Original Article

Bumblebees utilize floral cues differently on vertically and horizontally arranged flowers

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Pollinators have the capability of discriminating a wide variety of floral cues in order to identify rewarding flowers. However, little is known about how possible ecological or functional implications of horizontal and vertical positioning of flowers affect pollinator decision making. Flowers are commonly either arranged horizontally in meadows or vertically in inflorescences and blooming trees or bushes. Using bumblebees (*Bombus terrestris*), we here investigate if these 2 different foraging scenarios affect decision-making accuracy using an operant learning paradigm. Training foragers to feeders arranged either horizontally or vertically but bearing identical color or pattern cues, we found a highly significant and consistent difference in feeder choice accuracy. Bees presented with horizontally arranged feeders achieved accuracies of more than 90% by the end of the training. In contrast, bees foraging on vertically arranged feeders largely disregarded the feeder cues and accuracies remained well below 70%. Apart from feeder arrangement (horizontal, vertical) neither cue type (color, pattern), feeder display orientation (horizontal, vertical) nor vertical feeder distribution contributed significantly to choice accuracy. Training bees successively on vertical, horizontal, and vertical feeder arrays revealed that individual bees are capable of discriminating the presented feeder cues with high precision on the horizontal plane but did not use the acquired knowledge on subsequently presented vertically arranged feeders. Our results indicate that the spatial arrangement of flowers has marked effects on the foraging strategy employed by a generalist pollinator. We discuss the broader implications of foragers selectively allocating attention to focus on or disregard environmental information depending on spatial context.

Key words: **bumblebee, choice accuracy, ecological context, foraging strategy, perception, selective attention**.

INTRODUCTION

Foraging animals are well known to identify and use cues that distinguish useful resources from food types that have proved less rewarding (Hassell and Southwood 1978; Bell 1990; Real 1991; Dall et al. 2005). In doing so, spatial context is often integrated with the sensory cues that mark the food types themselves; for example, honeybees can learn to prefer flower color A over B in one spatial location and B over A in another location (Collett and Kelber 1988). In a few spectacular cases, foraging animals choose to disregard certain types of information altogether, even if this information is clearly accessible to them. Flower-visiting hummingbirds, for example, have excellent color vision (Goldsmith and Goldsmith 1979; Goldsmith 1980; Chen and Goldsmith 1986) yet disregard even strongly different flower colors if a particular food resource was previously identifiable unambiguously by spatial location (Hurly and Healy 1996; Healy and Hurly 2001). In this scenario, selective attention results in ignoring color information that is available at the sensory input level, whereas instead focusing on other salient cues that might identify a resource with the highest predictability (Zentall and Riley 2000; Dukas 2002; Dukas 2004). Here we explore the influence of spatial arrangement of artificial flowers on the attention that foraging bumblebees dedicate to floral cues.

Flowers of different species vary in the floral cues (and their combination) they provide (e.g., size, color, odor, shape) affecting the perception, signal processing, attention, and ultimately the behavior of foraging pollinators (e.g., Kunze and Gumbert 2001; Wertlen et al. 2008; Dyer and Griffiths 2012; Morawetz et al. 2013). For instance, both small flower size and floral cues with low ultraviolet (UV) reflectance can lead to increased search times and slower flight speeds in bumblebees (Spaethe et al. 2001). Once detected, cue similarity (Dyer and Chittka 2004a, 2004b; Dyer et al. 2008) and foraging context (e.g., Kunze and Gumbert 2001; Chittka et al. 2003; Dyer and Chittka 2004c; Giurfa 2004; Ings and Chittka 2008; Morawetz and Spaethe 2012; Morawetz et al. 2013) may strongly affect flower choice.

Flowers also vary in the way they present themselves to a pollinator. Many radially symmetrical flowers face upward, whereas

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many others (often bilaterally symmetrical [zygomorphic] flowers) face sideways affecting the way bees may perceive these flowers (Arnon et al. 2009). In honeybees, striking differences in the choice accuracy have been reported for cues displayed vertically or horizontally (Hertz 1929; von Frisch 1950), laterally, ventrally or dorsally (Giger and Srinivasan 1997). Hertz (1929) reported that bees could not discriminate horizontally displayed filled circles from triangles, which they are able to discriminate when displayed vertically (Horridge 2009). Honeybees discriminate pattern and color cues when presented to the lateral and frontal visual field, but neither cue could be discriminated when presented dorsally and only colors could be discriminated when presented ventrally (Giger and Srinivasan 1997). Such effects are commonly attributed to functional constraints associated with cue types and display orientation. Horizontally displayed patterns may render important features hard to recognize due to their different appearance from different approach directions. Also the visual angle with which cues are perceived may differ for differently displayed cues (e.g., Spaethe et al. 2001; Dyer et al. 2008; Dyer and Griffiths 2012). Frontally displayed vertical cues may be perceived with a visual angle maximal for the distance to the target. Horizontally displayed cues, on the other hand, are rarely seen from directly above but rather from a more peripheral aerial view during the approach flight reducing the visual angle and potentially increasing the limits of both target detectability and discrimination.

Perceptual limitations may also arise through functional differences in different regions of the eye (Wehner 1972; Chittka et al. 1988; Lehrer 1999). Regional morphological specialization is seen on the ommatidial level where both peripheral optics and receptor characteristics have been shown to facilitate a functional differentiation of the visual field in various insects (Horridge 1978; Horridge and Duelli 1979; Hardie 1986; Land 1997; Horridge 2005). However, while there is strong morphological regional specialization found in honeybee drones (Streinzer et al. 2013), worker honeybees show little regional differences in lens size or ommatidial divergence angles (Wakakuwa et al. 2005; Streinzer et al. 2013). Functional differentiation of the visual field may also be implemented through postreceptor neuronal organization. Evidence in both honeybees and bumblebees suggests a pronounced dorsal–ventral segregation of the neuronal wiring at various processing levels within the visual system (Hertel 1980; Ehmer and Gronenberg 2002; Paulk et al. 2008; Mota et al. 2011).

Although bees are in principle well capable of discriminating vertically displayed cues these may be processed differently depending on visual, attentional, and temporal constrains and on individual experience (e.g., Giurfa et al. 1999; Giurfa 2004; Stach and Giurfa 2005; Dyer et al. 2008; Dyer 2012; Dyer and Griffiths 2012; Morawetz and Spaethe 2012; Morawetz et al. 2013). For instance, Giurfa et al. (1999) found that honeybees presented with vertically displayed pattern cues learnt only the part pattern cue visible with the ventral (lower part of the cue) but not with the dorsal eye region (upper part of the cue) in absolute conditioning, that is, with only a rewarding pattern being presented during training. However, the bees discriminated these patterns using both dorsal and ventral information in differential conditioning (Giurfa et al. 1999) where both the rewarding pattern and the nonrewarding pattern were present simultaneously during training. This suggests that the bees, rather than being mechanistically constrained in the perception of the dorsal part of the cue, just did not use this information for discrimination in absolute conditioning. Likewise, in both honeybees (Giurfa 2004) and bumblebees (Dyer and Chittka 2004c)

discrimination of highly similar colors was only possible when both rewarded and nonrewarded feeder types were simultaneously available for direct comparison (differential conditioning). The same discrimination task was not mastered with the sequential presentation of the rewarding and nonrewarding cues (absolute conditioning) (Dyer and Chittka 2004c; Giurfa 2004). Giurfa (2004) argues that such behavioral differences may be due to differences in the attention paid to the available cue characteristics. Whereas in absolute conditioning bees associate the absolute properties of a cue with the reward, selective attention to the cue dimension along which feeders are most different (e.g. brightness, color contrast, size, etc.) may facilitate discrimination of simultaneously presented alternative cues (Zentall and Riley 2000). Attentional filtering of cues to improve choice accuracy may be also found under high foraging risks (Zentall and Riley 2000; Chittka et al. 2003; Ings and Chittka 2008, 2009; Avarguès-Weber et al. 2010) and limitations in time available for the decision making (Zentall and Riley 2000). The latter may entail filtering from the entirety of available information in order to provide a simplified and less precise but quickly processable guide to reward (Zentall and Riley 2000). On the other hand, under some circumstances not paying full attention to available cues or to the task at hand may be beneficial (Beilock et al. 2002; Burns 2005).

Evidently the foraging context is important for the way the bees utilize visual information to guide their flower choice. Clearly the horizontal distribution of flowers as found in meadows shapes the distribution and flower visitation patterns of bumblebees and other pollinators, in a way that foraging returns are maximized (Pyke 1978; Heinrich 1979a, 1979b; Dreisig 1995; Keasar et al. 1996; Chittka et al. 1997; Keasar 2000; Cresswell and Osborne 2004; Wolf and Moritz 2008; Lihoreau et al. 2012). In contrast, bumblebees on vertical foraging grounds show a more stereotypic behavior, predominantly starting to forage low within an inflorescence and progressing upwards (e.g., Pyke 1979; Waddington and Heinrich 1979). This has been interpreted as a template strategy to minimize a bees' flower re-visitation and thus maximize foraging returns (Pyke 1979; Waddington and Heinrich 1979; Kevan 1990; Orth and Waddington 1997a, 1997b). However, none of these studies directly compared the bees' choice accuracy in vertically versus horizontally arranged flowers. In both cases floral reward varies widely among flower species and may be predicted from plant-specific sets of floral cues. Additionally rewards within the same flower type may vary with, among other factors, genotype, plant size, flower sex, flower age, and time of day (Shuel 1952; Harder and Cruzan 1990; Klinkhamer and de Jong 1990; Aizen and Basilio 1998; Pacini et al. 2003; Leiss et al. 2004). Some of these intraspecific differences may also be advertised for pollinators, for instance in that some flowers change color after pollination (Weiss 1991, 1995). Likewise, recent depletion by other pollinators may be indicated by scent marks (Stout and Goulson 2001; Wilms and Eltz 2008) or electrostatic "traces" (Clarke et al. 2013).

However, floral cues may be differently utilized to guide foraging choices depending on the spatial arrangement of flowers. On a diverse and patchy meadow, species-specific cues provide a reliable predictor of reward, which may also determine the movement between inflorescences (Orth and Waddington 1997a). However, within vertically structured forage adjacent flowers are often of the same species and reward may be less readily predicted from plant species-specific cues. Here we investigate if these 2 different foraging scenarios affect bumblebees in their

choice accuracy of easy to discriminate feeder types controlling for potential mechanistic constraints based on cue type and cue orientation.

MATERIALS AND METHODS

Bees

Bumblebees (*Bombus terrestris audax*) originated from 2 commercial colonies (Biobest Belgium N.V.). Each nest-box was connected to a foraging arena ($70 \times 70 \times 100$ cm) where workers freely foraged for 30% sucrose solution (w/w) from clear Perspex feeders simultaneously present in horizontal and vertical arrangement to familiarize them with the feeder arrays. Successful foragers were individually marked with number tags (Opalithplättchen, Warnholz & Bienenvoigt, Germany) for identification during the testing. Pollen was provided ad libitum directly into the colony.

Training protocol

Bees were tasked with distinguishing 6 unrewarding from 6 rewarding feeders. The rewarding feeder type provided 5 µL of sucrose solution (30% w/w) (conditioned visual stimulus paired with reward CS+), whereas the unrewarding feeder (CS−) contained a 5 µL droplet of water. Depleted feeders were refilled with 5 µL of sucrose after the bee had left the feeder using a dispenser pipette ensuring that throughout the training all rewarding feeders provided sucrose on every visit.

During training one individual bee was repeatedly allowed access to the foraging arena until a total of 100 consecutive feeder visits were recorded. A feeder visit was defined as the bee actually landing on the feeding platform. After each foraging bout all feeders were cleaned and the positions of rewarding and nonrewarding feeders were randomized before the bee was allowed to enter the arena again. After the training was completed, the bees were removed from the colony.

We conducted 4 experiments with modified feeder arrangement and cue display. We tested at least 10 bees from 2 colonies for each of the experimental settings.

Experiment 1

The bees had to distinguish 6 blue, nonrewarding feeders from 6 purple rewarding ones. As floral colors in the UV blue spectrum are innately preferred by bumblebees (Raine and Chittka 2007, 2009), these 2 colors greatly facilitated the readiness of naive foragers to visit the artificial feeders. The colored plastic chips used as color cues were identical to the ones used by Raine and Chittka (2007) with the short wavelength reflectance peaks of the 2 colors at 435 and 460 nm for purple and blue, respectively. In the hexagonal bee color space, the color distance was determined with 0.3 hexagon units (Raine and Chittka 2007). This constitutes a color distance large enough to allow for easy discrimination by bumblebees (Dyer and Chittka 2004a, 2004b).

These feeders consisted of a clear landing platform (Perspex, 2.5×2.5 cm) and the square feeder cue (color chip, 2.5×2.5 cm) presented directly above (Figure 1a,b). These feeders were either arranged vertically on the back wall of the arena in 4 rows of 3 feeders (Figure 1a) or horizontally on the arena floor (Figure 1b). The used feeder cues were identical for both arrangements and were always displayed vertically either on the arena wall or, for the horizontally spaced feeders, on a white paper screen (6×10 cm) attached to each feeder (Figure 1b). In both settings the feeders

were evenly distributed with an area of approximately 70×70 cm ensuring similar interfeeder distances between 10 and 15 cm. For both horizontally and vertically arranged feeders, we randomized the locations of rewarding and nonrewarding feeders between each foraging bout. The vertically arranged feeders were shuffled in a pseudorandomized fashion to ensure equal numbers of rewarding and unrewarding feeders in the top and bottom half of the array.

Experiment 2

Similar to experiment 1, the feeder cues were displayed vertically but consisted of a vertical or horizontal black bar (30×4 mm) on a white square (3×3 cm) as simplest and maximally different pattern cue predicting reward (Figure 1c,d). Either the one or the other bar orientation was rewarding for a given bee.

Experiment 3

Here the purple and blue (CS+ and CS−, respectively) feeder cues were displayed horizontally forming the actual landing platform of both vertically (Figure 1e) and horizontally (Figure 1f) arranged feeders. In this way we tested for potential behavioral differences due to a changed presentation of the feeder cue as compared with experiment 1. As pattern orientation cannot be assessed by an approaching bee if displayed horizontally we did not repeat this experiment for pattern cues.

Experiment 4

Expanding experiment 1, we tested the performance of foragers on both feeder arrangements successively starting with 100 visits on the vertical feeder setting (Figure 1a), subsequently switching to the horizontal setting for the next 100 feeder visits (Figure 1b), followed by a final 100 visits on the vertical setting again (Figure 1a). In this way we investigated the ability of individual bees to utilize the feeder cues on both settings and potential changes with increasing experience.

Data analysis and statistics

Learning curves based on the mean choice accuracies ($\pm$ standard deviation [SD]) of the bees trained in each of the 6 feeder settings (Figure 1a–f) were generated from the percentage of correct choices for every consecutive block of 10 visits of all bees in that setting. We used a general linear model (GLM) fitted to a normal distribution with cue type (CT: color, pattern), cue display type (CD: horizontal, vertical), feeder arrangement (FA: horizontal, vertical), and colony of origin (C: colony 1, colony 2) as fixed models to compare the choice accuracies of the bees over the course of the training in each of the possible groups (i.e., factors defined in the GLM). Separate between-group comparisons were done for all pairs of blocks of 10 visits representing identical training length, thus controlling for increasing experience during training.

For the experiments with vertically arranged feeders we tested for potential differences in the precision in the bottom versus the top 2 feeder rows (Morawetz et al. 2014) using χ^2 test on the visitation rate of rewarding and unrewarding feeders (3 rewarding and 3 unrewarding feeders in each group). All analyses were done in R (version 2.11.1).

RESULTS

We found a highly significant difference in the choice accuracy over the course of training on the vertical as compared with the
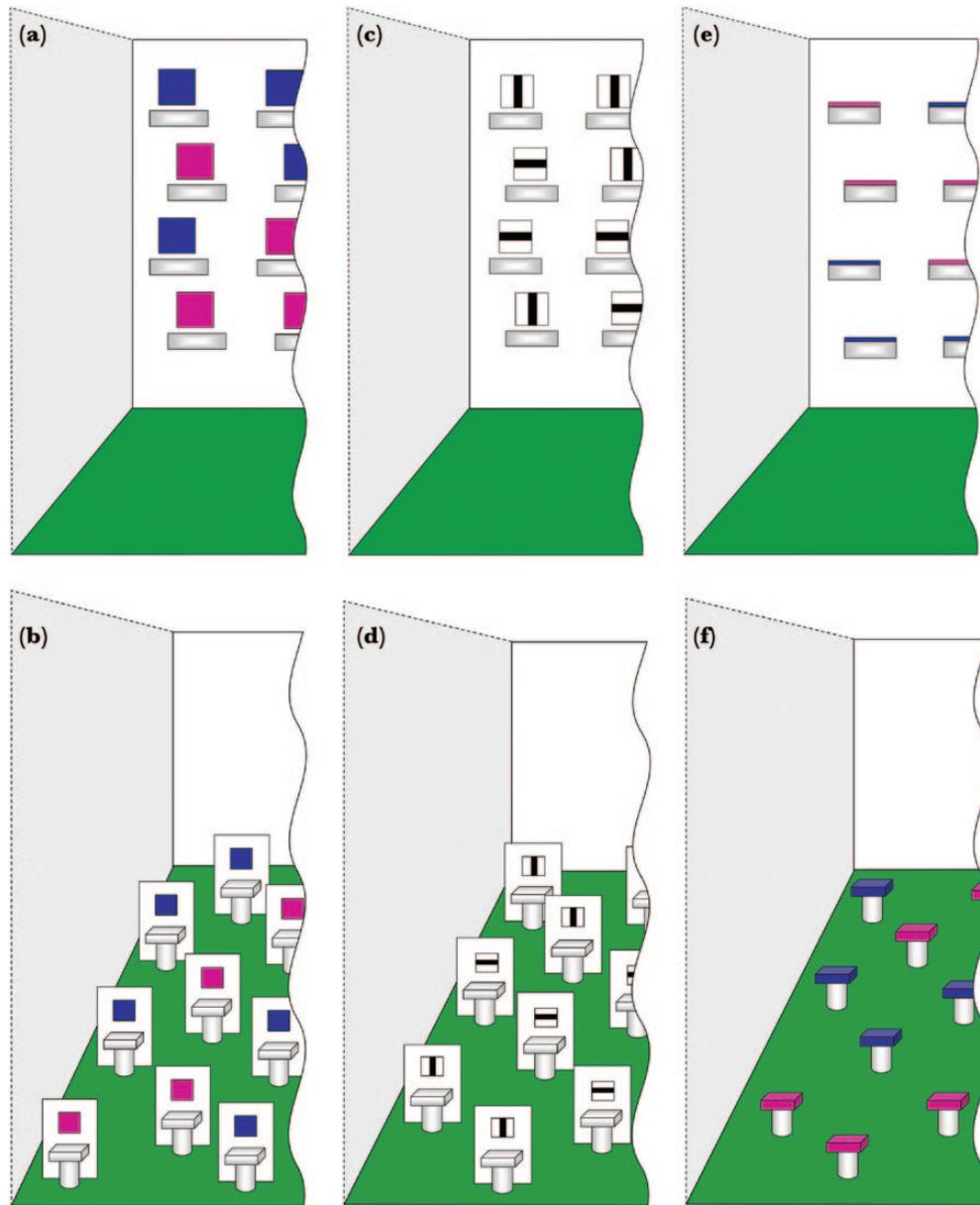
Figure 1
Graphical representation of the experimental setup to compare bee decision-making performance on (a, c, e) vertically and (b, d, f) horizontally arranged feeders. a versus b: comparison for vertically presented color cues (CS+: purple, CS−: blue); c versus d: comparison for vertically presented pattern cues (balanced design); e versus f: comparison for horizontally presented color cues (CS+: purple, CS−: blue). In all feeder settings the distance between the feeders was 10–15 cm.

horizontal feeder arrangement independent of the way feeder cues were displayed (Figures 2–4). On completion of the training, feeder arrangement was the sole significant driver of these differences in performance ($t_{56}^{FA100} = -6.274$, $P < 0.001$). At the beginning of training (first 10 visits) there was no significant difference between choice accuracy of bees with regard to cue types (color, pattern; $t_{56}^{CT10} = -1.718$, $P = 0.09$), cue display (horizontal, vertical; $t_{56}^{CD10} = 0.887$, $P = 0.38$), or spatial feeder arrangement ($t_{56}^{FA10} = -1.482$, $P = 0.14$). However, after 20 visits there was already a highly significant effect of feeder arrangement ($t_{56}^{FA20} = -2.849$, $P = 0.006$), whereas all other factors remain nonsignificant. Display orientation (CD) of the feeder cues remained nonsignificant throughout the training.

When exposing the foraging bees to vertically displayed color cues (experiment 1) or patterns (experiment 2) on feeders arranged either vertically (Figure 1a,c) or horizontally (Figure 1b,d), we found that bees on the vertical arrangement largely disregarded the cues and foraged with an overall choice accuracy of $53.1 \pm 13.2\%$ (mean $\pm$ SD) and $56.9 \pm 14.9\%$ correct choices after 50 and 100 visits, respectively. These were not significantly different from chance for both color (50: $\chi^2 = 1.22$, degrees of freedom [df] = 1, $P = 0.26$; 100: $\chi^2 = 3.6$, df = 1, $P > 0.05$) and pattern cues (50: $\chi^2 = 0.04$, df = 1, $P = 0.84$; 100: $\chi^2 = 1.44$, df = 1, $P = 0.23$). This is strongly contrasted by the performance on horizontally arranged feeders where bees overall averaged $77.1 \pm 19.5\%$ correct after 50 visits and $93.3 \pm 5.8\%$ after 100 visits (Figures 2 and 3).
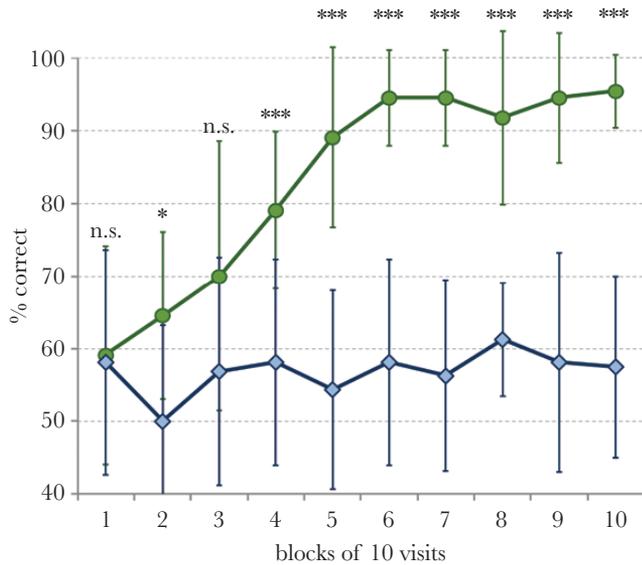
Figure 2
Learning curve (mean choice accuracy ± SD) over 100 visits of feeders with vertically displayed color cues arranged either horizontally (circles; $n = 11$) or vertically (diamonds; $n = 16$). There is a highly significant difference (n.s. = $P > 0.05$; *$P < 0.05$; ***$P < 0.001$; see text for details on the statistics) between the learning curves for the 2 feeder arrangements with only bees in the horizontal arrangement improving their decision making to more than 95% correct choices, whereas bees on the vertical arrangement remain below 60% correct choices at the end of training.
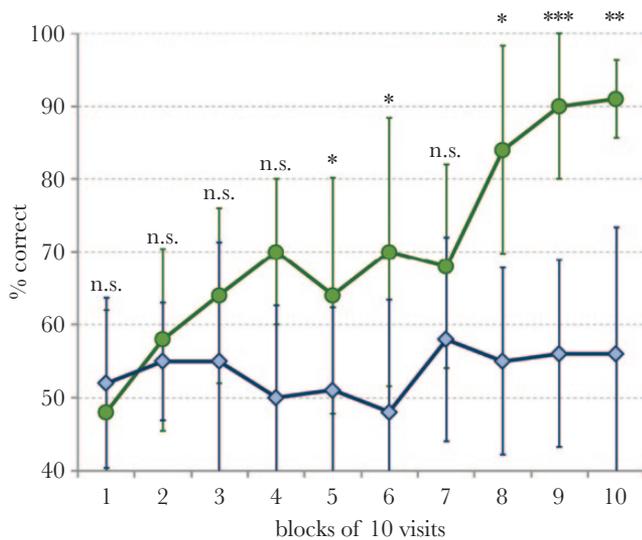
Figure 3
Learning curve (mean choice accuracy ± SD) over 100 visits of feeders with vertically displayed pattern cues arranged either horizontally (circles; $n = 10$) or vertically (diamonds; $n = 10$). There is a significant difference (n.s. = $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$) between the learning curves for the 2 feeder arrangements after the end of training with only bees in the horizontal arrangement improving their decision-making accuracy to more than 90%, whereas bees on the vertical arrangement remain below 60% correct choices.

When color cues were displayed horizontally (experiment 3, Figure 1e,f) the bees marginally improved performance on the vertical arrangement ($65.0 \pm 11.2\%$ and $69.0 \pm 18.1\%$ correct after
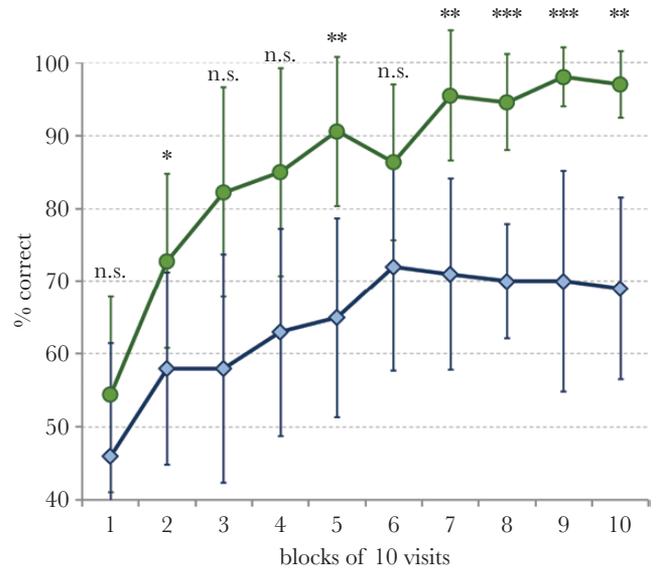
Figure 4
Learning curve (mean choice accuracy ± SD) over 100 visits of feeders with horizontally displayed color cues arranged either horizontally (circles; $n = 10$) or vertically (diamonds; $n = 10$). There is a highly significant difference (n.s. = $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$) between the learning curves for the 2 feeder arrangements with only bees in the horizontal arrangement improving their decision making to more than 95% correct choices, whereas bees on the vertical arrangement remain below 70% correct choices at the end of training.

50 and 100 visits, respectively) (Figure 4). However, the achieved performance on completion of the training was significantly below the performance on the horizontal feeder arrangement ($t_{16}^{FA100} = -3.897$, $P = 0.001$).

Analyzing the feeder visitation of a subsample of 15 individual trainings (i.e., 1500 individual feeder choices) on the vertical arrangement with both color or pattern cues, we found no significant preference for the bottom 2 (51.5%) versus the top 2 feeder rows (48.5%). There was also no difference ($\chi^2 = 0.047$, df = 1, $P = 0.83$) in the number of correct choices between top (53.0%) and bottom row feeders (52.6%).

In the transfer test from vertically to horizontally to vertically arranged feeders (experiment 4) individuals again foraged largely at random for the initial 100 feeder visits on the vertical feeder array. Being subsequently presented with the horizontally arranged feeders the bees quickly utilized the feeder cues to improve visitation rate on rewarding flowers to more than 90% after 50 visits ($98.0 \pm 4\%$ after 100 visits). However, after transitioning back to the vertical feeder array the bees did not apply the acquired knowledge about rewarding feeders and immediately reverted back to random feeder exploration reducing their decision-making precision from 98.0% to $53.0 \pm 13.5\%$. Accordingly the performance on the second leg of the vertical wall foraging showed no improvement in the decision-making accuracy as compared with the first (Figure 5).

DISCUSSION

We show that bumblebees in some foraging scenarios consistently disregard even easily distinguishable floral cues. The feeder cues were large enough to allow easy detection of adjacent feeders by foraging bees (Spaethe et al. 2001) and were sufficiently different to be discriminated (Dyer and Chittka 2004a, 2004b; Raine and Chittka 2007). Yet, only foraging on the horizontal feeder
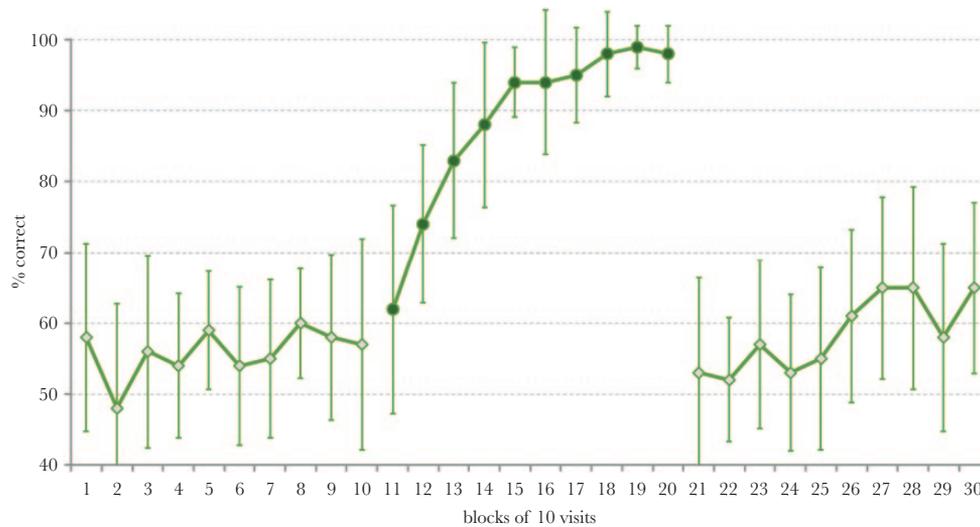
Figure 5

Learning curve (mean choice accuracy ± SD) over 300 feeder visits for bees ($n = 10$) successively transferred from vertical feeder arrangement (diamonds; first 100 visits) to horizontal feeder arrangement (circles, 100 visits) and back to the vertical arrangement (diamonds; last 100 visits). Reward was invariably predicted by vertically displayed color cues throughout the experiment. There is a striking difference in the bees' performance depending on feeder arrangement with performance improvement only observable in the horizontal setting. There was no significant difference in the performance of the first and second exposure to the vertical feeder setting.

arrangement resulted in the expected learning of the reward-predicting cue. The same cues displayed on vertically arranged feeders were largely disregarded and feeder choice was not significantly different from chance throughout the training. This is striking as cue characteristics, temporal and spatial scale of the foraging task, and reward predictability were highly similar in both arrangements and thus learning reward-predicting cues should be equally beneficial in both cases. Causes for this surprising difference in performance may be sought in perceptual limitations, attentional differences, or ecological implications inherent to either the spatial arrangement of flowers or the experimental design. Behavioral differences caused by training procedure (Dyer and Chittka 2004c; Giurfa 2004) and by the time available for decision making (Zentall and Riley 2000) could be ruled out because throughout the experiment we used differential conditioning and bees had temporary and spatially unrestricted access to all feeders.

However, marked differences in pattern discrimination depending on the way these cues are displayed have long been recognized in honeybees (Hertz 1929). Significant differences in the way differentially displayed pattern and color cues are used by bees to guide foraging decisions have been repeatedly demonstrated since (Horridge 1996; Giger and Srinivasan 1997; Fauria et al. 2000; Stach et al. 2004; Stach and Giurfa 2005; Arnon et al. 2009; Dyer and Griffiths 2012). Such differences have often been attributed to functional specializations of the honeybees' eye regions maximally exposed to the cue (Lehrer 1999) though this remains to be confirmed for bumblebees. Nonetheless, some studies clearly demonstrate that honeybees and bumblebees can successfully discriminate vertically displayed pattern cues in dual-choice experiments (e.g., Fauria et al. 2000; Stach et al. 2004; Stach and Giurfa 2005; Dyer and Griffiths 2012). However, these used 2 side-by-side feeders with vertically displayed cues which allowed simultaneous inspection of 2 patterns and in no case directly compared bees' performance in various spatial settings, for example, arrangements in the horizontal versus the vertical plane.

To separate the effects of cue display from the effects of the feeder arrangement we kept cue display strictly constant within

each experiment. On horizontally arranged feeders previous findings show that bumblebees learn horizontally displayed color cues better than vertically displayed ones (Arnon et al. 2009). This is in line with our finding that the bees on the vertical arrangement performed marginally better when color cues were displayed horizontally (Figure 1e) as compared with the performance on vertically arranged feeders with the color display being vertical (Figure 1a). However, it does not explain the significant difference between horizontal and vertical feeder arrangements. Even the improved vertical performance remained highly significantly below the accuracy achieved on horizontally arranged feeders. Overall, our data provide no evidence that the way the cues were displayed contributed significantly to the differences in the performance at any stage of the training.

Alternatively, new evidence suggests that honeybee decision-making accuracy is affected by feeder location within a vertical array (Morawetz et al. 2014). This could be explained by constraints in feeder perception depending on the position of the feeder within the visual field leading to differences in choice performance on the vertical plane. Therefore, this could provide a possible explanation for the observed reduction in choice accuracy on our vertically arranged feeders. Testing for any bias in the feeder visitation and accuracy in context of feeder height within the vertical array we found no evidence for such an effect in our data. Foragers on the vertical array had neither a preference for the bottom or top 2 rows of feeders (equally containing 3 rewarding and 3 nonrewarding feeders), nor did their accuracy differ with feeder position within the array. This again renders a mechanistic constraint on feeder perception as an explanation for the found results unlikely.

The most parsimonious explanation for the differences in choice accuracy between the vertical and horizontal plane is that attentional processes, depending on the spatial structure of the foraging grounds, lead to selective utilization of available cues resulting in distinct foraging strategies. In horizontally structured foraging grounds variation in reward is largely associated to specific sets of floral cues (flower type). Ignoring floral cues should greatly increase

the risk of visiting nonrewarding flower types, typically different in appearance. Therefore, capitalizing on the predictive value of such cues should be an advantageous strategy for both pollinators and pollinated plants. In contrast, vertically structured floral resources, such as vertical inflorescences, blooming bushes or trees often provide large numbers of a single flower type in close vicinity. These may be perceived by foragers as flowers of a single species (Orth and Waddington 1997a) and bees might not "expect" visual variation of flowers to be reliably associated with reward. Hence, bees may disregard individual flower cues in their flower-to-flower movement. Numerous insect pollinators in addition to *B. terrestris* have been shown to exhibit stereotypical bottom-to-top movement patterns within vertical inflorescences including other bumblebee species (*B. terricola*: Galen and Plowright 1985; *B. hortorum*: Corbet et al. 1981; *B. pennsylvanicus*: Orth and Waddington 1997b; 3 species: Valtueña et al. 2013), honeybees and non-*Apis* bees (*Xylocopa micans*: Orth and Waddington 1997; 5 species: Valtueña et al. 2013), and nectar foraging wasps (*Dolichovespula* and *Vespula* spp: Corbet et al. 1981; 7 species: Valtueña et al. 2013).

The context-specific allocation of attentional resources to available floral cues shown here in bumblebees may reflect a more widespread response to vertically structured resources, similar to the cue utilization proposed for foraging insects in hierarchically distributed resources in the horizontal plane (Hassell and Southwood 1978). Here, specific sets of cues may be selectively used to detect and discriminate patches of resources, whereas focusing on a different set of cues (if any) may guide foraging within a patch (Hassell and Southwood 1978; Bell 1990). Similar associations between foraging strategy and the spatial scale at which feeders are regarded as individual (patches of) resources have also been suggested for hummingbirds. Despite being equipped with acute color vision (Goldsmith and Goldsmith 1979; Goldsmith 1980; Chen and Goldsmith 1986), when foraging on arrays of multiple close-by feeders these birds seem to largely disregard salient color cues in favor of learned positional cues to identify previously rewarding feeders (Hurly and Healy 1996). Interestingly, distractor flowers in close proximity to the focal flower had similar effects on (within-patch) choice accuracy irrespective of their visual similarity to the focal flower. However, when an identical distractor flower was placed further away the birds increasingly visited both flowers potentially being perceived by the bird as 2 distinct, visually similar patches to choose from. A decrease in choice accuracy was not seen when a dissimilar distractor was moved further from the focal feeder thus representing a visually different patch (Hurly and Healy 1996). This is further supported by findings of Baum and Grant (2001) who predicted that for clustered resources (such as inflorescences) indiscriminately visiting adjacent feeders is the most efficient foraging strategy closely matching the foraging efficiency achieved in the field. Analyzing foraging returns of bumblebees foraging on vertically arranged and visually highly similar feeders, Burns (2005) found that bees, which foraged fast but less accurately collected on average more sucrose per time unit than accurate and slow foraging bees, thus making this a viable foraging strategy in this foraging condition (Burns 2005).

This not only explains why our bees disregarded the feeder cues in the vertical plane even though these cues were highly distinguishable, but also why there was little or no transfer of acquired information from one spatial arrangement to another. After having successfully mastered discrimination of the rewarding feeders in the horizontal setting, bees in the vertical arrangement, primed for discrimination of patches of flowers rather than individual flowers, show no significantly different performance to naive bees (Figure 5).

However, attention to or away from specific cues may be refocused under certain foraging conditions. Bees have been shown to be, at least in principle, capable of discriminating visual cues on vertically arranged feeders (Chittka et al. 2003; Ings and Chittka 2008, 2009; Morawetz and Spaethe 2012; Dawson et al. 2013) yet only achieved high choice accuracy if either chemical (quinine) or mechanical (mechanical crab spider) punishment for erroneous decisions was used. Likewise, bumblebees were able to selectively and correctly chose rewarding feeders on a vertical array after these had been socially communicated by informed demonstrator bees (Worden and Papaj 2005; Avarguès-Weber and Chittka 2014). Hence, although the foraging strategy of disregarding visual cues on the vertical plane may be maintained with varying floral cues, bees may abandon this approach if costs of visiting nonrewarding flowers become high or social cues facilitate feeder choice.

In conclusion, we provide a rare example of a generalist pollinator choosing not to discriminate flower types although clearly able to do so. Our results indicate that attentional processes associated to the spatial structure of the foraging resource may markedly affect the foraging strategies of bumblebees, and potentially a wide range of other insect pollinators.

FUNDING

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