the Feeder (GLM:  $P=0.001$ ,  $Z=-3.502$ ) and Mid-Route Control (GLM:  $P=0.002$ ,  $Z=-3.166$ ) release points. (D) Increase of scans of individual ants compared between Feeder and Mid-Route release as well as Mid-Route Control and Mid-Route release points.

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