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Avarguès-Weber

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1 **Evidence of cognitive specialization in an insect: proficiency is maintained across**
2 **elemental and higher-order visual learning but not between sensory modalities in honey**
3 **bees**

4 Valerie Finke^{1,2}, David Baracchi^{1,3}, Martin Giurfa^{1,4}, Ricarda Scheiner² and Aurore Avarguès-
5 Weber¹

6
7 ¹ *Centre de Recherches sur la Cognition Animale (CRCA), Centre de Biologie Intégrative*
8 *(CBI), Université de Toulouse; CNRS, UPS, 118 Route de Narbonne, 31062 Toulouse,*
9 *France*

10
11 ² *Biozentrum, Universität Würzburg, Am Hubland, 97074 Würzburg, Germany*

12
13 ³ *Department of Biology, University of Florence, Via Madonna del Piano 6, 50019 Sesto*
14 *Fiorentino, Italy*

15
16 ⁴ *Institut Universitaire de France, Paris, France*

17
18 Corresponding author:

19 Dr. Aurore Avarguès-Weber

20 Centre de Recherches sur la Cognition Animale

21 Université Toulouse 3

22 Bâtiment 4R3

23 118 Route de Narbonne

24 31062 Toulouse Cedex 09

25 France

26 E-mail : aurore.avargues-weber@univ-tlse3.fr

27 Tel: +33 561 556 572

28
29 ***Abstract***

30 Individuals differing in their cognitive abilities and foraging strategies may confer a valuable
31 benefit to their social groups as variability may help responding flexibly in scenarios with
32 different resource availability. Individual learning proficiency may either be absolute or vary
33 with the complexity or the nature of the problem considered. Determining if learning abilities
34 correlate between tasks of different complexity or between sensory modalities has a high
35 interest for research on brain modularity and task-dependent specialisation of neural circuits.
36 The honeybee *Apis mellifera* constitutes an attractive model to address this question due to its
37 capacity to successfully learn a large range of tasks in various sensory domains. Here we

38 studied whether the performance of individual bees in a simple visual discrimination task (a
39 discrimination between two visual shapes) is stable over time and correlates with their
40 capacity to solve either a higher-order visual task (a conceptual discrimination based on
41 spatial relations between objects) or an elemental olfactory task (a discrimination between
42 two odorants). We found that individual learning proficiency within a given task was
43 maintained over time and that some individuals performed consistently better than others
44 within the visual modality, thus showing consistent aptitude across visual tasks of different
45 complexity. By contrast, performance in the elemental visual-learning task did not predict
46 performance in the equivalent elemental olfactory task. Overall, our results suggest the
47 existence of cognitive specialisation within the hive, which may contribute to ecological
48 social success.

49

50 **Keywords**

51 *Apis mellifera* - Cognitive consistency – Honeybee – Insect cognition – Inter-individual
52 variability – Visual cognition

53

54 **1. Introduction**

55 Cognitive skills are often attributed to a species based on the ability of few representative
56 members to pass or fail key cognitive tests. Yet, depicting cognition at a species level ignores
57 the inter-individual variability that may reveal fundamental properties in terms of behavioural
58 plasticity and, in case of eusocial animals, specialization within a species. Indeed, inter-
59 individual differences may involve variation in different domains such as motivation to
60 complete the task, choice strategy, personality, or any combination of these factors. However,
61 variable performances between individuals may also be due to intrinsic differences in
62 cognitive abilities, which may be retraced to multiple dimensions, from differences in gene
63 expression to variability in neural population responses and hormonal levels (Akhund-Zade et
64 al., 2019; Honegger et al., 2019). Shifting the focus from the species to the individual level in
65 the study of cognitive abilities provides a remarkable opportunity to reveal key underpinning
66 mechanisms. Moreover, it also offers novel perspectives to understand the link between
67 fitness and cognition (Raine & Chittka, 2008; Thornton & Lukas, 2012; Thornton et al., 2014;
68 Evans et al., 2017; Boogert et al., 2018).

69 Social insects have attracted wide attention due to their remarkable cognitive feats
70 (Giurfa, 2007; Srinivasan, 2010; Avarguès-Weber & Giurfa, 2013; Chittka, 2017). The co-
71 existence of individuals with variable cognitive abilities within a social group may be
72 favoured due to the important energetic cost of investing in important learning faculties or
73 problem-solving abilities (Mery & Kawecki, 2003; Burns, 2005; Burns & Rodd, 2008;
74 Kawecki, 2009; Burns et al., 2011; Jaumann et al., 2013; Kotrschal et al., 2013). Such a co-
75 existence has been documented for example in bumblebees colonies where some individuals
76 consistently make fast but inaccurate foraging decisions while others decide more slowly yet
77 with higher accuracy (Chittka et al., 2003). Colony success indeed benefits from the co-
78 existence of costly but highly skilled foragers and cheaper but less accurate animals, as this
79 heterogeneity may improve exploitation of different food sources and information distribution
80 within the colony (Burns, 2005; Burns & Dyer, 2008; Muller & Chittka, 2008; Chittka et al.,
81 2009). For example, the distinction between scout foragers searching novel resources and
82 recruited bees relying on social information to exploit massively a unique resource as long as
83 it remains profitable might be based on different cognitive abilities (Cook et al., 2018).

84 Bees are particularly appealing to study inter-individual cognitive variability as
85 forager bees demonstrate diverse learning abilities ranging from elemental associative tasks to
86 higher-order forms of learning such as categorization, numerical tasks or concept formation,
87 among others (Srinivasan, 2010; Avarguès-Weber et al., 2011; Avarguès-Weber & Giurfa,
88 2013; Giurfa, 2013, 2019). Inter-individual variability has been generally neglected in
89 standard tests of bee learning, which rely on mean group performance. Exceptions to this
90 trend are the identification of individual variability in sucrose responsiveness as an important
91 factor determining individual learning performance in honeybees (Scheiner et al., 1999, 2001,
92 2005) and the analysis of variability in olfactory learning performances on an individual basis
93 (Pamir et al., 2011, 2014). Both show the importance of focusing on individual performances
94 as group-level analysis may lead to the misinterpretation of response dynamics.

95 Pioneer studies in bumblebees investigated whether such individual differences are
96 consistent between cognitive tasks. Thus, relative learning performances were compared
97 between visual and olfactory tasks with contradictory results between studies concerning the
98 existence of a correlation (Muller & Chittka, 2012; Smith & Raine, 2014). Bumblebees ability
99 to solve an elemental discrimination task (A+ vs. B-) seems correlated with the faculty to then
100 learn reversed reward contingencies in a non-elemental reversal learning phase (A- vs. B+)
101 (Raine & Chittka, 2012). On the contrary, recent studies on honeybees showed no correlation

102 between individual relative performance in odours discrimination tasks when the
103 reinforcement was appetitive or aversive (Junca et al., 2019) nor between landmark and
104 olfactory learning (Tait et al., 2019), which suggests some level of cognitive specialization.

105 Here we analysed individual learning performances in a simple visual discrimination
106 task in which bees had to discriminate a rewarded from a non-rewarded visual target. We
107 determined if learning proficiency was stable over time (three consecutive days) despite inter-
108 individual differences. After confirming that inter-individual differences were consistent and
109 unaffected by the kind of visual stimulus used in this task, we determined if performance
110 across visual tasks of different complexity, or across sensory modalities (visual versus
111 olfactory), was correlated. To this end we trained bees along two consecutive tasks: i) the
112 same elemental visual discrimination task described above and either ii) a conceptual visual
113 discrimination based on learning the constant spatial relationships between variable patterns
114 ('choosing the picture presenting an object *above/below* the other, or to the *left/right* of the
115 other, independently of the physical properties the objects present') (Avarguès-Weber et al.,
116 2012) or ii') a simple olfactory discrimination (a discrimination between a rewarded and a
117 non-rewarded odorant). While the simple visual and olfactory tasks represent basic forms of
118 learning in which two stimuli have unambiguous outcomes (A+ vs. B-), the conceptual task
119 requires transfer to novel unknown stimuli preserving the appropriate spatial relationship, and
120 represents, therefore, a higher-order learning form (Giurfa, 2003; Avarguès-Weber & Giurfa,
121 2013).

122

123 2. Methods

124 (a) General procedure

125 Free-flying honeybees (*Apis mellifera*) originating from a single hive and trained to forage for
126 nectar on a sucrose gravity feeder were used in all our experiments. Only bees with intact
127 wings were used as wing damage could account for reduced foraging performance (Higginson
128 & Barnard, 2004; Higginson et al., 2011). The age of the bees was not controlled. Bees were
129 recruited from the feeder to the setup by offering them a drop of sucrose solution with a
130 concentration (1.8 M) higher than that of the feeder (variable depending on foraging
131 motivation). While drinking, the bees were gently placed at the entrance of our Y-maze setup.
132 Once satiated, the bees flew back to their hive. Returning bees on their subsequent foraging
133 trip were colour-marked and individually trained in a stepwise fashion to enter the Y-maze to

134 collect a sucrose reward (1.8 M) placed on the back walls of the maze. This pre-training
135 usually took 1-2 hours per bee.

136 The maze consisted of a pre-chamber, a decision chamber and the two arms in which
137 the stimuli to be learned were presented. The pre-chamber was equipped with a sliding
138 door, which allowed controlling the traffic of foraging bees. Only one marked bee was
139 allowed at a time in the Y-maze. After entering the pre-chamber, the bee could fly into the
140 decision chamber through a hole (\varnothing 5 cm), leading to the two arms (40 cm x 20 cm x 20 cm,
141 L x H x W) of the apparatus. The stimuli were presented on a UV-reflecting white
142 background covering the back walls (20 x 20 cm) of the arms. Back walls were placed at 15
143 cm from the centre of the decision chamber. During the learning tasks, bees always had to
144 discriminate a stimulus rewarded with sucrose solution 1.8 M from an alternative stimulus
145 punished with quinine solution 60 mM (Avarguès-Weber et al., 2010). A choice was scored
146 when the bee approached one stimulus (< 5cm). If the bee chose the rewarded stimulus, it was
147 allowed to drink the sucrose solution *ad libitum* until it returned to the hive to deliver the
148 sucrose. An incorrect choice led to the tasting of quinine, which was followed by the
149 possibility to move to the alternative arm to collect sucrose on the rewarded stimulus. Only
150 the first choice within a foraging bout was recorded. The sides of the rewarded and punished
151 stimuli were exchanged in a pseudo-random sequence (i.e. a stimulus presented no more than
152 twice consecutively on the same side) throughout all experiments to prevent positional
153 learning. After the last training trial, non-reinforced tests were performed using fresh stimuli.
154 The tests were repeated twice to swap stimulus side and they were spaced by three refreshing
155 reinforced trials in order to maintain appetitive motivation. Each test lasted 45 seconds during
156 which the contacts the bees made with the surface of the stimuli were recorded. This period is
157 typically used in these tests as it allows uncovering the learning induced by the training;
158 longer periods may result in a switch of choice strategy due to the extinction conditions. The
159 percentage of correct choices for a given test was calculated for each bee using the number of
160 contacts with the stimuli in both repetitions of the test.

161

162 **(b) Experiment 1: Performance along three consecutive visual elemental**
163 **discriminations**

164 In this experiment, 18 bees were individually trained during three days to learn three
165 consecutive visual discriminations, one per day. A minimum of two, but more often, at least

166 three data points are typically used to show consistency in individual traits (Stamps &
167 Groothuis, 2010). We chose to replicate the visual task during three consecutive days to
168 determine the stability of individual performances. We did not extend the measurement period
169 beyond three days to avoid losing bees due to natural death or recruitment to alternative food
170 places. On each day, the bee experienced a 15-trial conditioning (i.e. 15 consecutive visits to
171 the maze) during which it had to learn to discriminate two visual achromatic patterns, one
172 (CS+) being consistently associated with reward (sucrose) and the other (CS-) with
173 punishment (quinine). Training was followed by a test in which the stimuli used for training
174 were presented without reinforcement (Fig. 1A). Training and testing took 1-2 hours per bee.
175 In the next two days, this procedure was repeated using a new set of visual stimuli every day.
176 All the bees that completed the experimental schedule returned voluntarily to the setup every
177 day. They were not maintained captive overnight in the laboratory. The bees returned reliably
178 to the experimental set-up throughout the three-day period and only one bee trained on day 1
179 did not come back on the next day to complete the training sequence.

180 The stimuli used were 7 x 7 cm black patterns printed on UV-reflecting white paper.
181 Six different patterns were used, which varied between bees and were presented as
182 counterbalanced pair combinations on each experimental day (Fig. S1). These patterns were
183 originally used in the study of Avarguès-Weber et al. (2012) and could be well resolved by
184 the visual system of honeybees.

185

186 (c) Experiment 2: Performance in elemental visual and olfactory discriminations

187 In this experiment, a novel set of bees (N = 18) were trained consecutively within a day to
188 solve a visual discrimination task and an olfactory discrimination task. The sequence of visual
189 and olfactory tasks was randomized between bees. The tasks were spaced by approximately
190 30 minutes during which the bees could collect sucrose solution outside of the Y-maze. This
191 delay allowed preparing the setup and stimuli for the next learning task. Both training phases
192 consisted of 15 trials in which the bees had to discriminate between a rewarded stimulus
193 (CS+) associated with sucrose solution and a second stimulus (CS-) associated with a quinine
194 solution (Fig. 2A). Both training phases were followed by a test in which the respective
195 stimuli were presented without reinforcement. The stimuli used in the visual task were the
196 same as those described for experiment 1. The pair combinations were counterbalanced across
197 bees. For the olfactory task, 10 µl of pure odorant (2-Octanol and Limonene, Sigma Aldrich)

198 were applied to 7x7 cm squares of filter paper. For each trial fresh stimuli were used to assure
199 that the odours could be well perceived throughout training. Between trials, when the bees
200 were absent from the set-up, the Y-maze was ventilated, and the arms of the maze were
201 cleaned with 30% ethanol to remove potential odour residues. In both tasks, reinforcement
202 contingencies were counterbalanced between bees. **The whole procedure took between 2-3.5**
203 **hours per bee.**

204

205 **(d) Experiment 3: Performance in visual discriminations of different cognitive**
206 **complexity**

207 An additional group of bees (N = 18) were trained within the same day along two successive
208 visual tasks, one elemental discrimination similar to the ones described in Experiment 1 and
209 one non-elemental conceptual discrimination based on spatial relational learning (Avarguès-
210 Weber et al., 2012). The sequence of the elemental and non-elemental tasks was randomized
211 between bees. Both tasks were spaced by approximately 30 minutes during which the bees
212 had access to a sucrose solution outside of the training apparatus. The tasks differed in the
213 number of conditioning trials (15 for the elemental task and 30 for the non-elemental task)
214 due to their different complexity. Training lengths were decided to ensure significant learning
215 of the majority of bees. The procedure and stimuli of the elemental task were identical to
216 those used in experiment 1 or in the visual task of experiment 2. In the non-elemental task, the
217 bees were trained to discriminate between two composite images, each consisting of two
218 coloured discs (Ø 7 cm), but arranged in two different spatial configurations – *above/below*
219 (discs aligned vertically, i.e. one above/below the other) and *left/right* (discs aligned
220 horizontally, i.e. one to the left/right of the other). The discs differed only in their chromatic
221 properties. They were cut from uncoated HKS papers (K+E Stuttgart, Stuttgart-Feuerbach,
222 Germany; 1N, 3N, 29N, 32N, 48N, 71N; Fig. S1). The reinforcement contingency
223 (above/below+ or left/right+) was counterbalanced between bees. The colour of the discs and
224 their positions within the back walls of the Y-maze were pseudo-randomized over trials, yet
225 keeping their alignment (Fig. 3A). By doing this, we ruled out that bees could use either the
226 absolute spatial locations or the centre of gravity as cue to solve the task (Avarguès-Weber et
227 al., 2012). The spatial relation between the discs was consequently the only reliable predictor
228 of the reward. The conditioning phase was followed by non-reinforced tests, in which novel
229 achromatic (black) geometric shapes were used to recreate the trained spatial relations. This
230 allowed examining whether bees learned the spatial concept, irrespective of the stimuli

231 properties. We took special care to choose shapes differing as much as possible from the
232 patterns used in the elemental learning task (Fig. 3A). Different shapes were used to this end
233 (Fig. S1). Stimuli were printed on UV-reflecting copy paper and had a size of 7 x 7 cm.
234 **Training and testing took 3-4.5 hours per bee.**

235

236 **(e) Statistical analysis**

237 Individual bee responses (correct or incorrect) during the acquisition phases were examined
238 using generalized linear mixed models (GLMM) with a binomial error structure - logit-link
239 function -, *glmer* function of R package *lme4* (Bates et al., 2014). In the models, the bee's
240 choices (0 or 1) were entered as the dependent variable, while the trial number, the task (Day
241 number (Experiment 1), Visual/Olfactory (Experiment 2) or Elemental/Non-Elemental
242 (Experiment 3)), the stimuli used and the order of the tasks were entered as fixed factors.
243 Subjects identity (ID) was entered as a random factor to account for the repeated-measure
244 design. Several models were run by testing interactions between factors and by dropping each
245 factor subsequently to select the significant model with the highest explanatory power (i.e. the
246 lowest AIC value) (see supplementary tables).

247 Performances during the non-reinforced tests were analysed with a generalized linear
248 mixed model (GLMM) with a binomial error structure and logit-link function, where the
249 proportion of correct choices for each bee was entered as dependent variable, while the task
250 and the task order were entered as fixed factors whenever appropriate. The intercept term
251 informed us on whether the mean proportion of correct choices is different from chance level.
252 Correlations were computed using both the Pearson and Spearman correlation coefficients.
253 All statistical analyses were performed with R 3.4.2 (R Development Core Team, 2016).

254

255 **3. Results**

256

257 **Experiment 1: Performance along three consecutive visual elemental discriminations**

258

259 Honeybees learned successfully the three elemental visual discriminations between the
260 achromatic visual patterns (Fig. 1A) as they significantly improved their performance during

261 the acquisition phases (GLMM, $n = 17$, $Trial: \chi^2 = 5.6, p = 0.02$; Fig.1B, table S1). There was
262 neither a significant effect of the pair of stimuli used ($Stimuli: \chi^2 = 15.4, p = 0.97$; table S1)
263 nor of the training sequence as performance did not improve along the three consecutive
264 visual discriminations ($Day: \chi^2 = 0.01, p = 0.92$; table S1). Accordingly, the performances in
265 the non-reinforced tests (Fig. 1C) were significantly higher than chance in all three days with
266 no significant influence of task repetition ($n = 17$; Day 1: 76.1 ± 3.3 % (mean \pm SEM), $Z =$
267 $6.17, p < 0.001$ (GLM); Day 2: 76.0 ± 2.3 %, $Z = 8.79, p < 0.001$; Day 3: 72.0 ± 2.7 %, $Z =$
268 $7.85, p < 0.001$; $Day: Z = 1.34, p = 0.17$ (GLMM)).

269 Individual learning performances (proportion of correct choices) were highly variable
270 between individuals (Fig. 1D), yet they were consistent along the three days (Day 1 vs. Day 2:
271 Spearman correlation, $r_s = 0.62, p = 0.009$, Pearson correlation, $r_p = 0.63, p = 0.007$; Day 2
272 vs. Day 3: $r_s = 0.66, p = 0.004$; $r_p = 0.78, p < 0.001$; Day 1 vs. Day 3: $r_s = 0.70, p = 0.002$; r_p
273 $= 0.66, p = 0.004$; Fig. 1D). This result indicates that despite population variability in learning
274 proficiency, individual proficiency remained stable across days and visual discrimination
275 tasks.

276

277 **Experiment 2: Performance in elemental visual and olfactory discriminations**

278

279 Although no significant improvement of performance could be detected over trials
280 (GLMM, $Trial: \chi^2 = 1.7, p = 0.19$; Fig.2B, table S2), the bees ($n = 18$) learned both tasks as
281 shown by their performance in the non-reinforced tests where they preferred the correct
282 stimulus, be it visual (74.9 ± 3.2 % of correct choices, GLM, $Z = 6.54, p < 0.001$; Fig. 2C) or
283 olfactory (84.0 ± 2.6 %, $Z = 8.24, p < 0.001$; Fig. 2C). Bees were generally more accurate in
284 the olfactory task than in the visual task (GLMM, $Task: Z = 3.58, p < 0.001$; Fig. 2C).

285 As in the previous experiment, a high variability in learning proficiency was observed
286 between the individuals trained (Fig. 2D). However, this time no correlation between
287 individual performances was found (Olf. vs. Vis: $r_s = 0.31, p = 0.21$; $r_p = 0.26, p = 0.29$; Fig.
288 2D), thus showing that individual proficiency is not stable between tasks involving different
289 sensory modalities.

290

291 **Experiment 3: Performance in visual discriminations of different cognitive complexity**

292

293 Honeybees improved their performance during the acquisition phase in both the elemental and
294 the conceptual task (GLMM, $n = 18$, *Trial*: $\chi^2 = 9.0$, $p = 0.003$; Fig. 3B, table S3). The task
295 sequence did not affect the bees' performance (*Order*, $\chi^2 = 0.05$, $p = 0.82$; Fig. S2, table S3).
296 Overall the bees' accuracy was higher in the elemental task than in the non-elemental task
297 (*Task*, $\chi^2 = 15.0$, $p < 0.001$, Fig. 3B, table S3), a result that is consistent with the different
298 levels of complexity of these tasks. Performance in the non-reinforced tests was significantly
299 higher than chance in both tasks (elemental task: 75.4 ± 2.7 % of correct choices, GLM, $Z =$
300 7.18 , $p < 0.001$; non-elemental task: 68.0 ± 2.9 % of correct choices, $Z = 4.73$, $p < 0.001$; Fig.
301 3B). Yet, it was also affected by the complexity of the task (GLMM, *Task*: $Z = 2.36$, $p = 0.02$,
302 Fig. 3B) as test performance was better after the elemental conditioning than after the non-
303 elemental conditioning.

304 Individual learning proficiency was variable but it correlated between individuals
305 across the two learning tasks ($r_S = 0.64$, $p = 0.004$; $r_P = 0.69$, $p = 0.002$; Fig. 3C), with some
306 individuals being consistently more error-prone than others in both tests.

307

308 **4. Discussion**

309 Our results highlight the importance of individual variability in cognitive tasks and its
310 relationship with the nature of the task considered. By testing the same bees on consecutive
311 days and tasks that were either similar (Experiment 1) or different (Experiments 2 and 3), we
312 observed an important inter-individual variability in learning performance as in all cases the
313 proportion of correct choices varied at the population level, with some bees being efficient
314 learners and others, on the contrary, poor learners. Importantly, this proficiency was
315 maintained across time when individuals were tested on three similar consecutive visual
316 discriminations (Experiment 1). Thus, the variable response observed within a given task
317 seems to be a consequence of individual stable factors rather than being noise resulting from
318 transitory variability in foraging activity, appetitive motivation or stochasticity in choice
319 persistence. In addition, we showed that proficiency is maintained across elemental and
320 higher-order learning tasks within the same sensory modality (Experiment 3), even if
321 performances were again highly variable at the population level. This result is important as it
322 shows that bees trained within the visual modality will conserve their success irrespective of

323 the cognitive complexity of the task, a problem that has never been addressed so far in
324 invertebrates. Finally, we showed that consistency in performance was not maintained when
325 bees were trained using tasks involving different modalities (vision and olfaction; Experiment
326 2), thus arguing in favour of within-modality cognitive specialization.

327

328 Several factors can account for the interindividual variability observed. Yet, some of
329 them can be ruled out in our study. In our experiments, only nectar foragers captured at a
330 sucrose feeder and consequently motivated for foraging were used, which discards differences
331 due to division of labour and appetitive motivation. In addition, the temporal sequence did
332 neither influence the performance of the bees. We expected that familiarization with the setup
333 and enhanced attention might be promoted by prior training experience, resulting in faster
334 acquisition in subsequent tasks. However, such improvement was not observed in our
335 conditions.

336 Consistent inter-individual difference in performances maintained within a visual task
337 or across elemental and higher-order visual tasks could have a genetic basis. *Drosophila* flies
338 from a population selected over several generations on the basis of their good learning
339 abilities in an aversive olfactory task exhibited an equally good performance in a different
340 aversive olfactory task (reinforced by an electric shock rather than a bitter substance), thus
341 highlighting the importance of genetic selection for learning abilities (Mery & Kawecki,
342 2002; Mery et al., 2007). Numerous studies suggest that genetic factors influence cognitive
343 performance in invertebrates (Raine et al., 2006; Ings et al., 2009; Orr et al., 2009; Raine &
344 Chittka, 2012; Scheiner et al., 2021). The bees of our study originated from a single hive, a
345 fact that reduces but does not abolish the genetic diversity among the bees tested, as different
346 patrines typically coexist within a hive due to multiple mating of the queen during the
347 nuptial flight. The learning performance of individual worker bees in elemental olfactory
348 tasks can indeed be predicted partially by their patriline (Brandes, 1988; Bhagavan et al.,
349 1994; Scheiner & Arnold, 2010; Junca et al., 2019). Genetic variability has a strong impact on
350 responsiveness to appetitive and aversive stimuli such as sucrose or thermic shocks,
351 respectively (Scheiner & Arnold, 2010; Junca et al., 2019). This variable responsiveness
352 translates into variation of performance observed in associative learning protocols in which
353 such stimuli are used as unconditioned stimuli (Scheiner et al., 2005; Roussel et al., 2009;
354 Scheiner & Arnold, 2010). Thus, the variable success of foragers co-opted for our
355 experiments could be due to their belonging to different genetic patrines within the colony.

356 Variability in learning performance in our study could also be influenced by prior
357 visual experience gathered on a larger time scale than the duration of our experiment during
358 foraging activities. Both age and sensory experience influence brain structural development of
359 forager bees, which, in turn, can modulate learning performance, although mostly in the form
360 of a cognitive decline with aging (Withers et al., 1993; Durst et al., 1994; Farris et al., 2001;
361 Münch et al., 2010; Groh et al., 2012; Scholl et al., 2014; Cabirol et al., 2018). The mushroom
362 bodies, the main higher-order structures of the insect brain, show experience-dependent
363 variations in their volume or density of synaptic buttons, following light exposure, age,
364 foraging experience or learning events (Hourcade et al., 2010; Scholl et al., 2014; Cabirol et
365 al., 2017; Cabirol et al., 2018). Individual variability in mushroom body development may
366 have an impact on cognitive faculties (Li et al., 2017). Therefore, it is likely that the stability
367 of learning proficiency observed across days or tasks of different complexity relies, at least
368 partially, on neurobiological variability resulting from different life experiences.

369 Learning differences could also emerge from variations in the processing of the stimuli
370 to be learned such as odours or visual cues. This possibility is supported by our study as we
371 found that some bees were relatively better at learning olfactory cues than visual cues, and
372 vice versa, thus reflecting potential variation in perceptual salience between modalities.
373 Honeybees are known to differ in their responsiveness to odours (Scheiner et al., 2004), which
374 could be retraced to inter-individual differences in the activity of olfactory neural circuits. In
375 fruit flies, for instance, stable inter-individual variability can be found in an odour-preference
376 assay, which translates into consistent inter-individual differences in Ca^{2+} activity levels in a
377 key structure of the olfactory circuit, the projection neurons of the antennal lobes (Honegger
378 et al., 2019). Similar arguments could apply to visual processing and its underlying visual
379 circuits.

380 The question of whether learning abilities correlate across problems of different
381 complexity or sensory domains is particularly relevant for the analysis of brain modularity
382 and for understanding the contributions of different neural circuits to different forms of
383 learning. In honeybees, different brain structures have been associated with different levels of
384 complexity in olfactory learning. The mushroom bodies are required for non-elemental
385 olfactory discrimination tasks such as the negative patterning problem (A+, B+, AB-)
386 (Devaud et al., 2015) or for reversal learning (A+ B- \rightarrow A- B+) (Boitard et al., 2015) but are
387 dispensable for elemental olfactory discrimination (A+, B+, CD-) (Devaud et al., 2015). From
388 this perspective, proficiency in non-elemental olfactory learning may not necessarily be

389 correlated with proficiency in elemental olfactory learning, given that these learning forms are
390 mediated by different brain structures. Applying this reasoning to our results in the visual
391 domain suggests that both learning forms, which are highly correlated, may require similar
392 visual circuits/structures. To date, the brain neuropils involved in different forms of visual
393 learning remain unknown due to the difficulty of reproducing successful visual learning in the
394 which would allow coupling with invasive recordings of neural activity (Avarguès-Weber &
395 Mota, 2016). Yet, given the massive visual afferences to the mushroom bodies (Ehmer &
396 Gronenberg, 2002; Paulk & Gronenberg, 2008) and to the central complex (Pfeiffer &
397 Homberg, 2014), participation of these structures is expected. For instance, in *Drosophila*,
398 both mushroom bodies and the central complex are involved in visual learning depending on
399 the specific task and setup used (Liu et al., 1999; Pan et al., 2009; Ofstad et al., 2011; Vogt et
400 al., 2014; Vogt et al., 2016).

401 The fact that we observed a positive correlation of performances across an elemental
402 task and a conceptual task in the visual modality suggests that a similar brain circuitry
403 underlies both discriminations. An alternative explanation may be that differences in general
404 visual processing abilities and attentional processes could have a major influence on the
405 performance in both tasks. In humans and rodents, general intelligence has been linked to
406 selective attention and working memory abilities (reviewed in Matzel & Kolata, 2010) which
407 encompassed both the storage of information and the processing and integration of
408 information (Baddeley, 2003; Jarrold & Towse, 2006)). Increasing evidence indicates that
409 insects are capable of selective attention mediated by several higher-order brain areas (van
410 Swinderen, 2011; Nityananda, 2016).

411 Shifting our focus from group to individual performances in cognitive studies could
412 thus contribute to the elucidation of the underlying mechanisms (Thornton & Lukas, 2012;
413 Pamir et al., 2014; Boogert et al., 2018; Klein, 2018). It also raises fascinating ecological
414 questions such as the possible existence of cognitive specialization between workers from
415 different patriline in a hive. In honeybees, the best learners might deal with more demanding,
416 complex tasks and concentrate their foraging effort towards the exploration of novel food
417 sources. Others might simply copy the former and use social information when facing
418 difficult tasks as occurs in bumblebees (Baracchi et al., 2018). This would explain the known
419 differentiation between scouts and recruits (Biesmeijer & de Vries, 2001; Beekman et al.,
420 2007). The diversity of foraging strategies within a colony has been shown to increase its
421 fitness (Burns, 2005; Burns & Dyer, 2008; Jeanson & Weidenmüller, 2014; Klein, 2018) but,

422 interestingly, the best learners are not necessarily the best foragers as demonstrated in
423 bumblebees, where bad learners foraged for a longer time frame and collected more resources,
424 potentially due to the energetic cost associated with cognition (Evans et al., 2017). Thus, the
425 complex interplay between interindividual cognitive skill diversity, task allocation and colony
426 fitness remains to be fully elucidated.

427

428 *References*

- 429 **Akhund-Zade, J., Ho, S., O'Leary, C., & de Bivort, B.** (2019). The effect of environmental
430 enrichment on behavioral variability depends on genotype, behavior, and type of
431 enrichment. *J Exp Biol*, **222**(19), jeb202234. doi: 10.1242/jeb.202234.
- 432 **Avarguès-Weber, A., de Brito Sanchez, M. G., Giurfa, M., & Dyer, A. G.** (2010).
433 Aversive reinforcement improves visual discrimination learning in free-flying
434 honeybees. *PLoS ONE*, **5**(10), e15370. doi: 10.1371/journal.pone.0015370.
- 435 **Avarguès-Weber, A., Deisig, N., & Giurfa, M.** (2011). Visual cognition in social insects.
436 *Ann Rev Entomol*, **56**, 423-443. doi: 10.1146/annurev-ento-120709-144855.
- 437 **Avarguès-Weber, A., Dyer, A. G., Combe, M., & Giurfa, M.** (2012). Simultaneous
438 mastering of two abstract concepts with a miniature brain. *Proc Natl Acad Sci USA*,
439 **109**(19), 7481-7486. doi: 10.1073/pnas.1202576109.
- 440 **Avarguès-Weber, A., & Giurfa, M.** (2013). Conceptual learning by miniature brains. *Proc R*
441 *Soc B*, **280**(1772), 20131907. doi: 10.1098/rspb.2013.1907.
- 442 **Avarguès-Weber, A., & Mota, T.** (2016). Advances and limitations of visual conditioning
443 protocols in harnessed bees. *J Physiol Paris*, **110**(3), 116-118. doi:
444 10.1016/j.jphysparis.2016.12.006.
- 445 **Baddeley, A.** (2003). Working memory: looking back and looking forward. *Nat Rev*
446 *Neurosci*, **4**(10), 829-839. doi: 10.1038/nrn1201.
- 447 **Baracchi, D., Vasas, V., Jamshed Iqbal, S., & Alem, S.** (2018). Foraging bumblebees use
448 social cues more when the task is difficult. [doi: 10.1093/beheco/arx143]. *Behavioral*
449 *Ecology*, **29**(1), 186-192. doi: 10.1093/beheco/arx143.
- 450 **Bates, D., Mächler, M., Bolker, B., & Walker, S.** (2014). Fitting linear mixed-effects
451 models using lme4. *arXiv*, 1406.5823.

452 **Beekman, M., Gilchrist, A. L., Duncan, M., & Sumpter, D. J. T.** (2007). What makes a
453 honeybee scout? *Behav Ecol Sociobiol*, **61**(7), 985-995. doi: 10.1007/s00265-006-
454 0331-9.

455 **Bhagavan, S., Benatar, S., Cobey, S., & Smith, B. H.** (1994). Effect of genotype but not of
456 age or caste on olfactory learning performance in the honey bee, *Apis mellifera*. *Anim*
457 *Behav*, **48**(6), 1357-1369. doi: 10.1006/anbe.1994.1372.

458 **Biesmeijer, J. C., & de Vries, H.** (2001). Exploration and exploitation of food sources by
459 social insect colonies: a revision of the scout-recruit concept. *Behav Ecol Sociobiol*,
460 **49**(2), 89-99. doi: 10.1007/s002650000289.

461 **Boitard, C., Devaud, J.-M., Isabel, G., & Giurfa, M.** (2015). GABAergic feedback
462 signaling into the calyces of the mushroom bodies enables olfactory reversal learning
463 in honey bees. *Front Behav Neurosci*, **9**. doi: 10.3389/fnbeh.2015.00198.

464 **Boogert, N. J., Madden, J. R., Morand-Ferron, J., & Thornton, A.** (2018). Measuring and
465 understanding individual differences in cognition. *Phil Trans R Soc B*, **373**(1756). doi:
466 10.1098/rstb.2017.0280.

467 **Brandes, C.** (1988). Estimation of heritability of learning behavior in honeybees (*Apis*
468 *mellifera capensis*). *Behav Gen*, **18**(1), 119-132. doi: 10.1007/bf01067081.

469 **Burns, J. G.** (2005). Impulsive bees forage better: the advantage of quick, sometimes
470 inaccurate foraging decisions. *Anim Behav*, **70**(6), e1-e5. doi:
471 10.1016/j.anbehav.2005.06.002.

472 **Burns, J. G., & Dyer, A. G.** (2008). Diversity of speed-accuracy strategies benefits social
473 insects. *Curr Biol*, **18**(20), R953-R954. doi: 10.1016/j.cub.2008.08.028.

474 **Burns, J. G., Foucaud, J., & Mery, F.** (2011). Costs of memory: lessons from 'mini' brains.
475 *Proc R Soc B*, **278**(1707), 923-929. doi: 10.1098/rspb.2010.2488.

476 **Burns, J. G., & Rodd, F. H.** (2008). Hastiness, brain size and predation regime affect the
477 performance of wild guppies in a spatial memory task. *Anim Behav*, **76**(3), 911-922.
478 doi: 10.1016/j.anbehav.2008.02.017.

479 **Cabirol, A., Brooks, R., Groh, C., Barron, A. B., & Devaud, J.-M.** (2017). Experience
480 during early adulthood shapes the learning capacities and the number of synaptic
481 boutons in the mushroom bodies of honey bees (*Apis mellifera*). *Learn & Mem*,
482 **24**(10), 557-562. doi: 10.1101/lm.045492.117.

483 **Cabirol, A., Cope, A. J., Barron, A. B., & Devaud, J.-M.** (2018). Relationship between
484 brain plasticity, learning and foraging performance in honey bees. *PLOS ONE*, **13**(4),
485 e0196749. doi: 10.1371/journal.pone.0196749.

- 486 **Chittka, L.** (2017). Bee cognition. *Curr Biol*, **27**(19), R1049-R1053. doi:
487 10.1016/j.cub.2017.08.008.
- 488 **Chittka, L., Dyer, A. G., Bock, F., & Dornhaus, A.** (2003). Psychophysics: Bees trade off
489 foraging speed for accuracy. *Nature*, **424**(6947), 388-388. doi: 10.1038/424388a.
- 490 **Chittka, L., Skorupski, P., & Raine, N. E.** (2009). Speed-accuracy tradeoffs in animal
491 decision making. *Trends Ecol & Evol*, **24**(7), 400-407. doi:
492 10.1016/j.tree.2009.02.010.
- 493 **Cook, C. N., Mosquero, T., Brent, C. S., Ozturk, C., Gadau, J., Pinter-Wollman, N., et**
494 **al.** (2018). Individual differences in learning and biogenic amine levels influence the
495 behavioural division between foraging honey bee scouts and recruits. *J Anim Ecol*,
496 **88**(2), 236-246. doi: 10.1111/1365-2656.12911.
- 497 **Devaud, J.-M., Papouin, T., Carcaud, J., Sandoz, J.-C., Grünewald, B., & Giurfa, M.**
498 (2015). Neural substrate for higher-order learning in an insect: Mushroom bodies are
499 necessary for configural discriminations. *Proc Natl Acad Sci USA*, **112**(43), E5854-
500 E5862. doi: 10.1073/pnas.1508422112.
- 501 **Durst, C., Eichmüller, S., & Menzel, R.** (1994). Development and experience lead to
502 increased volume of subcompartments of the honeybee mushroom body. *Behav Neur*
503 *Biol*, **62**(3), 259-263. doi: 10.1016/S0163-1047(05)80025-1.
- 504 **Ehmer, B., & Gronenberg, W.** (2002). Segregation of visual input to the mushroom bodies
505 in the honeybee (*Apis mellifera*). *J Comp Neurol*, **451**(4), 362-373. doi:
506 10.1002/cne.10355.
- 507 **Evans, L. J., Smith, K. E., & Raine, N. E.** (2017). Fast learning in free-foraging bumble
508 bees is negatively correlated with lifetime resource collection. *Scientific Reports*, **7**(1),
509 496. doi: 10.1038/s41598-017-00389-0.
- 510 **Farris, S. M., Robinson, G. E., & Fahrbach, S. E.** (2001). Experience-and age-related
511 outgrowth of intrinsic neurons in the mushroom bodies of the adult worker honeybee.
512 *J Neurosci*, **21**(16), 6395-6404. doi: 10.1523/JNEUROSCI.21-16-06395.2001.
- 513 **Giurfa, M.** (2003). Cognitive neuroethology: dissecting non-elemental learning in a honeybee
514 brain. *Curr Opin Neurobiol*, **13**(6), 726-735. doi: 10.1016/j.conb.2003.10.015.
- 515 **Giurfa, M.** (2007). Behavioral and neural analysis of associative learning in the honeybee: a
516 taste from the magic well. *J Comp Physiol A*, **193**(8), 801-824. doi: 10.1007/s00359-
517 007-0235-9.
- 518 **Giurfa, M.** (2013). Cognition with few neurons: higher-order learning in insects. *Trends*
519 *Neurosci*, **36**(5), 285-294. doi: 10.1016/j.tins.2012.12.011.

- 520 **Giurfa, M.** (2019). An Insect's sense of number. *Trends Cogn Sci*, **23**(9), 720-722. doi:
521 10.1016/j.tics.2019.06.010.
- 522 **Groh, C., Lu, Z., Meinertzhagen, I. A., & Rössler, W.** (2012). Age-related plasticity in the
523 synaptic ultrastructure of neurons in the mushroom body calyx of the adult honeybee
524 *Apis mellifera*. *J Comp Neurol*, **520**(15), 3509-3527. doi: 10.1002/cne.23102.
- 525 **Higginson, A. D., & Barnard, C. J.** (2004). Accumulating wing damage affects foraging
526 decisions in honeybees (*Apis mellifera* L.). *Ecol Entomol*, **29**(1), 52-59. doi:
527 10.1111/j.0307-6946.2004.00573.x.
- 528 **Higginson, A. D., Barnard, C. J., Tofilski, A., Medina, L., & Ratnieks, F.** (2011).
529 Experimental wing damage affects foraging effort and foraging distance in honeybees
530 *Apis mellifera*. *Psyche*, **2011**. doi: 10.1155/2011/419793.
- 531 **Honegger, K. S., Smith, M. A.-Y., Churgin, M. A., Turner, G. C., & de Bivort, B. L.**
532 (2019). Idiosyncratic neural coding and neuromodulation of olfactory individuality in
533 *Drosophila*. *Proc Natl Acad Sci*, 201901623. doi: 10.1073/pnas.1901623116.
- 534 **Hourcade, B., Muenz, T. M., Sandoz, J. C., Rössler, W., & Devaud, J. M.** (2010). Long-
535 term memory leads to synaptic reorganization in mushroom bodies: a memory trace in
536 the insect brain? *J Neurosci*, **30**, 6461-6465. doi: 10.1523/JNEUROSCI.0841-10.2010.
- 537 **Ings, T. C., Raine, N. E., & Chittka, L.** (2009). A population comparison of the strength and
538 persistence of innate colour preference and learning speed in the bumblebee *Bombus*
539 *terrestris*. *Behavioral Ecology and Sociobiology*, **63**(8), 1207-1218. doi:
540 10.1007/s00265-009-0731-8.
- 541 **Jarrold, C., & Towse, J. N.** (2006). Individual differences in working memory. *Neurosci*,
542 **139**(1), 39-50. doi: 10.1016/j.neuroscience.2005.07.002.
- 543 **Jaumann, S., Scudelari, R., & Naug, D.** (2013). Energetic cost of learning and memory can
544 cause cognitive impairment in honeybees. *Biol Lett*, **9**(4). doi: 10.1098/rsbl.2013.0149.
- 545 **Jeanson, R., & Weidenmüller, A.** (2014). Interindividual variability in social insects –
546 proximate causes and ultimate consequences. *Biol Rev*, **89**(3), 671-687. doi:
547 10.1111/brv.12074.
- 548 **Junca, P., Garnery, L., & Sandoz, J.-C.** (2019). Genotypic trade-off between appetitive and
549 aversive capacities in honeybees. *Sci Rep*, **9**(1), 10313. doi: 10.1038/s41598-019-
550 46482-4.
- 551 **Kawecki, T. J.** (2009). Evolutionary ecology of learning: insights from fruit flies. *Pop Ecol*,
552 **52**(1), 15. doi: 10.1007/s10144-009-0174-0.

553 Klein, S. (2018). *Causes and consequences of individual forager variability in social bees*.
554 Doctoral dissertation, Toulouse University III - Paul Sabatier.

555 **Kotrschal, A., Rogell, B., Bundsen, A., Svensson, B., Zajitschek, S., Brännström, I., et al.**
556 (2013). Artificial selection on relative brain size in the guppy reveals costs and
557 benefits of evolving a larger brain. *Curr Biol*, **23**(2), 168-171. doi:
558 10.1016/j.cub.2012.11.058.

559 **Li, L., MaBouDi, H., Egertová, M., Elphick, M. R., Chittka, L., & Perry, C. J.** (2017). A
560 possible structural correlate of learning performance on a colour discrimination task in
561 the brain of the bumblebee. *Proc R Soc B*, **284**(1864). doi: 10.1098/rspb.2017.1323.

562 **Liu, L., Wolf, R., Ernst, R., & Heisenberg, M.** (1999). Context generalization in
563 *Drosophila* visual learning requires the mushroom bodies. *Nature*, **400**(6746), 753-
564 756. doi: 10.1038/23456.

565 **Matzel, L. D., & Kolata, S.** (2010). Selective attention, working memory, and animal
566 intelligence. *Neurosci & Biobehav Rev*, **34**(1), 23-30. doi:
567 10.1016/j.neubiorev.2009.07.002.

568 **Mery, F., & Kawecki, T. J.** (2002). Experimental evolution of learning ability in fruit flies.
569 *Proc Natl Acad Sci*, **99**(22), 14274-14279. doi: 10.1073/pnas.222371199.

570 **Mery, F., & Kawecki, T. J.** (2003). A fitness cost of learning ability in *Drosophila*
571 *melanogaster*. *Proc R Soc B*, **270**(1532), 2465-2469. doi: 10.1098/rspb.2003.2548.

572 **Mery, F., Pont, J., Preat, T., & Kawecki, T. J.** (2007). Experimental evolution of olfactory
573 memory in *Drosophila melanogaster*. *Physiol Biochem Zool*, **80**(4), 399-405. doi:
574 10.1086/518014.

575 **Muller, H., & Chittka, L.** (2008). Animal personalities: The advantage of diversity. *Curr*
576 *Biol*, **18**(20), R961-R963. doi: 10.1016/j.cub.2008.09.001.

577 **Muller, H., & Chittka, L.** (2012). Consistent interindividual differences in discrimination
578 performance by bumblebees in colour, shape and odour learning tasks (Hymenoptera:
579 Apidae: *Bombus terrestris*). *Entomologia Generalis*, **34**(1), 1.

580 **Münch, D., Baker, N., Kreibich, C. D., Bråten, A. T., & Amdam, G. V.** (2010). In the
581 Laboratory and during Free-Flight: Old Honey Bees Reveal Learning and Extinction
582 Deficits that Mirror Mammalian Functional Decline. *PLOS ONE*, **5**(10), e13504. doi:
583 10.1371/journal.pone.0013504.

584 **Nityananda, V.** (2016). Attention-like processes in insects. *Proc R Soc B*, **283**(1842). doi:
585 10.1098/rspb.2016.1986.

- 586 **Ofstad, T. A., Zuker, C. S., & Reiser, M. B.** (2011). Visual place learning in *Drosophila*
587 *melanogaster*. [10.1038/nature10131]. *Nature*, **474**(7350), 204-207. doi: 10.1038-
588 nature10131.
- 589 **Orr, M., Hittel, K., Lukowiak, K., Han, J., & Lukowiak, K.** (2009). Differences in LTM-
590 forming capability between geographically different strains of Alberta *Lymnaea*
591 *stagnalis* are maintained whether they are trained in the lab or in the wild. *Journal of*
592 *Experimental Biology*, **212**(23), 3911-3918.
- 593 **Pamir, E., Chakraborty, N. K., Stollhoff, N., Gehring, K. B., Antemann, V.,**
594 **Morgenstern, L., et al.** (2011). Average group behavior does not represent individual
595 behavior in classical conditioning of the honeybee. *Learn Mem*, **18**(11), 733-741. doi:
596 10.1101/lm.2232711.
- 597 **Pamir, E., Szyszka, P., Scheiner, R., & Nawrot, M. P.** (2014). Rapid learning dynamics in
598 individual honeybees during classical conditioning. *Front Behav Neurosci*, **8**, 313. doi:
599 10.3389/fnbeh.2014.00313.
- 600 **Pan, Y., Zhou, Y., Guo, C., Gong, H., Gong, Z., & Liu, L.** (2009). Differential roles of the
601 fan-shaped body and the ellipsoid body in *Drosophila* visual pattern memory. *Learn &*
602 *Mem*, **16**(5), 289-295. doi: 10.1101/lm.1331809.
- 603 **Paulk, A., & Gronenberg, W.** (2008). Higher order visual input to the mushroom bodies in
604 the bee, *Bombus impatiens*. *Arthropod Structure and Development*, **37**(7), 443-458.
605 doi: 10.1016/j.asd.2008.03.002.
- 606 **Pfeiffer, K., & Homberg, U.** (2014). Organization and functional roles of the central
607 complex in the insect brain. *Ann Rev Entomol*, **59**, 165-184. doi: 10.1146/annurev-
608 ento-011613-162031.
- 609 **Raine, N. E., & Chittka, L.** (2008). The correlation of learning speed and natural foraging
610 success in bumble-bees. *Proc R Soc B*, **275**(1636), 803-808. doi:
611 10.1098/rspb.2007.1652.
- 612 **Raine, N. E., & Chittka, L.** (2012). No trade-off between learning speed and associative
613 flexibility in bumblebees: A reversal learning test with multiple colonies. *PLoS ONE*,
614 **7**(9), e45096. doi: 10.1371/journal.pone.0045096.
- 615 **Raine, N. E., Ings, T. C., Ramos-Rodriguez, O., & Chittka, L.** (2006). Intercolony
616 variation in learning performance of a wild British bumblebee population
617 Hymenoptera: apidae: *Bombus terrestris audax*. *Entomologia Generalis*, **28**(4), 241.

618 **Roussel, E., Carcaud, J., Sandoz, J.-C., & Giurfa, M.** (2009). Reappraising social insect
619 behavior through aversive responsiveness and learning. *PLoS ONE*, **4**(1), e4197. doi:
620 10.1371/journal.pone.0004197.

621 **Scheiner, R., & Arnold, G.** (2010). Effects of patriline on gustatory responsiveness and
622 olfactory learning in honey bees. [journal article]. *Apidologie*, **41**(1), 29-37. doi:
623 10.1051/apido/2009040.

624 **Scheiner, R., Erber, J., & Page Jr., R. E.** (1999). Tactile learning and the individual
625 evaluation of the reward in honey bees (*Apis mellifera* L.). *J Comp Physiol A*, **185**(1),
626 1-10. doi: 10.1007/s003590050360.

627 **Scheiner, R., Kuritz-Kaiser, A., Menzel, R., & Erber, J.** (2005). Sensory responsiveness
628 and the effects of equal subjective rewards on tactile learning and memory of
629 honeybees. *Learn & Mem*, **12**(6), 626-635. doi: 10.1101/lm.98105.

630 **Scheiner, R., Lim, K., Meixner, M., & Gabel, M.** (2021). Comparing the appetitive learning
631 performance of six European honeybee subspecies in a common apiary. *Insect*, **12**(9),
632 768. doi: 10.3390/insects12090768.

633 **Scheiner, R., Page, R., & Erber, J.** (2004). Sucrose responsiveness and behavioral plasticity
634 in honey bees (*Apis mellifera*). *Apidologie*, **35**(2), 133-142. doi:
635 10.1051/apido:2004001.

636 **Scheiner, R., Page, R. E., & Erber, J.** (2001). The effects of genotype, foraging role, and
637 sucrose responsiveness on the tactile learning performance of honey bees (*Apis*
638 *mellifera* L.). *Neurobiol Learn Mem*, **76**(2), 138-150. doi: 10.1006/nlme.2000.3996.

639 **Scholl, C., Wang, Y., Krischke, M., Mueller, M. J., Amdam, G. V., & Rössler, W.** (2014).
640 Light exposure leads to reorganization of microglomeruli in the mushroom bodies and
641 influences juvenile hormone levels in the honeybee. *Dev Neurobiol*, **74**(11), 1141-
642 1153. doi: 10.1002/dneu.22195.

643 **Smith, K. E., & Raine, N. E.** (2014). A comparison of visual and olfactory learning
644 performance in the bumblebee *Bombus terrestris*. *Behav Ecol Sociobiol*, **68**(9), 1549-
645 1559. doi: 10.1007/s00265-014-1765-0.

646 **Srinivasan, M. V.** (2010). Honey bees as a model for vision, perception, and cognition. *Ann*
647 *Rev Entomol*, **55**(1), 267-284. doi: 10.1146/annurev.ento.010908.164537.

648 **Stamps, J., & Groothuis, T. G. G.** (2010). The development of animal personality:
649 relevance, concepts and perspectives. *Biol Rev*, **85**(2), 301-325. doi: 10.1111/j.1469-
650 185X.2009.00103.x.

651 **Tait, C., Mattise-Lorenzen, A., Lark, A., & Naug, D.** (2019). Interindividual variation in
652 learning ability in honeybees. *Behav Process*, **167**, 103918. doi:
653 10.1016/j.beproc.2019.103918.

654 **Thornton, A., Isden, J., & Madden, J. R.** (2014). Toward wild psychometrics: linking
655 individual cognitive differences to fitness. *Behav Ecol*, **25**(6), 1299-1301. doi:
656 10.1093/beheco/aru095.

657 **Thornton, A., & Lukas, D.** (2012). Individual variation in cognitive performance:
658 developmental and evolutionary perspectives. *Phil Trans R Soc B*, **367**(1603), 2773-
659 2783. doi: 10.1098/rstb.2012.0214.

660 **van Swinderen, B.** (2011). Attention in drosophila. *Int Rev Neurobiol*, **99**, 51-85. doi:
661 10.1016/B978-0-12-387003-2.00003-3.

662 **Vogt, K., Aso, Y., Hige, T., Knapek, S., Ichinose, T., Friedrich, A. B., et al.** (2016). Direct
663 neural pathways convey distinct visual information to *Drosophila* mushroom bodies.
664 *eLife*, **5**, e14009. doi: 10.7554/eLife.14009.

665 **Vogt, K., Schnaitmann, C., Dylla, K. V., Knapek, S., Aso, Y., Rubin, G. M., et al.** (2014).
666 Shared mushroom body circuits underlie visual and olfactory memories in *Drosophila*.
667 *eLife*, **3**, e02395. doi: 10.7554/eLife.02395.

668 **Withers, G. S., Fahrbach, S. E., & Robinson, G. E.** (1993). Selective neuroanatomical
669 plasticity and division of labour in the honeybee. *Nature*, **364**(6434), 238-240. doi:
670 10.1038/364238a0.

671

672 *Figures legends*

673 **Figure 1: Experiment 1: Comparison of performance in three visual elemental**
674 **discriminations. A. Diagram of the Y-maze apparatus used to train bees in this study. B.**
675 Schematic presentation of one visual elemental learning task submitted to the bees. The visual
676 pattern to discriminate varied between bees and between days. **B.** Acquisition curves
677 expressed as proportion of correct choices \pm SEM of forager bees confronted with three
678 consecutive elemental visual tasks consisting of 15 trials over three days (Day 1, red curve;
679 Day 2, green curve; Day 3, blue curve). Bees improved performance over the course of the
680 training (GLMM, $n = 17$, $Trial: \chi^2 = 5.6$, $p = 0.02$). **C.** Choice accuracy expressed as
681 proportion of correct choices \pm SEM of forager bees in the non-reinforced learning tests
682 following each training session. Performances were significantly higher than chance level

683 (GLM, $n = 17$; Day 1: $Z = 6.17$, $p < 0.001$; Day 2: $Z = 8.79$, $p < 0.001$; Day 3: $Z = 7.85$, $p <$
684 0.001). **D.** Correlation between performances (proportion of correct choices) of individual
685 bees in the non-reinforced learning tests of the repetition of elemental visual tasks involving
686 different stimuli. Each dot shows data for one individual bee. The blue line represents the
687 regression line while the blue shadow indicates the 95% confidence interval. Performances
688 were correlated along the three days (Spearman correlation, Day 1 vs. Day 2: $r_s = 0.62$, $p =$
689 0.009 , Day 2 vs. Day 3: $r_s = 0.66$, $p = 0.004$; Day 1 vs. Day 3: $r_s = 0.70$, $p = 0.002$).

690

691 **Figure 2: Experiment 2: Comparison of performance in a visual and an olfactory**
692 **elemental discrimination.** **A.** Schematic presentation of the tasks submitted to the bees. **B**
693 Acquisition curves expressed as proportion of correct choices \pm SEM of forager bees ($n = 18$)
694 confronted with a visual task (V; red curve) and an olfactory task (O; blue curve) consisting
695 of 15 trials. No significant improvement of performance could be detected over trials
696 (GLMM, *Trial*: $\chi^2 = 1.7$, $p = 0.19$). **C.** Choice accuracy expressed as proportion of correct
697 choices \pm SEM of forager bees confronted with the V and the O tasks in the non-reinforced
698 learning test. Bees' performance was above chance level for both tasks (GLM, Vision: $Z =$
699 6.54 , $p < 0.001$; Olfaction: $Z = 8.24$, $p < 0.001$). **D.** Correlation between performances
700 (proportion of correct choices) of individual bees in the non-reinforced learning tests. Each
701 dot shows data for one individual bee. The blue line represents the regression line while the
702 blue shadow indicates the 95% confidence interval. No correlation between individual
703 performances was observed (Spearman correlation, $r_s = 0.31$, $p = 0.21$).

704

705 **Figure 3: Experiment 3: Comparison of performance in an Elemental and a Non-**
706 **Elemental visual task.** **A.** Schematic presentation of the visual learning tasks submitted to the
707 bees. **B** Acquisition curves expressed as proportion of correct choices \pm SEM of forager bees
708 ($n = 18$) confronted with an Elemental task (E; red curve) consisting of 15 trials and a Non-
709 Elemental task (NE; blue curve) consisting of 30 trials. There was a significant improvement
710 in performance over trial repetition (GLMM, $n = 18$, *Trial*: $\chi^2 = 9.0$, $p = 0.003$). **C.** Choice
711 accuracy expressed as proportion of correct choices \pm SEM of forager bees confronted with
712 the E and the NE tasks in the non-reinforced learning test. Bees' performance was
713 significantly above chance level in both tasks (GLM, $n = 18$, Elemental: $Z = 7.18$, $p < 0.001$;
714 Non-Elemental: $Z = 4.73$, $p < 0.001$). **D.** Correlation between performances (proportion of

715 correct choices) of individual bees in the Elemental (E) and Non-Elemental (NE) non-
716 reinforced learning tests (Spearman correlation, $r_s = 0.64$, $p = 0.004$). Each dot shows data for
717 one individual bee. The blue line represents the regression line while the blue shadow
718 indicates the 95% confidence interval.

719

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723

724 *Authors' contributions*

725 AAW conceived the project. VF and AAW designed the experiment. VF performed the
726 experiment. VF, AAW and DB analysed the data. VF, DB, MG, RS and AAW participated in
727 the interpretation of the results and in the redaction of the manuscript.

728

729 *Data accessibility*

730 The datasets supporting this article are accessible on Dryad:
731 https://datadryad.org/stash/share/xpGwh3DQUlu7QVY0afLB6w9Zg4ff63hqJzEIXI_SZrk

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739

740 *Competing interests*

741 We declare no competing interests.

742

743 *Ethical statement*

744 Our protocols comply with standard welfare practice in our field. The bees were not
745 manipulated and free to visit our apparatus. The experiment involved bees from an apiary
746 dedicated to research.

747





