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The effect of shape parameters on maximal detection distance of model targets by honeybee workers

Abstract The influence of several spatial parameters on the maximal detection distance of a target by approaching foraging honeybees was examined. The roles of target diameter, color and luminance contrasts have been already demonstrated in earlier studies. The present study used, for the first time, dissected flower like targets that differed in addition to diameter (D) and area ($\pi(D/2)^2 = A_{cir}$) also in the length of contour line (C), the area of the colored "petals" (A_{col}) and the degree of dissectedness as expressed mainly by the ratio A_{col}^2/C. The color and luminance contrasts were identical for all targets. Our results confirm the importance of size. However, we demonstrate for the first time, that full circular shapes have the greatest maximal detection distance among targets of equal diameters, and even more than dissected targets with equal A_{col} and double D. The parameter A_{col}^2/C was found as the best predictor of maximal detection distance of vertically presented targets with varying diameter and degree of dissection for honeybee workers. We propose that an increase in the colored area and decrease in contour line is advantageous due to the fact that it increases the amount of contrast that the target as a whole produces against its background.

Keywords Honeybee · Vision · Floral shape parameters · Detection distance

Abbreviations A_{cir} $\pi(D/2)^2$ · A_{col} the area of the colored "petals" · *ANOVA* analysis of variance · C length of contour line · D diameter · *MDD* maximal detection distance · *MVA* minimal visual angle

Introduction

The detection of flowers by their pollinators is the first step in a chain of events that finally may result in pollination and fertilization. Various stimuli produced by flowers can attract pollinators from afar, but visual stimuli are needed for exact localization and final orientation to the flower. The visual stimuli presented by flowers include three major components: color, size and shape. Eye structure, mainly inter-ommatidial angle, and the angular size of the receptive fields of individual photoreceptors are the main factors affecting acuity of bee vision (reviewed by Land 1997). However, optical characteristics of the target and the background are also important (Land 1997).

Two centuries ago Sprengel (1793) has already recognized the importance of floral size: "Because the final purpose of the corolla, which always applies, is that the flower catches the eye of the insect from afar, it must be as large as possible". The role of floral size as advertisement for pollinators was recently reviewed by Dafni et al. (1997) and Neal et al. (1998). Recent experiments have demonstrated that the maximal distance from which an object can be detected (MDD), or the minimal visual angle (MVA) an object subtends on the surface of the compound eye to be detectable is a function of its size and color. The MVA for honeybee workers was found to be 5° for full circular colored targets with both chromatic and green contrasts against the background, but only 15° for such targets with only chromatic but no green contrast (Giurfa et al. 1996). The importance of color intensity, color contrast and receptor-specific contrasts in flower discrimination is further explained by Lehrer (1997).

The importance of floral shape was also recognized by Sprengel (1793): "Each flower must always have a shape such that in the position which it occupies it can most

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easily catch the eye of the insect". The role of shape in floral advertisement was also recently reviewed by Dafni et al. (1997) and Neal et al. (1998). Lehrer et al. (1995) found that honeybees prefer less dissected radiating and symmetrical patterns over dissected and asymmetrical ones, and proposed that honeybees have an innate "knowledge" of the appearance of natural flowers. However, floral shape has not yet been experimentally examined as a factor affecting detection distance. All recent experiments were made only with full circular targets (Lehrer and Bischof 1995; Giurfa et al. 1996). Floral shapes and patterns within flowers are now considered mostly as characters important for short-distance recognition (within a few centimeters) and orientation by honeybees, but as less relevant at intermediate or long distances (Vorobyev et al. 1997; Kevan and Backhaus 1998). Moreover, floral shape has not been included in the calculations of the detection distances of various flower species by bees (Menzel et al. 1997).

Size and shape presumably combine in attracting pollinators to flowers (Dafni et al. 1997) and various characteristics such as perimeter and contour density seem to relate to general levels of attractiveness of flowers to pollinators (Kevan 1970; Dafni and Kevan 1997; Dafni et al. 1994; Dafni et al. 1997; Neal et al.

1998). However, experiments have not been made to determine the effect of those or other shape parameters on the distance at which a flower-like target can be detected.

The aims of our paper are: (1) to explain the effects of major geometrical floral shape parameters on the MDD, of a vertically oriented, colored target by foraging honeybee workers; and (2) to establish a regression equation that can be used to predict the distance from which honeybees can detect floral shapes that vary both in diameter and degree of dissectedness. We restricted our experiments to the use of vertical targets with chromatic and green contrasts against their background.

Materials and methods

Apparatus

Individually marked honeybees, *Apis mellifera*, were trained to enter a gray-colored, Y-shaped maze apparatus (Fig. 1), to collect 40% (weight/weight) sucrose solution (nectar) from the middle of a vertical target model. The Y-maze was similar to that used by Srinivasan and Lehrer (1988) and Giurfa et al. (1996). The whole apparatus was covered with an ultraviolet transmitting Plexiglas ceiling. The entrance wall had a central orifice, 5 cm in diameter, through which the bees could fly to find access to the two arms. A

Fig. 1 A Frontal view of Y-shaped maze apparatus in which honeybees were tested to determine the distance from which they could detect targets presented vertically on the back, movable, wall. **B** Overhead view of Y-shaped maze apparatus (after Giurfa et al. 1996)
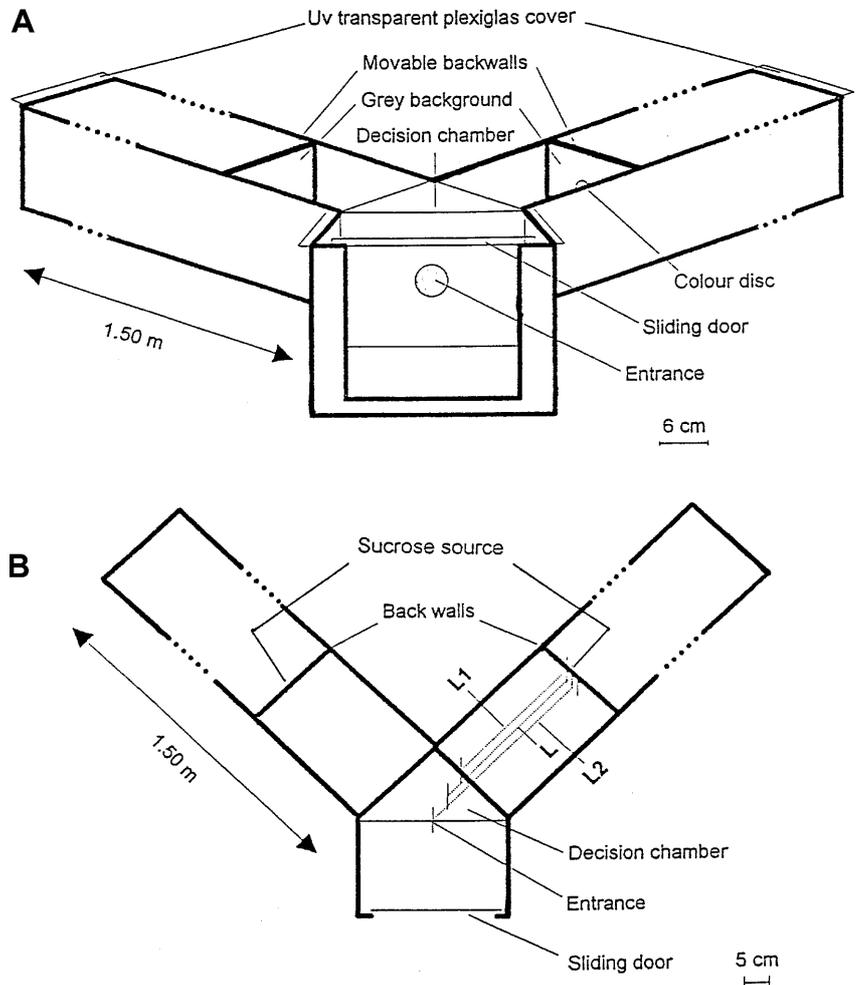
sliding door could close this orifice and allow the entrance of only one bee at a time into the maze.

The arms of the Y-maze were 1.50 m long and had movable back walls. Each back wall had a central orifice, 0.5 mm in diameter, through which nectar was offered by a capillary tube extended to the bottom of a plastic Petri dish (nectar reservoir), situated behind the back wall. Both arms could present a target with its central rewarding capillary tube. The bees were trained to feed at these targets and capillary tubes. A target model and reward were offered only on one arm of the maze at a time, while a gray paper identical to the target's background covered the target of the non-rewarding arm. The rewarding side was changed by flip of a coin, but no more than two successive times on the same side so as to prevent the bees from learning to feed on that side.

The bees were unable to see the target until they passed through the front entrance to the maze. The bees were thus forced to make their decision within the limits of the "decision chamber" (Fig. 1). A bee that crossed the line between the decision chamber and the non-rewarding arm was recorded as failed; those crossing toward the rewarding arm were recorded as passed. All distances given are those between the entrance and the target (L2 in Fig. 1b).

Targets

Following Giurfa et al. (1996), we used a bee-neutral achromatic gray paper (HKS-92N, K + E Stuttgart, Stuttgart-feuerbach, Germany) for the background. For the targets, we used HKS-43N paper (K + E Stuttgart, Stuttgart-feuerbach, Germany) that appears blue to the human eye. The chromaticity of the blue (HKS-43N) was 5.0 in COC units, the excitation of the UV, B and G receptors relatively to that of the gray background was 12.0%, 48.8%, and 14.0%, respectively, and the overall intensity contrast was 25% (Giurfa et al. 1996). For spectral reflectance curves, and further information on color reflectance and perception of the papers used for the models see Giurfa et al. (1996).

We define A_{cir} as the target area ($\pi(D/2)^2$); A_{col} as the area of the colored "petals"; C as the length of contour line; and D as diameter. Contour density is defined (Wehner 1981) as the ratio $C/\pi(D/2)^2$. Six circular targets (Fig. 2) of two different D and therefore different A_{cir} were used. The targets differed in their contour density and in the proportions of the contrasting areas A_{col}/A_{cir} (Table 1).

Procedure

Each experimental session began by training a group of honeybee foragers to enter the maze and feed at the capillary tube in the center of a vertical target (Ml, Fig. 2). At that stage, the bees were marked with acrylic colors on the dorsum of their thorax. During training, the distance of the target from the "decision chamber" was 20 cm and the rewarding side determined by flip of a coin. Only the bees that learned successfully to follow the rewarding target side were included in the next stages of the experiment. The learning criterion was that bees followed the target, a model of a given shape (Fig. 2), with a percentage of correct choices greater than 60%, which was easily achieved after 11–15 trails. Most of the bees reached a level of at least ten correct choices of 11 trails (91%). In each experimental session, no more than four marked bees participated, and only one bee was permitted into the maze at a time. Other marked bees and other foragers were excluded by the sliding door at the entrance. Only the first choice of bees returning from the hive to the experiment and entering the maze was recorded. During each visit, even if the bee failed in her decision, it was rewarded by letting it feed after passing to the rewarding arm, before leaving the maze to return to the hive.

After training was complete, the back wall was drawn backwards at 10-cm intervals, to increase the targets' distance from the choice point. The bees were tested at each distance. Each bee passed if she chose correctly more than 60% of the time at a significance level of 5% (using the Chi-square distribution table).

From our experience, a bee that failed five times in less than 20 trails never reached that passing level. Therefore, we recorded 20 visits, or until a bee failed five times at any distance. Each target model was tested at increasing distances until no bee passed. In that way, we recorded the maximal distance from which each bee could detect successfully a particular model. However, it is clear that the maximal distance from which the bee could see a model (MDD) was longer that the maximal distance at which she passed, but shorter than the minimal distance at which she failed. Therefore, we used the average of those two distances as the MDD.

When bees were tested using more than one target model, they were retrained and tested anew at 20 cm with the next model before testing them with longer distances. This was to verify that the bees followed the learned rule of entering the rewarding side with the target and were not using another clue previously learned.

The first set of experiments was done in August 1995, at the Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada (hereafter experiment I). In this set the Y-maze was placed in a laboratory room, near an open door, well illuminated by natural light, and with additional illumination of four Osram 40-W cool white fluorescent lamps. In these experiments, we used the models M0.6, M1, M6, M9, M60 and M90 (Fig. 2) and tested 15, 16, 14, 33, 15, and 15 individuals of local honeybees (*A. mellifera ligustica*), respectively. The second set of experiments was done in September 1997, at the Department of Biology, University of Haifa-Oranim, Tivon, Israel (hereafter experiment II). In this set, an identical Y-maze was placed outdoors on a table under a 50% black shade net, to obscure and diffuse direct solar radiation. In these experiments, we used the models M1, M6, and M60 (Fig. 2) and tested 11, 20 and 12 individuals of local honeybees (*A. mellifera carnica*), respectively.
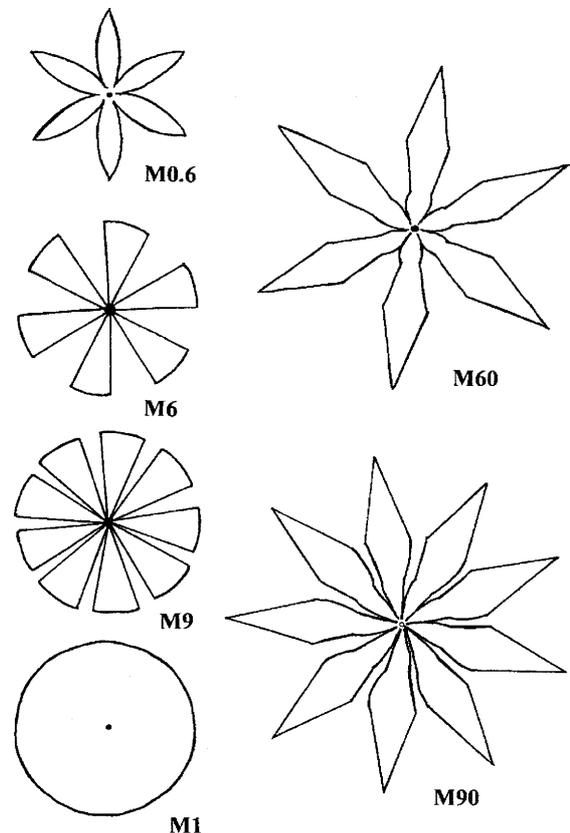

Fig. 2 Models used to determine the distances from which the honeybees could detect targets of different shapes presented vertically on the back, movable, wall of a Y-maze (Fig. 1; for geometric parameters see Table 1)

Table 1 The morphological parameters: colored area (A_{col}, cm^2), contour line length (C, cm), diameter (D, cm), various mathematical transformations of these parameters, A_{col}/A_{cir} and contour density $[C/\pi(D/2)^2]$ for all the experimental models

Parameter	Model number (see Fig. 2)					
	M0.6	M6	M9	M60	M90	M1
A_{col}	12.50	25.12	37.68	50.24	75.36	50.24
C	54.00	60.56	90.84	96.00	144.00	25.12
D	8.00	8.00	8.00	16.00	16.00	8.00
A_{col}/C	0.23	0.41	0.41	0.52	0.52	2.00
A_{col}^2/C	2.89	10.42	15.63	26.29	39.44	100.48
A_{col}/A_{cir}	0.25	0.50	0.75	0.25	0.38	1.00
Contour density	1.075	1.205	1.808	0.478	0.717	0.500

Data analysis

Chi-square value for the expected ratio of 60% correct and 40% incorrect choices at 5% confidence level was calculated for each bee, each model and each distance. The average Chi-square value was calculated for all bees in each model and each distance. We used the Chi-square values and not the percentage of correct choices because only this way is it possible to draw a line of significance ($P = 0.05$) above which the choices are not random, meaning that the bees could see the target, and below it the choices are random, meaning the bees could not see the targets (Fig. 3). This cannot be done when drawing the percentage of correct choices; having more than 50% correct choices does not always mean a significant deviation from random because the number of trails must be taken into account. A comparison among the maximal distances from which the various models could be seen was made by analysis of variance (ANOVA) followed by post hoc Tukey HSD multiple comparisons. The regression lines of the maximal detection distance and the main geometrical floral shape parameters of each model (D, C, A_{col}, various proportions among them, A_{col}/A_{cir} and contour line) were calculated. R^2 of significant ($P < 0.05$) linear regression, which indicates the proportion of the variation explained by the model, was used to select the best parameters for prediction of MDD by the floral shape parameters.

To compare the results of the two experiments we calculated the regression lines for detection distance versus the area square to contour line ratio (A_{col}^2/C) for each experiment separately and compared them by t-test (Zar 1984). All statistical analyses were made using Systat 8.0, SPSS (SYSTAT 1998).

Results

The mean Chi-square value for 60% correct choices for each tested target model at all distances tested, in both experiments are presented in Fig. 3a, b. It is clear that for all target models, the percentage of correct choices decreased with distance. For most models, the decrease was sharp over a relatively short distance, falling under the limit line of significance (Chi-square ≥ 3.84, $P = 0.05$), meaning that the bees could not see the target from that distance on. The intercept between the significance limit line and the graph of each model represents the MDD, namely the longest distance from which each model was detected (Table 2). One-way ANOVA revealed significant differences among the detection distances of the six models used in experiment I (Canada), and the effect of the models used in experiment II (Israel) was also significant (Table 2). Models M0.6, M1, M6 and M9 all of equal diameters (8 cm) differed in the maximal distances from which they could be detected, and the full circle (M1) was detected from a significantly longer distance than the all the others. Models of 16 cm diameter (M60 and M90) were detected from the same or even shorter distances than the M1 model, a full 8-cm-diameter circle. The hierarchy of the targets with respect to their MDD is M1 > M90 > M60 > M9 > M6 > M0.6 (Table 2). This result shows that the MDD is larger for a full disc than it is for any dissected circular target of the same diameter, and that a circular dissected target of a large diameter is detected at a larger distance than is a similarly dissected target of a smaller diameter. Thus decrease in dissectedness and increase of diameter improves MDD of a shape. These results were consistent in both experiments, even though the absolute values are not the same (Table 2, Fig. 3a, b). The mean ($\pm$SE) MDD of a full circle with diameter of 8 cm (M1) in experiment I was 56.9 ± 2.4 cm ($n = 33$) and in experiment II 36.0 ± 1.6 cm
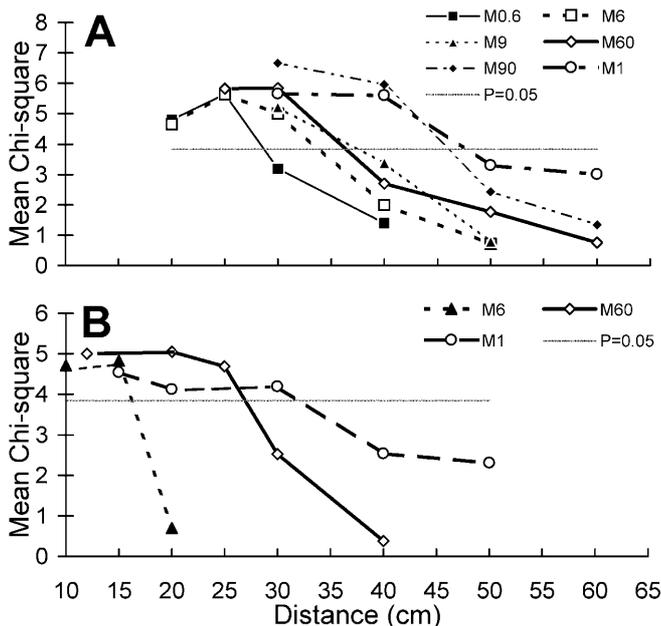

Fig. 3 Average Chi-square values for bee scores of the various models at different distances in experiment I in Canada (**A**) and in experiment II in Israel (**B**). The horizontal line is the border of significance for the Chi-square test (for 60% correct choices, $P < 0.05$)

Table 2 Mean ($\pm$SE) detection distances (cm) of various models (see Fig. 2) used in experiment I (Canada) and experiment II (Israel), and the number of bees tested with each model (n). Results of ANOVA for the effect of the model on detection distance. In each experiment, models with no common letter are significantly different (Tukey HDS, $P < 0.05$)

| ANOVA | Experiment I (Canada) | | | Experiment II (Israel) | | |
| | $F_{5,102} = 19.177$, $R^2 = 0.485$, $P < 0.001$ | | | $F_{2,30} = 15.686$, $R^2 = 0.44$, $P < 0.001$ | | |
Model	n	Mean ($\pm$SE)	Tukey HDS	n	Mean ($\pm$SE)	Tukey HDS
0.6	15	32.9 ± 1.5	C			
6	16	37.4 ± 1.7	C	11	22.2 ± 2.5	B
9	14	41.4 ± 1.7	BC			
60	15	41.7 ± 1.9	BC	12	28.5 ± 1.2	B
90	15	52.0 ± 7.4	AB			
1	33	56.9 ± 2.4	A	20	36.0 ± 1.6	A

($n = 20$), and the MVAs were 16.1° and 25.4°, respectively.

By linear regression, we first explored the effects of individual basic shape parameters of the models and some of their mathematical combinations on MDD of the models, and determined which parameter provided the greatest significant explanatory power of the variation in our results, i.e., the highest values of R^2 at $P < 0.05$. This was performed first for the 8-cm models in experiment I only, excluding the effect of D. The results show that within this group, A_{col} is the most important single parameter, and that contour line length and contour density had both an equally lower but still highly significant ($R^2 = 26.7\%$) explanatory power (Table 3).

In order to evaluate the relative importance of A_{col}, C and D, we performed the same regression to all models in experiment I (Table 3). The diameter, when tested separately, of the targets that vary much in their degree of dissectedness, has no significant effect on MDD. Contour line and contour density had a weak, but still significant explanatory power of 5% and 18%, respectively. A_{col} was the single parameter with the highest explanatory power (26.6%). Most combinations of any two parameters were highly explanatory, but no particular combination stands out as superb (Table 3).

The top ranking combination from experiment I, where six models with varying diameter and shape parameters were examined, was A_{col}^2/C, indicating a positive and dominant effect of the area on MDD and a negative one of contour line. The validity of that index was examined also for the results of experiment II where only three models were used (M1, M6, and M60). The regression line for A_{col}^2/C in experiments I is $y = 34.93 + 0.221x$ ($F_{1,76} = 74.117$, $P < 0.001$, $R^2 = 0.494$) and in experiment II $y = 19.60 + 0.1691x$ ($F_{1,41} = 56.517$, $P < 0.001$, $R^2 = 0.580$). There is no significant difference between the slopes of the regression lines (Fig. 4) of the two experiments ($t = 0.942$, $P = 0.30$), but there is a significant difference between elevations (intercept; $t = 34.675$, $P < 0.001$).

Discussion

Full circular targets were used in previous studies on target size and visual detectability to honeybees (Lehrer and Bischof 1995; Giurfa et al. 1996) and emphasized the importance of the visual angle for the determination of detection distance (as do other reports using those data (Giurfa and Vorobyev 1997; Menzel et al. 1997). Those studies imply that the diameter of a circular target is the only, or most, important feature concerning its visual detectability. This is demonstrated also in our results when comparing MDD of targets of identical shapes and different diameter M60 > M6 and M90 > M9 (Table 2). However, our data show, for the first time, that full circular targets are detected over the greatest

Table 3 Results of regressions of maximal detection distance (MDD) for each model versus its colored area (A_{col}, cm²), contour line length (C, cm), diameter (D, cm), various mathematical transformations of these parameters, A_{col}/A_{cir} and contour density $[C/\pi(D/2)^2]$ for the 8-cm-diameter experimental models (M0.6, M1, M6, M9) and for all six models (M0.6, M1, M6, M9, M60, M90) in experiment I (Canada). *Rows in boldface* are for those parameters with greatest explanatory power (R^2)

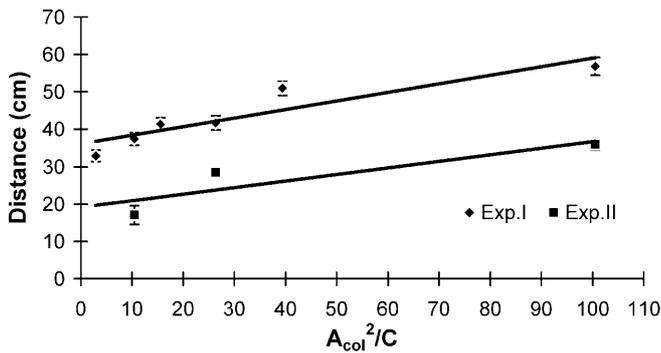| Parameter | 8-cm-diameter models | | | All models | | |
	R^2	$F_{(1,76)}$	P	R^2	$F_{(1,106)}$	P
A_{col}	0.467	66.712	< 0.001	0.266	38.398	< 0.001
C	0.267	27.669	< 0.001	0.050	5.603	0.020
D				0.001	0.087	0.769
A_{col}/C	**0.490**	**73.052**	**< 0.001**	0.338	67.321	< 0.001
A_{col}^2/C	**0.494**	**74.117**	**< 0.001**	**0.446**	**85.356**	**< 0.001**
A_{col}/A_{cir}	0.467	66.712	< 0.001	0.274	39.936	< 0.001
Contour density	0.267	27.669	< 0.001	0.181	23.366	< 0.001

Fig. 4 Regression lines for the average detection distance of the various models as a function of A_{col}^2/C in the first (experiment I in Canada) and second (experiment II in Israel) experiments. For n values see Table 2. Vertical bars represent $\pm SE$

distances, and that shape profoundly influences the distance over which honeybees can detect dissected circular colored targets, and that MDD is negatively correlated to the degree of dissectedness. When comparing targets with different shapes and sizes, we found that the colored area of a target is the most important single parameter affecting its MDD by approaching foraging honeybees.

The ratio of squared colored area to contour line length (A_{col}^2/C in Tables 1, 3) was the best index for the prediction ($R^2 = 0.45$) of MDD of dissected circular floral shaped target with color and green contrasts to the background in both experiments using local honeybees in Canada and Israel. The slopes of the regression lines of both experiments were not significantly different (Fig. 3a), meaning that A_{col}^2/C affected MDD in both experiments in the same way. We can only conjecture as to why the two data sets differ in their intercepts in spite of the use of exactly the same sizes, shapes and colors of the models and the maze. Perhaps differences in the light regimes during the experiments were a factor, or subtle differences in the races of the bees that we used. The consistency in the slopes indicates that the perceptual criteria used by the bees in both experiments were the same. We also note that our data for the minimum visual angles (MVAs) of detection of circular targets are different at 16.1° in Canada and 25.4° in Israel from those reported in Giurfa et al. (1996) at 5° in Germany. The fact that the highest R^2 value obtained was about 50% indicated that there are additional unexplored factors that affect MDD.

Contour density has been invoked as an important feature in visibility and attractiveness for flower visiting anthophiles (Dafni et al. 1997). However, our results show that its relationship with MDD is relatively weak ($R^2 = 0.27$). A_{col}^2/C is the best index of floral shape parameters we tested but other parameters (e.g., A_{col}/A_{cir}) that reflect the degree of dissectedness also have significant explanatory powers (Table 3). The lower correlation of MDD with contour density makes sense in the light of the fact that contour density is determined solely

by the number of periods contained in the pattern, whereas A_{col}^2/C and A_{col}/A_{cir} are based on the size of the colored areas within each period. We propose that an increase in the colored area and decrease in contour line and in the proportion of the colored area is advantageous due to the fact that it increases the amount of contrast that the target as a whole produces against its background.

A possible explanation of the results is that this ratio (A_{col}^2/C) is better correlated with the number of ommatidia that are fully covered by the shape from any distance than are other parameters. A_{col}^2/C of a shape is affected by of the number of repeated elements (periods) and by the size of each period, thus representing an integrated quantitative and reliable parameter describing the degree of dissectedness. Under any fixed A_{col}^2, increasing C increases the number of ommatidia that are only partially covered by the target's shape and thus would not be excited. However, this conjecture needs to be further tested. The higher R^2 value of A_{col}^2/C than of A_{col}/C for models differing in size and dissectedness may indicate that the positive effect of A_{col} on MDD is larger than the negative effect of C.

Detection of flowers

From the findings of Giurfa et al. (1996), it can be calculated that the ratio of distance of detectability per floral diameter is 11.5 if color and green contrast are evident, but only 3.8 if green contrast is lacking (Menzel et al. 1997). Our results provide ratios of 7.1 and 4.5, in two separate experiments, when color and green contrast are evident. Vorobyev et al. (1997) developed a method of reconstructing floral images as insects might see them. Even the striking flower of the orchid *Orchis caspia*, which is about 1 cm×0.5 cm can hardly be resolved as close as 4 cm. Vorobyev et al. (1997) conclude that although the character of the flower shape and patterns within the flower may be important for short-distance recognition, they are less relevant at long distances. Thus, it is clear that a flower's coloration, size, and shape are not the long-distance cues as has so often been assumed (see Kevan 1983; Dafni et al. 1997; Kevan and Backhaus 1998). Nevertheless, the size, and contour density have all been invoked as important features in the attractiveness of flowers to bees and other pollinators (Dafni and Kevan 1997; Dafni et al. 1997). Our results indicate that floral area is the most important single factor, and that dissected flowers with longer outlines would be less visible from a distance than ones with circular outlines and of the same diameter. Therefore, it is suggested that complex dissected flowers are detected by bees only from shorter distances than are un-dissected flowers of equal diameter. The preference of low frequency (less dissected) patterns from a distance of 30 cm (Lehrer et al. 1995) by honeybees accords with our results, namely that high frequency patterns (more dissected and with more elements) were not seen as well

from the distance at which the bees' decisions had to be made. Even so, complex shape features may allow insects to discriminate between different models (flowers) based on shape (Leppik 1953; Giurfa and Eichmann 1998) and disruption pattern (Horridge 1997a) at close range. Dissected patterns act as form and visual guides for orientation, landing, and foraging, or in concert with other floral cues (e.g., odor and coloration) in floral discrimination (Dafni et al 1997; Horridge 1997b). The ability to detect bilateral symmetry (Horridge 1996) and the innate preference of honeybees for symmetrically radiating patterns (Lehrer et al. 1995) does not indicate that they are seen better, only that they elicit reaction quickly.

Floral, en-face planar projected area (Dafni and Kevan 1997) allows comparisons of the sizes of attractive cues to pollinators (Dafni and Kevan 1997; Dafni and Neal 1997) and is an important component of attraction, as our results attest. Our results also indicate that the ratio of the colored area squared to contour line (A_{col}^2/C) is even more important and should not be ignored, mainly in comparison of floral shapes that vary simultaneously in shape and size. In the Israeli flora and that of the Canadian High Arctic, there is a negative correlation between the en-face planar projected area of flowers and contour densities, i.e., larger flowers are relatively less dissected than small flowers (Kevan 1970; Dafni and Kevan 1997). During the process of evolution, trade-offs always occur. Therefore, if dissectedness did not reduce floral detection distance, large dissected flower would presumably be favored in selection by being less costly to produce and retaining the efficiency of advertisement and attraction of pollinators. The fact that large flowers are less dissected is in accordance with our results that high A_{col}^2/C ratio increases detection distance in flowers and probably therefore floral attraction, the likelihood of pollination, and so the plant's reproductive fitness. Although larger flowers with relatively less dissectedness would appear to favor pollinator attractiveness, inflorescences of simultaneously blooming small flowers can accomplish the same effect through their corporate image (see Dafni et al. 1997). Resource constraints may operate to reduce floral biomass, as in self-pollinating flowers (Richards 1986), but cannot be invoked for explaining the optical size of flowers or inflorescences. It should also be noted that natural selection by pollinators might not be the only factor shaping all floral traits (Herrera 1996). Location of flowers by directional navigation, including the use of landmarks, and by the corporate effects of colors, and other features, of flowers in patches, on large plants, and in inflorescence occurs over large distances (see Dafni et al. 1997; Kevan and Backhaus 1998).

We conclude that color and shape of individual dissected flowers are important more for pollinators' recognition of flowers and their decision to land during final approach than for detection from long distances, but these two options are not exclusive (Kevan and Backhaus 1998).

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