

1 **How do backward walking ants (*Cataglyphis velox*) cope with navigational**  
2 **uncertainty?**

3

4 Sebastian Schwarz<sup>1</sup>, Leo Clement<sup>1</sup>, Evripides Gkaniias<sup>2</sup>, Antoine Wystrach<sup>1</sup>

5

6 <sup>1</sup>Centre de Recherches sur la Cognition Animale, CNRS, Université Paul Sabatier,  
7 Toulouse 31062 cedex 09, France

8

9 <sup>2</sup>School of Informatics, The University of Edinburgh, Crichton Street 10, Edinburgh  
10 EH8 9AB, U.K.

11

12

13

14

15 Address of correspondence:

16 Sebastian Schwarz

17 Université Paul Sabatier

18 Centre de Recherches sur la Cognition Animale, CNRS

19 31062 Toulouse

20 Email: [sebastian.schwarz@univ-tlse3.fr](mailto:sebastian.schwarz@univ-tlse3.fr)

21 Phone: +33561558444

22

23

24 **ABSTRACT**

25 Current opinion in insect navigation assumes that animals need to align with the goal  
26 direction to recognise familiar views and approach it. Yet, ants sometimes drag  
27 heavy food items backward to the nest and it is still unclear to what extent they rely  
28 on visual memories while doing so. In this study displacement experiments and  
29 alterations of the visual scenery reveal that ants do indeed recognise and use the  
30 learnt visual scenery to guide their path while walking backward. In addition, the  
31 results show that backward homing ants estimate their directional certainty by  
32 combining visual familiarity with other cues such as their path integrator and the time  
33 spent backward. A simple model that combines path integration with repulsive and  
34 attractive visual memories captures the results.

35

36 **Keywords:** ants, backward movement, navigation, peeking, route following,  
37 uncertainty, view-based navigation

38

39

40

## 41 INTRODUCTION

42

43 Central place foragers – such as desert ants – exhibit formidable navigational  
44 skills to find food and their way back home during numerous daily foraging trips  
45 (Collett, Graham, & Durier, 2003; Heinze, Narendra, & Cheung, 2018; Wehner,  
46 2003). These ground dwellers rely on a set of navigational strategies such as path  
47 integration (PI) (Wehner & Srinivasan, 2003; Wittlinger, Wehner, & Wolf, 2006) and  
48 visual scene navigation (Cheng, Narendra, Sommer, & Wehner, 2009; Zeil, 2012).  
49 The literature agrees that ants continuously integrate the directional dictates of these  
50 different strategies together, rather than switching between them (Collett, 2012;  
51 Hoinville & Wehner, 2018; Legge, Wystrach, Spetch, & Cheng, 2014; Reid,  
52 Narendra, Hemmi, & Zeil, 2011; Wystrach, Mangan, & Webb, 2015).

53 Current models of insect visual navigation capture well the behaviour of  
54 forward navigating ants (Baddeley, Graham, Husbands, & Philippides, 2012;  
55 Hoinville & Wehner, 2018; Wystrach, Beugnon, & Cheng, 2011; Wystrach, Cheng,  
56 Sosa, & Beugnon, 2011; Zeil, 2012) however, how ants navigate while dragging a  
57 heavy food item backward remains unclear (Ardin, Mangan, & Webb, 2016; Pfeffer &  
58 Wittlinger, 2016; Schwarz, Mangan, Zeil, Webb, & Wystrach, 2017). Despite their  
59 irregular backward foot strides the ants' PI system seems as accurate as during  
60 forward movement (Pfeffer, Wahl, & Wittlinger, 2016; Pfeffer & Wittlinger, 2016),  
61 however, guidance based on terrestrial visual cues seems disrupted (Schwarz et al.,  
62 2017). Evidence suggests that to recognise the familiar terrestrial scenery ants need  
63 to align their body in the familiar forward direction (Narendra, Gourmaud, & Zeil,  
64 2013; Wystrach, Cheng, et al., 2011; Zeil, 2012). This is probably why ants dragging  
65 a food item backward occasionally display a so-called 'peeking' behaviour: the ant  
66 stops pulling, drops its food item and turns around to look forward. If the scenery is  
67 familiar, the ant quickly returns to her food item and adjusts her backward path in the  
68 newly corrected homing direction. It seems clear that during these few moments  
69 facing forward in a familiar direction, ants recover and store the correct direction; and  
70 subsequently rely on celestial cues to maintain this new bearing when traveling  
71 backward (Schwarz et al., 2017). In this case navigation is discretised into different  
72 sources of information being used sequentially rather than simultaneously. Also,  
73 'peeking' involves the decision to trigger a distinct and observable behaviour when

74 navigational information is needed. This behaviour therefore provides a good  
75 opportunity to investigate how ants estimate their navigational uncertainty and as a  
76 corollary, which navigational information they have access to.  
77 Here two experiments with backward walking ants were carried out to investigate the  
78 following questions: (1) Can ants still perceive visual familiarity when walking  
79 backward? (2) How can this visual information enable ants to control their backward  
80 path. (3) Which information is used by ants to estimate uncertainty and trigger a  
81 peeking behaviour?

82

## 83 **METHODS**

84

### 85 **Study animal and site**

86

87 The experiments were carried out with Spanish desert ants *Cataglyphis velox*  
88 on a field site with diverse grass and bush vegetation at the outskirts of Seville during  
89 June 2017 and 18. *Cataglyphis velox* show typical characteristics of a desert ant  
90 such as diurnality, thermophily and solitary foraging (Cerdeira, 2001). As in other ant  
91 species, navigation and orientation in *C. velox* is predominantly based on vision  
92 derived from terrestrial and celestial cues (Mangan & Webb, 2012; Wystrach et al.,  
93 2015).

94

### 95 **General methods**

96 Two experiments were conducted: Experiment 1 in 2017 and Experiment 2 in  
97 2018. Both set-ups shared the following methods.

98 Ants were restricted to forage on a straight route between their nests and a  
99 feeder. The routes were mostly cleared from vegetation and enclosed by thin white  
100 plastic planks (10 cm high) that were dug halfway into the ground. The slippery  
101 surface of the planks prevented ants foraging elsewhere while minimising the  
102 obstruction of surrounding views (Wystrach, Beugnon, & Cheng, 2012). Ants could  
103 freely travel between nest and feeder, which was a ~15×15×15 cm plastic bowl sunk  
104 into the ground that contained several kinds of sweet buttery biscuit crumbs. The  
105 walls of the bowl were covered with a thin layer of Fluon® and prevented ants from  
106 climbing. Ants that dropped into the feeder and picked up a crumb were marked

107 individually with coloured acrylic or enamel paint (Tamiya™). During training, ants  
108 could leave the feeder via a small wooden ramp. Ants were considered trained and  
109 ready for testing once they had performed at least five foraging runs and were able to  
110 reach the feeder from the nest in a straight line (without colliding into any barriers).  
111 During tests (see below) the feeder ramp was removed to prevent other homing ants  
112 from interfering.

113

## 114 **Experiment 1**

115

116 Experiment 1, conducted during summer 2017, entailed a nest at the  
117 beginning of a straight 8×1.8 m long foraging route. Three large wooden boards  
118 (2.4×1.2 m) were connected (7.2×1.2 m) and placed onto the foraging route. These  
119 boards enhanced the tarsi grip of the ants and provided an even substrate that  
120 minimised potential interference with small grass haulms or pebbles during tests  
121 when ants dragged their food items backward (Fig. 1a).

122 During training, the individually marked foragers scuttled (forward) between  
123 the nest and feeder over the connected boards and familiarised themselves with the  
124 visual surroundings. After training, individual ants were subjected to one test  
125 conditions. All tests comprised of a forager that dragged a large biscuit crumb  
126 backward. For that, trained foragers with a small food item (~0.2×0.2×0.2 cm) were  
127 caught and transferred into a plastic vial. The food item was carefully and manually  
128 removed and a larger biscuit piece (~2.0×0.5×0.2 cm) was offered to the ant instead.  
129 The biscuit provided was large enough to force the ants to drag it backward. After the  
130 ant locked mandibles onto the large biscuit, she was transferred to the appropriate  
131 release point. Four possible test conditions were carried out with either FV- (i.e., ants  
132 with their PI vector information, captured at the feeder) or ZV-ants (i.e., foragers  
133 without PI information captured just before they enter the nest; Fig. 1a). To test the  
134 effect of the level of visual familiarity in backward movements, ants were either  
135 released at the familiar feeder (FV) or at the feeder with unfamiliar visual  
136 surroundings (FVU). A few seconds after the FVU-ant had started to home backward  
137 the visual surroundings were altered by adding large black plastic bags (~0.8×0.6 m)  
138 on one side and a large dark tarp (0.9×3.4 m) on the other side of the route. The  
139 objects were always placed parallel to the backward path of the ants to avoid

140 behavioural interferences and potential obstructions. To test the effect of route  
141 location, backward moving ants were tested either at the feeder (beginning of the  
142 route; ZV) or at the middle of the route (ZVmid).

143

#### 144 **Experiment 1: data and analysis**

145

146 For all tests, the distance between the release point and the location at which  
147 peeking behaviours occurred was noted. Tests ended as soon as the backward  
148 walking ant reached the end of the wooden boards (i.e., ~0.5 m in front of the nest  
149 entrance) or abandoned her food item for more than one minute. Individual ants were  
150 tested only once per test but were subjected to different test conditions with at least  
151 one un-interfered training trial between tests. The sequence of tests was evenly  
152 counter-balanced across individuals.

153 Comparison were made between FV- vs. FVU-ants and ZV- vs. ZVmid-ants  
154 (Fig. 1a). Given the large inter-individual variations, paired-data was applied and thus  
155 only ants that were tested on both FV and FVU or ZV and ZVmid conditions,  
156 respectively were kept for analysis. Both the distance at which the first peeking  
157 behaviour occurred (1<sup>st</sup> peek distance) and the overall peek rate of individuals (i.e.,  
158 number of peek/distance walked) were compared using Wilcoxon ranksum tests a  
159 nonparametric statistic for paired data (Matlab™, Mathworks, Matick, MA, USA).  
160 Given that all ants walked rather straight toward the nest along the route, distance  
161 walked could be simply approximated by the beeline distance walked along the route.  
162 Most ants walked the full route (7.2 m) except obviously ants in the ZVmid condition  
163 and some foragers that abandoned their biscuit. For the comparison of peek rate, the  
164 7.2 m long route was divided approx. into half (Section 1: 0 - 3.4 m; Section 2: 3.4 -  
165 7.2 m; Figure 1A). Thus, during ZVmid tests ants ran only Section 2. Comparisons  
166 between ZV- vs. ZVmid-ants were conducted to separate the effect of distance  
167 walked (i.e., ZVmid vs. ZV on Section 1) from the actual location along the route (i.e.,  
168 ZVmid vs. ZV on Section 2). Bayesian statistics were applied to evaluate which of  
169 these alternative hypotheses explain peek rate best.

170 Backward paths were recorded by using GoPro HERO3+ cameras which were  
171 manually held approx. 0.6 m above the tested ant. Therefore, a quantification of the  
172 movement speed of the ants before and after peeking could be calculated. For that

173 the relative distance walked by the backward ants during the five seconds preceding  
174 the onset of the first peek (i.e., before the moment when the ants released the  
175 biscuit) and five seconds after the peek (i.e., after the ant resumed backward motion)  
176 was estimated.

177

## 178 **Experiment 2**

179

180 Experiment 2 was conducted in the summer months of 2018 with two different  
181 nests of *C. velox* ants. For each nest, a 5.0×2.0 m straight foraging route was built  
182 with the nest entrance at one end and the feeder at the other end (Fig. 2a). As in  
183 Experiment 1, the route was enclosed by white plastic planks and ants were given a  
184 choice of biscuit crumbs inside the feeder to prompt foraging. However, here the ants  
185 scuttled back and forth directly on the natural ground during training. Once trained  
186 (see General methods), individual ants were captured on their way home 0.5 m  
187 before reaching their nest and subsequently released at one out of four possible  
188 locations (Fig. 2a):

189 Feeder (F): Ants were released 0.5 m after the feeder.

190 Before nest (BeN): Ants were released on the route, 0.5 m before their nest.

191 Beyond nest (ByN): Ants were released 0.5 m beyond the nest in the feeder-nest  
192 direction.

193 Unfamiliar (U): Ants were released ~30.0 m away from the nest in a visually  
194 unfamiliar location.

195 For all tests, ants were captured in a plastic vial, offered a large biscuit crumb  
196 to incite backward walking and, once the ant had grabbed the cookie, released within  
197 a lampshade at the middle of a large wooden board (2.4×1.2 m). Individual ants were  
198 tested only once per test, but could be subjected to different tests conditions, with at  
199 least one un-interfered training trial between tests. The wooden board was set in  
200 place just before and removed just after each test. The board was centred on the  
201 current release location with the long side along the feeder-nest direction (Fig. 2a) as  
202 it represents the expected homing direction. The board provided an even substrate  
203 during tests and prevented ants to use potential familiar olfactory cues from the  
204 ground or the nest (BeN and ByN tests). A grid pattern (0.25×0.25 m) drawn on the  
205 board enabled paths to be transcribed onto gridded paper. The lampshade (beige

206 opaque fabric, 0.5 m diameter; 0.4 m height) surrounded the ant upon release and  
207 obstructed any familiar terrestrial views; the top of the lampshade was open providing  
208 the ant with celestial compass cues. Once the ant had pulled the large crumb  
209 backward for 0.1 m, the lampshade was lifted and the visual surrounding was  
210 revealed. This ensured that the ants could not utilise any familiar scenes before  
211 starting their backward path.

212 The backward paths and locations of peeking behaviour were noted. For each  
213 peek, the duration (i.e., the time the ant was not dragging the biscuit) was recorded  
214 but not the forward paths during the peek itself. Recording continued until the ants  
215 either reached the edge of the board or abandoned their large crumb for more than 1  
216 min.

217

## 218 **Experiment 2: data and analysis.**

219

220 The recorded paths were digitised as (x, y) coordinates using GraphClick (Arizona  
221 Software). Path characteristics such as direction, meander (for details see Schwarz,  
222 Albert, Wystrach, & Cheng, 2011) and peek location were computed and analysed  
223 with Matlab™ (Mathworks, Matick, MA, USA). Differences between test locations  
224 were determined using a generalised linear mixed effect model with repeated ants as  
225 random effect and Tukey's post hoc corrections. For peek durations, a model for  
226 proportional (binomial) data was applied with 0 to 60 s (the duration at which we  
227 stopped recording) reported between 0 and 1.

228

## 229 **RESULTS**

230

### 231 **Experiment 1**

232

233 In this experiment ants were free to scuttle forward along an 8.0 m straight route  
234 between the nest and a feeder to become familiarised with the visual scenery of the  
235 route. For tests, trained homing ants were captured either directly at the feeder (FV-  
236 ants) or upon reaching their nest (ZV-ants). Captured ants were given a large biscuit  
237 crumb that had to be dragged backward along the route home (Fig. 1a) and the  
238 occurrence of peeking behaviour was recorded.



239

240 *FV vs. ZV: effect of path integration*

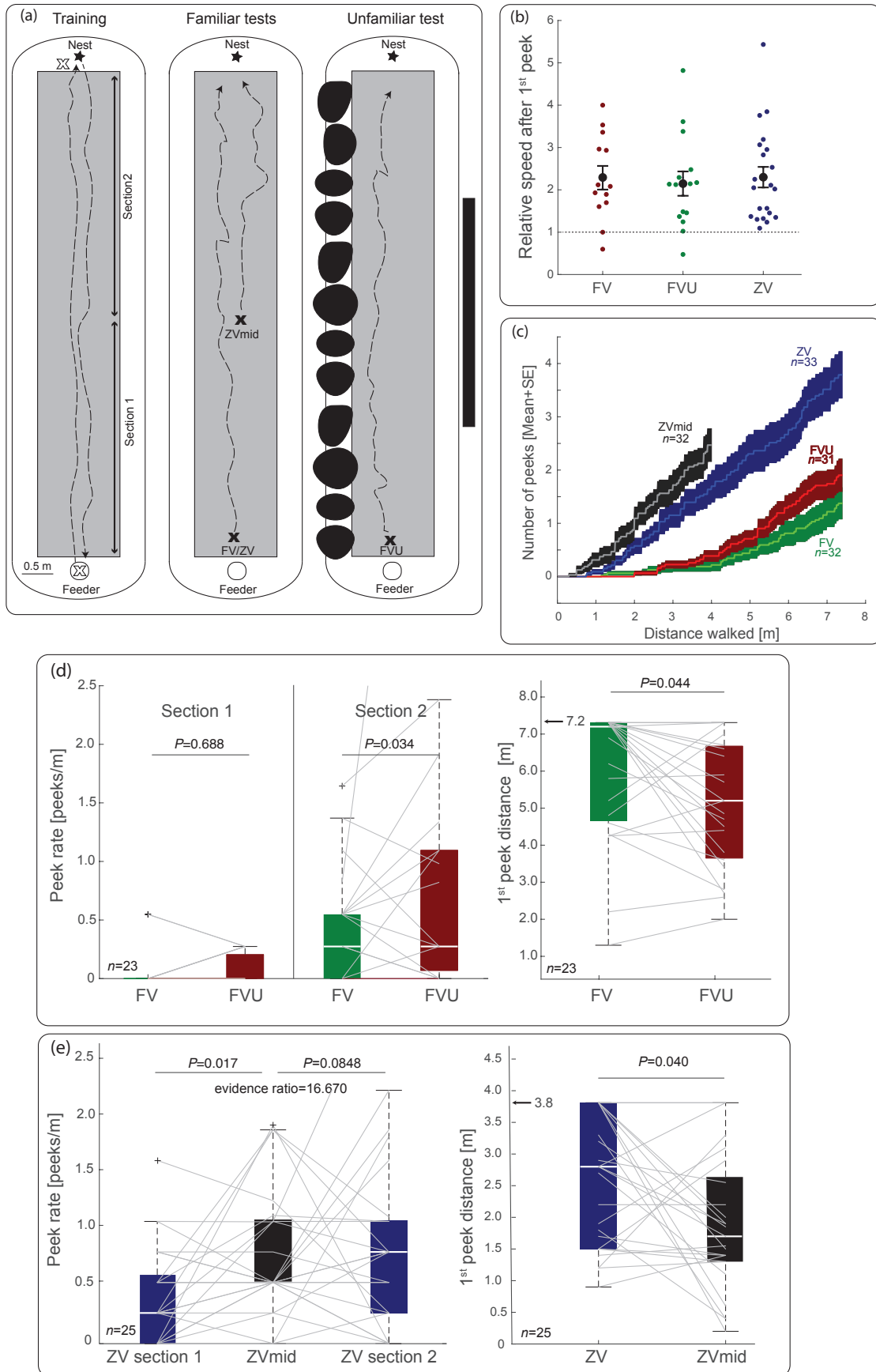
241

242 In both FV and ZV conditions, ants started to pull their biscuit toward the nest and  
243 mostly maintained that direction. The ability of ZV-ants to do so suggests that the  
244 foragers were able to perceive the familiar terrestrial cues although they might have  
245 had a chance to take a glimpse forward upon release and before starting their  
246 backward movements. In any case, the PI state had a strong effect. As seen by the  
247 standard errors of the data population, ZV-ants peeked earlier (first peek distance  
248 ZV-ants:  $M \pm SD = 3.28 \pm 2.19$  m; FV-ants:  $M \pm SD = 5.90 \pm 1.93$  m) and thrice as much  
249 (overall peek rate ZV-ants:  $M \pm SD = 0.63 \pm 0.63$  peek/m; FV-ants:  $M \pm SD = 0.19 \pm 0.29$   
250 peek/m) than FV-ants (Fig. 1c). Also, ZV-ants occasionally abandoned their large  
251 food item and did not resume backward movements (6 out of 33), whereas no FV-  
252 ants abandoned theirs (0 out of 32). A Fisher's exact test verified a significant  
253 difference ( $P = 0.032$ ). It seems clear that a lack of (or conflicting) PI information  
254 decreases the ants' directional certainty.

255

256

257



259 **Figure1.** Dynamics of peeking behaviours in terms of path integration and visual  
260 familiarity (Experiment 1). (a) Schematics of experimental set-up with training and  
261 test conditions. During training ants foraged between nest and feeder (~8.0 m) on  
262 three thin wooden boards serving as an even substrate (grey rectangles). The route  
263 was divided into two sections corresponding to the first and second half of the route.  
264 For tests, trained ants were either captured at the feeder (full-vector ants, FV) or just  
265 before entering the nest after foraging (zero-vector ants, ZV; open crosses) and  
266 released at the feeder (as FV- FVU or ZV-ants) or on the middle of the route (ZVmid-  
267 ants; black crosses). For FVU (unfamiliar), the familiarity of the route was  
268 manipulated by adding large black visual objects (black blobs) on one side and a  
269 dark tarp (black vertical bar) on the other side of the route. Dashed lines depict  
270 example paths of the ants. (b) Change in speed after the first peek. Each dot shows  
271 the relative change in speed (5s after/5s before) the first peek for each ant. Dotted  
272 line at 1 indicates no change in speed. Almost all ants increase their speed after their  
273 first peek. (c) Cumulated number of peeks displayed against the distance walked  
274 along the route ( $M \pm SE$  across individuals). A clear separation between FV- and ZV-  
275 ants is visible where ZV-ants peek earlier than FV-ants. (d) Overall peek rate (left)  
276 and distance of the first peek (right) for both FV-ant conditions. FV-ants peek less  
277 often than FVU-ants in Section 2 and travel a longer distance before displaying their  
278 first peek. 7.3 m indicates the end of the route. (e) Overall peek rate (left) and  
279 distance of the first peek (right) for both ZV-ant conditions. ZVmid-ants peek more  
280 often than ZV-ants from Section 1 but not from Section 2 (Bayesian evidence ratio  
281 strongly favour similarity with Section 2). ZVmid-ants travel a shorter distance before  
282 first peek as compared to ZV-ants. 3.8 m indicates the end of the route (ZV-ant paths  
283 were truncated at 3.8 m to match the maximum homing distance of ZVmid-ants).  
284 Grey lines (d, e) represent individually tested ants across conditions. See main text  
285 for statistical details.

286

### 287 *FV vs. FVU: effect of visual unfamiliarity*

288

289 To test the potential effect of the level of visual unfamiliarity on backward walking  
290 ants, two conditions were conducted: (1) FV-ants homing backward on the unaltered,  
291 usual route, and (2) Full-Vector-Unfamiliar (FVU) ants, homing backward on the  
292 same route but this time the visual surrounding was altered by additional large black  
293 plastic bags (~0.8×0.6 m) and a rectangular dark tarp (0.9×3.4 m) on each side of the  
294 route (Fig. 1a). The objects were added only after the tested FVU-ants had started  
295 their backward path to ensure that they could not monitor the visual change before  
296 engaging in dragging the biscuit. If ants trigger peeks because of navigational  
297 uncertainty then they should peek more often in unfamiliar environments. Results  
298 confirm the prediction.

299 First, FVU-ants peeked more often than FV-ants. However, this effect was weak,  
300 and reaches significance only in Section 2 (Wilcoxon ranksum test:  $P = 0.027$ ,  $Z =$

301 3.751) but not in Section 1 of the route (Wilcoxon ranksum test:  $P = 0.688$ ,  $Z \sim 0$ ; Fig.  
302 1d), due to a statistical floor effect. Indeed, a low rate of peeking in the first section of  
303 the route was expected, given that the path integration vector is longer and thus  
304 stronger at the beginning of the route home (Wystrach et al., 2015).

305 Second and most importantly, FVU-ants travelling in the unfamiliar environment  
306 displayed their first peek earlier along the route as compared to FV-ants on the  
307 familiar route (Wilcoxon ranksum test:  $P = 0.044$ ,  $Z = 2.016$ ; Fig. 1d). The results  
308 suggest that ants could perceive the difference in visual familiarity while walking  
309 backward given that the visual surrounding was altered only after the ants had  
310 started they journey backward,

311 As for ZV-ants (see above), FVU-ants tested in the unfamiliar condition  
312 abandoned their biscuits significantly more than FV-ants (FVU: 6 out of 31 vs. FV: 0  
313 out of 32. Fisher's exact test:  $P = 0.022$ ). Here again, it seems that visual  
314 unfamiliarity decreases directional certainty of backward walking ants.

315

#### 316 *ZV vs ZVmid: effect of location*

317 We investigated the potential effect of the location along the route by releasing zero  
318 vector ants either at the beginning of the familiar route (ZV) or directly in the middle  
319 of the familiar route (ZVmid; Fig. 1a, c). Consequently, ZVmid-ants walked only  
320 Section 2, while ZV-ants moved along both sections. Ants displayed their first peek  
321 on average slightly earlier when released at the middle of the route (ZVmid) than  
322 when released at the beginning of the route (ZV; Wilcoxon ranksum test:  $P = 0.040$ ,  
323  $Z = 2.062$ ; Fig. 1e). Also, the peek rate displayed by ZVmid-ants along Section 2 (the  
324 only section they walked) was higher than ZV-ants along Section 1 (Wilcoxon  
325 ranksum test:  $P = 0.005$ ,  $Z = -2.814$ ) but similar to the peek rate displayed by these  
326 ZV-ants along Section 2 of the route (Wilcoxon ranksum test:  $P = 0.796$ ,  $Z = -$   
327  $0.2585$ ; Fig. 1e). A Bayesian evidence ratio was computed to estimate whether  
328 Section 1 or Section 2 of ZV-ants' peek rate resembles most ZVmid-ants' peek rate.  
329 The obtained evidence ratio was 50.74 in favour of Section 2, which equals  
330 'overwhelming evidence' for an effect on peek rate of the actual location along the  
331 route rather than the distance walked.

332

#### 333 *Peeking and walking speed*

334 Interestingly, in all conditions, and for the vast majority of the individuals, ants walked  
335 backward on average twice as quickly after peeking than before peeking (Fig. 1b).  
336 This supports the idea that a peeking event increases the ant's directional certainty  
337 for some time.

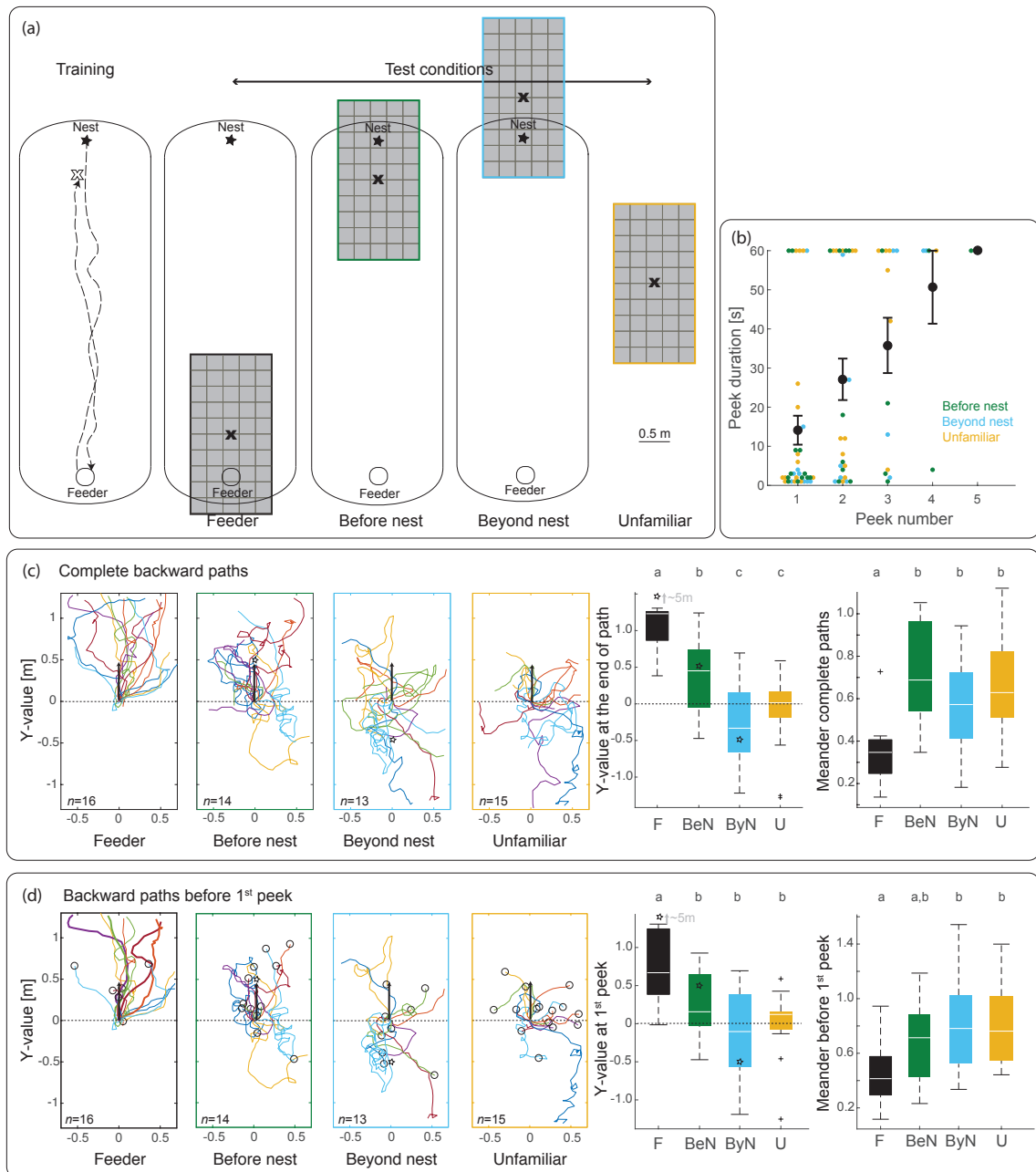
338

## 339 **Experiment 2**

340

341 In this experiment, homing foragers were trained along a route, captured 0.5 m  
342 before they reached their nest, provided with a large biscuit crumb and released on  
343 top of a wooden board (Fig. 2a) at different test locations: namely, 0.5 m after the  
344 feeder (F), 0.5 m before the nest (BeN), 0.5 m beyond the nest (ByN) and at a distant  
345 unfamiliar location (U) ~30.0 m away (Fig. 2a). Crucially, in this experiment all tested  
346 ants were prevented from monitoring the visual surrounding before dragging their  
347 food item backward as a lampshade was blocking the whole panoramic view (see  
348 Methods). Hence, any evident effect of the scenery on the backward path must result  
349 from visual information perceived while the ants were dragging their crumb backward  
350 – at least until they peeked for the first time.

351



352

353 **Figure 2.** Backward path characteristics and peeking behaviour at different release  
 354 points (Experiment 2). (a) Schematics of experimental set-up with training and  
 355 test conditions. During training ants foraged between nest and feeder (~5.0 m). Trained  
 356 ants with a remaining homing vector of 0.5 m (open cross depicts capture point) were  
 357 tested backward at different release points: feeder (F), before nest (BeN), beyond  
 358 nest (ByN) and unfamiliar (U) test site. Ants were released (black crosses) on the  
 359 middle of a thin wooden board (grey) to rule out the use of olfactory cues. Boards  
 360 had a 0.25×0.25 m squared pattern to enable path recording. Dashed lines depict  
 361 example paths of ants during training. (b) Duration of peek (the time the ant spent  
 362 away from the cookie) as a function of peek number for each individual. Regardless  
 363 of test condition, peek duration increases with number of peeks. Max. threshold of  
 364 peek duration was set to 60s and 'Feeder condition' was removed from this analysis  
 365 as peek number correlates with position along the board. (c) Complete recorded  
 366 backward paths of ants across conditions. Paths ended either because ants left the

367 board or abandoned their cookie (peek duration > 60s). Boxplots show distance  
368 reached at the end of the path along the feeder nest axis (Y axis) and meander of the  
369 paths across individuals. Differences in top letters (a, b, c) indicate significant  
370 differences between groups ( $\alpha=0.05$ ). Except for unfamiliar (U) all other  
371 conditions were directed toward the actual nest position, showing that ants used  
372 familiar visual cues. Black dotted lines depict release point, black arrows remaining  
373 vector length (0.5 m) and open stars actual nest position. (d) As in (c), except that  
374 paths were truncated at the first peek or when exiting the board. Hence all  
375 navigational information gathered by ants was obtained while walking backward.  
376 Thick paths (left panel) emphasise four ants in the feeder conditions that displayed  
377 nest-directed backward paths without facing the nest direction. Open circles  
378 represent positions of 1<sup>st</sup> peeks. For statistical details see text.  
379

### 380 *Ants can guide their backwards path*

381

382 Analysis of the complete paths trajectory revealed differences between test  
383 conditions. The Y-values – the position along the feeder-to-nest line – at the end of  
384 the foragers' path varied across conditions (ANOVA:  $F=21.96$ ,  $P<0.001$ ; Fig. 2c).  
385 Ants from the feeder test displayed paths directed toward the nest and hence  
386 obtained higher Y-values at the end of their recorded paths than any other conditions  
387 (Tukey's post-hoc test F vs. BeN, ByN and U:  $Zs > 3.75$ ,  $Ps < 0.001$ ; Fig. 2c). Ants in  
388 unfamiliar tests showed no directional preference along the Y-axis (Fig. 2c), as  
389 expected given the lack of familiar visual information at this location. Interestingly,  
390 ants from BeN and ByN conditions differed significantly in their final Y-values on the  
391 board (Tukey's post-hoc test BeN vs. ByN:  $Z = 3.47$ ,  $P = 0.003$ ). The medians of both  
392 of these groups are close to the actual nest location, showing that they used familiar  
393 visual cues to search at the nest (Fig. 2c). Differences between conditions could also  
394 be observed in path meander (ANOVA:  $F=9.07$   $P < 0.001$ ). Ants from the feeder test  
395 showed straighter paths than ants from all other conditions (Tukey's post-hoc test F  
396 vs. BeN, ByN and U:  $Zs > 3.68$   $Ps < 0.002$ ; Fig. 2c). No difference in meander among  
397 the remaining test conditions could be determined. Indeed, BeN, ByN and U ants  
398 were expected to search on the board: BeN- and ByN-ants due to the proximity of the  
399 nest and U-ants due to the of the lack of familiar visual information. Overall, these  
400 data show that ants could use familiar visual cues to adequately direct their backward  
401 paths.

402 Remarkably, analysis of the paths displayed before the first peek (or until the ant  
403 left the board if she did not peek) showed a similar pattern of results for both distance

404 reached along the Y-axis (ANOVA:  $F = 11.37$   $P < 0.001$ ) and path meander (ANOVA:  
405  $F = 3.52$   $P = 0.024$ ). Ants released at the feeder travelled significantly longer  
406 distances along the feeder-nest direction before peeking than all other test conditions  
407 (Tukey's post-hoc test: F vs. BeN, ByN and U:  $Z_s > 3.29$   $P_s < 0.006$ ; Fig. 2d) and  
408 displayed straighter paths (Tukey's post-hoc F vs. ByN and U:  $Z_s > 2.65$   $P_s < 0.03$ ; F  
409 vs. BeN:  $Z = 1.88$   $P = 0.235$ ; Fig. 2d). The three other groups (BeN, ByN, U) were  
410 expected to search on the board and to perform a similar level of path meander.  
411 Differences in the feeder-nest distance between these conditions (BeN, ByN, U) were  
412 not significant using Tukey's post-hoc test. However, the pattern of results followed  
413 what was expected if ants were using views to direct their path toward the nest. Ants  
414 released before (BeN) and beyond (ByN) their nest both moved on average toward  
415 the nest location, that is, in opposite direction from their release points; and ants  
416 released at the unfamiliar test site (U) showed less directed paths (Fig. 2d). The  
417 differences in paths characteristics is also reflected if one considers the probability of  
418 obtaining the expected order of path endpoint across the four test conditions (Y-  
419 value:  $F > \text{BeN} > \text{U} > \text{ByN}$ ) is  $1/4! = 0.042$ . Interestingly, several ants released at the  
420 feeder (4 out of 16 ants) displayed nest-directed backward paths across the whole  
421 recording board without performing a single peek and by keeping their body  
422 orientation away from the feeder-nest direction by at least  $90^\circ$  (bold paths in Fig. 2d).

423 Because nest-directed path sections were achieved before the ants triggered their  
424 first peek and the visual panorama was revealed to them only after they had started  
425 backward motion, the differences across locations show that ants can recognise and  
426 use the familiar visual cues to guide their path while moving backward and without  
427 the need of peeking.

428

#### 429 *Peek duration and past information*

430

431 We also tested whether peek duration was influence by the test condition and the  
432 number of previously displayed peeks (Fig. 2b). The feeder condition was excluded  
433 from this analysis as these ants were expected to move in a straight line and exit the  
434 board so that the actual peek number of a given ant may correlate with the location  
435 where the ant peeks instead of being based on the previous peek(s): the higher the  
436 peek number the larger the distance from the feeder. The three other groups (BeN,



437 ByN, U) on the other hand, are expected to search on the board so any effect of the  
438 peek number is unlikely to be attributed to a specific location on the board.  
439 Interestingly, peek duration, which was recorded up to 60 s, was strongly influenced  
440 by the number of peeks previously displayed by the ant (GLM peek number:  $F =$   
441  $17.09$ ,  $P < 0.001$ ; Fig. 2b) and not the actual test condition (GLM condition:  $F = 0.17$ ,  
442  $P = 0.841$ ; Fig. 2b). The more peeks an ant had previously displayed the longer its  
443 current peeking duration. This shows that the ant's peeking behaviour is modulated  
444 by past information but whether it is the time passed or the number of peek  
445 previously displayed cannot be disentangled here.

446

## 447 **DISCUSSION**

448

449 Ants dragging a heavy food item backward occasionally trigger a so-called  
450 'peeking behaviour' or 'peek': ants drop their food and turn around to look forward.  
451 Aligning their body in a familiar direction enables them to recognise the learnt visual  
452 panorama and hence adjust the direction of their subsequent backward path  
453 (Schwarz et al., 2017). It is clear that ants gain directional information from learnt  
454 terrestrial cues when peeking forward. However, whether or not they can recognise  
455 terrestrial cues while dragging their food item backward is less clear. Several of the  
456 current results demonstrate that ants are indeed able to do so, raising question about  
457 the underlying mechanisms.

458

### 459 **Ants still recognise terrestrial cues while walking backwards**

460

461 Experiment 1 shows that the visual scenery experienced while walking backwards  
462 influenced the occurrence of peeking behaviour. First, ZVmid-ants displayed their  
463 first peek earlier when starting their backward journey halfway along the route rather  
464 than ZV-ants at the beginning of the route (Fig. 1e). Second, FV-ants displayed their  
465 first peek earlier along the route if the surrounding scenery was artificially altered  
466 (FVU, Fig. 1d). This was true even though the scene was manipulated only after the  
467 ants had started dragging their biscuit backward and thus indicates that ants  
468 perceived the alteration of the familiar scene while walking backward. It should be

469 noted that this effect was weak (Fig. 1d), possibly because the alteration of the scene  
470 was not obvious enough (Schwarz et al., 2014).

471 In Experiment 2, ants could guide their trajectories based on terrestrial cues while  
472 walking backward. Ants were released on a board (ruling out the use of olfactory  
473 cues) and within a lampshade. The visual world was revealed to them once they had  
474 started their backward journey. Nonetheless and despite the lack of PI homing  
475 vector, their paths were oriented in the expected direction (i.e., the nest) resulting in  
476 differences between test conditions. Importantly, this was also true for the portion of  
477 path displayed before their first peek, that is, displayed purely backward (Fig. 2d).

478 In sum, ants can use learnt terrestrial visual cues while walking backward to guide  
479 their path as well as decide whether and when to peek forward. The next section  
480 discusses potential explanations.

481

## 482 **Mental rotation or combining attractive and repulsive views?**

483

484 How can ants recognise views backward? This is a puzzling question given that  
485 the assumption of current models of visual homing states that views must be  
486 retinotopically aligned to provide directional information (Ardin, Peng, Mangan,  
487 Lagogiannis, & Webb, 2016; Baddeley et al., 2012; Collett, Graham, & Collett, 2017;  
488 Möller, 2012; Wystrach, Mangan, Philippides, & Graham, 2013; Zeil, 2003). This idea  
489 seems to be supported by data in freely navigating ants (Narendra et al., 2013;  
490 Wystrach, Cheng, et al., 2011) although some other processes may be also at work  
491 (Wystrach et al., 2012). Recently, it has been suggested that ants may perform some  
492 sort of mental rotation to compare misaligned views (Ardin, Mangan, Wystrach, &  
493 Webb, 2015; Ardin et al., 2016), which could be achieved if views are encoded in the  
494 frequency domain (Stone et al., 2017). But, this idea is hard to reconcile with the  
495 result of previous experiments where ants would not adjust their backward trajectory  
496 at all unless they peeked to align their body in the correct direction (Schwarz et al.,  
497 2017).

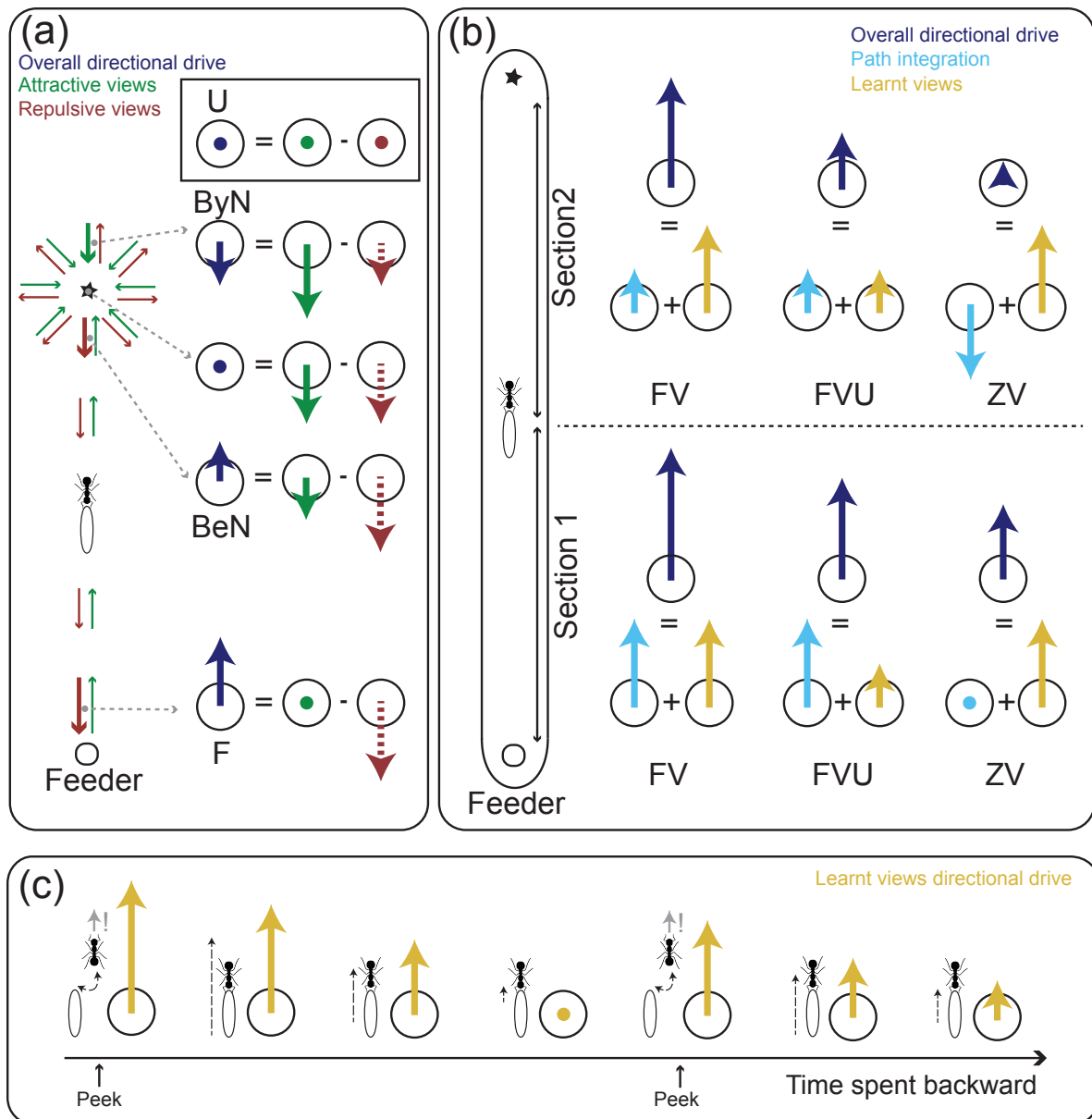
498 Here we suggest an alternative hypothesis to mental rotation: ants may still need to  
499 align their body to recognise views retinotopically but possess a memory bank of  
500 views learnt while facing in multiple directions and not only toward the nest. Notably,  
501 views learnt while facing in the anti-nest direction could be treated as repulsive when

502 homing (Fig. 3a). The familiarities resulting from the comparison of the currently  
503 perceived view with both attractive (nest facing) and aversive (feeder facing) visual  
504 memories could simply be compared in a way somewhat analogous to an opponent  
505 process. The signal resulting from this comparison informs the ant about whether to  
506 move toward or away from the currently faced direction. In addition, homing ants  
507 might use the visual memories stored during their outbound trips (i.e., when they  
508 went from the nest to the feeder) as repulsive. This idea challenges the opinion that  
509 ants treat in- and outbound trip visually separately depending on the motivational  
510 state (Harris, Hempel de Ibarra, Graham, & Collett, 2005; Wehner, Boyer,  
511 Loertscher, Sommer, & Menzi, 2006). Instead, ants may always recall both their  
512 memorised in- and outbound facing views but treat them as repulsive or attractive  
513 depending on their current motivational state.

514 Such a hypothesis explains several observed phenomena of the current study. (1)  
515 In a former experiment (Schwarz et al., 2017) backward ants were not able to correct  
516 their path at all while walking backward because, in this particular set-up, in- and out-  
517 bound routes were spatially separated (as a one-way circuit) so that no outbound  
518 views were available to potentially help out backward homing ants. (2) In the current  
519 Experiment 2, backward ants released at the feeder (F) carried on in the correct nest  
520 direction (Fig. 2d) because they recognised outbound views oriented toward the  
521 feeder, driving them away from (or opposite to) this direction (Fig. 3a). (3) Alteration  
522 of the visual surrounding would trigger earlier peeking behaviours because the  
523 familiarity of the feeder facing (outbound) views would be equally altered, disrupting  
524 the repulsive effect and thus reducing the overall directional drive (Fig. 1d). (4)  
525 Assuming that outbound views near the feeder are more familiar than in the middle of  
526 the route (ants perform learning walks at the feeder: Nicholson, Judd, Cartwright, &  
527 Collett, 1999), the repulsive effect would be stronger for ants released at the feeder  
528 than in the middle of the route, yielding to a stronger directional drive and hence less  
529 peeking near the feeder (Fig. 1d). (5) Further, it was surprising in Experiment 2 that  
530 ants released close to the nest could direct their backward paths toward the nest  
531 (BeN, ByN; Figure 2c, d). Although this verifies that they recognised familiar views  
532 they nonetheless tended to peek often and even abandoned their cookie close to the  
533 nest (9 out of 28 in BeN- and 4 out of 20 in ByN-test). This seems counter-intuitive,  
534 yet it can be explained in the light of the 'repulsive view' hypothesis. During learning

535 walks around the nest, ants appear to store indeed both nest and anti-nest oriented  
536 views (Jayatilaka, Murray, Narendra, & Zeil, 2018). Even if these nest views may be  
537 all extremely familiar, the integration of attractive (nest-oriented) and repulsive (anti-  
538 nest oriented) views would result in a low overall directional drive, which would thus  
539 lead to high peek rates (and a high probability for abandoning the crumb) but  
540 nonetheless guide the ants toward the nest. Fig. 3a illustrates further the functionality  
541 of this simple model. (6) Finally, two recent studies revealed the importance of  
542 outbound trips for homing ants. Ants with outbound views during training were more  
543 efficient in homing than ants with only inbound views during training (Freas & Cheng,  
544 2018; Freas & Spetch, 2019). But whether homing ants actually used their outbound  
545 view as suggested here, or simply learnt homing views by turning back during their  
546 outbound trips remains to be seen.

547



548

549 **Figure 3.** Models on how ants may combine navigational information. The longer the  
 550 length of the drawn vectors the higher the directional drive. Dots represent cases with  
 551 no directional drive and stars nest locations. (a) Illustration of the ‘repulsive view  
 552 hypothesis’. Overall directional drive results from the integration of attractive homing  
 553 views (green arrows) minus repulsive outbound views (red arrows). Left scheme  
 554 represents theoretical positions and orientations of memorised views. The ant  
 555 recognises only views that are aligned with its current body orientation (here, always  
 556 facing downward). The larger the distance from the current location to the closest  
 557 aligned view, the lower the familiarity and directional drive. This principle provides  
 558 appropriate guidance toward the nest. Right scheme shows examples of integration  
 559 for different locations (grey dashed arrows) with the ant always facing downward. For  
 560 instance, when facing downward at the BeN location, the closest aligned view is  
 561 repulsive (bold red arrow on right left scheme). Given that the neighbouring green  
 562 arrow is not aligned, the closest aligned attractive view is further away, beyond the  
 563 nest (bold green arrow on left scheme). Overall, the ants at this position (still facing  
 564 downward) will be more repulsed than attracted by the current facing direction and

565 thus walk backward toward the nest. In contrast, when beyond the nest ByN (still  
566 facing downward), the attractive views will match better than the repulsive views and  
567 the ants will thus turn around and walk backward toward the nest. Whatever the  
568 position and orientation of the ants around the nest, the agent will be drawn towards  
569 the nest (b) Directional drive across test conditions of Experiment 1 in Section 1 and  
570 2. Ants are tested in FV (full-vector), FVU (full-vector unfamiliar) and ZV (zero-vector)  
571 conditions. Overall directional drive (dark blue vectors) results from the integration of  
572 path integration (cyan vectors, the longer the path integration vector the stronger its  
573 directional drive) and learnt view (yellow vectors, the more familiar the view the  
574 stronger its directional drive). (c) Directional drive resulting from the recognition of a  
575 learnt view (yellow vectors) decrease with time spent facing in a different direction.  
576 Low directional drive results in lower speed (dashed arrow) and eventually peeking.  
577 Here memorised views are assumed to be facing upward and are thus recognised  
578 only when facing upward during peeking (small grey arrow) and not while facing  
579 downward during backward motion. Note that the second peek triggers a lower  
580 directional drive than the first (see also Fig. 1b).

581

### 582 **Ants combine multiple cues to estimate directional uncertainty and trigger** 583 **peeks.**

584

585 It is known that ants combine the directional dictates of the current visual  
586 familiarity with their PI in a weighted fashion (Wehner, Hoinville, Cruse, & Cheng,  
587 2018). Notably, the direction indicated by the current view is more weighted as the  
588 current view is familiar (Legge et al., 2014) and the direction indicated by the PI is  
589 more weighted as the PI vector length increases (Wystrach et al., 2015). Backward  
590 walking ants appear to weight these cues in the same fashion. Fig. 3b shows how  
591 such an integration of cues captures the peek rate observed across our conditions  
592 and distance walked along the route. Notably, this explains why ZV-ants peeked  
593 earlier and more often than FV-ants (Fig. 1b), as observed in North African  
594 *Cataglyphis fortis* ants (Pfeffer & Wittlinger, 2016) and why peek rate increases as  
595 the distance along the route increase (Fig. 1d, e).

596 Interestingly, such an estimate of directional certainty seems not only to influence  
597 the occurrence of peeking but also whether the peeking ants decided to return to  
598 their biscuit or abandon it. FV-ants in familiar visual surroundings and therefore with  
599 the highest directional certainty, dragged their biscuit all along the 7.20 m route  
600 without exception (32 out of 32). In contrast, some ants abandoned their biscuits in  
601 both FV unfamiliar (6 out of 31) and ZV (6 out of 33) conditions.

602 Finally, it is worth mentioning that ants clearly increased the speed of their  
603 backward motion after peeking (Fig. 1c). The increase in speed is likely not only a  
604 mere consequence of a short recovery from the dragging activity but also a gain in  
605 navigational certainty as this sudden speed increase is also apparent when displaced  
606 foragers reach their familiar route and recognise the familiar scenery (pers. observ.).  
607 Furthermore, a decrease in speed when ants run off their PI has been observed  
608 (Buehlmann, Fernandes, & Graham, 2018). Hence it seems that the speed of  
609 movement reflects the strength of the directional drive and therefore directional  
610 certainty. Taken together, peeking behaviour seem to increase directional certainty,  
611 at least temporally (Fig. 3c)

612

### 613 **Ants gather information about the time spent backward.**

614

615 Recently, it has been shown that directional information based on terrestrial cues  
616 is obtained when ants face forward during peeks and must therefore be stored in a  
617 short-term memory while the ant is subsequently walking backward (Schwarz et al.,  
618 2017). Our results suggest that short-term memory also influences the ants'  
619 navigational certainty. The time spent peeking forward varied (as already noted by  
620 Pfeffer and Wittlinger (2016)) with some ants 'peeking' for less than a second while  
621 other spent more than 60s (after which recording was stopped) without returning to  
622 their cookie. Interestingly, the more an ant had peeked before during a test run the  
623 longer her current peek lasted (Fig. 2b). This was true for the conditions where ants  
624 searched around a given location such as the nest or when released in completely  
625 unfamiliar location. In these conditions (BeN, ByN, U), the elapsed time, which  
626 necessarily correlates with the number of previous peeks, does not correlate with  
627 specific locations in the world (contrary to the 'F' condition). This shows that ants  
628 somehow gather information across time: either information about the overall time  
629 spent backwards or information about the number of peek previously displayed (see  
630 also Fig. 3c).

631 Former experiments have already shown that the behaviour of ants can be  
632 modulated by recent experience in the order of seconds to minutes – a form of  
633 hysteresis (Graham & Mangan, 2015). For instance, ants display a so-called  
634 backtracking behaviour only if they have recently perceived the nest surrounding

635 (Wystrach, Schwarz, Baniel, & Cheng, 2013). Also, homing ants display higher  
636 meander in their paths when recapitulating a well-known route for the second time in  
637 a row (Collett, 2014; Wystrach, Schwarz, Graham, & Cheng, 2019). Finally, ants can  
638 remember the compass direction of a wind gust after being blown (Wystrach &  
639 Schwarz, 2013). In the present case, ants seem to also build up information about  
640 the recent past. Even though it makes functional sense it remains to be seen what  
641 neural or physiological mechanisms underlie this phenomenon.

642

### 643 **Conclusion**

644 This study confirmed that ants walking backward are not just paying attention to  
645 celestial cues but combine multiple information from their PI, the recognition of  
646 terrestrial cues and temporal information such as the time they spent backward. All  
647 this information seems to be integrated in an overall directional drive. This drive,  
648 which reflects the current directional certainty, seems to (1) guide the ants backward  
649 path, (2) triggers peeking behaviour and (3) finally dictates whether or not to return to  
650 their food item during peeks. Importantly, this study shows that ants can recognise  
651 familiar terrestrial cues backward. In addition to the attractive memories facing  
652 toward the nest, the hypothesis that homing ants use a collection of repulsive visual  
653 memories facing away from the nest and possibly stored during their outbound trip  
654 was put forward. In the light of this hypothesis, visual navigation forward or backward  
655 can then simply be achieved by using the relative familiarity between both sets of  
656 opposite valence memories. As often with research on insect navigation, remarkably  
657 flexible behaviours incite researchers to endorse the simplest explanations (Wystrach  
658 & Graham, 2012).

659

### 660 **ACKNOWLEDGEMENTS**

661

662 We are grateful for Xim Cerda and his helpful team at CSIC Seville for permanent  
663 assistance in logistics and administration during field work. We also thank Cornelia  
664 Buehlmann, Scarlett Dell-Cronin, Cody Freas and Michael Mangan for manual and  
665 moral support during field preparation and data collection. Finally, we are grateful for  
666 the constructive comments of Paul Graham on the manuscript. The study was partly  
667 financed by The European Research Council, 759817-EMERG-ANT ERC-2017-STG.



668

669 **AUTHOR CONTRIBUTIONS**

670

671 SS, Conceptualization, Methodology, Validation, Formal analysis, Investigation,  
672 Writing – original draft preparation, Writing – review & editing, Visualization,  
673 Supervision, Project administration; LC, Investigation, Validation; EG, Investigation,  
674 Validation; AW, Conceptualization, Methodology, Validation, Formal analysis,  
675 Investigation, Writing – original draft preparation, Writing – review & editing,  
676 Visualization, Supervision, Project administration, Funding acquisition.

677

678

679 **REFERENCES**

680

681 Ardin, P., Mangan, M., Wystrach, A., & Webb, B. (2015). How variation in head pitch  
682 could affect image matching algorithms for ant navigation. *Journal of*  
683 *Comparative Physiology A*, 201(6), 585–597.

684 Ardin, P., Peng, F., Mangan, M., Lagogiannis, K., & Webb, B. (2016). Using an insect  
685 mushroom body circuit to encode route memory in complex natural  
686 environments. *PLoS Computational Biology*, 12(2), e1004683.

687 Ardin, P. B., Mangan, M., & Webb, B. (2016). Ant homing ability is not diminished  
688 when traveling backwards. *Frontiers in Behavioral Neuroscience*, 10:69.

689 Baddeley, B., Graham, P., Husbands, P., & Philippides, A. (2012). A Model of Ant  
690 Route Navigation Driven by Scene Familiarity. *PLoS Computational Biology*,  
691 8(1), 1002336.

692 Buehlmann, C., Fernandes, A., & Graham, P. (2018). The interaction of path  
693 integration and terrestrial visual cues in navigating desert ants: what can we  
694 learn from path characteristics? *The Journal of Experimental Biology*, 221.

695 Cerda, X. (2001). Behavioural and physiological traits to thermal stress tolerance in  
696 two Spanish desert ants. *Etologia*, 9, 15-27.

697 Cheng, K., Narendra, A., Sommer, S., & Wehner, R. (2009). Traveling in clutter:  
698 navigation in the Central Australian desert ant *Melophorus bagoti*. *Behavioural*  
699 *Processes*, 80, 261-268.

700 Collett, M. (2012). How navigational guidance systems are combined in a desert ant.  
701 *Current Biology*, 22, 927-932.

702 Collett, M. (2014). A desert ant's memory of recent visual experience and the control  
703 of route guidance. *Proceedings of the Royal Society B: Biological Sciences*,  
704 281, 20140634.

705 Collett, M., Graham, P., & Collett, T. S. (2017). Insect navigation: what backward  
706 walking reveals about the control of movement. 27, 141-143.

707 Collett, T., Graham, P., & Durier, V. (2003). Route learning by insects. *Current*  
708 *Opinion in Neurobiology*, 13(6), 718-725.

709 Freas, C. A., & Cheng, K. (2018). Landmark learning, cue conflict, and outbound  
710 view sequence in navigating desert ants. *Journal of Experimental Psychology:*  
711 *Animal Learning and Cognition*, 44(4), 409-421.

- 712 Freas, C. A., & Spetch, M. L. (2019). Terrestrial cue learning and retention during the  
713 outbound and inbound foraging trip in the desert ant, *Cataglyphis velox*.  
714 *Journal of Comparative Physiology A*, doi.org/10.1007/s00359-00019-01316-  
715 00356.
- 716 Graham, P., & Mangan, M. (2015). Insect navigation: do ants live in the now? *The*  
717 *Journal of Experimental Biology*, 218(819-823).
- 718 Harris, R. A., Hempel de Ibarra, N., Graham, P., & Collett, T. S. (2005). Priming of  
719 visual route memories. *Nature*, 438, 302.
- 720 Heinze, S., Narendra, A., & Cheung, A. (2018). Principles of insect path integration.  
721 *Current Biology*, 28, 1023-1058.
- 722 Hoinville, T., & Wehner, R. (2018). Optimal multiguideance integration in insect  
723 navigation. *Proceedings of the National Academy of Sciences of the United*  
724 *States of America*, 115(11), 2824-2829.
- 725 Jayatilaka, P., Murray, T., Narendra, A., & Zeil, J. (2018). The choreography of  
726 learning walks in the Australian jack jumper ant *Myrmecia croslandi*. *The*  
727 *Journal of Experimental Biology*, 221, 185306.
- 728 Legge, E., Wystrach, A., Spetch, M., & Cheng, K. (2014). Combining sky and earth:  
729 desert ants (*Melophorus bagoti*) show weighted integration of celestial and  
730 terrestrial cues. *The Journal of Experimental Biology*, 217, 4159-4166.
- 731 Mangan, M., & Webb, B. (2012). Spontaneous formation of multiple routes in  
732 individual desert ants (*Cataglyphis velox*). *Behavioral Ecology*, 23(5), 944-954.
- 733 Möller, R. (2012). A model of ant navigation based on visual prediction. *Journal of*  
734 *Theoretical Biology*, 305, 118-130.
- 735 Narendra, A., Gourmaud, S., & Zeil, J. (2013). Mapping the navigational knowledge  
736 of individually foraging ants, *Myrmecia croslandi*. 280, 20130683.
- 737 Nicholson, D. J., Judd, S. P. D., Cartwright, B. A., & Collett, T. S. (1999). Learning  
738 walks and landmark guidance in wood ants (*Formica rufa*). *The Journal of*  
739 *Experimental Biology*, 202, 1831-1838.
- 740 Pfeffer, S., Wahl, V., & Wittlinger, M. (2016). How to find home backwards?  
741 Locomotion and inter-leg coordination during rearward walking of *Cataglyphis*  
742 *fortis* desert ants. *The Journal of Experimental Biology*, 219, 2110-2118.

- 743 Pfeffer, S., & Wittlinger, M. (2016). How to find home backwards? Navigation during  
744 rearward homing of *Cataglyphis fortis* desert ants. *The Journal of*  
745 *Experimental Biology*, *219*, 2119-2126.
- 746 Reid, S. F., Narendra, A., Hemmi, J. M., & Zeil, J. (2011). Polarised skylight and the  
747 landmark panorama provide night-active bull ants with compass information  
748 during route following. *The Journal of Experimental Biology*, *214*, 363-370.
- 749 Schwarz, S., Albert, L., Wystrach, A., & Cheng, K. (2011). Ocelli contribute to the  
750 encoding of celestial compass information in the Australian desert ant  
751 *Melophorus bagoti*. *The Journal of Experimental Biology*, *214*, 901-906.
- 752 Schwarz, S., Julle-Daniere, E., Morin, L., Schultheiss, P., Wystrach, A., Ives, J., &  
753 Cheng, K. (2014). Desert ants (*Melophorus bagoti*) navigating with robustness  
754 to distortions of the natural panorama. *Insectes Sociaux*, *61*, 371-383.
- 755 Schwarz, S., Mangan, M., Zeil, J., Webb, B., & Wystrach, A. (2017). How Ants Use  
756 Vision When Homing Backward. *Current Biology*, *27*(3), 401-407.
- 757 Stone, T., Webb, B., Adden, A., Weddig, N., Honkanen, A., Templin, R., . . . Heinze,  
758 S. (2017). An anatomically constrained model for path integration in the bee  
759 brain. *Current Biology*, *27*(20), 3069-3085.e3011.
- 760 Wehner, R. (2003). Desert ant navigation: how miniature brains solve complex tasks.  
761 *Journal of Comparative Physiology A*, *189*, 579-588.
- 762 Wehner, R., Boyer, M., Loertscher, F., Sommer, S., & Menzi, U. (2006). Ant  
763 navigation: one-way routes rather than maps. *Current Biology*, *16*, 75-79.
- 764 Wehner, R., Hoinville, T., Cruse, H., & Cheng, K. (2018). Steering intermediate  
765 courses: desert ants combine information from various navigational routines.  
766 *Journal of Comparative Physiology A*, *202*(7), 459–472.
- 767 Wehner, R., & Srinivasan, M. V. (2003). Path integration in insects. In K. K. Jeffrey  
768 (Ed.), *The neurobiology of spatial behaviour* (pp. 9-30). Oxford: Oxford  
769 University Press.
- 770 Wittlinger, M., Wehner, R., & Wolf, H. (2006). The ant odometer: stepping on stilts  
771 and stumps. *Science*, *312*, 1965-1966.
- 772 Wystrach, A., Beugnon, G., & Cheng, K. (2011). Landmarks or panoramas: what do  
773 navigating ants attend to for guidance? *Frontiers in Zoology*, *8*, 21.

- 774 Wystrach, A., Beugnon, G., & Cheng, K. (2012). Ants might use different view-  
775 matching strategies on and off the route. *The Journal of Experimental Biology*,  
776 *215*, 44-55.
- 777 Wystrach, A., Cheng, K., Sosa, S., & Beugnon, G. (2011). Geometry, features, and  
778 panoramic views: Ants in rectangular arenas. *Journal of Experimental*  
779 *Psychology: Animal Behavior Processes*, *37*(4), 420-435.
- 780 Wystrach, A., & Graham, P. (2012). What can we learn from studies of insect  
781 navigation? *Animal Behaviour*, *84*, 13-20.
- 782 Wystrach, A., Mangan, M., Philippides, A., & Graham, P. (2013). Snapshots in ants?  
783 New interpretations of paradigmatic experiments. *The Journal of Experimental*  
784 *Biology*, *216*, 1766-1770.
- 785 Wystrach, A., Mangan, M., & Webb, B. (2015). Optimal cue integration in ants.  
786 *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20151484.
- 787 Wystrach, A., & Schwarz, S. (2013). Ants use a predictive mechanism to compensate  
788 for passive displacements by wind. *Current Biology*, *23*, 1083-1085.
- 789 Wystrach, A., Schwarz, S., Baniël, A., & Cheng, K. (2013). Backtracking behaviour in  
790 lost ants: an additional strategy in their navigational toolkit. *Proceedings of the*  
791 *Royal Society B: Biological Sciences*, *280*, 20131677.
- 792 Wystrach, A., Schwarz, S., Graham, P., & Cheng, K. (2019). Running paths to  
793 nowhere: repetition of routes shows how navigating ants modulate online the  
794 weights accorded to cues. *Animal Cognition*, *22*(2), 213–222.
- 795 Zeil, J. (2003). Catchment areas of panoramic snapshots in outdoor scenes. *Journal*  
796 *of the Optical Society of America A*, *20*(3), 450-469.
- 797 Zeil, J. (2012). Visual homing: an insect perspective. *Current Opinion in*  
798 *Neurobiology*, *22*, 285–293.
- 799