

RESEARCH ARTICLE

Bumblebee visual search for multiple learned target types

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SUMMARY

Visual search is well studied in human psychology, but we know comparatively little about similar capacities in non-human animals. It is sometimes assumed that animal visual search is restricted to a single target at a time. In bees, for example, this limitation has been evoked to explain flower constancy, the tendency of bees to specialise on a single flower type. Few studies, however, have investigated bee visual search for multiple target types after extended learning and controlling for prior visual experience. We trained colour-naive bumblebees (*Bombus terrestris*) extensively in separate discrimination tasks to recognise two rewarding colours in interspersed block training sessions. We then tested them with the two colours simultaneously in the presence of distracting colours to examine whether and how quickly they were able to switch between the target colours. We found that bees switched between visual targets quickly and often. The median time taken to switch between targets was shorter than known estimates of how long traces last in bees' working memory, suggesting that their capacity to recall more than one learned target was not restricted by working memory limitations. Following our results, we propose a model of memory and learning that integrates our findings with those of previous studies investigating flower constancy.

Key words: visual search, bee, search template, flower constancy, working memory.

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INTRODUCTION

Visual search is an essential component of our lives and is an extremely well-researched field in human psychology and neuroscience (Chun and Wolfe, 2000; Verghese, 2001; Wolfe, 1998; Wolfe, 2003). We know comparatively little, however, about visual search in other animals despite the fact that several animals also use visual search for vital biological functions like foraging, searching for mates or avoiding predators (Bond and Kamil, 2002; Ings and Chittka, 2008; Spaethe et al., 2006). Bees, for example, have to discriminate highly rewarding flowers from poorly rewarding flowers while foraging (Benard et al., 2006; Chittka et al., 1999). Several studies have shown that while performing this task, they tend to specialise on a single rewarding target type while occasionally sampling other flowers as well, a phenomenon referred to as flower constancy (Waser, 1986). It has been suggested that flower constancy reflects memory and cognitive limitations on the ability of bees to rapidly retrieve memories for multiple targets (Raine and Chittka, 2007; Waser, 1986). Other studies have, however, hinted that either of two targets can be recalled, albeit not simultaneously (Chittka and Thomson, 1997; Hill et al., 1997), but few control for prior experience and learning as well as odour cues. Those that do (Chittka and Thomson, 1997), have found that target recall might be better explained by training schedules than memory capacity, suggesting that prior learning experience must be controlled to allow adequate tests of visual search limitations.

Another consideration is the distinction between working memory capacity and an immediate search template, as has been made for humans (Olivers et al., 2011). If a bee learns a search template (Goulson, 2000) and fails to learn further targets while a 'primary'

template is active in the working memory, this could be because of two non-mutually exclusive mechanisms: the primary search template might prevent new templates from being learned (Chittka et al., 1999) or it could prevent all use of other search templates – even if previously learnt – for as long as the primary template lasts in the working memory. In the latter case, bees should be unable to use or recall other learnt target templates soon after using a search template for a particular target. In order to investigate visual search capacity for learned targets, the experimental design should therefore allow bees to learn multiple targets with separate training tasks for each target such that each target can form a search template. One could then ask whether the bee can switch between search templates, or whether it is restricted to a single template until its memory trace decays.

We therefore designed an experiment with a controlled training schedule on bumblebees, *Bombus terrestris* (Linnaeus 1758) with limited previous visual experience. We tested the hypothesis that they can flexibly and rapidly retrieve more than one learned visual target as a search template when faced with a simultaneous choice between multiple learned target types.

MATERIALS AND METHODS

Animals

Bees were obtained from a commercial supplier (Syngenta Bioline, Weert, The Netherlands), tagged with Opalith number tags (Christian Graze KG, Weinstadt-Endersbach, Germany) to enable individual identification, and colonies were transferred from the commercially supplied nest boxes, under red light, to one compartment of a two-chambered wooden nest box (28×16×11 cm length×width×height).

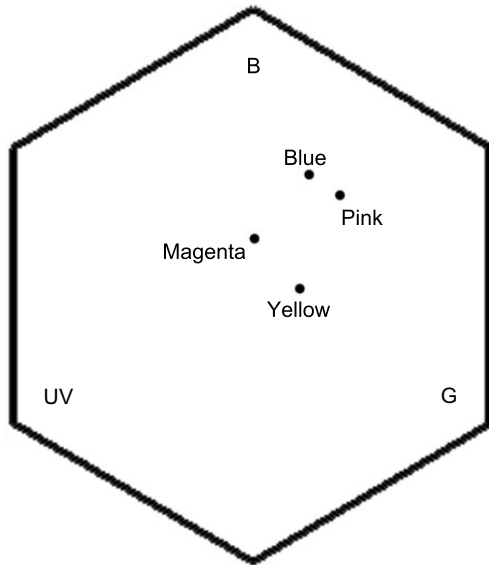


Fig. 1. Colour loci of the artificial flowers in the colour hexagon. The three vertices indicated correspond to the bumblebee photoreceptors sensitive to ultraviolet (UV), blue (B) and green (G). The angular distance from the centre represents the hue as perceived by the bee, and distances between points indicate the discriminability of the hues. The distance between the centre and any vertex is 1 and distances above 0.1 are perceptually distinguishable. The calculated distances between colour loci plotted here based on the measured spectra show that blue–magenta (colour distance=0.31), pink–yellow (colour distance=0.38), blue–pink (colour distance=0.13) and magenta–yellow (0.25) are all distinguishable.

The floor of the other compartment was covered with cat litter for bees to discard refuse. Bees were allowed to forage for 50% sucrose (v/v) in an arena consisting of a wooden box (100×60×29 cm length×width×height) with a UV-transparent Plexiglas lid, which they entered *via* a 24.5 cm long Perspex tunnel. The arena floor was covered with green card and the arena was illuminated by two twin lamps [TMS 24 F with HF-B 236 TLD (4.3 kHz) ballasts; Philips, The Netherlands] fitted with Activa daylight fluorescent tubes (Sylvania, New Haven, UK) from above. Bees were supplied with pollen *ad libitum* directly into the colony on alternate evenings.

Calculating stimuli spectral properties

The reflectance spectra of the artificial flowers used in the experiments were analysed using an Avantes AvaSpec 2048 spectrophotometer (Anglia Instruments Limited, Soham, UK) with a deuterium–halogen light source, relative to a BaSO₄ white standard. As the sensitivity of bee photoreceptors differs from ours, we converted the spectra of targets into a bee-specific hexagonal colour space (Fig. 1) (Chittka, 1992) considering the spectral sensitivity of bumblebee photoreceptors (Skorupski et al., 2007), the spectral reflectance of the background and the spectral distribution of the illuminant. The colour hexagon has three vertices corresponding to the three bee photoreceptors tuned to ultraviolet (UV), blue and green light, with the Euclidean distance between the centre and any of the vertices being 1 and colour distances above 0.1 being distinguishable. Plotting the colour loci in this space thus allows the calculation of colour distances between pairs of colours in the bee colour space, which in turn indicate the perceptual discriminability of the colours. The colour distance between blue and magenta (0.31) was similar to the colour distance between

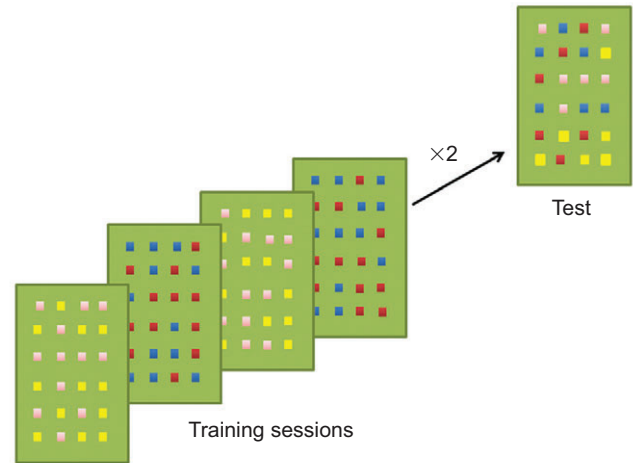


Fig. 2. Training tasks and test protocol used in the main experiment. Bees were trained to discriminate between a rewarding and an unrewarding colour in two alternating colour discrimination tasks. The starting colour discrimination task alternated between bees. After four training sessions on each task, bees were tested with all four colours and no reward. There were two experimental conditions, with different rewarding colours in each: Condition 1: pink and blue; Condition 2: yellow and magenta.

magenta and yellow (0.25) and between pink and yellow (0.38). The colour distance between blue and pink was lower (0.13) but sufficient for the colours to be distinguished. To verify that these relatively similar colours could be behaviourally distinguished, the discriminability of the blue and pink flowers was also assessed in a control experiment (see below).

Pretraining

Colour-naïve foragers were trained to forage from transparent square Perspex chips (side: 25 mm, thickness: 4 mm), carrying drops of 50% (v/v) sucrose, for two to three bouts. They were subsequently trained to feed from artificial flowers consisting of chips placed on glass vials (4 cm tall, 1.5 cm diameter) arranged in a 6×4 horizontal grid with vials placed 15 cm apart from each other. Twelve randomly chosen artificial flowers had 12 μl of 50% sucrose on them, while others remained empty. Training began after bees had foraged on this grid for two to three bouts.

Training

Bees from three different colonies were trained in two experimental conditions each consisting of two alternating visual discrimination tasks (Fig. 2) in which bees had to discriminate target colours from distractors. In Condition 1, 12 bees were trained in the two separate tasks to discriminate blue target flowers from magenta distractor flowers and pink target flowers from yellow distractor flowers. In Condition 2, the target and distractor colours were reversed, and 10 other bees were trained to discriminate magenta target flowers from blue distractor flowers and yellow target flowers from pink distractor flowers.

Each bee was individually trained on one of the two tasks until it reached a success criterion of 80% correct choices (probing of the flowers for reward) out of the last 20 choices made. The bee was then trained on the second task until it reached the same success criterion. The two tasks were subsequently alternated until the bee had successfully performed both tasks four times. Each task had 12 rewarding or ‘target’ flowers (Condition 1: blue/pink; Condition 2:

magenta/yellow) holding 12 μ l of 50% sucrose, and 12 non-rewarding or 'distractor' flowers (Condition 1: magenta/yellow; Condition 2: blue/pink) holding 12 μ l of distilled water. The target and distractor flowers in this and the other experiments below were positioned according to previously decided random spatial configurations on every foraging bout. The flowers were not refilled during a bout and bees were allowed to revisit flowers in all experiments. Between bouts, the artificial flowers were cleaned with 99% ethanol to remove scent markings, and water to remove traces of ethanol. Half the bees began training with one of the two discrimination tasks and the other half with the other task, and data from the two regimes were combined in the analysis. Two bees did not complete training in Condition 1 and data from these bees was discarded.

Test

Post-training, bees were tested on their ability to flexibly choose the two target colours. Six flowers of each target and distractor colour were presented to the bee. All flowers contained 12 μ l of distilled water, to prevent reinforcement of any colour during the test. The choices of the bee and the order of the choices were noted. The entire foraging bout was video recorded using a Sony DCR-SR58E Handycam. The recordings were later examined to obtain the times taken and the distances between consecutive artificial flowers chosen. The tests were carried out until 5 min were over or the bee returned to the colony after a minimum of 12 choices, whichever was sooner.

Control

To determine whether the blue and pink flowers were discriminable, we conducted a control experiment. Each of 10 new bees was pre-trained as above and tested on an array of 12 blue and 12 pink flowers, with flowers of one colour carrying 12 μ l 50% sucrose and flowers of the other carrying 12 μ l of distilled water. Half the bees tested encountered rewarding pink flowers and the other half encountered rewarding blue flowers. The choices of the bees were noted and analysed to see whether the bees could successfully learn one colour and meet a criterion of 80% correct choices out of the last 20 choices. Successful learning would show that bees could visually discriminate between the two colours.

Data analysis

The choices made by the bees were divided into the four possible transitions between the two target colours. We compared the number of choices of each transition type using pairwise Wilcoxon signed rank tests ($\alpha=0.05$) to examine whether bees were more likely to make constant transitions (Condition 1: blue–blue, pink–pink; Condition 2: magenta–magenta, yellow–yellow) than switches (Condition 1: blue–pink, pink–blue; Condition 2: magenta–yellow, yellow–magenta). We also examined the number of constant transitions made before each switch to investigate whether bees switched often or only occasionally. Finally, we calculated a sequence index (Heinrich, 1979) for each bee, dividing the number of constant transitions by the total number of transitions. This gives the probability of a transition being constant rather than a switch. If the bees were flower constant, the expected index value would be close to 1, while if they visited two targets with equal probability the expected value would be close to 0.5. We compared the observed number of constant choices with the expected values corresponding to indices of 1 and 0.5 using a chi-square test ($\alpha=0.05$).

To examine how quickly the bees made their choices, we compared the median times taken to make each of the four possible

choice types using pairwise Wilcoxon signed rank tests ($\alpha=0.05$). We investigated whether the time taken to make choices correlated with the distance between the choices made by calculating the Pearson's correlation coefficient between the two measures. All statistical analyses were carried out using PASW Statistics v 18.0 (SPSS Inc. 2009, Chicago, IL, USA; www.spss.com).

RESULTS

Training

Bees learnt to discriminate both blue flowers from magenta ones and pink flowers from yellow ones but took longer to learn the blue–magenta discrimination than the pink–yellow discrimination. The mean (\pm s.d.) number of choices per bout was 12.2 \pm 4.8. In Condition 1, the mean number of choices taken to learn the rewarding colour was 33.5 \pm 14.6 for the blue flowers and 20.3 \pm 0.95 for the pink flowers. In Condition 2, the mean number of choices to learn the rewarding colour was 24.3 \pm 3.2 for yellow flowers and 27.1 \pm 5.1 for the magenta flowers. Bees also made more errors initially on the blue–magenta, magenta–blue and yellow–pink tasks, with accuracies of 75 \pm 9%, 73.5 \pm 4.9% and 73.7 \pm 10.4%, respectively, in the very first training session compared with 91 \pm 8% in the pink–yellow task. On the final training session, however, the accuracy of bees in all tasks in both conditions was near perfect (Condition 1: 97 \pm 3% for the blue–magenta, 100% for the pink–yellow; Condition 2: 96 \pm 5% for the magenta–blue, 98.8 \pm 2.7% for the yellow–pink). The time taken for the entire training ranged from 1 h 59 min to 6 h 28 min and the mean time was 3 h 39 min.

Test

Condition 1 – target colours: blue and pink

All 10 bees tested in Condition 1 showed a high degree of accuracy with only one choice of a distractor out of all 281 choices made. Thus, they were not choosing randomly but focusing on the two target colours. The mean (\pm s.d.) number of choices made by each bee was 27.3 \pm 12.0. The mean number of pink choices made (16.5 \pm 8.1) was greater than the mean number of blue choices made (11.6 \pm 5.9). The difference between the number of pink and blue choices, however, just failed to reach significance at the 5% level (paired *t*-test; $t_9=-2.156$; $P=0.06$).

We divided the choices according to the four possible transitions: blue–blue, pink–pink, blue–pink and pink–blue and compared the numbers of each transition type. We found that while the numbers of constant choices (pink–pink and blue–blue) were higher, the median number of choices made did not differ significantly across transition types (Fig. 3A; pairwise Wilcoxon signed rank tests, all $P>0.2$), suggesting that bees made an approximately equal number of choices for each transition, whether they switched colours or stayed constant.

To further investigate whether bees stayed flower constant over several consecutive choices or switched colours often, we examined the number of choices each bee made before switching. The median number of consecutive blue choices made before switching to pink was 1 and the median number of consecutive pink choices made before switching to blue was 2 (Fig. 3C). The respective means were 1.9 \pm 1.5 and 2.8 \pm 2.1. The mean sequence index across all bees was 0.6 \pm 0.1 and the proportion of constant choices made was significantly different from 1 ($\chi^2=48.2$, d.f.=9, $P<0.05$) but not from 0.5 ($\chi^2=11.4$, d.f.=9, $P>0.2$), indicating that bees were switching frequently and only rarely stayed constant to a single colour.

An examination of the transition times showed that the median times between choices were not significantly different across the

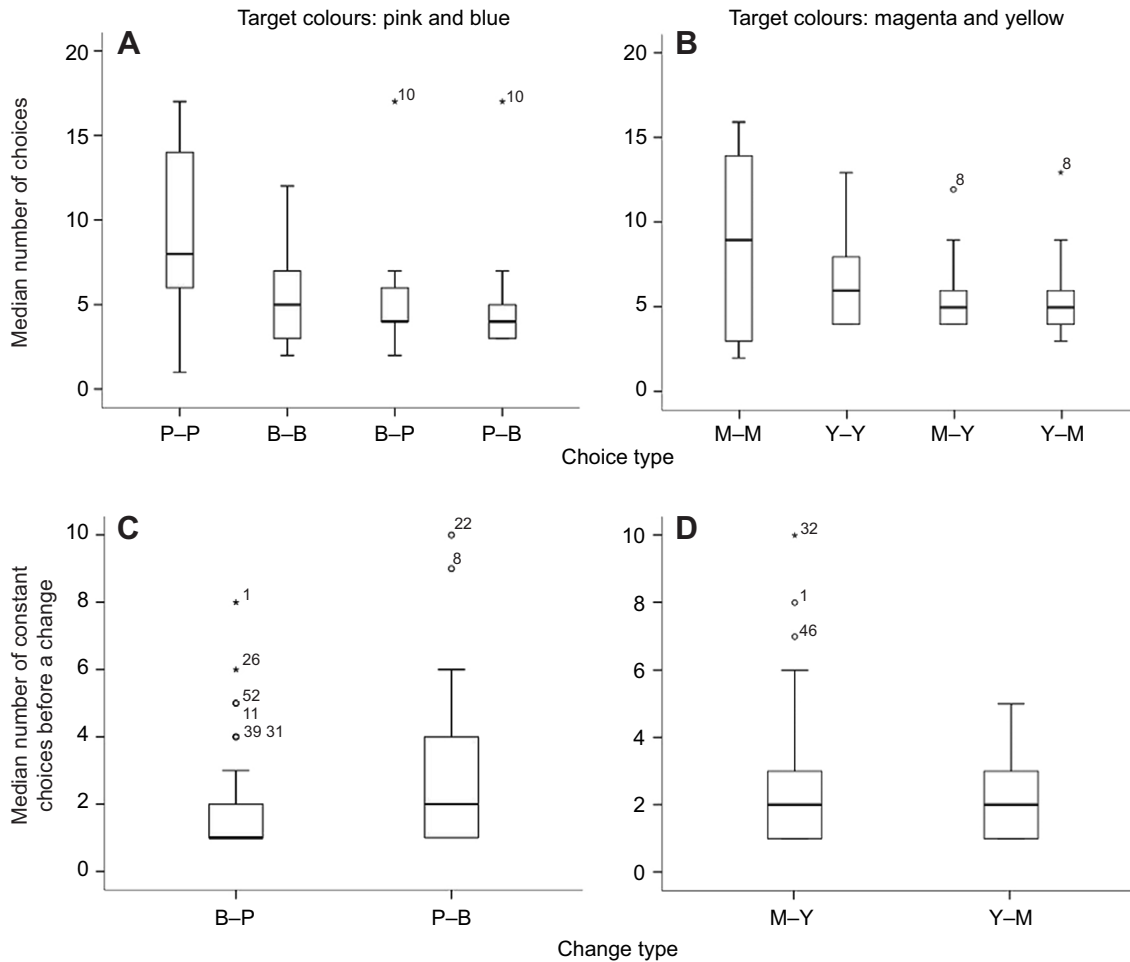


Fig. 3. Median number of choices made by bees with inter-quartile range (IQR, boxes) and range (whiskers) in experimental conditions 1 (A,C) and 2 (B,D). (A,B) Median number of choices in each transition type during the test. (C,D) Median number of constant choices made by bees before switching colours. Transition types are indicated on the x-axis: P–P, pink to pink; B–B, blue to blue; B–P, blue to pink; P–B, pink to blue; M–M, magenta to magenta; Y–Y, yellow to yellow; M–Y, magenta to yellow; Y–M, yellow to magenta.

different transition types (Fig. 4A; pairwise Wilcoxon signed rank tests, all $P > 0.2$), staying at 5–6 s across all transition types. The low transition times were not well explained by the physical distances between the targets chosen, with a low but significant correlation between transition time and distance (Pearson's correlation coefficient = 0.1, $N = 270$, $P = 0.03$).

We compared the times taken by the bees when switching between colours (blue–pink or pink–blue) with estimates of bee working memory duration to examine whether the bees switched before the memory trace of the previous search template could have completely decayed. Working memory completely decays before 8.7 s but is still robust at 6 s in the honeybee (Zhang et al., 2005). Field studies on bumblebees have indicated similar working memory dynamics (Chittka et al., 1999). We used both these estimates and examined the proportion of the choices made by bees below either. A total of 77.6% (45 out of 58) of all blue–pink transitions and 75% of all pink–blue transitions were under 9 s (Fig. 4C). Furthermore, 62.1% (36 out of 58) of all blue–pink transitions and 65.4% of all pink–blue transitions were 6 s or under (Fig. 4C). The lowest transition time was 1 and 2 s, respectively, for the blue–pink and the pink–blue transitions. Bees were, therefore, able to quickly switch between target colours before their working memory traces of the previous colour decayed and did so frequently. An inspection

of the distributions of the transition times did not indicate any bimodality, which would have suggested that the choices were split – perhaps by some memory threshold – between shorter and longer times. There was also no qualitative difference between the transition time distributions between the transition types.

Condition 2 – target colours: magenta and yellow

Similar to Condition 1, all 10 bees tested in Condition 2 were highly accurate and chose no distractors across all 293 choices made. The mean (\pm s.d.) number of choices made by each bee was 28.3 ± 11.5 . The mean number of magenta choices made (15.2 ± 8.1) and the mean number of yellow choices made (13.1 ± 4.6) were not significantly different (paired t -test; $t_9 = 1.0$; $P = 0.34$).

The median number of choices did not differ across the different transition types (magenta–magenta, yellow–yellow, magenta–yellow and yellow–magenta; Fig. 3B; pairwise Wilcoxon signed rank tests, all $P > 0.07$). The median number of consecutive magenta choices made before switching to yellow and the median number of consecutive yellow choices made before switching to magenta was 2 in both cases (Fig. 3D). The respective means were 2.5 ± 2.3 and 2.0 ± 1.2 . The mean sequence index across all bees was 0.6 ± 0.1 and the proportion of constant choices made was significantly different from 1 ($\chi^2 = 51.8$, d.f. = 9, $P < 0.05$) but not from 0.5 ($\chi^2 = 6.1$, d.f. = 9, $P > 0.2$). This shows

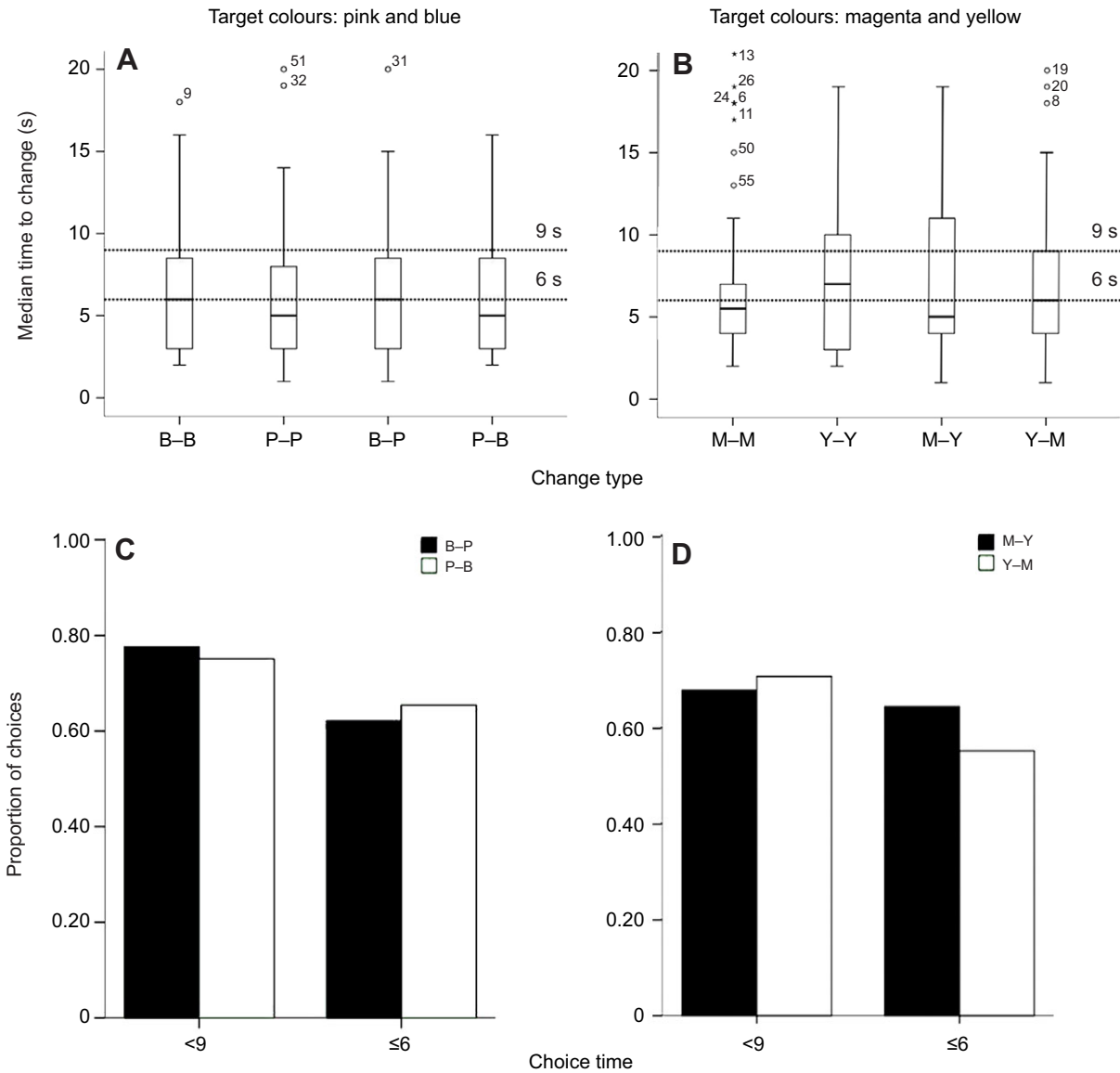


Fig. 4. Transition times compared with estimates of bee working memory: 9 s, complete decay of traces in the working memory; 6 s, memory traces still robust. (A,B) Median time spent between choices split according to transition type with IQR (boxes) and range (whiskers) in experimental conditions 1 (A) and 2 (B). Some outliers have been excluded for ease of representation. Dotted lines represent known estimates of bee working memory. (C,D) Proportion of non-constant choices (switches) made within estimates of bee working memory in experimental conditions 1 (C) and 2 (D). Transition types are indicated on the x-axis and legends as for Fig. 3.

that in this condition too, bees switched between the two target types often rather than staying constant to a single colour.

The median times between choices in Condition 2 were not significantly different between the different transition types (Fig. 4B; pairwise Wilcoxon signed rank tests, all $P > 0.19$), and similar to Condition 1, were either 5 or 6 s across all transition types. The transition times and distances between targets were again weakly but significantly correlated (Pearson's correlation coefficient = 0.2, $N = 273$, $P = 0.001$), once more suggesting that the low transition times were not adequately explained by the distance between the targets.

A total of 68% (40 out of 59) of all magenta–yellow transitions and 71% (41 out of 58) of all yellow–magenta transitions were under 9 s (Fig. 4D). Furthermore, 64% (38 out of 59) of all magenta–yellow transitions and 55% (32 out of 58) of all yellow–magenta transitions

were 6 s or under (Fig. 4D). Both transitions had lowest transition times of 1 s. As with the first experimental condition, the distributions of the transition times were not bimodal and the different transition types did not differ in the distribution of transition times.

Thus, the results of Condition 2 were qualitatively similar to those of Condition 1 and, again, bees switched between target colours frequently and often before estimates of the time taken for their working memory traces to decay.

Control

All 10 bees learnt the rewarding colour in the control experiments. Bees took on average only 20.4 ± 4.7 choices since first choosing the rewarding colour to reach an accuracy of 80% correct choices out of the last 20. Bees were therefore clearly able to distinguish the blue flowers from the pink flowers.

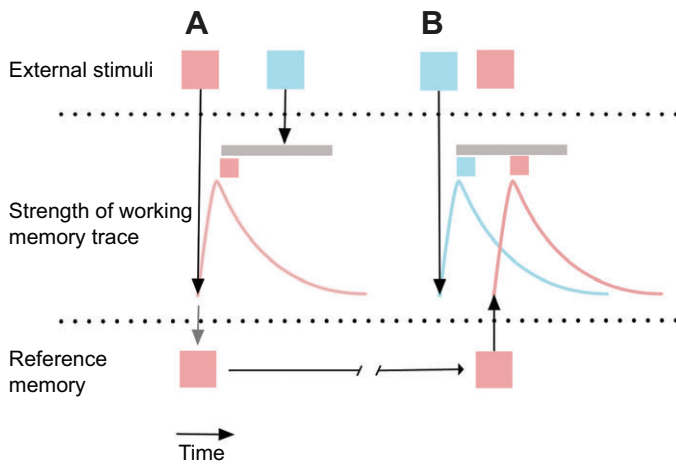


Fig. 5. Model of working memory dynamics. (A) Stimuli that are visually encountered create working memory traces that decay with time. The creation of a working memory trace is followed by an inhibitory period (grey bars) during which new stimuli (blue square) cannot enter the working memory and therefore cannot be learned. (B) Stimuli encountered after this period (blue square) can enter the working memory. Stimuli that have previously entered the reference memory (pink square) can be recalled to the working memory if encountered externally, even during the inhibitory period.

DISCUSSION

We tested bees with carefully controlled visual experience trained on a fixed schedule to examine whether they flexibly search for multiple target types, and investigated the sequence and speed with which they switched between search templates, explicitly comparing this with estimates of how long working memory lasts in bees. We found that bees that have trained for a relatively extended period of time on two alternating targets can recall both targets flexibly and quickly. The times taken to switch between targets were below estimates of how long bee working memory traces take to decay, suggesting that bumblebees can utilise at least two target types, accessing multiple search templates within a short duration of time.

Visual search experiments in humans have typically found that people ignore distractors and focus on the target stimuli when there is only a single target type (Wolfe, 1994) but fail to ignore distractors when instructed to attend to multiple targets (Houtkamp and Roelfsema, 2009; Menner et al., 2009). This has led to the suggestion that while multiple items can be held in the working memory, we are unable to process different search templates concurrently (Olivers et al., 2011). Here, our results suggest that bees can activate two different search templates within 1 s of each other. The bees chose almost no distractors in our experiment, indicating that they were using search templates for particular targets rather than choosing colours in a non-specific manner.

This conclusion is especially supported by results from Condition 2 and the control experiment. In Condition 2, the target colours were both less saturated than the distractors. They were also well separated in the bee colour space and one of the target colours (magenta) was close to one of the distractors (blue) as well as the other target colour. Thus, the bees could not simply rely on the similarity of target colours during visual search and any natural preference for saturated colours would be insufficient to explain our results. The control experiment further shows that bees could distinguish between the blue and the pink flowers, reinforcing the idea that even for similar target colours they can use two different search templates rather than relying on one template that was non-

specific enough to include both the pink and blue flowers. These results, and the clear concordance of our results from Condition 1 and Condition 2, support the idea that the bees were using separate search templates for the target colours.

It is possible that what seems like an extension of working memory capacity might be explained by better and more rapid retrieval from the reference memory (Ericsson and Kintsch, 1995; Gobet, 2000). Here, however, we cannot distinguish whether the bees were simultaneously holding the two search templates in their working memory or rapidly retrieving the templates from their reference memory. One potential mechanism by which bees might switch between target types is suggested by human psychophysical studies that use the same target from trial to trial, across multiple trials (Schneider and Shiffrin, 1977). This is similar to the training phase of our study where bees were extensively 'block-trained' on the same two targets, on average for over 4 h. Studies like this found a quicker recall of items in memory and this seemed to be enabled by a transition from an 'effortful' working memory to a more automated process that recognises the target items (Rossi et al., 2007; Woodman et al., 2007). Given the potentially lower computational and storage capabilities of the bee nervous system, the idea that similar processes might explain our results is appealing.

Our results have implications for flower constancy, the tendency of bees to specialise on a single flower species amongst all available flowers (Waser, 1986). Even in studies demonstrating that bees visit multiple targets, bees predominantly visited one flower type and only sampled other flower types (Heinrich, 1976; Heinrich, 1979). We, however, show that when colour-naïve bees have extended training, they do not specialise on a single target but choose either of two targets more or less equally, often switching between them. The disparity between our results and previous findings could be due to several factors. Our training schedule with alternate blocks of different tasks might have enabled bees to learn both the colours better and store them effectively in their reference memory. In addition, we used colour-naïve bees for our study, which prevented previously learnt colour biases from interfering with the learning of new targets. Our experiment also excluded the possibility of learnt olfactory cues influencing the decisions of bees, which could potentially play a role in field studies.

Several researchers have implicated memory limitations in flower constancy (Chittka et al., 1997; Lewis, 1986; Waser, 1986). Our results suggest that if flower constancy is due to cognitive constraints, this does not reflect a limitation of working memory, but rather represents a difficulty with learning novel targets immediately after learning a target (Chittka and Thomson, 1997). One should note, however, that in our experiment the flowers differed in only one attribute (colour) and in nature, flowers might differ in other attributes such as morphology and odour as well. It would be important to test whether memory or learning constraints determine flower constancy on flowers with these multiple attributes. Our results, in combination with previous work, however, support a model where newly learned targets hamper the learning of further targets not yet stored in the reference memory, whereas targets that were previously learned are easily recalled (Fig. 5).

In our model, a newly learnt search template enters the working memory and is utilised to find targets. This template prevents further templates from being learnt during an inhibitory period that lasts for as long as the trace of the primary template lasts in the working memory (Fig. 5A, grey bars). This template could enter the reference memory after repeated use for a longer duration of time. After the inhibitory period, i.e. after ' t_w ' seconds, another target can be learnt

and similarly stored in both working and later, reference memories. Now either of these two targets can be recalled from the reference memory. The recall of learnt targets is, however, not restricted by the inhibitory period following the use of a particular search template. Hence, multiple learnt search templates can be used within seconds of each other with the minimum time ' t_p ' between switches being determined by the processing time taken to recall templates rather than by working memory duration (Fig. 5B). The model would therefore predict that the time taken by bees to recall and use secondary learnt templates after using a primary search template should be less than the time taken by bees to choose a completely novel target, i.e. $t_p < t_w$. This could be tested in experiments where bees trained on two target colours are subsequently tested in a condition with both the targets and novel colours present. Our model would predict that the transition times between the learnt targets would be less than the transition times between targets and novel colours.

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AUTHOR CONTRIBUTIONS

V.N. conceived and designed the experiments and analysed the results. V.N. and J.G.P. performed the experiments and wrote the paper.

COMPETING INTERESTS

No competing interests declared.

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