

1 **A lateralised design for the interaction of visual memories and heading representations in
2 navigating ants.**

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10 **Abstract:**

11 The navigational skills of ants, bees and wasps represent one of the most baffling examples
12 of the powers of minuscule brains. Insects store long-term memories of the visual scenes
13 they experience ¹, and they use compass cues to build a robust representation of directions
14 ^{2,3}. We know reasonably well how long-term memories are formed, in a brain area called the
15 Mushroom Bodies (MB) ^{4–8}, as well as how heading representations are formed in another
16 brain area called the Central Complex (CX) ^{9–12}. However, how such memories and heading
17 representations interact to produce powerful navigational behaviours remains unclear ^{7,13,14}.
18 Here we combine behavioural experiments with computational modelling that is strictly
19 based on connectomic data to provide a new perspective on how navigation might be
20 orchestrated in these insects. Our results reveal a lateralised design, where signals about
21 whether to turn left or right are segregated in the left and right hemispheres, respectively.
22 Furthermore, we show that guidance is a two-stage process: the recognition of visual
23 memories – presumably in the MBs – does not directly drive the motor command, but
24 instead updates a “desired heading” – presumably in the CX – which in turn is used to
25 control guidance using celestial compass information. Overall, this circuit enables ants to
26 recognise views independently of their body orientation, and combines terrestrial and
27 celestial cues in a way that produces exceptionally robust navigation.

28

29 ***Bilaterally decorrelated input to the CX produces goal-oriented paths.***

30 We first investigated how information about the visual familiarity of the scenes – as
31 computed in the MB – could plausibly be sent to the CX for guidance given the known
32 circuitry of insect brains. Even though our current approach is an experimental one, the CX
33 circuitry is understood and conserved enough to make such effort possible using biologically
34 constrained neural modelling^{12,15–17}.

35 Recent studies have shown that the CX circuits can: 1) track the current heading, in two
36 substructures called Ellipsoid Body (EB) and Protocerebral Bridge (PB)^{10,11,18}; 2) retain a
37 desired heading representation for tens of seconds in the Fan-shaped Body (FB)¹⁴; and 3)
38 compare both current and desired headings to output compensatory left/right steering
39 commands^{14,19}. The desired heading can be updated by bilateral signals to the FB from
40 external regions¹⁴. Such a signal can plausibly come from the recognition of long-term visual
41 memories in the MB, which sends bilateral input to the FB through one relay in the Superior
42 Intermediate Protocerebrum (SIP). These observations led to the idea that navigation, such
43 as learnt route following, could emerge by having the MBs signalling to the CX when the
44 insect is facing its familiar route direction or not^{7,13,14}.

45 We thus tested the viability of this hypothesis by building a model of the CX, strictly based
46 on this connectivity (Fig. 1). Contrary to what was expected, our model shows that having
47 the bilateral ‘visual familiarity’ signals to the FB correspond with the moments when the
48 agent is facing the correct route direction did not allow straight routes to emerge. A
49 thorough search through the parameter space revealed that this configuration produces a
50 mediocre directionality at best, and is very sensitive to parameter change (Extended data fig.
51 1). Contrastingly, route following becomes extremely stable and robust to parameter
52 changes as soon as the signals to the FB from the left and right brain hemispheres
53 correspond to moments where the agent is oriented to the right or the left of its goal,
54 respectively (Fig. 1). Impressively, varying parameters (such as the time during which FB
55 neurons sustain their activity, or the heading angle away from the goal for which left or right
56 input signals are strongest) hardly has any effect: straight routes emerge as long as left and
57 right hemispheric inputs roughly correlate with a right and left heading bias, respectively
58 (Fig. 1, Extended data fig. 1). As a corollary, if left and right hemispheric inputs correlate
59 instead with left and right (rather than right and left) heading biases, a straight route in the

60 reverse direction emerges (Fig. 1). Thus, having the input signal correlate with moments
61 where the agent faces the goal direction corresponds to a zone of transition between two
62 stable regimes of route-following in opposite directions.

63 In other words, this suggests that recognising views when facing the goal may not be a good
64 solution, and instead, it shows that the CX circuitry is remarkably adapted to control a visual
65 course as long as the input signals from the visual familiarity of the scene to both
66 hemispheres are distinct, with one hemisphere signalling when the agent's heading is biased
67 towards the right and the other, towards the left. This model makes particular predictions,
68 which we next tested with behavioural experiments.

69

70 ***The recognition of familiar views triggers compensatory left or right turns.***

71 Previous studies assumed that ants memorise views while facing the goal ^{20–22} and anti-goal
72 ^{23–25}) directions, and that they must consequently align their body in these same directions
73 to recognise a learnt view as familiar ^{26–28}. On the contrary, our modelling effort suggests
74 that ants should rather recognise views based on whether the route direction stands on
75 their 'left or right' rather than 'in front or behind'. We put this idea to the test using an
76 open-loop trackball system enabling the experimenter to choose both the position and body
77 orientation of tethered ants directly in their natural environment ²⁹. We trained ants along a
78 route and captured homing individuals just before they entered their nest to ensure that
79 these so-called zero-vector ants (ZV) could no longer rely on their path integration homing
80 vector ³⁰. We recorded the motor response of these ants while mounted on the trackball
81 system, in the middle of their familiar route, far from the catchment area of the nest, when
82 fixed in eight different body orientations (Fig. 2a, b). Results show that, irrespective of their
83 body orientation, ants turned mostly towards the correct route direction (Fig. 2c). When the
84 body was oriented towards (0°, nest direction) or away (180°) from the route direction, ants
85 still showed a strong preference for turning on one side (to the left or to the right,
86 depending on individuals) (Fig. 2d). This was not the case when ants were tested in
87 unfamiliar surroundings (Fig. 2c, d), showing that the lateralised responses observed on the
88 familiar route was triggered by the recognition of the visual scene. This implies that ants can
89 recognise their route independently of their body orientation, and can derive whether the

90 route direction is towards their left or their right. Importantly, even when facing the route or
91 anti-route direction, recognition of familiar views appears to trigger a 'left vs. right' decision
92 rather than a 'go forward vs. turn' decision.

93

94 ***Guidance based on memorised views involves the celestial compass.***

95 We showed that the recognition of familiar views indicates whether the goal direction is
96 towards the left or right. In principle, guidance could thus be achieved by having these
97 left/right signals directly trigger the left or right motor command. An alternative would be,
98 as in our model, that such left/right signals can be used to update the 'desired heading
99 directions' in the CX, which in turn uses its own compass information to control steering (Fig.
100 1). This makes a counterintuitive prediction: if the recognition of familiar views triggers a
101 turn towards the correct side, reversing the direction of the compass representation in the
102 CX should immediately reverse the motor decision. We tested this prediction by mirroring
103 the apparent position of the sun in the sky by 180° to *Cataglyphis velox* ants tethered to our
104 trackball system. A previous study had shown that this manipulation was sufficient to shift
105 this species' compass heading representation ³¹.

106 We first tethered well-trained ZV ants (i.e., captured just before entering the nest) on our
107 trackball system with their body orientation fixed perpendicularly to their familiar route
108 direction. As expected, ants in this situation turned towards the correct route direction (Fig.
109 3, left panels, natural sun), indicating that they correctly recognised familiar visual terrestrial
110 cues. When mirroring the apparent sun's position by 180°, these ants responded by turning
111 in the opposite direction within one second (Fig. 3, left panel, mirrored sun). We repeated
112 the experiment by placing such ZV ants in the same compass direction but in an unfamiliar
113 location. In this situation, the ants turned in random directions (Fig. 3, middle panels),
114 showing that the direction initially chosen by the ants on their familiar route (Fig. 3, left
115 panels) was based on the recognition of terrestrial rather than celestial cues. It however
116 remains unclear whether the sun rotation had an impact on ants in unfamiliar terrain, as
117 ants in this situation regularly alternate between left and right turns anyway ²⁵. Finally, to
118 ensure that the observed effect on route was not due to an innate bias at this particular
119 location, we repeated this experiment with ants tethered at the exact same route location

120 and body orientation, but this time only with ants that were trained to an alternative
121 straight route, which was aligned with the tethered direction of the trackball (Fig. 3, right
122 panel). As expected, these ants showed no preference in turning direction at the group level,
123 although most individuals still strongly favoured one side rather than walking straight (Fig. 3
124 right panels). Interestingly, mirroring the sun significantly reversed the individual's chosen
125 direction (even though they were aligned with their goal direction) (Fig. 3c right panels).

126 Taken together these results show that guidance based on learnt views is a two-stage
127 process: the recognition of visual memories – presumably through the MBs – does not
128 directly drive the motor command, but it instead signals a desired heading – presumably
129 through the CX –, which in turn is used to control guidance using celestial compass
130 information.

131

132 ***A complex interaction between terrestrial and celestial guidance***

133 The results from above point at a complex interaction between the use of long-term
134 memory of terrestrial cues – indicating whether the goal is left or right – and the heading
135 estimate based on compass cues. To further endorse the credibility of our proposed
136 guidance system, we used our model to explore how agents navigating along their familiar
137 route would react to a sudden 135° shift of the CX current celestial compass estimate, and
138 compared their behaviour to that of real homing ZV ants tested in a similar scenario, where
139 we shifted the sun position by 135° using a mirror (Fig. 4). Impressively, and despite the
140 nonlinear dynamics at play, the simulated shift in the CX model closely resembled the
141 response of the ants to the sun manipulation, adding credibility to the model and helping us
142 grasp the mechanisms at play (Fig. 4).

143

144 ***General discussion***

145 We showed that during view-based navigation, ants recognise views when oriented left and
146 right from their goal to trigger left and right turns. Facing in the correct route direction does
147 not trigger a 'go forward' command, but marks some kind of labile equilibrium point in the
148 system. Also, we show that the recognition of left or right familiar views does not drive the

149 motor decision directly but is perfectly suited to inform the CX, which in turn maintains the
150 desired heading using its own compass information. The advantage of this design is clear
151 considering that the recognition of learnt visual terrestrial cues is sensitive to variables such
152 as body orientation ^{31,32} or partial visual obstructions that must happen continuously when
153 navigating through grassy or leafy environments, making the visual familiarity signal
154 mediated by the MBs inherently noisy. In contrast, the CX provides a stable and sustained
155 heading representation by integrating self-motion ¹¹ with multiple wide-field celestial ¹⁰ and
156 terrestrial cues ^{9,33}. The CX is thus well suited to act as a heading buffer from the noisy MBs
157 signal, resulting in smooth and stable guidance control. In addition, the compass
158 representation in the CX enables to steer the direction of travel independently of the actual
159 body orientation ¹². Our results thus explain how ants visually recognise a view using the
160 MBs and subsequently follow such direction backwards using the CX ³¹ or how ants can
161 estimate the actual angular error between the current and goal directions before initiating
162 their turn ³⁴. Also, in addition to route following, such a lateralised design can produce
163 remarkably robust homing in complex environments (Wystrach et al., 2020 in prep).

164 Finally, the proposed circuit offers an interesting take on the evolution of navigation.
165 Segregating 'turn left' and 'turn right' signals between hemispheres evokes the widespread
166 tropotaxis, where orientation along a gradient is achieved by directly comparing the signals
167 intensities between physically distinct left and right sensors (e.g., antennae or eyes) in
168 bilateral animals ^{35–41}. Comparing signals between hemispheres could thus be an ancestral
169 strategy in arthropods; and ancestral brain structures such as the CX accommodates well
170 such a bilateral design and may be constrained to receive such lateralised input to function
171 properly. The evolution of visual route-following in hymenoptera is a relatively recent
172 adaptation, and it cannot be achieved by directly comparing left and right visual inputs –
173 which is probably why each eye can afford to project to both hemispheres' MBs ^{42,43}.
174 Categorising learnt views as indicators of whether the goal is to the left or to the right, and
175 subsequently segregating this information in the left and right hemispheres may thus be an
176 evolutionary adaptation to fit the ancestrally needed bilateral inputs to the CX (Fig. 1).

177 How left and right visual memories are acquired and learnt when naive insects explore the
178 world for the first time remains to be seen. During their learning flights, wasps regularly
179 alternate between moments facing 45° to the left and 45° to the right of their goal, strongly

180 supporting our claim that insect form such left and right memories ⁴⁴. During their
181 meandering learning walks, ants tend to reverse turning direction when facing the nest or
182 anti-nest direction ^{21,23,45}, however, they do expose their gaze in all directions, providing
183 ample opportunities to form a rich set of left and right visual memories ⁴⁵. Our model shows
184 that the angle at which views are learnt does not need to be precisely controlled (Fig. 1c,d).
185 Views facing the nest may as well be included during learning and categorised as left, right or
186 both, explaining why most ants facing their goal usually choose to turn in one particular
187 direction while others turned less strongly. During learning, the first source of information
188 about whether the current body orientation is left or right from the goal probably results
189 from path integration. Interestingly, lateralised dopaminergic feedback from the Lateral
190 Accessory Lobes (LAL, a pre-motor area) to the MBs could represent an ideal candidate to
191 orchestrate such a categorisation of left/right memories (Wystrach et al., 2020 in prep).
192 Revisiting current questions in insect and robot navigation such as early exploration, route
193 following and homing ^{20,46–49}; the integration of aversive memories ^{8,24,50}, path integration
194 and views (^{51–54} or other sensory modalities (^{55–58} as well as seeking for underlying neural
195 correlates ^{5–7} – with such a lateralised design as a framework promises an interesting
196 research agenda.

197

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203 **Authors contributions**

204 Research design: AW. Data collection: AW, SS, FLM, LC. Trackball system design: FLM. Data
205 analysis: AW, SS, FLM. Modelling: AW. Manuscript writing: AW.

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208

209 **Method**

210 *The trackball setup:*

211 For both experiments (fig 2 and 3) we used the air-suspended trackball setup as described in
212 Dahmen et al., 2017²⁹; and chose the configuration where the ants are fixed in a given
213 direction and cannot physically rotate (if the ant tries to turn, the ball counter-rotates under
214 its legs). To fix ants on the ball, we used a micro-magnet and metallic paint applied directly
215 on the ant's thorax. The trackball air pump, battery and computer were connected to the
216 trackball through 10 m long cables and hidden in a remote part of the panorama. The
217 trackball movements were recorded using custom software in C++, data was analysed with
218 Matlab and can be provided upon request.

219

220 *Routes setups and ant training in *Cataglyphis velox*:*

221 For all experiments (fig. 2 and 3 and 4), *Cataglyphis velox* ants were constrained to forage
222 within a route using dug wood planks that prevented them to escape, while leaving the
223 surrounding panoramic view of the scenery intact (as described in Wystrach et al., 2012⁵⁹).
224 Cookie crumbs were provided ad libitum in the feeder positions for at least two days before
225 any tests. Some barriers dug into the ground created baffles, enabling us to control whether
226 ants were experienced with the route. Ants were considered trained when able to home
227 along the route without bumping into any such obstacle. These ants were captured just
228 before they entered their nest to ensure that they could not rely on path integration (so-
229 called ZV ants), marked with a metallic paint on the thorax and a colour code for individual
230 identification, and subjected to tests (see next sections).

231

232 *Routes setups and ant training in *Myrmecia croslandi*:*

233 For the experiment with *Myrmecia croslandi* ants (fig. 2), we used each individual's natural
234 route, for which these long-lived ants have extensive experience⁶⁰. Individuals were
235 captured on their foraging trees, marked with both metallic paint and a colour code for
236 individual identification, given a sucrose solution or a prey and released where they had
237 been captured (on their foraging tree). Upon release, most of these ants immediately started

238 to return home. We followed them while marking their route using flag pins every 50 cm (so
239 that their exact route was known). We captured the ants just before they entered their nests
240 and subjected them to the test on the trackball (see next section).

241

242 *Experimental protocol for the left/right trackball experiment (figure 2):*

243

244 1- An experienced ant was captured just before entering its nest, and marked with a drop of
245 metallic paint on the thorax.

246 2- A large opaque ring (30 cm diameter, 30 cm high) was set around the trackball setup.

247 3- The ant was fixed on the trackball within the opaque ring, which prevented her to see the
248 surroundings. Only a portion of sky above was accessible to the ant.

249 4- The trackball system (together with the opaque ring and the fixed ant within) was moved
250 to the desired position and rotated so that the ant was facing the desired direction.

251 5- One experimenter started recording the trackball movements (from the remote
252 computer), when another lifted the ring (so the ant could see the scenery) before leaving the
253 scene, letting the ant behave for at least 15 seconds post ring lifting.

254 6- The experimenter came back, replaced the ring around the trackball system, and rotated
255 the trackball system (following a pre-established pseudo random sequence) for the ant to
256 face in a novel direction.

257 7- We repeated steps 5 and 6 until the 8 possible orientations were achieved (the sequence
258 of orientations were chosen in a pseudo-random order so as to counter-balance orientation
259 and direction of rotation).

260 The data shown in fig. 2 for each orientation is averaged across 12 sec of recording (from 3
261 sec to 15 sec assuming ring lifting is at 0 sec). We decided to let 3 sec after ring lifting, as the
262 movements of the experimenter before he leaves the scenery might disturb the ants).

263 In all experiments, ants were tested only once.

264

265 *Experimental protocol for the mirror trackball experiments (figure 3):*

266

267 1- An experienced ant was captured just before entering its nest, and marked with a drop of
268 metallic paint on the thorax.

269 2- A large opaque ring (30 cm diameter, 30 cm high) was set around the trackball setup.
270 3- The ant was fixed on the trackball within the opaque ring, which prevented her to see the
271 surroundings. Only a portion of sky above was accessible to the ant.
272 4- The trackball system (together with the opaque ring and the fixed ant within) was moved
273 to the desired position and rotated so that the ant was facing the desired direction.
274 5- One experimenter started recording the trackball movements, when another lifted the
275 ring (so the ant could see the scenery) before leaving the scene, letting the ant behave for at
276 least 10 seconds post ring lifting.
277 5- Two experimenters simultaneously hid the real sun and projected the reflected sun using
278 a mirror, so that the sun appeared in the opposite position of the sky to the ant for at least 8
279 seconds.
280 Ants were tested only once, in one of the conditions.

281
282 *Experimental design and protocol for the mirror experiment with ants on the floor (figure 4):*
283
284 *Cataglyphis velox* ants were trained to a 10 meters-long route for at least two consecutive
285 days. A 240 × 120 cm thin wood board was placed on the floor in the middle of the route,
286 ensuring that the navigating ants walked smoothly without encountering small clutter over
287 this portion of the route. Homing ants were captured just before entering their nest and
288 released at the feeder as ZV ants. Upon release, these ZV ants typically resume their route
289 homing behaviour; at mid-parkour (halfway along the board section) the real sun was hidden
290 by one experimenter and reflected by another, using a mirror, for the sun to appear to the
291 ant 135° away from its original position in the sky. To ensure that each individual was tested
292 only once, tested ants were marked with a drop of paint after the procedure.
293 The ZV ants walking on the board were recorded using a Panasonic Lumix DMC-FZ200
294 camera on a tripod, and their paths were digitised frame by frame at 10 fps using image J.
295 We used four marks on the board to correct for the distortion due to the tilted perspective
296 of the camera's visual field. Analysis of the paths were achieved with Matlab.

297

298

299 *The CX neural model.*

300 The CX model circuitry and input signals are described in Extended data figure 2 (a-d), and
301 the different parameters used to obtain the output (motor command) are described in
302 Extended data figure 1. All the modelling has been achieved with Matlab, and can be
303 provided upon request.

304

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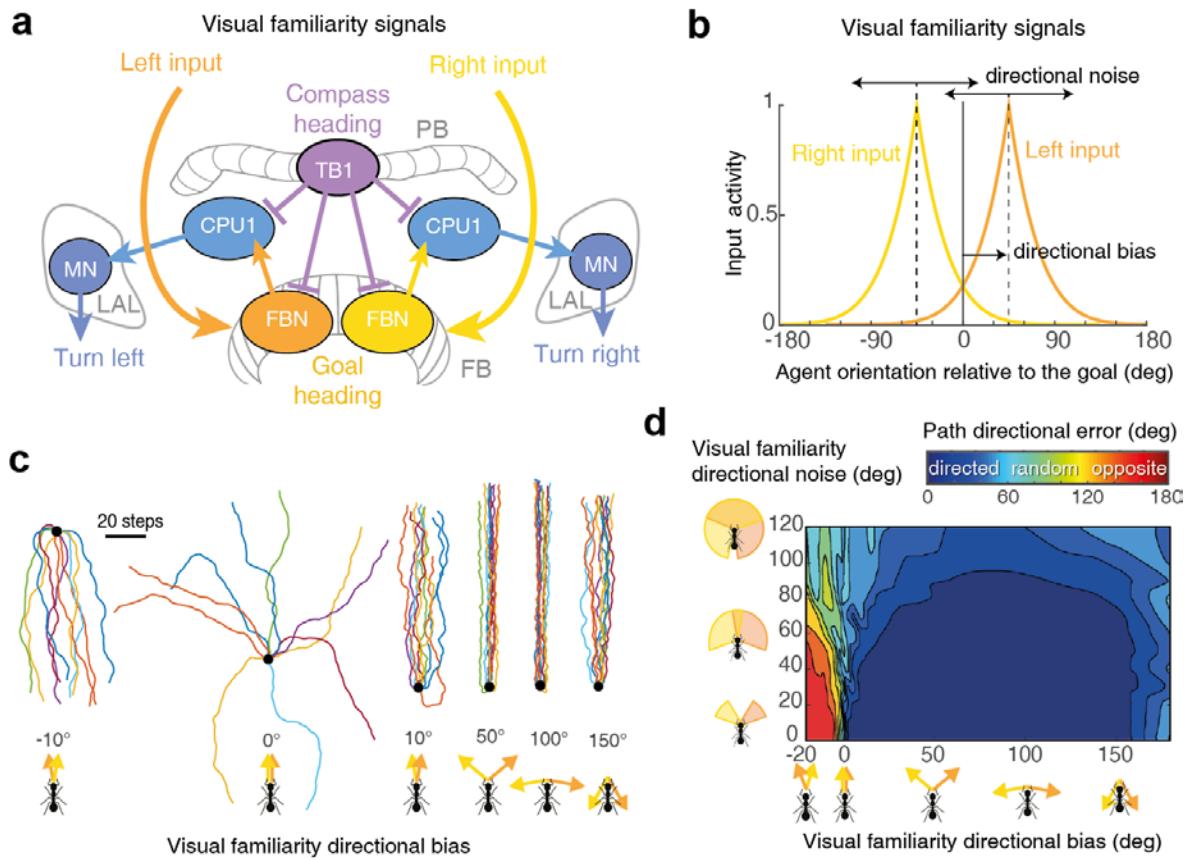
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438

439 **Figure 1**



440

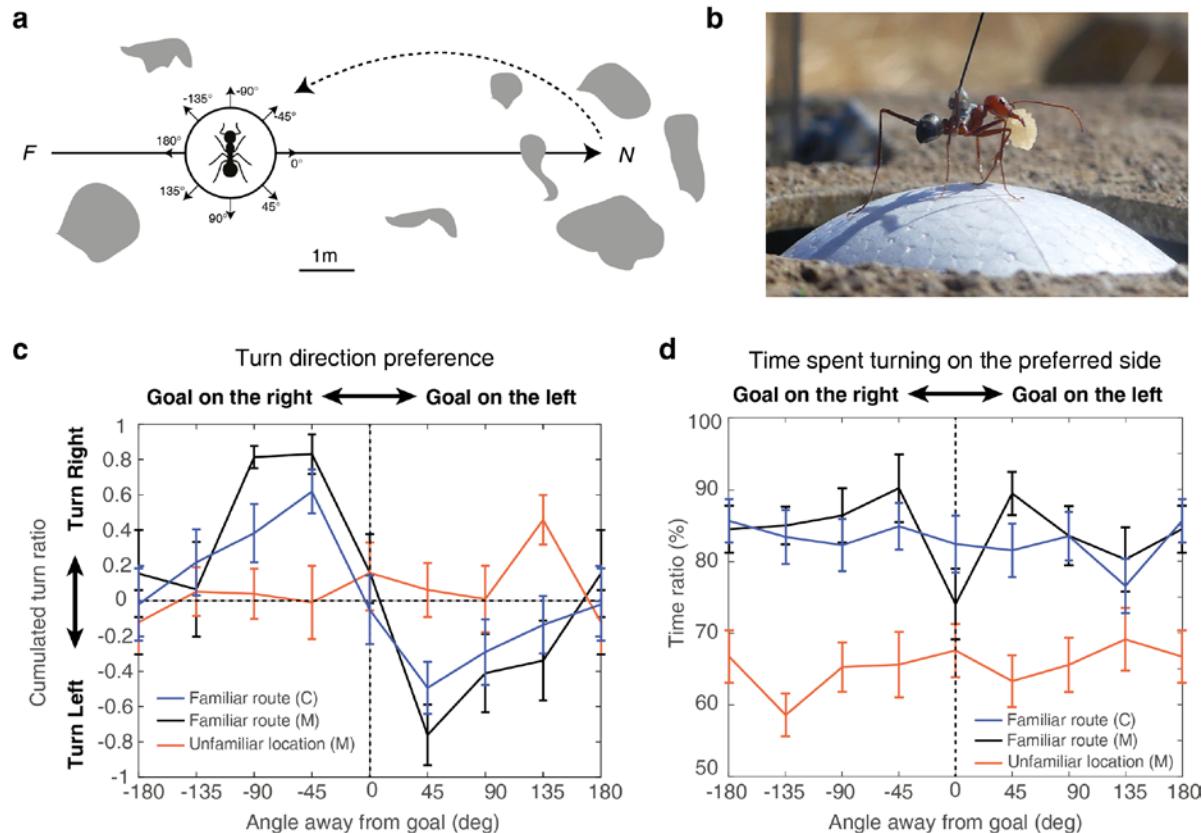
441 **Figure 1. Bilaterally decorrelated input to Central Complex produces stable route heading.**

442 **a.** The central complex (CX) sits at the centre of the brain but is wired to both hemispheres.
443 It receives bilateral inputs in the Fan-shaped Body (FB), where sustained activity of the FB
444 neurons (FBN) forms two representations of the goal heading. CPU1 neurons compare such
445 'goal heading' representations to the 'compass-based current heading' representation of the
446 Protocerebral Bridge (PB) neurons (TB1) and outputs bilateral signals to the left and right
447 Lateral Accessory Lobes (LALs), where they modulate motor neurons (MN) descending to the
448 thorax to control left and right turns, respectively (see **extended figure 2, d, g** for details of
449 the circuitry). **b.** Simulated inputs to the FBN neurons. We assumed that the input signals to
450 the FBN are body-orientation-dependant (as expected if resulting from visual familiarity of
451 the scene²⁸ such as outputted by the MBs⁴. 'directional bias' indicates the direction relative
452 to the goal direction (0°) at which the left visual familiarity signals is highest in average (+45°
453 in this example). Right signal responds symmetrically for the other direction (-directional
454 bias). 'Directional noise' in the visual familiarity was implemented by shifting the input curve
455 response around its mean (i.e. the 'directional bias') at each time step by a random value

456 (normal distribution with standard deviation given by 'directional noise'). **c.** Paths resulting
457 given different directional biases. **d.** Path directional error (absolute angular error between
458 start-to-arrival beeline, and start-to-goal direction) after 200 steps, as a function of the visual
459 familiarity 'directional bias' (x axis) and 'directional noise' (y axis). **c, d.** Straight route
460 headings robustly emerge as long as left and right inputs send a signal when the body is
461 oriented right and left from the goal, respectively (i.e., directional bias $> 0^\circ$) but not if both
462 inputs send a signal when facing the goal (i.e., directional bias $= 0^\circ$). Orientation towards the
463 opposite direction emerges if left and right inputs signal inversely, that is, when the body is
464 oriented right and left from the goal respectively (i.e., directional bias $< 0^\circ$). Robustness to
465 visual familiarity directional noise indicate that the direction in which views are learnt does
466 not need to be precisely controlled. See further analysis in Extended Data Fig. 1.

467

468 **Figure 2.**

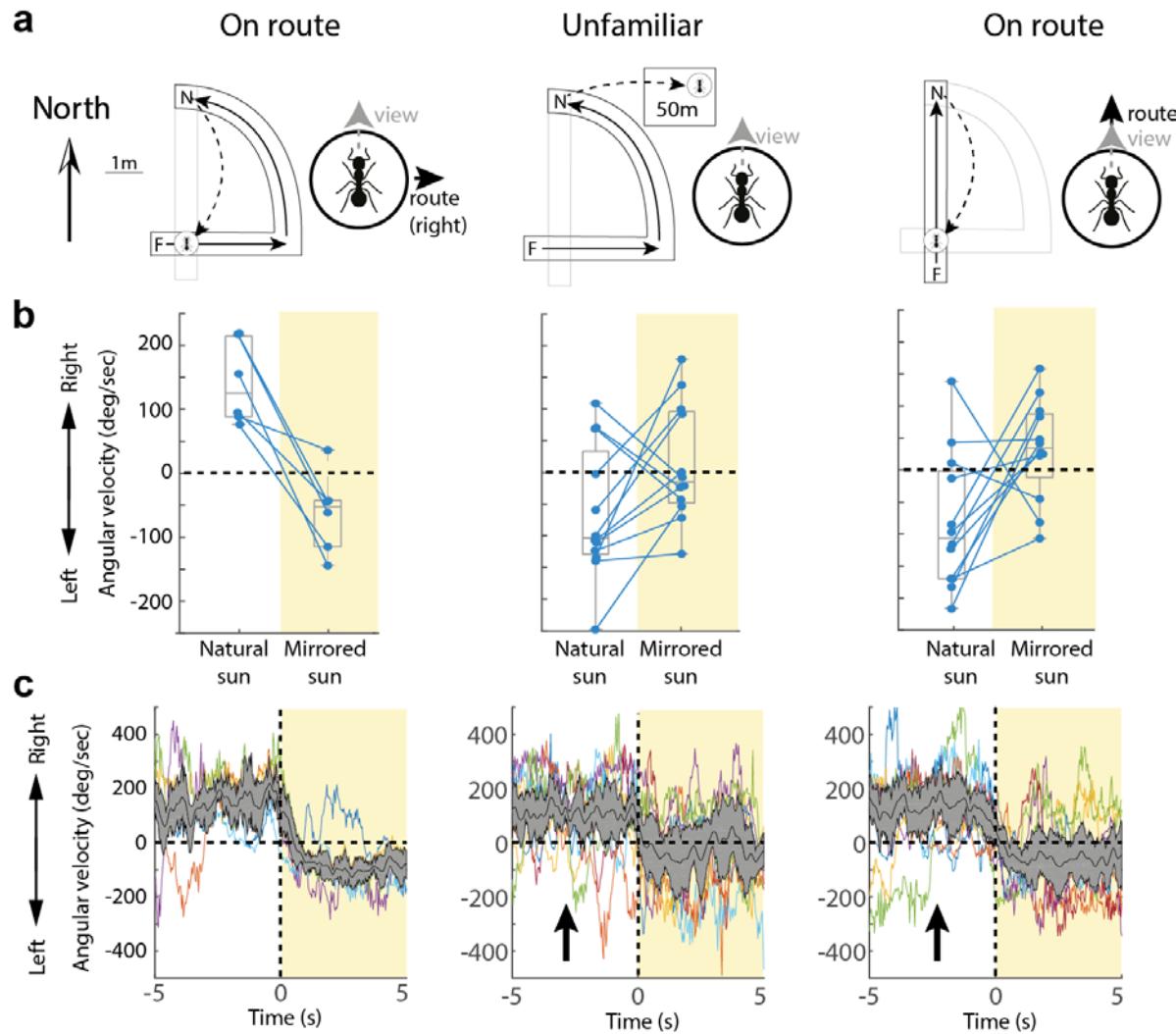


469

470 **Figure 2. Ants visually recognise whether the goal direction is left or right. a.** Homing ants
471 were captured at the end of their familiar route and fixed on the trackball (**b**) in 8 different
472 compass orientations. The route was rich in visual terrestrial cues (grey blobs). **F**: feeder, **N**:
473 nest. **b**. An individual *Cataglyphis velox* mounted on the trackball setup, holding its precious
474 cookie crumb. **c**. Turn ratio (degrees (right - left) / (right + left); mean ± se across individuals)
475 for the eight compass directions, on the familiar route or in the unfamiliar location (same
476 compass directions but unfamiliar surroundings) across 12 seconds of recording. **d**.
477 Proportion of time spent turning on the preferred side of each individual (mean ± se across
478 individuals). **C**: *Cataglyphis velox* ($n=17$), **M**: *Myrmecia crosslandi* ($n=11$).

479

480 **Figure 3**



481

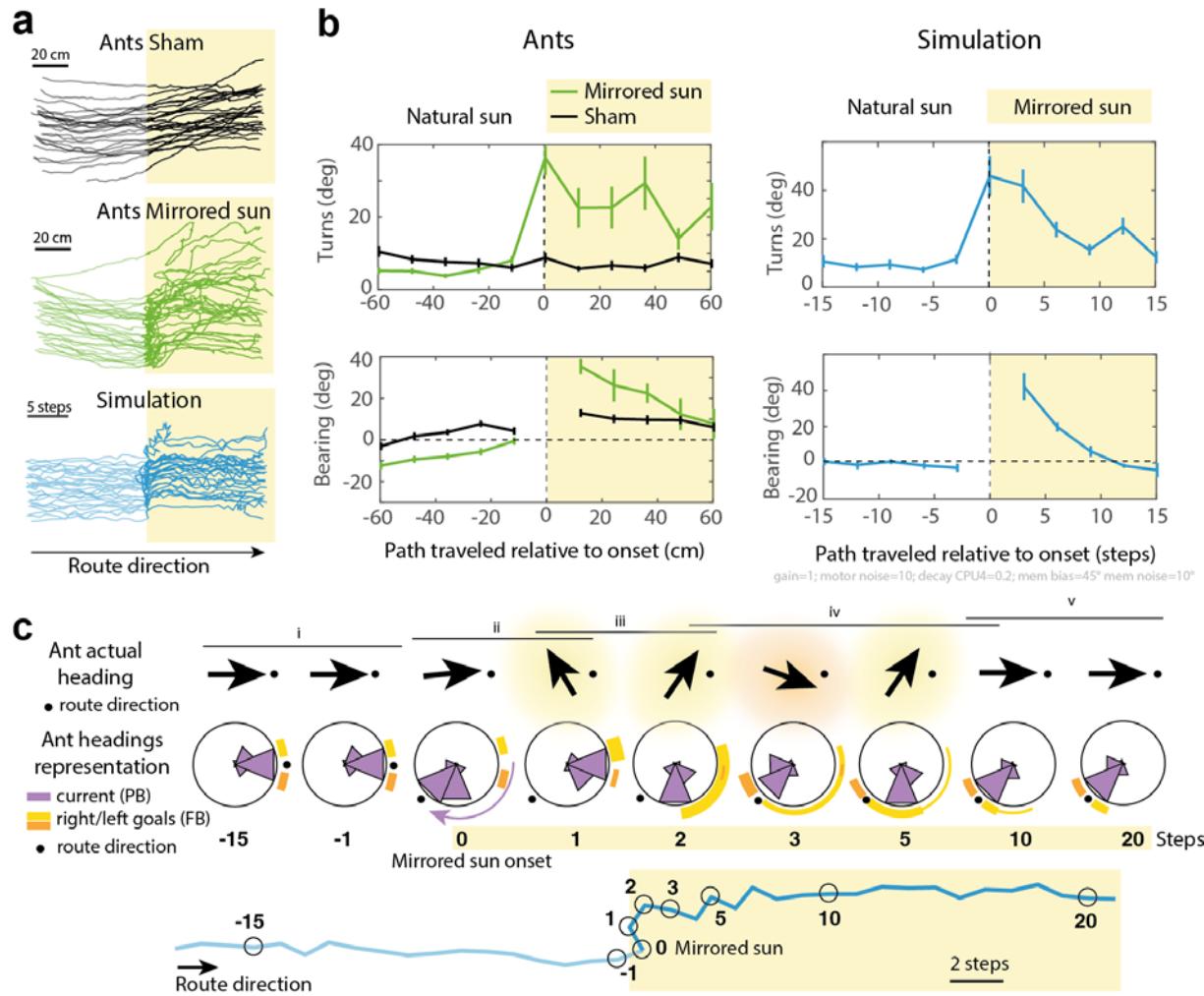
482 **Figure 3. Rotation of celestial cues shift turning direction based on familiar terrestrial cues.**

483 **a.** Schemes of the training and test condition. Homing ants were captured at the end of their
484 familiar route (black arrows: familiar route, F: feeder, N: nest) and fixed on the trackball with
485 their body always facing north, either on their route with the route direction 90° to the right
486 (left panel); or within unfamiliar surroundings (middle panel); or ants were trained along a
487 route oriented 90° to the previous one and released on their familiar route in the same
488 location and orientation, which this time is facing their route direction. **b.** Box plots indicate
489 average angular velocity (positive = right turn) each ant (dots) 5s before (white) and 5s after
490 (yellow) the apparent sun's position is mirrored by 180°. Wilcoxon test for: 'turn towards
491 the right with natural sun' (left panel: n=6, p=0.0156; middle panel: n=12 p=0.9788; right
492 panel: n=12 p=0.9866), 'mirror effect: turn direction reversal' (left panel: n=6, p=0.0156,
493 power=0.9994; middle panel: n=12 p=0.3955; right panel: n=12 p=0.0320). **c.** Turning

494 velocities (individuals in colour; median \pm iqr of the distribution in grey) across time, before
495 and after the sun manipulation (t_0). Arrows in the middle and left panels: the velocities of
496 some individuals have been inverted so that all individuals' mean turn directions before the
497 manipulation are positive.

498

499 **Figure 4**



500

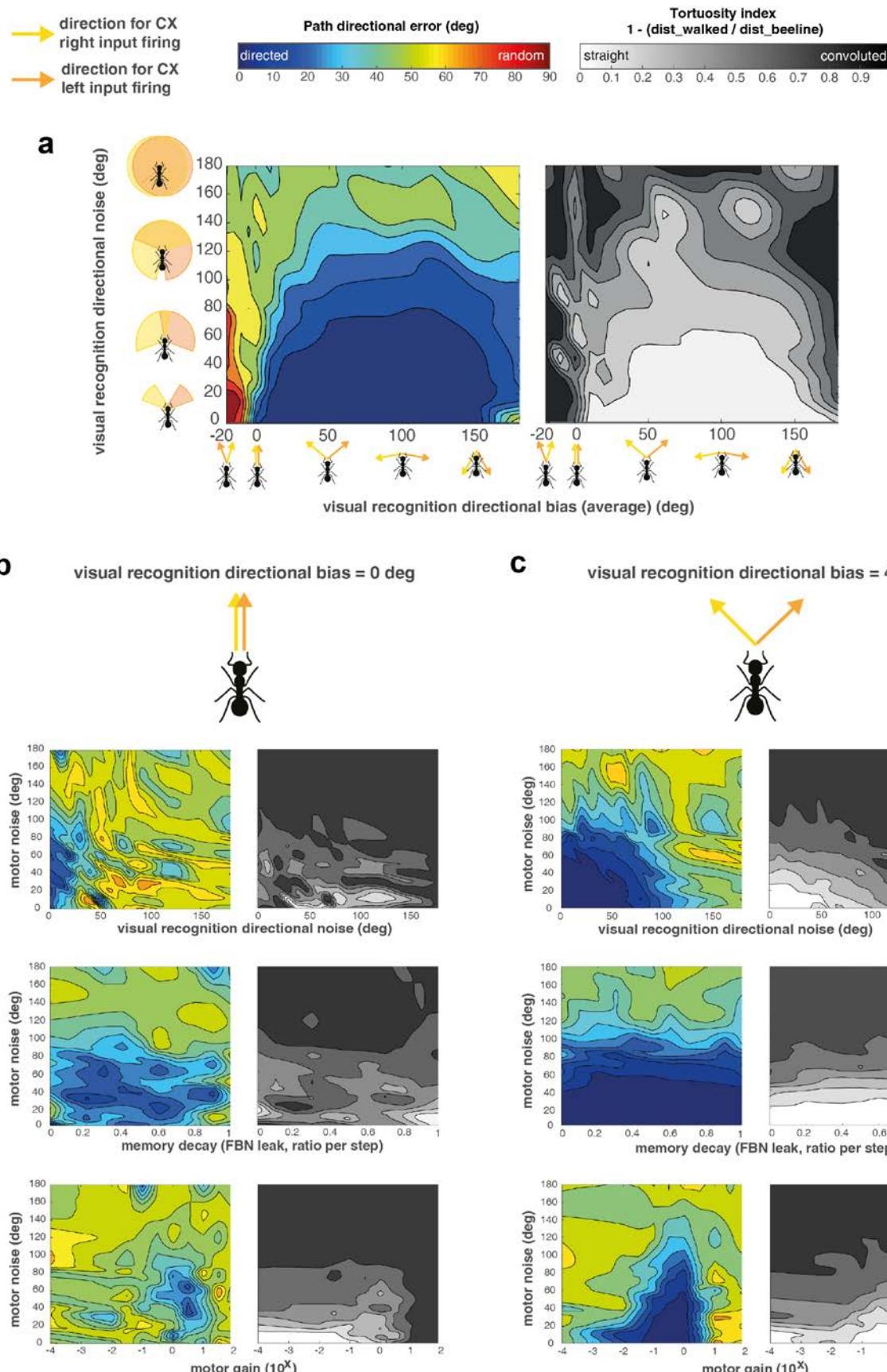
501 **Figure 4. Rotation of celestial cues affect ants route following as predicted.** Paths (a) and
 502 quantification of bearing and turns (b) of real (black and green) and simulated (blue) zero-
 503 vector ants (i.e., deprived of path integration information) recapitulating a familiar straight
 504 route while entering an area where we manipulated celestial compass cues (yellow). For the
 505 'Mirrored sun' condition (green) the real sun was hidden from the ants and mirrored so as to
 506 appear rotated by 135° counter clockwise in the sky. For the 'sham' condition (black), the
 507 experimenters were standing in the same place and the real sun was also hidden, but only a
 508 small piece of the sky (close to, but not including the sun) was mirrored for the ants.
 509 Simulated ants (blue) result from the model presented in fig. 1. Sun rotation was modelled
 510 as a 135° shift in the current heading representation (3-cell shift of the bump of activity in
 511 the Protocerebral Bridge). Paths of both real and simulated ants were discretised (segments
 512 of 12 cm for real ants, and of 3 steps for the simulations), before and after the sun rotation
 513 onset point. Turns correspond to the absolute angle between two successive segments,

514 bearing indicates the direction of segments relative to the route (0°). Turns at '0' on the x-
515 axes correspond to the angle between the segment preceding and following the shift of the
516 celestial compass. **c.** The effect observed in the simulations is quantitatively dependant on
517 the model's parameters (here gain=1; motor noise=10; decay FBN=0.2; visual familiarity
518 directional bias ± noise=45°±10° see Extended Data Fig. 1 for a description of parameters),
519 but its key signature can be explained qualitatively. (i) Under normal situation the current
520 heading is maintained between the right and left goal heading representation in the Fan-
521 shaped Body (FB) (yellow and orange marks) and updated by right and left visual familiarity
522 signals. (ii) The sun rotation creates a sudden shift of the current heading representation in
523 the Protocerebral Bridge (PB) (purple curved arrow), although the agent is still physically
524 facing the actual route direction (black dot). This leads the agent to display a sudden left
525 turn to re-align its shifted heading representation with the FB goal heading that is held in
526 short term memory. (iii) This novel direction of travel is visually recognised as being 'left of
527 the goal', causing a strong lateralised signal in the right FB's goal heading representation
528 (yellow). This biased activity triggers right turns, exposing the agent to new headings
529 recognised as 'right of the goal', and thus more signal sent to the right FB (yellow arcs),
530 favouring further right turns. (iv) Turning right eventually leads the agent to overshoot the
531 actual goal direction, recognise view as 'right from the goal' and thus signalling in the left FB
532 (orange). These signals are, at first, superimposed with the previous desired heading
533 representation, resulting in a period of conflicting guidance information causing meandering.
534 (v) The agent progressively updates its novel goal heading representation as the trace of the
535 previous desired heading fades out and the new one strengthens due to the incoming signals
536 from visual familiarity. In sum, motor decision results from complex dynamics between two
537 main factors: 1- how strong are the left and right visual familiarity signals updating the goal
538 heading representations (orange and yellow glow around the 'Ant actual heading' arrows),
539 which depend on whether the agent is oriented left or right from its goal; and 2- how well
540 the current heading representation (PB) matches the goal heading representation (more
541 detail in Extended Data Fig. 2).

542

543

544 **Extended data figure 1.**



546 **Extended data figure 1. Parameter exploration of the Central Complex model (see fig 3). a.**

547 This shows a parameter exploration for the CX model presented in **Fig. 1** (see **extended fig. 2**
548 for details of the circuitry). - Path directional error (absolute angular error between start-to-
549 arrival and start-to-goal directions) and path tortuosity (index = $1 -$
550 $(\text{beeline_distance}/\text{distance_walked})$) after 200 steps are shown according to various
551 parameter ranges. For each point on the map, all the other parameters are chosen to
552 maximise for lowest path directionality error.

553 **a.** Same as **Fig. 1d**, except that for each point of the map, the other parameters are chosen
554 to maximise for lowest path directionality error instead of being fixed at an average range.

555 Note that in **Fig. 1d**, visual familiarity direction bias < 0 typically results in routes leading to
556 the opposite direction (i.e., path directional error close to 180° , **see Fig. 1**). Here, maximising
557 for lowest path directional error did not result in goal-oriented path, but selected
558 parameters yielding very high tortuosity, thus indicated that no parameter regime can yield
559 straight, directed route when visual familiarity bias is < 0 . Note that straight, goal-oriented
560 paths emerge as long as the visual familiarity direction bias is > 0 , that is, if the left
561 hemisphere inputs correlate with moments when the nest is on the left, and vice versa.

562 **b.** Visual familiarity directional bias is fixed at a value of 0° , meaning that both CX inputs
563 respond maximally when the agent is facing the goal direction. Note that in this condition,
564 regions of low path directional errors (blue) and region of low path tortuosity (white) do not
565 overlap. This means that one cannot obtain straight, goal-directed paths if left and right CX
566 inputs respond when the nest is located in front.

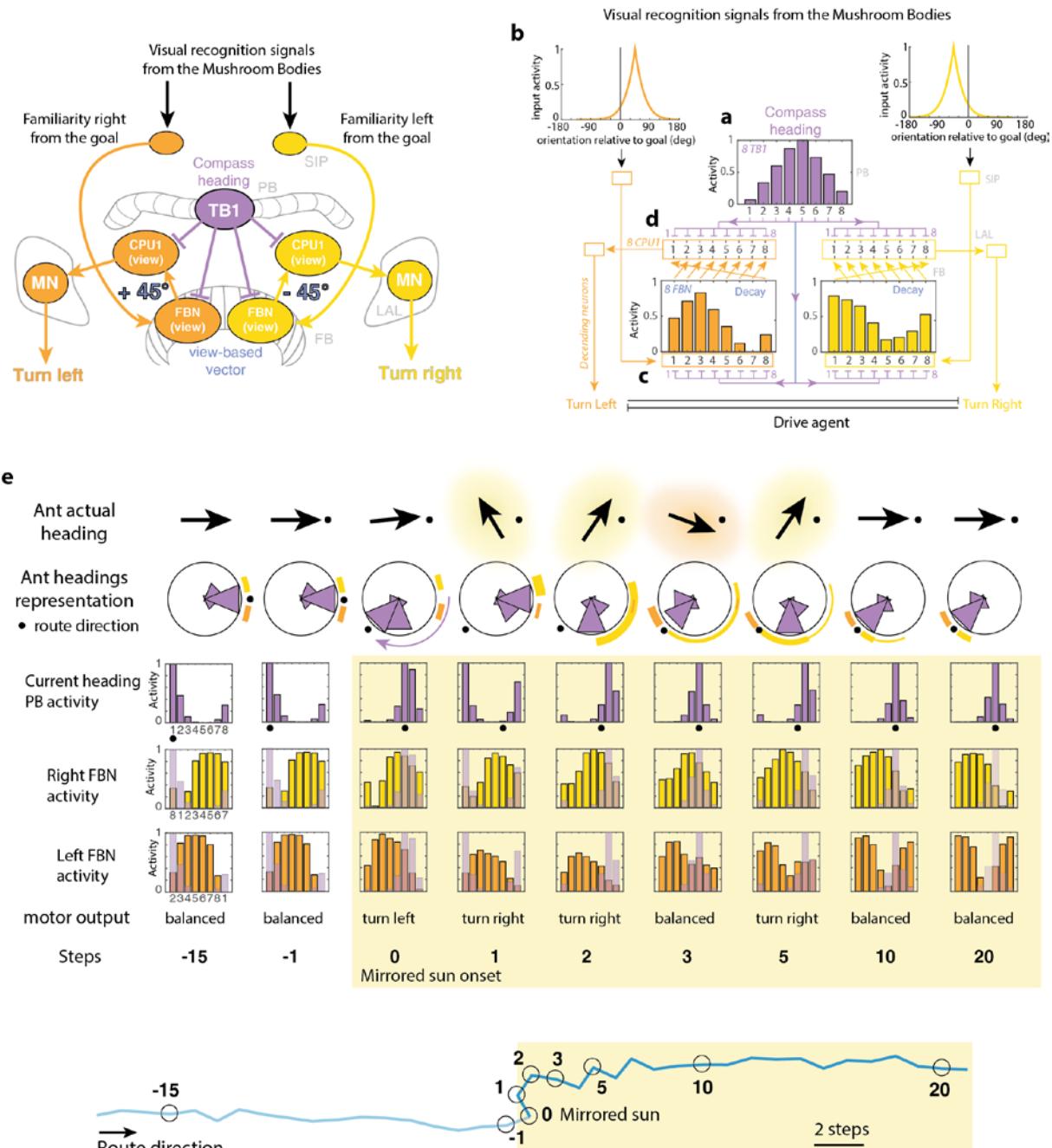
567 **c.** Visual familiarity directional bias is fixed at a value of $+45^\circ$, meaning that left and right CX
568 inputs respond maximally when the agent is oriented 45° to the right or left from the goal
569 direction, respectively. Note that regions with low path directional errors (blue) and regions
570 of low path tortuosity (white) overlap well, showing a very large range of parameters for
571 which we can obtain straight, goal-directed paths. We found the robustness to parameters
572 remarkable: the model copes with motor noise up to 80° , visual familiarity direction noise up
573 to 90° , is insensitive to its vector-memory decay and operates across several orders of
574 magnitude for the gain.

575

576 **Parameters' description:**

577 **Visual familiarity directional bias:** Indicates the absolute angle away from the goal at which
578 visual familiarity signals (i.e., the CX inputs) are highest, assuming 0° indicates the correct
579 goal direction. 0° indicates that both left and right inputs fire when the nest direction is
580 aligned with the current body orientation. Inversely, 180° indicates that left and right input
581 fire when the nest is right behind. Positive values (between 0° and 180°) indicate that the
582 left and right inputs fire when the nest direction is on the left and right hand side
583 respectively (the extent of the angular bias is given by the value). Negative values (between
584 0° and -180°) indicate a reversal, so that left and right input fire when the nest direction is on
585 the right and left hand side respectively. **Visual familiarity directional noise:** Represents the
586 extent of a systematic deviation from the visual familiarity directional bias angle. It is
587 implemented by shifting the input curve response (horizontal arrows in **Fig. 1b**) around its
588 mean (given by the 'directional bias') at each time step by random values drawn from a
589 normal distribution with standard deviation given by 'directional noise'. It can be seen as
590 representing a directional noise when storing visual memories. High directional noise means
591 that the input signal will occasionally respond strongest when oriented in the other direction
592 than indicated by the visual familiarity directional bias. Robustness to visual familiarity
593 directional noise indicates that the orientation of the body does not need to be precisely
594 controlled during memory acquisition. **Motor noise:** at each time step, a directional 'noise
595 angle' is drawn randomly from a Gaussian distribution of $\pm SD = \text{motor noise}$, and added to
596 the agent's current direction. **Memory decay:** proportion of Fan-shaped Body Neurons (FBN,
597 see extended fig 2 for details) activity lost at each time step: For each FBN: $\text{Activity}_{(t+1)} =$
598 $\text{Activity}_{(t)} \times (1 - \text{memory decay})$. This corresponds to the speed at which the memory of the
599 vector representation in the FBN decays. A memory decay = 1 means that the vector
600 representation in the FBN is used only for the current time step and entirely overridden by
601 the next inputs. A memory decay = 0 means that the vectors representation acts as a perfect
602 accumulator across the whole paths (as in PI), which is probably unrealistic. **Motor gain:** Sets
603 the gain to convert the motor neuron signals (see extended fig 2 for details) into an actual
604 turn amplitude ($\text{turn amplitude} = \text{turning neuron signal} \times \text{gain}$). Note that here, the motor
605 gain is presented across orders of magnitude. One order of magnitude higher means that the
606 agent will be one order of magnitude more sensitive to the turning signal.

607 **Extended data figure 2.**



608

609

610 **Extended data figure 2. Details of the CX model's circuitry.**

611 **a-d. General scheme of the CX model as presented in figure 1 (left panel) and the**
 612 **corresponding detailed circuitry (right panel). This model exploits the same circuit as the CX**
 613 **model used for PI^{12,14}, except that FB input indicate visual familiarity rather than speed of**
 614 **movement.**

615 **a.** Current heading direction is modelled in the Protocerebral Bridge (PB) as a bump of
616 activity across 8 neurons forming a ring-attractor (purple), as observed in insects¹⁴. Each
617 neuron responds maximally for a preferred compass direction, 45° apart from the neighbour
618 neurons (neuron 1 and 8 are functionally neighbours, closing the ring structure). Change in
619 the agent's current compass orientation results in a shift of the bump of activity across the 8
620 neurons (we did not model how this is achieved from sensory cues, see^{9,10,61} for studies
621 dedicated on this).

622 **b.** Visual familiarity signals fire according to the agent orientation relative to the goal
623 direction. Here the input curve indicates that right and left signals fire maximally when the
624 agent is oriented 50° (in average) left and right from its goal respectively (but see Fig. 1 and
625 Extended fig. 1 for variation of these parameters: 'directional bias' and 'directional noise').

626 **c.** These lateralised input signals excite two dedicated sets of FBN. These FBNs are
627 simultaneously inhibited by the current heading representation (purple), resulting in two
628 negative imprints of the current heading activity across the FBNs, which can be viewed as
629 two 'view-based vectors'. FBNs show some sustained activity so that, across time, successive
630 imprints are superimposed, thus updating the 'view-based-vectors' (as for Path integration,
631 except that this sustained activity is not crucial). The sustainability of such a 'view-based
632 vector' depends on the FBN activity's decaying rate, which can be varied in our model and
633 has little incidence on the agent's success (Extended figure 1, parameter decay).

634 **d.** Motor control is achieved using the same circuitry as for Path integration¹². On each brain
635 hemisphere, neurons (called CPU1 in some species), compare the current compass heading
636 (purple) with their version of the FBN 'view-based-vector'. Crucially, both FBN
637 representations are neurally shifted by 1 neuron (as if rotating the view-based-vector by 45°
638 clockwise or counter-clockwise depending on the hemisphere), resulting in an overall activity
639 in the CPU1 (sum of the 8 CPU1) indicating whether the view-based-vector points rather on
640 the left- (higher resulting activity in the left hemisphere) or right-hand side (higher resulting
641 activity in the right hemisphere). The CPU1 neurons sum their activity on descending motor
642 neurons (MN), which difference in activity across hemispheres triggers a left or right turn of
643 various amplitude, given a 'motor gain' that can be varied to make the agent more or less
644 reactive (Extended figure 1 for detailed parameter description). Numbers on the left indicate
645 neurons numbers. Letters on the right indicate brain areas (SIP: Superior Intermediate

646 Protocerebrum, PB: Protocerebral Bridge, FB: Fan-shaped Body, LAL: Lateral Accessory
647 Lobe).

648 **e.** Same as Fig. 4c, with added details of the PB (purple) and right and left FB (yellow and
649 orange) neural activity. Note that the FBNs order has been shifted (2,3,4,5,6,7,8,1 and
650 8,1,2,3,4,5,6,7) and inhibition exerted by the PB is represented (overlaid transparent purple,
651 1,2,3,4,5,6,7,8) as happens in the left and right CPU1 neuron (**d**). This way, the strength of
652 the motor signal for turning right and left – which correspond to the sum of non-inhibited
653 right and left CPU1 activity – can be inferred by looking at the area covered by non-occluded
654 yellow and orange FBN columns respectively.

655 With manipulation such as rotating the current compass information, it becomes apparent
656 that motor decision results from complex dynamics between two main factors: 1- how
657 strong are the left and right visual input signal updating the view-based-vectors
658 representation (represented by orange and yellow glow around the actual ant heading
659 arrows), which depend on whether the agent is oriented left or right from its goal and 2-
660 how well the current heading representation (PB) matches the rotated left and right shifted
661 FB view-based-vector current representations.