# 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

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## *Abstract*

Individuals differing in their cognitive abilities and foraging strategies may confer a valuable benefit to their social groups as variability may help responding 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 if learning abilities correlate between tasks of different complexity or between sensory modalities has a high interest for research on brain modularity and task-dependent specialisation of neural circuits. The honeybee *Apis mellifera* constitutes an attractive model to address this question due to 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 relations 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 specialisation within the hive, which may contribute to ecological social success.

## 1. Introduction

Cognitive skills are often attributed to a species based on the ability of 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 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 performances between individuals may also be due to intrinsic differences in cognitive abilities, which may be retraced to multiple dimensions, from differences in gene expression to variability in neural population responses and hormonal levels (Akhund-Zade et al., 2019; Honegger et al., 2019). 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 & Chittka, 2008; Thornton & Lukas, 2012; Thornton et al., 2014; Evans et al., 2017; Boogert et al., 2018).

Social insects have attracted wide attention due to their remarkable cognitive feats (Giurfa, 2007; Srinivasan, 2010; Avarguès-Weber & Giurfa, 2013; Chittka, 2017). The co-existence of individuals with variable cognitive abilities within a social group may be favoured due to the important energetic cost of investing in important learning faculties or problem-solving abilities (Mery & Kawecki, 2003; Burns, 2005; Burns & Rodd, 2008; Kawecki, 2009; 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 & Dyer, 2008; Muller & Chittka, 2008; Chittka et al., 2009). For example, the distinction between scout foragers searching novel resources and recruited bees relying on social information to exploit massively a unique resource as long as it remains profitable might be based on different cognitive abilities (Cook et al., 2018).

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 & 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 performances on an individual basis (Pamir et al., 2011, 2014). Both show the importance of focusing on individual performances 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 performances were compared between visual and olfactory tasks with contradictory results between studies concerning the existence of a correlation (Muller & Chittka, 2012; Smith & Raine, 2014). Bumblebees ability to solve an elemental discrimination task (A+ vs. B-) seems correlated with the faculty to then learn reversed reward contingencies in a non-elemental reversal learning phase (A- vs. B+) (Raine & Chittka, 2012). On the contrary, recent studies on honeybees showed no correlation

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

Here we analysed individual learning performances in a simple visual discrimination task in which bees had to discriminate a rewarded from a non-rewarded visual target. We determined if learning proficiency was stable over time (three 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 if performance across visual tasks of different complexity, or across sensory modalities (visual versus olfactory), was correlated. To this end we trained bees along 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 (a 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+ vs. B-), the conceptual task requires transfer to novel unknown stimuli preserving the appropriate spatial relationship, and represents, therefore, a higher-order learning form (Giurfa, 2003; Avarguès-Weber & Giurfa, 2013).

## 2. Methods

### (a) General procedure

Free-flying honeybees (*Apis mellifera*) 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 & 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 M) 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 M) placed on the back walls of the maze. This pre-training usually took 1-2 hours 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 controlling the traffic of foraging bees. 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 (Ø 5 cm), leading to the two arms (40 cm x 20 cm x 20 cm, L x H x W) of the apparatus. The stimuli were presented on a UV-reflecting white background covering the back walls (20 x 20 cm) of the arms. Back walls were placed at 15 cm from the centre of the decision chamber. During the learning tasks, bees always had to discriminate a stimulus rewarded with sucrose solution 1.8 M from an alternative stimulus punished with quinine solution 60 mM (Avarguès-Weber et al., 2010). A choice was scored when the bee approached one stimulus (< 5cm). 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 to move 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 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 seconds during which the contacts the bees made with the surface of the stimuli were recorded. This period is typically used in these tests as it allows uncovering the learning induced by the training; longer periods may result in a switch of choice strategy due 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.

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

In this experiment, 18 bees were individually trained during three 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 &

Groothuis, 2010). We chose to replicate the visual task during three consecutive days to determine the stability of individual performances. We did not extend the measurement period beyond three days to avoid losing bees due to 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 hours per bee. In the next two 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 three-day period and only one bee trained on day 1 did not come back on the next day to complete the training sequence.

The stimuli used were 7 x 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.

**(c) 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 minutes during which the bees could collect sucrose solution outside of the Y-maze. This delay allowed preparing 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 7x7 cm squares of filter paper. For each trial fresh stimuli were used to assure

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 2-3.5 hours per bee.

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

An additional group of bees (N = 18) were trained within the same day along 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. Both tasks were spaced by approximately 30 minutes 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) due to 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 (Ø 7 cm), 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 papers (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 positions within the back walls of the Y-maze were pseudo-randomized over trials, yet 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 relation 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 relations. This allowed examining 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 x 7 cm. Training and testing took 3-4.5 hours per bee.

### (e) 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 - logit-link function -, *glmer* function of R package *lme4* (Bates et al., 2014). 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. Subjects 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 supplementary tables).

Performances during the non-reinforced tests were analysed with a generalized linear mixed model (GLMM) with a binomial error structure and logit-link function, where the proportion of correct choices for each bee was entered as dependent variable, while the task and the task order were entered as fixed factors whenever appropriate. The intercept term informed us on 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 (R Development Core Team, 2016).

### 3. Results

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

Honeybees learned successfully the three elemental visual discriminations between the achromatic visual patterns (Fig. 1A) as they significantly improved their performance during the acquisition phases (GLMM, $n = 17$, *Trial*: $\chi^2 = 5.6$, $p = 0.02$; Fig.1B, 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 of the training sequence as performance did not improve along the three consecutive visual discriminations (*Day*: $\chi^2 = 0.01$, $p = 0.92$; table S1). Accordingly, the performances in the non-reinforced tests (Fig. 1C) were significantly higher than chance in all three days with no significant influence of task repetition ($n = 17$; Day 1: 76.1 ± 3.3 % (mean ± SEM), $Z = 6.17$, $p < 0.001$ (GLM); Day 2: 76.0 ± 2.3 %, $Z = 8.79$, $p < 0.001$; Day 3: 72.0 ± 2.7 %, $Z = 7.85$, $p < 0.001$; *Day*: $Z = 1.34$, $p = 0.17$ (GLMM)).

Individual learning performances (proportion of correct choices) were highly variable between individuals (Fig. 1D), yet they were consistent along the three days (Day 1 vs. Day 2: Spearman correlation, $r_S = 0.62$, $p = 0.009$, Pearson correlation, $r_p = 0.63$, $p = 0.007$; Day 2 vs. Day 3: $r_S = 0.66$, $p = 0.004$; $r_p = 0.78$, $p < 0.001$; Day 1 vs. Day 3: $r_S = 0.70$, $p = 0.002$; $r_p = 0.66$, $p = 0.004$; Fig. 1D). 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 performance in the non-reinforced tests where they preferred the correct stimulus, be it visual (74.9 ± 3.2 % of correct choices, GLM, $Z = 6.54$, $p < 0.001$; 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 individuals trained (Fig. 2D). However, this time no correlation between individual performances was found (Olf. vs. Vis: $r_S = 0.31$, $p = 0.21$; $r_p = 0.26$, $p = 0.29$; 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*: $\chi^2 = 9.0$, $p = 0.003$; Fig. 3B, table S3). The task sequence did not affect the bees' performance (*Order*, $\chi^2 = 0.05$, $p = 0.82$; Fig. S2, table S3). Overall the bees' accuracy was higher in the elemental task than in the non-elemental task (*Task*, $\chi^2 = 15.0$, $p < 0.001$, Fig. 3B, table S3), a 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: $75.4 \pm 2.7$ % of correct choices, GLM, $Z = 7.18$, $p < 0.001$; non-elemental task: $68.0 \pm 2.9$ % of correct choices, $Z = 4.73$, $p < 0.001$; Fig. 3B). Yet, it was also affected by the complexity of the task (GLMM, *Task*: $Z = 2.36$, $p = 0.02$, Fig. 3B) 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. 3C), with some individuals being consistently more error-prone than others in both tests.

## 4. 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 and 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, on the contrary, 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 performances were 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 been addressed so far 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 interindividual variability observed. Yet, 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 neither 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 improvement was not observed in our conditions.

Consistent inter-individual difference in performances maintained within a visual task or across elemental and higher-order visual tasks could have a genetic basis. *Drosophila* flies from a population selected over several generations on the basis of their good learning abilities 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 abilities (Mery & 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 & 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 due to 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 & 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 & 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 & 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 aging (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 variations 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; Cabirol et al., 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 variations 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 retraced to inter-individual differences in the activity of olfactory neural circuits. In fruit flies, for instance, stable inter-individual variability can be found in an odour-preference assay, which translates 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., 2019). Similar arguments could apply to visual processing and its underlying visual circuits.

The question of whether learning abilities correlate 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 both 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 due to the difficulty of reproducing successful visual learning in the which would allow coupling with invasive recordings of neural activity (Avarguès-Weber & Mota, 2016). Yet, given the massive visual afferences to the mushroom bodies (Ehmer & Gronenberg, 2002; Paulk & Gronenberg, 2008) and to the central complex (Pfeiffer & 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; Vogt et al., 2016).

The fact that we observed a positive correlation of performances across an elemental task and a conceptual task in the visual modality suggests that a similar brain circuitry underlies both discriminations. An alternative explanation may be that differences in general visual processing abilities and attentional processes could have a major influence on the performance in both tasks. In humans and rodents, general intelligence has been linked to selective attention and working memory abilities (reviewed in Matzel & Kolata, 2010) which encompassed both the storage of information and the processing and integration of information (Baddeley, 2003; Jarrold & 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 performances in cognitive studies could thus contribute to the elucidation of the underlying mechanisms (Thornton & 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 & 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 & Dyer, 2008; Jeanson & 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 due to the energetic cost associated with cognition (Evans et al., 2017). Thus, the complex interplay between interindividual cognitive skill diversity, task allocation and colony fitness remains to be fully elucidated.

*Ethical statement*

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

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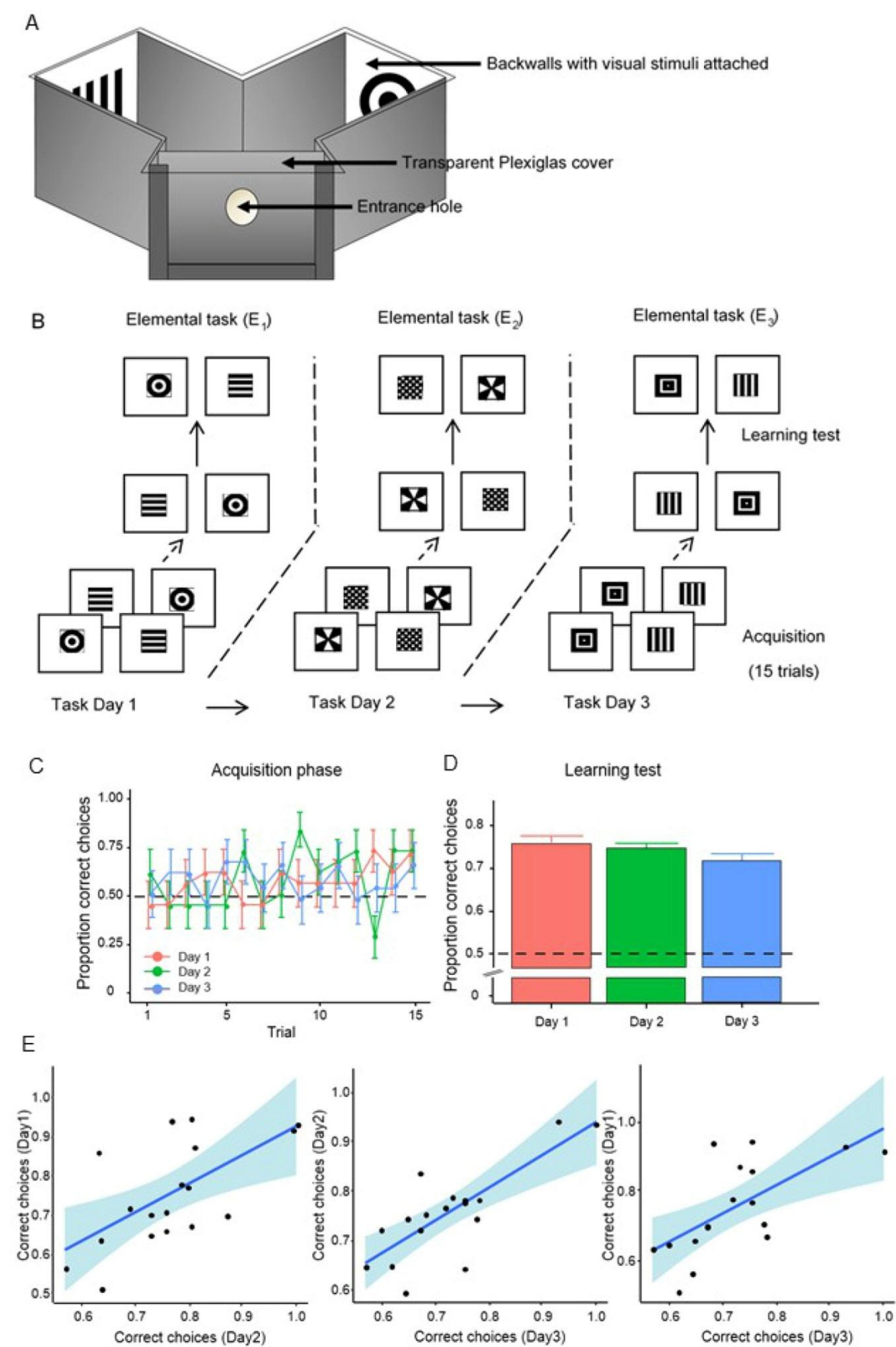
**Figures**

**Figure 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 presentation of one visual elemental learning task submitted to the bees. The visual pattern to discriminate varied between bees and between days**. B.** Acquisition curves expressed as proportion of correct choices ± SEM of forager bees confronted with three consecutive elemental visual tasks consisting of 15 trials over three days (Day 1, red curve; Day 2, green curve; Day 3, blue curve). Bees improved performance over the course of the training (GLMM, $n = 17$, *Trial*: $\chi^2 = 5.6$, $p = 0.02$). **C.** Choice accuracy expressed as proportion of correct choices ± SEM of forager bees in the non-reinforced learning tests following each training session. Performances were significantly higher than chance level (GLM, $n = 17$; Day 1: $Z = 6.17$, $p < 0.001$; Day 2: $Z = 8.79$, $p < 0.001$; Day 3: $Z = 7.85$, $p < 0.001$). **D**. Correlation between performances (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 while the blue shadow indicates the 95% confidence interval. Performances were correlated along the three days (Spearman correlation, Day 1 vs. Day 2: $r_S = 0.62$, $p = 0.009$, Day 2 vs. Day 3: $r_S = 0.66$, $p = 0.004$; Day 1 vs. Day 3: $r_S = 0.70$, $p = 0.002$).
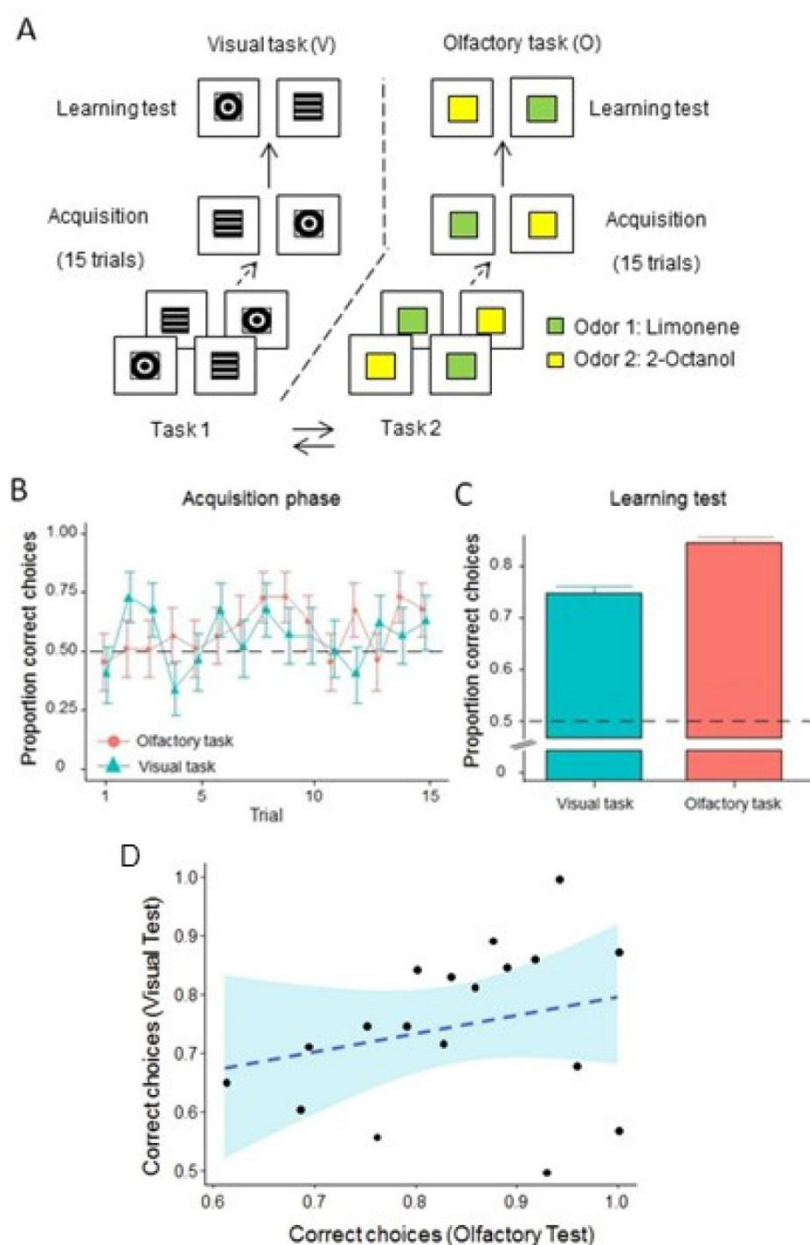
**Figure 2: Experiment 2: Comparison of performance in a visual and an olfactory elemental discrimination. A.** Schematic presentation of the tasks submitted to the bees. **B** Acquisition curves expressed as proportion of correct choices ± SEM of forager bees ($n = 18$) confronted with a visual task (V; red curve) and an olfactory task (O; blue curve) consisting of 15 trials. No significant improvement of performance could be detected over trials (GLMM, *Trial*: $\chi^2 = 1.7$, $p = 0.19$). **C.** Choice accuracy expressed as proportion of correct choices ± SEM of forager bees confronted with the V and the O tasks in the non-reinforced learning test. Bees' performance was above chance level for both tasks (GLM, Vision: $Z = 6.54$, $p < 0.001$; Olfaction: $Z = 8.24$, $p < 0.001$). **D**. Correlation between performances

(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 while the blue shadow indicates the 95% confidence interval. No correlation between individual performances was observed (Spearman correlation, $r_S = 0.31$, $p = 0.21$).
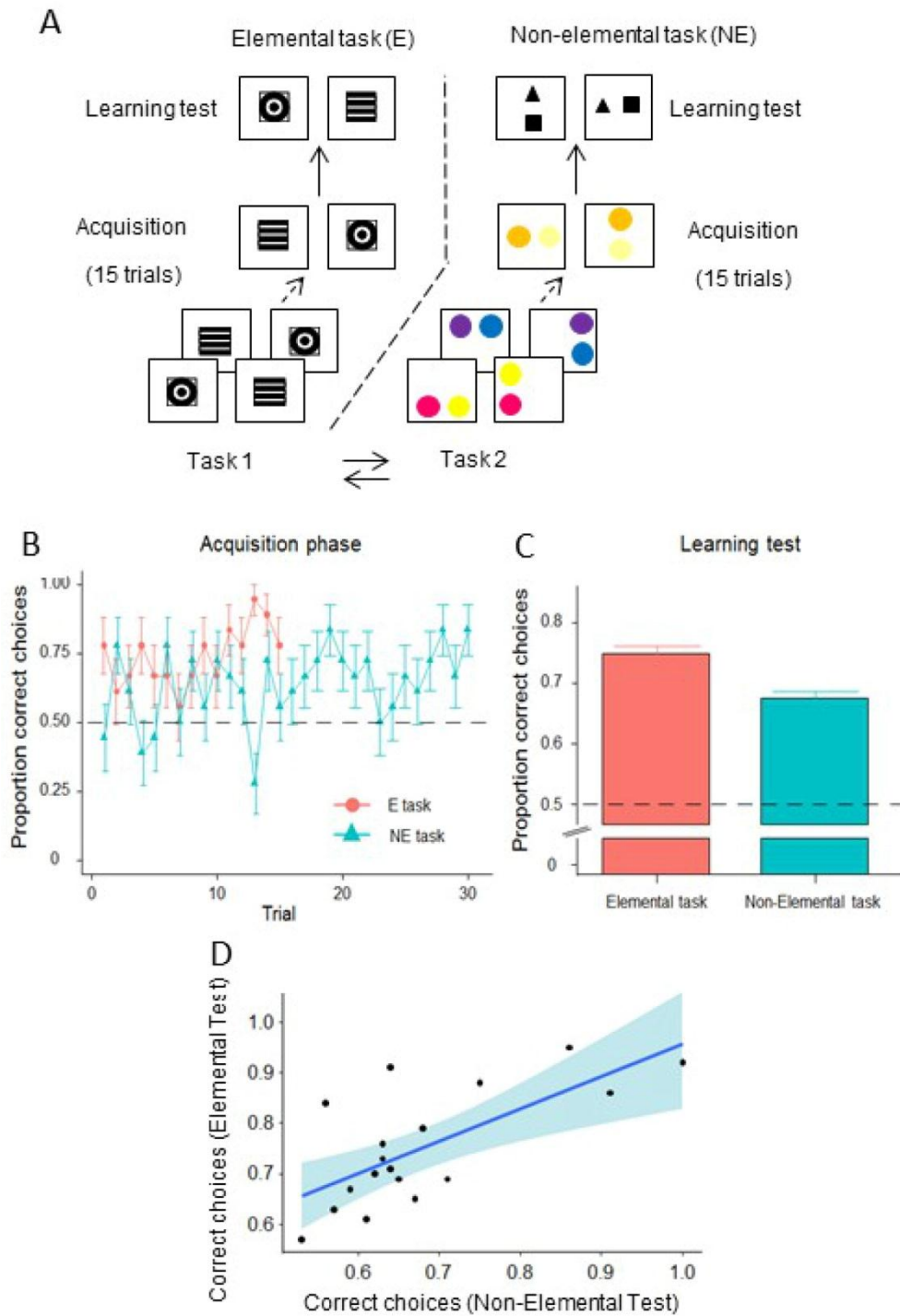
**Figure 3: Experiment 3: Comparison of performance in an Elemental and a Non-Elemental visual task. A.** Schematic presentation of the visual learning tasks submitted to the bees. **B** Acquisition curves expressed as proportion of correct choices ± SEM of forager bees (n = 18) confronted with an Elemental task (E; red curve) consisting of 15 trials and a Non-Elemental task (NE; blue curve) consisting of 30 trials. There was a significant improvement

in performance over trial repetition (GLMM, $n = 18$, *Trial*: $\chi^2 = 9.0$, $p = 0.003$). **C.** Choice accuracy expressed as proportion of correct choices $\pm$ SEM of forager bees confronted with the E and the NE tasks in the non-reinforced learning test. Bees' performance was significantly above chance level in both tasks (GLM, $n = 18$, Elemental: $Z = 7.18$, $p < 0.001$; Non-Elemental: $Z = 4.73$, $p < 0.001$). **D**. Correlation between performances (proportion of correct choices) of individual bees in the Elemental (E) and Non-Elemental (NE) 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 while the blue shadow indicates the 95% confidence interval.
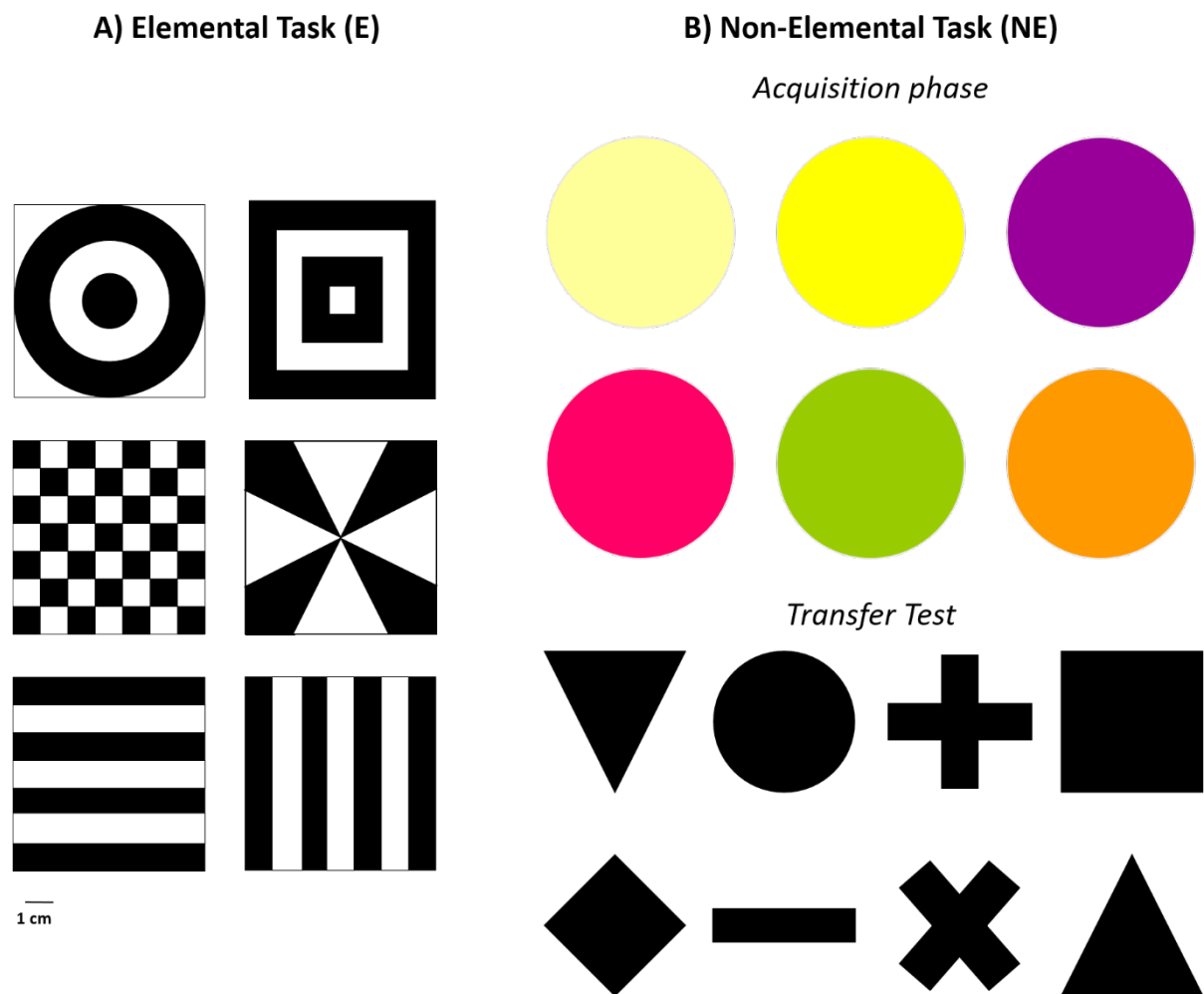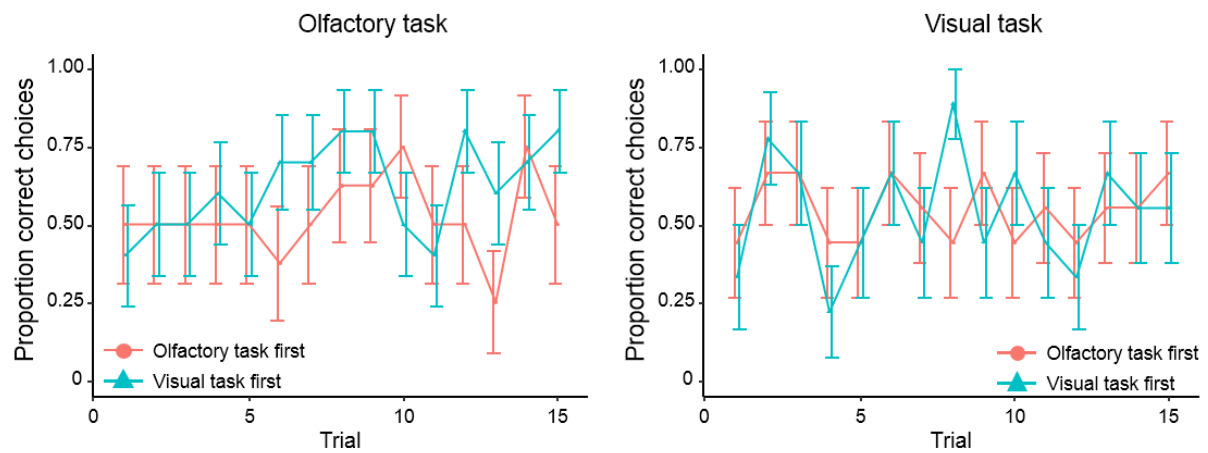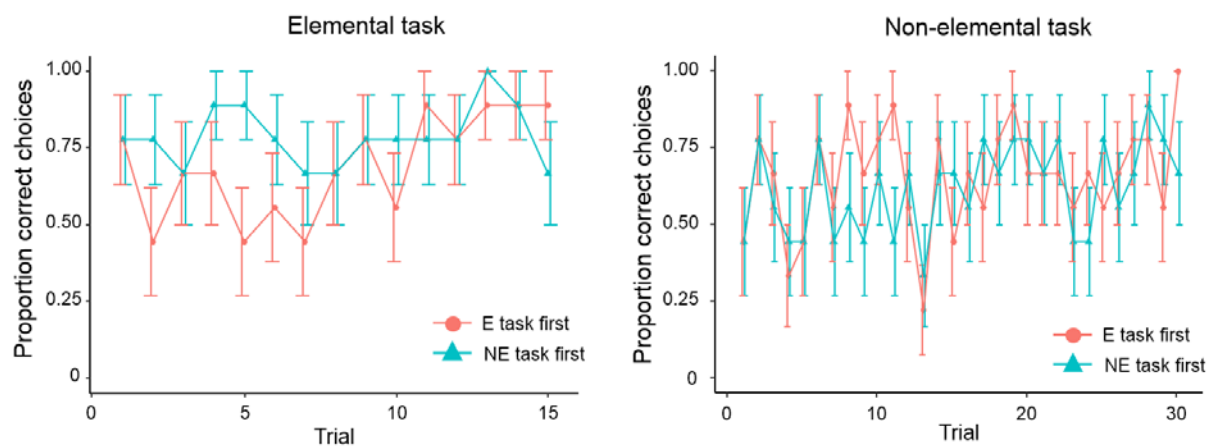
## A) Elemental Task (E)

## B) Non-Elemental Task (NE)

*Acquisition phase*

*Transfer Test*



1 cm

### Fig. S1. Stimuli used in our visual-learning experiments

**A)** In the Elemental discrimination (Experiments 1, 2 and 3), bees had to differentiate between a pair of stimuli randomly chosen between the six alternatives available: one stimulus was rewarded with sucrose solution (CS+) while the other was punished with quinine solution (CS-). After training, a learning test using the same stimuli that were trained but in the absence of reinforcement, was performed. **B)** In the Non-Elemental conceptual discrimination, all six alternative colour stimuli were used during the acquisition phase for all bees, which had to learn to choose a specific spatial relationship vs. a different spatial relationship (above/left vs. left/right). Each possible pair of stimuli was used to build the spatial relationships that had to be discriminated. Stimuli varied randomly from one trial to the other in order to vary stimuli appearance while keeping constant the spatial relations. After training, a non-reinforced transfer test was conducted with a pair of achromatic stimuli randomly chosen for each individual among the eight alternatives.

Experiment 2: Acquisition curves expressed as the proportion of correct choices ± SEM across trials of forager bees (n = 18) confronted to the Olfactory Elemental task (left panel) or the Visual Elemental task (right panel) depending on this task being performed at first or after the other task.



Experiment 3: Acquisition curves expressed as the proportion of correct choices ± SEM across trials of forager bees (n = 18) confronted to the Elemental task (left panel) or the Non-Elemental task (right panel) depending on this task being performed at first or after the other task.

**Fig. S2. Representation of the tasks sequence effect**