Grouping of visual objects by honeybees

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Summary

Recent work has revealed that monkeys as well as pigeons are able to categorise complex visual objects. We show here that the ability to group similar, natural, visual images together extends to an invertebrate – the honeybee. Bees can be trained to distinguish between different types of naturally occurring scenes in a rather general way, and to group them into four distinct categories: landscapes, plant stems and two different kinds of flowers. They exhibit the same response to novel visual objects that differ greatly in their individual, low-level features, but belong to one of the four categories. We exclude the possibility that they might be using single, low-level features as a cue to categorise these natural visual images and suggest that the categorisation is based on a combination of low-level features and configurational cues.

Key words: honeybee, learning, memory, grouping, categorization, matching-to-sample, cue.

Introduction

Recent research is revealing that honeybees possess sophisticated sensory and perceptual mechanisms that enable them to navigate to food sources accurately and efficiently. They are able to use a series of visual images of the environment acquired *en route* to get to their destination (Collett, 1996; Collett et al., 1993; Judd and Collett, 1998; Wehner et al., 1990, 1996). Bees are also able to associatively group and recall visual stimuli along their foraging paths, enabling them to organize and retrieve navigational information pertaining to multiple routes (Zhang et al., 1999). They can learn to use symbolic rules for navigating through complex mazes and to apply these rules in flexible ways (Zhang et al., 1996, 1999, 2000). Honeybees are able to form 'concepts' of sameness and difference. They can learn to solve matching-to-sample and non-matching-to-sample discriminations, and transfer the learned rules to novel stimuli of the same or a different sensory modality (Giurfa et al., 2001). Bees can also extract general properties of a stimulus, such as orientation (Wehner, 1971; van Hateren et al., 1990) or symmetry (Horridge and Zhang, 1995; Giurfa et al., 1996; Horridge, 1996), and apply them to distinguish between other stimuli, which they have never previously encountered. This demonstrates that honeybees are able to categorise artificial geometrical objects by using abstract features. Although the bee has only a tiny brain, many of the behaviours referred to above require considerable perceptual capabilities and central storage and evaluation mechanisms associated with experience-dependent adaptations (Srinivasan and Zhang, 1998; Menzel and Giurfa, 2001).

The natural environment in which a bee operates is composed of a variety of landscapes and a variety of objects within them, such as trees, plants and flowers. How do honeybees look at objects and scenes? Can bees group the different types of objects that they encounter into different categories? Such a capacity would facilitate rapid and accurate recognition of important landmarks and targets, and enhance foraging efficiency.

Object grouping can be thought of as the ability to link together items that are 'similar', even though they are distinguishable from one another. A rose is a rose, regardless of its exact size, colour or orientation; it can thus be considered to belong to a group that is different from the group of rocks, for example, or trees, or ponds.

Recent work has revealed that monkeys and other primates are able to categorise complex visual images, such as photographs of human faces, trees and other animals (Davenport and Rogers, 1971; Vogels, 1999; Freedman et al., 2000). Martin-Malivel suggested that the baboon can form amodal abstract concepts of human and baboon categories (Martin-Malivel and Fagot, 2001). Pigeons have the capacity to group objects into a number of different categories, such as people, other pigeons, trees, water, landscapes and so on (Mallott and Siddall, 1972; Herrnstein, 1984; Roitblat, 1987; Huber et al., 2000). They can even learn to distinguish between outline drawings of the leaves of different tree species (Cerella, 1979). Bumblebees can learn to associate colour with a reward, irrespective of other visual parameters such as size or shape (Dukas and Waser, 1994). So far, however, there have been no

studies investigating the ability of invertebrates to classify complex, natural objects.

Here we explore whether bees can learn to distinguish between four different categories of natural visual images that are likely to be relevant to their foraging behaviour. The categories examined are flowers of two different shapes, plant stems and landscapes. The items belonging to the different categories possess distinct characteristics, and are unambiguously perceived, at least by humans, as belonging to different perceptual classes. On the other hand, items belonging to a given category are perceived, at least by humans, as being 'similar', and belonging to the same class.

Materials and methods
General

The experiments were carried out in the All Weather Bee Flight Facility at the Australian National University's Research School of Biological Sciences. The facility consists of a modified glasshouse in which the internal temperature is regulated by a computer to maintain $24\pm5°C$ during the day and $17\pm3°C$ at night. A beehive with two entrances, one allowing bees access to the inside of the facility and the other to the outside, was mounted on the wall of the facility. Bees foraging indoors obtained sugar water from feeders in the facility. For each experiment, about 20 bees were marked individually at the beginning of the experiment and trained to visit a feeder containing $0.5\,\mathrm{mol\,l^{-1}}$ sugar solution in the maze. The experiment commenced with pre-training for 2 days (training bees to enter the maze and choose among test stimuli), followed by training on the actual task. The latter phase included training periods, learning tests and transfer tests (Type 1 and Type 2, described below). The entire experiment ran for 11 days. 8 bees remained at the end of the experiment.

Experimental setup

A multiple-choice maze, located inside the facility, was used for training and tests. Bees entering the maze encountered a 'sample' stimulus at the entrance chamber (C1), a connecting chamber (C2) and four additional 'test' stimuli in a subsequent test chamber (C3; Fig. 1A,B). The bees were trained to fly through chambers C1, C2 and C3 in succession. The back wall of the entrance chamber C1 carried the sample stimulus. The bees flew through a 3 cm hole in the sample stimulus to chamber C2, the back wall of which consisted of a transparent film with a 3 cm diameter aperture in the centre. The transmission of the film is approximately uniform in the human visible spectrum and is reduced in the UV. The latter, however, is irrelevant, as there is relatively little UV light within the bee flight facility, because the roof blocks most of it. This aperture restricted the bees' speed of flight through the apparatus, and the transparent film provided the bees with a view from C2 of
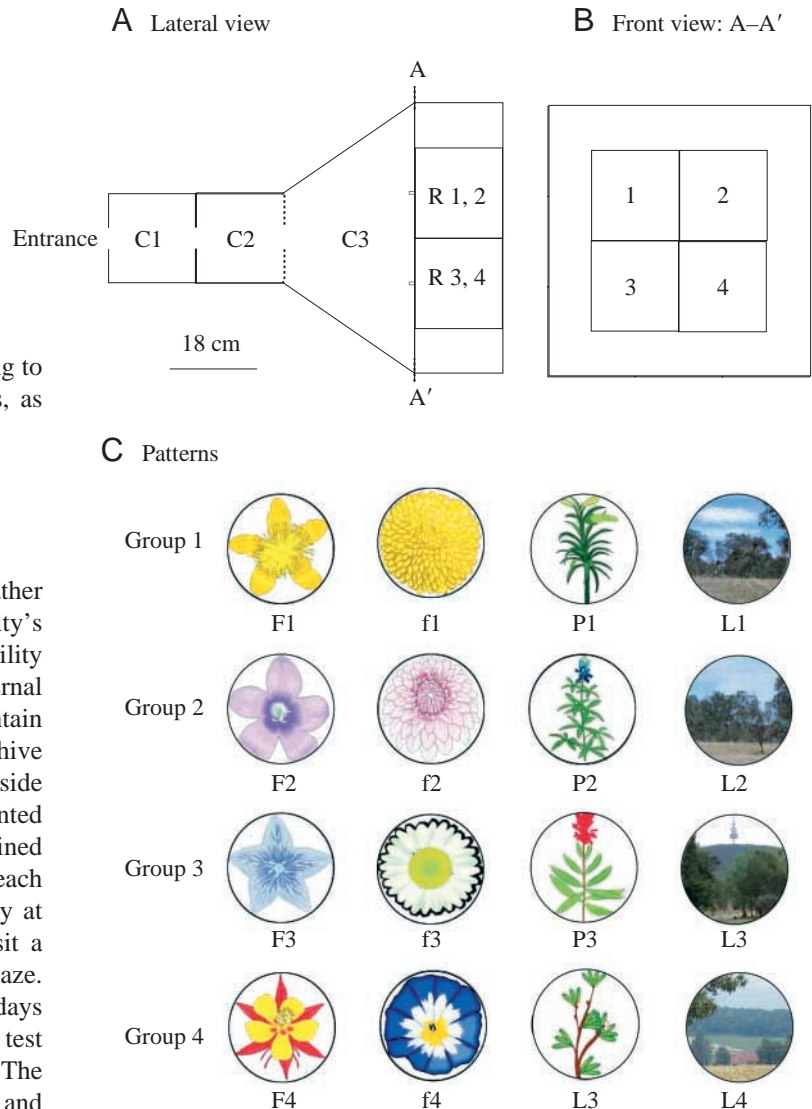

Fig. 1. Illustration of experiments showing (A,B) the multiple-choice maze apparatus and (C) the four groups of stimuli that were used. See text for details.

the four test stimuli, that were mounted on a 'choice board', forming the back wall of the test chamber C3. If the bee chose the correct test stimulus in C3, she would be able to receive a reward of sugar solution from a feeder that was placed in the reward box, R, behind that stimulus, by landing on and crawling through a tube in the centre of the stimulus.

Visual stimuli

Four groups of complex images (G1, G2, G3 and G4), printed on disks of diameter 18 cm using a colour laser printer (Tektronix Phaser 780 Graphics, NWS Corp., NY, USA), were used in the training and the tests. Each group consisted of four stimuli, each stimulus belonging to a different category (Fig. 1C). The categories were as follows. One category (F) consisted of images of flowers that were star-shaped, but of different colours. A second category (f) comprised images of

flowers that were nearly circular in shape, again of different colours. The third category (P) consisted of images of plant stems, of various shapes. The final category (L) was composed of images of landscapes. Within each category, individual images differed in the details of their shape, texture and, sometimes, colour. In transfer tests, the sample stimulus was always from Group 1 and the four test stimuli on the choice board were from one of the three other groups (G2, G3 or G4). Each test stimulus, again, was from a different category, as shown in Fig. 1C.

Training and testing procedures

During training and learning tests, the sample stimulus and the four test stimuli on the choice board were from Group 1. Each of the four test stimuli was from a different category, as shown in Fig. 1C. During training, the sample pattern was changed every 10 min (after an average of two rewarded visits per bee). The relative positions of the four test stimuli were also randomly shuffled every 10 min. This ensured that the bees learned to match the stimuli by visual comparison, and not by associating a specific feeder location with each sample. Learning tests began on the third day of training.

There were two types of transfer tests. In Type 1 transfer tests, the sample stimulus and the four test stimuli on the choice board were all from the same group, but this group was different from that used during training. In other words, these transfer tests were conducted using Group 2 (in some tests) or Group 3 (in others). In Type 2 transfer tests, the sample stimulus was from Group 1 and the four test stimuli on the choice board were from a different group (Group 2, Group 3 or Group 4). The two types of transfer tests were interleaved.

The bees' performances were measured in learning tests as well as transfer tests. In each case, performance was evaluated by noting which test stimulus the bee chose first upon entering the test chamber (by landing on the corresponding entrance tube).

Each transfer test was carried out only for a brief period (10 min, involving about two visits per bee). The reward continued to be present during the tests, in order to minimize extinction and maintain the bees' motivation to visit the apparatus. The brevity of each transfer test ensured that no learning occurred during the test. Transfer tests were interleaved between segments of continued training that were at least 40 min long, using Group 1 stimuli. Each transfer test was repeated 4–5 times to gather sufficient data.

Controls to check for the use of olfactory cues

Controls were carried out to check whether the bees' choice behaviour in the learning and transfer tests was influenced by possible olfactory cues emanating from the feeder, which was placed in a box behind the appropriate test stimulus. Two types of controls were used. In order to minimise the effects of extinction of learning, one type of control was carried out briefly at the end of the day, whereby bees were continuously tested in the transfer test, which had been carried out just before the control check (but with the feeder removed). Another type of control was carried out at the end of the whole series of experiments. In these controls, all four test stimuli, as well as the sample, were identical. The stimulus used in these tests was a grey-level version of F1 (Fig. 5). The feeder was placed behind one of the test stimuli (this position was varied randomly from one control test to the next). Four control tests of this type were performed, each with the feeder in a different position.

Data analysis

Each type of transfer test was performed 4–5 times to gather sufficient data. For each test, the choice frequency for each stimulus was calculated from the total number of first choices for each of the four test stimuli. The performance of each bee was evaluated separately by pooling all of the choices that it made for a given test stimulus in a given type of test. The average performance for a given type of test was obtained by averaging the choice frequencies across bees. The sample size (N) was taken to be the number of bees, rather than the number of individual choices, to ensure that the samples were truly statistically independent. The data was analysed to obtain mean values of choice frequency, standard deviations (S.D.) and standard errors of means (S.E.M.). Student t-tests were used to determine whether each choice frequency was significantly different from the random choice level of 25%. The Kolmogorov–Smirnov two-sample test (Groebner and Shannon, 1985) was used to test for significant differences between histograms obtained in a given type of test with different samples. For each given type of experimental test, six such statistical tests were done (details are given in the figure legends).

Results

Learning tests

Bees were initially trained using the four stimuli labelled as Group 1 in Fig. 1C. Each test stimulus belonged to a different category. The sample stimulus was identical to one of the test stimuli, and the bees had to learn to choose the test stimulus that matched the sample. This task was, in effect, a 'matching-to-sample' task. The learning tests were commenced on the third day of training (after ca. 80 rewarded visits per bee, on average). The bees learned this task well. For each sample, the bees showed a strong and statistically significant preference for the matching test stimulus (Fig. 2A). Performance for the learning tests was measured over a total of 1132 visits of 19 bees. The choice frequency in favour of the matching stimulus was significantly greater than the random choice level of 25% ($P<0.001$), for each of the four sample stimuli. The average choice frequency in favour of the matching stimulus was 60%. However, the choice frequencies for the other (non-matching) stimuli were always either significantly lower than 25%, or not significantly different from it (details in Fig. 2A). Differences between the histograms for different sample stimuli were tested

using the Kolmogorov–Smirnov two-sample test. All the histograms are found to be significantly different from each other ($P<0.001$).

Type 1 transfer tests

Type 1 transfer tests are described in Materials and methods. The trained bees were then briefly tested on two novel groups of stimuli (Groups 2 and 3), which they had never previously encountered. Each group consisted of four stimuli, one belonging to each category (Fig. 1C). In each test, the sample was identical to one of the stimuli of the group that was being tested. The bees were immediately able to find the matching stimulus in each of the novel groups, without any training on them. Performance for Type 1 transfer tests using Group 2 was measured over a total 797 visits of 14 bees, and for Group 3 over a total 383 visits of 12 bees. The bees showed a strong and statistically significant preference for the matching test stimulus: the choice frequency in favour of the matching stimulus was significantly greater than the random choice level of 25% for each of the four samples. The average choice frequency for the matching stimulus was 62% for Group 2 and 61% for Group 3. The differences between the histograms for different sample stimuli in Group 2 as well as Group 3 were significant ($P<0.001$). The results of these transfer tests (Fig. 2B,C) show that the bees performed well with each group. Thus, the bees were able to apply to Group 2 and Group 3 the concept of matching that they had acquired whilst being trained on Group 1. These results confirm and extend earlier work in our and other laboratories, which demonstrated that bees can learn to match colours, stripes or scents and transfer this matching ability to novel stimuli (Giurfa et al., 2001).

Type 2 transfer tests

Type 2 transfer tests are described in Materials and methods. The experiments described so far demonstrate the ability of bees to learn to match stimuli that are identical. Can bees go one step further, and identify 'similar' stimuli as belonging to the same category? To investigate this, we asked
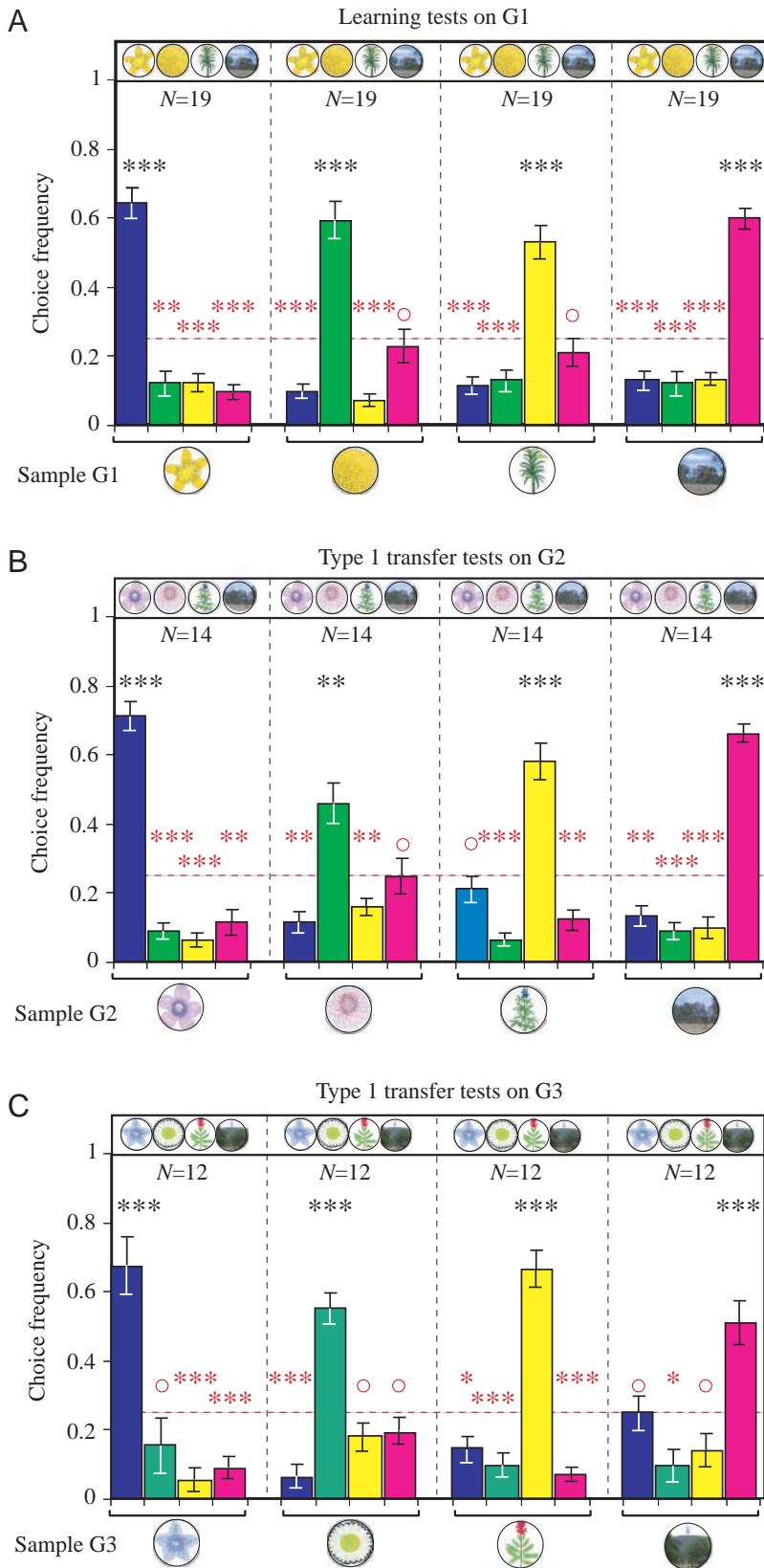
Fig. 2. Results of (A) learning tests and (B,C) Type 1 transfer tests. For each group, the bars show the relative preferences for the four test stimuli when the sample was a star-shaped flower, a circular flower, a plant stem or a landscape, as shown underneath the abscissa. In each panel, N denotes the number of bees that were tested in each experiment. Asterisks denote statistically significant differences from the random choice level of 25% (broken horizontal lines). ***$P<0.001$; **$P<0.01$; *$P<0.05$. Black asterisks refer to levels that are significantly greater than 25%, and red asterisks to levels significantly lower than 25%. The circles denote no significant difference from 25%. Values are means ± S.E.M. of the data. In each case, the bees are able to learn to choose the test stimulus that matches the sample.

whether the bees, trained as above, could match a sample stimulus from one group, with a stimulus of the same category from a *different* group. In these tests, the sample was always a stimulus from Group 1, but the test stimuli were from Group 2, Group 3 or Group 4 (see Fig. 1C). Performance was measured over a total of 262 visits of 10 bees for Type 2 transfer tests from Group 1 to Group 2, over a total of 256 visits of 10 bees for the transfer tests from Group 1 to Group 3, and over a total of 281 visits of 10 bees for the transfer tests from Group 1 to Group 4. The transfer tests were brief, and were interleaved between segments of the training session.

The bees performed very well in these transfer tests. In each case, the bees showed a clear and significant preference for the test stimulus that belonged to the same category as the sample (Fig. 3A,B). Particularly noteworthy is the transfer test using Group 4, in which the test stimuli were entirely novel (Group 4, Fig. 1C). These stimuli had never been used in the training phase, or in the learning tests or Type 1 transfer tests. Again, the bees performed very well at picking the test stimulus that was in the same category as the sample (Fig. 3C). We tested for differences between the histograms obtained using the four different sample stimuli for each of the three types of transfer tests, namely, Group 1 to Group 2, Group 1 to Group 3 and Group 1 to Group 4. In each type of transfer test, the four histograms were significantly different from each other ($P<0.001$).

In a final set of transfer tests, we examined the trained bees' ability to match coloured stimuli with grey-level versions of them. Here the sample stimuli were from Group 3, and the test stimuli were grey-level versions of these stimuli (Group 3*, Fig. 4). These transfer tests represent data from a total of 219 visits of 11 bees. The bees performed well at this task, too (Fig. 4).

Control tests to check for the use of olfactory cues

Fig. 5 shows the results of control tests that were carried out at the end of all transfer tests. Here, all four test stimuli and the sample were identical, and the feeder was placed behind one of the test stimuli. The data were collected over a total of 108 visits by 5 bees. The bees chose randomly among all four test stimuli, exhibiting no preference for the stimulus that was associated with the feeder ($P>0.05$). Thus, the bees' choices in our experiments were driven
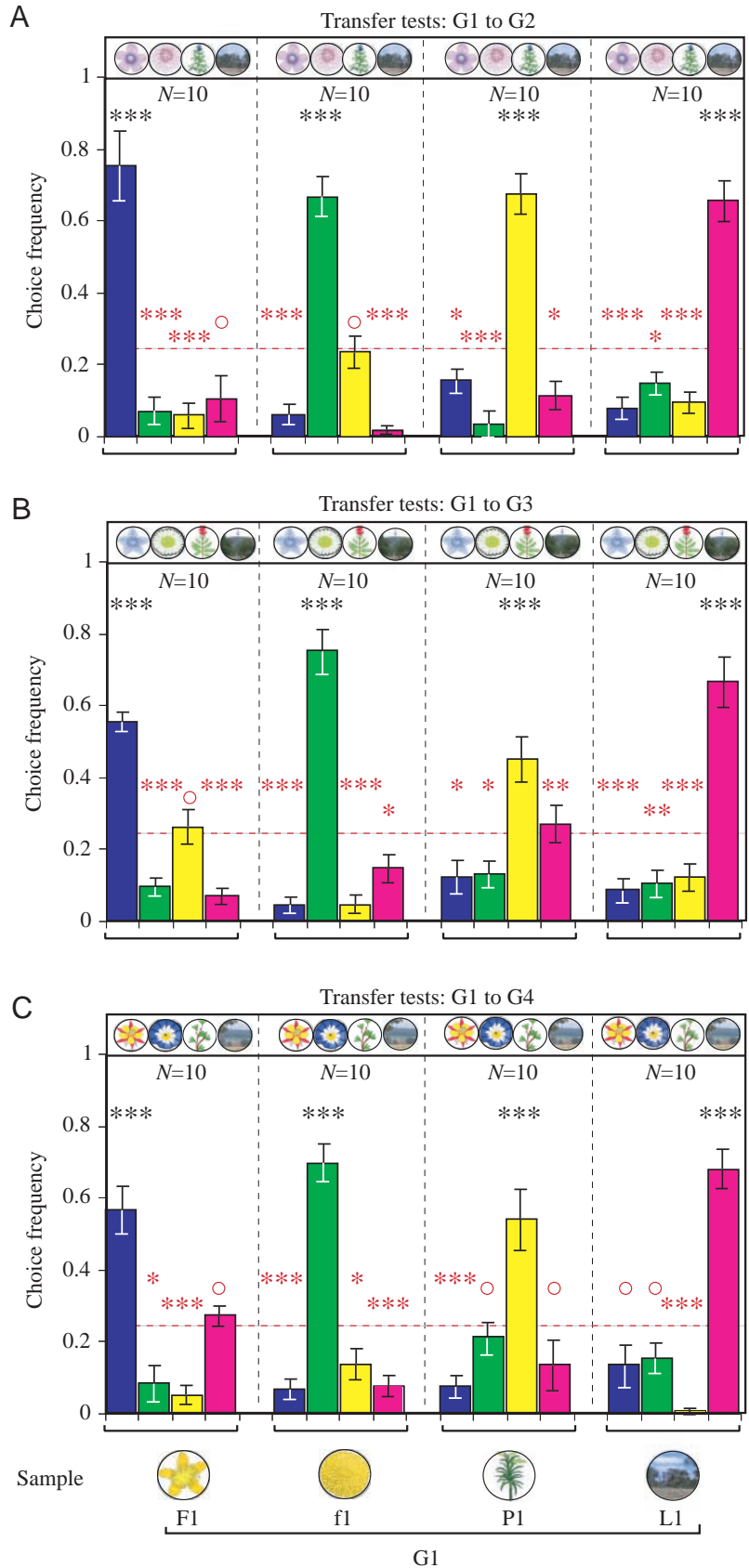

Fig. 3. Results of Type 2 transfer tests examining the ability of bees, having encountered a sample stimulus from Group 1, to choose a test stimulus of the same category in (A) Group 2, (B) Group 3 and (C) a novel Group 4. In each case, the bees are able to learn to choose the test stimulus that belonged to the same category as the sample. Details as in Fig. 2.
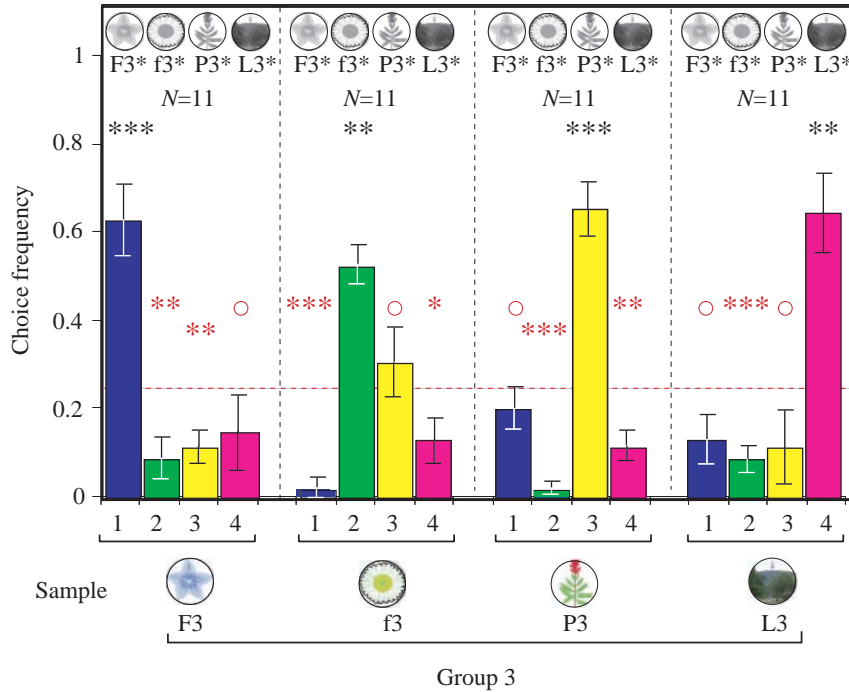
Fig. 4. Transfer tests examining the ability of bees, having encountered a sample stimulus from Group 3, to choose a test stimulus of the same category in Group 3*, which is composed of grey-level versions of the stimuli in Group 3. Bees are clearly able to perform this task. Details as in Fig. 2.
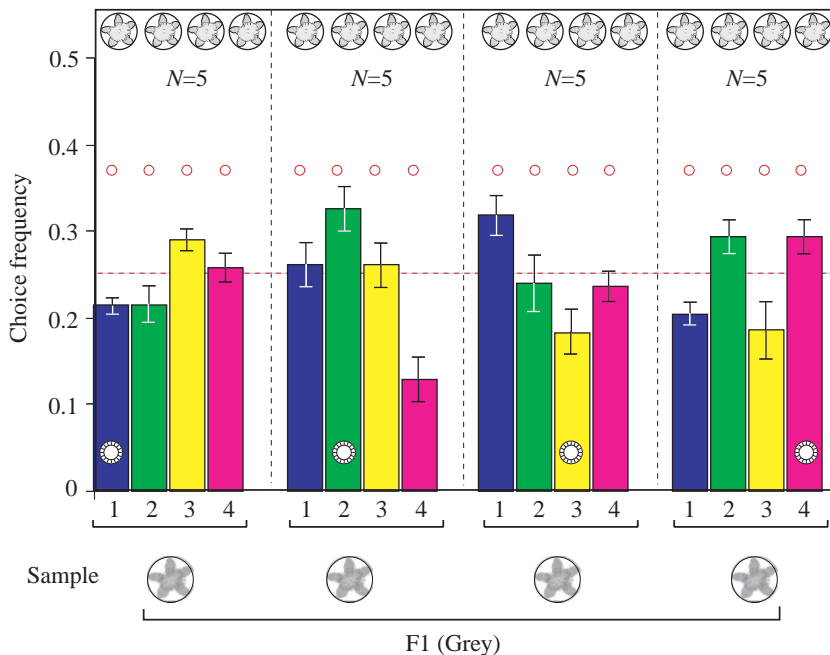

Fig. 5. Results of four control tests to check for the possible use of olfactory cues. Bees trained in the category discrimination experiments of Fig. 2 were presented with tests in which the sample as well as the four test stimuli were identical (in this case, they were grey-level versions of F1). The feeder was placed behind one of the test stimuli, as shown by the circular symbol. The bees chose randomly among the four stimuli, indicating that they were not using olfactory cues to make their discriminations in our experiments.

only by the visual cues provided by the patterns, and not by pheromonal cues emanating from the feeder.

Analysis of possible biases arising from previously rewarded patterns and positions

To check whether a bee's choice was influenced by the identity or the position of the pattern at which it had been previously rewarded, we analysed the choice frequencies for the previously rewarded pattern and position immediately after the sample stimulus was changed, or the test stimuli were rearranged. The results are summarized in Tables 1 and 2. Table 1 pertains to the learning tests and Type 1 transfer tests. Table 2 pertains to the Type 2 transfer tests. Statistical analysis shows that the choice frequencies for previously rewarded patterns and positions are significantly smaller than random choice level (25%) or are not significantly different from it (Tables 1 and 2). Thus, there is no preference for the previously rewarded pattern or position. For example, if a stimulus belonging to the category of star-shaped flowers was used as a rewarding stimulus in a previous trail, and a stimulus from a different category (circular flower, landscape or plant) was rewarded in the following experiments, only 15% of the visits would still be to the star-shaped flower stimulus in the subsequent trails. This level is significantly lower than 25% ($P<0.05$, Group1, Table 1). Similarly, if the correct (rewarded) test stimulus was in Position 3 in a previous trail, and in a different position (1, 2 or 4) in a subsequent trail, then only 31% of the visits would be to the formerly rewarded position (Position 3). This is not significantly different from 25% ($P>0.05$, Group 1, Table 1). Thus, it is clear that the bees' performance in choosing the matching or similar stimulus was not significantly affected by previously rewarded patterns or their positions.

Performance of individual bees

While space constraints prevent us from listing the choice frequencies of each bee in each situation, data from two individual bees (Table 3) demonstrate consistent performance. The results from the two bees are statistically indistinguishable. Both bees performed well in all of the various tests.

Table 1. *Bias analysis for learning tests and Type 1 transfer tests*

Previously rewarded category or position	Group 1			Group 2			Group 3		
	Fr	N	P	Fr	N	P	Fr	N	P
Flower F	0.15	136	<0.05	0.11	140	>0.50	0.05	104	<0.001
Flower f	0.20	82	>0.05	0.25	134	>0.50	0.10	102	<0.001
Plant	0.15	155	<0.01	0.06	153	<0.001	0.12	100	<0.01
Landscape	0.15	149	<0.05	0.09	140	<0.001	0.20	96	>0.05
Position 1	0.15	250	<0.001	0.22	168	>0.05	0.28	116	>0.50
Position 2	0.18	287	<0.05	0.21	171	>0.05	0.17	108	>0.05
Position 3	0.31	240	>0.05	0.27	226	>0.50	0.29	127	>0.05
Position 4	0.24	287	>0.50	0.22	198	>0.05	0.15	97	<0.05

Bias analysis for learning tests and Type 1 transfer tests. Fr, mean choice frequency; N, total number of visits. The P values are results of t-tests for a statistically significant difference from the random-choice level of 0.25.

Table 2. *Bias analysis for Type 2 transfer tests*

Previously rewarded category or position	G1 to G2			G1 to G3			G1 to G4			G3 to G3*		
	Fr	N	P	Fr	N	P	Fr	N	P	Fr	N	P
Flower F	0.13	45	>0.05	0.06	55	<0.01	0.07	60	<0.01	0.04	52	<0.01
Flower f	0.06	61	<0.01	0.14	59	>0.05	0.22	58	>0.50	0.13	56	>0.05
Plant	0.05	38	<0.01	0.13	56	>0.05	0.02	41	<0.01	0.11	27	>0.05
Landscape	0.02	45	<0.05	0.02	66	<0.001	0.17	48	>0.05	0.02	53	<0.001
Position 1	0.31	49	>0.05	0.21	56	>0.50	0.16	44	>0.05	0.23	61	>0.50
Position 2	0.21	34	>0.50	0.18	55	>0.05	0.14	56	>0.05	0.27	52	>0.50
Position 3	0.19	36	>0.05	0.14	59	>0.05	0.08	53	<0.01	0.37	27	>0.05
Position 4	0.25	70	>0.50	0.11	66	<0.05	0.09	54	<0.05	0.21	53	>0.05

Details as in Table 1.

Table 3. *Performance of two individual bees in the learning and transfer tests*

Test type	Choice frequency for correct test	
	Bee number 001	Bee number 010
Learning test: G1 to G1	48/83=0.58	30/45=0.67
Type 1 transfer test: G2 to G2	55/74=0.74	45/64=0.70
Type 1 transfer test: G3 to G3	38/46=0.83	29/43=0.67
Type 2 transfer test: G1 to G2	21/30=0.70	27/28=0.71
Type 2 transfer test: G1 to G3	24/42=0.57	21/37=0.57
Type 2 transfer test: G1 to G4	26/34=0.76	29/34=0.85

The numerator and denominator in each fraction denote the numbers of correct and total choices, respectively.

Discussion

The results of the present study show clearly that bees can learn a match-to-sample task that involves choosing between four different complex images. Furthermore, bees can generalize this learned matching concept to (1) match novel stimuli that they have never previously encountered and (2) match stimuli that are not identical, but 'similar'.

Our results do not reveal the specific cues by which similarity is judged. The landscape scenes were all characterized by blue sky in the upper half of the scene and green/brown bush in the lower half, separated by a horizon. The plant scenes all consisted of a green stem with leaves and, in one case, a red flower at the top. The flower scenes comprised images that were either roughly circular, or roughly star-shaped. The colours of the flowers were variable. Given that the colours of the stimuli were not consistent within categories, it is unlikely that the bees were only using colour *per se* as a cue to distinguish between the categories. Rather, form and, possibly, visual textures are likely to be relevant cues as well. This is supported by the observation that category discrimination was not compromised when the colours of the stimuli were removed (Fig. 4).

Were the bees distinguishing between the patterns by using their mean luminance as a cue? To investigate this possibility, we measured the mean luminance of the patterns (Table 4). The measurements show that the star-shaped flowers, circular flowers and plants display very similar luminance. Furthermore, the luminance rankings of the patterns in these three categories are different from group to group. The landscapes are slightly dimmer. Thus, the bees could not have used mean luminance as the sole cue to distinguish between categories.

Were the bees distinguishing between the patterns in terms of what M. Hertz termed 'figural intensity' (length of contour

Table 4. *Mean luminance of patterns*

	Mean luminance of patterns (lux)			
	Star-type flowers	Circular-type flowers	Plants	Landscapes
Group 1	106.3	105	109	86.3
Group 2	101	105.7	112.7	88.7
Group 3	106.7	106	108.7	88
Group 4	106.7	96.3	110.3	88

Mean luminance of patterns was measured by a TES 1330 Digital Lux Meter (TES Electrical Electronic Corp., Taipei, Taiwan). The luminances were measured 20 cm in front of the patterns.

per unit area; Hertz, 1933)? With the complex images used in our experiments, it is virtually impossible to measure this parameter, because many of the patterns contain complex internal textures. In this circumstance, we believe that the spatial frequency content of the patterns provides a measure that is approximately equivalent to figural intensity. We therefore computed the spatial power spectra of the patterns (Fig. 6). Visual inspection suggests that the spectra do indeed differ between categories. For example, the images belonging

to the circular flower category all possess spectra that are roughly circular symmetrical, whereas the images in the landscape category all exhibit spectra that contain enhanced power along the x and y axes. To measure these differences quantitatively, we compared power levels, within a certain spatial frequency band, of patterns belonging to the same category, as well as across categories. The band chosen for analysis was the region spanning 0.853–1.0 cycles cm^{-1} spatial frequency along the positive and negative directions of the v axis in the spatial frequency domain. The results show that, in most cases, the power in this band is similar for patterns that belong to a given category, but different for patterns that belong to different categories. Table 5 shows the relative power levels for patterns in the various categories. It also shows the results of tests for statistically significant difference between the power levels of various categories. The power levels of the Landscape images are significantly different from those of the star-shaped flowers ('Flower') and the circular flowers ('flowers') ($P<0.05$). The Flower images also differ significantly from the 'Plant' images ($P<0.05$). Other comparisons, however, reveal no significant difference.

The above analysis raises the possibility that spatial frequency content is one cue by which honeybees classify natural scenes. It is unlikely to be the only cue, however. Other cues might be circular symmetry (for the circular flowers), angular periodicity (for the star-shaped flowers), bilateral symmetry (for the plant stems) and the presence of a horizontal, high-contrast edge, the horizon (for the landscape scenes). Further work is required to evaluate the possible roles of these other cues.
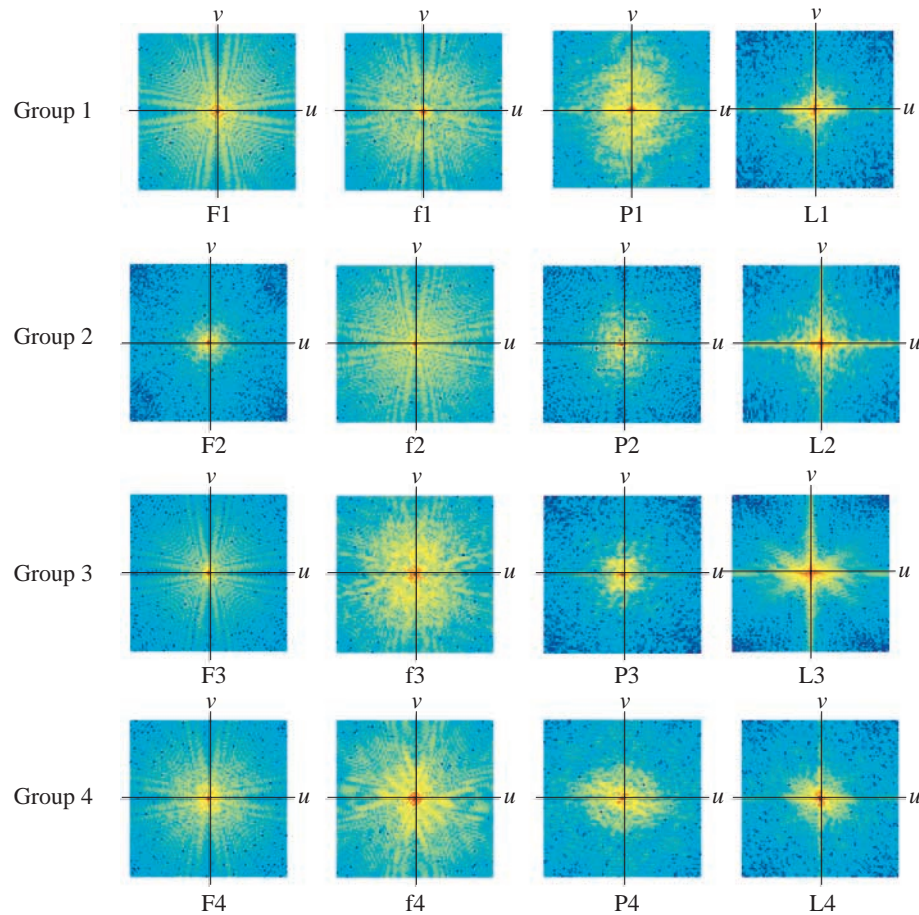
The results of the transfer tests with novel stimuli (Fig. 3C) show that the bees performed very well at picking the novel test stimulus that was in the same category as the sample. The honeybees exhibit the same response to novel stimuli that differ greatly in their individual, low-level features. That is, bees treat these highly variable stimuli as equivalent. Clearly, the bees' performance is not merely due to rote learning of each of the exemplars.

When bees display an apparent ability to distinguish between different classes of stimuli, are they also displaying a true ability to 'generalize' across stimuli that belong to the same category? Or does this apparent generalization come about simply because they cannot distinguish between stimuli that belong to the same category? The latter possibility seems unlikely because, at least in some of the

Fig. 6. Power spectra of patterns in each of the four groups of stimuli used in the experiments. Spatial frequency ranges from –2.22 cycles cm^{-1} to +2.22 cycles cm^{-1} along the u and v axes, where the unit spatial frequency represents a period equal to the diameter of the full image.

Table 5. *Comparison of the spatial power spectra of different categories and statistical test*

	Flowers F (0.5525±0.0106)	Flowers f (0.5835±0.02437)	Plants (0.6151±0.0212)	Landscapes (0.6502±0.0267)
Flowers F (0.5525±0.0106)		$t=2.12$, $f=6$, $P<0.085$	$t=5.04$, $f=6$, $P<0.05$	$t=6.61$, $f=6$, $P<0.05$
Flowers f (0.5835±0.02437)			$t=1.95$, $f=6$, $P<0.10$	$t=3.69$, $f=6$, $P<0.05$
Plants (0.6151±0.0212)				$t=2.05$, $f=6$, $P<0.09$

For each category, values are means ± S.D. of the power in the frequency range 0.825–1.0 cycles cm^{-1} along the positive and negative directions of the v axis in the spatial frequency domain.

Also shown are the results of Student *t*-tests for statistically significant differences between the power levels for different categories.

cases, the stimuli belonging to a given category differed substantially in colour. It is well known that bees are generally very good at learning to discriminate between stimuli on the basis of colour, orientation, shape or other attributes (Srinivasan, 1994; Lehrer et al., 1995; Chittka et al., 1993; Vorobyev and Menzel, 1999; Wehner, 1981). Nevertheless, we investigated this question rigorously by examining whether bees could be trained, in a Y-maze, to distinguish between two stimuli that belonged to the same category. The training and testing procedure used for these Y-maze experiments was as employed by Srinivasan and Lehrer (1988). In four separate training experiments, we examined whether bees could be trained to distinguish between F2 and F3 in Category 1, between f3 and f4 in Category 2, between P1 and P2 in Category 3 and between L1 and L2 in Category 4. We deliberately chose pairs of stimuli that were likely to be the most difficult to discriminate. The results showed that honeybees could learn each of these discrimination tasks. The choice frequency in favour of the positive stimulus ranged from 62.9% to 78.4%, depending upon the particular experiment, but in each case this frequency was significantly higher than the random-choice level of 50% ($P<0.001$ in three cases, and $P<0.05$ in one case). Thus, while the bees were learning to distinguish between four different classes of stimuli in our main experiments, they were also exhibiting true perceptual generalization across stimuli that belonged to a given class. It is clear that the highly variable complex images in the same category are discriminable by the honeybee. However, they are treated as equivalent when bees are required to distinguish between images in different categories.

So far we have excluded the possibility that bees might be using some single low-level features as a cue to categorise these complex visual objects. Some other configurational properties could still be used in this categorisation. This might include circular symmetry (for the circular flowers), angular periodicity (for the star-shaped flowers), bilateral symmetry (for the plant stems) and the presence of a horizontal, high-contrast edge, the horizon (for the landscape scenes). It is likely that this categorisation is based on a combination of low-level features as well as some configurational properties.

It is also clear that that the behaviour of the trained bees does not necessarily represent categorization in the sense of associating a specific concept, meaning or relevance, to each of the stimulus classes, as is likely to be the case in humans.

With bees, establishing the similarity between images belonging to a given category could simply be based on a comparison of the responses evoked by the images across multiple neural channels representing different features. Recently, Halford distinguished and ranked a series of different levels of cognitive processes that provides a theoretical basis for interpreting findings about simpler cognitive processes by infants and younger children as well as humanlike competencies in animals. (Halford et al., 1998; G. S. Halford, S. Phillips and W. H. Wilson, manuscript submitted). The apparent ability of bees to classify objects may be a process that works at a lower level than that in humans.

Our findings suggest that the honeybee possesses an ability to group similar stimuli into categories. Further work is required to determine whether the four classes of complex images that we have used in our experiments represent four categories of natural scenes that are important to a foraging honeybee, and if so, whether these categories are innately programmed by evolution, or learned individually through experience.

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