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COGNITIVE NEUROSCIENCE

Bees flexibly adjust decision strategies to information content in a foraging task

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When making decisions, animals often rely on multiple cues simultaneously. These provide complementary sources of information, which can increase the accuracy of decisions. In this study, we tested the decision and learning strategies of insects faced with multiple cues in a foraging task, using the bumblebee *Bombus terrestris*. We presented combinations of visual-only features, as found in natural flowers: colors of varying discriminability, paired with shapes or patterns. We found that the bees relied exclusively on colors when these were easy to discriminate, and did not learn pattern or shape features simultaneously. With harder to discriminate colors, the bees learned both color 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 investment in learning time and accuracy during multicue learning and decision making. A difference in learning dynamics suggests that blocking could serve as a mechanism to implement this strategy switch.

INTRODUCTION

When animals make decisions based on 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 color and size, scent, and haptic properties. Such complementary sources of information can help overcome ambiguity when choosing between multiple options, as well as improve robustness to 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*). Although 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 increase in accuracy outweighs the additional costs, for example, when cues are hard to detect or noisy (*27*–*29*). When a decision can be made with high accuracy using a single cue, integrating multiple cues simultaneously might be an optimal decision-making strategy in terms of accuracy, but not in terms of efficiency (*22*, *30*).

In this study, we investigated how insects adjust their learning and decision strategies to the sensory context, using the bumblebee *Bombus terrestris* (Hymenoptera, Apidae) as a model. Insects provide an ideal model system for these investigations, as they are able to take fast and accurate decisions, despite 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, particularly of pollinating insects selecting and memorizing flowers with visual and olfactory attributes (*32*, *33*, *34*). 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 (*34*, *35*) and maximize comparability between cues, we presented combinations of visual-only features, as they are found on real flowers that bees visit: colors, shapes, and patterns (*36*, *37*). We presented cue combinations that varied in the discriminability in one of the visual attributes to assess the strategies bees followed in tasks of varying difficulty.

RESULTS

To test which attributes bumblebees retained from flowers displaying multiple visual cues simultaneously (Fig. 1A), we used an experimental design in which the bees first learned to associate a combination of color and configural cue (either pattern or shape; Fig. 1B) with a sucrose reward, and a second combination of these cues with a drop of water (Fig. 1C). We then set the two attributes in conflict, by swapping them across the stimulus pair [as in (*38*, *39*)], 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 had learned the attribute they did not choose in the first test. To assess whether the bees used the same learning and decision strategy in different contexts, we designed two color categories: distant color pairs and close color pairs (Fig. 1B), which were easier and harder to discriminate perceptually, respectively (fig. S1).

Before training, we assessed the initial preferences of all bees for the combination of stimuli used in training and testing (fig. S2, A and B). They were then trained on the stimulus that they preferred less, to ensure that training did not reinforce innate preferences. With both configural cues, bees preferred blue over orange and teal over blue in the initial preference test, irrespective of the pattern or shape the colors were combined with (fig. S2, E and F). Across colors, no significant preference for either pattern or shape emerged (fig. S2, C and D). These preferences also held up when stimuli were tested as single attributes (fig. S2G).

Bees consistently chose colors over other flower features when in conflict

When presented with a conflicting combination of stimuli, bees chose color significantly more often than the shape or pattern attributes (Fig. 2, A and B). The relative fraction of choices for color depended

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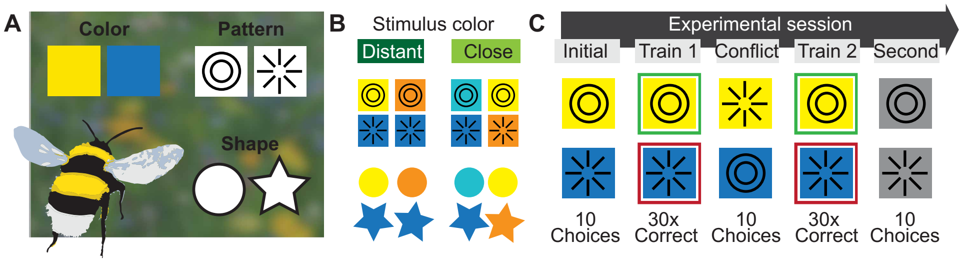

Fig. 1. The importance of color, pattern, and shape for pollinator flower selection. (**A**) Flowers provide a combination of different visual cues used by insect pollinators for detection and discrimination: most prominently color, patterns, and shapes (representative examples shown). (**B**) In this study, bumblebees (*B. terrestris*) were presented with a stimulus pair out of four color combinations (yellow-blue, orange-blue, teal-blue, or yellow-orange) for either patterns (radial-concentric) or shapes (circle-star). Two of the color pairs were distant in perception, while the other two were close (see fig. S1). (**C**) To assess which of these attributes the insects attend to and learn when presented in combination, we presented individual bumblebees with a combination of cues: color and configuration (patterns or shapes). We first assessed the bee's preference for one pair of cue combinations in an unrewarded initial test (see fig. S2). In the subsequent differential conditioning (train 1), each bee was trained differentially to a color pair, combined with either a pair of patterns or shapes. Bees were always rewarded on the less preferred cue combination. In the example pair shown, green frames represent the rewarded cue combination, and red frames represent the unrewarded combination. After training, bees then had to choose between the rewarded color or configural attribute in a conflict test (conflict). The conflict was created by swapping the trained attributes across the stimulus pair, so that each stimulus displayed only one of the two rewarded attributes. Subsequently, the animals' training was reinforced (train 2), and a second test with single attribute pairs was used to assessed whether they learned the attribute they did not preferentially choose in the conflict test.

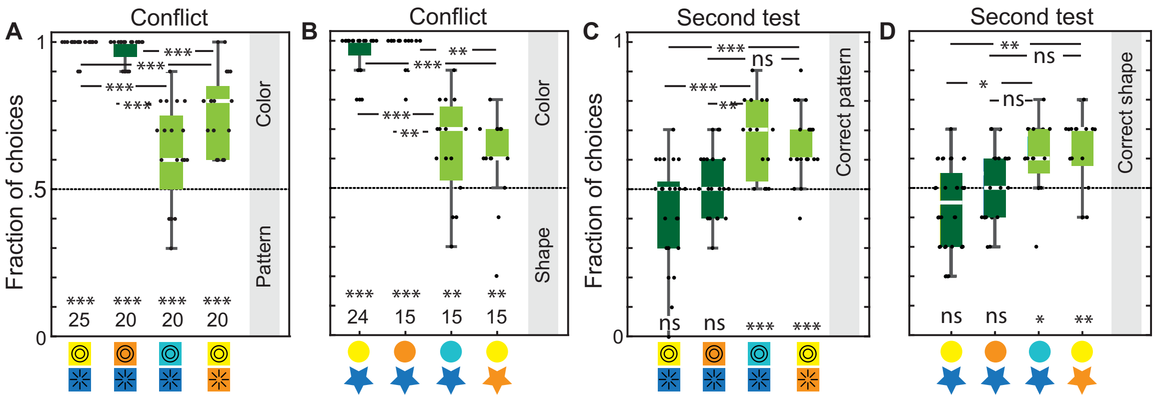

Fig. 2. Choices for flower attributes when set into conflict. (**A** and **B**) Fraction of choices for the color attribute (choices above 0.5) or the pattern or shape attribute (choices below 0.5) in the conflict test. The symbols below the plot show the trained stimulus combinations. Each group contains bees rewarded on either of the two cue combinations. (**C** and **D**) Fraction of choices for the second attribute, which was not chosen in the conflict test, and thus subsequently tested individually. Since configural cues were chosen less frequently in the conflict test, the results of their individual tests are shown here. For the results of bees that chose pattern or shape first, see fig. S4 [(B) and (D)]. The number of bees tested is indicated in (A) and (B), for pattern and shape combinations, respectively. The results of a GLMM 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 where statistically significant. All statistical results are abbreviated as $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$; ns, not significant. Boxplots depict the median and 25 to 75% range, and the whiskers represent the data exceeding the box by more than 1.5 interquartile ranges. Individual data points are shown in black. The light and dark green fill colors highlight the close and distant color cue combinations, respectively.

on the color condition: while bees chose color over the configural attribute nearly exclusively under the distant color conditions, the median choice rates for color were only between 60 to 80% under the close color conditions. Moreover, the individual variation was much lower with distant colors pairs than with close color pairs, where the variation ranged from bees choosing pattern or shape preferentially, to those choosing color at up to 90%.

As in many other cases of decision making in vertebrates (*25*, *40*) and insects (*34*, *41*), and specifically in a flower recognition context (*39*, *42*–*45*), we observed a clear hierarchy of cues the bumblebees relied on: They primarily relied on colors over configural attributes under all conditions. Our results were highly robust, holding up qualitatively and quantitatively across multiple bumblebee colonies and different experimenters, and were quantitatively similar across the different pattern and shape features, even though these likely activate pattern and shape recognition circuits quite differently (*46*–*50*), as they varied 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 preferentially relied on color when recalling memorized combinations of color, shapes, or patterns (*38*, *51*). When cues are combined additively for decision making, the overwhelming majority of studies suggest that more reliable, or less noisy, cues are given more weight (*3*, *12*, *14*, *52*–*54*). In our experiment it seems reasonable that colors would represent the more reliable cue, because they are easier to detect at a distance than patterns and shapes (*55*–*57*), which require high-resolution vision and are likely used at a more close-range stage of flower interactions (*58*, *59*). Moreover, under natural conditions, patterns and shapes suffer more readily from obstruction by foliage than flower colors.

Bees learned the pattern and shape attributes only with close color pairs

Because most of the individuals chose color over the pattern or shape attributes in all cue combinations, we asked whether bumblebees did indeed learn both attributes of the flowers, or only the color feature. Bumblebees provided with distant color pairs chose patterns or shapes at random (Fig. 2, C and D), suggesting that they only learned the color, but not the pattern or shape attributes. Bees trained on the close color pairs, however, chose the trained pattern or shape attribute significantly above the random choice rate (Fig. 2, C and D). The few bees that did prefer the pattern or shape attribute in the conflict tests also chose the color attributes above random choice (fig. S4, B and D), demonstrating that they learned both attributes of the combined stimuli with close color pairs.

In previous studies with combined attributes (*38*, *51*), honeybees learned both color and shape or pattern attributes [although see (*60*) for various learning strategies with combined cues], whereas in our experiments, they only learned both when the two colors were perceptually close. Thus, although honeybees and bumblebees are clearly capable of learning and integrating multiple object attributes (*61*) and even generalize object gestalt across modalities (*62*), we here demonstrate that bumblebees do not automatically learn all object attributes, but only do so in certain contexts.

Bees switched their decision strategy between distant and close color pairs

We next assessed the strategy the bumblebees used to choose between cues in the conflict test for the distant and close color conditions, in particular with respect to the weights they assigned to color as compared to patterns or shapes, respectively. To this end, we designed a Bayesian decision model, which included the bees' reliance on color, pattern, and shape cues, modeled as priors, which were weighted relative to each other (see Materials and Methods). In order to obtain priors for the distant and close color conditions, as well as patterns and shapes, we trained a new set of animals to individual features instead of cue combinations: one distant (orange-blue) and one close (teal-blue) color pair, as well as patterns and shapes on gray 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 patterns and shapes after the combined attribute training (second test; Fig. 2, C and D). Qualitatively, the same holds true for the fraction of choices for close colors in the second test (fig. S4, B and D), although the small number of individuals choosing the configural category first did not allow us to confirm this statistically. 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 predict the bee's decisions for color in the conflict situation (Fig. 3B), in which the prior probabilities for color and shape or pattern were linearly combined and weighted (see Materials and Methods). A weighting factor of 1 indicated that the bees only relied on their prior for color, a factor of 0.5 that they relied on color and patterns or shapes equally, and a factor below 0.5 that they relied more strongly on patterns or shapes than color. The resulting weights for the four tested conditions (distant and close colors for both patterns and shapes) supported the intuitive interpretation of the conflict test results (Fig. 2, A and B): The bees relied (almost) exclusively on color with distant color pairs (Fig. 3C), while they relied on both color and configural cues with close color pairs, with a stronger weighting of color (Fig. 3C).

Combining complementary sources of information about an object is only one of two possible integration strategies—the other is a winner-takes-all approach, where one cue is primarily relied on (*63*, *64*). Our results suggest that the bees switch between strategies: from an additive combination of information under the close color condition, to a winner-takes-all strategy under the distant color condition (Fig. 3C).

Combined cues were learned faster than individual cues in close color combinations, but not with distant colors

In search of a mechanistic explanation for this switch in decision strategies, we analyzed the learning rates of the bees with distant and close color pairs. With combined color and configural attributes, the

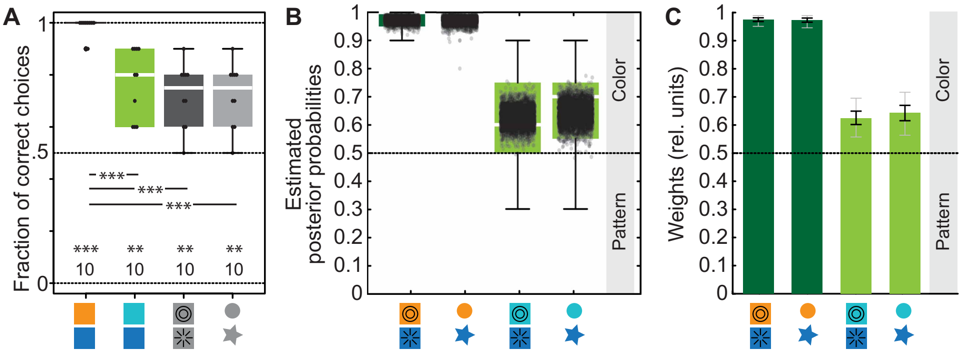

Fig. 3. Single choices and Bayesian model with decision weights. (**A**) Fraction of choices after training to individual attributes (distant: orange-blue and close: blue-teal colors, patterns and shapes on gray background; see symbols below the plot). Each group contains bees rewarded on either of the two cue combinations. Individual data points are shown in black. The statistical results were obtained with GLMM with a binomial family using the logit link. They compare the choice fractions to random choice at 0.5, depicted at the bottom of each graph, and across conditions where statistically significant. All results are abbreviated as $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$. (**B**) The predicted population choices under the conflict condition, modeled as posterior probabilities using a Bayesian decision model (see Materials and Methods) are shown in black, for 4000 post–warm-up iterations of the model. The corresponding experimental data to which the model was fitted are shown as colored boxplots (data from Fig. 2, A and B). (**C**) Estimated weighting factors, resulting from 4000 post–warm-up iterations of the model (depicted are median estimates and its 50 and 95% credible intervals, in gray and black, respectively). See fig. S3 for the distributions of weighting factors. [(A) and (B)] Boxplots depict the median and 25 to 75% range, the whiskers represent the data exceeding the box by more than 1.5 interquartile ranges. The light and dark green fill colors highlight the close and distant color-cue combinations, respectively.

bumblebees required fewer trials to reach a high fraction of correct choices for the distant color pairs than for close ones (Fig. 4, A and B). The fraction of correct choices was already significantly higher in the first learning block and remained higher throughout all learning trials. Across combined-attribute and single-attribute learning of distant colors, the final learning outcome, quantified as the fraction of correct choices in the final learning block, was not significantly different (Fig. 4D).

The combined-attribute learning rates for the close color pairs were distinctly less steep than those of the distant color pairs or, in other words, required more flower visits to reach the same level of performance. Even after the six learning blocks performed during training, the fraction of correct choices was lower for all close color pairs than all distant color pairs (Fig. 4, A and B). One might argue this was the case because the bees did learn both attributes, color and pattern or shape (Fig. 2, C and D), and therefore required more learning trials. However, the learning rates of attribute combinations with close colors were equally steep, if not steeper, with those for the respective single attributes (Fig. 4, C and D). This suggests that multicue learning did not diminish the learning rate, but that the slower learning of the individual attributes under these conditions was responsible for the comparably slow rates of the combined attributes. The single-attribute learning curves for close color pairs reached a significantly lower fraction of correct choices in the final learning block than the multiattribute ones (Fig. 4D). Thus, multicue learning under these conditions enhanced learning rates, as well as the final learning outcome.

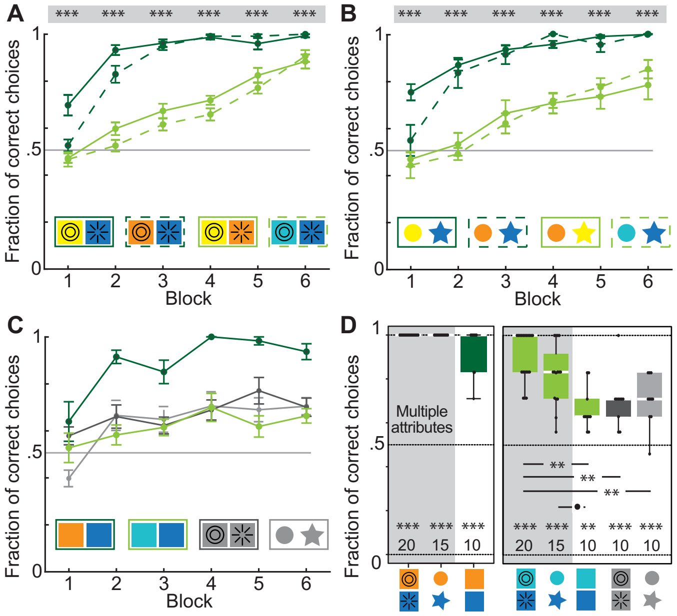

Fig. 4. Learning performance with multi- and single-attribute stimuli. (**A** and **B**) Learning rates of the bumblebees for all combined attributes, as well as (**C**) single-attribute training. Shown are the group means and standard errors for each learning block (fraction of correct and incorrect choices the bees made until they accumulated five correct choices). (**D**) Learning performance in the final training block, compared across multi- and single-attribute learning (see symbols below the plot for the cue combination during training). All statistical results were obtained with GLMM with a binomial family using the logit link, in (A) and (B), comparing the choice fractions for each block of animals with close and distant color pairs, and 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 between groups, and only statistically significant results are depicted. All statistical results are abbreviated as *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$. Boxplots depict the median and 25 to 75% range, and the whiskers represent the data exceeding the box by more than 1.5 interquartile ranges. Individual data points are shown in black. The light and dark green fill colors highlight the close and distant color-cue combinations, respectively.

Decision strategies traded off efficiency (learning speed) and accuracy

The switch in learning strategy we observed in the two sensory contexts, either learning only the most salient cue or learning both cues might be puzzling at first glance. It contradicts the notion that more information about a target is always better, and thus, integrating complementary sources of information is optimal (*7*, *8*), suggesting that the best general strategy would be learning all cues. However, this does not account for time and energy as a resource.

With the distant color pairs, the bees required distinctly fewer flower visits to reach similar levels of correct choices than with the close color pairs (Fig. 4, A to C), while obtaining very high levels of correct choices after training with the color cue alone (Fig. 4D). Thus, with distant color pairs, the bees could arrive at a reliable decision strategy much faster by learning only the color attribute, rather than also learning the pattern or shape attributes, which required more trials and reached less accurate decision levels than distant colors when learned individually. Other systems demonstrate that 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*). Under the close color condition, where the learning rate was not reduced by learning combined attributes, compared to only individual attributes, the bees did acquire the additional information of shapes and patterns and indeed improved their decision accuracy for some of the attributes (Fig. 4D). This supports the notion that learning time, or efficiency, is an important factor in learning and decision strategies in insects, which is balanced with obtaining maximal information to optimize decision accuracy. Further experiments would be required to determine how efficiency (time requirement) is weighted relative to decision accuracy. This could be achieved by 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 bees switch from a single cue to multicue learning and decision strategy, and whether this point differs between individuals or remains stable for the entire population.

The observed trade-off between accuracy and learning speed has important similarities, as well as principal differences between a similar trade-off previously observed in honeybees and bumblebees: When tested with individual cues, particularly of low discriminability, bees that took longer to make an individual flower choice were more accurate at their decision (*65*–*69*), likely because it afforded them a longer inspection and integration time of the sensory information, which could be described by an evidence accumulation framework with different thresholds (*70*). The trade-off between decision time and accuracy applies to individual decisions, representing individual flower visits. In our paradigm, the trade-off applies to the learning strategy, for example, whether to learn only the distant color attribute with a steeper learning rate and thus reduced time and energy investment, rather than learning both attributes for potentially higher reliability but at a lower speed. This trade-off operated on a population level, as all bees we tested changed strategy in the two different sensory contexts presented. Moreover, the decision of which strategy to take, i.e., whether to learn both cues or only a single one, is not adaptive to re-evaluate at every flower visit, but should rather be consistent across visits. Thus, the underlying mechanism of this switch is likely different from the time versus accuracy trade-off that individual bees make at each consecutive flower visit.

DISCUSSION

Blocking as a possible mechanism underlying the switch in learning strategy

How might the switch in learning strategies be implemented mechanistically? One answer could lie in the discriminability of the sensory features presented, which were reflected in the learning rates for distant and close color pairs, as well as patterns and shapes. Our findings mirror results from previous studies that showed slower learning rates for perceptually close than for distant colors (*17*, *65*), and fit with previous results demonstrating that colors can be learned at a glance by bumblebees, while more complex spatial cues such as patterns require longer viewing times (*71*).

Learning two attributes did not principally require more learning trials than a single attribute: Bees learned combined attributes with close colors with the same, if not a smaller, number of visits than when the attributes were presented individually (Fig. 4, A and B, versus C). This suggests that learning two attributes might benefit from synergistic effects, such as attentional cueing (*72*), or valence signaling (*17*, *18*) by one of the attributes, which are suggested to improve multicue learning rates compared to single cue ones (*15*, *17*) [but see (*23*)]. Moreover, the choice rates for either of the cues learned in combined training tested individually were similar to those trained with single attributes (compare Figs. 2, C and D, and 4D; and fig. S4, B and D), demonstrating that learning both cues simultaneously provided equally high choice accuracy as learning either one individually. Thus, any saliency or attentional effects that might have occurred during learning the combined cues did not reduce learning rates or learning outcomes compared to learning the cues individually.

A possible mechanism explaining why the bees did not learn the pattern or shape cues when paired with distant color cues is that their recognition might require longer inspection time, while it has been demonstrated that bumblebees can recognize and learn blue-yellow color combinations with presentation times as short as 25 ms (*71*). Thus, in our study, bumblebees might have learned the distant color combination so rapidly that they did not have sufficient inspection time to learn the shapes or patterns. However, bumblebees also learn close colors (such as yellow and orange) at short presentation times of 50 to 100 ms. Thus, applying the same logic, pattern or shape learning should also not have been possible under the close color condition, if the bees shaped their inspection time of the flower by the time required for color recognition (*58*). Thus, it is unlikely that the bees did not learn the pattern and shape attributes because of sensory constraints under the distant color condition, because similar sensory constraints would have applied to the close color condition.

We therefore propose that the mechanism underlying the difference in learning outcomes between the close and distant color combinations is not due to limitations in sensory perception, but the generation of associations while forming the memory. The different learning rates could provide a mechanism for the change in learning and decision strategy between the two conditions: blocking (*73*). Blocking is a phenomenon typically described when animals learn multiple attributes of an object or stimulus source sequentially. 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 (*74*, *75*). Blocking has been demonstrated across the animal kingdom, from invertebrates to vertebrates, including humans. In insects, it has been described across modalities and in a variety of tasks (*75*–*77*), although the occurrence of the phenomenon can vary with the stimulus type (*78*) and can be confounded by experimental designs (*79*, *80*).

In our experiments, the stimuli were not presented sequentially, as typically done when testing for blocking. But since the bees learned the distant colors 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 color was already formed after a few trials when pattern or shape associations were not yet formed, any further association of the configural attribute with the reward was blocked, as if the combination of cues had been presented only after the initial color training. Using blocking to enact the switch in decision strategies would be a very effective mechanism on which evolutionary selection can act, to trade off learning speed with decision accuracy, as blocking only comes into effect when one cue is learned much faster than the other associated one (*31*, *81*, *82*).

Conclusion

We found that the bumblebee, *B. terrestris*, flexibly adjusted their learning and decision strategies when presented with visual attributes of varying discriminability, to balance decision accuracy and learning efficiency. Our analysis of the bees' 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*, *83*).

MATERIALS AND METHODS

Ethics statement

No ethical permissions were required for experimentation on bees in Germany.

Animals

Colonies of *B. terrestris* were obtained from commercial breeders (Biobest, Westerlo, Belgium). The colonies were housed in a two-chamber wooden box (28 cm by 16 cm by 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% w/v sucrose solution, and with pollen grains (Bio-Blütenpollen, Naturwaren-Niederrhein, Germany).

Setup

All experiments were conducted in a flight arena as previously described (*58*). In brief, the bees' nesting box was connected to the arena (120 cm by 100 cm by 35 cm) via an acrylic tube. The floor of the arena was covered with gray cardboard (Mi-Taintes no. 122, Canson SAS, Annonay Cedex, France). The same cardboard was used for the training feeders (see the "Stimuli" section). The experiments were performed on several different bumblebee colonies per experimental condition (see the "Experimental procedure" section), to ensure that the observed effects were robust against individual colony variation (*84*).

Stimuli

All artificial flowers were constructed from cardboard cutouts, mounted on 10-mm tall, dark gray platforms 40 mm in diameter. The gray training stimuli were made from same cardboard as the floor of the arena. For testing, yellow, orange, teal, and blue cards were used (tinted drawing paper nos. 12, 19, 32, and 31, respectively; Buntpapierfabrik Ludwig Bähr, Kassel, Germany). The relative reflectance spectra for all stimuli are shown in fig. S1A. To test the configural 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. 1B). For the configural category pattern, we printed a concentric-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. 1B).

We performed two sets of experiments, in which combinations of shape-color and pattern-color were shown to separate groups of bumblebees. Both categories used the same pairs of colors. Two of which were distant in bumblebee color space (fig.S1) and thus should be easily distinguishable: yellow-blue, orange-blue; while two were close and thus harder to distinguish: yellow-orange, teal-blue, either in combination with shapes (circle-star) or patterns (circle-radial). Neutral colored stimuli were gray 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 color and pattern or color and shape, including the respective conflict and control tests (see the "Experimental procedure" section).

Spectral measurements and color vision modeling

The relative reflectance spectra of the colored cardboard from which the stimuli were constructed, as well as that of the gray 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, USA). The spectrometer was calibrated against a Spectralon white diffuse reflectance standard (WS-1-SL, Ocean Optics). Color loci in the color triangle were calculated using the method described in (*85*) using the spectral sensitivities of *B. terrestris*' three photoreceptor classes from (*86*) (fig. S1B).

Experimental procedure

Foragers of *B. terrestris* were selected for experiments by scoring their prior foraging activity in the flight arena on gray 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 gray training stimuli with 10 μl of 50% sucrose solution in the center 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 gray flowers. Each artificial flower was refilled immediately by the experimenter after the bumblebee departed, while it was feeding on a different one.

During this initial training, the bees learned that in order to retrieve the reward, they had to land on the flowers. As the bees predominantly approached flowers from the side rather than land directly in the center [likely due to the geometry of the flowers; see also (*58*) for a quantification and discussion of the landing strategies in a similar setup], they were not able to antennate the sucrose or water droplets in the center before making a landing decision.

Conflict experiments

The experiment began with an initial preference test (Fig. 1C), during which each bee was individually presented with a combination of color and shape or pattern (for example, a yellow star and an orange circle, or a teal square with a concentric pattern 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 avoid pairing either with a reward. The first 10 choices of each bee were recorded. Subsequently, the bee was allowed to feed ad libitum from a gray feeder, which was introduced to the arena after the test, and returned to the colony.

The color-pattern or color-shape combination of the pair that the bee least preferred was then chosen as the rewarded stimulus for training (Fig. 1C). If both stimulus pairs were preferred equally, the stimulus that had been tested on fewer individuals was selected as the rewarded one. All instances of the rewarded stimulus were supplied with 10 μl of a 1 M sucrose solution, while the unrewarded pair was supplied with the same volume of water. During training, the artificial flowers were resupplied immediately after the bee approached the next one. Care was taken to only refill it while the bee was occupied feeding on a different artificial flower, to not train bees to following the pipette that contained sugar water. Training continued until a bee had made 30 correct choices, and as many incorrect choices as were necessary to reach 30 correct choices. When the bee returned to the colony during training, the order of the stimuli in the arena was rearranged to prevent spatial learning. After training, sucrose solution was provided ad libitum on a gray feeder, which was introduced to the arena after the bee finished training, so that the bee would fill her crop and return to the colony.

When the bee subsequently returned to the foraging arena, a conflict test was performed (Fig. 1C). It was conducted in the same way as the initial preference test, but the attributes of the stimuli were swapped: The rewarded color 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). Five instances of each stimulus pair were presented in the arena, each with 10 μl of water, to avoid pairing either with a reward. The first 10 choices of each bee were recorded. Afterward, a second training session was conducted using the original cue combination, in the same manner as the first training session, until the bee again reached 30 correct choices (Fig. 1C and fig. S4, A and C).

Subsequently, a second test was conducted in the same way as the unrewarded initial preference and the conflict test: Five instances of each stimulus pair were presented in the arena, each with 10 μl of water, to avoid pairing either with a reward. The first 10 choices of each bee were recorded. In this second test, the presented stimuli only had one attribute (either color, or pattern, or shape). This attribute was the one the bee did not choose preferentially in the conflict test (Fig. 1C; for example, if she chose color over shape in the conflict test, in the second test, the bee was presented with gray stars and circles. If she chose shape over color, the bee was presented with square-shaped colored 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 color: orange-blue, close color: blue-teal, pattern or shape on gray background). The experiment began with an initial preference test composed of 10 unrewarded choices, followed by a training session until 30 correct choices were performed, and an unrewarded session, in which the stimulus pair, which was presented for training, was presented, and 10 unrewarded choices were recorded.

Scoring of behavioral decisions

In keeping with long-established methodology in honeybee and bumblebee training, we scored the bee's choices for a flower stimulus under the training condition based on human observation of the live experiments (ensuring high resolution and depth information). The criterion for a choice during training was the following: Bees landed and probed the sucrose or water solution in the center of the flower, to ensure that each training visit that was scored entailed an experience of the rewarding or aversive substance. In unrewarded test trials, we scored landing of the bees, defined as a contact of the front legs with the flower, as a choice for a particular stimulus. These criteria are state of the art in similar studies of (artificial) flower choice across different research groups (*87*–*89*). The scoring criteria proved highly repeatable, as they were applied by multiple experimenters to different bumblebee colonies in separate subsets of experiments (see the "Number of bees, colonies, and experimenters" section), which led to highly consistent results across different color groups, as well as shapes and patterns.

Number of bees, colonies, and experimenters

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

Bayesian decision model

We constructed a Bayesian decision model (*90*, *91*), predicting the choice rates of bees for color 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

$$p(H\,|\,O) = \frac{p(O\,|\,H) \times p(H)}{p(O)} \tag{1}$$

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

$$p(O) = \int p(O\,|\,H) \times p(H)\, dH \tag{2}$$

Since the decision model was designed to predict choices in the conflict situation, the priors needed to reflect both prior probability of color $p(H|C_1)$ 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*, *63*, *92*)

$$p(H) = \frac{p\left(H\,|\,C_1\right)^{w} \times p\left(H\,|\,C_2\right)^{1-w}}{\int p\left(H\,|\,C_1\right)^{w} \times p\left(H\,|\,C_2\right)^{1-w}\, d(H)} \tag{3}$$

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

$$p(H\,|\,O) = \frac{p(O\,|\,H) \times p\left(H\,|\,C_1\right)^{w} \times p\left(H\,|\,C_2\right)^{1-w}}{\int p(O\,|\,H) \times p\left(H\,|\,C_1\right)^{w} \times p\left(H\,|\,C_2\right)^{1-w}\, d(H)} \tag{4}$$

We implemented the model in discrete terms in R v4.4.1 (R Foundation for Statistical Computing, Vienna, Austria) 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 color or pattern/shape obtained in the individual attribute experiments, in which the animals were only trained to a single attribute (distant or close color, pattern, or shape), instead of a color combination (Fig. 3A). Since the single-attribute data were obtained from a different set of bumblebees than those that performed the conflict experiments, we used logit-scale prior distributions for our model rather than point estimates. To obtain these, we estimated population-level variation in preferences by fitting binomial generalized linear mixed-effects model (GLMM) in lme4 (*93*) to each single-attribute dataset, calculating prior mean as the logit transform of the mean choice rates, and the standard deviation as sum of the fitted individual and population standard deviations. Weightings were also estimated on a logit scale, with a normally distributed prior distribution centered at 0 (50%) with a standard deviation of 4. The model was fitted as a binomially distributed Bayesian GLM in Stan v2.32.2 using the R package BRMS (*94*), generating 4000 post–warm-up estimates for each posterior choice probability (Fig. 3B), cue prior and weighting (Fig. 3C and fig. S4).

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. This assured equal possibility for forming a positive association to the stimulus across bees. For all unrewarded preference tests, the fraction of choices for either of the stimuli in a pair was calculated. Statistical analysis was performed using R v4.1.2 (R Foundation for Statistical Computing, Vienna, Austria). To assess whether the preference for color in the conflict experiment differed from random choice (50:50, since all stimuli were presented in pairs), a GLMM with the following formula was used

$$\text{correct choice} \sim \text{color} + (1|\text{animalID}) \tag{5}$$

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

To analyze 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 second test, a GLMM with the following formula was used

$$\text{correct choice} \sim \text{pattern} + (1|\text{animalID}) \tag{6}$$

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 color in the conflict test, and the nonpreferred attribute in the second test for patterns and shapes, we used a GLM of the family "quasibinomial"

$$\text{choice} \sim \text{pattern} \times \text{color} \tag{7}$$

To assess the fraction of choices for bees in the initial preference test for color, shape, or pattern, and the effects of their interaction, we used a GLM of the family "quasibinomial"

$$\text{choice} \sim \text{pattern} \times \text{color} \tag{8}$$

Supplementary Materials

This PDF file includes:

Figs. S1 to S4

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