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Title: Individual Learning Phenotypes Drive Collective Cognition

Authors: Chelsea N. Cook^{1*}, Natalie J. Lemanski², Thiago Mosqueiro², Cahit Ozturk¹,
Jürgen Gadau³, Noa Pinter-Wollman^{2◇}, Brian H. Smith^{1◇}

Affiliations:

¹ School of Life Sciences, Arizona State University, Tempe, USA
² Department of Ecology and Evolutionary Biology, University of California Los Angeles,
Los Angeles, USA
³ Institute for Evolution and Biodiversity, University of Münster, Münster, Germany

◇Co-Senior Authors

*Corresponding Author

One Sentence Summary: Attentive individuals more strongly influence collective foraging decisions by focusing on and recruiting to preferred food locations.

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25 **ABSTRACT:** Collective cognition emerges from individuals responding to local
26 information to make decisions. However, animals vary in how they learn to pay attention
27 to important information, which has unknown consequences on collective behavior. We
28 tested whether honey bee colonies comprised of individuals that differ in their capacity
29 to focus their attention would choose to continue to visit learned, familiar food locations or
30 switch to novel food locations. We found that colonies of focused bees preferred familiar
31 food location, while colonies of less focused bees visited novel and familiar food sites
32 equally. In mixed colonies, both types of bees preferred the familiar food location.
33 Attention-focused individuals drive nestmates to their preferred location by recruiting
34 them more intensely compared to unfocused individuals. Our results reveal that
35 emergent collective behavior is driven by the attention-focusing abilities of individuals.

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38 **Main Text:**

39 Collective cognition allows animal groups to more effectively respond to a rapidly
40 changing environment compared to their individual counterparts, such as schools of fish
41 avoiding predators (1), flocks of birds migrating across the Earth (2), or honey bee
42 colonies finding and visiting millions of flowers (3). Individuals in groups utilize local
43 information to quickly adjust to ecological changes by implicitly or explicitly
44 communicating information with group members to form collective behavior (4–6).
45 Collective cognition emerges from interactions between individuals that vary in their
46 cognitive abilities (3, 4). Variation in the cognitive task of attention can shape critical

47 individual behaviors, such as effectively cueing in on the correct prey or mate (7), and
48 can have severe consequences on learning and productivity in humans (8–10).
49 However, little is known about how individual variation in attention may influence
50 emergent collective behavior.

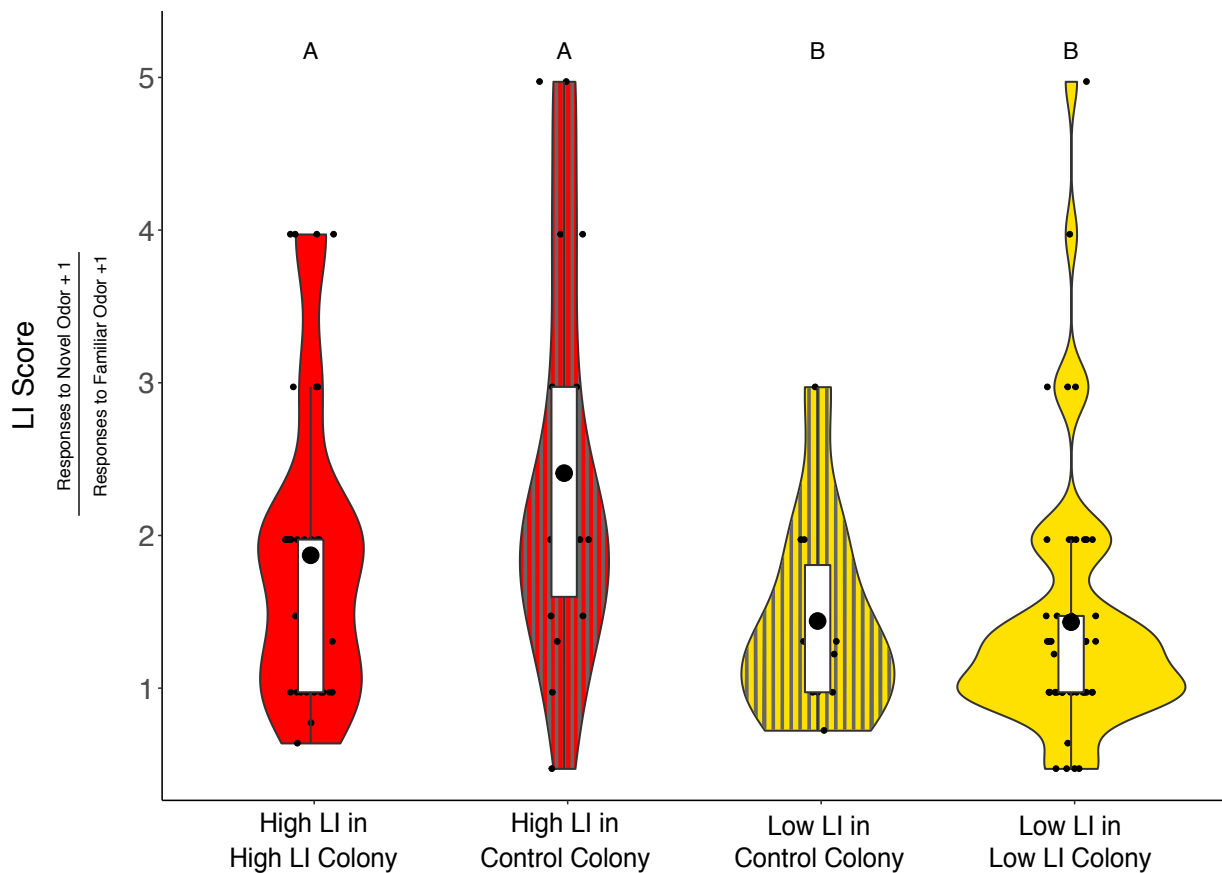
51 We therefore tested how individual differences in learning to focus attention
52 scales to shape collective foraging behavior in honey bees by utilizing a learning
53 behavior called latent inhibition (LI) (11). Latent inhibition is a form of non-associative
54 learning related to the ability to ignore familiar, unrewarding stimuli to pay attention to
55 novel, important stimuli (12). Specifically, after exposure to an odor that is not followed
56 by reward, some forager bees take longer to learn about this now ‘familiar’ odor, relative
57 to a novel odor, when both types of odor are later paired with reward, or “high LI”. Other
58 bees that learn both familiar and novel odors quickly are “low LI”. Moreover, differences
59 in expression of LI correlate to foraging specializations. LI has been mostly studied in
60 vertebrates (12–16). However, honey bees (*Apis mellifera*) also exhibit (17, 18) and
61 show heritable variation in LI (11). Scout bees, who search for novel food sources, show
62 high LI whereas recruited bees that forage at known food locations show low LI (19). To
63 uncover how individual variation in learning to pay attention impacts collective behavior,
64 we investigated how an individual’s latent inhibition (LI) may scale to influence collective
65 foraging behavior in honey bee colonies.

66 The reproductive queens and haploid males (drones) of a honey bee colony
67 exhibit variation in LI (11, 18). This allowed us to select for distinct high and low LI
68 phenotypes to generate lines from queens singly inseminated with sperm from like-
69 performing drones to produce workers that exhibit similar LI to their parents (20). We

70 then created colonies composed of age-matched single cohorts of only low, only high,
71 50/50 mixed high and low LI workers, as well as age-matched non-selected control
72 bees. In semi-natural foraging conditions, we counted the number of forager visits, first
73 visits, and revisits to the familiar or novel food locations. To explore the mechanisms
74 underlying how individual variation in LI affects collective foraging, we quantified the
75 round recruitment dance activity in mixed colonies while foraging.

76 To ensure that selected bees in different social environments exhibited the
77 predicted heritable LI phenotype, we evaluated the LI score of foragers from selected
78 lines that spent their adult life in either their natal colony or a control colony. Foragers
79 retained the expected LI based on the LI of their parents, regardless of whether they
80 were housed with same or with variable learning phenotypes (GLM: $\chi^2 = 6.54$, $df=1$,
81 $p=0.011$, Fig. 1). We did not detect an effect of the identity of the colony in which the
82 bees were housed on LI phenotype ($\chi^2 = 3.766$, $df=2$, $p=0.152$, Fig. 1).

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Figure 1: Social environment does not alter expression of genetically selected latent inhibition. LI scores of individuals from high LI lines that spent their adult life either in high LI only colonies (red, $n=36$) or in a control colony with a variety of LI phenotypes from an open mated queen (red with gray vertical lines, $n=18$); individuals from low LI lines that spent their adult life either in low LI only colonies (yellow, $n=52$) or in control colonies (yellow with gray vertical lines, $n=10$). Different letters above boxes indicate statistically significant differences according GLM comparison ($p<0.05$). In this and subsequent figures, the large black dot is the mean, the white box is the interquartile range (IQR), whiskers extend to $1.5 \times \text{IQR}$, and the small points beyond the whiskers are outliers. Color shaded areas show the

96 *distribution of the data. Additionally, here and in all following figures, yellow are low LI*
97 *colonies and individuals, gray are control colonies and individuals, and red are high LI*
98 *colonies and individuals.*

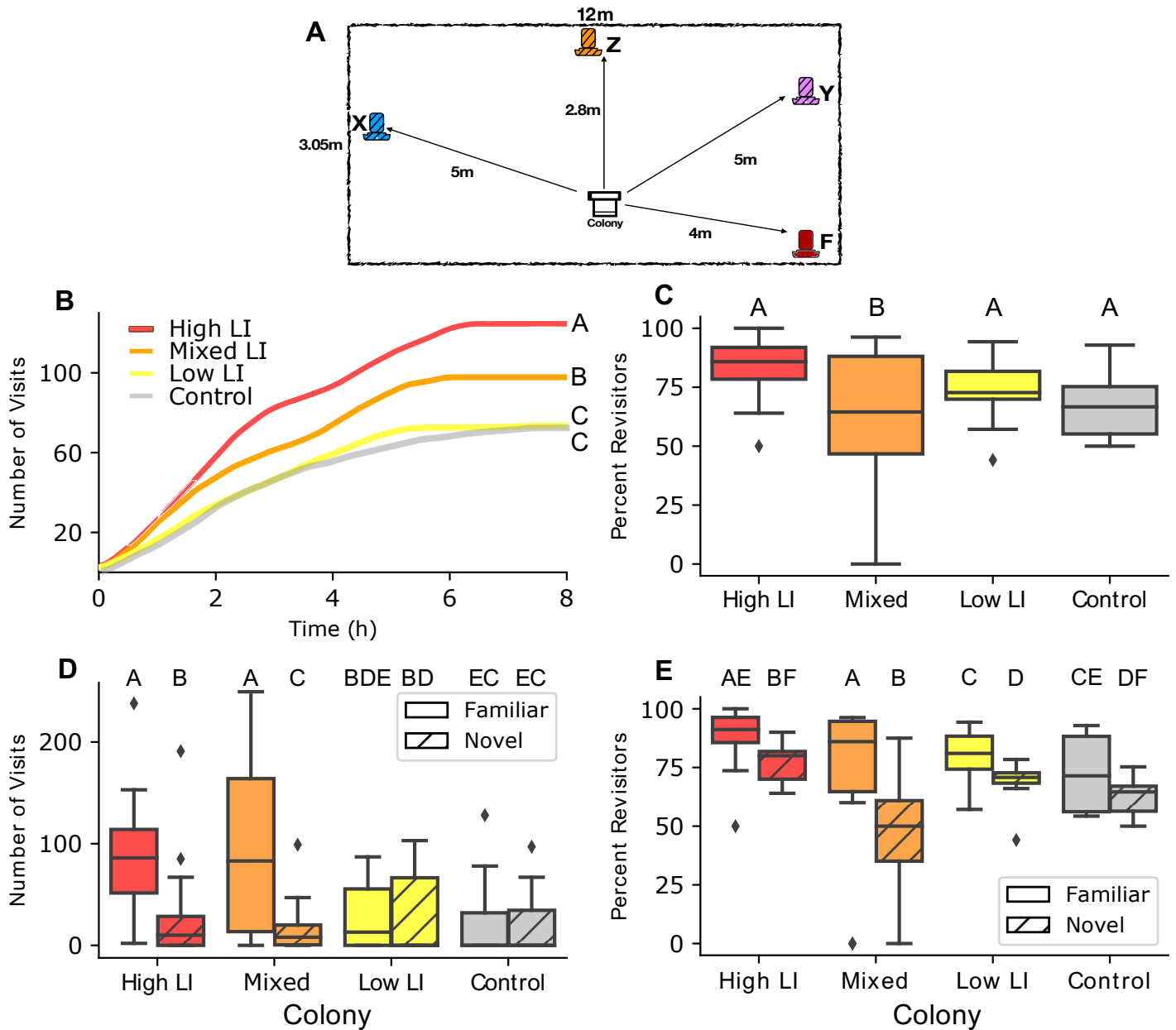
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101 To determine how the learning phenotypes influenced colony-level foraging
102 behavior, we placed small single-cohort age-matched colonies into a flight cage and
103 monitored foraging activity to familiar or novel feeders (Fig. 2A). To evaluate the
104 collective feeder choice, we recorded the number of visits to each feeder by bees from
105 each selected line according to the color of paint on the bees' thorax. We further
106 marked bees with a feeder-specific color on their abdomen when they visited the feeder
107 for the first time to determine if bees revisited that feeder.

108 Colony learning phenotype strongly influenced overall number of visits to the
109 food locations (GLM: $\chi^2 = 1270$, $df = 3$, $p < 0.0001$, Fig. 2B). Foraging in the high, low,
110 and control colonies was largely performed by bees revisiting the feeders, while mixed
111 colonies had more new visitors to the feeders (GLM, $\chi^2 = 22.32$, $df = 3$, $p < 0.0001$, Fig.
112 2C, table). A colony's LI phenotype composition also determined its preference
113 between the novel and familiar feeders, with high LI and mixed colonies preferring the
114 familiar and low and control colonies showing no preference (GLM: Feeder*Colony χ^2
115 =473.64, $df=3$, $p<0.0001$; Fig. 2D). Revisits to feeders drive foraging for all colonies
116 (Fig. 2E: Colony*Feeder $\chi^2=53.67$, $p<0.0001$). However, new foragers in the mixed
117 colonies that visited the novel feeder were less likely to return to it compared to foragers
118 who visited the novel feeders in other colonies (Table S6).

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121 **Figure 2: Colonies constructed from different genetic lines selected for high or**

122 **low latent inhibition exhibited differences in collective foraging behavior. (A) The**

123 **experimental set up illustrating the location of feeders in relation to the location of the**

124 **colony (center, white) within the experimental arena (large rectangle) (See table S2 for**

125 *feeder placement and odors) (B) Cumulative number of visits of all bees (bees from*
126 *selected lines and controls) to all feeders over time by colony type. Different letters to*
127 *the right of the lines indicate statistically significant differences according to a post hoc*
128 *test ($p < 0.05$) (See fig S1 for individual visitation). (C) Percent of re-visits out of the total*
129 *number of visits to all feeders by colony type. Here and in all following panels, different*
130 *letters above boxes indicate statistically significant differences according to a post hoc*
131 *test ($p < 0.05$, table S4). (D) Number of all visits to the familiar feeder (solid boxes) and a*
132 *novel feeder (hatched boxes) for each type of colony, when both novel and familiar*
133 *feeders were presented simultaneously (days 2-4) (for post-hoc results see table S5).*
134 *(E) Percent of re-visits out of the total number of visits to either the familiar or the novel*
135 *feeder by type of colony when both novel and familiar feeders were presented*
136 *simultaneously (days 2-4) (for post-hoc results see table S6). N=24 colonies, 6 colonies*
137 *per colony type, 6172 total visits.*

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140 To determine why the mixed colonies showed a preference for the familiar feeder
141 (Fig. 2D), we examined how individual lines visited each feeder (Fig. 3). In 2017, we
142 tested mixed colonies placed in a flight cage. In 2018, we reselected lines and then
143 placed mixed colonies into two-frame observation hives to evaluate recruitment dances
144 along with visitation to the feeders in the flight cages. We found that there was a
145 significant year effect (table S7), likely due to reselection and different hive placement.
146 We therefore statistically analyzed each year separately to focus on the within-year
147 variation between the selected lines.

148 Low LI and control individuals shift their preference to the familiar feeder when
149 mixed with high LI bees. In 2017, we found a significant interaction between the
150 selected line and which feeder foragers visited (GLM: $\chi^2 = 7.79$, $df=2$, $p=0.02$; Fig. 3A).
151 Although low LI and control colonies did not show a preference to a novel or familiar
152 feeder when they had a uniform colony composition (Fig. 2E), when mixed with high LI
153 individuals, low LI and control individuals exhibited a preference to the familiar feeder
154 (Fig. 3A, table S8). High LI individuals showed a preference to familiar feeders just as
155 colonies comprised of only high LI individuals did (Fig. 2E). We found a significant
156 interaction between selected line and feeder again in 2018 (GLM: $\chi^2 = 85.27$, $df=2$,
157 $p<0.0001$; Fig. 3B), with low LI and control individuals showing preference to the familiar
158 feeder over the novel feeder (Fig. 3B, table S9) similar to high LI individuals preferring
159 the familiar feeders.

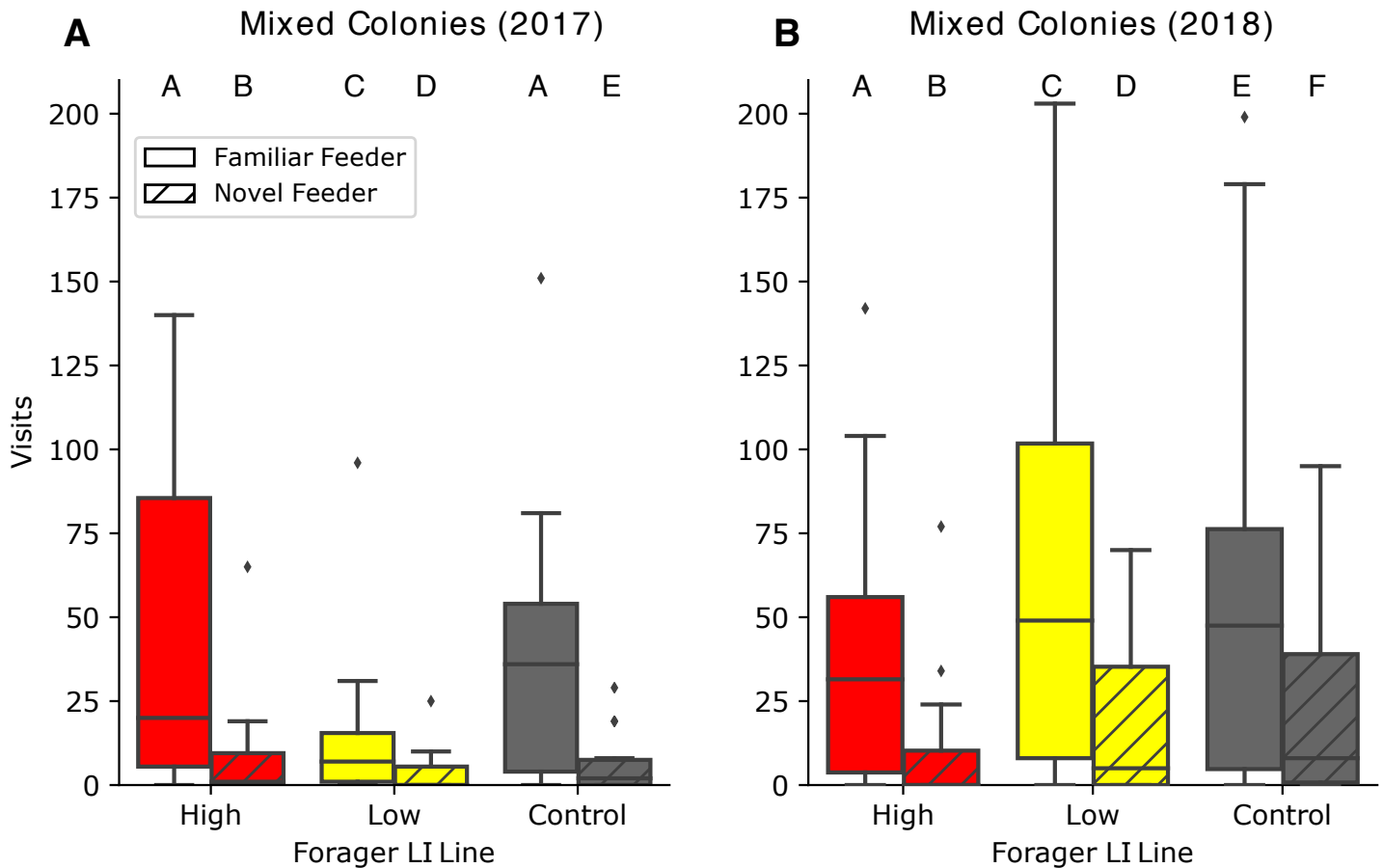
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167 **Figure 3: Visits of individuals from different genetically selected lines when in a**

168 **mixed colony.** Daily visits to the familiar and novel feeders by individual bees in mixed

169 colonies from low LI parents (yellow), high LI parents (red) or open mated queens (grey)

170 in (A) 2017, N=6 mixed colonies, 2347 overall visits and (B) in mixed colonies from lines

171 that were re-selected in 2018, N=6 colonies, 6272 overall visits. In both years, low LI

172 and control bees switched to prefer the familiar feeder.

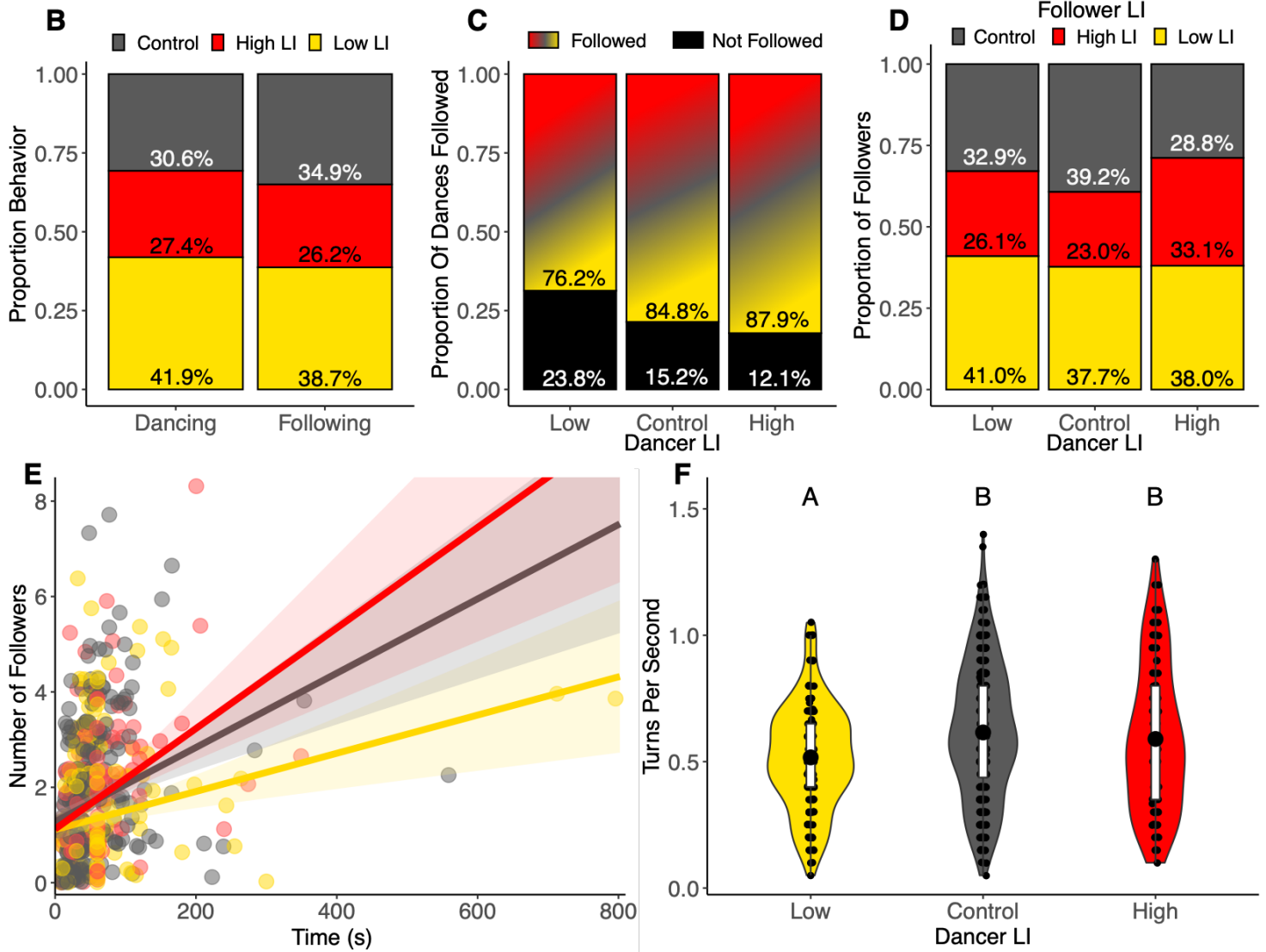
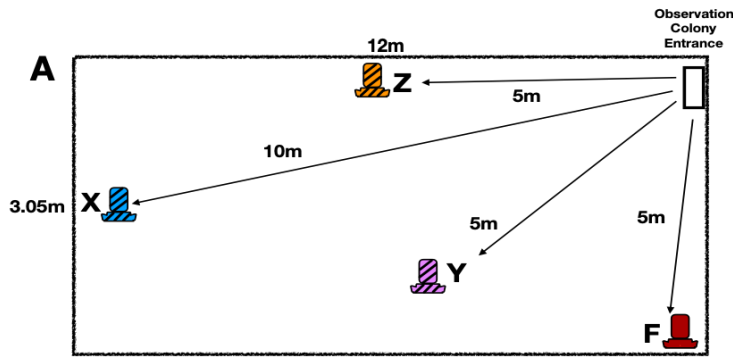
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175 To uncover the behavioral mechanisms that underlie why low LI and control bees
176 switch feeder preference when housed with high LI bees, we evaluated how each line
177 performed the round dance, the modified waggle dance used for recruitment to food at
178 short distances (21). Individuals from the lines differed in their likelihood to perform a
179 round dance (Chi-square test: $\chi^2=26.61$, $df=2$, $p<0.0001$; Fig. 4B). Low LI individuals
180 were significantly more likely to perform a dance compared to high LI individuals
181 (pairwise chi-square test: $p=0.0001$) and controls (pairwise chi-squared test: $p=0.004$).
182 High LI individuals were just as likely to perform a dance as controls ($p=0.36$).
183 Individuals differed in their likelihood to follow a dance based on their selected line (Chi-
184 square test: $\chi^2=28.26$, $df=2$, $p<0.0001$; Fig. 4B). Low LI individuals were significantly
185 more likely to follow a dance compared to high LI bees (pairwise chi-square test:
186 $p<0.0001$) and controls ($p<0.003$). High LI and control individuals were equally likely to
187 follow a dance ($p=0.240$).

188 Although the high LI individuals danced less often, high LI dances had
189 significantly more followers compared to low and control bees (Chi-square test: $\chi^2=$
190 13.93 , $df=2$, $p<0.001$; Fig. 4C). Low LI bees performed more dances that had no
191 followers compared to high LI and control dances. Low LI individuals spent more time
192 dancing; however, they attracted fewer followers than high and control dancers,
193 indicated by the significant interaction between the LI of the dancer and dance duration
194 when predicting the number of followers (GLMM: $\chi^2= 6.42$, $df=2$, $p=0.04$; Fig. 4E). The
195 relative attraction of dances of high LI bees could be due to the intensity of the dance.
196 High LI bees performed more turns per second during their dances (ANOVA: $\chi^2=12.8$,
197 $df=2$, $p=0.002$; Fig. 4F).

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200 **Figure 4: Recruitment dances facilitate integration of information from different**
201 **genetically selected lines.** (A) The experimental set up illustrating the location of
202 feeders in relation to the location of the colony entrance (top right, white) within the
203 experimental arena (large rectangle). (See SI Table 2 for feeder placement and odors)
204 (B) Proportion of dances (N=667) or follows (N=1201) across 6 colonies performed by
205 bees from each line, relative to their abundance in the mixed colony (350 high, 350 low,
206 700 control). We accounted for the difference in abundance of each selected line by
207 dividing the number of observed control dancers by 2 before calculating these
208 proportions. (C) Proportion of dances performed per LI line type that were either
209 followed by at least one individual (colored) or not followed by any other bees (black).
210 (D) Proportion of dances by LI line type that were followed (from panel B) broken down
211 by LI of the follower. (E) Relationship between number of followers and duration of a
212 dance by line. Point and line colors indicate LI of dancer. Best fit line represents the
213 GLM, shaded area represents the 95% confidence interval. (F) Rate of turns per second
214 in a dance by line.

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217 By combining techniques from experimental psychology and behavioral ecology,
218 we have developed a system for investigating how variation in individual learning
219 behavior drives collective cognition. We demonstrate that a laboratory-selected
220 heritable learning behavior with natural individual variation scales to shape the collective
221 performance of honey bee colonies on quasi-natural foraging tasks. In the lab, high LI

222 bees learn to ignore familiar odors that they experienced without reinforcement, while
223 readily learning novel odors.

224 One interpretation of reduced learning to a familiar, unrewarding, stimulus is that
225 pre-exposure reduces attention to, and thus associability of, that stimulus (22, 23). In
226 this interpretation, latent inhibition allows animals to focus attention on important
227 information (15, 24, 25). Our observations of field behavior of low and high LI individuals
228 and colonies are consistent with this interpretation, whereby high LI individuals have
229 stronger attention capacities to food compared to low LI individuals. Once high LI
230 individuals have found a food location, they continue to revisit it, 'attending' more
231 strongly to reinforced feeders over new ones. The increased impact of the resource on
232 these bees could translate into stronger, more vigorous dances. In contrast, low LI
233 individuals learn and visit both known and new feeders equally, dividing their attention
234 across resources and acting more like generalist foragers. In mixed colonies, this
235 broadened attention by low LI individuals may therefore make them the perfect
236 audience for the high LI dancers, driving them to prefer feeders that high LI individuals
237 preferentially visit. Under natural conditions, where queens mate with many different
238 drones, most colonies would possess both types of learners, perhaps more closely
239 resembling our mixed colonies (26). We propose that this diversity of 'attention' aspect
240 of individual cognitive phenotypes may enhance the overall efficacy with which a colony
241 finds and exploits resources (27). In summary, our work indicates that individual
242 cognition scales to shape the collective cognition of animals solving critical ecologically
243 relevant tasks.

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245 REFERENCES AND NOTES

- 246 1. A. J. W. Ward, J. E. Herbert-Read, D. J. T. Sumpter, J. Krause, Fast and accurate
247 decisions through collective vigilance in fish shoals. *Proc. Natl. Acad. Sci.* **108**,
248 2312–2315 (2011).
- 249 2. T. Sasaki, D. Biro, Cumulative culture can emerge from collective intelligence in
250 animal groups. *Nat. Commun.* **8**, 15049 (2017).
- 251 3. I. D. Couzin, Collective cognition in animal groups. *Trends Cogn. Sci.* **13**, 36–43
252 (2009).
- 253 4. D. J. Sumpter, *Collective animal behavior* (Princeton University Press, 2010).
- 254 5. S. Camazine, J.-L. Deneubourg, N. R. Franks, J. Sneyd, E. Bonabeau, G. Theraula,
255 *Self-organization in biological systems* (Princeton university press, 2003).
- 256 6. I. D. Couzin, J. Krause, in *Advances in the Study of Behavior* (Elsevier, 2003;
257 <https://linkinghub.elsevier.com/retrieve/pii/S0065345403010015>), vol. 32, pp. 1–75.
- 258 7. R. Dukas, Behavioural and ecological consequences of limited attention. *Philos.*
259 *Trans. R. Soc. Lond. B. Biol. Sci.* **357**, 1539–1547 (2002).
- 260 8. R. Schachar, G. D. Logan, P. Robaey, S. Chen, A. Ickowicz, C. Barr, Restraint and
261 Cancellation: Multiple Inhibition Deficits in Attention Deficit Hyperactivity Disorder.
262 *J. Abnorm. Child Psychol.* **35**, 229–238 (2007).
- 263 9. P. Dayan, S. Kakade, P. R. Montague, Learning and selective attention. *Nat.*
264 *Neurosci.* **3**, 1218–1223 (2000).
- 265 10. C. J. Mitchell, M. E. Le Pelley, *Attention and associative learning: From brain to*
266 *behaviour* (Oxford University Press, USA, 2010).
- 267 11. S. B. C. Chandra, J. S. Hosler, B. H. Smith, Heritable variation for latent inhibition
268 and its correlation with reversal learning in honeybees (*Apis mellifera*). *J. Comp.*
269 *Psychol.* **114**, 86–97 (2000).
- 270 12. R. E. Lubow, Latent inhibition. *Psychol. Bull.* **79**, 398 (1973).
- 271 13. M. D. Mitchell, M. I. McCormick, M. C. O. Ferrari, D. P. Chivers, Friend or foe? The
272 role of latent inhibition in predator and non-predator labelling by coral reef fishes.
273 *Anim. Cogn.* **14**, 707–714 (2011).
- 274 14. M. C. O. Ferrari, D. P. Chivers, Latent inhibition of predator recognition by
275 embryonic amphibians. *Biol. Lett.* **5**, 160–162 (2009).
- 276 15. R. E. Lubow, Latent inhibition as a measure of learned inattention: some problems
277 and solutions. *Behav. Brain Res.* **88**, 75–83 (1997).

- 278 16. R. E. Lubow, Latent inhibition: Effects of frequency of nonreinforced pre-exposure
279 of the CS. *J. Comp. Physiol. Psychol.* **60**, 454–457 (1965).
- 280 17. C. I. Abramson, M. E. Bitterman, Latent inhibition in honeybees. *Anim. Learning*
281 *Behav.* **14**, 184–189 (1986).
- 282 18. H. J. Ferguson, S. Cobey, B. H. Smith, Sensitivity to a change in reward is heritable
283 in the honeybee, *Apis mellifera*. *Anim. Behav.* **61**, 527–534 (2001).
- 284 19. C. N. Cook, T. Mosqueiro, C. S. Brent, C. Ozturk, J. Gadau, N. Pinter-Wollman, B.
285 H. Smith, Individual differences in learning and biogenic amine levels influence the
286 behavioural division between foraging honeybee scouts and recruits. *J. Anim. Ecol.*
287 **88**, 236–246 (2018).
- 288 20. J. S. Latshaw, B. H. Smith, Heritable variation in learning performance affects
289 foraging preferences in the honey bee (*Apis mellifera*). *Behav. Ecol. Sociobiol.* **58**,
290 200–207 (2005).
- 291 21. K. D. Waddington, Honey bee foraging profitability and round dance correlates. *J.*
292 *Comp. Physiol.* **148**, 297–301 (1982).
- 293 22. P. I. Pavlov, Conditioned reflexes: an investigation of the physiological activity of
294 the cerebral cortex. *Ann. Neurosci.* **17**, 136 (1927).
- 295 23. R. E. Lubow, I. Weiner, P. Schnur, in *The Psychology of Learning and Motivation:*
296 *Advances in Research and Theory*. (Academic Press, New York, 1981;
297 <http://site.ebrary.com/id/10244511>), vol. 15, pp. 1–49.
- 298 24. S. J. Gershman, D. M. Blei, Y. Niv, Context, learning, and extinction. *Psychol. Rev.*
299 **117**, 197–209 (2010).
- 300 25. R. E. Lubow, *Latent inhibition and conditioned attention theory* (Cambridge
301 University Press, 1989), vol. 9.
- 302 26. H. R. Mattila, K. M. Burke, T. D. Seeley, Genetic diversity within honeybee colonies
303 increases signal production by waggle-dancing foragers. *Proc. R. Soc. B Biol. Sci.*
304 **275**, 809–816 (2008).
- 305 27. T. T. Hills, P. M. Todd, D. Lazer, A. D. Redish, I. D. Couzin, Exploration versus
306 exploitation in space, mind, and society. *Trends Cogn. Sci.* **19**, 46–54 (2015).
- 307 28. S. B. C. Chandra, J. S. Hosler, B. H. Smith, Heritable variation for latent inhibition
308 and its correlation with reversal learning in honeybees (*Apis mellifera*). *J. Comp.*
309 *Psychol.* **114**, 86–97 (2000).
- 310 29. C. N. Cook, T. Mosqueiro, C. S. Brent, C. Ozturk, J. Gadau, N. Pinter-Wollman, B.
311 H. Smith, Individual differences in learning and biogenic amine levels influence the

- 312 behavioural division between foraging honeybee scouts and recruits. *J. Anim. Ecol.*
313 **88**, 236–246 (2018).
- 314 30. S. W. Cobey, D. R. Tarpy, J. Woyke, Standard methods for instrumental
315 insemination of *Apis mellifera* queens. *J. Apic. Res.* **52**, 1–18 (2013).
- 316 31. J. R. Harbo, in *Bee Breeding and Genetics*, (Academic Press, Inc, Rinderer T.E.,
317 1986), pp. 361–389.
- 318 32. Z. S. Liang, T. Nguyen, H. R. Mattila, S. L. Rodriguez-Zas, T. D. Seeley, G. E.
319 Robinson, Molecular Determinants of Scouting Behavior in Honey Bees. *Science*.
320 **335**, 1225–1228 (2012).
- 321 33. B. Ripley, B. Venables, D. M. Bates, K. Hornik, A. Gebhardt, D. Firth, M. B. Ripley,
322 Package ‘mass.’ *Cran R* (2013).
- 323 34. D. Bates, M. Maechler, B. Bolker, S. Walker, lme4: Linear mixed-effects models
324 using Eigen and S4. *R Package Version.* **1**, 1–23 (2014).
- 325 35. R. Lenth, M. R. Lenth, Package ‘lsmeans.’ *Am. Stat.* **34**, 216–221 (2018).
- 326 36. R. C. Team, R: A language and environment for statistical computing (2018).

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334 genetically selected lines and CO maintained them. CNC carried out data collection
335 and wrote the first draft of the manuscript. CNC, TM, NJL, NPW, BHS discussed
336 results. All authors commented on the manuscript. **Competing Interests:** The
337 authors declare no competing financial interests **Data Availability:** Data will be
338 available on FigShare and code will be available on Github upon publication.

339

340 **SUPPLEMENTAL MATERIALS**

341 **Materials and Methods**

342 **Tables S1-S9**

343 **Fig. S1**

344 **References 28-36**