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**Title: Individual Learning Phenotypes Drive Collective Cognition**

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

24

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.

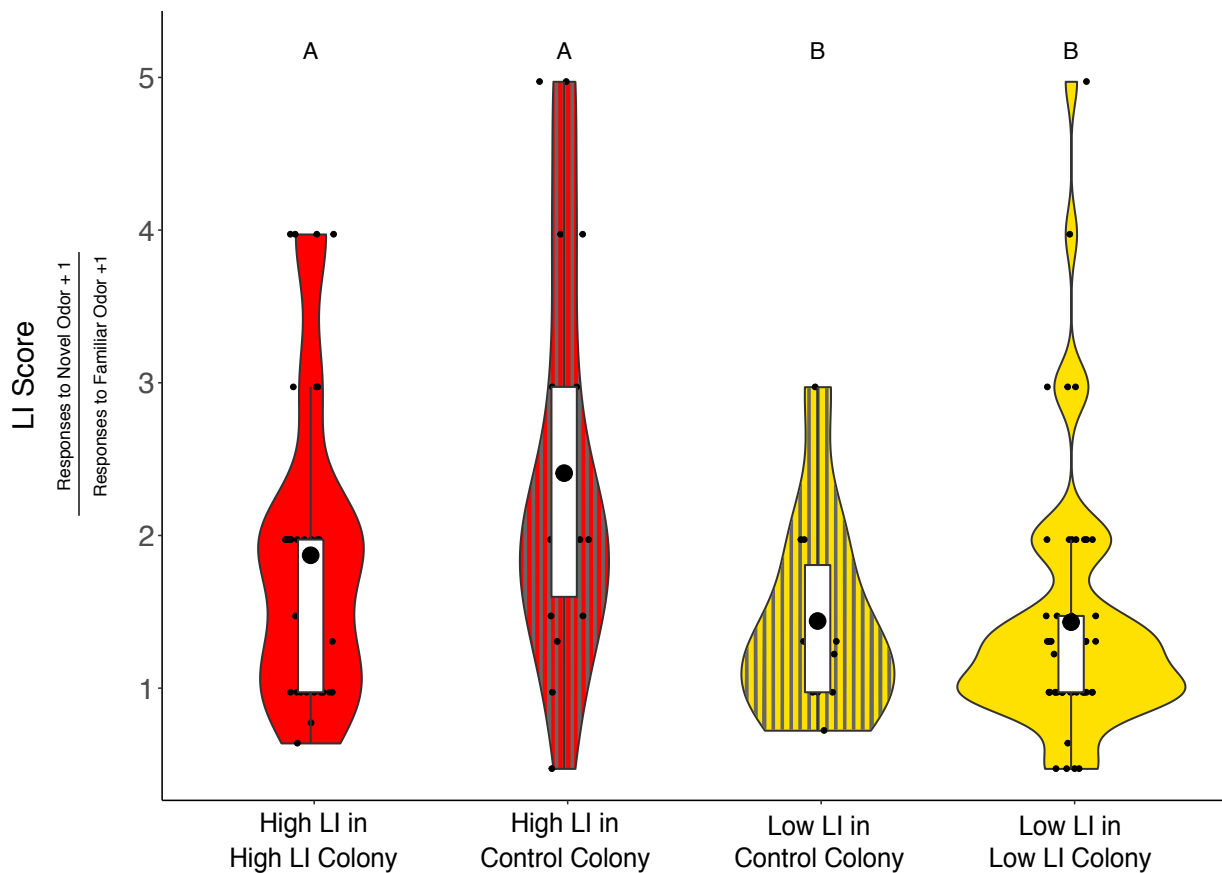
51 We therefore tested how individual differences in learning to focus attention  
52 scales to shape collective foraging behavior in honey bees by utilizing a learning  
53 behavior called latent inhibition (LI) (11). Latent inhibition is a form of non-associative  
54 learning related to the ability 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.*

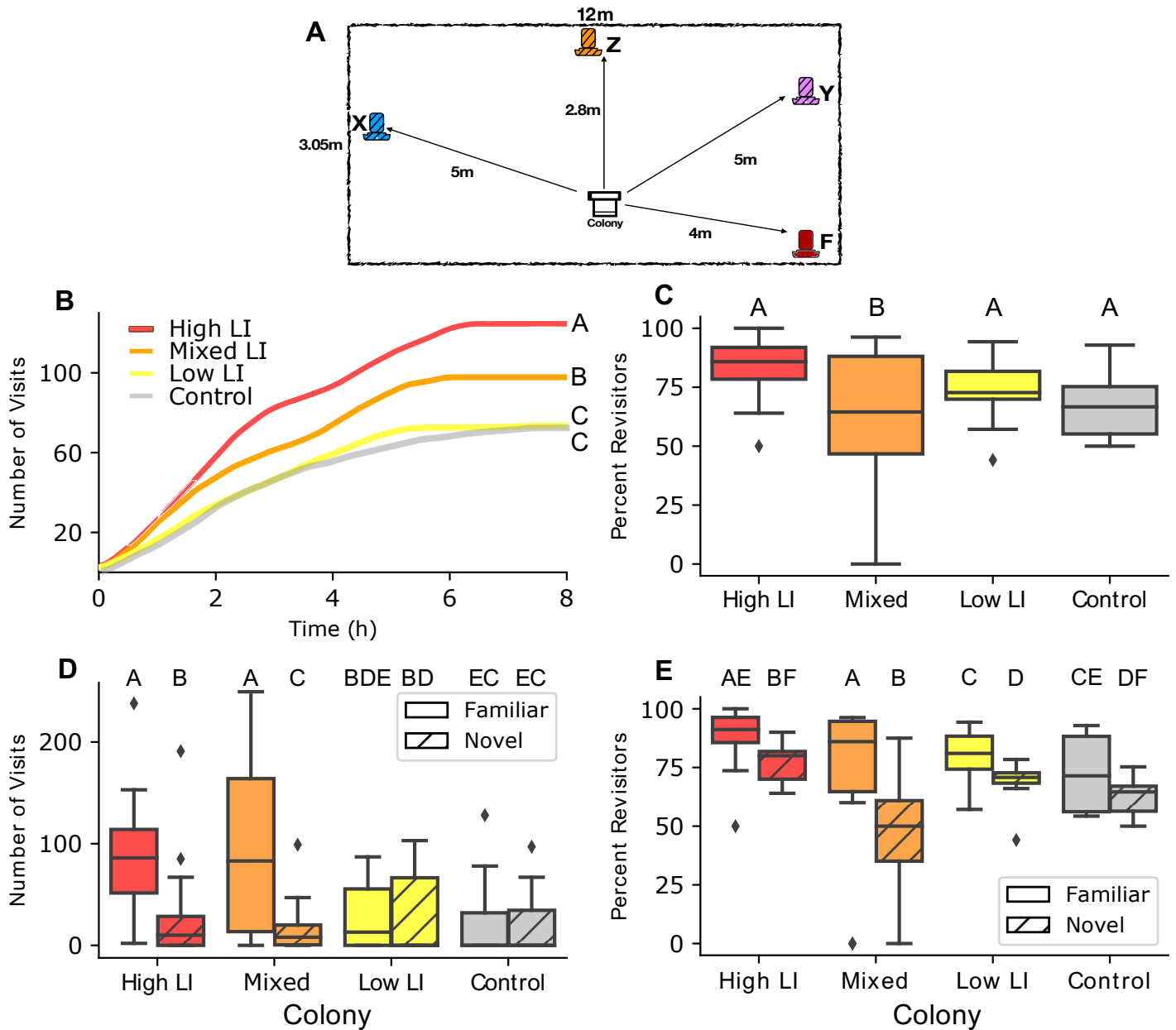
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101 To determine how the learning phenotypes influenced colony-level foraging  
102 behavior, we placed small single-cohort age-matched colonies into a flight cage and  
103 monitored foraging activity to familiar or novel feeders (Fig. 2A). To evaluate 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  $\chi^2$   
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.

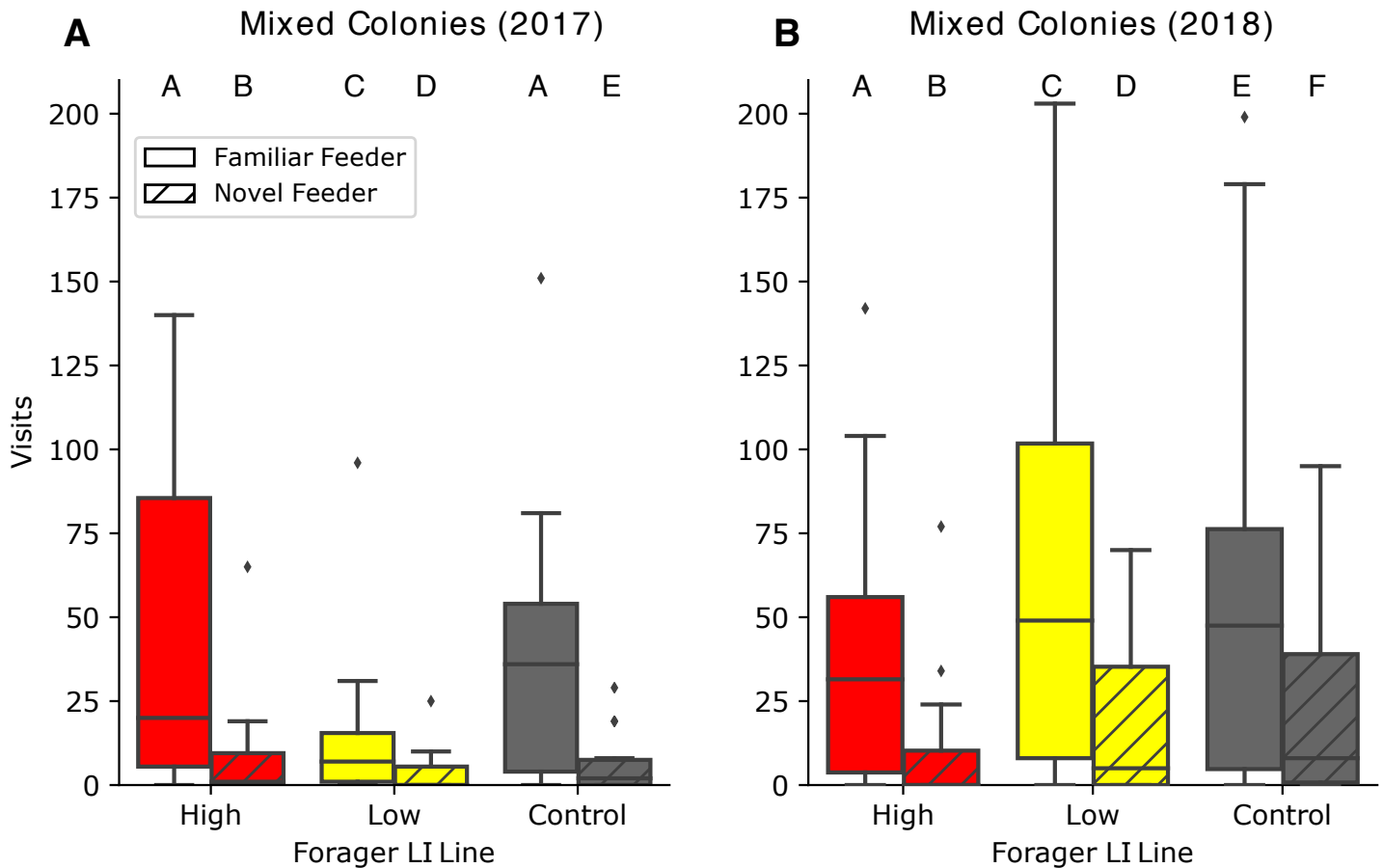
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167 **Figure 3: Visits of individuals from different genetically selected lines when in a**  
168 **mixed colony.** Daily visits to the familiar and novel feeders by individual bees in mixed  
169 colonies from low LI parents (yellow), high LI parents (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.

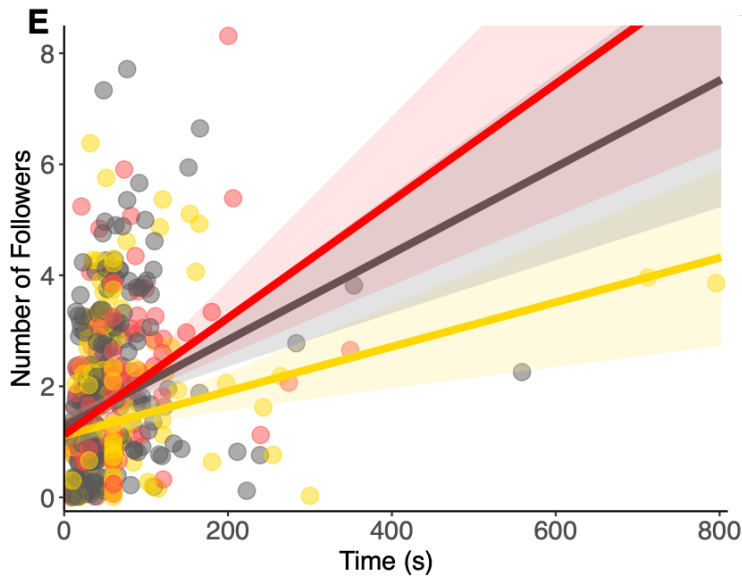
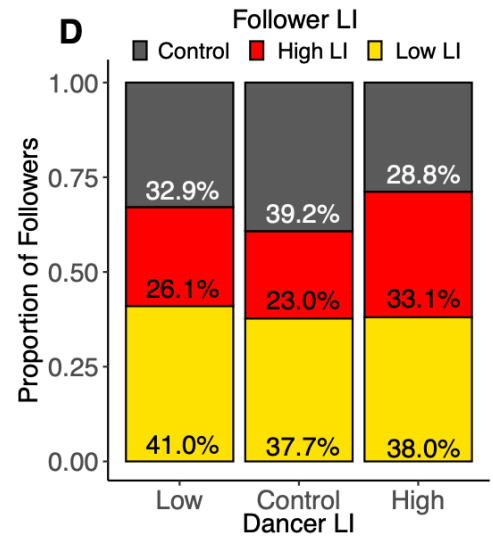
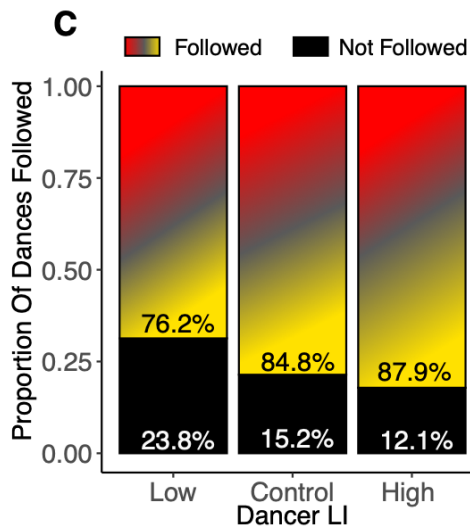
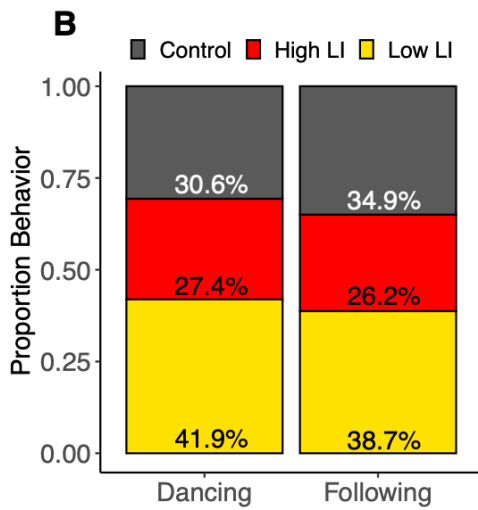
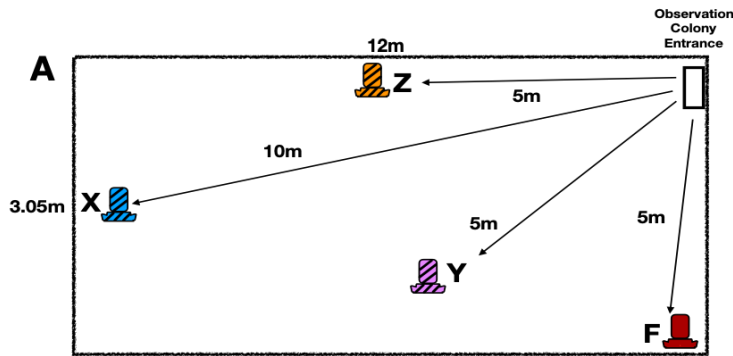
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175 To uncover the behavioral mechanisms that underlie why low LI and control bees  
176 switch feeder preference when housed with high LI bees, we evaluated how each line  
177 performed the round dance, the modified waggle dance used for recruitment 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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327

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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**