# Bumblebees flexibly adjust learning and decision strategies to sensory information content in a foraging task

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When animals and humans make decisions based on their sensory input, they often rely on multiple cues at once. These provide complementary sources of information, which can help overcome ambiguity and noise, and increase the accuracy of decisions. While most studies have focused on the benefits of multimodal and within-modal integration for learning and decision making, their costs have received less attention. Processing multiple inputs, and learning and memorizing them requires more neural resources than single cues, and might also require more time. When a decision can be made with high accuracy based on a single cue alone, adhering and memorizing multiple ones simultaneously might thus concur higher costs than benefits, and not be an optimal decision-making strategy. In this study, we tested if insects trade-off the costs and benefits of learning multiple cues in a foraging task, using the buff-tailed bumblebee *Bombus terrestris*. To maximize comparability between cues, we presented combinations of visual-only features, such as are found on natural flowers: colours of varying discriminability, paired with shapes or patterns. We found that the bees relied exclusively on colours when these were easy to discriminate, and did not learn pattern or shape features presented simultaneously. With harder to discriminate colours, the bees learned both colour and shape or pattern features. Our results demonstrate that bumblebees flexibly adjust their learning strategies when presented with visual features of varying discriminability, to balance the costs and benefits of multi-cue learning. Our analysis of the learning rates of the bees with multi- and single attribute stimuli suggests that blocking could serve as a mechanism to implement this strategy switch. These results shed light on trade-offs in learning and decision making with multiple cues, and can directly be compared to studies in other insects, animals and humans.

Keywords: decision making, insect, multi-modal, foraging, trade-off, learning

## Introduction

When animals and humans make decisions based on their sensory input, they often rely on multiple simultaneous cues, both within and across modalities [1-5]. We can, for example, hear and see an approaching car, and can tell a ripe from an unripe strawberry by its colour and size, scent and touch. Such complementary sources of information can help overcome ambiguity when choosing between multiple options, or noise associated with one or multiple of the sensory cues [6-10], and thereby increase the accuracy of decisions in diverse species ranging from primates [11-14] to insects [15-20]. While the benefits of multimodal and within-modal integration of cues for learning and decision making are well demonstrated, the trade-offs between these benefits and potential costs have received less attention. Processing multiple inputs [21, 22], and even more so learning and memorizing them might be more costly in terms of time [23] (but see also [15, 17]), and can further lead to conflicts between the sensory inputs [24-26]. Thus, learning and integrating multiple cues might only be beneficial for decision making, when the added accuracy outweighs the costs, for example when cues are hard to detect or noisy [27-29]. When a decision can be made with high accuracy based on a single cue, integrating multiple cues simultaneously might not be an optimal decision-making strategy [22, 30].

In this study, we tested if insects trade-off between costs and benefits for learning multiple cues in a choice task, using the buff-tailed bumblebee, *Bombus terrestris,* as a model. Insects make an ideal model system for these investigations, as they are able to take fast and accurate decisions, but have to do so with very limited processing power [31, 32]. Much of our understanding of multimodal decision-making in insects is based on visual and olfactory cues in a foraging context, for example of pollinating insects selecting and memorising rewarded flowers with visual and olfactory attributes [32, 33]. Integrating cues in this context has been demonstrated to increase decision accuracy [15, 16, 18], reduce response time [15] and overcome ambiguity caused by noisy stimuli [19]. To avoid context dependent modulation as generated by olfactory cues [33, 34] and maximize comparability between cues, we presented combinations of visual-only features, as they are found on real flowers that bees visit: colours, shapes and patterns [35, 36]. We presented cue combinations which varied in the discriminability in one of the visual attributes to assess the strategies bees followed in these learning and decision tasks of varying difficulty levels.

## Materials and Methods

### Animals

Colonies of *Bombus terrestris* were obtained from commercial breeders (Biobest, Westerlo, Belgium). The colonies were housed in a two-chamber wooden box (28 cm×16 cm×11 cm), which provided one chamber for nest-building and one for feeding. Before experiments started, the bees were fed ad libitum with APIinvert (Südzucker, Germany), a 70% sucrose solution, and with pollen grains (Bio-Blütenpollen, Naturwaren-Niederrhein, Germany).

### Setup and Experimental Procedure

All experiments were conducted in a flight arena as previously described [37]. In short, the bee's nesting boxes were connected to the arena (120 cm × 100 cm × 35 cm) via an acrylic tube. The floor of the arena was covered in grey cardboard (Mi-Taintes #122, Canson SAS, Annonay Cedex, France). The same cardboard was used for the training feeders (see *Stimuli*). The experiments were performed on several different bumblebee colonies per experimental condition (see *Experimental Procedures*), to ensure that the observed effects were robust against individual colony variation [38].

### Stimuli

All artificial flowers were constructed from cardboard cut-outs, mounted on 10 mm high, dark grey platforms of 40 mm diameter. The grey training stimuli were made from same cardboard as the floor of the arena. For testing, yellow, orange, teal and blue cardboard was used (Tinted drawing paper #12, #19, #32 and #31, respectively; Buntpapierfabrik Ludwig Bähr, Kassel, Germany). The relative reflectance spectra for all stimuli are show in Fig. S1A. To test the category *shape*, squares of 40 mm side length were used as neutral stimuli. For testing, circles of 40 mm diameter and five-armed star shapes with the same overall area were used for comparison (see Fig. 1E, insets). As patterns, we printed a circle-pattern consisting of two concentric black rings, and a radial pattern consisting of eight radially arranged stripes, each of 2.1 mm width onto square-shaped cardboard stimuli (see Fig. 1C, insets).

We performed two sets of experiments, in which the categories shape-colour and pattern-colour were shown to separate groups of bumblebees. Both categories used the same pairs of colours. Two of which were *distant* in bumblebee colour space (Fig.S1), and thus should be easily distinguishable: yellow-blue, orange-blue; while two were more *close*, and thus harder to distinguish: yellow-orange, teal-blue, either in combination with shapes (circle – star) or patterns (circle – radial). Stimuli with neutral colour were grey, and had a square shape in the pattern category, and star – circle shape in the shape category. Each bumblebee was only presented with one combination of colour and pattern or colour and shape, including the respective conflict and control tests (see *Experimental Procedure*).

### Spectral measurements and colour vision modelling

The relative reflectance spectra of the colour carton from which the stimuli were constructed, as well as that of the grey background on which the stimuli were presented (Fig. S1A), were measured using a JAZ spectrometer equipped with a pulsed Xenon light source (Ocean Optics, Dunedin, FL, United States). The spectrometer was calibrated against a white standard (WS-1-SL, Ocean Optics). Colour loci in the colour triangle were calculated using the method described by [39] with the bumblebee's photoreceptor spectral sensitivities used from [40] (Fig. S1B).

**Experimental Procedure**

Foragers of *B. terrestris* were selected for experiments by scoring their foraging activity in the flight arena on grey training flowers supplied with 30% sucrose solution. For individual identification, bees were marked on the thorax with number tags. During experiments, only a single bee was allowed to enter the arena. Before being presented with the test stimuli, five grey training stimuli with 10 µl of 50 % sugar solution in the centre were positioned in the arena in a random arrangement. The bees performed three to five foraging bouts, separated by the forager returning to the colony, on the grey flowers. Each stimulus was refilled immediately after the bumblebee departed.

*Conflict experiments*

The experiment began with a preference test (Fig. 1B), during which the bee was presented with a combination of colour and shape or pattern (for example a yellow star and an orange circle, or a teal square with a concentric patterns and a blue square with a radial pattern). Five instances of each stimulus pair were presented in the arena, each with 10 µl of water, to not pair either of them with a reward. The first 10 choices of each bee were recorded. Subsequently, the bee was allowed to feed ad libitum from a grey feeder and returned to the colony.

The colour-pattern or colour-shape combination of the pair that the bee preferred less was then chosen as the rewarded stimulus for training (Fig. 1B). If both stimulus pairs were preferred equally, the stimulus that had been tested on less individuals was selected as the rewarded one. All instances of the rewarded stimulus were supplied with 10 µl of a 1M sucrose solution, while the un-rewarded pair was supplied with the same volume of water. During training, the stimuli were re-supplied immediately after the bee approached the next stimulus. Training continued until a bee had made 30 correct choices, and as many incorrect choices as it took her to reach the default value. When the bee returned to the colony during training, the order of the stimuli in the arena was re-arranged to prevent spatial learning. After training, sucrose solution was provided ad libitum on a grey feeder, so the bee would return to the colony.

When the bee subsequently returned to the foraging arena, a conflict test was performed (Fig. 1B). It was conducted in the same way as the preference test, but the features of the stimuli were swapped: the rewarded colour was combined with the unrewarded pattern / shape and vice versa (for example,instead of a yellow star and an orange circle, the bee was tested with a yellow circle and an orange star).

Afterwards, a second training with the original stimuli was conducted, until the bee again reached thirty correct choices (Fig. 1B, Fig. S3A,C).

Subsequently, a final test was conducted, which assessed the preference for the attribute the bee did not choose preferentially in the conflict test (Fig. 1B; for example, if she chose colour over shape in the conflict test, in the final test the bee were presented with grey shapes. If she chose shape over colour, the bee was presented with square-shaped colour stimuli). This test was conducted in the same way as the preference test.

*Single attribute experiment*

This experiment was performed as above, but with stimuli that comprised only one visual attribute (distant colour: orange-blue, close colour: blue-teal, pattern or shape on grey background). The experiment began with a preference test comprised of ten unrewarded

choices, followed by a training until thirty correct choices were performed, and an unrewarded, in which the stimulus pair, which was presented for training, was shown unaltered.

**Number of bees and colonies per experiment**

For the colour and pattern conflict experiment, bumblebee foragers of four colonies were trained and tested by two different experimenters (25 individuals in the yellow-blue, and 20 each in the orange-blue, teal-blue, and yellow-orange conditions), while four colonies were tested by three different experimenters for the colour and shape experiment (24 individuals in the yellow-blue, and 15 each in the orange-blue, teal-blue, and yellow-orange conditions). Two additional colonies were used to test 10 foragers in each condition with single attribute stimuli by one experimenter.

**Bayesian decision model**

We constructed a Bayesian decision model [41, 42], estimating the choice rates of bees for colour in the conflict test as posterior probabilities p(H|O), which are generated by the likelihood of the observations given the hypothesis p(O|H), and the prior probability of the hypothesis p(H), which entails the animals' prior knowledge about the probability of a reward on a given stimulus.

$$p(H \mid \mathrm{O}) = \frac{p(O \mid \mathrm{H}) \times p(H)}{p(O)}$$

The likelihood of the observations given the hypothesis p(O|H) was 0.5 in all experiments, since we presented 2 choices of stimuli in equal numbers. The term p(O) provides a normalising term, to retain the resulting probability within the bounds of [0,1], calculated as:

$$p(O) = \int p(O \mid \mathrm{H}) \times p(H)\, dH$$

Since the decision model was designed to predict choices in the conflict situation, the priors needed to reflect both prior probability of colour $p(H|C_1)$ and pattern or shape $p(H|C_2)$, respectively. We therefore generated a combined prior, with a relative weighting (weighting factor w) between the two terms [12, 43, 44]:

$$p(H) = \frac{p(H \mid \mathrm{C}_1)^w \times p(H \mid \mathrm{C}_2)^{1-w}}{\int p(H \mid \mathrm{C}_1)^w \times p(H \mid \mathrm{C}_2)^{1-w}\, d(H)}$$

The combined prior also included a normalising term, which integrates all possible prior probabilities for H. The full model thus reads:

$$p(H \mid \mathrm{O}) = \frac{p(O \mid \mathrm{H}) \times p(H \mid \mathrm{C}_1)^w \times p(H \mid \mathrm{C}_2)^{1-w}}{\int p(O \mid \mathrm{H}) \times p(H \mid \mathrm{C}_1)^w \times p(H \mid \mathrm{C}_2)^{1-w}\, d(H)}$$

We implemented the model in discrete terms in Matlab 2022a, and fitted the resulting posterior probabilities to the observed choices of the animals in the conflict test, to obtain the weighting factor for each of the four conditions. As priors, we assigned the fraction of choices for the rewarded colour or pattern/ shape obtained in the individual attribute experiments, in which the animals were only trained two a single attribute (distant or close colour, pattern, shape), instead of a colour combination (Fig. 3A). Since the single attribute data was obtained from a different set of bumblebees than those which performed the conflict experiments, we used a permutation approach: every choice data point for the colour attribute was combined with

every point for the pattern or shape attribute to calculate the combined prior, resulting in a 10x10 prior matrix (as 10 bees were tested in both single attribute colour and pattern or shape tests). From the resulting 100 posterior probabilities, we randomly selected a subset matched to the number of observed choices in the respective conflict conditions (15 or 20). For these, a weighting factor was fitted, using a sum of mean square error between the posterior probabilities and observed choice frequencies (using fmincon with bounds at 0 and 1 and a maximum of 1000000 iterations). This procedure was repeated 10000 times for different subsets, to arrive at the same number of estimates for the weighting factor for each of the four conditions (Fig. 3C). Posterior probabilities were calculated for the mean of the weighting factor distribution, using the full 10x10 posterior matrix (Fig. 3B), for visual inspection of the goodness of fit.

**Data analysis**

To assess learning progress, the fraction of correct choices was calculated for each block of five correct choices, and as many incorrect choices as were made to arrive at the default value (Fig. 1C,D). This assured equal possibility for forming a positive association to the stimulus across bees. For all unrewarded preference tests, the fraction of correct choices was calculated. Statistical analysis was performed using with R v4.1.2 (R Foundation for Statistical Computing).

To analyse whether the preference for colour in the conflict experiment differed from random choice (50:50, since all stimuli were presented in pairs), a generalised linear mixed-effects model with the following formula was used:

$$correct\ choice \sim colour\ +\ (1 \mid animalID)$$

These estimated the fixed-effect of the stimulus colour on the relative probability of choosing the stimulus – scored for each individual as 0 or 1, accounting for individual biases.

To analyse whether the preference for pattern or shape, if they were not preferred in the conflict experiment, differed from random choice (50:50, since all stimuli were presented in pairs) in the final test, a generalised linear mixed-effects model with the following formula was used:

$$correct\ choice \sim pattern/shape\ +\ (1 \mid animalID)$$

These estimated the fixed-effect of the stimulus pattern or shape on the relative probability of choosing the stimulus – scored for each individual as 0 or 1, accounting for individual biases.

To compare the choice fraction for colour in the conflict test, and the non-preferred attribute in the final test for patterns and shapes, we used a generalised linear model of the family “quasibinomial”:

$$choice \sim\ pattern/shape \times colour$$

To assess if the fraction of choices of naïve bees for colour, shape or pattern, and the effects of their interaction, we used a generalised linear model of the family “quasibinomial”:

$$choice \sim pattern\ \times \mathrm{colour}$$

## Results

To test which attributes bumblebees retained from flowers with multiple visual cues simultaneously, we used an experimental design in which the bees first learned to associate a combination of colour and pattern (or shape) with a sugar reward, and a second combination with a drop of water (Fig. 1B). We then set the two attributes in conflict, by swapping them across the stimulus pair (as in [45, 46]), to test which attribute the bees relied on more strongly to make their decisions. Subsequently, bees were trained on the original cue combination again, to then test whether they learned the attribute they did not choose in the first test. To assess if the bees used the same learning and decision strategy in different contexts, we designed two colour categories which were combined with patterns and shapes: *distant* colours and *close* colours (Fig. 1C), which were easier and harder to discriminate perceptually, respectively (Fig. S1).

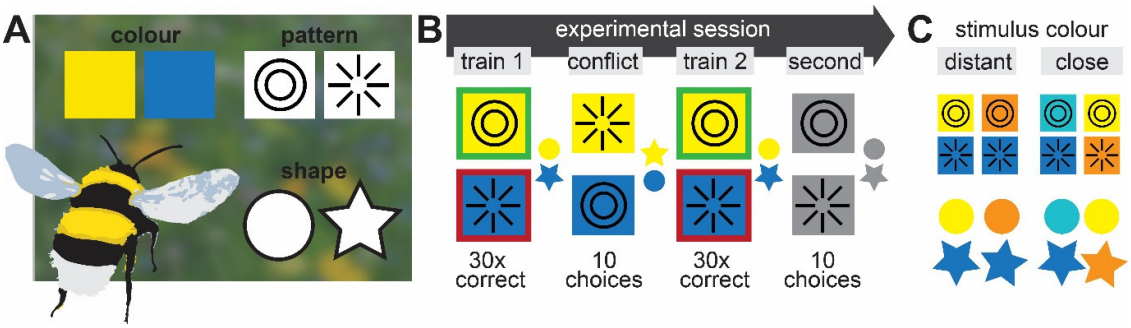


**Fig. 1 The importance of colour, pattern and shape for pollinator flower selection.**
**A** Flowers provide a combination of different visual cues used by insect visitors for detection and discrimination; most prominently colour, patterns and shapes. **B** To assess which of these features insects attend to and learn, we presented bumblebees (*Bombus terrestris*) with a combination of cues: colour and patterns, or colour and shape. The bees were trained differentially to a combination of one colour and one pattern (or shape), and then had to choose between either the colour or pattern (shape) feature in a conflict test. Subsequently, the animals' training was reinforced, and a second test assessed whether they learned the feature they did not preferentially choose in the conflict test. **C** Each bee was presented with a stimulus pair out of four colour combinations for either patterns or shapes. Two of the colour pairs were distant in sensory perception, while the other two were close (see Fig. S1).

Before the training, the naïve preferences of all bees for the pair of stimuli they were trained on was assessed (Fig. S2A,B). They were then trained on the stimulus which they preferred less, to ensure that training did not reinforce innate preferences. In both the pattern and shape condition, bees naively preferred blue over orange and teal over blue, irrespective of the pattern or shape the colours were combined with (Fig. S2E,F). Across colours, no significant preference for either pattern or shape emerged (Fig. S2C,D). These innate preferences also held up when stimuli were tested as single attributes (Fig. S2G).

### Bees always chose colours over other flower features when in conflict

When presented with a conflicting combination of stimuli, bees chose colour significantly more often than the shape or pattern attributes (Fig. 2A,B). This is similar to previous experiments with honeybees, which always chose the colour attribute over either shapes or patterns combined with colour [45, 47]. However, in our experiments, the fraction of choices for colour depended on the colour condition: while both pattern and shape-trained bees chose colour over the other attribute nearly exclusively in the *distant* colour pairs, the median choice rates for colour were only between 60-80% in the *close* colour pairs. Moreover, the individual variation was much lower in the distant colours pairs, while it ranged from bees choosing pattern or shape preferentially, to those choosing colour at up to 90% in the close colour pairs.

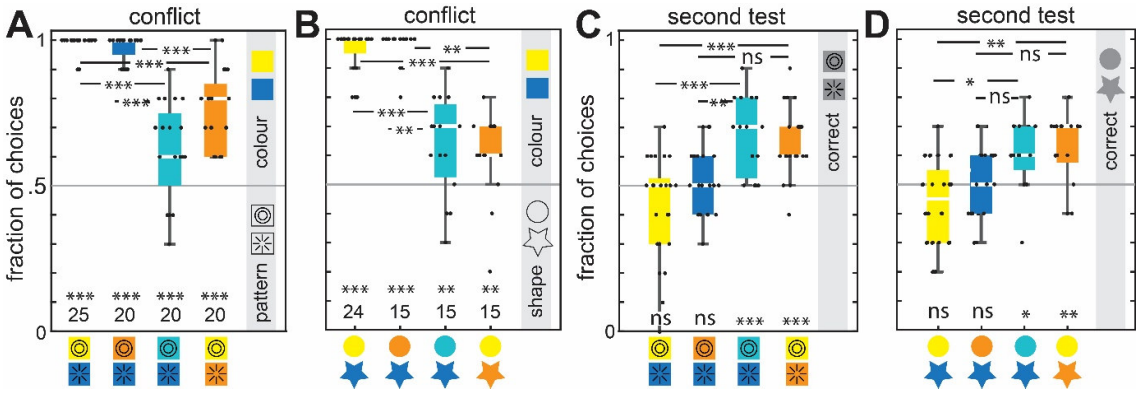


**Fig. 2 Choices for flower attributes when set into conflict.**
**A,B** Fraction of choices for the colour (above 0.5) or the pattern or shape (below 0.5) attribute in the conflict test, when the learned attributes were swapped across the stimulus pair, compared to the training. **C,D** Fraction of choices for the second attribute, not chosen in the conflict test (which in majority was the pattern, or shape, respectively). For the results of animals that chose pattern or shape first, see Fig. S3B,D. Number of bees tested is indicated in A and B, for pattern and shape combinations, respectively. The results of a generalised linear mixed-effects model with a binomial family via the logit link, comparing the choice distributions to random choice at 0.5 are shown at the bottom of each graph. Comparisons across groups were performed with the same model, and are depicted were statistically significant. All statistical results are abbreviated as * < 0.05, ** < 0.01, *** < 0.001, *n.s.* not significant.

### Bees learned the pattern and shape attributes only with close colour pairs

Since most of the bees chose colour over the pattern or shape attributes in all cue combinations, we asked whether bees indeed learned both attributes of the flowers, or only the colour feature. Unlike honeybees in previous studies, which always learned the second attribute in combination training experiments [45, 47], bumblebees provided with *distant* colour pairs chose patterns or shapes at random (Fig. 2C,D), suggesting they only learned the colour, but not the pattern or shape attributes. Bees trained on the *close* colour pairs, however, chose the trained pattern or shape attribute significantly above random choice (Fig. 2C,D). The few bees that did prefer the pattern or shape attribute in the conflict tests also chose the colour attributes above random choice (Fig. S2B,D), demonstrating that they learned both attributes of the combined stimuli with close colour pairs.

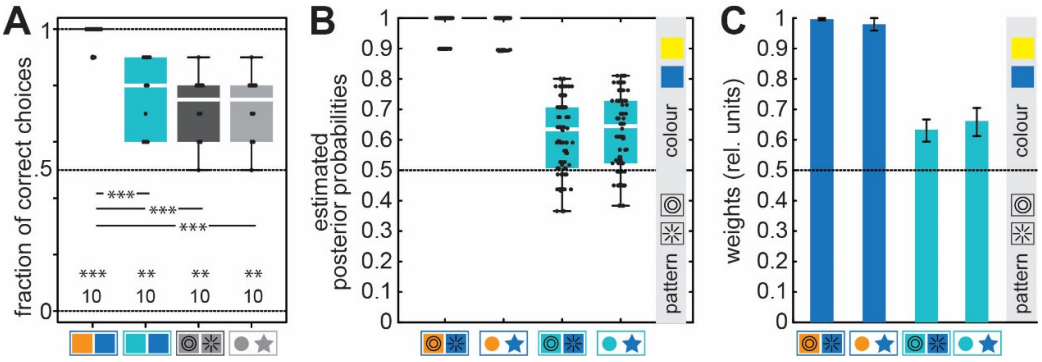


**Fig. 3 Single choices and Bayesian model with decision weights.**
**A** Fraction of choices after training individual attributes (distant: orange-blue and close: blue-teal colours, patterns and shapes on grey background). The statistical results were obtained with generalised linear mixed-effects models with a binomial logit link. They compare the choice fractions to random choice at 0.5, depicted at the bottom of each graph, and across conditions. All results are

abbreviated as * < 0.05, ** < 0.01, *** < 0.001. **B** Results of a Bayesian decision model (see methods), estimating the choice distributions in the conflict condition as posterior probabilities, using the test results for individual attributes (**A**) as priors. The priors for colour and pattern or shape, respectively, were combined with a weighting factor, which was estimated by fitting the estimated posterior probabilities to the observed choices (Fig. 2A,B). **C** Estimated weighting factors, resulting from 10000 iterations of the model (depicted are mean values and the interquartile range).

### Bees changed their decision strategy between distant and close colour pairs

We next assessed the strategy bees used to choose between cues in the conflict test for the distant and close colour conditions, in particular with respect to the weights they assigned to colour and patterns or shapes, respectively. To this aim, we designed a Bayesian decision model, which included the bees' reliance on colour, pattern and shape cues, modelled as priors, which were weighted relative to each other (see Methods). In order to obtain priors for the distant and close colour conditions, as well as patterns and shapes, we trained a new set of bees to individual features, instead of cue combinations: one distant (orange-blue) and one close (teal-blue) colour pair, as well as patterns and shapes on grey background, using the same methods as for the cue combination experiment. We then tested their choices for the trained attributes (Fig. 3A). For both patterns and shapes, the resulting fractions of correct choices were not significantly different from the fraction of choices for pattern and shapes after the combined attribute training (second test, Fig. 2C,D). Qualitatively, the same holds for the fraction of choices for close colours in the second test (Fig. S3B,D), though the number of individuals was not sufficient for a statistical assessment. This comparison demonstrates that priors derived from individual attribute training can serve as priors for the combined cue experiment.

Using these priors, we fitted a decision model, to estimate the bee's decisions for colour in the conflict situation (Fig. 3B), in which the prior probabilities for colour and shape or pattern were linearly combined and weighted. A weighting factor of 1 indicated that the bees only relied on their prior for colour, a factor of 0.5 that they relied on colour and patterns or shapes equally, and a factor below 0.5 that they relied more strongly on patterns or shapes than colour.
The resulting weights for the four tested conditions (distant and close colours for both patterns and shapes) support the intuitive interpretation of the conflict test results (Fig. 2A,B): the bees relied (almost) exclusively on colour in the distant colour conditions (Fig. 3C), while they relied on both colour and pattern or shape attributes in the close colour condition, with a stronger weight on colour (Fig. 3C).

### Different learning rates for distant and close colour conditions suggest that blocking could be underlying the switch in decision strategies.

In search for a mechanistic explanation of this switch in decision strategies, we analysed the learning rates of the bees in the distant and close colour conditions. With combined cues, the bees required fewer trials to reach a high fraction of correct choices for the distant colour pairs than the close ones (Fig. 4A,B). The fraction of correct choices was significantly higher already in the first learning block and remained higher throughout all learning trials. Across combined cue and single cue learning of distant colours, the final learning outcome, quantified as the fraction of correct choices in the last learning block, was not significantly different (Fig. 4D).

The combined cue learning rates of the close colour pairs were distinctly slower than those of the distant colour pairs (Fig. 4A,B). One might argue this was the case because the bees did learn two attributes, colour and pattern or shape (Fig. 2C,D), and therefore required more learning trials. However, the learning rates of cue combinations with close colours were not slower than those for the respective single attributes (Fig. 4C,D). This suggests that multi-cue

learning did not limit the learning rate, but that the slow learning rates for the single attributed in these conditions were responsible for the comparably slow rates. Indeed, the learning curves with single attributes used in the close colour conditions were even flatter than their multi-cue counterparts, and reached a significantly lower fraction of correct choices in the last learning block for the pattern condition (Fig. 4D). Thus, multi-cue learning in these conditions improved learning rates, and the final learning outcome.

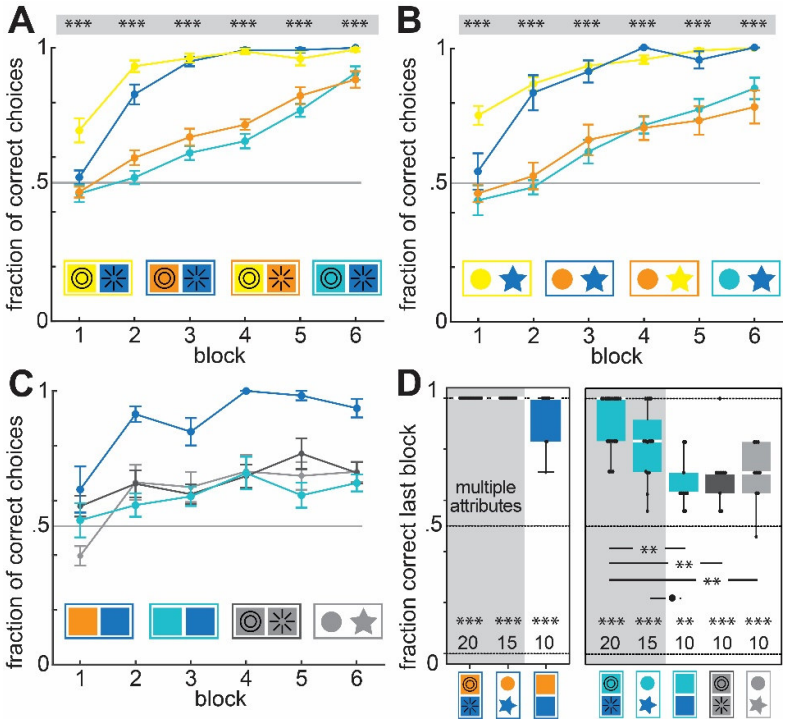


**Fig. 4 Learning performance with multi- and single attribute stimuli.**
**A,B** Learning rates of the bumblebees for all combined stimuli, as well as **C** single attribute training. **D** Learning performance in the last training block, compared across multi – and single attribute learning. All statistical results were obtained with generalised linear mixed-effects models with a binomial logit link, in A,B comparing the choice fractions for each block of animals in the close and distant colour conditions, in D comparing the choice fractions to random choice at 0.5, depicted at the bottom of each graph. The same model was used to compare across groups, the results of which are depicted were statistically significant. All statistical results are abbreviated as * < 0.05, ** < 0.01, *** < 0.001.

The difference in learning rates for distant and close colours, as well as patterns and shapes, were likely linked to the discriminability of the features, and thus the complexity of the learning task. They mirrored results from previous studies which showed slower learning rates for close than distant colours [17, 48]. The different learning rates could provide a mechanism for the change in learning and decision strategy between the two conditions: the fast colour learning in the distant condition could block the memory formation for additional features of the same target. It has been shown in numerous invertebrates and vertebrates that such blocking occurs when different visual features, or visual and olfactory features, are presented sequentially in reference to the same target [49-52]. While the two cues were presented simultaneously in this experiment, the rapid learning of the distant colours might nevertheless have acted in a similar fashion to sequential presentation to block any further attribute learning. In the close colour condition, learning of pattern and shape features likely occurred simultaneous with colour learning, as the learning rates were highly similar.

## Discussion

In this study we investigated how an insect trades off the costs and benefits of decision-making by multiple cues in a foraging task. We found that the buff-tailed bumblebee *B. terrestris* flexibly adjusted their learning and decision strategies when presented with visual features of varying discriminability, to balance decision accuracy and learning efficiency.

### Cue hierarchy in multimodal decision making

In previous studies with combined attributes [45, 47], honeybees learned both colour and shape or pattern attributes (though see [53] for various learning strategies with combined cues), while in our experiments, they only learned both when the two colours to be distinguished were perceptually similar. Thus, while honeybees and bumblebees are clearly capable of learning and integrating multiple attributes of an object [54], and even generalise object *gestalt* across modalities [55], we here demonstrate that bumblebees do not automatically learn all object features, but only do so in certain contexts.

As in many other cases of decision making in vertebrates [25, 56] and insects [33, 57], and specifically in a flower recognition context [46, 58-61], we observed a clear hierarchy of the cues the bumblebees relied on for their decision: they primarily used colours over patterns and shapes, in all conditions. Our results were highly robust, holding up qualitatively and quantitatively across multiple bumblebee colonies and different experimenters, and were quantitatively similar across pattern and shape stimuli, even though these likely activate pattern and shape recognition circuits quite differently [62-66], as they differed in edge contrasts and spatial extents .

Not only was the observed hierarchy very robust, but it was also similar to that of honeybees in a comparable task with combined visual attributes. Across studies, honeybees preferably relied on colour, when recalling memorised combinations of colour, shapes or patterns [45, 47]. When cues are combined additively for decision making, the overwhelming majority of studies suggests that the more reliable, or less noisy, cues, obtains more weight [3, 12, 14, 67-69]. In our experiment it seems intuitive that colours represented the more reliable cue, since they are easier to detect from a distance than patterns and shapes [70-72], which require high resolution vision and are likely used at a more close-range stage of flower interactions [37, 73]. Moreover, under natural conditions, patterns and shapes suffer more readily from obstruction by foliage than flower colours.

### A switch in decision strategy trades off between efficiency and accuracy

Combining complementary information sources about an object is only one of two possible integration strategies – the other is a winner-takes it all approach, where the more reliable cue is selected to rely on [43, 74]. Our results suggest that the bees switch between strategies: from an additive combination of information in the close colour condition, to a winner-takes all strategy in the distant colour condition (Fig. 3C). At an individual level, honeybees and bumblebees have been shown to trade off foraging speed for accuracy, though these were individual traits, not a switch in strategy across the population [48, 75-78].

We observed a general strategy, across all tested individuals, from an additive to a winner-takes all approach with stimulus context, and specifically, the discriminability of one of the cues. At first glance, this might be puzzling, as one might assume that more information about a target is always better, and thus integrating complementary sources of information is optimal [7, 8]. But this does not take into account time as a factor. The bees learned the distant colour combination much faster than the close ones (Fig. 4C), which is in line with previous results on learning rates with perceptually similar and distant colours [17, 48]. Interestingly, in the

contexts with close colours, where the bees learned both attributes, the bees learned the two attributes equally fast, if not faster than when presented individually (Fig. 4A-C). This might be due to attentional cueing [79], or valence signalling [17, 18] by one of the cues, which are suggested to improve multi-cue learning rates compared to single cue ones [15, 17] (though see [23]).

Thus, with distant colours, the bees could arrive at a reliable decision strategy much quicker by relying only on distant colours. Indeed, accounting for time as an important factor for decisions, instead of only the available sensory information, can change the statistically optimal decision strategy [21, 22]. This suggests that also in insects, learning time, or efficiency, is an important factor in decision making. How efficiency is weighted relative to decision accuracy requires further tests, varying the perceptual discriminability and resulting decision accuracy of one of the cues relative to the other over a larger range, to find the point(s) at which the bees switch from a single cue to multi-cue learning and decision strategy.

**Blocking as a mechanism to switch learning and decision strategies**

Our data provides a possible explanation for a simple underlying mechanism for this switch in decision strategy, which directly ties to the differences in learning speed: blocking [80]. Blocking is a phenomenon typically described when animals, ranging from different invertebrates to vertebrates, learn multiple attributes of an object or a stimulus source sequentially [49, 51]. When one attribute is presented alone and learned, a second attribute which is presented simultaneously with the first one is not learned (as readily) any more. Blocking has been demonstrated in insects across modalities and in a variety of tasks [51, 81, 82], though the occurrence of the phenomenon can vary with the type of stimuli [83] and can be confounded by experimental designs [50, 84] .

In our experiments, the stimuli were not presented sequentially, as typically done when testing for blocking. But since the bees learned the distant colours much faster than shapes or patterns when presented individually (Fig. 4C), the effect might have been similar to a blocking paradigm: as the association of the reward and distant colour was already formed after a few trials, when pattern or shape associations were not yet formed, any further association of patterns or shapes with the reward was blocked, as if the combination of cues had been presented only after the initial colour training. Using blocking to enact the switch in decision strategies would be a very simple, yet effective mechanism, to trade off learning speed (as blocking only comes in effect when one cue is learned much faster than the other associated one) with decision accuracy. This keeps well with the general idea that the computationally limited insect brain enabled simple, yet effective and adaptive strategies to perform complex behaviour, with a limited set of neurons [31, 52, 85].

**Conclusion**

We found that the buff-tailed bumblebee *B. terrestris* flexibly adjusted their learning and decision strategies when presented with visual features of varying discriminability, to balance decision accuracy and learning efficiency. Our analysis of the bee's learning rates suggests that blocking during learning could implement this strategy switch. This opens the door for future investigations into the underlying neural control strategies, which will enable in-depth comparisons of context-dependent learning and decision strategies in insects with the current focus in vertebrates [6, 86].

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**Data Availability**

Source data for all behavioural experiments and spectral measurements:
https://figshare.com/s/c4c912de7dd7e24a9ec8

Custom-written analysis code: https://github.com/stoeckl-lab/Spaethe_et_al_2024_beeDecisions

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