RESEARCH ARTICLE

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

Valerie Finke[1,2], David Baracchi[1,3], Martin Giurfa[1,4], Ricarda Scheiner[2] and Aurore Avarguès-Weber[1,*]

ABSTRACT

Individuals differing in their cognitive abilities and foraging strategies may confer a valuable benefit to their social groups as variability may help them to respond flexibly in scenarios with different resource availability. Individual learning proficiency may either be absolute or vary with the complexity or the nature of the problem considered. Determining whether learning ability correlates between tasks of different complexity or between sensory modalities is of high interest for research on brain modularity and task-dependent specialization of neural circuits. The honeybee *Apis mellifera* constitutes an attractive model to address this question because of its capacity to successfully learn a large range of tasks in various sensory domains. Here, we studied whether the performance of individual bees in a simple visual discrimination task (a discrimination between two visual shapes) is stable over time and correlates with their capacity to solve either a higher-order visual task (a conceptual discrimination based on spatial relationships between objects) or an elemental olfactory task (a discrimination between two odorants). We found that individual learning proficiency within a given task was maintained over time and that some individuals performed consistently better than others within the visual modality, thus showing consistent aptitude across visual tasks of different complexity. By contrast, performance in the elemental visual-learning task did not predict performance in the equivalent elemental olfactory task. Overall, our results suggest the existence of cognitive specialization within the hive, which may contribute to ecological social success.

KEY WORDS: *Apis mellifera*, Cognitive consistency, Honey bee, Insect cognition, Inter-individual variability, Visual cognition

INTRODUCTION

Cognitive skills are often attributed to a species based on the ability of a few representative members to pass or fail key cognitive tests. Yet, depicting cognition at a species level ignores the inter-individual variability that may reveal fundamental properties in terms of behavioural plasticity and, in the case of eusocial animals, specialization within a species. Indeed, inter-individual differences may involve variation in different domains such as motivation to complete the task, choice strategy, personality, or any combination of these factors. However, variable performance between individuals may also be due to intrinsic differences in cognitive abilities, which may occur in multiple dimensions, from differences in gene expression to variability in neural population responses and hormonal levels (Akhund-Zade et al., 2019; Honegger et al., 2020). Shifting the focus from the species to the individual level in the study of cognitive abilities provides a remarkable opportunity to reveal key underpinning mechanisms. Moreover, it also offers novel perspectives to understand the link between fitness and cognition (Raine and Chittka, 2008; Thornton and Lukas, 2012; Thornton et al., 2014; Evans et al., 2017; Boogert et al., 2018).

Social insects have attracted wide attention as a result of their remarkable cognitive feats (Giurfa, 2007; Srinivasan, 2010; Avarguès-Weber and Giurfa, 2013; Chittka, 2017). The co-existence of individuals with variable cognitive abilities within a social group may be favoured because of the significant energetic cost of investing in important learning faculties or problem-solving abilities (Mery and Kawecki, 2003; Burns, 2005; Burns and Rodd, 2008; Kawecki, 2010; Burns et al., 2011; Jaumann et al., 2013; Kotrschal et al., 2013). Such a co-existence has been documented, for example, in bumblebees colonies where some individuals consistently make fast but inaccurate foraging decisions while others decide more slowly yet with higher accuracy (Chittka et al., 2003). Colony success indeed benefits from the co-existence of costly but highly skilled foragers and cheaper but less accurate animals, as this heterogeneity may improve exploitation of different food sources and information distribution within the colony (Burns, 2005; Burns and Dyer, 2008; Muller and Chittka, 2008; Chittka et al., 2009). For example, the distinction between scout foragers searching novel resources and recruited bees relying on social information to massively exploit a unique resource as long as it remains profitable might be based on different cognitive abilities (Cook et al., 2019).

Bees are particularly appealing to study inter-individual cognitive variability as forager bees demonstrate diverse learning abilities ranging from elemental associative tasks to higher-order forms of learning such as categorization, numerical tasks or concept formation, among others (Srinivasan, 2010; Avarguès-Weber et al., 2011; Avarguès-Weber and Giurfa, 2013; Giurfa, 2013, 2019). Inter-individual variability has been generally neglected in standard tests of bee learning, which rely on mean group performance. Exceptions to this trend are the identification of individual variability in sucrose responsiveness as an important factor determining individual learning performance in honeybees (Scheiner et al., 1999; 2001, 2005) and the analysis of variability in olfactory learning performance on an individual basis (Pamir et al.,

[1]Centre de Recherches sur la Cognition Animale (CRCA), Centre de Biologie Intégrative (CBI), Université de Toulouse; CNRS, UPS, 118 Route de Narbonne, 31062 Toulouse, France. [2]Biozentrum, Universität Würzburg, Am Hubland, 97074 Würzburg, Germany. [3]Department of Biology, University of Florence, Via Madonna del Piano 6, 50019 Sesto Fiorentino, Italy. [4]Institut Universitaire de France, 75005 Paris, France.

*Author for correspondence (aurore.avargues-weber@univ-tlse3.fr)

D.B., 0000-0003-1308-0612; M.G., 0000-0001-7173-769X; R.S., 0000-0002-7515-4253; A.A., 0000-0003-3160-6710

1

2011, 2014). Both show the importance of focusing on individual performance as group-level analysis may lead to the misinterpretation of response dynamics.

Pioneer studies in bumblebees investigated whether such individual differences are consistent between cognitive tasks. Thus, relative learning performance was compared between visual and olfactory tasks, with contradictory results between studies concerning the existence of a correlation (Muller and Chittka, 2012; Smith and Raine, 2014). Bumblebees' ability to solve an elemental discrimination task (A+ versus B−) seems to be correlated with the faculty to then learn reversed reward contingencies in a non-elemental reversal learning phase (A− versus B+) (Raine and Chittka, 2012). In contrast, recent studies on honeybees showed no correlation between individual relative performance in odour discrimination tasks when the reinforcement was appetitive or aversive (Junca et al., 2019), or between landmark and olfactory learning (Tait et al., 2019), which suggests some level of cognitive specialization.

Here, we analysed individual learning performance in a simple visual discrimination task in which bees had to discriminate a rewarded from a non-rewarded visual target. We determined whether learning proficiency was stable over time (3 consecutive days) despite inter-individual differences. After confirming that inter-individual differences were consistent and unaffected by the kind of visual stimulus used in this task, we determined whether performance across visual tasks of different complexity, or across sensory modalities (visual versus olfactory), was correlated. To this end, we trained bees in two consecutive tasks: (i) the same elemental visual discrimination task described above and either (ii) a conceptual visual discrimination based on learning the constant spatial relationships between variable patterns ('choosing the picture presenting an object above/below the other, or to the left/right of the other, independently of the physical properties the objects present') (Avarguès-Weber et al., 2012) or (ii′) a simple olfactory discrimination (discrimination between a rewarded and a non-rewarded odorant). While the simple visual and olfactory tasks represent basic forms of learning in which two stimuli have unambiguous outcomes (A+ versus B−), the conceptual task requires transfer to novel unknown stimuli preserving the appropriate spatial relationship, and therefore represents a higher-order learning form (Giurfa, 2003; Avarguès-Weber and Giurfa, 2013).

MATERIALS AND METHODS
Ethical statement
Our protocols comply with standard welfare practice in our field. The bees were not manipulated and were free to visit our apparatus. The experiment involved bees from an apiary dedicated to research.

General procedure
Free-flying honeybees (*Apis mellifera* Linnaeus 1758) originating from a single hive and trained to forage for nectar on a sucrose gravity feeder were used in all our experiments. Only bees with intact wings were used, as wing damage could account for reduced foraging performance (Higginson and Barnard, 2004; Higginson et al., 2011). The age of the bees was not controlled. Bees were recruited from the feeder to the setup by offering them a drop of sucrose solution with a concentration (1.8 mol l^{-1}) higher than that of the feeder (variable depending on foraging motivation). While drinking, the bees were gently placed at the entrance of our Y-maze setup. Once satiated, the bees flew back to their hive. Returning bees on their subsequent foraging trip were colour marked and individually trained in a stepwise fashion to enter the Y-maze to collect a sucrose reward (1.8 mol l^{-1}) placed on the back walls of the maze. This pre-training usually took 1–2 h per bee.

The maze consisted of a pre-chamber, a decision chamber and the two arms in which the stimuli to be learned were presented. The pre-chamber was equipped with a sliding door, which allowed the traffic of foraging bees to be controlled. Only one marked bee was allowed at a time in the Y-maze. After entering the pre-chamber, the bee could fly into the decision chamber through a hole (5 cm diameter), leading to the two arms (40×20×20 cm, L×H×W) of the apparatus. The stimuli were presented on a UV-reflecting white background covering the back walls (20×20 cm) of the arms. The back walls were placed 15 cm from the centre of the decision chamber. During the learning tasks, bees always had to discriminate a stimulus rewarded with 1.8 mol l^{-1} sucrose solution from an alternative stimulus punished with 60 mmol l^{-1} quinine solution (Avarguès-Weber et al., 2010). A choice was scored when the bee approached one stimulus (<5 cm). If the bee chose the rewarded stimulus, it was allowed to drink the sucrose solution *ad libitum* until it returned to the hive to deliver the sucrose. An incorrect choice led to the tasting of quinine, which was followed by the possibility of flying to the alternative arm to collect sucrose on the rewarded stimulus. Only the first choice within a foraging bout was recorded. The sides of the rewarded and punished stimuli were exchanged in a pseudo-random sequence (i.e. a stimulus was presented no more than twice consecutively on the same side) throughout all experiments to prevent positional learning. After the last training trial, non-reinforced tests were performed using fresh stimuli. The tests were repeated twice to swap stimulus side and they were spaced by three refreshing reinforced trials in order to maintain appetitive motivation. Each test lasted 45 s, during which the contacts the bees made with the surface of the stimuli were recorded. This period is typically used in such tests as it allows uncovering of the learning induced by the training; longer periods may result in a switch of choice strategy owing to the extinction conditions. The percentage of correct choices for a given test was calculated for each bee using the number of contacts with the stimuli in both repetitions of the test.

Experiment 1: performance over three consecutive visual elemental discriminations
In this experiment, 18 bees were individually trained over 3 days to learn three consecutive visual discriminations, one per day. A minimum of two, but more often at least three, data points are typically used to show consistency in individual traits (Stamps and Groothuis, 2010). We chose to replicate the visual task over 3 consecutive days to determine the stability of individual performance. We did not extend the measurement period beyond 3 days to avoid losing bees as a result of natural death or recruitment to alternative food places. On each day, the bee experienced a 15-trial conditioning (i.e. 15 consecutive visits to the maze) during which it had to learn to discriminate two visual achromatic patterns, one (CS+) being consistently associated with reward (sucrose) and the other (CS−) with punishment (quinine). Training was followed by a test in which the stimuli used for training were presented without reinforcement (Fig. 1A). Training and testing took 1–2 h per bee. In the next 2 days, this procedure was repeated using a new set of visual stimuli every day. All the bees that completed the experimental schedule returned voluntarily to the setup every day. They were not maintained captive overnight in the laboratory. The bees returned reliably to the experimental set-up throughout the 3 day period and only one bee trained on day 1 did not come back the next day to complete the training sequence.
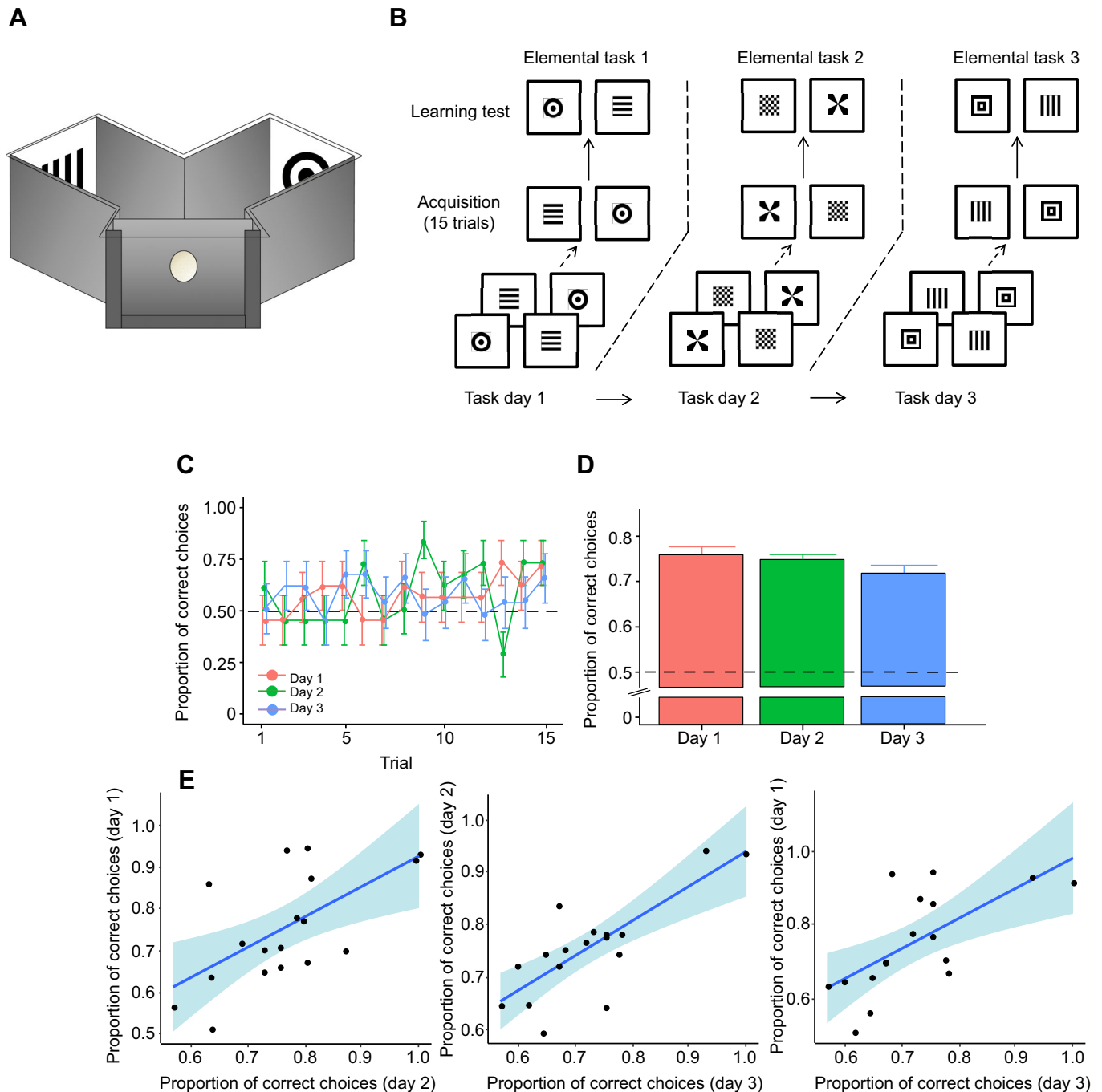
Fig. 1. Experiment 1: comparison of performance in three visual elemental discriminations. (A) Diagram of the Y-maze apparatus used to train bees in this study. (B) Schematic representation of one visual elemental learning task that bees were subjected to. The visual pattern that bees had to discriminate varied between bees and between days. (C) Acquisition curves expressed as the proportion of correct choices (±s.e.m.) of forager bees confronted with three consecutive elemental visual tasks consisting of 15 trials over 3 days. Bees improved their performance over the course of training (GLMM, n=17, Trial: χ^2=5.6, P=0.02). (D) Choice accuracy expressed as the proportion of correct choices (±s.e.m.) of forager bees in the non-reinforced learning tests following each training session. Performance was significantly higher than chance level (GLMM, n=17; day 1: Z=6.17, P<0.001; day 2: Z=8.79, P<0.001; day 3: Z=7.85, P<0.001). (E) Correlation between performance (proportion of correct choices) of individual bees in the non-reinforced learning tests of the repetition of elemental visual tasks involving different stimuli. Each dot shows data for one individual bee. The blue line represents the regression line; blue shading indicates the 95% confidence interval. Performance was correlated over the 3 days (Spearman correlation, day 1 versus day 2: r_S=0.62, P=0.009, day 2 versus day 3: r_S=0.66, P=0.004; day 1 versus day 3: r_S=0.70, P=0.002).

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

Experiment 2: performance in elemental visual and olfactory discriminations

In this experiment, a novel set of bees (N=18) were trained consecutively within a day to solve a visual discrimination task and an olfactory discrimination task. The sequence of visual and olfactory tasks was randomized between bees. The tasks were spaced by approximately 30 min during which the bees could collect sucrose solution outside of the Y-maze. This delay allowed preparation of the setup and stimuli for the next learning task. Both training phases consisted of 15 trials in which the bees had to discriminate between a rewarded stimulus (CS+) associated with sucrose solution and a second stimulus (CS−) associated with a quinine solution (Fig. 2A). Both training phases were followed by a test in which the respective stimuli were presented without reinforcement. The stimuli used in the visual task were the same as those described for experiment 1. The pair combinations were counterbalanced across bees. For the olfactory task, 10 µl of pure odorant (2-octanol and limonene, Sigma-Aldrich) were applied to 7×7 cm squares of filter paper. For each trial, fresh stimuli were used to ensure that the odours could be well perceived throughout training. Between trials, when the bees were absent from the set-up, the Y-maze was ventilated, and the arms of the maze were cleaned with 30% ethanol to remove potential odour residues. In both tasks, reinforcement contingencies were counterbalanced between bees. The whole procedure took between 2 and 3.5 h per bee.

Experiment 3: performance in visual discriminations of different cognitive complexity

An additional group of bees (N=18) were trained within the same day in two successive visual tasks, one elemental discrimination similar to the ones described in experiment 1 and one non-elemental conceptual discrimination based on spatial relational learning (Avarguès-Weber et al., 2012). The sequence of the elemental and non-elemental tasks was randomized between bees. The tasks were spaced by approximately 30 min during which the bees had access to a sucrose solution outside of the training apparatus. The tasks differed in the number of conditioning trials (15 for the elemental task and 30 for the non-elemental task) because of their different complexity. Training lengths were decided to ensure significant learning of the majority of bees. The procedure and stimuli of the elemental task were identical to those used in experiment 1 or in the visual task of experiment 2. In the non-elemental task, the bees were trained to discriminate between two composite images, each consisting of two coloured discs (7 cm diameter), but arranged in two different spatial configurations: above/below (discs aligned vertically, i.e. one above/below the other) and left/right (discs aligned horizontally, i.e. one to the left/right of the other). The discs differed only in their chromatic properties. They were cut from uncoated HKS paper (K+E Stuttgart, Stuttgart-Feuerbach, Germany; 1N, 3N, 29N, 32N, 48N, 71N; Fig. S1). The reinforcement contingency (above/below+ or left/right+) was counterbalanced between bees. The colour of the discs and their position on the back walls of the Y-maze were pseudo-randomized over trials, but keeping their alignment (Fig. 3A). By doing this, we ruled out that bees could use either the absolute spatial locations or the centre of gravity as cue to solve the task (Avarguès-Weber et al., 2012). The spatial relationship between the discs was consequently the only reliable predictor of the reward. The conditioning phase was followed by non-reinforced tests, in which novel achromatic (black) geometric shapes were used to recreate the trained spatial relationships. This allowed us to examine whether bees learned the spatial concept, irrespective of the stimuli properties. We took special care to choose

shapes differing as much as possible from the patterns used in the elemental learning task (Fig. 3A). Different shapes were used to this end (Fig. S1). Stimuli were printed on UV-reflecting copy paper and had a size of 7×7 cm. Training and testing took 3–4.5 h per bee.

Statistical analysis

Individual bee responses (correct or incorrect) during the acquisition phases were examined using generalized linear mixed models (GLMM) with a binomial error structure and logit-link function, glmer function of R package lme4 (Bates et al., 2015). In the models, the bee's choices (0 or 1) were entered as the dependent variable, while the trial number, the task [Day number (experiment 1), Visual/Olfactory (experiment 2) or Elemental/Non-Elemental (experiment 3)], the stimuli used and the order of the tasks were entered as fixed factors. Subject identity (ID) was entered as a random factor to account for the repeated-measure design. Several models were run by testing interactions between factors and by dropping each factor subsequently to select the significant model with the highest explanatory power (i.e. the lowest AIC value) (see Tables S1–S3).

Performance during the non-reinforced tests was analysed with a GLMM with a binomial error structure and logit-link function, where the proportion of correct choices for each bee was entered as a dependent variable, and the task and the task order were entered as fixed factors when appropriate. The intercept term informed us whether the mean proportion of correct choices is different from chance level. Correlations were computed using both the Pearson and Spearman correlation coefficients. All statistical analyses were performed with R 3.4.2 (http://www.R-project.org/).

RESULTS
Experiment 1: performance over three consecutive visual elemental discriminations

Honeybees successfully learned the three elemental visual discriminations between the achromatic visual patterns (Fig. 1B) as they significantly improved their performance during the acquisition phases (GLMM, $n=17$, Trial: $\chi^2=5.6$, $P=0.02$; Fig. 1C; Table S1). There was neither a significant effect of the pair of stimuli used (Stimuli: $\chi^2=15.4$, $P=0.97$; Table S1) nor a significant effect of the training sequence as performance did not improve over the three consecutive visual discriminations (Day: $\chi^2=0.01$, $P=0.92$; Table S1). Accordingly, performance in the non-reinforced tests (Fig. 1D) was significantly higher than chance on all 3 days with no significant influence of task repetition [$n=17$; day 1: 76.1±3.3% (mean±s.e.m.), $Z=6.17$, $P<0.001$ (GLMM); day 2: 76.0±2.3%, $Z=8.79$, $P<0.001$; day 3: 72.0±2.7%, $Z=7.85$, $P<0.001$; Day: $Z=1.34$, $P=0.17$ (GLMM)].

Individual learning performance (proportion of correct choices) was highly variable between individuals (Fig. 1E), yet it was consistent over the 3 days (day 1 versus day 2: Spearman correlation, $r_S=0.62$, $P=0.009$, Pearson correlation, $r_p=0.63$, $P=0.007$; day 2 versus day 3: $r_S=0.66$, $P=0.004$; $r_p=0.78$, $P<0.001$; day 1 versus day 3: $r_S=0.70$, $P=0.002$; $r_p=0.66$, $P=0.004$; Fig. 1E). This result indicates that despite population variability in learning proficiency, individual proficiency remained stable across days and visual discrimination tasks.

Experiment 2: performance in elemental visual and olfactory discriminations

Although no significant improvement of performance could be detected over trials (GLMM, Trial: $\chi^2=1.7$, $P=0.19$; Fig. 2B; Table S2), the bees ($n=18$) learned both tasks as shown by their
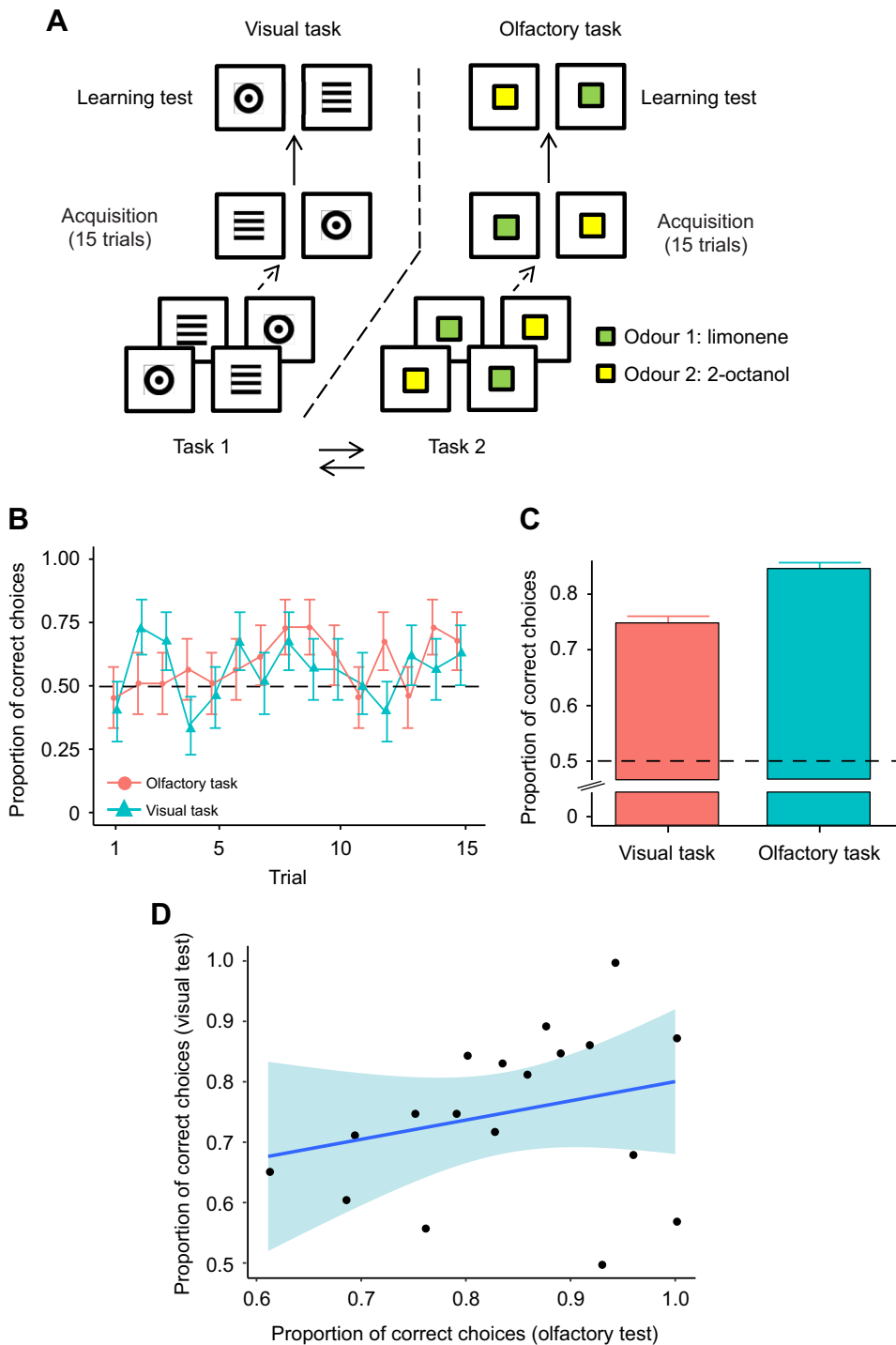
Fig. 2. Experiment 2: comparison of performance in a visual and an olfactory elemental discrimination. (A) Schematic representation of the tasks that bees were subjected to. (B) Acquisition curves expressed as the proportion of correct choices (±s.e.m.) of forager bees (n=18) confronted with a visual task and an olfactory task consisting of 15 trials. No significant improvement of performance could be detected over trials (GLMM, Trial: χ^2=1.7, P=0.19). (C) Choice accuracy expressed as the proportion of correct choices (±s.e.m.) of forager bees confronted with the visual and the olfactory tasks in the non-reinforced learning test. Bee performance was above chance level for both tasks (GLMM, Vision: Z=6.54, P<0.001; Olfaction: Z=8.24, P<0.001). (D) Correlation between the performance (proportion of correct choices) of individual bees in the non-reinforced learning tests. Each dot shows data for one individual bee. The blue line represents the regression line; blue shading indicates the 95% confidence interval. No correlation between individual performances was observed (Spearman correlation, r_S=0.31, P=0.21).

performance in the non-reinforced tests where they preferred the correct stimulus, be it visual (74.9±3.2% of correct choices, GLMM, Z=6.54, P<0.001; Fig. 2C) or olfactory (84.0±2.6%, Z=8.24, P<0.001; Fig. 2C). Bees were generally more accurate in the olfactory task than in the visual task (GLMM, Task: Z=3.58, P<0.001; Fig. 2C).

As in the previous experiment, a high variability in learning proficiency was observed between the trained individuals (Fig. 2D). However, this time no correlation between individual performances was found (Olfactory versus Visual: r_S=0.31, P=0.21; r_p=0.26, P=0.29; Fig. 2D), thus showing that individual

proficiency is not stable between tasks involving different sensory modalities.

Experiment 3: performance in visual discriminations of different cognitive complexity

Honeybees improved their performance during the acquisition phase in both the elemental and the conceptual task (GLMM, n=18, Trial: χ^2=9.0, P=0.003; Fig. 3B; Table S3). The task sequence did not affect the bees' performance (Order, χ^2=0.05, P=0.82; Fig. S2, Table S3). Overall, the bees' accuracy was higher in the elemental task than in the non-elemental task (Task, χ^2=15.0, P<0.001, Fig. 3C; Table S3), a
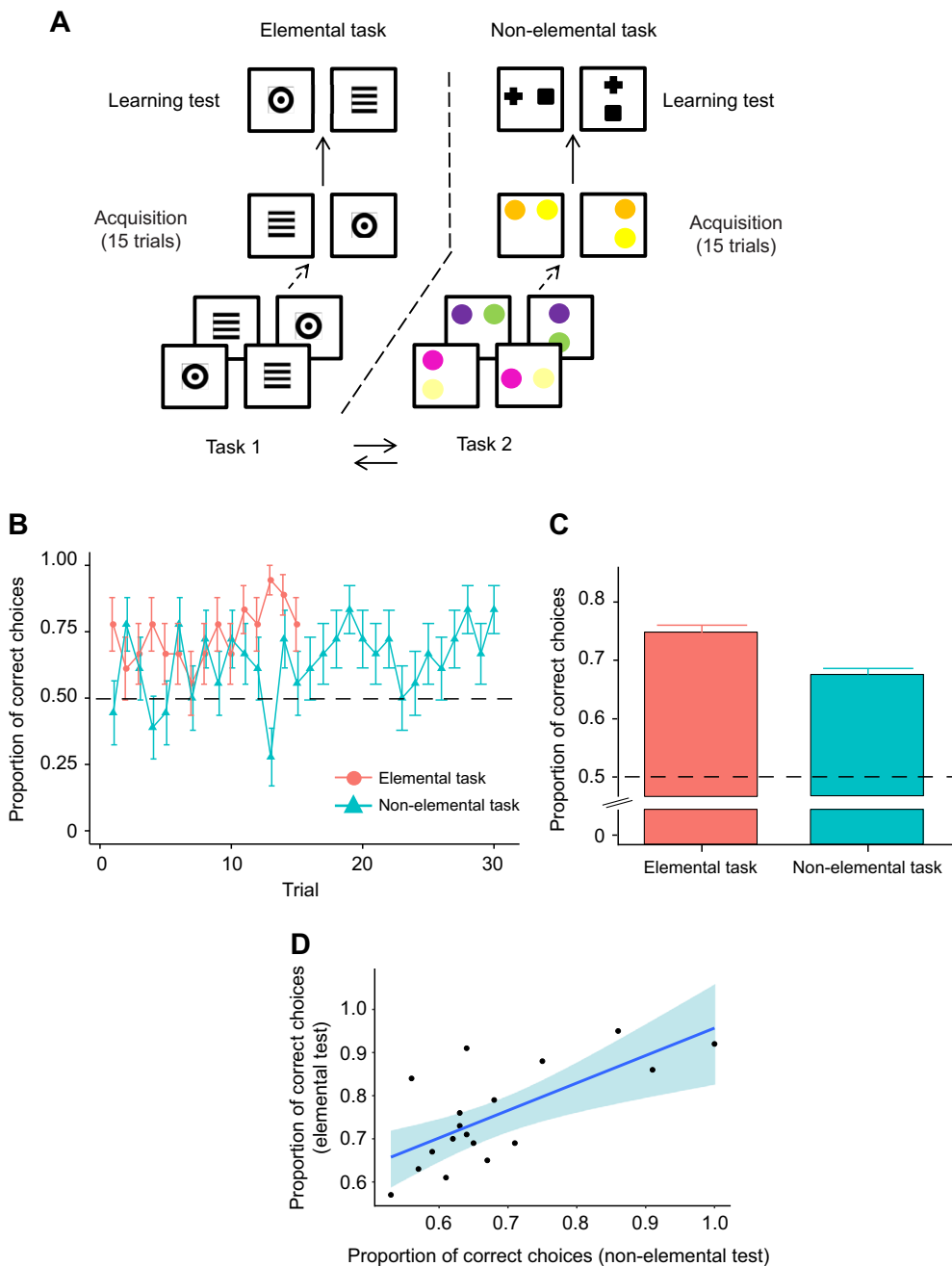
Fig. 3. Experiment 3: comparison of performance in an elemental and a non-elemental visual task. (A) Schematic representation of the visual learning tasks that bees were subjected to. (B) Acquisition curves expressed as the proportion of correct choices (±s.e.m.) of forager bees (n=18) confronted with an elemental task consisting of 15 trials and a non-elemental task consisting of 30 trials. There was a significant improvement in performance over trial repetition (GLMM, n=18, Trial: χ^2=9.0, P=0.003). (C) Choice accuracy expressed as the proportion of correct choices (±s.e.m.) of forager bees confronted with the elemental and the non-elemental tasks in the non-reinforced learning test. Bee performance was significantly above chance level in both tasks (GLMM, n=18, Elemental: Z=7.18, P<0.001; Non-Elemental: Z=4.73, P<0.001). (D) Correlation between the performance (proportion of correct choices) of individual bees in the elemental and non-elemental non-reinforced learning tests (Spearman correlation, r_S=0.64, P=0.004). Each dot shows data for one individual bee. The blue line represents the regression line; blue shading indicates the 95% confidence interval.

result that is consistent with the different levels of complexity of these tasks. Performance in the non-reinforced tests was significantly higher than chance in both tasks (Elemental task: 75.4±2.7% of correct choices, GLMM, Z=7.18, P<0.001; Non-Elemental task: 68.0±2.9% of correct choices, Z=4.73, P<0.001; Fig. 3C). Yet, it was also affected by the complexity of the task (GLMM, Task: Z=2.36, P=0.02; Fig. 3C) as test performance was better after the elemental conditioning than after the non-elemental conditioning.

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

DISCUSSION
Our results highlight the importance of individual variability in cognitive tasks and its relationship with the nature of the task

considered. By testing the same bees on consecutive days with tasks that were either similar (experiment 1) or different (experiments 2 and 3), we observed an important inter-individual variability in learning performance as in all cases the proportion of correct choices varied at the population level, with some bees being efficient learners and others, in contrast, poor learners. Importantly, this proficiency was maintained across time when individuals were tested on three similar consecutive visual discriminations (experiment 1). Thus, the variable response observed within a given task seems to be a consequence of individual stable factors rather than being noise resulting from transitory variability in foraging activity, appetitive motivation or stochasticity in choice persistence. In addition, we showed that proficiency is maintained across elemental and higher-order learning tasks within the same sensory modality (experiment 3), even if performance was again highly variable at the population level. This result is important as it shows

that bees trained within the visual modality will conserve their success irrespective of the cognitive complexity of the task, a problem that has never previously been addressed in invertebrates. Finally, we showed that consistency in performance was not maintained when bees were trained using tasks involving different modalities (vision and olfaction; experiment 2), thus arguing in favour of within-modality cognitive specialization.

Several factors can account for the inter-individual variability observed. But, some of them can be ruled out in our study. In our experiments, only nectar foragers captured at a sucrose feeder and consequently motivated for foraging were used, which discards differences due to division of labour and appetitive motivation. In addition, the temporal sequence did not influence the performance of the bees. We expected that familiarization with the setup and enhanced attention might be promoted by prior training experience, resulting in faster acquisition in subsequent tasks. However, such an improvement was not observed in our conditions.

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

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

complexity relies, at least partially, on neurobiological variability resulting from different life experiences.

Learning differences could also emerge from variation in the processing of the stimuli to be learned such as odours or visual cues. This possibility is supported by our study as we found that some bees were relatively better at learning olfactory cues than visual cues, and vice versa, thus reflecting potential variation in perceptual salience between modalities. Honeybees are known to differ in their responsiveness to odours (Scheiner et al., 2004), which could be linked to inter-individual differences in the activity of olfactory neural circuits. In fruit flies, for instance, stable inter-individual variability was found in an odour-preference assay, which translated into consistent inter-individual differences in Ca^{2+} activity levels in a key structure of the olfactory circuit, the projection neurons of the antennal lobes (Honegger et al., 2020). Similar arguments could apply to visual processing and its underlying visual circuits.

The question of whether learning ability correlates across problems of different complexity or sensory domains is particularly relevant for the analysis of brain modularity and for understanding the contributions of different neural circuits to different forms of learning. In honeybees, different brain structures have been associated with different levels of complexity in olfactory learning. The mushroom bodies are required for non-elemental olfactory discrimination tasks such as the negative patterning problem (A+, B+, AB−) (Devaud et al., 2015) or for reversal learning (A+ B−→A− B+) (Boitard et al., 2015) but are dispensable for elemental olfactory discrimination (A+, B+, CD−) (Devaud et al., 2015). From this perspective, proficiency in non-elemental olfactory learning may not necessarily be correlated with proficiency in elemental olfactory learning, given that these learning forms are mediated by different brain structures. Applying this reasoning to our results in the visual domain suggests that the two learning forms, which are highly correlated, may require similar visual circuits/structures. To date, the brain neuropils involved in different forms of visual learning remain unknown because of the difficulty of reproducing successful visual learning in the laboratory, which would allow coupling with invasive recordings of neural activity (Avarguès-Weber and Mota, 2016). However, given the massive visual afferences to the mushroom bodies (Ehmer and Gronenberg, 2002; Paulk and Gronenberg, 2008) and to the central complex (Pfeiffer and Homberg, 2014), participation of these structures is expected. For instance, in *Drosophila*, both mushroom bodies and the central complex are involved in visual learning depending on the specific task and setup used (Liu et al., 1999; Pan et al., 2009; Ofstad et al., 2011; Vogt et al., 2014, 2016).

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

Shifting our focus from group to individual performance in cognitive studies could thus contribute to the elucidation of the underlying mechanisms (Thornton and Lukas, 2012; Pamir et al.,

2014; Boogert et al., 2018; Klein, 2018). It also raises fascinating ecological questions such as the possible existence of cognitive specialization between workers from different patrilines in a hive. In honeybees, the best learners might deal with more demanding, complex tasks and concentrate their foraging effort towards the exploration of novel food sources. Others might simply copy the former and use social information when facing difficult tasks, as occurs in bumblebees (Baracchi et al., 2018). This would explain the known differentiation between scouts and recruits (Biesmeijer and de Vries, 2001; Beekman et al., 2007). The diversity of foraging strategies within a colony has been shown to increase its fitness (Burns, 2005; Burns and Dyer, 2008; Jeanson and Weidenmüller, 2014; Klein, 2018) but, interestingly, the best learners are not necessarily the best foragers, as demonstrated in bumblebees, where bad learners foraged for a longer time frame and collected more resources, potentially as a result of the energetic cost associated with cognition (Evans et al., 2017). Thus, the complex interplay between inter-individual cognitive skill diversity, task allocation and colony fitness remains to be fully elucidated.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: A.A.-W.; Methodology: A.A.-W., V.F.; Validation: V.F., M.G., R.S., A.A.-W.; Formal analysis: D.B., A.A.-W., V.F.; Investigation: V.F.; Resources: A.A.-W.; Writing - original draft: A.A.-W., V.F.; Writing - review & editing: D.B., M.G., R.S.; Visualization: D.B., A.A.-W.; Supervision: M.G., R.S., A.A.-W.; Project administration: A.A.-W.; Funding acquisition: A.A.-W.

Data availability
The datasets supporting this article are available from the Dryad digital repository (Finke et al., 2021): doi:10.5061/dryad.1ns1rn8v5.

References
Akhund-Zade, J., Ho, S., O'Leary, C. and de Bivort, B. (2019). The effect of environmental enrichment on behavioral variability depends on genotype, behavior, and type of enrichment. *J. Exp. Biol.* **222**, jeb202234. doi:10.1242/jeb.202234

Avarguès-Weber, A. and Giurfa, M. (2013). Conceptual learning by miniature brains. *Proc. R. Soc. B Biol. Sci.* **280**, 20131907. doi:10.1098/rspb.2013.1907

Avarguès-Weber, A. and Mota, T. (2016). Advances and limitations of visual conditioning protocols in harnessed bees. *J. Physiol. Paris* **110**, 107-118. doi:10.1016/j.jphysparis.2016.12.006

Avarguès-Weber, A., de Brito Sanchez, M. G., Giurfa, M. and Dyer, A. G. (2010). Aversive reinforcement improves visual discrimination learning in free-flying honeybees. *PLoS ONE* **5**, e15370. doi:10.1371/journal.pone.0015370

Avarguès-Weber, A., Deisig, N. and Giurfa, M. (2011). Visual cognition in social insects. *Annu. Rev. Entomol.* **56**, 423-443. doi:10.1146/annurev-ento-120709-144855

Avarguès-Weber, A., Dyer, A. G., Combe, M. and Giurfa, M. (2012). Simultaneous mastering of two abstract concepts by the miniature brain of bees. *Proc. Natl. Acad. Sci. USA* **109**, 7481-7486. doi:10.1073/pnas.1202576109

Baddeley, A. (2003). Working memory: looking back and looking forward. *Nat. Rev. Neurosci.* **4**, 829-839. doi:10.1038/nrn1201

Baracchi, D., Vasas, V., Jamshed Iqbal, S. and Alem, S. (2018). Foraging bumblebees use social cues more when the task is difficult. *Behav. Ecol.* **29**, 186-192. doi:10.1093/beheco/arx143

Bates, D., Mächler, M., Bolker, B. and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1-48. doi:10.18637/jss.v067.i01

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

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

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

Boitard, C., Devaud, J.-M., Isabel, G. and Giurfa, M. (2015). GABAergic feedback signaling into the calyces of the mushroom bodies enables olfactory reversal learning in honey bees. *Front. Behav. Neurosci.* **9**, 198. doi:10.3389/fnbeh.2015.00198

Boogert, N. J., Madden, J. R., Morand-Ferron, J. and Thornton, A. (2018). Measuring and understanding individual differences in cognition. *Phil. Trans. R. Soc. B Biol. Sci.* **373**, 20170280. doi:10.1098/rstb.2017.0280

Brandes, C. (1988). Estimation of heritability of learning behavior in honeybees (*Apis mellifera capensis*). *Behav. Genet.* **18**, 119-132. doi:10.1007/BF01067081

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

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

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

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

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

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

Chittka, L. (2017). Bee cognition. *Curr. Biol.* **27**, R1049-R1053. doi:10.1016/j.cub.2017.08.008

Chittka, L., Dyer, A. G., Bock, F. and Dornhaus, A. (2003). Psychophysics: bees trade off foraging speed for accuracy. *Nature* **424**, 388-388. doi:10.1038/424388a

Chittka, L., Skorupski, P. and Raine, N. E. (2009). Speed-accuracy tradeoffs in animal decision making. *Trends Ecol. Evol.* **24**, 400-407. doi:10.1016/j.tree.2009.02.010

Cook, C. N., Mosqueiro, T., Brent, C. S., Ozturk, C., Gadau, J., Pinter-Wollman, N., Smith, B. H. and Resasco, J. (2019). Individual differences in learning and biogenic amine levels influence the behavioural division between foraging honeybee scouts and recruits. *J. Anim. Ecol.* **88**, 236-246. doi:10.1111/1365-2656.12911

Devaud, J.-M., Papouin, T., Carcaud, J., Sandoz, J.-C., Grünewald, B. and Giurfa, M. (2015). Neural substrate for higher-order learning in an insect: mushroom bodies are necessary for configural discriminations. *Proc. Natl. Acad. Sci. USA* **112**, E5854-E5862. doi:10.1073/pnas.1508422112

Durst, C., Eichmüller, S. and Menzel, R. (1994). Development and experience lead to increased volume of subcompartments of the honeybee mushroom body. *Behav. Neural. Biol.* **62**, 259-263. doi:10.1016/S0163-1047(05)80025-1

Ehmer, B. and Gronenberg, W. (2002). Segregation of visual input to the mushroom bodies in the honeybee (*Apis mellifera*). *J. Comp. Neurol.* **451**, 362-373. doi:10.1002/cne.10355

Evans, L. J., Smith, K. E. and Raine, N. E. (2017). Fast learning in free-foraging bumble bees is negatively correlated with lifetime resource collection. *Sci. Rep.* **7**, 496. doi:10.1038/s41598-017-00389-0

Farris, S. M., Robinson, G. E. and Fahrbach, S. E. (2001). Experience- and age-related outgrowth of intrinsic neurons in the mushroom bodies of the adult worker honeybee. *J. Neurosci.* **21**, 6395-6404. doi:10.1523/JNEUROSCI.21-16-06395.2001

Finke, V., Baracchi, D., Giurfa, M., Scheiner, R. and Avarguès-Weber, A. (2021). Evidence of cognitive specialization in an insect: proficiency is maintained across elemental and higher-order visual learning but not between sensory modalities in honey bees. *Dryad, Dataset*, doi:10.5061/dryad.1ns1rn8v5

Giurfa, M. (2003). Cognitive neuroethology: dissecting non-elemental learning in a honeybee brain. *Curr. Opin. Neurobiol.* **13**, 726-735. doi:10.1016/j.conb.2003.10.015

Giurfa, M. (2007). Behavioral and neural analysis of associative learning in the honeybee: a taste from the magic well. *J. Comp. Physiol. A* **193**, 801-824. doi:10.1007/s00359-007-0235-9

Giurfa, M. (2013). Cognition with few neurons: higher-order learning in insects. *Trends Neurosci.* **36**, 285-294. doi:10.1016/j.tins.2012.12.011

Giurfa, M. (2019). An Insect's sense of number. *Trends Cogn. Sci.* **23**, 720-722. doi:10.1016/j.tics.2019.06.010

Groh, C., Lu, Z., Meinertzhagen, I. A. and Rössler, W. (2012). Age-related plasticity in the synaptic ultrastructure of neurons in the mushroom body calyx of the adult honeybee Apis mellifera. *J. Comp. Neurol.* **520**, 3509-3527. doi:10.1002/cne.23102

Higginson, A. D. and Barnard, C. J. (2004). Accumulating wing damage affects foraging decisions in honeybees (Apis mellifera L.). *Ecol. Entomol.* **29**, 52-59. doi:10.1111/j.0307-6946.2004.00573.x

Higginson, A. D., Barnard, C. J., Tofilski, A., Medina, L. and Ratnieks, F. (2011). Experimental wing damage affects foraging effort and foraging distance in honeybees Apis mellifera. *Psyche: A J. Entomol.* **2011**, 419793. doi:10.1155/2011/419793

Honegger, K. S., Smith, M. A.-Y., Churgin, M. A., Turner, G. C. and de Bivort, B. L. (2020). Idiosyncratic neural coding and neuromodulation of olfactory individuality in Drosophila. *Proc. Natl. Acad. Sci. USA* **117**, 23292-23297. doi:10.1073/pnas.1901623116

Hourcade, B., Muenz, T. S., Sandoz, J.-C., Rössler, W. and Devaud, J.-M. (2010). Long-term memory leads to synaptic reorganization in the mushroom bodies: a memory trace in the insect brain? *J. Neurosci.* **30**, 6461-6465. doi:10.1523/JNEUROSCI.0841-10.2010

Ings, T. C., Raine, N. E. and Chittka, L. (2009). A population comparison of the strength and persistence of innate colour preference and learning speed in the bumblebee Bombus terrestris. *Behav. Ecol. Sociobiol.* **63**, 1207-1218. doi:10.1007/s00265-009-0731-8

Jarrold, C. and Towse, J. N. (2006). Individual differences in working memory. *Neuroscience* **139**, 39-50. doi:10.1016/j.neuroscience.2005.07.002

Jaumann, S., Scudelari, R. and Naug, D. (2013). Energetic cost of learning and memory can cause cognitive impairment in honeybees. *Biol. Lett.* **9**, 20130149. doi:10.1098/rsbl.2013.0149

Jeanson, R. and Weidenmüller, A. (2014). Interindividual variability in social insects - proximate causes and ultimate consequences. *Biol. Rev.* **89**, 671-687. doi:10.1111/brv.12074

Junca, P., Garnery, L. and Sandoz, J.-C. (2019). Genotypic trade-off between appetitive and aversive capacities in honeybees. *Sci. Rep.* **9**, 10313. doi:10.1038/s41598-019-46482-4

Kawecki, T. J. (2010). Evolutionary ecology of learning: insights from fruit flies. *Popul. Ecol.* **52**, 15-25. doi:10.1007/s10144-009-0174-0

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

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

Li, L., MaBouDi, H., Egertová, M., Elphick, M. R., Chittka, L. and Perry, C. J. (2017). A possible structural correlate of learning performance on a colour discrimination task in the brain of the bumblebee. *Proc. R. Soc. B Biol. Sci.* **284**, 20171323. doi:10.1098/rspb.2017.1323

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

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

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

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

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

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

Muller, H. and Chittka, L. (2012). Consistent interindividual differences in discrimination performance by bumblebees in colour, shape and odour learning tasks (Hymenoptera: Apidae: Bombus terrestris). *Entomol. Gen.* **34**, 1-8. doi:10.1127/entom.gen/34/2012/1

Münch, D., Baker, N., Kreibich, C. D., Bråten, A. T. and Amdam, G. V. (2010). In the laboratory and during free-flight: old honey bees reveal learning and extinction deficits that mirror mammalian functional decline. *PLoS ONE* **5**, e13504. doi:10.1371/journal.pone.0013504

Nityananda, V. (2016). Attention-like processes in insects. *Proc. R. Soc. B Biol. Sci.* **283**, 20161986. doi:10.1098/rspb.2016.1986

Ofstad, T. A., Zuker, C. S. and Reiser, M. B. (2011). Visual place learning in Drosophila melanogaster. *Nature* **474**, 204-207. doi:10.1038/nature10131

Orr, M., Hittel, K., Lukowiak, K. S., Han, J. and Lukowiak, K. (2009). Differences in LTM-forming capability between geographically different strains of Alberta Lymnaea stagnalis are maintained whether they are trained in the lab or in the wild. *J. Exp. Biol.* **212**, 3911-3918. doi:10.1242/jeb.024281

Pamir, E., Chakroborty, N. K., Stollhoff, N., Gehring, K. B., Antemann, V., Morgenstern, L., Felsenberg, J., Eisenhardt, D., Menzel, R. and Nawrot, M. P. (2011). Average group behavior does not represent individual behavior in classical conditioning of the honeybee. *Learn. Mem.* **18**, 733-741. doi:10.1101/lm.2232711

Pamir, E., Szyszka, P., Scheiner, R. and Nawrot, M. P. (2014). Rapid learning dynamics in individual honeybees during classical conditioning. *Front. Behav. Neurosci.* **8**, 313. doi:10.3389/fnbeh.2014.00313

Pan, Y., Zhou, Y., Guo, C., Gong, H., Gong, Z. and Liu, L. (2009). Differential roles of the fan-shaped body and the ellipsoid body in Drosophila visual pattern memory. *Learn. Mem.* **16**, 289-295. doi:10.1101/lm.1331809

Paulk, A. C. and Gronenberg, W. (2008). Higher order visual input to the mushroom bodies in the bee, Bombus impatiens. *Arthropod Struct. Dev.* **37**, 443-458. doi:10.1016/j.asd.2008.03.002

Pfeiffer, K. and Homberg, U. (2014). Organization and functional roles of the central complex in the insect brain. *Annu. Rev. Entomol.* **59**, 165-184. doi:10.1146/annurev-ento-011613-162031

Raine, N. E. and Chittka, L. (2008). The correlation of learning speed and natural foraging success in bumble-bees. *Proc. R. Soc. B Biol. Sci.* **275**, 803-808. doi:10.1098/rspb.2007.1652

Raine, N. E. and Chittka, L. (2012). No trade-off between learning speed and associative flexibility in bumblebees: a reversal learning test with multiple colonies. *PLoS ONE* **7**, e45096. doi:10.1371/journal.pone.0045096

Raine, N. E., Ings, T. C., Ramos-Rodriguez, O. and Chittka, L. (2006). Intercolony variation in learning performance of a wild British bumblebee population Hymenoptera: apidae: bombus terrestris audax. *Entomol. Gen.* **28**, 241. doi:10.1127/entom.gen/28/2006/241

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

Scheiner, R. and Arnold, G. (2010). Effects of patriline on gustatory responsiveness and olfactory learning in honey bees. *Apidologie* **41**, 29-37. doi:10.1051/apido/2009040

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

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

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

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

Scheiner, R., Lim, K., Meixner, M. D. and Gabel, M. S. (2021). Comparing the appetitive learning performance of six European honeybee subspecies in a common apiary. *Insects* **12**, 768. doi:10.3390/insects12090768

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

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

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

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

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

Thornton, A. and Lukas, D. (2012). Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2773-2783. doi:10.1098/rstb.2012.0214

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

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

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

Vogt, K., Aso, Y., Hige, T., Knapek, S., Ichinose, T., Friedrich, A. B., Turner, G. C., Rubin, G. M. and Tanimoto, H. (2016). Direct neural pathways convey distinct visual information to Drosophila mushroom bodies. *eLife* **5**, e14009. doi:10.7554/eLife.14009

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