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1 **An intrinsic oscillator underlies visual navigation in ants**

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21 **Highlights**

- 22 • Ants show regular oscillations while navigating.
- 23 • Amplitude of oscillations are modulated by both learnt and innate visual cues.
- 24 • This modulation optimizes the balance between exploration and exploitation.
- 25 • Oscillations are produced internally as reproduce with a simple neural model.

26

27 **Abstract**

28 Many insects display lateral oscillations while moving, but how they are produced and
29 participate in visual navigation remains unclear. Here we show that visually navigating ants
30 continuously display regular lateral oscillations coupled with variations of forward speed that
31 strongly optimise the distance covered while simultaneously enabling them to scan left and
32 right directions. This pattern of movement is produced endogenously and conserved across
33 navigational contexts in two phylogenetically distant ant species. Moreover, the oscillations'
34 amplitude can be modulated by both innate or learnt visual cues to adjust the
35 exploration/exploitation balance to the current need. This lower-level motor pattern thus
36 drastically reduces the degree of freedom needed for higher level strategies to control
37 behaviour. The observed dynamical signature readily emerges from a simple neural-circuit
38 model of the insect's conserved pre-motor area known as the lateral accessory lobe, offering
39 a surprisingly simple but effective neural control, and endorsing oscillations as a core,
40 ancestral way of moving in insects.

41

42 **Keywords:** insect navigation, time series analysis, intrinsic oscillator, lateral accessory lobe.

43

44 **Introduction**

45

46 Navigating through space implies both to acquire information (exploration) and to use this
47 information to move in the correct direction (exploitation). A way to acquire information is to
48 sample the environment by actively moving. Such 'active-sampling' is common across the
49 animal kingdom spanning from invertebrates¹⁻³ to vertebrates⁴⁻⁸. However, active sampling
50 entails movements that are typically different than moving towards the goal and thus requires
51 the animal to solve a trade-off. Achieving a balance between sampling actions (exploration)
52 and goal-directed actions (exploitation) lies at the core of the behavioural control, but how it is
53 achieved and evolved in animals remains unclear.

54 A way of sampling the world is through the production of regular alternations between left and
55 right turns along the path: lateral oscillations. Lateral oscillations are observed in wide range
56 of taxa (vertebrates^{8,9}; invertebrates¹⁰⁻¹⁴) and have been mainly studied in the context of
57 olfactory behaviours such as plume following in moths^{12,15-17}, trail following in ants¹⁸ or odour
58 gradient climbing in *Drosophila* larvae¹⁴ and *Caenorhabditis elegans*¹⁹. The intrinsic
59 production of oscillations enables an efficient sampling of odour across locations and models
60 show that oscillations modulated by odour perception enables to reach the source in a
61 remarkably effective way^{14,19,20}.

62 Modelling studies have shown that lateral oscillations can also be useful for visual navigation.
63 For instance, having the amplitude of oscillation modulated by the familiarity of the perceived
64 visual scenes, can produce robust visual navigational behaviours such as route-following²¹ or
65 homing²², and captures particular behavioural signatures observed in ants²³. Moreover, visually
66 guided insects such as ants²³⁻²⁸, wasps^{29,30} or bumblebees³¹ do display oscillations, whose
67 expression appears to be coupled with visual perceptual cues. But whether these lateral
68 oscillations are produced internally, how exactly they interact with visual cues and how they
69 participate to the visual navigational task remains unclear.

70 We focused on the expression of oscillations in two ecologically and phylogenetically distant
71 ant species: *Myrmecia croslandi* are solitary foragers relying heavily on vision^{23,27,32-34} ; and
72 *Iridomyrmex purpureus* that uses mass recruitment and pheromone trails but also other
73 modalities for navigation³⁵. The replication of the experiments in two distant species enables
74 to tell apart whether the observed signatures are species-specific or shared across ants.

75 As most central place foragers, these ants species are known to rely on two main strategies to
76 guide their foraging journeys^{33,35}. The first strategy, commonly called Path Integration, allows
77 individuals to continuously estimate the distance and compass direction that separates them
78 from their nest (or other starting points) during their foraging trip³⁶⁻³⁸. The second, commonly
79 called view-based navigation, involves the learning and subsequent recognition of the learnt
80 visual panorama³⁸⁻⁴⁰. To see how these navigational strategies interact with oscillations, we
81 mounted ants on a spherical treadmill device⁴¹ (see Star methods), directly in their natural
82 environment. This device enables to record the ants motor behaviour in detail, without
83 interference of the uneven ground, while facilitating the control of the surrounding visual cue
84 perceived. We characterised whether the obtained trajectories show a regular oscillatory pattern
85 of movements and how these patterns are influenced by the presence or absence of: (1) visual
86 input, (2) learnt visual terrestrial cues, (3) path integration homing vector and (4) rotational
87 visual feedback. In both species, our results revealed the presence of a conserved pattern of
88 oscillations generated intrinsically, which comprises both angular and forward velocity
89 components. This pattern of movement provides a remarkable trade-off between exploration
90 and exploitation and the amplitude of the oscillations can be flexibly adjusted by visual
91 information in a way that is adapted to the navigational tasks at hand. Finally, we propose a
92 simple neural circuit model of reciprocal inhibition between left and right pre-motor area to
93 explore how these movement dynamics could be produced.

95 **Results**

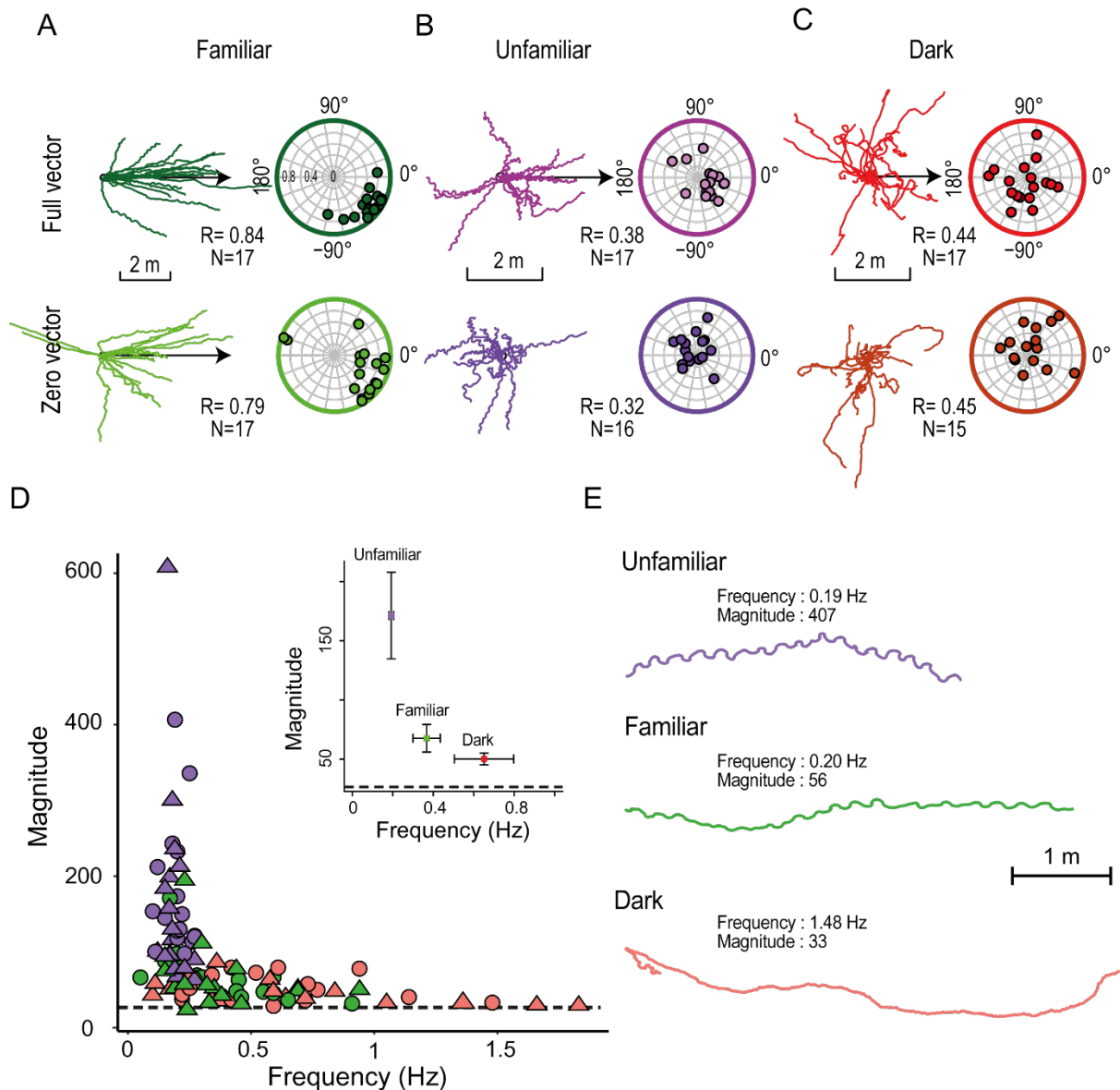
96

97 **Ants mounted on the trackball display their natural navigational behaviour**

98 We first investigated whether ants mounted on the trackball display their natural navigational
99 behaviours across different experimental conditions. When released on the ground in their
100 natural environment, both species studied here (*Myrmecia croslandi* and *Iridomyrmex*
101 *purpureus* see Figure S1) are known to rely on learnt terrestrial cues as well as, to a lesser
102 extent, on Path Integration (PI)^{23,33-35}. We first tethered ants and placed them on top of the
103 trackball in a way that enabled them to physically rotate and control their actual body
104 orientation⁴¹ (Figure S2). The trackball was placed in three distinct visual conditions: (1) along
105 the individual ant's familiar route (F) therefore in presence of familiar terrestrial cues; (2) in
106 an unfamiliar location (U) 50 meters away from their usual route; or (3) without any visual
107 input: in complete darkness (D). For each of these visual conditions, ants were tested either
108 with (full-vector (FV) ants) or without (zero-vector (ZV) ants) PI information. While FV ants
109 were captured at their feeding place and thus possess a PI homing vector pointing in the food-
110 to-nest compass direction, ZV ants were caught just before entering their nest and thus no
111 longer possess a PI homing vector.

112

113



114

115 **Figure 1. Oscillation characteristics vary across visual conditions.** Trajectories of *M.*
 116 *croslandi* tested on the trackball in a familiar panorama along their known route ((A) green),
 117 an unfamiliar panorama ((B) purple) or in the dark ((C) red). For each condition, individuals
 118 were tested either with (full-vector, top row) or without (zero-vector, bottom row) path
 119 integration information. Reconstructed paths over 60 s are displayed relative to the real (in
 120 familiar) or theoretical (in full-vector) direction of the nest (arrow). In the circular plots, each
 121 dot indicates the average circular vector calculated over the entire path of an individual,
 122 showing the mean direction and the average vector length (i.e., a point closer to the periphery
 123 indicates straighter paths). The R values ('Straightness' between 0 and 1) indicate the length
 124 of the average resulting vector of the population. The direction (in familiar terrain) or
 125 theoretical direction (for FV in unfamiliar terrain) of the nest is 0°. (D) The graphs show the
 126 frequency and spectral density magnitude of the dominant oscillation (highest magnitude) for
 127 method see method see Figure S2). High frequencies indicate a fast-oscillatory rhythm and
 128 high magnitudes indicate a strong presence of this oscillation. Individuals were tested within
 129 a familiar panorama (green), an unfamiliar panorama (purple) or in the dark (red). Symbols
 130 indicate whether the state of the Path Integration vector was full (round) or zero (triangles) at
 131 the beginning of the experiment. Inserts show the mean frequency against the mean
 132 magnitude of each visual condition with the associated 95% confidence interval around the

133 mean. The dashed black line represents the mean of the spectral density peak magnitudes
134 resulting from 200 Gaussian white noise signals. (E) example path for each condition for *M.*
135 *croslandi* across 100s.

136
137

138 Irrespectively of the PI state (FV or ZV), ants mounted on the trackball within their familiar
139 visual route (i.e., in the presence of learnt terrestrial cues) displayed paths that were oriented
140 toward the nest direction (Figure 1A; Rayleigh test with nest as theoretical direction ps: FV &
141 ZV < 0.001), proving that they recognised and used the familiar terrestrial cues to orient even
142 without PI information (ZV). When tested in unfamiliar surroundings, FV ants were oriented
143 towards the theoretical direction of the nest as indicated by their PI (Figure 1B first row;
144 Rayleigh test with PI as theoretical direction p: FV< 0.001); but ZV ants (Figure 1B second
145 row) showed random orientations (Rayleigh test p: ZV=0.443). This confirms that the distant
146 release points were indeed unfamiliar to the ants and that the ants relied on their PI when tested
147 as FV ants. When tested in total darkness, ants displayed randomly orientated paths in all
148 conditions (Figure 1C; Rayleigh test p: FV=0.354; ZV=0.360;), showing that the chosen dark
149 condition was effective in preventing the ants to use neither terrestrial nor celestial cues for
150 orientation. Overall, these results demonstrate that *M. croslandi* foragers rely on learnt
151 terrestrial cues as well as their PI to navigate when mounted on the trackball system (Figure 1).

152 We then looked at the individual's path straightness (R values in Figure 1 that indicate
153 whether the ant's travel directions were rather constant across time (R=1) or not (R=0)).
154 Independent of the PI state, the ants' paths were straighter in familiar terrain as compared to
155 the other conditions (Figure 1; Familiar vs. Unfamiliar & Familiar vs. Dark: ps < 0.001),
156 showing that the recognition of learnt terrestrial cues was most effective at helping the ant to
157 maintain a constant direction of travel. With regards to the effect of PI state, there was no
158 difference on the path straightness within each visual condition (FV vs ZV ps <0.1, Figure 1)

159 Overall, these results show that *M.croslandi* rely greatly on learnt visual cues and to a
160 lesser extent on their PI. The latter still enables them to guide their general direction in
161 unfamiliar terrain, but has only a limited impact on their path's straightness. Qualitatively
162 similar results were obtained with our second species *I. purpureus* (see Figure S1). These
163 results are consistent with what is observed in these species when navigating on their natural
164 grounds^{33,35}.

165

166 **Ants display regular lateral oscillations**

167 To determine whether ants display regular lateral oscillations – that is, alternate between left
168 and right turns at a steady rhythm – we first used our video recordings to track the ant's
169 change in body orientation when mounted on the trackball. The body angular velocity signal
170 is independent of the ant's actual forward movement and thus a direct reading of its motor
171 control for turning. We conducted a Fourier analysis on autocorrelation coefficients of the
172 angular velocity time series to obtain a 'power spectral density' (PSD) (see Figure S2 C-E)
173 for detailed method). This PSD provides information about the regularity and frequency of
174 oscillation, with higher magnitude values (y axis; Figure S2E) indicating more regular
175 oscillation at the corresponding frequency (x axis; Figure S2E). For each ant, we selected the
176 frequency corresponding to the highest magnitude (peak), that is, the most salient rhythm in
177 the signal. In all experimental conditions, the obtained peak fell in the expected range of 0.2
178 to 1.5 Hz, as observed in other insect species^{14,42}. It should be noted that this rhythm is 10 to
179 50 times slower than ants' typical stepping frequency⁴³ and thus are not the consequence of
180 their rhythmic walking gait and hence must be the product of a different oscillatory
181 mechanism. For both species, the obtained highest PSD magnitudes obtained with the ants
182 signal were higher than the ones obtained with a Gaussian white noise (Figure 1D dashed
183 line; Wilcoxon one-tail test: $p \leq 0.001$, see Figure S3 A, C for *I. purpureus*), showing that ants

184 displayed lateral oscillations with a higher regularity than random. We also replicated the
185 same analysis using tracks of *M. croslandi* ants recorded directly on the ground while
186 displaying learning walks around their nest (Figure S4), which confirms that these regular
187 oscillations are not a consequence of being mounted on the trackball set-up.

188

189 **The navigational context modifies the regularity and frequency of oscillations**

190 We tested whether the visual condition and the state of the path integrator influenced how
191 regular the oscillations are, which can be measure with the magnitude of the individuals'
192 power spectral density peak, (PSD, see S2 C-E for individual example and method) (Figure
193 1D, E). The statistical model revealed no interaction between both effects (AIC=-198.8,
194 $F_{2,101}=0.434$, $p=0.647$) however the additive model (i.e., without interaction AIC=-215.8)
195 explains the variation of the magnitude peaks relatively well (R^2 marginal=56% &
196 conditional=67%). PI state did not affect the regularity of oscillations (PSD peak magnitudes
197 (Fig, 1D; Anova: vector effect: $F_{1,101}=1.291$, $p>0.200$)), however, the three visual conditions
198 did (Fig, 1D; Anova: visual condition effect: $F_{2,101}=83.663$, $p < 0.001$; Post-hoc: F vs. U:
199 $p<0.001$; F vs. D: $p=0.016$; U vs. D: $p<0.001$): oscillations were most regular in unfamiliar
200 terrain, intermediate in familiar environment and least regular in the dark (Fig, 1D, E;
201 mean±se: $U_{(FV+ZV)}=171±19$; $F_{(FV+ZV)}=68±6$; $D_{(FV+ZV)}=50±3$). The effect of individuality is
202 significant ($p=0.015$), indicating that some individuals show more regular oscillations than
203 others, across conditions.

204 We then investigated whether our different conditions influenced the oscillations'
205 frequencies (Figure 1D, x axis), which indicates how quick the turn alternation happens. Here
206 again, the PI state had no observable effect (Wilcoxon test for repeated measures; F: FV vs.
207 ZV $p=0.635$; U: FV vs. ZV $p=0.343$, mean±se in F: FV=0.38±0.05 Hz, ZV=0.34±0.04 Hz; U:
208 FV=0.19±0.01Hz, ZV=0.18±0.0009 Hz, Fig 1 D), however, independent of the PI state, the

209 oscillatory frequencies were significantly higher in a familiar (F) than in an unfamiliar (U)
210 visual panorama ($p=0.023$, $\text{mean}\pm\text{se}$: $F_{(FV+ZV)}=0.37\pm0.036$ Hz; $U_{(FV+ZV)}=0.19\pm0.008$ Hz;
211 Figure 1D). Thus, the presence of familiar visual cues tends to increase the frequency of
212 oscillations.

213 In the dark however, peak magnitudes are significantly weaker, closer to Gaussian
214 noise and with a wider frequency range, suggesting that the PSD peak in some individuals
215 may result from noise (Figure 1D, E). Oscillations seems to persist in the dark, however their
216 expression is greatly inhibited suggesting that visual input is important for the expression of
217 oscillation (Figure2).

218 Overall, these results confirm the existence of regular oscillations and that their
219 expression are influenced by the perceived familiarity of the visual surrounding, with slower
220 and most regular oscillations being expressed in unfamiliar terrain (Figures 1D, E, S4A). The
221 second ant species *I. purpureus* showed significantly regular oscillations, too, with the same
222 tendency to produce slower oscillation in visually unfamiliar terrain and to inhibit their
223 expression when in the dark (Figure S3).

224

225 **The navigational context modulates the angular and forward velocity of oscillations**

226

227 To investigate the dynamics of the ant oscillatory movements in more details, we combined
228 for each ant its body angular velocity signal – obtained from video recording – with the
229 forward movement signal – obtained from the trackball movements. We reconstructed
230 ‘average cycles’ for each individual by pooling the angular and forward velocity recordings
231 3s before and 3s after the moments when ants switch from a left to a right turn (i.e., when the
232 time series of the angular velocity crosses zero from negative to positive; see Figure S5). That

233 way, we can quantify each individual's average dynamic of angular and forward velocity and
234 compare them across conditions.

235 The visual surrounding had a strong effect ($p < 0.001$): ants displayed higher peak of
236 angular velocities (Figure 3B, upper row; mean \pm se: $U_{(FV+ZV)} = 129 \pm 4.8$ deg/s;
237 $F_{(FV+ZV)} = 67.5 \pm 4.4$ deg/s) and higher forward velocities amplitude (Figure 3B, second row,
238 mean \pm se: $U_{(FV+ZV)} = 4.8 \pm 0.34$ cm/s; $F_{(FV+ZV)} = 2.3 \pm 0.2$ cm/s) in an unfamiliar environment.
239 There was however neither an effect of the PI state on turn or forward velocity ($p > 0.05$) nor
240 an interaction between the visual surrounding and the PI state (mean peak of angular velocity
241 model: AIC=160.9, interaction $p > 0.05$; amplitude of forward velocity model: AIC=109.9,
242 interaction $p = 0.22$). Therefore, the amplitude of lateral oscillations within the path are larger
243 in an unfamiliar panorama than in a familiar one, independently of the PI state (Figure 1E).

244

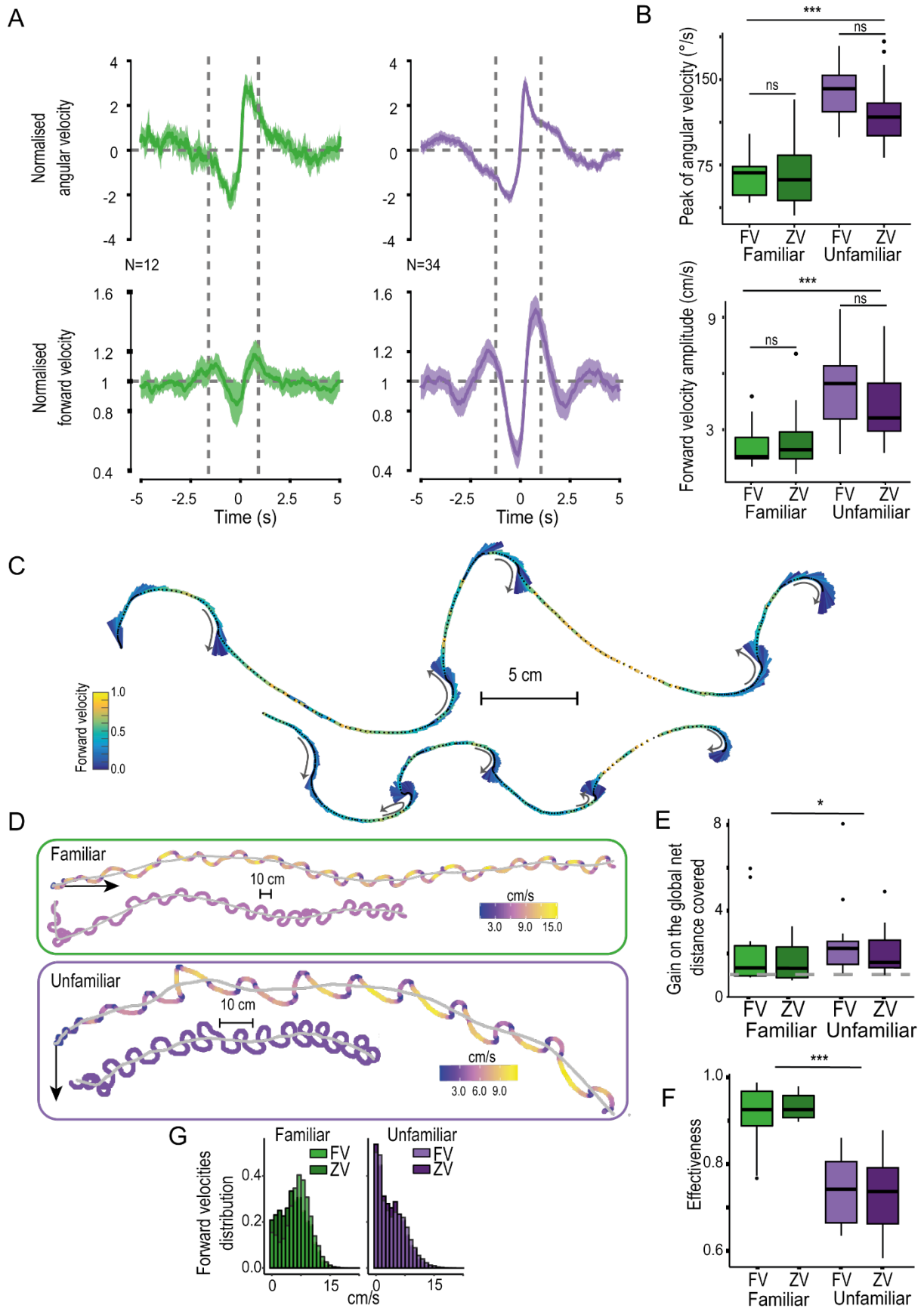
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246 **Lateral oscillations are combined with specific forward velocities variations.**

247

248 To test for the existence of conserved oscillatory dynamics across individuals, each
249 individual average cycle (Figure S2 F-I for method example) was normalised and averaged to
250 obtain a cycle at the population level. To ensure that we pooled ants oscillating at similar
251 frequency ranges, we separated data from familiar and unfamiliar terrain and selected only
252 individuals showing a peak frequency within 0.1 to 0.27 Hz for *M. croslandi* (N=12). These
253 frequency ranges correspond to high magnitude, ensuring that they are not a consequence of
254 noise. The emerging population-averaged oscillation patterns show the existence of
255 movement dynamics that are consistent across individuals, for both familiar and unfamiliar
256 environments (Figure 2 A). Forward velocity co-varies with angular velocity in a particular
257 way. Forward velocity is quite low when the ants reverse their turning direction (i.e., when

258 angular velocity crosses zero). In contrast, we observe significant peaks of forward velocity,
259 which happen briefly (up to 1s) while the ant is sweeping to the left or right (Figure 2A).
260 Remarkably, these peaks coincide well with the moment when the ants' body orientation is
261 aligned with its overall direction of travel (Figure 2A, dashed lines) even though during these
262 moments the ants' angular velocity is quite high. The same covariation is present in our
263 second species *I. purpureus* (Fig S3C, D), showing that this signature is not a specificity of
264 *M. croslandi*.
265 We replicated the same analysis using tracks of *M. croslandi* ants recorded directly on the
266 ground while displaying learning walks around their nest and observed the same relationship
267 between forward and angular speed (Figure S4), which confirms that these dynamics are not
268 a consequence of being mounted on the trackball set-up.
269



270

271
272

Figure 2: Co-variation of forward velocity and angular velocities optimize the distance covered and visual exploration. (A) Angular velocities (top-row) and forward velocity

273 (bottom row) co-vary in a way that seem conserved across visual condition (on familiar route
274 (green) or in unfamiliar terrain (purple)). Population cycles have been reconstructed by
275 merging full- (FV) and zero-vector (ZV) data and normalising the data amplitude within the
276 individual's average cycle (Figure S2 F-I). Colour areas around the mean curves represent the
277 95% confidence interval, based on the inter-individual variation. Dashed lines represent the
278 moment when the ants are facing their overall direction of travels. (B) boxplots show the
279 actual distribution of the non-normalised mean peak of angular speed (top row) and forward
280 velocity amplitude (bottom row) for the individuals' average cycle (FV on the left, ZV on the
281 right). (C) Details of paths (12s) displayed by two different individuals in unfamiliar terrain.
282 Black dots indicate the successive positions of the animal and vectors indicate the current
283 heading direction. Variation of forward velocities are indicated by both the colour and the
284 length of the vectors (the longer the vector, the smaller the forward speed and thus the higher
285 the time spent in this direction). Grey arrows emphasise the directions of turns. (D)
286 Reconstructed path (100s) of two individuals recorded in a familiar (green panel) and in an
287 unfamiliar (purple panel) panorama. Each path has been either reconstructed with the actual
288 forward velocity signal of the ant (top path) or with a constant speed (mean of the
289 individual's forward velocity signal, bottom path). Colour scales indicate the forward
290 velocity. For each path, the global trajectory is shown in grey (i.e., path smoothed to remove
291 the lateral oscillations). Straight black arrows indicate the direction of the nest. (E-G)
292 Population statistics across conditions. (E) Ratio of the effective distance covered (length of
293 grey path in (D)) between the reconstructed path with variation speed against path with
294 constant speed for the different condition. A ratio >1 (dashed grey line) indicates that the
295 effective distance covered is longer with forward speed variation than without. (F) Ratio
296 between the effective distance covered (length of grey path in (D)) and the actual distance
297 walked. (G) Distribution of the forward velocity in cm/s for each condition.
298

299

300 Thus, ants (Figure 2, S4, S3) display large sweeps from one side to the other and thus spend a
301 minimal amount of time facing their goal direction (i.e. the middle of the sweep), as angular
302 speed is high at this moment. However, they produce a burst of forward velocity during this
303 moment, that is, when aligned with their direction of travel (Figure 2A, C, D). On the
304 contrary, they slow down, sometimes up to a pause, at the end of each left and right sweep,
305 that is, when their body is facing away from their overall direction of travel (Figure 2A, C, D,
306 G).

307

308

309 **The dynamics of lateral oscillations optimise the distance covered.**

310

311 To investigate the benefit of such regular variations of forward movements within the
312 oscillations' cycle, we compared the ant's real paths with reconstructed versions of their path
313 where we kept the original angular speed signal but averaged the forward speed, so it became
314 constant (Figure 2D). By doing so the actual distance walked remains identical, but
315 remarkably, the effective ground distance covered (length of the grey paths in Figure 2D) by
316 the original paths (with forward speed variation) increased by up to a factor 8 (median =1.5;
317 25 / 75 percentiles = 1.08 / 2.5) compared to the paths with constant speed. This positive gain
318 concerns 81% of our individuals and is significant in all our conditions (ratio above 1:
319 $p < 0.009$, Figure 2E).

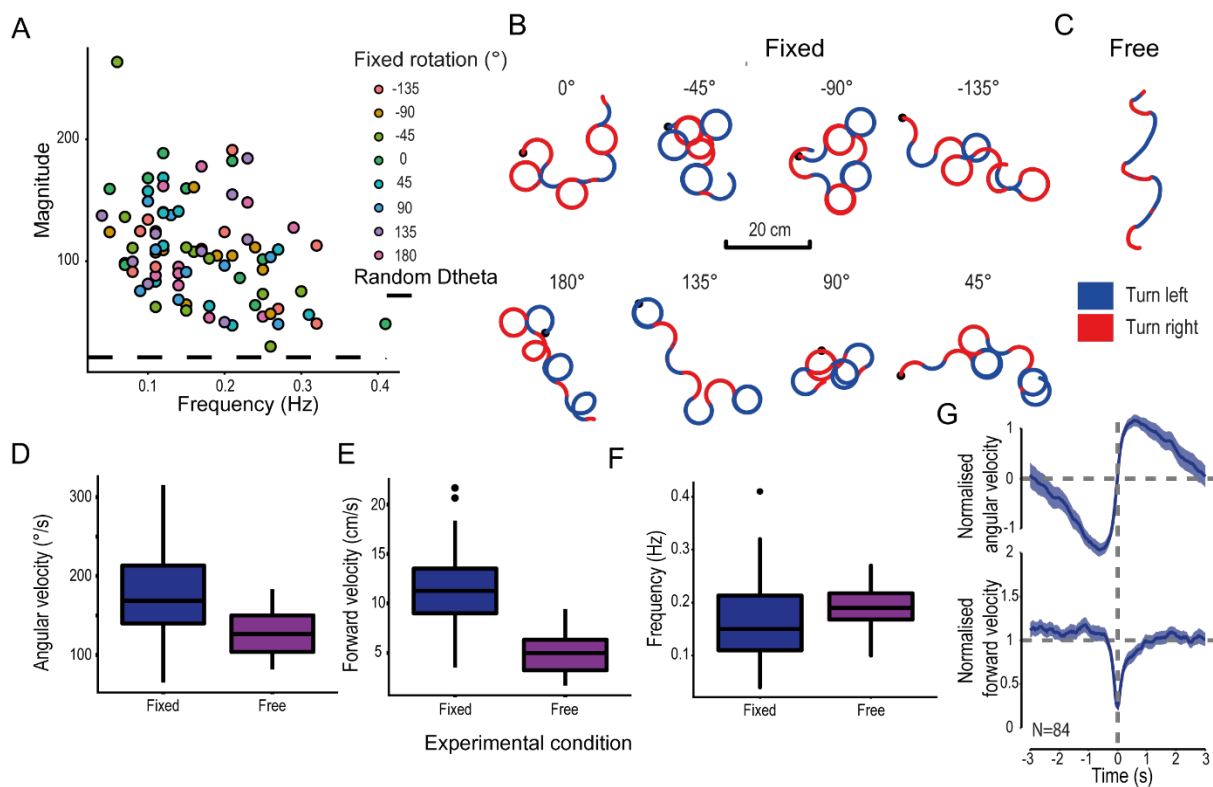
320 We then looked at the ratio between the effective ground distance covered (length of the grey
321 path in Figure 2F) and the actual distance walked across conditions. The smaller the ratio the
322 more local oscillations are impeding the ants to cover effective ground (a ratio of 1 indicates
323 a straight path, without local oscillations). Such an 'effectiveness ratio' is impacted by the
324 presence of familiar visual surrounding but not by the PI state (panorama effect:
325 $F_{1,101}=142.090$, $p < 0.001$; PI effect: $F_{1,101}=0.683$, $p = 0.407$). Paths displayed when on
326 familiar terrain are more effective to cover ground than in an unfamiliar environment (Post-
327 hoc, Figure 4D, F vs. U: $p < 0.001$). This is in line with the fact that ants displayed smaller
328 amplitude of oscillation in the presence of a familiar panorama (Fig 2A, B). In addition, we
329 observed that ants in familiar environment displayed less pauses (Fig 2G) and higher forward
330 velocities (N =34, $p < 0.001$, mean \pm se: F =6.087 \pm 0.336, U=3.961 \pm 0.182 cm/s).

331

332 **Oscillations are modulated by rotational feedback**

333 To test whether oscillations result from an intrinsic oscillator rather than a control mechanism
334 based on an external directional reference (i.e., servo-mechanism), we investigated whether
335 ants deprived of rotational feedback (either via optic-flow or compass cues) would still

336 oscillate. To do so, ants were mounted on the trackball in a way that prevented them from
 337 physically rotating their body on the ball: when the ant tries to turn, it is the ball that
 338 counterturns. In other words, the fixed ant experiences neither a change of body orientation
 339 nor visual rotational feedback when trying to turn (see Figure S2B). For this experiment, we
 340 recorded *M. croslandi* ants in unfamiliar terrain as this condition produced the clearest
 341 oscillations in our previous experiments (Figure 1D). To control for potential effects of facing
 342 directions (depending on celestial or terrestrial visual cues), we tested each ant fixed in eight
 343 subsequent different orientations with a 45° rotational shift.
 344



345

346

347 **Figure 3. Ants still oscillate in the absence of rotational feedback.** Zero-vector ants were
 348 tethered on the trackball in a way that prevented actual body rotation and tested in an
 349 unfamiliar environment. (A) Distribution of the individual Fourier dominant peak frequency
 350 and magnitude based on the angular velocity's spectral density time series (as in Figure 1D),
 351 method see Figure S2 B, C, D, E). High frequency indicates a fast-oscillatory rhythm, and a
 352 high magnitude indicates a strong presence of this oscillatory rhythm. The colour symbols
 353 represent the rotation relative to the theoretical nest direction (0°). The dashed black line
 354 represents the mean magnitude obtained from 200 Gaussian white noise signals (18.75). (B)

355 Example paths of different individuals fixed in different orientations. (C) Example path from
356 an ant that was free to rotate on the trackball, recorded in unfamiliar terrain in previous
357 experiments. (B, C) In both situations, ants alternate regularly between right (blue) and left
358 (red), but turns are sharper in the absence of rotational feedback. Peak of angular velocity
359 (D), peak of forward velocity (E) and Frequency (F) of the individual's average oscillation
360 cycle show that ants move faster, turn faster and slightly longer in the absence of rotation
361 feedback. (G) Angular velocities (top-row) and forward velocities (bottom row) co-vary in a
362 way that seem conserved across experimental conditions. Population cycles have been
363 reconstructed by merging all rotational condition as there is no differences of amplitude of
364 mean peak of angular velocity and mean forward amplitude cycles between rotational
365 conditions (Anova: $Df = F_{7,84} = 1.0103$, $p \geq 0.432$). Each individual signal has been normalised
366 before pooling. Coloured areas around mean curves represent the 95% confidence interval,
367 based on the inter-individual variation.

368
369

370 Despite the absence of visual rotational feedback, the obtained peak magnitudes of the
371 angular velocity power spectral density (PSD: see Star Method) were much higher than
372 expected from a Gaussian white noise ($p < 0.001$) clearly showing the presence of a regular
373 alternation between left and right turns (Figure 3A, B). The ants' body orientation relative to
374 the world had no effect on the magnitudes (orientation: $F_{7,83} = 0.3729$, $p = 0.914$) nor did the
375 other random parameters (individual $p = 0.933$, sequence $p = 0.473$). The mean oscillation
376 frequencies (mean \pm se: 0.17 ± 0.007 Hz) were quite close to what we observed when these ants
377 were free to rotate in an unfamiliar environment (Wilcoxon test for repeated measures: $p = 1$,
378 $N = 88$, Figure 3F). Thus, ants can display regular turning oscillations without rotational
379 feedback, whether as a result of optic flow or a change of orientation relative to directional
380 cues such as the visual panorama, wind, celestial compass cues or the magnetic field. Here
381 again, the lateral oscillations displayed by the fixed ants showed the simultaneous variation of
382 forward speed, as observed in the other conditions (Figure 3G). Consequently, we are left
383 with the conclusion that these oscillatory dynamics are generated intrinsically.
384 Interestingly, the absence of rotational feedback led to higher angular velocities (mean:
385 fixed = 176 deg/s; free = 128 deg/s; $p < 0.001$), higher forward velocity (mean: fixed = 11 cm/s;
386 free = 5 cm/s; $p < 0.001$) and slightly slower turn alternation (i.e., lower frequency: fixed = 0.16

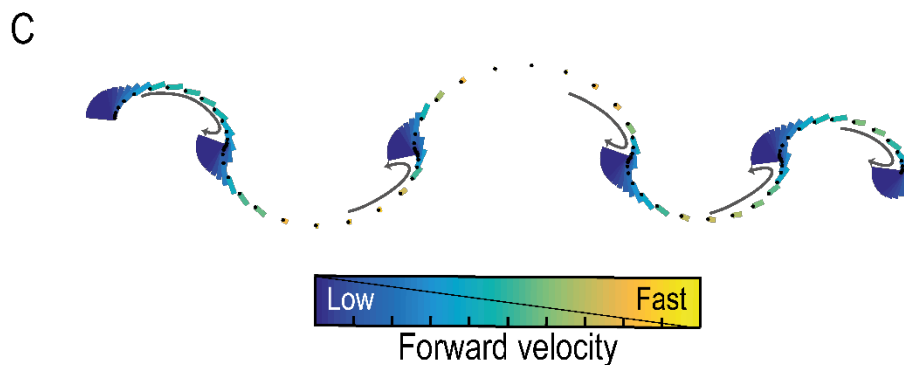
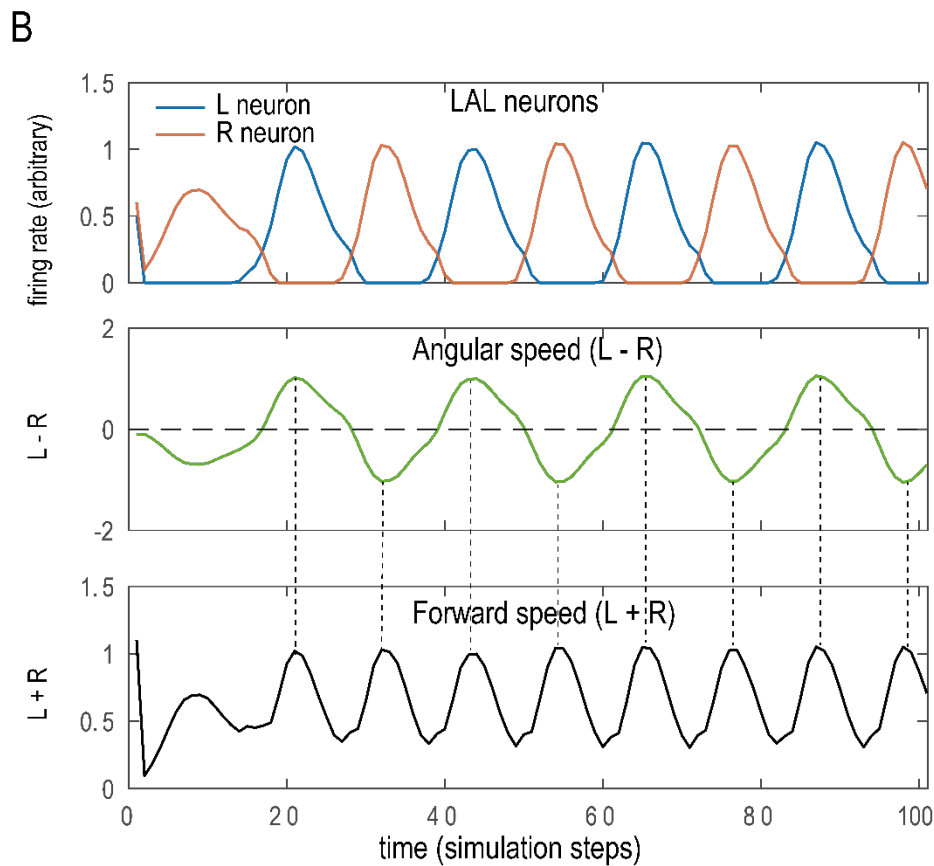
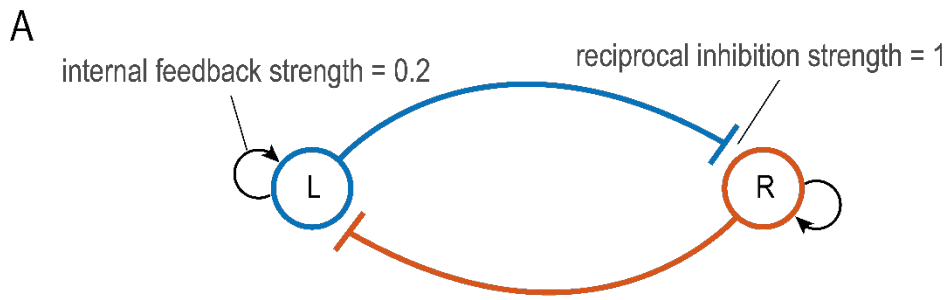
387 Hz; free=0.19 Hz, $p=0.0189$) than ants that were free to physically rotate on the ball (Figure
388 3A-F). Rotational sensory feedback is thus involved in limiting the amplitude of the
389 oscillations.

390
391

392 **The observed movement signature emerges readily from a simple neural circuit.**

393
394 Similarly to previous work^{44,45}, we designed a simplistic neural model based on the circuitry
395 of the insect pre-motor area so-called lateral accessory lobes (LAL). The purpose of this
396 model was not to match observed data quantitatively²⁰ but simply to test whether the co-
397 varying relationship observed between angular and forward velocity could emerge from this
398 type of circuit. Activation of the neurons in the left and right pre-motor areas are known to
399 mediate left and right turns respectively in insects^{11,13,45-48}. Furthermore, these left and right
400 regions are known to reciprocally inhibit each other^{11,13,45,47}. Modelling two reciprocally
401 inhibiting neurons with internal feedback – that tries to maintain a basal activity – is
402 sufficient to obtain the typical oscillatory activity between left and right LAL^{11,45} (Figure 4)
403 and thus provides an explanation for the regular oscillations between left and right turns
404 observed in insects. Interestingly, we show here that simply assuming that forward velocity is
405 controlled by the sum of left and right output – while angular velocity results from their
406 difference^{14,20,45} – is sufficient for the covariation observed in ants to emerge (Figure 4).
407 Bursts of forward speed appear when one side largely dominates over the other, that is when
408 the ant is at the maximum speed of its angular sweep and thus roughly aligned with its overall
409 direction of travel. Inversely, a break of forward speed occurs when the dominance is
410 reverted between LAL neurons, that is at the moment where ant reverts their turning direction
411 (Figure 4). Importantly, the emergence of this particular relationship is robust to parameter
412 change (Figure S5) and thus a stable feature of these types of circuits.

413



414

415 **Figure 4. Reciprocal inhibition between two units produces the observed relationship**
 416 **between angular and forward velocity.**

417 (A) Scheme of the model abstracted from the lateral accessory lobe (LAL). The Right (R) and
 418 Left (L) hemisphere neurons reciprocally inhibit each other (blue and red connection), while
 419 trying to sustain a basal firing rate through internal feedback (black arrow). (B) This results in

420 the emergence of stable anti-phasic oscillatory activity between the R and L neurons (B,
421 upper row). Assuming that angular velocity is controlled by the difference (B, middle row) –
422 and forward speed by the sum (B, bottom row) – between left and right activation is
423 sufficient to elicit the movement dynamics observed in ants (compare Figure 4C with Figure
424 2C). (C) Details of the dynamic of the path generated by the model. Colour indicates forward
425 velocity (scales are arbitrary). Black dots indicate the successive positions of the agent and
426 vectors indicate the current heading direction. Variation of forward velocities are indicated by
427 both the colour and the length of the vectors (the longer the vector, the smaller the forward
428 speed and thus the higher the time spent in this direction). As ants, the model results in a
429 zigzagging path where velocity drops during turn reversal and increases when facing the
430 overall direction of travel (Figure 2A, C, D). While the model enables the modulation of
431 amplitude and frequency of the oscillations, the forward/angular velocities relationship is
432 quite robust to parameter change (Figure S5).

433
434

435 **Discussion**

436

437 **An embedded solution for the compromise between exploration/exploitation**

438

439 We recorded the detailed locomotor movements of two distantly related ant species – *M.*
440 *croslandi* and *I. purpureus* – using a trackball-treadmill device directly in their natural
441 environment. Despite that one species is a solitary visual navigator (*M. croslandi*) and the
442 other (*I. purpureus*) uses pheromone trails and mass recruitment, we noticed a remarkable
443 similar behavioural signature. Both species continuously display regular lateral oscillations
444 with a synchronised burst of forward speed when facing the general direction of travel (Figure
445 1, 2A, C, S3). This pattern movement strongly optimises the overall ground distance covered
446 while simultaneously enabling the ant to slow down when scanning to left and right directions,
447 which may extend up to a full U-turn in some ants (Fig 2 C-F).

448 Previous observations assumed that ants accelerate when facing their goal direction as a
449 response to the recognition of familiar views when aligned in this particular direction^{49–51}. Here
450 we show that this acceleration is the product of an endogenous process, as it is still expressed
451 in unfamiliar terrain or when the ant body is artificially fixed on our trackball in a given

452 orientation (Figure 3). This findings stresses the often disregarded importance of internally
453 generated movement within the ‘sensorimotor’ loop^{2,8,52–54}.

454

455 The described internally generated movement dynamic provides an embedded solution for the
456 compromise between exploration (looking on the side) and exploitation (covering ground in
457 the desired direction). External visual cues can then modulate the exploration/exploitation
458 balance to the task at hand by simply adjusting the amplitude of this endogenous dynamic.
459 Higher amplitude oscillations optimise ‘exploration’ (higher amplitude scans) in an unfamiliar
460 environment, while lower amplitudes favour ‘exploitation’ (straighter paths) on a familiar route
461 (Fig 2, S3).

462 Interestingly, this movement signature is equally useful, and used, during the acquisition of
463 learnt visual information, when naïve ants display their learning walk around the nest²⁷ (Fig
464 S4). Optimising the learning of visual cues in naïve ants requires to bias the balance towards
465 ‘exploration’ in the same manner as searching for familiar cues in an unfamiliar environment
466 does in experienced ants; thus, it is not surprising to see here also high amplitude oscillations
467 (Figure 2A-D, S3). The apparent different needs for the acquisition of information on the one
468 hand and the use of that information on the other hand, are thus solved with the same sensory-
469 motor solution. The weaker modulation observed in *I. purpureus* (Figure S3) may be explained
470 by their strong reliance on chemical trails³⁵, whose absence on the trackball may favour
471 exploration in both visually familiar and unfamiliar conditions.

472 Finally, we see in both species that the internally generated oscillations can be strongly
473 inhibited when not needed, such as when moving in the dark (Figure 1C, D, S3A, B). Indeed,
474 oscillations are not always useful and it may be advantageous to repress them in situations like
475 when inside the nest or when trying to escape an aversive situation. Thus, both the animal’s
476 internal state and the presence/absence of relevant contextual information – such as a visual

477 panorama by opposition to no panorama at all – modulates the expression of the internally
478 produced oscillations in a similar vein as the male fly’s internal state continuously tunes up or
479 down the gain of circuits promoting visual pursuit⁵⁵. However, what specific type of visual
480 information promotes the expression of oscillations remains to be seen.

481

482 **Evolutionary consideration and neural Implementation.**

483

484 Lateral oscillations around 0.3-1Hz are also observed in moths^{12,15,16,56} *Drosophila* larvae¹⁴,

485 Colorado beetles⁴², flying hymenopteran^{29,30,57} and other insects¹³, suggesting an ancestral

486 way of moving, which predates at least the holometabolous insects’ common ancestor

487 (around 300 Myr ago).

488 In the insect brain, regular lateral oscillations seem to result from reciprocal contra-lateral

489 inhibitions between left and right hemispheric premotor areas, so-called Lateral Accessory

490 Lobes (LAL) an ancestral brain structure, highly conserved across insects^{13,44,45}. These circuits

491 – analogous to central pattern generators (CPG) – result in the internal production of

492 asymmetrical and rhythmical excitation between left and right motor commands, so-called flip-

493 flop neurons^{11,13,45-48}. However, while CPG are well known to sustain a wide range of

494 rhythmical limb movements^{8,53,58,59}, the LAL controls the displacement of the whole animal

495 across space and thus directly contributes to the navigational task.

496 Some have suggested that neural systems evolved at first to coordinate movements

497 endogenously^{54,60} whereas the modulation of these movements by external sensory

498 information originated only as a second step⁶⁰. This view is supported by the current

499 demonstration of an internally produced rhythm at the core of the navigational behaviour in

500 ants, as well as the observation that, across species, various multi-modal sensory cue

501 converge to the same conserved region (the LAL) to produce the remarkable variety of

502 navigational behaviours across species^{13,17,44,45}. Modulation of oscillations by olfactory cues

503 helps *Drosophila* larvae¹⁴ to climb odour gradient, male moths to track pheromone
504 plume^{12,13,15-17} and ants to follow chemical trails¹⁸. Modulation of oscillations by vision for
505 navigation, as observed in wasps^{29,30} bumblebees³¹ and ants²³⁻²⁸ may have appeared later
506 with the evolution of visual navigation in hymenopteran, through direct or indirect
507 connections between the mushroom bodies – the seat of navigational visual memories^{50,61,62}
508 – and the LAL (Figure 4). Modulation of oscillations by re-afferent rotational visual cues, as
509 we showed here in ants (Figure 3), might be ancestral to insects as we equally observe it in
510 moths^{16,17,63}. This likely evolved through connections between horizontal optic-flow detectors
511 in the optic lobes^{16,64} and the LAL (Figure 4), providing a useful feedback-control to calibrate
512 the amplitude of turns, and more generally participating in the widespread opto-motor
513 response¹⁶.

514

515 The forward speed variation within the oscillation cycles presented here has not been
516 reported in other insects' species and the fact that it is shared in two phylogenetically and
517 ecologically distant ants (Fig S3) suggests that it is a shared feature in the ant family. This
518 may be an adaptation for the use of vision while walking. Scanning multiple direction
519 through body rotation is key for visual scene recognition in hymenopteran^{40,65,66}, and because
520 ants are ground dwellers, they are reluctant to decouple their body orientation from their
521 direction of travel; even though they can⁶⁷. Ants thus benefit to pause when looking on the
522 side, otherwise they would depart away from their general direction of travel. Conversely, the
523 timely burst of forward speed when facing the overall direction of travel (Fig 2A, C, D)
524 enables to stretch the oscillations and thus strongly improves the amount of ground covered
525 (Fig 2 D-F). In addition, pausing when looking on the side must improve the efficiency of
526 visual recognition due to gaze stabilization, which accommodates remarkably well the idea

527 that views are learnt and recognized when oriented left and right – rather than towards and
528 away – from the goal^{29,68}.

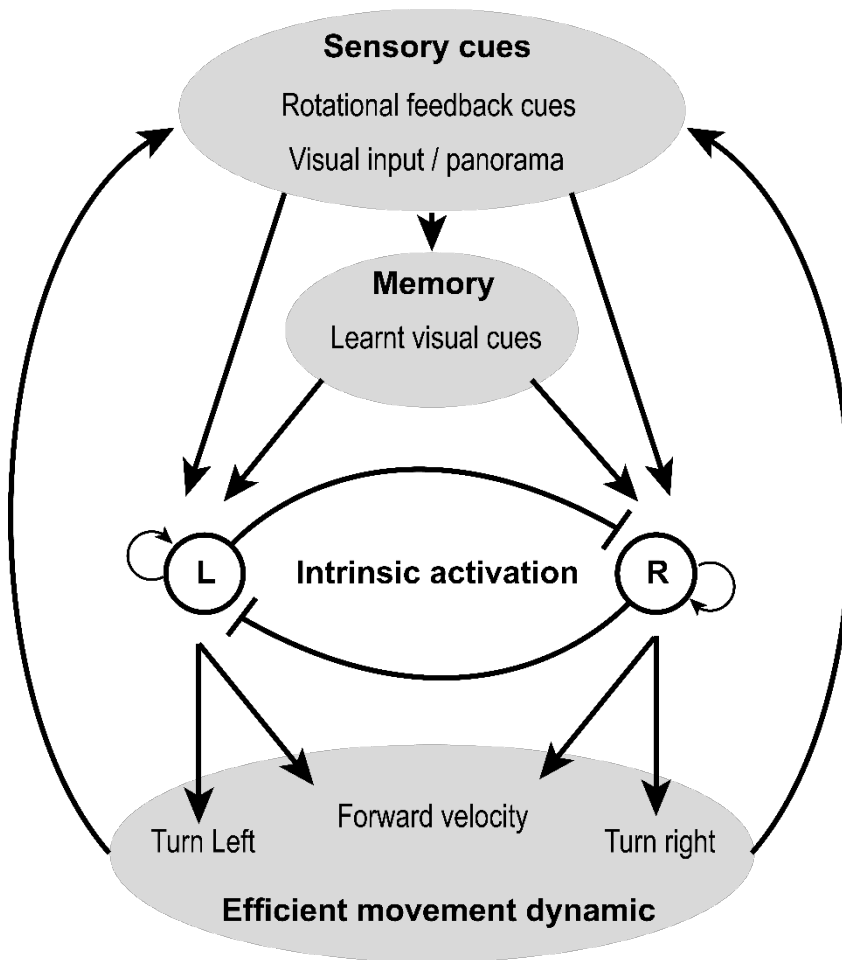
529

530 Interestingly, the efficient covariation between forward and angular velocity observed here in
531 ants is captured by a model of the LAL by simply assuming that forward speed results from
532 the summed excitation of both hemisphere motor commands; while turning velocities results
533 from the difference between left and right excitation (Figure 4). Certainly, we do not exclude
534 that more complex circuitry could produce other regimes of covariations, but our simple
535 model shows that this particular relationship between forward and angular speed is robust to
536 parameter change (Figure S5), and thus can readily emerge from the LAL. However, the
537 oscillations' amplitude and frequencies vary with parameter change, at least across a factor of
538 2 (Figure S5). Therefore, we can easily envision how various inputs into the LAL (such as
539 pictured in Figure 5) could modulate the amplitude and frequency of the emerging
540 oscillations, without altering the fundamental relationship between forward and angular
541 velocities. For instance, inputs from the central complex such as PFL2 neurons project
542 bilaterally to the LAL⁶⁹⁻⁷¹ and could thus promote the overall modulation of oscillations
543 amplitude as shown here. Inversely, PFL3 neurons, which project unilaterally to the LAL,
544 could mediate lateralised information, whether from memorised views⁶⁸ or path
545 integration^{72,73} to bias the oscillations toward one side⁷¹. Understanding precisely how such
546 inputs interact with oscillations in insects opens the door to a complexity that would be too
547 vast to tackle here, but given the rapid development of neurobiological tools and knowledge
548 about the circuitry of the lateral accessory lobes, this may constitute a realistic endeavour in
549 the near future.

550

551

552
553



554

555 **Figure 5. An intrinsic oscillator at the core of visual navigation.**

556 We propose a simple scheme to encompass our results. In this view, sensory input (in this
557 case various innate and learnt visual information) act on behaviour only indirectly, through
558 the systematic modulation of an intrinsic oscillator. The latter ensures that an efficient
559 movement dynamic is preserved across navigational contexts, which would not necessarily be
560 the case if various and potentially conflicting sensory information were directly modulating
561 movement. This scheme also highlights the idea that action is not merely the product of
562 perception. At the core of behaviour lies an intrinsic, self-generated dynamic, which are
563 modulated, rather than controlled, by sensory perception.

564

565 **STAR methods**

566

567 **RESOURCE AVAILABILITY :**

568 **Lead contact**

569

570 Further information and requests for resources and reagents should be directed to and will be
571 fulfilled by the lead contact, Leo Clement (clement.leo@univ-tlse3.fr).

572

573 **Materials availability**

574 As experiments took place in the natural environment this study did not generate new unique
575 reagents.

576

577 **Data and code availability**

578

579 Any data or code information required to generate this results paper is available from the lead
580 contact upon request.

- 581
- All data reported in this paper will be shared by the lead contact upon request
 - All original code has been deposited at: https://github.com/awystrac/Neural_oscillator
583 and is publicly available as of the date of publication.
 - Any additional information required to reanalyze the data reported in this paper is
585 available from the lead contact upon request

586

587 EXPERIMENTAL MODEL AND SUBJECT DETAILS

588 **Study Animal & Experimental site**

589 All experiments took place within an open grassy woodland at the National Australian
590 University, Canberra from Feb. to Mar. 2019. We had the opportunity to work with two
591 Australian endemic ant species: *Myrmecia croslandi* and *Iridomyrmex purpureus*. *Myrmecia*
592 *croslandi* workers are known to forage solitarily, with each individual either hunting on the
593 ground in the vicinity of the nest or navigating routinely back and forth toward the same
594 favorite foraging tree throughout her life span⁶⁶. These ants rely mainly on learnt terrestrial
595 visual cues to navigate but are also able to resort to PI when the visual environment does not
596 provide guidance^{27,32,39,66}. Eight nests of *M. croslandi*, that foraged on two distinct trees
597 between 6.0 and 30.0 m away from the colony, were used in this study. *Iridomyrmex*
598 *purpureus* ants form large colonies and forage along pheromone trails that lead to food
599 patches. Despite employing pheromone trails for recruitment, this species also uses both
600 learnt visual information and path integration for navigation³¹. We also performed
601 navigational experiments with two *I. purpureus* nests to ensure that this species relies indeed
602 on both learnt visual terrestrial cues and path integration, which they did surprisingly well
603 (see Figure S1). For the main experiment, a feeder was placed 7.0 m away from the nest and
604 foragers were free to familiarize themselves with the route for 72 h before being tested.

605 METHOD DETAILS

606 **Trackball system and data extraction**

607

608 During tests, ants were mounted on a trackball device³⁸. This device consists of a polystyrene
609 ball held in levitation in an aluminum cup by an air flow. The trackball has two sensors
610 placed at 90° to the azimuth of the sphere, which record the movements of this sphere and

611 translate them into X and Y data retracing the path of the ant. The X and Y acquisition of the
612 trackball rotations happened at a 30 Hz frequency (i.e., 30 data points per second), enabling
613 us to reconstruct the ant's movements with high precision. Additionally, a camera (640×480
614 pixels) recording from above provided details of the ant's body orientation, also at 30 Hz. We
615 also analyzed *M. croslandi* learning walks recorded directly on the natural ground. Head
616 directions were obtained via video recordings at 25 Hz (provided by Jochen Zeil).

617 In this study, we used two different trackball configurations to record the ants' motor
618 responses: further referred to as 'Free ant' and 'Fixed ant' experiments, respectively.

619 Free ant experiments: two small wheels prevented the polystyrene ball from rotating
620 in the horizontal plane, however, all other degrees of freedom of the ball rotation were
621 accessible (Figure S2 A; 'closed-loop'³⁸). Ants were attached on top of the ball by putting
622 magnetic paint on their thorax and a micro-magnet fixed at the bottom end of a single dental
623 thread that was in turn attached to a 0.5 mm pin. Crucially, the pin was placed within a glass
624 capillary. This procedure enabled the ants to execute physical rotations on the ball (the ball is
625 not rotating horizontally) but prevented any translational movement. Ants could thus execute
626 body rotations and control the direction in which they faced but any attempt to go forward or
627 backward resulted in ball rotations. We used the recorded videos to manually track the ants'
628 body orientation through time using the free software Kinovea (v-0.9.1).

629 Fixed ant experiment: the two small wheels were no longer in place. Hence, the ball
630 could now turn in any direction, including the horizontal plane (Figure S2B; 'open-loop'³⁸).
631 Ants were tethered directly to a needle with a micro magnet (glued at the end of the needle)
632 and magnetic paint on their thorax. The top end of the needle was glued to a small piece of
633 paper sheet (0.5×2.5 cm). Consequently, the fixed ant could no longer rotate, and the
634 experimenter could choose in which direction individual was facing. Any attempt to move,

635 including turning, by the ants resulted in ball rotations. This trackball configuration was only
636 conducted with the more robust *M. croslandi*.

637

638 **Free ant experiments: protocol**

639 At the start of each test, the ant was mounted on the trackball device but surrounded by an
640 opaque cylinder (30×30 cm) that prevented the ant from seeing any cues from the visual
641 scenery around her. Once the ant was in place on the device, the whole apparatus was moved
642 to the desired test location in the field. Afterward, the surrounding cylinder was removed,
643 revealing the visual scenery to the ant and data recording began. To ensure a high level of
644 homing motivation, only individuals who had previously received a 40% sucrose solution
645 (for *M. croslandi*) or a food item (for *I. purpureus*) were tested. The recording period was 3.5
646 min for the robust *M. croslandi* and 1.5 min for the flimsier *I. purpureus*.

647 To test the impact of terrestrial visual cues on the oscillation behavior, ants were
648 tested under three distinct conditions.

649 Familiar (F): ants were tested along their habitual route, which therefore presents a
650 familiar visual view.

651 Unfamiliar (U): ants were tested at least 50 m away from the habitual route, which
652 therefore presents an unfamiliar panorama.

653 Dark (D): ants were tested in total darkness, within an opaque cylinder (30×30 cm)
654 covered with a red Plexiglas plate that transmitted only the low red wavelengths, which ants
655 cannot perceive^{67,68}.

656 To test the impact of PI on oscillation behavior, ants were tested as either full- or zero
657 vector ants. Full vector (FV): ants were caught at the start of their inbound trip to the nest

658 (i.e., at the foraging tree for *M. croslandi* and at the feeder for *I. purpureus*). FV ants have an
659 informative homing PI vector, which points in the food-to-nest compass direction.
660 Consequently, FV ants can rely on both PI vector and the learnt visual scenery while being
661 tested. Zero vector (ZV): homing ants were captured just before entering the nest, that is, at
662 the end of their inbound trip. Hence, their PI homing vector is reduced to zero and thus no
663 longer directionally informative. Consequently, ZV ants can only rely on the learnt visual
664 scenery while being tested. For each of the three visual conditions FV and ZV ants were
665 tested, resulting in a total of six conditions.

666 For *I. purpureus*, at least 16 ants were tested in each of the six conditions (F: FV&ZV
667 =16; U: FV&ZV =17; D: FV=16 & ZV=17). Since *I. purpureus* forms very populous
668 colonies with an abundance of foragers, all individuals were tested only once, in one of the
669 six conditions. The data obtained are therefore statistically independent. On the contrary, *M.*
670 *croslandi* forms sparsely populated colonies and individuals usually make only one foraging
671 trip per day⁶⁶. Thus, it is time-consuming and challenging to capture, mark and follow
672 individuals throughout foraging trips. Individuals were therefore captured (either at the
673 foraging tree (FV) or before reaching their nest (ZV)) and tested successively in a pseudo-
674 random order in all three visual panoramas: Familiar (F), Unfamiliar (U) and in the Dark (D).
675 Both the sequence in which the visual conditions were experienced and the individuality were
676 included in the statistical models as it is likely that the state of the PI vector will be modified
677 across successive tests. Overall, 32 *M. croslandi* ants were tested with some individuals
678 tested as ZV or FV ants on two different days. At least 16 *M. croslandi* ants were tested in
679 each of the six conditions (F: FV&ZV =17; U: FV&ZV =17; D: FV=17 & ZV =16). Overall,
680 101 recordings were obtained.

681 In the 'free ant' experiments, the ant's body axis can turn without the ball movement.
682 We used the recorded videos to manually track the ants' body orientation through time using

683 the free software Kinovea. We removed the first 3s of recording of each ant as the removal of
684 the opaque ring may have disrupted the behavior. Overall, the analyzed recording length was
685 100s (except for two ants: 84 and 99s) for *M. croslandi* individuals and 50s (except for two
686 ants: 49s) for *I. purpureus* ants. For details of the Fourier analysis (see below); nine paths of
687 *I. purpureus* were discarded (F FV=1, U FV = 1, U ZV =2, D FV =2, D ZV = 3) as the ants
688 displayed too many pauses.

689

690 **Fixed ant experiments: protocol**

691 To test if oscillations are due to an intrinsic oscillator or caused by the fact that ants try to
692 keep a bearing toward an external stimulus, we conducted an additional experiment on *M.*
693 *croslandi* ants. We recorded foragers without an informative integration vector (ZV) in the
694 same unfamiliar environment (U) as before. Ants were tested in eight different fixed
695 orientations, covering the 360° azimuth by bins of 45°; and with one direction corresponding
696 to the food-to-nest compass direction. Each ant was tested in all eight orientations in a
697 pseudo-random sequence. To change the ant's orientation, the experimenter would first place
698 the opaque cylinder (30×30 cm) around the trackball system to prevent the ant from
699 perceiving the visual panorama, then rotate the whole set-up (trackball and mounted ant) and
700 finally remove the opaque cylinder to re-start data collection. Ants were recorded for at least
701 15s up to 20s in each orientation. Eleven ants were tested in all eight orientations. Since the
702 ants were fixed, trackball rotations along the horizontal axis provided a direct measure of the
703 angular velocity of the attempted turn generated by the ant. Angular velocity time series were
704 then extracted from the trackball data. At the end, the available length of the recordings for
705 the analysis had 512 frames (~17s) except for 5 individuals (294,394,456,474,494 frames). It
706 should be noted here that prior to the Fourier analysis (see below) we added a series of 0s

707 (zero padding) at the end of the time series until it had a length of 3000 data points to match
708 the same recording length obtained in the free ant experiment). This permits to increase the
709 precision in the frequency range obtained from the Fourier analysis.

710

711 QUANTIFICATION AND STATISTICAL ANALYSIS

712 All statistical analyses have been run using the free software R (v 3.6.2. R Core Development
713 Team). For all statistical tests, the p-values were compared to the critical alpha risk at 0.05,
714 with the appropriate correction if needed. Statistical parameters mean and the associated
715 standard error is given within the text and/or on figures: N represents the number of
716 individuals.

717 **Fourier analysis**

718 To reveal the occurrence of regular lateral oscillations, we choose to focus on the angular
719 velocity value (Figure S2C), which constitutes a direct reading from the left/right motor
720 control. This time series was processed through three successive steps to obtain its ‘spectral
721 density’, according to the Wiener-Khinchin theorem. First, the signal was parsimoniously
722 smoothed with a moving median running of a length of five frames (0.17s) to reduce the
723 influence of the recording noise (Figure S2D, dashed blue line). Then, the recorded time
724 series was passed through an autocorrelation function (Figure S2D). Finally, a Fourier
725 transform was performed on these autocorrelation coefficients, providing the power spectral
726 density (Figure S2E). With this approach, the magnitudes obtained are independent from
727 angular drift and amplitudes of the oscillations and thus can be directly compared across
728 individuals. A high magnitude indicates a strong oscillation for a given frequency. For each
729 individual, the dominant frequency (i.e., presenting the highest peak magnitude) and its
730 magnitude were extracted (Figure S2E, dashed blue lines). To check whether these

731 magnitudes indicate a significant regular oscillation, we compared them to the average
732 spectral density magnitude resulting from 200 Gaussian white noise signals of the same
733 length (within each species and experiment). Gaussian white noise signals were obtained by
734 drawing a sequence of random values drawn from a normal law. These simulated signals
735 were then processed through the exact same operations as the ants' angular velocity
736 recording: namely smoothing, autocorrelation, Fourier transformation and extraction of the
737 highest peak magnitude. The mean of the 200 highest magnitudes obtained was then
738 compared to the real ants' equivalent magnitudes with a Wilcoxon one-tail test. As each
739 experimental group has been compared with this mean magnitude of the simulated angular
740 velocity signal, the p-value is subsequently adjusted using the Bonferroni correction.

741

742 **Average oscillatory cycle**

743 To extract the average dynamics of an oscillation cycle, the mean cycles at the individual and
744 population levels were reconstructed as follows. First, we smoothed the angular velocity time
745 series of each individual by running twice a median with a window length of 31 frames for
746 *M. croslandi* (for both free and fixed experiments), 25 frames for data during learning walks
747 on the natural ground and seven frames for *I. purpureus*. This window length is much smaller
748 than one oscillatory cycle and thus smoothens the data without altering the cycle general
749 dynamics (Figure S2 F). Second, we indexed moments when the time series crosses 0 (from –
750 to +) as t_0 ; and extracted a window of ± 90 frames around the t_0 indices (± 60 frames for *I.*
751 *purpureus*; Figure S2 F). We then reconstructed a mean cycle for each individual by
752 averaging the individual's extracted windows, aligned at t_0 (Figure S2 G). The individuals'
753 average forward speed dynamics during one cycle was obtained in the same way by using the
754 same indices t_0 obtained from the angular velocity data (Figure S2 H). For each ant, the mean

755 angular velocity peak and amplitude of forward velocity cycles were extracted for analysis.
756 Finally, we reconstructed the average cycle at the level of the population by averaging the
757 mean cycle of all individuals. Note that to do so, each individual's mean cycle was first
758 normalized to show similar amplitudes ($\text{mean_cycle_normalised} =$
759 $\text{mean_cycle}/\text{mean}(|\text{mean_cycle_values}|)$). The goal was here to observe the cycle dynamics
760 through time and not to estimate the inter-individual variation in amplitude, which was
761 analyzed previously using the individual's mean cycle amplitude. Note that the criterion used
762 to align the time series (the change from a left to a right turn) necessarily creates an artefact
763 in the averaged angular velocity obtained. Namely, an average change from left turn to right
764 turn at t_0 . However, several factors indicate the relevance of such pooling at the population
765 level: (1) the period of the average cycle corresponds to the mean frequency obtained from
766 the Fourier transform. (2) we can observe a significant reversal of the angular velocity before
767 and after the mean oscillation cycle. (3) the associated forward velocities co-vary in a
768 significant way, indicating the existence of conserved dynamics.

769

770 **Analysis of the ants' direction of movement**

771 We reconstructed the ant paths of time that derived from the trackball recording for a fixed
772 period to determine the mean direction of movement (μ) as well as the mean circular vector
773 length (r , a measure of dispersion) of each individual. The mean directions (μ) were
774 analyzed using a Rayleigh test (from R package: Circular) that also includes a theoretical
775 direction (analogous to the V-test). To test whether the angular data are distributed uniformly
776 as a null hypothesis or if they are oriented toward the theoretical direction of the nest as
777 indicated by the state of the PI or the familiar panorama, the average vectors lengths (r) were

778 analyzed via a Wilcoxon-Mann-Whitney test with a Bonferroni correction for multiple
779 testing.

780

781 **Analysis of optimization**

782

783 To investigate the benefit of variation of forward and angular velocities signal on the
784 overall ground distance covered we reconstructed for each individual a fictive path where
785 forward speed was maintained constant (we took the average forward speed, so that the total
786 distance walked remain the same as in the original path). To estimate the overall ground
787 distance covered for a given path, we computed a ‘global trajectory’ by smoothing the path
788 with a sliding window, until effectively removing the oscillations component (Figure 4B grey
789 paths). To estimate the actual benefit of variation of forward speed on the distance covered,
790 we compared the length of the ‘global trajectories’ between the fictive path (with constant
791 forward speed) and original path (Fig 2D, E). A ratio >1 mean that the original path covered
792 more ground distance, and vice versa. Ratios were compared with Wilcoxon one-tail test to
793 the threshold one.

794 To test for an effect of the familiarity and vector on the distance covered we calculated an
795 ‘Effectiveness ratio’ for each individual as the ratio between the length of the ‘global
796 trajectory’ / ‘actual distance walked’ on the original paths with oscillations (Figure 2D, F). To
797 enable a fair comparison across individuals, we computed the “effectiveness ratio” on a 100s
798 portion of paths, using an additive mixed model.

799

800 **Statistical models**

801 For the free ant experiment, two types of models were tested: the first considering the
802 interaction between visual panorama and vector modalities, the second with simple additive
803 effect. It should be noted here that in case of deviation of the residuals of these models from
804 normality and or homoscedasticity, the response variables have been transformed. Only the
805 model presenting the lowest Akaike information criterion was retained and subsequently
806 analyzed via an analysis of variance (Anova), followed by a post-hoc analysis of Tukey's
807 rank comparison. Finally, for *M. croslandi* whose individuals were tested across several
808 conditions, the models are mixed models that controlled the sequence and the individuality
809 effect as random variable. For some models, we removed the sequence effect because of a
810 singularity problem of this factor (i.e., the information given by this variable is already
811 contained in other variables). For fixed ant experiments (which were tested only as ZV ants in
812 an unfamiliar environment), the model analyzed the effect of the condition of the subsequent
813 rotations.

814

815 COMPUTATIONAL MODEL

816 The computational model presented in Figure 5 has been built and run using Matlab®

817 R2016b. The code is open access and available at :

818 https://github.com/awystrac/Neural_oscillator

819 It is a step-based model ('For loop'). Two neurons (Left and Right neurons) reciprocally
820 inhibit each other, while trying to maintain a baseline activity through self-excitation and
821 internal feedback.

Variable	Description
----------	-------------

L	Left neuron activity
R	Right neuron activity
LNF	Left neuron internal feedback
RNF	Right neuron internal feedback

822

Parameters	Description
W	Reciprocal inhibition synaptic weight
Baseline	Firing rate of the oscillator neurons without any external modulation (default at 0.5)
Exhaust rate	Rate at which the negative internal feedback is modulated between each time step
Noise	Standard error of the normal distribution of the noise added to the activity of the neurons of the oscillator (default at 0.1)

823

824 Initialization

825 $R_1 = \text{random}(0 \text{ to } 1)$

826 $L_1 = \text{random}(0 \text{ to } 1)$

827 $RNF_1 = 0$

828 $LNF_1 = 0$

829

830 At each time step

831 L and R neuron update their activity due to their self-excitation, internal feedback, inhibition
832 from the other neuron, and noise.

833

$$834 \quad L_{t+1} = L_t - LNF_t - (R_t \times W) + (random(-1 to 1) \times noise)$$

$$835 \quad R_{t+1} = R_t - RNF_t - (L_t \times W) + (random(-1 to 1) \times noise)$$

836

837 Set a hard limit to the activity both neurons

838

$$839 \quad LM_{t+1} = \begin{cases} L_{t+1} & \text{if } L_{t+1} > 0 \\ 0 & \text{if } L_{t+1} \leq 0 \end{cases} \quad RM_{t+1} = \begin{cases} R_{t+1} & \text{if } R_{t+1} > 0 \\ 0 & \text{if } R_{t+1} \leq 0 \end{cases}$$

840

841 Update the internal negative feedback for the left and right motor neurons. The internal
842 feedback changes proportionally to the difference between its own activity and the neuron
843 activity (relative to the baseline activity)

$$844 \quad RNF_{t+1} = RNF_t + Exhaust\ rate \times (R_{t+1} - RNF_t - Baseline)$$

$$845 \quad LNF_{t+1} = LNF_t + Exhaust\ rate \times (L_{t+1} - LNF_t - Baseline)$$

846

847

848 Computation of the angular and forward velocities

849

$$850 \quad Angular_velocity = R - L$$

$$851 \quad Foward_velocity = R + L$$

852

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854

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868 Author contributions

869 LC Conception and Design of experiment, Data collection, Analysis and interpretation of

870 data, Drafting and revising the article. SS Conception and Design of experiment, Data

871 collection, Drafting and revising the article. AW Conception and Design of experiment, Data

872 collection, Analysis and interpretation of data, Drafting and revising the article, Supervision

873 of project.

874

876 **References**

- 877 1. Dittmar, L., Stürzl, W., Baird, E., Boeddeker, N. & Egelhaaf, M. Goal seeking in honeybees:
878 matching of optic flow snapshots? *Journal of Experimental Biology* **213**, 2913–2923 (2010).
- 879 2. Gomez-Marin, A., Stephens, G. J. & Louis, M. Active sampling and decision making in *Drosophila*
880 chemotaxis. *Nat Commun* **2**, 441 (2011).
- 881 3. Lehrer, M. SMALL-SCALE NAVIGATION IN THE HONEYBEE: ACTIVE ACQUISITION OF VISUAL
882 INFORMATION ABOUT THE GOAL. *The Journal of Experimental Biology* **199**, 253–261 (1996).
- 883 4. Dawkins, M. S. & Woodington, A. Pattern recognition and active vision in chickens. *Nature* **403**,
884 652–655 (2000).
- 885 5. Otero-Millan, J., Troncoso, X. G., Macknik, S. L., Serrano-Pedraza, I. & Martinez-Conde, S.
886 Saccades and microsaccades during visual fixation, exploration, and search: Foundations for a
887 common saccadic generator. *Journal of Vision* **8**, 21–21 (2008).
- 888 6. Wachowiak, M. All in a Sniff: Olfaction as a Model for Active Sensing. *Neuron* **71**, 962–973
889 (2011).
- 890 7. Wesson, D. W., Donahou, T. N., Johnson, M. O. & Wachowiak, M. Sniffing Behavior of Mice
891 during Performance in Odor-Guided Tasks. *Chemical Senses* **33**, 581–596 (2008).
- 892 8. Wolf, S. *et al.* Sensorimotor computation underlying phototaxis in zebrafish. *Nat Commun* **8**, 651
893 (2017).
- 894 9. DeBose, J. L. & Nevitt, G. A. The use of Odors at Different Spatial Scales: Comparing Birds with
895 Fish. *J Chem Ecol* **34**, 867–881 (2008).
- 896 10. Freas, C. A. & Cheng, K. The Basis of Navigation Across Species. *Annu. Rev. Psychol.* **73**, 217–241
897 (2022).
- 898 11. Iwano, M. *et al.* Neurons associated with the flip-flop activity in the lateral accessory lobe and
899 ventral protocerebrum of the silkworm moth brain. *J. Comp. Neurol.* **518**, 366–388 (2010).

- 900 12. Kanzaki, R., Sugi, N. & Shibuya, T. Self-generated Zigzag Turning of Bombyx mori Males during
901 Pheromone-mediated Upwind Walking(Physology). *Zoological science*. **9**, 515–527 (1992).
- 902 13. Namiki, S. & Kanzaki, R. The neurobiological basis of orientation in insects: insights from the
903 silkmoth mating dance. *Current Opinion in Insect Science* **15**, 16–26 (2016).
- 904 14. Wystrach, A., Lagogiannis, K. & Webb, B. Continuous lateral oscillations as a core mechanism for
905 taxis in Drosophila larvae. *eLife* **5**, e15504 (2016).
- 906 15. Kuenen, L. P. S. & Baker, T. C. A non-anemotactic mechanism used in pheromone source
907 location by flying moths. *Physiol Entomol* **8**, 277–289 (1983).
- 908 16. Olberg, R. M. Pheromone-triggered flip-flopping interneurons in the ventral nerve cord of the
909 silkworm moth, Bombyx mori. *J. Comp. Physiol.* **152**, 297–307 (1983).
- 910 17. Namiki, S., Iwabuchi, S., Pansopha Kono, P. & Kanzaki, R. Information flow through neural
911 circuits for pheromone orientation. *Nat Commun* **5**, 5919 (2014).
- 912 18. Hangartner, W. Spezifität und Inaktivierung des Spurpheromons von Lasius fuliginosus Latr. und
913 Orientierung der Arbeiterinnen im Duftfeld. *Springer* **57**, 34 (1967).
- 914 19. Izquierdo, E. J. & Lockery, S. R. Evolution and Analysis of Minimal Neural Circuits for Klinotaxis in
915 Caenorhabditis elegans. *Journal of Neuroscience* **30**, 12908–12917 (2010).
- 916 20. Adden, A., Stewart, T. C., Webb, B. & Heinze, S. A neural model for insect steering applied to
917 olfaction and path integration. <http://biorxiv.org/lookup/doi/10.1101/2020.08.25.266247>
918 (2020) doi:10.1101/2020.08.25.266247.
- 919 21. Kodzhabashev, A. & Mangan, M. Route Following Without Scanning. in *Biomimetic and*
920 *Biohybrid Systems* (eds. Wilson, S. P., Verschure, P. F. M. J., Mura, A. & Prescott, T. J.) vol. 9222
921 199–210 (Springer International Publishing, 2015).
- 922 22. Le Möel, F. & Wystrach, A. Opponent processes in visual memories: A model of attraction and
923 repulsion in navigating insects' mushroom bodies. *PLoS Comput Biol* **16**, e1007631 (2020).
- 924 23. Murray, T. *et al.* The role of attractive and repellent scene memories in ant homing (*Myrmecia*
925 *croslandi*). *J Exp Biol* **223**, jeb210021 (2020).

- 926 24. Graham, P. & Collett, T. S. View-based navigation in insects: how wood ants (*Formica rufa* L.)
927 look at and are guided by extended landmarks. *Journal of Experimental Biology* **205**, 2499–2509
928 (2002).
- 929 25. Lent, D. D., Graham, P. & Collett, T. S. Phase-Dependent Visual Control of the Zigzag Paths of
930 Navigating Wood Ants. *Current Biology* **23**, 2393–2399 (2013).
- 931 26. Lent, D. D., Graham, P. & Collett, T. S. Image-matching during ant navigation occurs through
932 saccade-like body turns controlled by learned visual features. *Proceedings of the National*
933 *Academy of Sciences* **107**, 16348–16353 (2010).
- 934 27. Jayatilaka, P., Murray, T., Narendra, A. & Zeil, J. The choreography of learning walks in the
935 Australian jack jumper ant *Myrmecia croslandi*. *J Exp Biol* **221**, jeb185306 (2018).
- 936 28. Zeil, J. & Fleischmann, P. N. The learning walks of ants (Hymenoptera: Formicidae). (2019)
937 doi:10.25849/MYRMECOL.NEWS_029:093.
- 938 29. Stürzl, W., Zeil, J., Boeddeker, N. & Hemmi, J. M. How Wasps Acquire and Use Views for Homing.
939 *Current Biology* **26**, 470–482 (2016).
- 940 30. Voss, R. & Zeil, J. Active vision in insects: an analysis of object-directed zig-zag flights in wasps (
941 *Odynerus spinipes* ?, Eumenidae). *Journal of Comparative Physiology A: Sensory, Neural, and*
942 *Behavioral Physiology* **182**, 377–387 (1998).
- 943 31. Philippides, A., de Ibarra, N. H., Riabinina, O. & Collett, T. S. Bumblebee calligraphy: the design
944 and control of flight motifs in the learning and return flights of *Bombus terrestris*. *Journal of*
945 *Experimental Biology* **216**, 1093–1104 (2013).
- 946 32. Jayatilaka, P., Raderschall, C. A., Narendra, A. & Zeil, J. Individual foraging patterns of the jack
947 jumper ant *Myrmecia croslandi* (Hymenoptera: Formicidae). *Myrmecological News* **19**, 75–83
948 (2013).
- 949 33. Narendra, A., Gourmaud, S. & Zeil, J. Mapping the navigational knowledge of individually
950 foraging ants, *Myrmecia croslandi*. *Proc. R. Soc. B* **280**, 20130683 (2013).

- 951 34. Zeil, J., Narendra, A. & Stürzl, W. Looking and homing: how displaced ants decide where to go.
952 *Phil. Trans. R. Soc. B* **369**, 20130034 (2014).
- 953 35. Card, A., McDermott, C. & Narendra, A. Multiple orientation cues in an Australian trunk-trail-
954 forming ant, *Iridomyrmex purpureus*. *Aust. J. Zool.* **64**, 227 (2016).
- 955 36. Collett, M. & Collett, T. S. Path Integration: Combining Optic Flow with Compass Orientation.
956 *Current Biology* **27**, R1113–R1116 (2017).
- 957 37. Heinze, S., Narendra, A. & Cheung, A. Principles of Insect Path Integration. *Current Biology* **28**,
958 R1043–R1058 (2018).
- 959 38. Muller, M. & Wehner, R. Path integration in desert ants, *Cataglyphis fortis*. *Proceedings of the*
960 *National Academy of Sciences* **85**, 5287–5290 (1988).
- 961 39. Collett, T. S. & Cartwright, B. A. Eidetic images in insects: their role in navigation. at
962 [https://doi.org/10.1016/0166-2236\(83\)90048-6](https://doi.org/10.1016/0166-2236(83)90048-6). (1983).
- 963 40. Zeil, J. Visual homing: an insect perspective. *Current Opinion in Neurobiology* **22**, 285–293
964 (2012).
- 965 41. Dahmen, H., Wahl, V. L., Pfeffer, S. E., Mallot, H. A. & Wittlinger, M. Naturalistic path integration
966 of *Cataglyphis* desert ants on an air-cushioned lightweight spherical treadmill. *J Exp Biol* **220**,
967 634–644 (2017).
- 968 42. Lonnendonker, U. DYNAMIC PROPERTIES OF ORIENTATION TO A VISUALLY FIXATED TARGET BY
969 WALKING COLORADO BEETLES. *Journal of Experimental Biology* **158**, 16 (1991).
- 970 43. Zollikofer, C. P. E. STEPPING PATTERNS IN ANTS. *Journal of Experimental Biology* **192**, 107–118
971 (1994).
- 972 44. Namiki, S. & Kanzaki, R. Comparative Neuroanatomy of the Lateral Accessory Lobe in the Insect
973 Brain. *Front. Physiol.* **7**, (2016).
- 974 45. Steinbeck, F., Adden, A. & Graham, P. Connecting brain to behaviour: a role for general purpose
975 steering circuits in insect orientation? *J Exp Biol* **223**, jeb212332 (2020).

- 976 46. Berni, J. Genetic Dissection of a Regionally Differentiated Network for Exploratory Behavior in
977 *Drosophila Larvae*. *Current Biology* **25**, 1319–1326 (2015).
- 978 47. Berni, J., pulver, S. R., Griffith, L. C. & Bate, M. Autonomous Circuitry for Substrate Exploration in
979 Freely Moving *Drosophila Larvae*. *Current Biology* **22**, 10 (2012).
- 980 48. Kanzaki, R. Neural Basis of Odor-source Searching Behavior in Insect Brain Systems Evaluated
981 with a Mobile Robot. *Chemical Senses* **30**, i285–i286 (2005).
- 982 49. Baddeley, B., Graham, P., Husbands, P. & Philippides, A. A Model of Ant Route Navigation Driven
983 by Scene Familiarity. *PLoS Comput Biol* **8**, e1002336 (2012).
- 984 50. Kamhi, J. F., Barron, A. B. & Narendra, A. Vertical Lobes of the Mushroom Bodies Are Essential
985 for View-Based Navigation in Australian *Myrmecia* Ants. *Current Biology* **30**, 3432–3437.e3
986 (2020).
- 987 51. Wystrach, A., Mangan, M., Philippides, A. & Graham, P. Snapshots in ants? New interpretations
988 of paradigmatic experiments. *Journal of Experimental Biology* **216**, 1766–1770 (2013).
- 989 52. Brembs, B. The brain as a dynamically active organ. *Biochemical and Biophysical Research*
990 *Communications* **564**, 55–69 (2021).
- 991 53. Schroeder, C. E., Wilson, D. A., Radman, T., Scharfman, H. & Lakatos, P. Dynamics of Active
992 Sensing and perceptual selection. *Current Opinion in Neurobiology* **20**, 172–176 (2010).
- 993 54. Yuste, R., MacLean, J. N., Smith, J. & Lansner, A. The cortex as a central pattern generator. *Nat*
994 *Rev Neurosci* **6**, 477–483 (2005).
- 995 55. Hindmarsh Sten, T., Li, R., Otopalik, A. & Ruta, V. Sexual arousal gates visual processing during
996 *Drosophila* courtship. *Nature* **595**, 549–553 (2021).
- 997 56. Kanzaki, R. & Mishima, T. Pheromone-Triggered ‘fiipflopping’ Neural Signals Correlate with
998 Activities of Neck Motor Neurons of a Male Moth, *Bombyx mori*. *Zoological Science* **13**, 79–87
999 (1996).

- 1000 57. Egelhaaf, M., Boeddeker, N., Kern, R., Kurtz, R. & Lindemann, J. P. Spatial vision in insects is
1001 facilitated by shaping the dynamics of visual input through behavioral action. *Front. Neural*
1002 *Circuits* **6**, (2012).
- 1003 58. Marder, E. & Calabrese, R. L. Principles of rhythmic motor pattern generation. *Physiological*
1004 *Reviews* **76**, 687–717 (1996).
- 1005 59. McAuley, J. H., Rothwell, J. C. & Marsden, C. D. Human anticipatory eye movements may reflect
1006 rhythmic central nervous activity. *Neuroscience* **94**, 339–350 (1999).
- 1007 60. Keijzer, F., van Duijn, M. & Lyon, P. What nervous systems do: early evolution, input–output, and
1008 the skin brain thesis. *Adaptive Behavior* **21**, 67–85 (2013).
- 1009 61. Buehlmann, C. *et al.* Mushroom Bodies Are Required for Learned Visual Navigation, but Not for
1010 Innate Visual Behavior, in *Ants. Current Biology* **30**, 3438-3443.e2 (2020).
- 1011 62. Webb, B. & Wystrach, A. Neural mechanisms of insect navigation. *Current Opinion in Insect*
1012 *Science* **15**, 27–39 (2016).
- 1013 63. Pansopha, P., Ando, N. & Kanzaki, R. Dynamic use of optic flow during pheromone tracking by
1014 the male silkworm, *Bombyx mori*. *Journal of Experimental Biology* **217**, 1811–1820 (2014).
- 1015 64. Busch, C., Borst, A. & Mauss, A. S. Bi-directional Control of Walking Behavior by Horizontal Optic
1016 Flow Sensors. *Current Biology* **28**, 4037-4045.e5 (2018).
- 1017 65. Wystrach, A. Movements, embodiment and the emergence of decisions. Insights from insect
1018 navigation. *Biochemical and Biophysical Research Communications* S0006291X21007348 (2021)
1019 doi:10.1016/j.bbrc.2021.04.114.
- 1020 66. Wystrach, A., Philippides, A., Aurejac, A., Cheng, K. & Graham, P. Visual scanning behaviours and
1021 their role in the navigation of the Australian desert ant *Melophorus bagoti*. *J Comp Physiol A*
1022 **200**, 615–626 (2014).
- 1023 67. Schwarz, S., Clement, L., Gkaniyas, E. & Wystrach, A. *How do backward walking ants (Cataglyphis*
1024 *velox) cope with navigational uncertainty?*

- 1025 <http://biorxiv.org/lookup/doi/10.1101/2019.12.16.877704> (2019)
- 1026 doi:10.1101/2019.12.16.877704.
- 1027 68. Wystrach, A., Le Moël, F., Clement, L. & Schwarz, S. *A lateralised design for the interaction of*
- 1028 *visual memories and heading representations in navigating ants.*
- 1029 <http://biorxiv.org/lookup/doi/10.1101/2020.08.13.249193> (2020)
- 1030 doi:10.1101/2020.08.13.249193.
- 1031 69. Heinze, S., Florman, J., Asokaraj, S., el Jundi, B. & Reppert, S. M. Anatomical basis of sun
- 1032 compass navigation II: The neuronal composition of the central complex of the monarch
- 1033 butterfly. *J. Comp. Neurol.* **521**, 267–298 (2013).
- 1034 70. Sayre, M. E., Templin, R., Chavez, J., Kempenaers, J. & Heinze, S. A projectome of the bumblebee
- 1035 central complex. *eLife* **10**, e68911 (2021).
- 1036 71. Hulse, B. K. *et al.* A connectome of the *Drosophila* central complex reveals network motifs
- 1037 suitable for flexible navigation and context-- dependent action selection. 180.
- 1038 72. Stone, T. *et al.* An Anatomically Constrained Model for Path Integration in the Bee Brain. *Current*
- 1039 *Biology* **27**, 3069-3085.e11 (2017).
- 1040 73. Le Moël, F., Stone, T., Lihoreau, M., Wystrach, A. & Webb, B. The Central Complex as a Potential
- 1041 Substrate for Vector Based Navigation. *Front. Psychol.* **10**, 690 (2019).
- 1042

STAR methods

RESOURCE AVAILABILITY :

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Leo Clement (clement.leo@univ-tlse3.fr).

Materials availability

As experiments took place in the natural environment this study did not generate new unique reagents.

Data and code availability

Any data or code information required to generate this results paper is available from the lead contact upon request.

- All data reported in this paper will be shared by the lead contact upon request
- All original code has been deposited at: https://github.com/awystrac/Neural_oscillator and is publicly available as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study Animal & Experimental site

All experiments took place within an open grassy woodland at the National Australian University, Canberra from Feb. to Mar. 2019. We had the opportunity to work with two Australian endemic ant species: *Myrmecia croslandi* and *Iridomyrmex purpureus*. *Myrmecia croslandi* workers are known to forage solitarily, with each individual either hunting on the ground in the vicinity of the nest or navigating routinely back and forth toward the same favorite foraging tree throughout her life span⁶⁶. These ants rely mainly on learnt terrestrial visual cues to navigate but are also able to resort to PI when the visual environment does not provide guidance^{27,32,39,66}. Eight nests of *M. croslandi*, that foraged on two distinct trees between 6.0 and 30.0 m away from the colony, were used in this study. *Iridomyrmex purpureus* ants form large colonies and forage along pheromone trails that lead to food patches. Despite employing pheromone trails for recruitment, this species also uses both learnt visual information and path integration for navigation³¹. We also performed navigational experiments with two *I. purpureus* nests to ensure that this species relies indeed on both learnt visual terrestrial cues and path integration, which they did surprisingly well (see Figure S1). For the main experiment, a feeder was placed 7.0 m away from the nest and foragers were free to familiarize themselves with the route for 72 h before being tested.

METHOD DETAILS

Trackball system and data extraction

During tests, ants were mounted on a trackball device³⁸. This device consists of a polystyrene ball held in levitation in an aluminum cup by an air flow. The trackball has two sensors placed at 90° to the azimuth of the sphere, which record the movements of this sphere and translate them into X and Y data retracing the path of the ant. The X and Y acquisition of the trackball rotations happened at a 30 Hz frequency (i.e., 30 data points per second), enabling us to reconstruct the ant's movements with high precision. Additionally, a camera (640×480 pixels) recording from above provided details of the ant's body orientation, also at 30 Hz. We also analyzed *M. croslandi* learning walks recorded directly on the natural ground. Head directions were obtained via video recordings at 25 Hz (provided by Jochen Zeil).

In this study, we used two different trackball configurations to record the ants' motor responses: further referred to as 'Free ant' and 'Fixed ant' experiments, respectively.

Free ant experiments: two small wheels prevented the polystyrene ball from rotating in the horizontal plane, however, all other degrees of freedom of the ball rotation were accessible (Figure S2 A; 'closed-loop'³⁸). Ants were attached on top of the ball by putting magnetic paint on their thorax and a micro-magnet fixed at the bottom end of a single dental thread that was in turn attached to a 0.5 mm pin. Crucially, the pin was placed within a glass capillary. This procedure enabled the ants to execute physical rotations on the ball (the ball is not rotating horizontally) but prevented any translational movement. Ants could thus execute body rotations and control the direction in which they faced but any attempt to go forward or backward resulted in ball rotations. We used the recorded videos to manually track the ants' body orientation through time using the free software Kinovea (v-0.9.1).

Fixed ant experiment: the two small wheels were no longer in place. Hence, the ball could now turn in any direction, including the horizontal plane (Figure S2B; 'open-loop'³⁸). Ants were tethered directly to a needle with a micro magnet (glued at the end of the needle)

and magnetic paint on their thorax. The top end of the needle was glued to a small piece of paper sheet (0.5×2.5 cm). Consequently, the fixed ant could no longer rotate, and the experimenter could choose in which direction she was facing. Any attempt to move, including turning, by the ants resulted in ball rotations. This trackball configuration was only conducted with the more robust *M. croslandi*.

Free ant experiments: protocol

At the start of each test, the ant was mounted on the trackball device but surrounded by an opaque cylinder (30×30 cm) that prevented the ant from seeing any cues from the visual scenery around her. Once the ant was in place on the device, the whole apparatus was moved to the desired test location in the field. Afterward, the surrounding cylinder was removed, revealing the visual scenery to the ant and data recording began. To ensure a high level of homing motivation, only individuals who had previously received a 40% sucrose solution (for *M. croslandi*) or a food item (for *I. purpureus*) were tested. The recording period was 3.5 min for the robust *M. croslandi* and 1.5 min for the flimsier *I. purpureus*.

To test the impact of terrestrial visual cues on the oscillation behavior, ants were tested under three distinct conditions.

Familiar (F): ants were tested along their habitual route, which therefore presents a familiar visual view.

Unfamiliar (U): ants were tested at least 50 m away from the habitual route, which therefore presents an unfamiliar panorama.

Dark (D): ants were tested in total darkness, within an opaque cylinder (30×30 cm) covered with a red Plexiglas plate that transmitted only the low red wavelengths, which ants cannot perceive^{67,68}.

To test the impact of PI on oscillation behavior, ants were tested as either full- or zero vector ants. Full vector (FV): ants were caught at the start of their inbound trip to the nest (i.e., at the foraging tree for *M. croslandi* and at the feeder for *I. purpureus*). FV ants have an informative homing PI vector, which points in the food-to-nest compass direction. Consequently, FV ants can rely on both PI vector and the learnt visual scenery while being tested. Zero vector (ZV): homing ants were captured just before entering the nest, that is, at the end of their inbound trip. Hence, their PI homing vector is reduced to zero and thus no longer directionally informative. Consequently, ZV ants can only rely on the learnt visual scenery while being tested. For each of the three visual conditions FV and ZV ants were tested, resulting in a total of six conditions.

For *I. purpureus*, at least 16 ants were tested in each of the six conditions (F: FV&ZV =16; U: FV&ZV =17; D: FV=16 & ZV=17). Since *I. purpureus* forms very populous colonies with an abundance of foragers, all individuals were tested only once, in one of the six conditions. The data obtained are therefore statistically independent. On the contrary, *M. croslandi* forms sparsely populated colonies and individuals usually make only one foraging trip per day⁶⁶. Thus, it is time-consuming and challenging to capture, mark and follow individuals throughout foraging trips. Individuals were therefore captured (either at the foraging tree (FV) or before reaching their nest (ZV)) and tested successively in a pseudo-random order in all three visual panoramas: Familiar (F), Unfamiliar (U) and in the Dark (D). Both the sequence in which the visual conditions were experienced and the individuality were included in the statistical models as it is likely that the state of the PI vector will be modified across successive tests. Overall, 32 *M. croslandi* ants were tested with some individuals

tested as ZV or FV ants on two different days. At least 16 *M. croslandi* ants were tested in each of the six conditions (F: FV&ZV =17; U: FV&ZV =17; D: FV=17 & ZV =16). Overall, 101 recordings were obtained.

In the ‘free ant’ experiments, the ant’s body axis can turn without the ball movement. We used the recorded videos to manually track the ants’ body orientation through time using the free software Kinovea. We removed the first 3s of recording of each ant as the removal of the opaque ring may have disrupted the behavior. Overall, the analyzed recording length was 100s (except for two ants: 84 and 99s) for *M. croslandi* individuals and 50s (except for two ants: 49s) for *I. purpureus* ants. For details of the Fourier analysis (see below); nine paths of *I. purpureus* were discarded (F FV=1, U FV = 1, U ZV =2, D FV =2, D ZV = 3) as the ants displayed too many pauses.

Fixed ant experiments: protocol

To test if oscillations are due to an intrinsic oscillator or caused by the fact that ants try to keep a bearing toward an external stimulus, we conducted an additional experiment on *M. croslandi* ants. We recorded foragers without an informative integration vector (ZV) in the same unfamiliar environment (U) as before. Ants were tested in eight different fixed orientations, covering the 360° azimuth by bins of 45°; and with one direction corresponding to the food-to-nest compass direction. Each ant was tested in all eight orientations in a pseudo-random sequence. To change the ant’s orientation, the experimenter would first place the opaque cylinder (30×30 cm) around the trackball system to prevent the ant from perceiving the visual panorama, then rotate the whole set-up (trackball and mounted ant) and finally remove the opaque cylinder to re-start data collection. Ants were recorded for at least 15s up to 20s in each orientation. Eleven ants were tested in all eight orientations. Since the

ants were fixed, trackball rotations along the horizontal axis provided a direct measure of the angular velocity of the attempted turn generated by the ant. Angular velocity time series were then extracted from the trackball data. At the end, the available length of the recordings for the analysis had 512 frames (~17s) except for 5 individuals (294,394,456,474,494 frames). It should be noted here that prior to the Fourier analysis (see below) we added a series of 0s (zero padding) at the end of the time series until it had a length of 3000 data points to match the same recording length obtained in the free ant experiment). This permits to increase the precision in the frequency range obtained from the Fourier analysis.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses have been run using the free software R (v 3.6.2. R Core Development Team). For all statistical tests, the p-values were compared to the critical alpha risk at 0.05, with the appropriate correction if needed. Statistical parameters mean and the associated standard error is given within the text and/or on figures: N represents the number of individuals.

Fourier analysis

To reveal the occurrence of regular lateral oscillations, we choose to focus on the angular velocity value (Figure S2C), which constitutes a direct reading from the left/right motor control. This time series was processed through three successive steps to obtain its 'spectral density', according to the Wiener-Khinchin theorem. First, the signal was parsimoniously smoothed with a moving median running of a length of five frames (0.17s) to reduce the influence of the recording noise (Figure S2D, dashed blue line). Then, the recorded time series was passed through an autocorrelation function (Figure S2D). Finally, a Fourier transform was performed on these autocorrelation coefficients, providing the power spectral

density (Figure S2E). With this approach, the magnitudes obtained are independent from angular drift and amplitudes of the oscillations and thus can be directly compared across individuals. A high magnitude indicates a strong oscillation for a given frequency. For each individual, the dominant frequency (i.e., presenting the highest peak magnitude) and its magnitude were extracted (Figure S2E, dashed blue lines). To check whether these magnitudes indicate a significant regular oscillation, we compared them to the average spectral density magnitude resulting from 200 Gaussian white noise signals of the same length (within each species and experiment). Gaussian white noise signals were obtained by drawing a sequence of random values drawn from a normal law. These simulated signals were then processed through the exact same operations as the ants' angular velocity recording: namely smoothing, autocorrelation, Fourier transformation and extraction of the highest peak magnitude. The mean of the 200 highest magnitudes obtained was then compared to the real ants' equivalent magnitudes with a Wilcoxon one-tail test. As each experimental group has been compared with this mean magnitude of the simulated angular velocity signal, the p-value is subsequently adjusted using the Bonferroni correction.

Average oscillatory cycle

To extract the average dynamics of an oscillation cycle, the mean cycles at the individual and population levels were reconstructed as follows. First, we smoothed the angular velocity time series of each individual by running twice a median with a window length of 31 frames for *M. croslandi* (for both free and fixed experiments), 25 frames for data during learning walks on the natural ground and seven frames for *I. purpureus*. This window length is much smaller than one oscillatory cycle and thus smoothens the data without altering the cycle general dynamics (Figure S5 A). Second, we indexed moments when the time series crosses 0 (from

– to +) as t_0 ; and extracted a window of ± 90 frames around the t_0 indices (± 60 frames for *I. purpureus*; Figure S5 A). We then reconstructed a mean cycle for each individual by averaging the individual's extracted windows, aligned at t_0 (Figure S5 B). The individuals' average forward speed dynamics during one cycle was obtained in the same way by using the same indices t_0 obtained from the angular velocity data (Figure S5 C). For each ant, the mean angular velocity peak and amplitude of forward velocity cycles were extracted for analysis. Finally, we reconstructed the average cycle at the level of the population by averaging the mean cycle of all individuals. Note that to do so, each individual's mean cycle was first normalized to show similar amplitudes ($\text{mean_cycle_normalised} = \text{mean_cycle}/\text{mean}(|\text{mean_cycle_values}|)$). The goal was here to observe the cycle dynamics through time and not to estimate the inter-individual variation in amplitude, which was analyzed previously using the individual's mean cycle amplitude. Note that the criterion used to align the time series (the change from a left to a right turn) necessarily creates an artefact in the averaged angular velocity obtained. Namely, an average change from left turn to right turn at t_0 . However, several factors indicate the relevance of such pooling at the population level: (1) the period of the average cycle corresponds to the mean frequency obtained from the Fourier transform. (2) we can observe a significant reversal of the angular velocity before and after the mean oscillation cycle. (3) the associated forward velocities co-vary in a significant way, indicating the existence of conserved dynamics.

Analysis of the ants' direction of movement

We reconstructed the ant paths of time that derived from the trackball recording for a fixed period to determine the mean direction of movement (μ) as well as the mean circular vector length (r , a measure of dispersion) of each individual. The mean directions (μ) were

analyzed using a Rayleigh test (from R package: Circular) that also includes a theoretical direction (analogous to the V-test). To test whether the angular data are distributed uniformly as a null hypothesis or if they are oriented toward the theoretical direction of the nest as indicated by the state of the PI or the familiar panorama, the average vectors lengths (r) were analyzed via a Wilcoxon-Mann-Whitney test with a Bonferroni correction for multiple testing.

Analysis of optimization

To investigate the benefit of variation of forward and angular velocities signal on the overall ground distance covered we reconstructed for each individual a fictive path where forward speed was maintained constant (we took the average forward speed, so that the total distance walked remain the same as in the original path). To estimate the overall ground distance covered for a given path, we computed a ‘global trajectory’ by smoothing the path with a sliding window, until effectively removing the oscillations component (Figure 4B grey paths). To estimate the actual benefit of variation of forward speed on the distance covered, we compared the length of the ‘global trajectories’ between the fictive path (with constant forward speed) and original path (Fig 4C). A ratio >1 mean that the original path covered more ground distance, and vice versa. Ratios were compared with Wilcoxon one-tail test to the threshold one.

To test for an effect of the familiarity and vector on the distance covered we calculated an ‘Effectiveness ratio’ for each individual as the ratio between the length of the ‘global trajectory’ / ‘actual distance walked’ on the original paths with oscillations (Figure 4D). To

enable a fair comparison across individuals, we computed the “effectiveness ratio” on a 100s portion of paths, using an additive mixed model.

Statistical models

For the free ant experiment, two types of models were tested: the first considering the interaction between visual panorama and vector modalities, the second with simple additive effect. It should be noted here that in case of deviation of the residuals of these models from normality and or homoscedasticity, the response variables have been transformed. Only the model presenting the lowest Akaike information criterion was retained and subsequently analyzed via an analysis of variance (Anova), followed by a post-hoc analysis of Tukey's rank comparison. Finally, for *M. croslandi* whose individuals were tested across several conditions, the models are mixed models that controlled the sequence and the individuality effect as random variable. For some models, we removed the sequence effect because of a singularity problem of this factor (i.e., the information given by this variable is already contained in other variables). For fixed ant experiments (which were tested only as ZV ants in an unfamiliar environment), the model analyzed the effect of the condition of the subsequent rotations.

COMPUTATIONAL MODEL

The computational model presented in Figure6 has been built and run using Matlab®

R2016b. The code is open access and available at :

https://github.com/awystrac/Neural_oscillator

It is a step based model ('For loop'). Two neurons (Left and Right neurons) reciprocally inhibit each other, while trying to maintain a baseline activity through self-excitation and internal feedback.

Variable	Description
L	Left neuron activity
R	Right neuron activity
LNF	Left neuron internal feedback
RNF	Right neuron internal feedback

Parameters	Description
W	Reciprocal inhibition synaptic weight
Baseline	Firing rate of the oscillator neurons without any external modulation (default at 0.5)
Exhaust rate	Rate at which the negative internal feedback is modulated between each time step
Noise	Standard error of the normal distribution of the noise added to the activity of the neurons of the oscillator (default at 0.1)

Initialization

$R_1 = \text{random}(0 \text{ to } 1)$

$L_1 = \text{random}(0 \text{ to } 1)$

$RNF_1 = 0$

$LNF_1 = 0$

At each time step

L and R neuron update their activity due to their self-excitation, internal feedback, inhibition from the other neuron, and noise.

$$L_{t+1} = L_t - LNF_t - (R_t \times W) + (random(-1 to 1) \times noise)$$

$$R_{t+1} = R_t - RNF_t - (L_t \times W) + (random(-1 to 1) \times noise)$$

Set a hard limit to the activity both neurons

$$LM_{t+1} = \begin{cases} L_{t+1} & \text{if } L_{t+1} > 0 \\ 0 & \text{if } L_{t+1} \leq 0 \end{cases}$$

$$RM_{t+1} = \begin{cases} R_{t+1} & \text{if } R_{t+1} > 0 \\ 0 & \text{if } R_{t+1} \leq 0 \end{cases}$$

Update the internal negative feedback for the left and right motor neurons. The internal feedback changes proportionally to the difference between its own activity and the neuron activity (relative to the baseline activity)

$$RNF_{t+1} = RNF_t + Exhaust\ rate \times (R_{t+1} - RNF_t - Baseline)$$

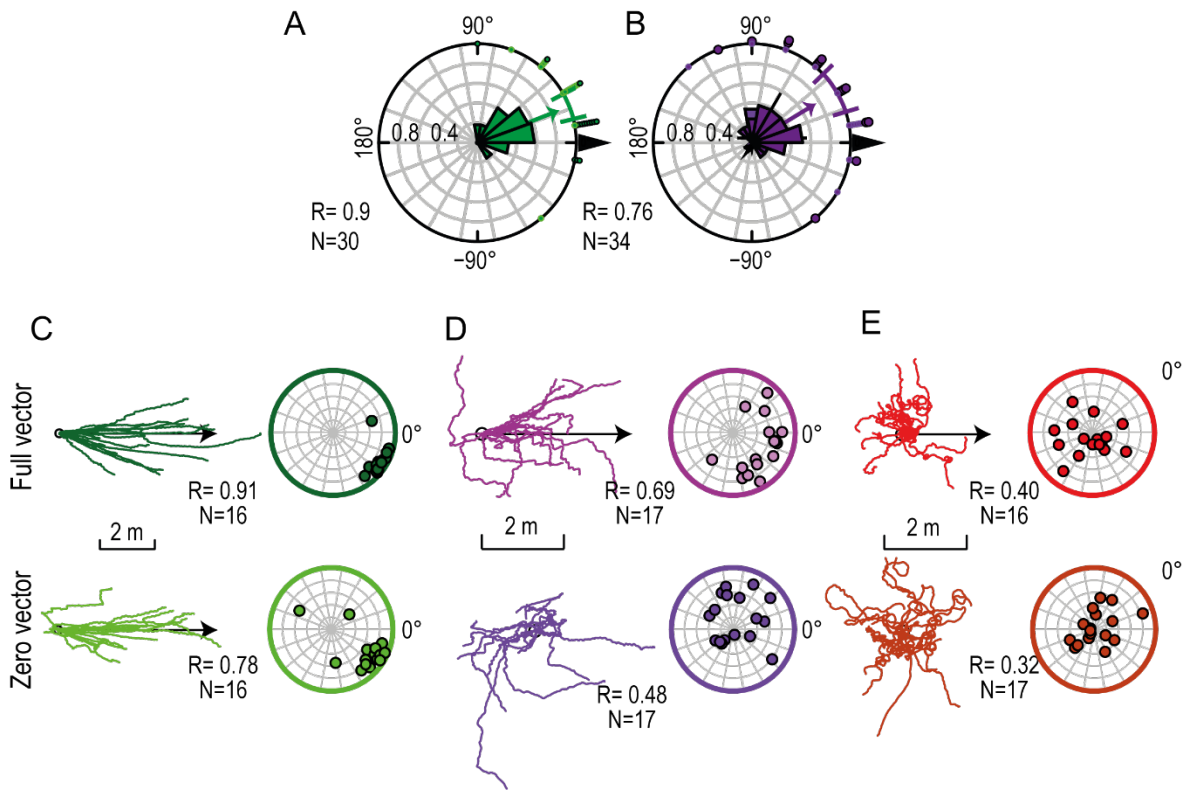
$$LNF_{t+1} = LNF_t + Exhaust\ rate \times (L_{t+1} - LNF_t - Baseline)$$

Computation of the angular and forward velocities

$$Angular_velocity = R - L$$

$$Foward_velocity = R + L$$

1 **Supplemental information 1**



2

3 **Figure S1: The meat ant *Iridomyrmex purpureus* uses both visual and celestial cues to**
 4 **navigate.** (A-B) Ants were released at the center of a goniometer divided in 18 sectors (20°
 5 each) either in a familiar (green) or unfamiliar (purple) surroundings. The taken directions of
 6 the tested ants were recorded at two points. (A) Circular histogram depicting the directional
 7 decisions of tested zero-vector (ZV) ants (without informative integration vector) in presence
 8 of familiar surroundings. (B) Circular histogram depicting the directional decisions of tested
 9 full-vector (FV) ants (with informative integration vector) in unfamiliar surroundings. The
 10 arrow corresponds to the mean vector of the distribution. The 95% confidence interval of the
 11 mean is displayed as a coloured arc. Each dot corresponds to one corrected direction obtained
 12 from one individual. after several tested individuals, the goniometers were rotated (180°) to
 13 prevent the use of chemical trails. Dots with a black rim are data recorded before rotation of
 14 the goniometers and the dots without black rim after rotation.
 15 (C-E) Path of ant reconstructed over 25 s from the trackball, in a familiar ((C) green) or an
 16 unfamiliar panorama ((D) purple) and in the dark ((E) red). For each condition, individuals
 17 were tested either as FV- or ZV vector ant. The first column of each condition shows the
 18 paths oriented to the theoretical direction of the nest (arrow). In the second column, each dot
 19 indicates the average circular vector calculated over the entire path of an individual, showing
 20 the mean direction and the average vector length (i.e., a point closer to the periphery indicates
 21 straighter paths). The R values indicate the length of the average resulting vector of the
 22 population. In all graphs, the direction (in familiar terrain) or theoretical direction (for FV in
 23 unfamiliar terrain) of the nest is set at 0°.
 24 The results show that ants in presence of familiar panorama were oriented toward their nest
 25 irrespectively of the PI state (FV or ZV) (Rayleigh test: on goniometers (A): $p < 0.001$; path
 26 displayed on the trackball (B): $p_s = \text{FV} \ \& \ \text{ZV} < 0.001$). Secondly, when tested in unfamiliar
 27 surroundings, FV ants followed their PI vector (Rayleigh test: on goniometers (B): $p < 0.001$;
 28 path displayed on the trackball (D, first row): $p = \text{FV} < 0.001$). But ZV ants (Figure 1D

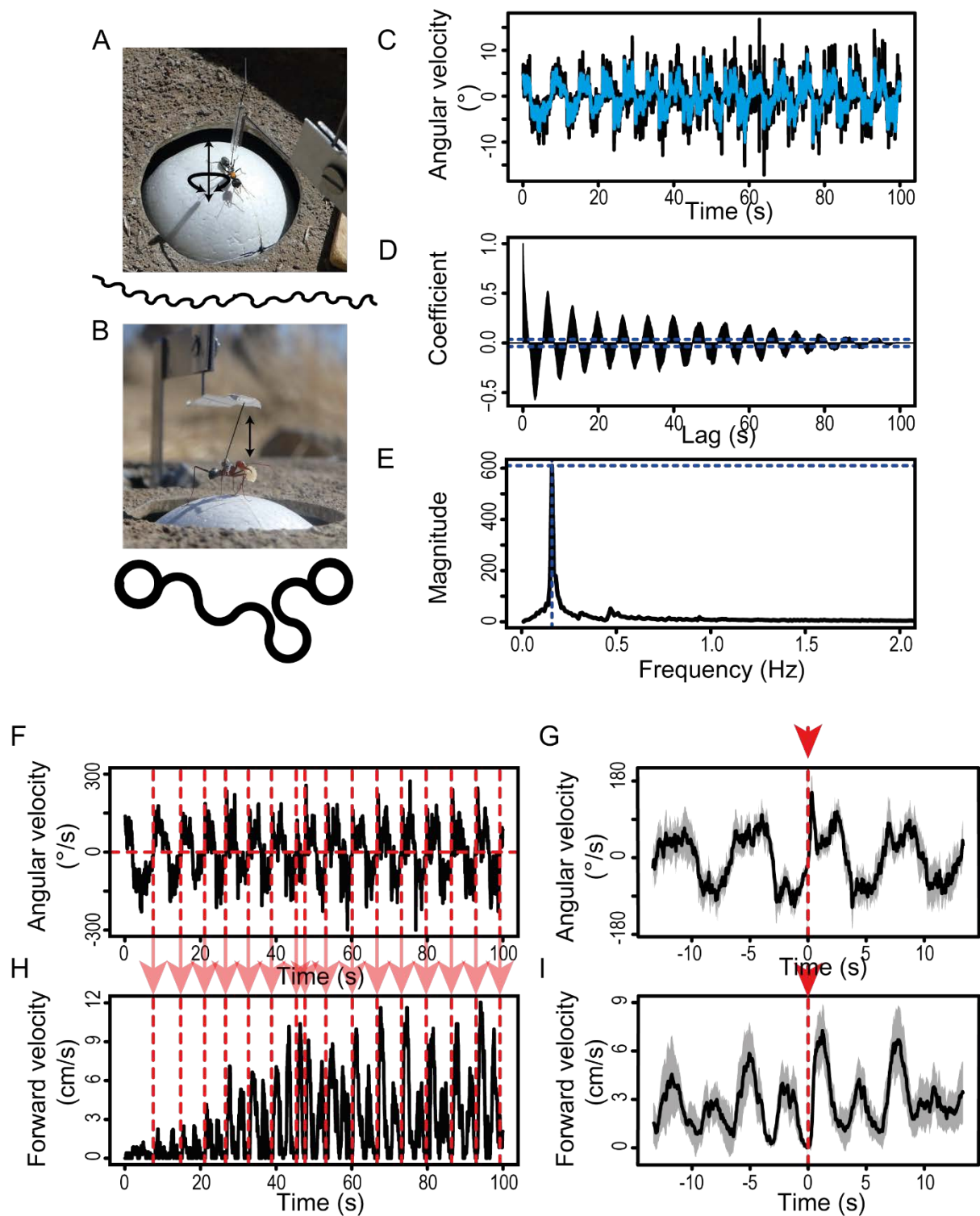
29 second row) showed random orientations (Rayleigh test p: $ZV=0.672$). Finally, ants
30 displayed randomly orientated paths in all darkness conditions (Figure 1E; Rayleigh test p:
31 $FV=0.213$, $ZV=0.866$). Overall, these results demonstrate that this species use learnt
32 terrestrial cues as well as their PI to navigate when released on the goniometers or mounted
33 on the trackball system. Therefore, in both experiment this species does not only rely on
34 chemical trails but also on the visual panorama and the path integration during foraging.
35

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39 **Supplemental information 2**



40

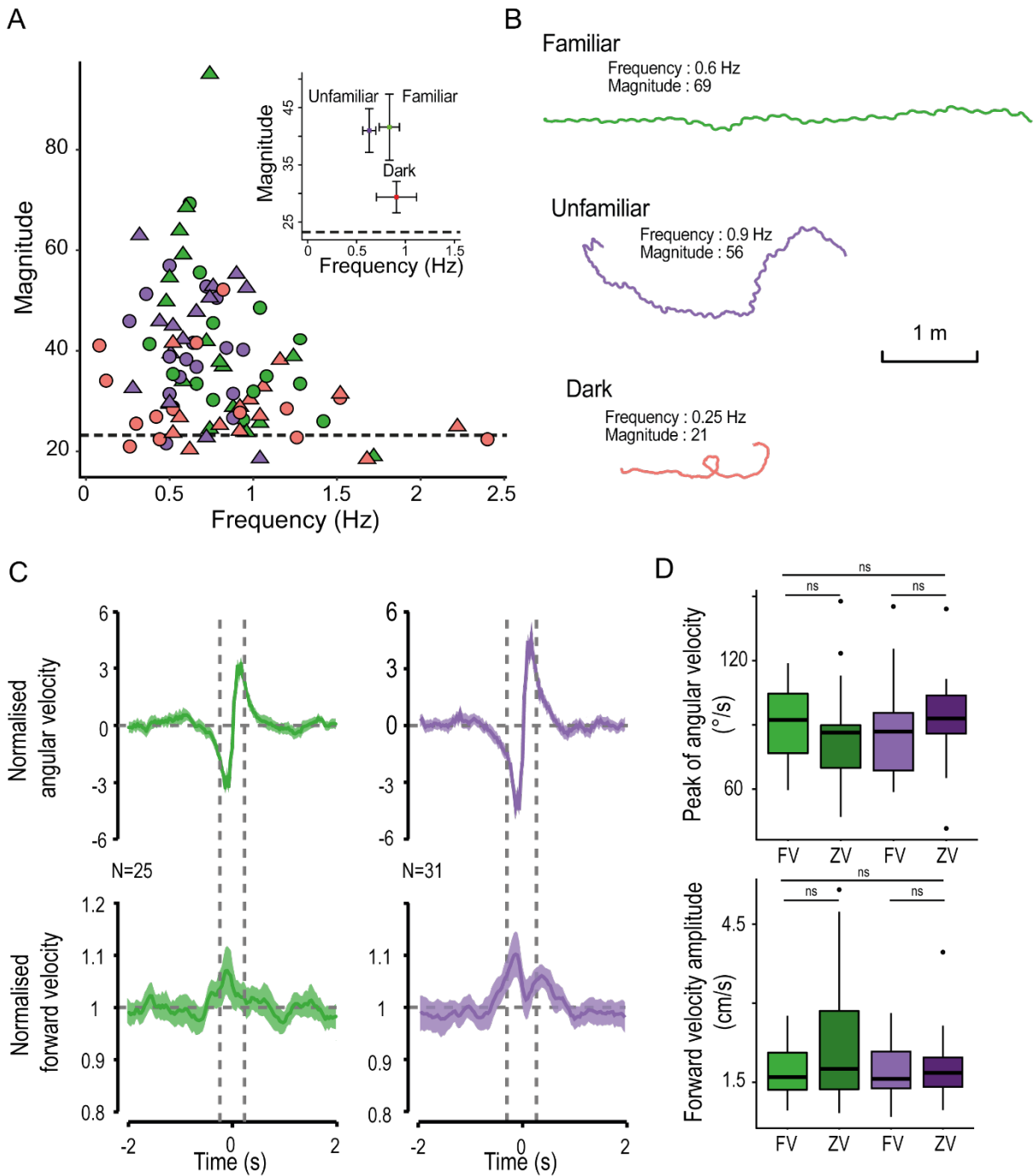
41

42 **Figure S2: Trackball set-ups, recording and processing of the ants' trajectory.** (A)
 43 Trackball set-up for 'free ant experiment' (top view). Two wheels prevent the sphere from
 44 rotating along the horizontal plane. Ants are free to rotate their body along the yaw axis to
 45 control in which direction they perceive the world. (B) Trackball set-up for 'fixed ant
 46 experiment' (side view). The two wheels have been removed, so the ball can turn in every
 47 direction. Ants are fixed in a way that prevent body rotations along the yaw axis, so they are

48 forced to keep their bearing in the imposed direction. For A and B an example path has been
49 plotted below the picture. (C) Angular velocity signal over time (recorded at 30 readings/s) in
50 an individual of the species *M. croslandi* (black) with smoothed signal superimposed (blue).
51 (D) Autocorrelation carried out on the entire smoothed angular velocity signal. (E) Fourier
52 transformation of the autocorrelation coefficients signal (shown in D) provides the ‘spectral
53 density’. This approach has the advantage to provide magnitudes that are directly comparable
54 between individuals. For each individual, the frequency peak with the highest magnitude was
55 extracted, indicating a strong oscillation of the angular velocity signal at that frequency
56 (dashed blue lines). F-I Methodology to obtain an average oscillation cycle. (F) We used the
57 angular velocity signal to flag moments when the signal crosses 0 and goes up to positive
58 angles (vertical dashed red lines). (G) We extracted portions of the signal of $\pm 3s$ (large
59 enough to contain a full oscillation cycle) around each of the flags, aligned them at flag = t_0
60 and averaged them to obtain the individual’s average cycle ($\pm 95\%$ confidence interval in
61 grey) of the angular velocity signal. (I) The individual’s average cycle for the forward
62 velocity signal was achieved using the angular velocity flags (vertical dashed red lines as in
63 F) on the forward velocities (H).
64

65 **Supplemental information 3**

66



67

68 **Figure S3: Oscillation characteristics across visual conditions.**

69 Individuals were tested within a familiar panorama (green), an unfamiliar panorama (purple)

70 or in the dark (red).

71 (A) shows the frequency and spectral density magnitude of the dominant oscillation (highest

72 magnitude) (A) (for method see Star method and Figure S2 F-I). High frequencies indicate a

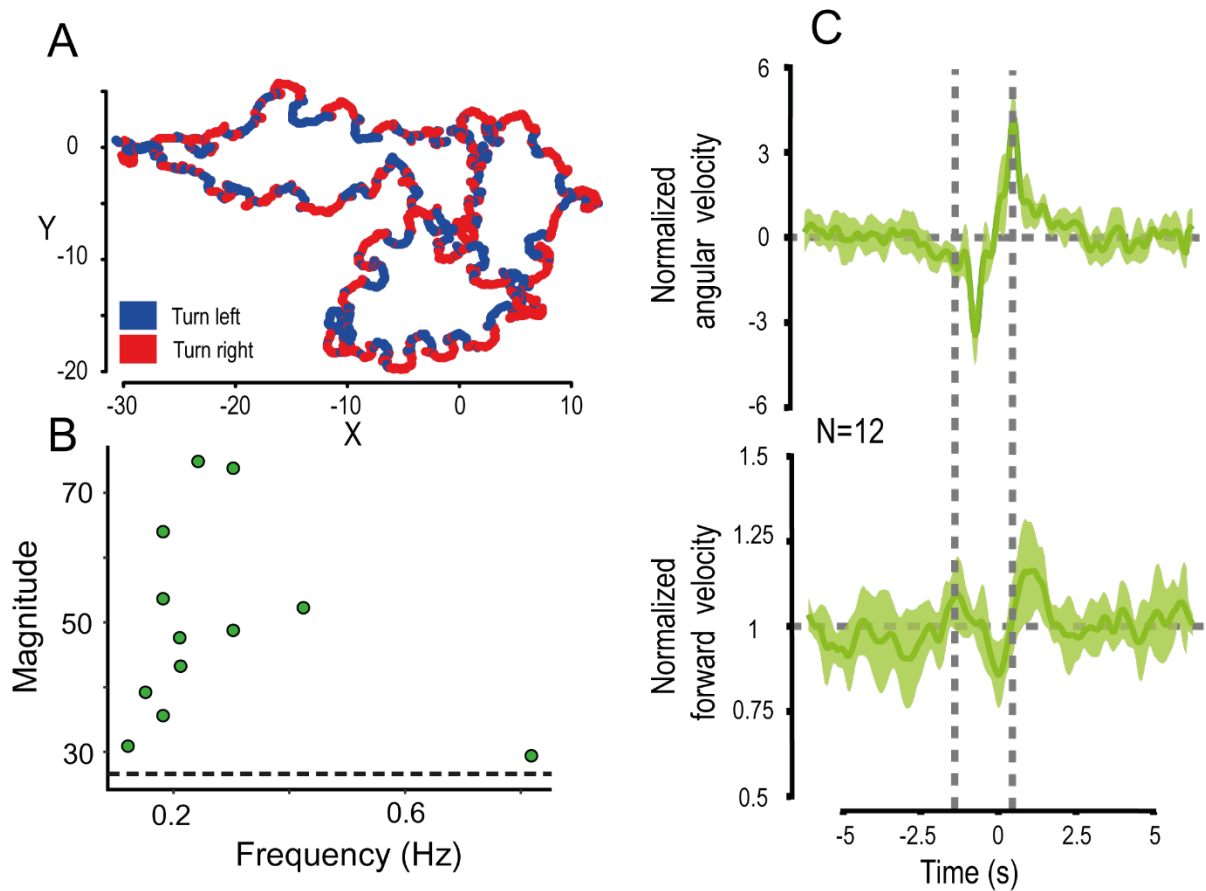
73 fast-oscillatory rhythm and high magnitudes indicate a strong presence of this oscillation.

74 Symbols indicate whether the state of the path integration vector was full (round) or set to

75 zero (triangles). Inserts show the mean frequency against the mean magnitude of each visual

76 condition with the associated 95% confidence interval around the mean. The dashed black

77 line represents the mean of the spectral density peak magnitudes resulting from 200 Gaussian
78 white noise signals. Magnitudes were higher than those obtained with the spectral density of
79 a Gaussian white noise ((A) dashed line; Wilcoxon one-tail test: $p \leq 0.01$), showing that ants
80 displayed lateral oscillations with a higher regularity than random. Analysis reveals that the
81 regularity differ between visual panoramas with ants tested in familiar and unfamiliar terrain
82 yield more regular oscillations than in the dark ((A) Anova: $F_{2,90} = 10.038$, $p < 0.001$, F vs U =
83 $p > 0.96$, $df = 86$, $\text{mean} \pm \text{se}$: $F_{(FV+ZV)} = 41.59 \pm 3$; $U_{(FV+ZV)} = 41 \pm 2$; D vs U or F = $p < 0.001$,
84 $\text{mean} \pm \text{se}$: $D_{(FV+ZV)} = 29.4 \pm 1.45$). However, independent of the PI state, ants showed a
85 tendency to oscillate quicker in familiar than in unfamiliar terrain ($p \geq 0.180$, $\text{mean} \pm \text{se}$:
86 $\text{mean} \pm \text{se}$: $F_{(FV+ZV)} = 0.83 \pm 0.056$ Hz; $U_{(FV+ZV)} = 0.63 \pm 0.037$).
87 (B) shows an example path for each condition across 83 s.
88 (C) Population-average cycle (see Star method and Figure S3) shows how angular and
89 forward velocities co-vary. Angular velocities (top-row) and forward velocity (bottom row)
90 co-vary in a way that is conserved across conditions: when on familiar route (green) or in
91 unfamiliar terrain (purple). Population cycles have been reconstructed by merging full- (FV)
92 and zero-vector (ZV) data and normalising the data amplitude within the individual's average
93 cycle. Colour areas around the mean curves represent the 95% confidence interval, based on
94 the inter-individual variation. Dashed lines represent the moment when the ants are facing
95 their overall direction of travels. Angular velocities (top-row) and forward velocity (bottom
96 row) co-varies in a way that seem conserved across experimental conditions and species (see
97 Figure 3). (D) Boxplots show the actual distribution of the non-normalized mean peak of
98 angular speed and forward velocity amplitude for the individuals' average cycle (FV on the
99 left, ZV on the right). The mean peak of angular velocities and forward velocity amplitude
100 underlying the oscillations are rather constant across navigational context ((D), ($p \geq 0.05$)).
101 Therefore, there is no clear effect on the amplitude of oscillation display within the path (A,
102 B).
103
104



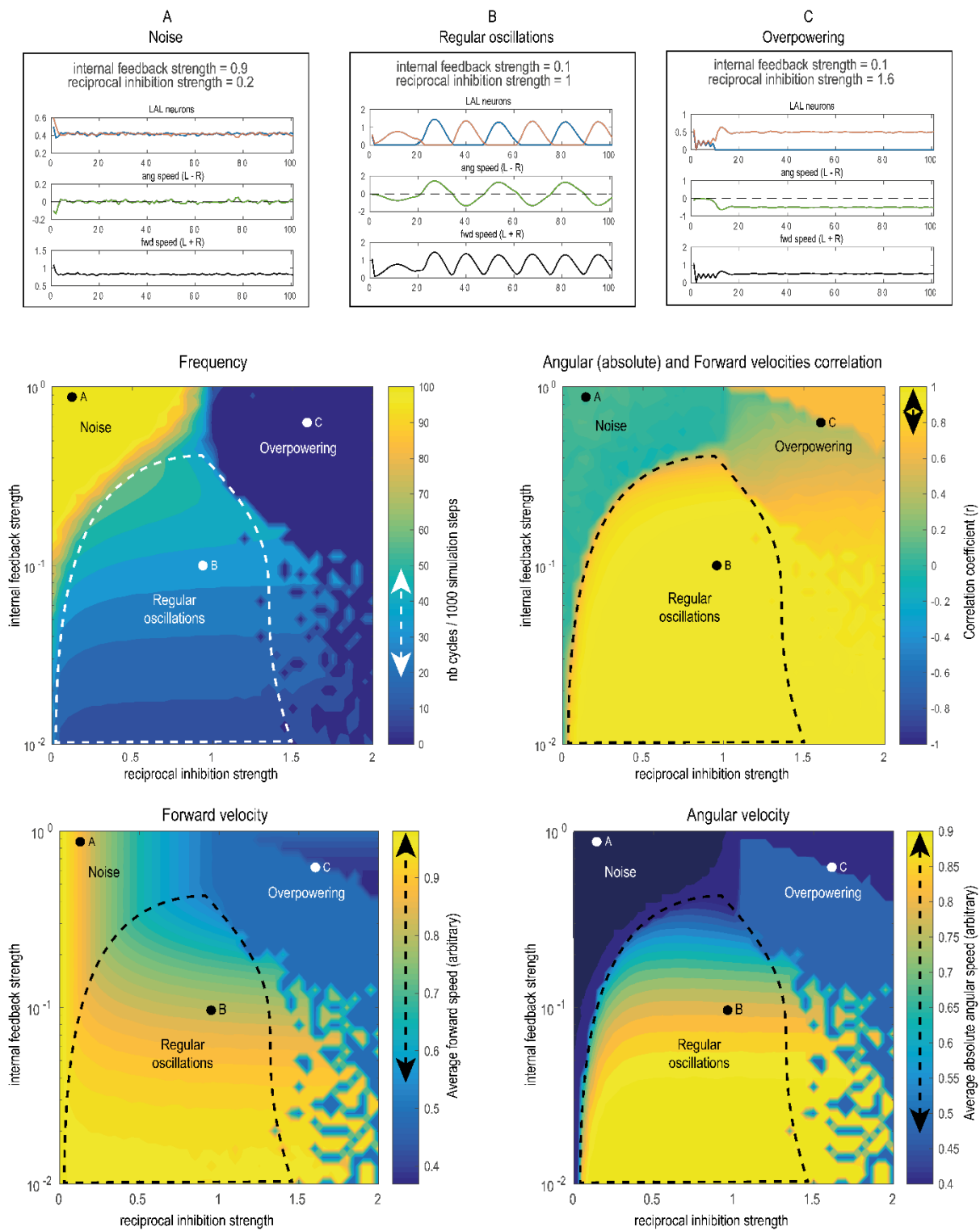
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108

109 **Figure S4. Ant learning walks show similar dynamics of oscillation.** Ants path and head
 110 orientation were recorded (25 Hz) during their learning walks directly on the ground
 111 (courtesy of Jochen Zeil, see Jayatilaka et al, 2018). (A) Example path of an individual
 112 showing clear alternation between right (red) and left (blue) turn. (B) Frequency and spectral
 113 density magnitude of the dominant oscillation (highest magnitude) of angular velocities times
 114 series of 25s (for method see Star method and Figure S2 F-I). Magnitudes were higher than
 115 those obtained with the spectral density of a Gaussian white noise ((A) dashed line; Wilcoxon
 116 one-tail test: $p \leq 0.001$). (C) Angular velocity (top-row) and forward velocity (bottom row)
 117 covary in a similar way than when recorded on the track ball (see Figure 3). Population cycles
 118 have been normalised by the data amplitude within the individuals mean cycle (see Figure S3
 119 for example). Colour areas around the mean curves represent the 95% confidence interval,
 120 based on the inter-individual variation. The natural learning walks showed regular
 121 oscillations as well as the same dynamical relationship between angular and forward
 122 velocities than trackball data. Ants walking on the ground also tend to increase their forward
 123 velocity when they are aligned with their general direction of travel. Data provide by Jochen
 124 Zeil, see²⁷

125



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129

130

131 **Figure S5. The covariation between angular and forward velocity is robust to**
 132 **parameter change.** Exploration of our abstract LAL model's (Figure 5) sensitivity to
 133 change in the two free parameters (inhibition strength and internal feedback strength).

134 Regular oscillations between LAL neurons emerge in a wide space of parameters (functional
135 range delineated by the dashed line, an example for a given parameter set (dot) is shown in
136 (B)). While frequencies (right of middle row), forward and angular velocities (bottom row)
137 can vary roughly across a factor 2 across the functional parameter range, the correlation
138 between absolute angular and forward velocity is constrained around 1 (dashed arrows in the
139 colour bars indicate the variation in the functional range). This positive covariation indicates
140 that the agent slows down (low forward velocity) when reversing turning direction (low
141 absolute angular velocity) and accelerates (high forward velocity) in between, that is when
142 sweeping past its general direction of travel. Outside of this functional range, regular
143 oscillations disappear for extreme parameter sets. For instance, if one neuron overpowers the
144 other due to too strong reciprocal inhibitory strength (C, overpowering); or inversely, due to
145 the absence of reciprocal inhibition (strength <0.01) or a too strong internal adaptation
146 preventing the neurons to modulate their baseline activity, and thus resulting in noise (A).
147