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Detection of patches of coloured discs by bees

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SUMMARY

To find out how grouping of flowers into patches improves their detectability by hymenopteran pollinators, we trained honeybees and bumblebees to detect groups of three spatially separated disks and compared results with the detection limit for single disks. When the discs presented contrast to the long-wavelength-sensitive (L) receptor, grouping of disks improved the detectability. The disks were optically resolvable for the honeybee eye. The improvement of detectability was stronger for bumblebees than for honeybees. When disks did not present contrast to the L-receptor, the grouping did not improve the detectability, i.e. the detection limit was set by the size of a single disk. We conclude that in bees the neural mechanisms that improve detectability of grouped elements require input from the L-receptor. Our results indicate that grouping of flowers into sparse patches can improve their detectability by bees, even when individual flowers can be optically resolved by the eyes of bees, as long as flowers can be detected by the long-wavelength-sensitive receptor.

INTRODUCTION

Although insect compound eyes have low spatial resolution (Land, 1997), insects effectively use vision for foraging and navigation. In particular, bees rely on visual cues for detecting and discriminating profitable flowers. Flowers are often grouped into inflorescences, forming patches – an arrangement that is likely to increase the distance from which flowers are detected by pollinators. Here we ask how grouping of coloured targets into patches improves their detectability.

Pattern perception in bees has been in the focus of research for more than a century (e.g. von Frisch, 1914; Baumgärtner, 1928; Hertz, 1929a; Hertz, 1929b; Hertz, 1931; Hertz, 1933; Hertz, 1935; Schnetter, 1968; Wehner, 1969; Cruse, 1972; Anderson, 1977; Srinivasan and Lehrer, 1988; Collett and Cartwright, 1983; Menzel and Lieke, 1983; Giger and Srinivasan, 1995; Giurfa et al., 1996a; Efler and Ronacher, 2000; Stach et al., 2004; Zhang et al., 2004; Dyer et al., 2005) (for reviews, see Wehner, 1972; Wehner, 1981). The early attempts were devoted to discover which particular features such as pattern border length, density, edge orientation or degree of disruptiveness could be discriminated by bees. Later studies showed that the brain of the bees effectively encodes low-level spatial features of many different patterns (for reviews, see Lehrer, 1987; Srinivasan et al., 1994; Heisenberg, 1995; Giurfa and Menzel, 1997; Horridge, 1999; Horridge, 2005).

A pattern can be a feature of a single target, but it can also be formed by spatially arranging several visual elements or targets. Our present study is related to the latter, and is based on previous work which showed that honeybees detect targets using two largely independent mechanisms (Giurfa et al., 1996b; Giurfa et al., 1997; Giurfa and Vorobyev, 1998). An achromatic mechanism is mediated by the long-wavelength (L) or green-sensitive photoreceptor. This mechanism can detect relatively small circular targets [angular subtenses down to 5° (Lehrer and Bischof, 1995; Giurfa et al., 1996b; Hempel de Ibarra et al., 2001)], but this mechanism is not sensitive to targets subtending visual angles larger than 15° (Giurfa and Vorobyev, 1998). The second mechanism is chromatic, i.e. it is not sensitive to changes in stimulus intensity, receiving inputs from all three spectral types of bee photoreceptors. This mechanism has low spatial resolution – the limiting visual angle for a single circular targets is about 15° (Giurfa et al., 1997). The same mechanisms operate when bees look at targets that display two colours arranged in concentric patterns (Hempel de Ibarra et al., 2001; Hempel de Ibarra et al., 2002). However, for such patterns the minimum distance at which the target can still be detected is decreased, i.e. the angular detection limit increased. The critical parameter that determines this change in detectability is the distribution of L-receptor contrasts. In previous experiments we found that if a central disc with a weak L-receptor contrast (dim) was surrounded by a ring with strong L-receptor contrast (bright), the target yielded a detection limit of 6.5° (Hempel de Ibarra et al., 2001). Detection of the reciprocal arrangement of the pattern colours, i.e. where the ring was dim and the central disc was bright, was only worse when its visual angle subtended more than 10°.

Here we explored a different spatial pattern, presenting bees with single discs and triplet patterns composed of three spatially separated discs. We expected that the detection performance would be limited by the detectability of a single disc in these triplets, and we expected to find two angular detection limits related to the presence or absence of L-receptor contrast in the colours of the stimuli. We used bumble bees (*Bombus terrestris*) and compared the experimental outcomes with those obtained with honeybees (*Apis mellifera*) trained in a similar way. In these two species of hymenopteran pollinators the spectral sensitivities of their photoreceptors is similar (Peitsch et al., 1992), but the optical resolution of their eyes differ (Macuda et al., 2001; Spaethe and Chittka, 2003) and the processing properties of their visual pathways may also differ.

MATERIALS AND METHODS

The method and apparatus were identical to that described by Giurfa et al. (Giurfa et al., 1996b). Individually marked bees were trained to find a sucrose reward on a target presented in a Y-maze. Honeybees, *Apis mellifera* L., entered through a large open window of a laboratory room (for details, see Hempel de Ibarra et al., 2001), whereas bumblebees *Bombus terrestris* L. (purchased from STB Control, Aarbergen, Germany) were kept within a flight cage, situated in a glass house. The experimental procedure was the same for the two species.

After flying into the maze a bee was able to see both back walls simultaneously. It learned to choose the arm containing a visible target rather than the arm containing no target while flying within the decision chamber. This enabled us to control the stimulus size seen by the bee during decision making. At each visit the first choice was recorded. When the animal entered the arm with the rewarded stimulus, its choice was recorded as correct and it was allowed to feed *ad libitum*. If it entered the unrewarded arm, its choice at this visit was recorded as incorrect. It was then either allowed to return to the maze entrance or it was gently pushed out of the maze to repeat the task until it found the reward.

The back walls displaying the target on either-way side were placed at different distances along the maze arm or the target size was reduced to vary the visual angle (α) subtended by the target (Giurfa et al., 1996b). The target's angular subtense was decreased as soon as an animal performed a number of subsequent visits (between six and 29) with a correct performance significantly above the 60% threshold of correct choices, as determined by the binomial distribution. If at one step targets were no longer detectable and arms were thus chosen randomly, the bees' choices were recorded during 30 visits, followed by a performance check with the target subtending the largest visual angle. The smallest angular subtense at which a target was detected by the bees of each experimental group was determined as α_{det} whereas the smaller subtense tested subsequently was determined as α_{indet}. Bees could move within the decision chamber of the maze before entering one of the arms. The minimal and maximal distance from which a bee could see the back walls in both arms differed by the distance from the centre of the decision chamber by 5 cm. We calculated the maximum and minimum angular size of the target for all distances tested estimating the error of the visual angle (Giurfa et al., 1996b). The detection limit (α_{lim}) was defined by the transection between the behavioural function of correct choices and the statistical criterion of significance (P_0=0.6).

Each bee learned only one target. This could be either a single coloured disc with a diameter of 8 cm (bumblebees) or 4.6 cm [honeybees, for comparison of detectability of differently sized targets (see Giurfa et al., 1996b)] or to detect a triplet pattern consisting of three discs of the same colour and size (each 4.6 cm in diameter) arranged in an upright triangle. A distance of 4.6 cm was kept between neighbouring discs (border to border) to prevent a merging of the triplet elements at small angular subtenses. Single disc detection was tested in bumblebees with angular subtenses of 29.9°, 16.9°, 13.0°, 10.2°, 7.6°, 7.0°, 5.1°, 4.3°, 2.5°, 2.3°, 1.3°, and triplet detection with 17.5°, 7.6°, 5.9°, 4.1°, 2.5°, 1.3°, 0.6° of visual angle subtended by a triplet disk. Honeybees were tested with discs and triplets subtending 17.4°, 5.9°, 4.1°, 3.3°.

We chose the same yellow and violet colour used in previous studies (Giurfa et al., 1996b) that differed in their L-receptor contrast to the background. Stimuli were cut from standard graphic papers (HKS 3N and 33N; background grey HKS 92N; K+E Druckfarben, Germany). Glasshouse illumination and the reflectance spectra of the papers were measured with a calibrated photospectrometer (Ocean Optics, Dunedin, FL, USA). Receptor signals were calculated as quantum catches integrating illumination spectrum, reflection spectrum and the spectral sensitivity of each bee's photoreceptors (Wyszecki and Stiles, 1982). Contrasts for each receptor type were calculated by normalising stimulus quantum catch to the quantum catch of the grey background (for details, see Hempel de Ibarra et al., 2001). If values of these ratios are close to 1, a stimulus has no receptor contrast for the particular receptor type, because receptor signals do not change between stimulus and background. Under the glasshouse illumination the yellow stimuli presented a slightly smaller L-receptor contrast to the background than under daylight conditions in the experiments with the honeybees (3.2 and 3.6, respectively). Violet stimuli had no L-receptor contrast under both illuminations. Chromaticity of both colours was well above threshold [RNL model of bee colour vision (Vorobyev et al., 2001)]. Bumblebees were selected by eye to be similarly sized in order to reduce variability in eye-size (Spaethe and Chittka, 2003), and in addition, their thorax width (from 3.5–4.5 mm; mean 4.0 mm) was measured after the experiment.

RESULTS

We found that bumblebees detected yellow targets from further away or at smaller angular subtenses than violet ones. The single yellow disc subtended a visual angle of α_{det}=2.3° when it was last detected by the bumblebees (binomial test, P=0.035) and α_{indet}=1.3° when it was not detectable anymore (N=10 bees, P=0.99). The behaviourally determined detection limit was thus α_{lim}=1.8° (see Fig. 1). The violet disc was last detected when subtending α_{det}=4.3° (P<0.001) and not detected anymore subtending α_{indet}=2.5° (P=0.79, N=6 bees). Thus, the absence of L-receptor contrast resulted in an impaired distance range for the detection of the violet disc (with an detection limit of α_{lim}=3.2°, see Fig. 2). These results resemble previous findings with honeybees where the presence of L-receptor contrast in a coloured target increased the distance over which a stimulus was detected (Giurfa et al., 1996b). The better detection limit for the bumblebee eye as compared with the honeybee can be attributed to the larger size of its eyes, which is correlated with its

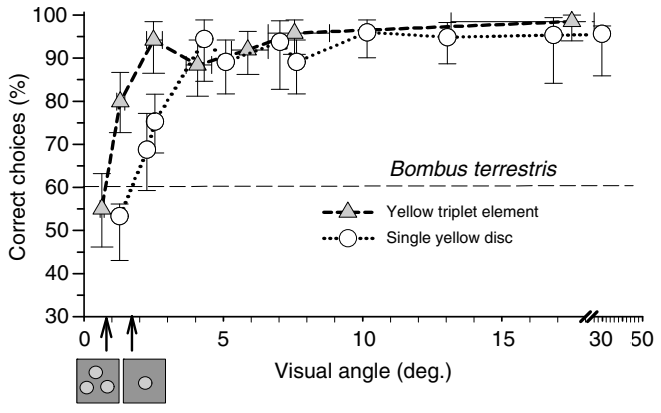

Fig. 1. Detection of yellow discs and triplets by bumblebees. The performance of bees is plotted as a function of the visual angle subtended by a single disc presented either alone (open symbols) or as an element of a triplet (grey symbols). The yellow colour of the targets provided chromatic contrast as well as L-receptor contrast against the background. The detection limit (arrow) for a disc presented alone (α_{lim}=1.8°) was worse than that of a disc presented in a triplet (α^{e}_{lim}=0.6°). The horizontal broken line indicates the discrimination threshold of 60%.

larger body size allowing reduced interommatidial angles and improved optical resolution (Macuda et al., 2001; Spaethe and Chittka, 2003).

When trained to detect the yellow triplet (Fig. 1), bumblebees could detect the target over a larger distance than the distance predicted from the detectability of a triplet element. The triplet was detectable for bees over a large distance, while the triplet's element subtended angles larger and equal to α^{e}_{det}=0.6° and/or the whole triplet in its largest lateral extension α^{t}_{det}=1.9° (binomial test, P=0.03, N=11 bees). At this angular subtense, individual bees were tested over 30 trials but did not display significant levels of correct choices. We therefore did not test them further with smaller patterns. Since the summed choices were significantly correct, we concluded that at this angular subtense detectability of the pattern was close to the detection limit and therefore set α^{e}_{lim}=0.6° (α^{t}_{lim}=1.9°). This is a more realistic estimate in this case as compared to the one that can be derived from the graphical definition of detection limit (α^{e-g}_{lim}=0.8°, α^{t-g}_{lim}=2.4°) since individual bees did not detect the triplet. For comparison, a single disc was not detectable for bumblebees at this angular subtense (Fisher exact test, P=0.02). Thus, the detection limit for the triplet was improved as compared to single discs. Interestingly, the limiting visual angle for a yellow triplet in its largest lateral extension, α^{t}_{det}=1.9°, is similar to the limiting visual angle for a single yellow disc (α_{lim}=1.8°).

Bumblebees were able to detect the violet triplet, presenting only chromatic contrast to the background but no L-receptor contrast, at a distance where a triplet element subtended α^{e}_{det}=4.1° and the whole triplet in its lateral extension α^{t}_{det}=12.3° (binomial test, P<0.001, N=11 bees; Fig. 2). When the single element subtended α^{e}_{det}=2.5° and the triplet α^{t}_{det}=7.4°, bees were unable to detect the stimulus. Thus the detection limit for the violet triplet was a^{e}_{lim}=2.6° and a^{t}_{lim}=7.8° (Fig. 2). Since the bumblebees trained with the single violet disc were reaching a detection limit between α_{det}=4.3° and α_{indet}=2.5° the result indicates that the detectability of the triplet was limited by the detectability of the single element.

We repeated the experiment with honeybees, testing whether they would detect yellow discs differently if presented alone or in a triplet. The single disc was detected until α_{det}=5.9° (N=9 bees, P=0.008)

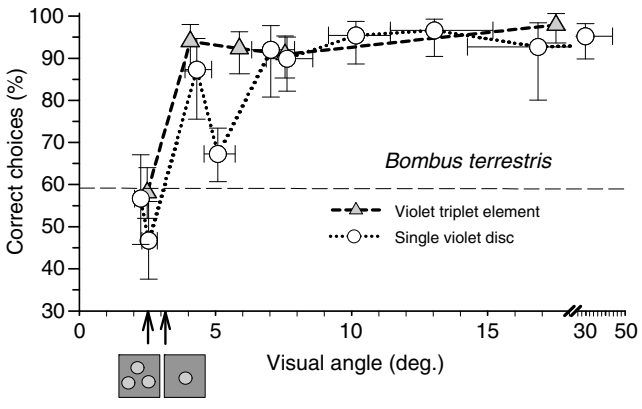

Fig. 2. Detection of violet discs and triplets by bumblebees. The violet stimulus colour provided only chromatic contrast against the background but no L-receptor contrast. The detection limit for a disc did not change significantly if presented alone (α_{lim}=3.2°) or in a triplet (a^{e}_{lim}=2.6°). The lack of coincidence between a modelled response to the triplet's area (grey symbols) and to a single target (open symbols) is obvious, supporting the assumption that detectability of the violet triplet was based on the detectability of its elements.

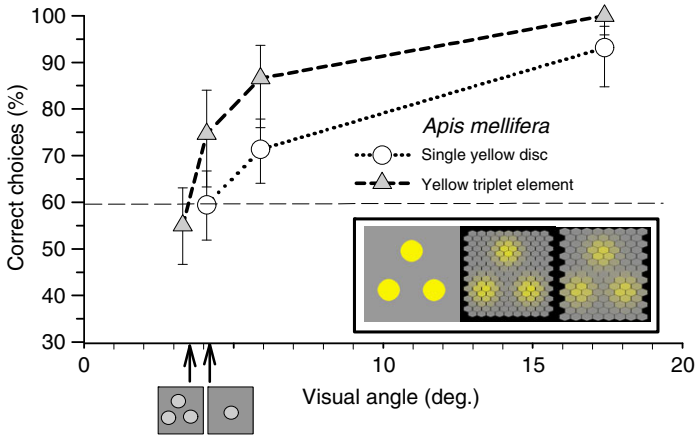

Fig. 3. Detection of yellow discs and triplets by honeybees. Honeybees had to detect a disc being presented alone (open symbols) or in a triplet (grey symbols). The colour of the discs provided chromatic contrast as well as L-receptor contrast. Similarly to bumblebees, the detectability of a disc presented in a triplet was enhanced. Inset: projection of the triplet on the honeybee's ommatidial lattice shows that the elements did not merge at small angular subtenses. In the middle panel the triplet subtended 4.1°, an angular subtense at which it was still detected by honeybees. The triplet at an angular subtense of 3.3° (right panel) was undetectable for bees.

and not detected at α_{indet}=4.1° (N=6 bees, P=0.63; α_{lim}=4.2°; Fig. 3). These results were similar to that described previously in identical experiments (Giurfa et al., 1996b; Hempel de Ibarra et al., 2001). The detection performance changed for discs arranged in a triplet. The yellow triplet was still detectable for honeybees when the triplet elements subtended α^{e}_{det}=4.1° (α^{t}_{det}=12.3°; N=8 bees, binomial test, P=0.006). At this angular subtense a single disc cannot be seen by the bee: the performance difference between the two groups was significant (Fisher exact test, P<0.0001). At α^{e}_{indet}=3.3° (N=6 bees, α^{t}_{indet}=10.0°) bees were no longer able to detect the yellow triplet (P=0.82, NS). Thus the arrangement of yellow elements into a triplet improved the detection range for honeybees. However, this improvement was not as strong as that observed for bumblebees.

We simulated the appearance of the triplet to the bee eye at different distances projecting it onto the honeybee ommatidial lattice (Vorobyev et al., 1997) (Fig. 3, inset). The disc elements covered ommatidia which were clearly separated in space at any angular size tested. We conclude that the improvement of detectability at small angular subtenses was not achieved because the triplet discs appeared to merge for the honeybee.

DISCUSSION

What bees see through their low-resolution eye depends on both the distance to a target and the target's size, i.e. the angular subtense. Previous work has shown that in order to be detected by honeybees a uniformly coloured circular target must cover at least seven ommatidia if this target presents L-receptor contrast to the background, and at least 59 ommatidia if L-contrast is absent and the target is detected on the basis of chromatic cues alone (Giurfa et al., 1996b). This limiting number of ommatidia is largely independent of the strength of the target's contrast to the background, indicating that detection requires comparison of signals of neighbouring ommatidia and hence a neural processing that goes beyond summation of signals of single ommatidia. Further studies of targets with centre-surround structure demonstrated that the

limiting visual angle depends on the distribution of L-receptor contrast within the target (Hempel de Ibarra et al., 2001). However, it remained uncertain whether the rules of target detection revealed in honeybees can be extrapolated to other hymenopteran pollinators, such as bumblebees. Bumblebees detect targets from further distance than honeybees (Macuda et al., 2001; Spaethe and Chittka, 2003). This improvement of visual angle can be explained by better optical resolution of the bumblebee eye (Spaethe and Chittka, 2003). It is also possible that neural processing of ommatidia signals is different in honeybees and bumblebees.

Our results reveal both similarity and differences between honeybees and bumblebees in neural processing of ommatidial signals. Bumblebees, like honeybees, have two largely separate pathways for processing of visual information – achromatic vision mediated by the L-receptor has high resolution, and chromatic vision has low resolution. This was also found by Dyer and colleagues (Dyer et al., 2008) in a new study carried out independently from ours. The fact that the detectability by chromatic vision alone of a triplet is determined by detectability of single elements indicates that chromatic cues are not used to group elements of a target to increase its detection range. Where L-receptor cues are available the detection is improved by grouping the elements. In the case of bumblebees this improvement is consistent with the assumption that the longest diameter of a triplet determines the limiting visual angle. However, in the case of the honeybees the improvement is weaker than that predicted from the size of a whole triplet, which may indicate that honeybees and bumblebees process ommatidial signals differently.

It is important to note that in the case of honeybees the elements of the triplet can be optically resolved, and therefore the improvement of the detection range cannot be explained by optical merging of the elements. Optical modelling of the honeybee eye gives very reliable results, because the geometry of honeybee foragers eyes are almost identical, which is confirmed by practically identical results obtained by different researchers (e.g. Kirschfeld, 1973; Seidl, 1980). However, because bumblebee eyes differ in size, any optical model may give unreliable estimates of optical resolution of animals used in our behavioural experiments. Therefore, we cannot estimate the number of bumblebee ommatidia corresponding to the limiting visual angle and it remains uncertain whether the elements of a triplet could be optically resolved by bumblebees at the detection limit.

Our findings show that insect-pollinated flowers may benefit by evolving inflorescences composed of small flowers that are clearly separated from each other, given that such flowers have L-receptor contrast to the background.

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