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A. D. Giger · M. V. Srinivasan

Pattern recognition in honeybees: eidetic imagery and orientation discrimination

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Abstract The roles of eidetic imagery and orientational cues, respectively, in the discrimination of visual patterns by honeybees (*Apis mellifera*) were evaluated by training the bees to discriminate between patterns consisting of periodic, black and white square wave gratings. Training and tests with a number of different pairs of patterns revealed that bees use orientational cues almost exclusively, if such are present, and make use of eidetic images only when orientational cues are not available. On the other hand, if a pattern carries strong orientational cues, bees learn the orientation even if it is irrelevant to the discrimination task on which they are trained.

Key words Vision · Template · Orientation analysis · Honeybees · *Apis mellifera*

Introduction

Although visual pattern recognition has been studied extensively both in animals and humans, much remains to be learned about the principles involved. Honeybee workers are optimal subjects in which to study pattern recognition: As flying foragers they rely heavily on visual information, and as social insects they are ideal experimental animals.

How do bees recognise and discriminate patterns? Previous work, studying the discrimination of patterns presented in the vertical plane, suggests that at least two processes may be involved. Firstly, a pattern may be stored as an eidetic image or template, similar to a photographic picture. In the learning phase, the bee memorises the spatial intensity distribution of the rewarded pattern as a "snapshot" by hovering stably in front of and close to it (rev. Wehner 1981). The trained bee then distinguishes between the rewarded pattern and a different pattern by comparing the extent to which the stored image matches each of these patterns (Collett and Cartwright 1983; Gould 1985; rev. Wehner 1981). Alternatively, or additionally, patterns may be represented in a more abstract fashion on the basis of a set of parameters, such as size (Ronacher 1979a, b), spatial frequency, orientation of edges or bars, etc. (Wehner 1971, rev. 1981).

Recently van Hateren et al. (1990) suggested that bees can discriminate patterns on the basis of orientation as a parameter, without memorising intensity distributions. In their experiments, bees were trained to distinguish between patterns with different orientations, under experimental conditions in which they had to choose between the patterns at a distance. Their postulate was that, while approaching the patterns, the bees would first use orientational cues and then, when close enough to fixate the patterns, use eidetic imagery to distinguish between the patterns (see also Srinivasan et al. 1994).

Here we test bees under experimental conditions in which they can inspect patterns close up and fixate them before they make a decision. We ask whether they use only memorised intensity distributions, only orientational cues, or a combination of the two in making a discrimination.

Methods

For each experiment a group of ca. 6 individually marked worker honeybees (*Apis mellifera*) were trained to enter the apparatus and collect a reward of sugar water. The apparatus consisted of a transparent perspex box in which the training and test patterns could be presented on two opaque walls perpendicular to each other (Fig. 1). In the centre of each pattern there was a perspex tube protruding circa 0.5cm. In the case of the positive pattern (+), this tube led into a dark reward box containing a feeder with sugar water. With the negative pattern (–), the tube was blocked after ca. 5 cm.

A. D. Giger (✉) · M. V. Srinivasan
Centre for Visual Sciences, Research School of Biological Sciences, Australian National University, G.P.O. Box 475, Canberra ACT 2601, Australia

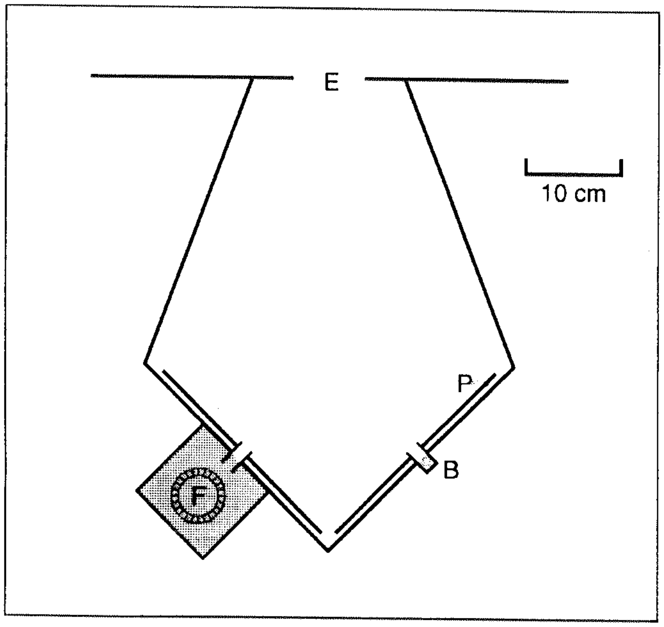

Fig. 1 The experimental setup. *B*: blocked tube; *E*: entrance (through an aperture in the window); *F*: feeder; *P*: pattern

The patterns were presented on cardboard disks 24 cm in diameter and consisted of periodic, black and white square wave gratings (wavelength 6 cm, Figs. 2 and 4). They were prepared by gluing stripes of black paper (cut out of laser printer print outs of high quality) onto white photocopying paper.

During training and throughout the whole experiment, the positions of the positive and negative patterns were interchanged every 10 mins to ensure that the bees did not associate the reward with a particular site. In such a 10 mins interval each bee would visit the apparatus twice, on average.

Once the bees had learned the training task, tests were conducted approximately once an hour. Before each test the reward box and both tubes were removed and replaced with two clean tubes identical to the blocked tube used in the training. The patterns were also replaced with fresh, unscented patterns. This procedure prevented the bees from using possible olfactory cues. Then, during a period of 4 mins, the bees' performance was measured by counting the number of times they touched or landed on either of the tubes. The effects of any side preferences were ruled out by interchanging the patterns' positions halfway through the test period. The bees' preference for each pattern was measured by counting the number of landings and touches, and quantifying these by giving landings a weight of 2 and touches a weight of 1. The resulting numbers were then used to calculate the choice frequency α in favour of the positive pattern (α = ratio of the number of positive choices to the total number of choices). Each test was repeated several times until the total number of choices was sufficient for statistical analysis.

To determine whether a measured α was significantly different from 0.5 (corresponding to random choice), we used an estimated standard deviation of the mean based on the assumption that the binary choice behaviour of the bees follows a binomial distribution. For details of this procedure see van Hateren et al. (1990).

During the course of each experiment control experiments were run frequently to ensure that the bees were not using olfactory cues to discriminate between the patterns. These controls were done by testing the bees with two identical patterns. Under these conditions the bees chose randomly between the two patterns ($\alpha = 0.48 \pm 0.07$, $P > 0.1$), indicating that non-visual cues were not important.

Results and discussion

In the first experiment we trained the bees to discriminate between a horizontally oriented grating (+) and a vertically oriented one. The learning test (test on training patterns, Fig. 2a) revealed a choice frequency of 0.93 for the positive pattern. Apparently, this was a very easy task for the bees. Similar levels of performance have been reported in earlier work with such

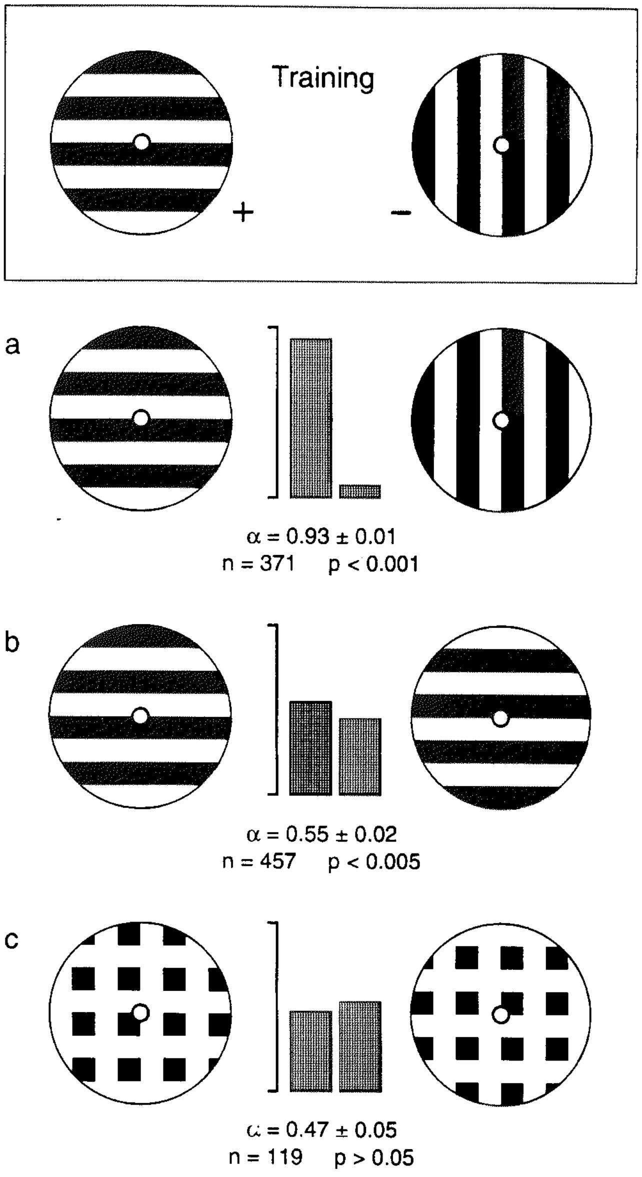

Fig. 2a–c Training on horizontal (rewarded, +) versus vertical (unrewarded, −) gratings. **a** Learning test. **b** Test on positive training pattern (+) versus the same pattern oriented vertically. *Histograms* show the choice frequencies with respect to the corresponding patterns. The *calibration bar* to the left of each histogram equals 1. α: choice frequency in favour of the left pattern; *n*: total number of choices; *p*: significance level for α being different from random choice. **c** Test on patterns which differ in intensity distribution overlap with training patterns (see text)

patterns (Lehrer et al. 1985; Srinivasan and Lehrer 1988).

We then asked what cues the bees used in this discrimination. What were the contributions of a memorised intensity distribution and pattern orientation, respectively? To investigate this question, bees, trained to distinguish between a horizontal and a vertical grating as described above, were tested on two horizontally oriented gratings. One grating was identical to the rewarded pattern, while the other was displaced by half a period, as shown in Fig. 2b. If the bees were using only the memorised intensity distribution to distinguish between the patterns of Fig. 2a, one would expect them to distinguish the patterns in Fig. 2b very well. In fact, they should prefer the positive training pattern even more strongly than in Fig. 2a, because the negative pattern produces less overlap with the memorised intensity distribution than does the vertically oriented pattern in Fig. 2a. However, the bees' preference for the positive training pattern was considerably lower than in the learning test. Clearly, the bees found it very difficult to distinguish between the two patterns when both had the same orientation and differed only in their spatial intensity distributions. Evidently, the bees were not distinguishing between the original horizontal and vertical training patterns of Fig. 2a purely on the basis of a photographic image: the orientation as such played an important role in the discrimination.

The possibility remains that patterns which carry strong orientation signals (such as the gratings we used) suppress the use of memorised intensity distributions, even if such intensity distributions are acquired from the training patterns. This was ruled out by the test shown in Fig. 2c. In the left test pattern the positions of the black squares overlap with the positions of the black stripes in the positive training pattern, but not with the black stripes in the negative training pattern. In the right test pattern, on the other hand, the black squares are positioned to overlap with black areas in the negative training pattern and with white areas in the positive one. These test patterns do not carry any orientation signals (i.e. the different orientations contained in a pattern cancel each other out), so the use of memorised intensity distributions of the training patterns would not be suppressed. If, under these conditions, the bees made their decisions based on intensity distribution, they should choose the left test pattern more often, because this shows more overlap with the memorised positive training pattern. As the bees showed no preference for either of the patterns (see Fig. 2c), we conclude that orientation signals do not suppress the use of intensity distribution cues in the test.

To examine whether memorised intensity distributions play a role at all, a separate experiment was carried out in which the bees were trained to distinguish between two horizontal gratings, one displaced by half a period relative to the other (Fig. 3a, same patterns as in Fig. 2b). Now the bees were able to discriminate the two patterns in a statistically significant way ($\alpha = 0.63$, $P < 0.001$). This shows that, if necessary, bees can use the difference in the intensity distributions as a cue to perform the discrimination. (Wehner (1981, p. 477) has obtained similar results with radial gratings, as have we (data not shown)). However, when these trained bees were tested for their ability to distinguish between the negative training pattern and a vertically oriented pattern, they showed a strong preference for the negative pattern, although its intensity distribution was inverted with respect to the positive training pattern and therefore would not have shown any overlap with a memorised intensity distribution (Fig. 3b). Clearly, although the vertically oriented pattern would have shown a 50% overlap with a memorised intensity distribution, the negative pattern was preferred because it was the one bearing the correct orientation.

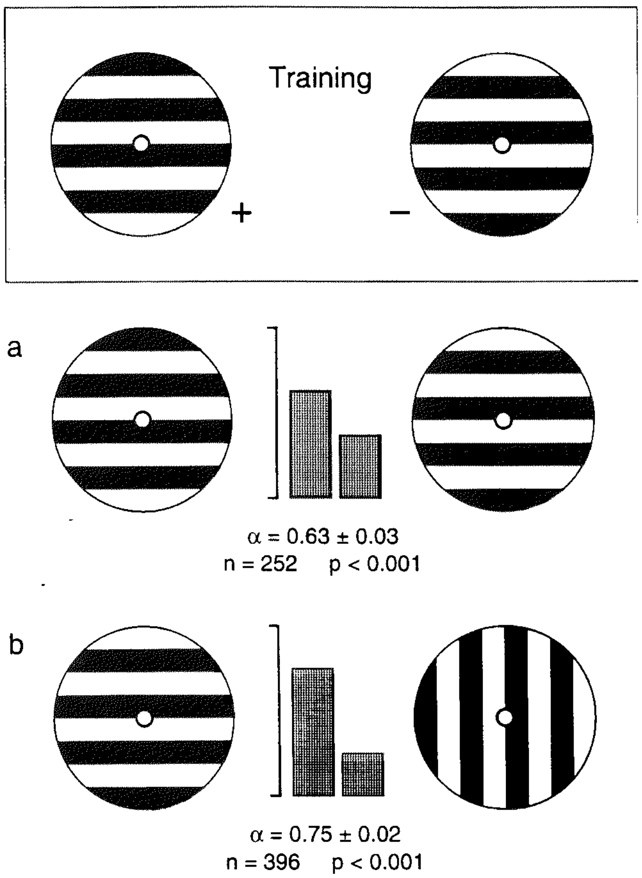

Fig. 3a, b Training on horizontal grating (rewarded, +) versus the same pattern shifted by half a period (unrewarded, −). **a** Learning test. **b** Test on negative training pattern (−) versus the positive training pattern oriented vertically

In the two experiments described above we assumed that the bees fixate the patterns when they compare their intensity distributions with the memorised distribution of the positive training pattern. That is, if the test pattern is the contrast-inverted version of the training pattern, they see no overlap at all. On the other hand, with a vertically oriented version of the training pattern, the ratio of overlapping to non-overlapping areas is 50%, neglecting boundary effects. One could argue that, if the bees test the match continually while they are in motion, the amount of overlap between the seen and the memorised intensity distribution would fluctuate between 0 and 100% for the contrast-inverted pattern, but remain constant at 50% for the rotated pattern (neglecting boundary effects). The bees would then choose the pattern that produces the maximal overlap at any time, and therefore choose the pattern with the same orientation as the training pattern. This would explain the results in Figs. 2a and 3b (but not the result in 3a). However, the experiment depicted in Fig. 4 illustrates that bees do not always use just a scan-and-match strategy. Here bees are again trained to distinguish between two horizontally oriented patterns, but the black bars are only 1cm wide, while the white bars have a width of 5 cm. The negative pattern is displaced by half a period relative to the positive one. The bees learned to make this discrimination quite well (Fig. 4a). The trained bees were then tested on a contrast-inverted version versus a vertically oriented version of the positive training pattern (Fig. 4b). They showed a clear preference for the horizontally oriented pattern. If a template of the positive training pattern is swept over its contrast-inverted version, the overlap of the intensity distributions would fluctuate only between 0 and 33% (neglecting boundary effects). With the vertically oriented pattern, on the other hand, the overlap would always be 72% – a much greater value. Therefore, in this case, if the bees had learned the patterns in a purely photographic sense, they should have preferred the vertically oriented pattern. The finding that they favoured the horizontally oriented, contrast-inverted pattern instead, shows again that orientation is a very strong cue.

The overlap calculations above assume both an infinitely large pattern and an infinitely large receptive field. The latter can be argued against, as both Wehner (1972) and ourselves (unpublished data) have shown that, under certain conditions, the region of the pattern just ventral to the fixation point is more important to pattern discrimination than other regions. Nevertheless, it is unlikely that the bees include only small areas in their snapshots. The smaller a snapshot is, the less useful it must be to identify a food source, because it would match many other scenes as well.

Figure 4c presents another argument against the use of small regions for orientation processing. In this test we used patterns that showed different global orientations (horizontal and vertical, respectively), but could not be discriminated when only a small area of a pattern was considered at a time. The fact that the bees preferred the pattern with the correct global orientation indicates that they are computing orientation in a global sense, rather than extracting it from small patches.

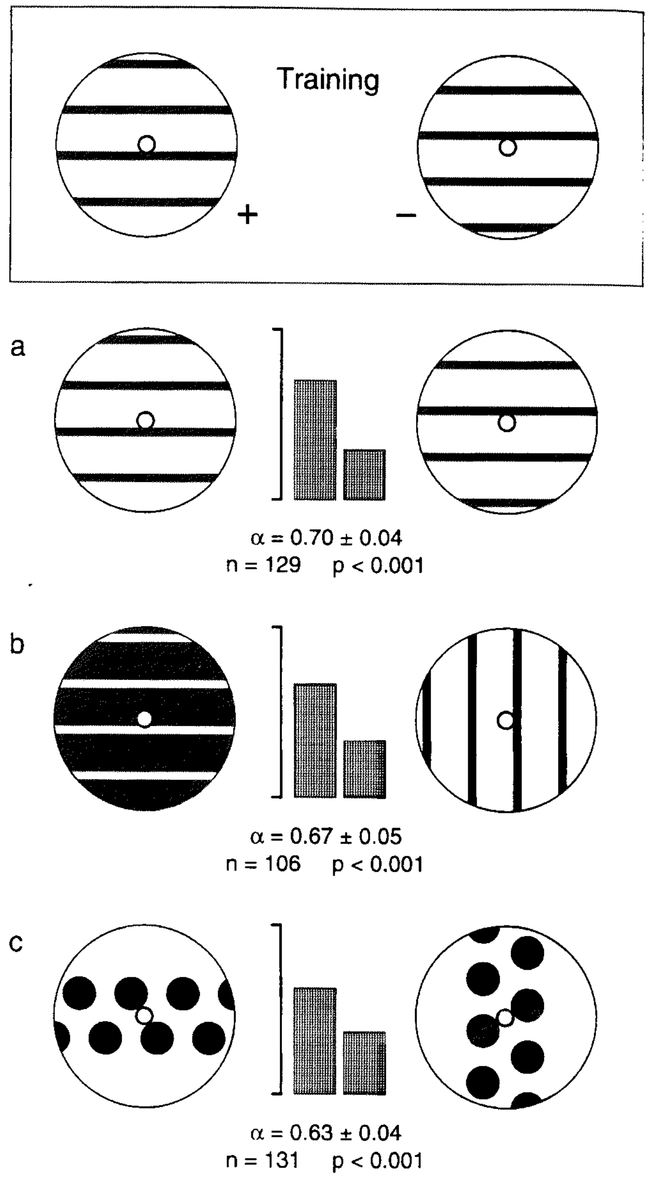

Fig. 4a–c Training on horizontal pattern with black (width 1cm) and white (width 5cm) bars (rewarded, +) versus the same pattern shifted by half a period (unrewarded, −). **a** Learning test. **b** Test on contrast-inverted positive training pattern versus the positive training pattern oriented vertically. **c** Test on patterns with black dots arranged in horizontal and vertical rows, respectively

One important result of the experiments of Figs. 3b, 4b and 4c is that the bees acquire orientation information during training, irrespective of whether this information is actually needed in the discrimination task. In other words, if both training patterns are horizontally oriented, the bees use their intensity distributions to distinguish between them, but they also learn the orientation of the patterns. On the other hand, when bees are required to distinguish between patterns that differ strongly in their orientations, they barely use the intensity distribution as a cue even when this would provide them with the information necessary to make the discrimination. Thus, it appears that bees discriminate between patterns on the basis of memorised intensity distributions only when they are forced to do so. Evidently, the weight assigned to a particular mechanism of pattern discrimination depends on the nature of the cues that are available.

How pattern orientation is represented by the bees' visual system is still largely unknown. One possibility is that patterns are represented as eidetic images, but that the images are not purely "photographic" – they may encode the positions and orientations of edges, or other salient features in the pattern. Alternatively, orientation could be extracted as an abstract, position-independent cue, in terms of the responses of a number of orientation-tuned channels (e.g. O'Carroll 1993; Srinivasan et al. 1993, 1994).

In conclusion we can say that honeybees do not use just memorised distributions of intensity to discriminate between patterns, when the patterns carry strong orientational cues and are differently oriented. This is true not only for patterns viewed from a distance (as shown by van Hateren et al. 1990), but also at close range where they can be fixated. However, bees do discriminate between patterns on the basis of memorised intensity distributions (or other representations which preserve spatial information) when orientational information cannot be used to make the discrimination.

Memorising patterns purely "photographically" in terms of their spatial intensity distributions, could impose severe demands on the limited information-storage capacity of an insect's brain, especially when a number of different patterns have to be learned. In many cases, it may be more economical to represent patterns in a more abstract fashion and merely in terms of their distinguishing features. This may be one reason why photographic imagery is not used unless it is absolutely essential.

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References

Collett TS, Cartwright BA (1983) Eidetic images in insects: their role in navigation. Trends Neurosci 6: 101–105

Gould JL (1985) How bees remember flower shapes. Science 227: 1492–1494

Hateren JH van, Srinivasan MV, Wait PB (1990) Pattern recognition in bees: orientation discrimination. J Comp Physiol A 167: 649–654

Lehrer M, Wehner R, Srinivasan M (1985) Visual scanning behaviour in honeybees. J Comp Physiol A 157: 405–415

O'Carroll D (1993) Feature-detecting neurons in dragonflies. Nature 362: 541–543

Ronacher B (1979a) Äquivalenz zwischen Grössen- und Helligkeitsunterschieden im Rahmen der visuellen Wahrnehmung der Honigbiene. Biol Cybernetics 32: 63–75

Ronacher B (1979b) Beitrag einzelner Parameter zum wahrnehmungsgemässen Unterschied von zusammengesetzten Reizen bei der Honigbiene. Biol Cybernetics 32: 77–83

Srinivasan MV, Lehrer M (1988) Spatial acuity of honeybee vision and its spectral properties. J Comp Physiol A 162: 159–172

Srinivasan MV, Zhang SW, Rolfe B (1993) Is pattern vision in insects mediated by 'cortical' processing? Nature 362: 539–540

Srinivasan MV, Zhang SW, Witney K (1994) Visual discrimination of pattern orientation by honeybees: performance and implications for 'cortical' processing. Phil Trans R Soc Lond B 343: 199–210

Wehner R (1971) The generalization of directional visual stimuli in the honey bee, *Apis mellifera*. J Insect Physiol 17: 1579–1591

Wehner R (1972) Dorsoventral asymmetry in the visual field of the bee, *Apis mellifica*. J Comp Physiol 77: 256–277

Wehner R (1981) Spatial vision in arthropods. In: Autrum H (ed) Vision in invertebrates (Handbook of sensory physiology, vol VII/6C). Springer, Berlin Heidelberg New York, pp 287–616