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Hateren, J.H. van; Srinivasan, M.V.; Wait, P.B.

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Pattern recognition in bees: orientation discrimination

J.H. van Hateren[1,2], M.V. Srinivasan[2] and P.B. Wait[2]

[1] Department of Biophysics, University of Groningen, Westersingel 34, NL-9718 CM Groningen, The Netherlands
[2] Visual Sciences, RSBS, Australian National University, Canberra, ACT 2601, Australia

Summary. 1. Honey bees (*Apis mellifera*, worker) were trained to discriminate between two random gratings oriented perpendicularly to each other. This task was quickly learned with vertical, horizontal, and oblique gratings. After being trained on perpendicularly-oriented random gratings, bees could discriminate between other perpendicularly-oriented patterns (black bars, white bars, thin lines, edges, spatial sinusoids, broken bars) as well.

2. Several tests indicate that the stimuli were not discriminated on the basis of a literal image (eidetic template), but, rather, on the basis of orientation as a single parameter. An attempt to train bees to discriminate between two different random gratings oriented in the same direction was not successful, also indicating that the bees were not able to form a template of random gratings.

3. Preliminary experiments with oriented 'Kanizsa rectangles' (analogue of Kanizsa triangle) suggest that edge detection in the bee may involve mechanisms similar to those that lead to the percept of illusory contours in humans.

Introduction

Broadly speaking, there are two theories of visual pattern recognition in bees. One theory postulates that patterns are classified and discriminated on the basis of one or more parameters, such as content of high spatial frequencies ('contour density'), orientation of contours, etc. (rev. Wehner 1981). The other theory proposes that a pattern is stored as a literal image, in much the same way as a photographic plate (eidetic template, Collett and Cartwright 1983; Gould 1985). Recognition then depends on the degree to which a newly encountered pattern matches this stored template, i.e. the extent to which their intensity profiles overlap (Wehner 1972; Cruse 1974; rev. Wehner 1981). The extent to which these two possibilities are 'rivals' is unclear because, firstly, they could coexist, and, secondly, the differences between the theories could be due partly to the differences in the tasks that have been investigated: identifying a food source, or using landmark patterns in navigation.

The main aim of this study is to examine whether it is possible to train bees to discriminate patterns purely on the basis of their orientation, without any reference to a template. In order to prevent the possible formation of a template we trained bees on several pairs of oriented random gratings. With this training procedure, any template that would yield a good match with a particular random grating would yield a poor match with at least several of the other random gratings that were used. Thus, if bees only use templates for pattern discrimination, we expect a poor performance on this task. If, on the other hand, they are able to use orientation per se as a parameter for pattern discrimination, we expect that they would be good at discriminating the orientation not only of random gratings, but also of other patterns which they had not previously seen.

Materials and methods

Apparatus. Honey bees (*Apis mellifera*, worker) were marked and trained to enter a Y-shaped, dual-tunnel apparatus, similar to that described in Srinivasan and Lehrer (1988). Bees entered the apparatus through an aperture in the window, and could view simultaneously two stimulus patterns, each mounted on the vertical end wall of one tunnel. One of the patterns offered a reward of sugar water, dispensed by a feeder located in a box behind the pattern. The box was accessible via a small connecting tube running through the centre of the pattern and protruding approximately 0.5 cm. The other pattern offered no reward and merely carried a short central tube, closed at its far end and painted black on the inside so as to be optically indistinguishable from the tube on the rewarded pattern.

Stimuli. Stimuli were prepared on disks of 24 cm diameter. The random gratings consisted of 12 bars, each 2 cm wide, with each bar having an equal probability of being black or white (see Fig. 1 for the 10 random gratings we used). This was determined using the random number generator of a Turbo Pascal program. As laser printouts of these gratings did not have the required blackness and homogeneity, we constructed the patterns by gluing black paper on white paper. Unless stated otherwise, the contrast was 0.9 for all stimuli used. The disks were mounted on the vertical end wall of each tunnel, 17 cm from the tunnel entrance. At this distance, each disk subtended a visual angle of 70.4°, and the width of each bar 6.7°. The bars could thus be well resolved by the optical apparatus of the bees: $\Delta\rho$, the half-width of the angular sensitivity of the photoreceptors, is about 2.6° for frontal vision (Laughlin and Horridge 1971; Eheim and Wehner 1972; Labhart 1980; van Hateren and Backhaus, unpublished), and $\Delta\phi$, the inter-ommatidial angle, is about 1.9° (van Hateren and Backhaus, unpublished; see also Seidl 1982, cited in Land 1989). Moreover, behavioural experiments (e.g. Srinivasan and Lehrer 1988) have demonstrated that bees can resolve periodic gratings of 2° stripe width (4° period).

Training and testing procedure. Each experiment was commenced by training a fresh, naive group of 4–7 bees to enter the apparatus and collect the reward. On a warm day, all of these bees would visit the apparatus twice every 7–9 min (the hive was about 50 m from the laboratory which housed the apparatus). Each bee was allowed to receive two rewards, on average, after which the positions of the rewarded and unrewarded gratings were interchanged in order to ensure that the bees did not associate the reward with one particular tunnel. After two more rewards per bee, the reward was returned to the original tunnel and the gratings were replaced by a new pair of random gratings, the combination being determined by a long list of random, pairwise combinations of the 10 gratings. This procedure was continued throughout the experiment.

The learning performance of the bees was evaluated as follows. A bee's entry into one of the tunnels was scored either as a correct response (if it entered the tunnel leading to the rewarded pattern) or an incorrect one (if it entered the other tunnel). In analysing the responses (see below) we only took into account the first response of each bee on each visit, in order to eliminate the possibility that the second choice might be influenced by the outcome of the first, particularly if the first choice happened to be the incorrect tunnel. As individual bees usually visited the apparatus at different times, there was seldom more than one bee in the apparatus and thus there was very little chance of one bee's choice being influenced by that of another. Since different bees visited the tunnel about equally often, all bees contributed approximately equally to the results.

After the bees had learned to respond correctly to the oriented gratings (the learning curve reaching a plateau of about 90% correct responses after 20–40 rewards), we continued to train them on random gratings while occasionally interspersing tests with other pairs of patterns. Bees were rewarded on these other patterns as well, but only 4 times, on average, per test: twice with the rewarded pattern in one tunnel, and twice with it in the other tunnel, as in the training on the random gratings. A given training and testing experiment with a group of bees typically ran for several days. A particular combination of test patterns would be repeated only after presentation of many pairs of random gratings and other pairs of test patterns, so that a given pair of test patterns was rarely presented more than twice per day. In principle the procedure of rewarding test patterns might cause the bees to learn these particular patterns, but we could not find any indication that this was indeed happening. In particular, we found that performance on test patterns was immediately at the final level and did not improve with successive presentations of them.

The choices of the bees might have been influenced by olfactory cues due, for example, to pheromones used by the bees to mark the site of the reward. We controlled for this possibility by occasionally testing bees, which were trained to discriminate between gratings of two different orientations, on two gratings, both having the same orientation as the one rewarded in the training. The patterns remained in their respective tunnels throughout each test, but the reward was switched to the other tunnel halfway through the test (i.e. after two rewards per bee). There was no indication that the bees' responses favoured the tunnel that happened to contain the reward ($\alpha=0.49\pm0.06$; $n=68$, $P>0.80$, see section on analysis of responses below). If the bees had used olfactory cues, they would have preferred the tunnel with the reward, as the patterns themselves were identically oriented and therefore equally attractive to the bees.

Analysis and statistical evaluation of responses. To quantify discrimination performance, we analysed the bees' responses in terms of the choice frequency, α, in favour of the correct pattern. We define α as the ratio of the number of correct choices to the total number of choices. Thus, $\alpha=0.5$ implies that the bees do not discriminate between the two patterns, while $\alpha=1$ indicates perfect discrimination. To determine whether a measured α is different from random choice behaviour ($\alpha=0.5$), we used two procedures. The first is to assume that the binary choice behaviour of the bees follows a binomial distribution (i.e. each consecutive response has a fixed probability of being correct). For a measured α on the basis of n responses, an estimate of the standard deviation of the mean, σ_α, is given by $\sigma_\alpha=(\alpha(1-\alpha)/n)^{1/2}$ (e.g. Schefler 1979). As a rule of thumb, α is significantly different from 0.5 if it is more than $2\sigma_\alpha$ (at 5% significance level) or $3\sigma_\alpha$ (at 0.1% significance level) away from 0.5. We also estimated the standard deviation of the mean in a different way by grouping the responses, determining the means of these groups, and finally calculating the standard deviation of the mean of this series of means. We found a close correspondence with the expression given above, indicating that the assumption of a binomial distribution is a reasonable one, at least for the first responses on consecutive visits. In the Results section we give $\alpha\pm\sigma_\alpha$.

A second procedure that we used for assessing the significance of α being different from 0.5 was the application of a χ^2-test. This always yielded results consistent with the procedure outlined above. In the Results section, the probability that the null-hypothesis that $\alpha=0.5$ is correct is given as P, determined from the χ^2-test. Thus $P<0.001$ means that there is less than 0.1% chance that the measured α is different from 0.5 only because of random fluctuations in the data. Finally, for determining whether α in a particular test was significantly different from the α in another test, we used a 2×2 χ^2-test, with P now specifying the probability that the two measured α's are different by chance.

Results

The set of random gratings that was used to train the bees is shown in Fig. 1. During the training, bees were presented with a pair of these gratings, one oriented perpendicularly to the other, with one grating located in each tunnel. The pattern oriented in one direction (e.g. vertical) was rewarded, while that oriented along the other direction (e.g. horizontal) was not. Patterns and rewarded sides were changed regularly, as described in Materials and methods, in order to prevent bees from associating a particular pattern or a particular tunnel with the reward. Bees quickly learned to fly directly to the grating with the correct orientation. Figure 2 shows the results when bees were trained to vertical (rewarded) vs. horizontal patterns (a), horizontal (rewarded) vs. vertical patterns (b), and two mutually perpendicular oblique orientations (c). The fractions of correct responses, α, was about 0.9 in each of these cases. The correct responses to vertical gratings (Fig. 2a) might in principle
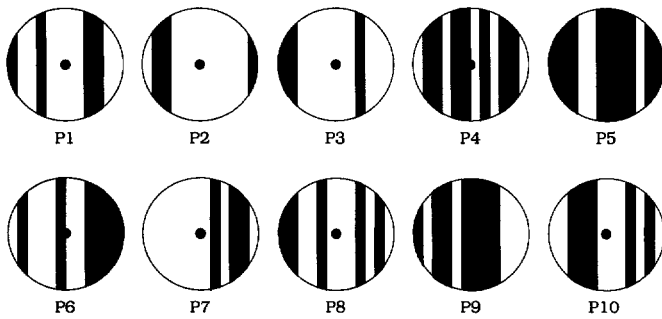
Fig. 1. The 10 random gratings used in this study. Each pattern had a diameter of 24 cm, and consisted of 12 bars, each 2 cm wide. Each bar had an equal probability of being black or white. A bar of 2 cm width subtends a visual angle of 6.7° at the entrance to each tunnel of the Y-maze. The dot in the centre of each disk depicts the 2 cm diameter entrance of the tube, possibly leading to a reward
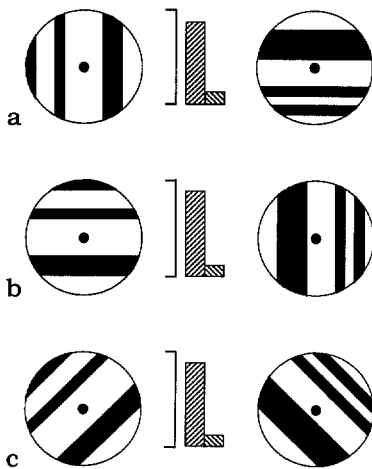

Fig. 2. a. Bees trained to discriminate a series of vertical random gratings (rewarded) from horizontal random gratings (unrewarded) yielded $\alpha = 0.87 \pm 0.02$ ($n = 232$, $P < 0.001$). The random gratings shown in the figure represent the complete set shown in Fig. 1. The histogram shows the fractions of correct choices (α) and incorrect choices ($1-\alpha$). The calibration bar to the left of each histogram equals 1. **b.** As **a**, but with the horizontal gratings rewarded; $\alpha = 0.89 \pm 0.01$ ($n = 645$, $P < 0.001$). **c.** As **a**, but with the oblique gratings shown in the left part of the figure rewarded; $\alpha = 0.88 \pm 0.02$ ($n = 409$, $P < 0.001$)

Fig. 3a–f. Responses to various oriented stimuli after training to random gratings oriented as in Fig. 2c. **a.** Black bars of 2 cm width, each subtending a visual angle of 6.7° × 70.4° as seen from the entrance of each tunnel; $\alpha = 0.91 \pm 0.04$ ($n = 64$, $P < 0.001$). **b.** White bars of 2 cm width; $\alpha = 0.90 \pm 0.04$ ($n = 59$, $P < 0.001$). **c.** Black lines of 0.5 cm width, subtending 1.7° × 70.4° as seen from the entrance of each tunnel; $\alpha = 0.73 \pm 0.04$ ($n = 138$, $P < 0.001$). **d.** Edges; $\alpha = 0.77 \pm 0.03$ ($n = 197$, $P < 0.001$). **e.** Sinusoidal gratings, of period 12 cm (39°), and contrast 0.7; the stripes in the figure only symbolize the sinusoid, in reality the grey level of the sinusoid varied continuously; $\alpha = 0.89 \pm 0.04$ ($n = 54$, $P < 0.001$). **f.** Broken black bars of 2 cm width; each part of the bar was 5 cm long; $\alpha = 0.81 \pm 0.06$ ($n = 47$, $P < 0.001$)

be explained as the consequence of a simple optomotor behaviour, rather than the result of learning an orientation: when bees fly into the Y-maze, they will see more horizontal movement in the vertical pattern than in the horizontal one, and may thus be deflected toward the vertical pattern. The other trainings, however, especially that on the oblique gratings, make such an explanation very unlikely. Therefore, we decided to carry out most of the tests in conjunction with the training on oblique gratings, though we have replicated most of the results with bees trained to either vertical or horizontal gratings.

Although the random gratings used were changed very frequently (approximately 30 times during a typical day's training), each grating was presented many times.
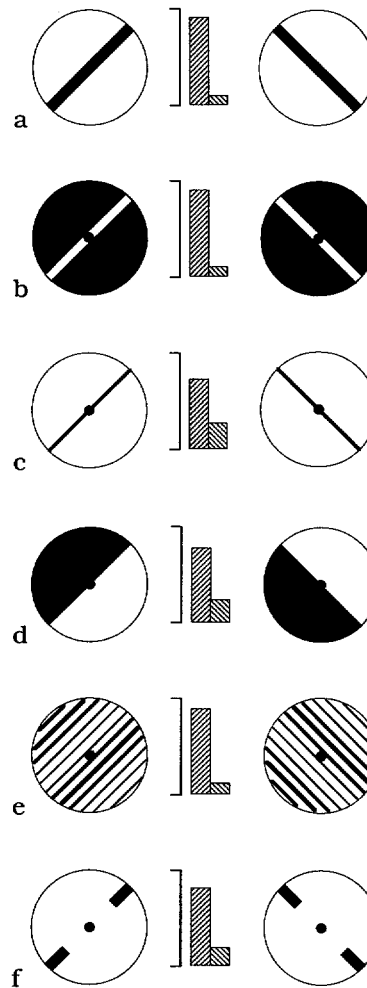
It is conceivable, therefore, that the bees mastered the task by memorizing each of the 10 random gratings individually. As a control, therefore, we tested bees, being trained to the random gratings of Fig. 1, on pairs of new random gratings they had not encountered previously. We found that orientation discrimination was immediately as good with these new pairs as with the original ones, with α again close to 0.9 ($\alpha = 0.85 \pm 0.03$; $n = 162$, $P < 0.001$). If the bees trained on the random gratings learned to make their decision on the basis of orientation only, we would expect them to be able to discriminate the same set of orientations even with patterns they had not seen previously. The results depicted in Fig. 3 show that this is indeed the case. Bees trained

on gratings can discriminate the orientation of black bars (a), white bars (b), thin lines (c, angular width smaller than both $\Delta\rho$ and $\Delta\phi$, see Materials and methods), single edges (d), sinusoidal gratings (e), and broken bars (f). Apparently, although the patterns are very different from each other and from the random gratings, bees are able to utilize effectively the one property that is common to all of the patterns, namely, orientation.

The results of Fig. 3 suggest that it is merely a single parameter, orientation, rather than a specific template, that is used for discriminating these patterns. It is conceivable, however, that the bees use a template in addition to orientation for discriminating the pairs of random gratings (results of Fig. 2). Bees rewarded a few times on a particular grating might form a (weak) template of that grating. Even if the next grating that is presented is randomly different from this template, there will always be some overlap between the two, leading to a partial match. We should also take into account that the bees are making their decision on the wing, and that they are free to direct their gaze to different parts of the patterns. Thus they may select that part of the pattern that produces the best possible match with the template. In order to test this possibility we occasionally interspersed tests where the grating that was rewarded in the previous presentation was presented again, but now together with another grating not in the perpendicular but in the same orientation in the other tunnel. If the bees had formed a template, it would match the original grating perfectly, thus one would expect them to prefer the original grating over the new one. If, on the other hand, the bees only used the cue of orientation for the task, they would not prefer either of the gratings, as both gratings were oriented in the same direction. Our results support the latter hypothesis: α in favour of the original grating is not significantly different from the random choice level ($\alpha = 0.53 \pm 0.05$; $n = 87$, $P > 0.50$).

In an extension of this test we trained bees to discriminate between two fixed perpendicularly-oriented gratings [P4 (rewarded) versus P8, see Fig. 1, oriented as in Fig. 2c]. Again, they learned this task well ($\alpha = 0.98 \pm 0.01$; $n = 409$, $P < 0.001$). We then rotated P8 to the same orientation as P4. If a template had been formed, we would expect $\alpha > 0.5$, but we found instead that α in favour of P4 was not significantly different from the random choice level ($\alpha = 0.51 \pm 0.04$; $n = 193$, $P > 0.80$). Evidently, even with a fixed pair of gratings presented in two different orientations, only orientation is used as a criterion for discrimination. This was confirmed by training bees on a single pair of perpendicularly-oriented gratings, and then testing them on other pairs of random gratings. Immediately, the bees were performing well in discriminating all other random gratings on the basis of their orientation ($\alpha = 0.98 \pm 0.01$; $n = 110$, $P < 0.001$).

These findings led us to question whether bees can form a template of a random grating at all. Therefore we tried to train 7 bees to discriminate between two identically-oriented gratings, P4 and P8. These two gratings differ substantially in individual structure. They ex-

hibit only average overlap even when shifted relative to each other, but do not differ very much in trivial properties such as average brightness or contour density (number of edges). We found that even after each bee had received 70–90 rewards, none of the 7 bees responded above chance level (all bees together yielded $\alpha = 0.51 \pm 0.02$; $n = 646$, $P > 0.40$). Apparently, bees find it very difficult to discriminate two similarly oriented random gratings, and it is unlikely that they form or utilize templates for this task.

Discussion

Recently it has been argued (Gould 1985) that bees do use an eidetic template for discriminating certain patterns. Though this may be true, we think it has by no means been proven. As there are presently no limits to the type, number, or complexity of possible parameters that could be used in lieu of a literal template, it is certainly possible to contrive a set of parameters that could be used to discriminate patterns such as those employed in Gould's study. Nevertheless, it is likely that bees use both template-based and parameter-based strategies in recognizing patterns, emphasizing one or the other depending on the stimuli and the behavioural setting (see also Cartwright and Collett 1983; Ronacher 1979).

It has been surmised that the formation of a template is facilitated by the presence of a visual landmark (such as the entrance tube in the centre of each pattern) which the bees can fixate, thus stabilizing the image of the pattern on their retina (Wehner and Flatt 1977; rev. Wehner 1981). Although such a tube was present in our experiments, it seems unlikely that the bees were able to use it as a fixation device. This is because the choice had to be made before entering one of the tunnels, relatively far away (at least 17 cm) from the tubes. Therefore, it is possible that our experimental design precluded easy fixation and thus the acquisition of a template. Furthermore, Gould (1986) argues that patterns can be remembered only as low-resolution pictures (resolution ca. 10°). If this is the case, it might also preclude template acquisition for the patterns we used, as the narrowest bars in the random grating were 6.7° wide. Nevertheless, our findings demonstrate clearly that bees can utilize the orientation of a pattern as a parameter, without acquiring a template.

Wehner (1971) showed that bees trained on oriented black bars can utilize orientation information in other patterns as well, such as black bars of different dimensions, interrupted black bars, and white bars. However, because the training pattern was kept fixed in this and related studies, it is difficult to exclude the possibility that this apparent generalization of orientation was performed using a template. If we assume that the bees had some freedom in what area of the training stimulus to use for a template, and where to direct their gaze in the tests, the results in Wehner's transfer tests can be explained on the basis that the positive test stimuli were more strongly correlated with the template ac-

quired from the training stimulus, than were the negative test stimuli. Our study confirms and extends several of Wehner's findings, showing that bees can utilize orientation information in a pattern from a variety of features, such as individual bars, edges, thin lines, and even from features with low spatial intensity-gradients, as in sinusoidal gratings. More importantly, our experiments show explicitly that this is accomplished without the use of pattern templates.

The experiments described here do not reveal whether bees can distinguish between the various test patterns that were used, when presented in the same orientation. We have been able to train bees to distinguish between a random grating (rewarded) and a similarly-oriented single bar (unrewarded; $\alpha = 0.78 \pm 0.03$; $n = 159$, $P < 0.001$), but not between a random grating (rewarded) and a sinusoidal (unrewarded; $\alpha = 0.50 \pm 0.04$; $n = 177$, $P > 0.95$), or between two similarly-oriented random gratings (see Results, last paragraph). Therefore, we cannot claim that bees are capable of 'generalizing' pattern orientation in the sense implied by Anderson (1972) or Wehner (1981, p. 540). What our findings do demonstrate, however, is that bees are capable of comparing the dominant orientation of two patterns, irrespective of their structural details.

How might the visual system of the bee extract information on pattern orientation? It is conceivable that bees discriminate between horizontally and vertically oriented features, for example, in terms of the characteristic temporal fluctuations of intensity that are produced when the features are scanned. A horizontal scan (induced, for example, by a yaw turn) would cause individual photoreceptors to register fluctuations of intensity while viewing vertically-oriented features, but not while viewing horizontally-oriented ones. A vertical scan (induced, for example, by a pitching motion) would have the opposite effect. Similar strategies have been suggested, for example, by Zerrahn (1933) and Wolf (1933) for the discrimination of patterns in the horizontal plane (rev. Wehner 1981). Information on orientation can also be obtained by using the signals of motion detectors that are selectively tuned to motion in horizontal and vertical directions, respectively (Srinivasan and Lehrer 1988). While it is not implausible that vertical and horizontal features are discriminated on the basis of their temporal or motion signatures, it is more difficult to explain the discrimination of oblique gratings on this basis. This would necessitate invoking other processes such as scanning along oblique directions, or a more elaborate analysis of spatiotemporal intensity patterns or motion signals (van Hateren 1990). An alternative possibility is analysis of the visual pattern by interneurons with orientation-sensitive receptive fields, as in the visual cortex of higher vertebrates.

Having established a way to train bees to 'abstract' a particular orientation, we can use this paradigm to test other properties of the bee's visual system. A preliminary example is shown in Fig. 4. For the human visual system it is known that aligned contours are more effective in creating the percept of a boundary, than are non-aligned contours or contours interrupted by other struc-
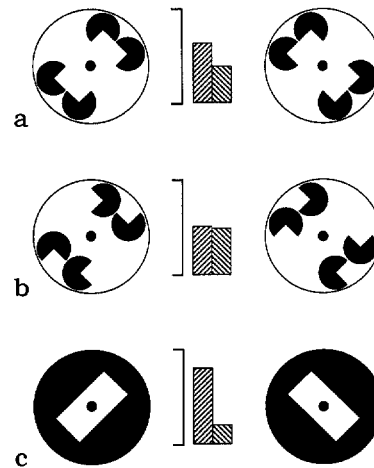

Fig. 4a–c. Test of the presence in the bee visual system of edge detecting mechanisms producing effects similar to those produced in the human visual system while perceiving illusory contours. **a.** 'Kanizsa rectangles', producing in the human visual system the percept of a white rectangle bounded partly by illusory contours; figure to scale; $\alpha = 0.62 \pm 0.03$ ($n = 275$, $P < 0.001$). **b.** Variation on the pattern of **a**, lacking illusory contours; figure to scale; $\alpha = 0.51 \pm 0.03$ ($n = 241$, $P > 0.80$). **c.** White rectangles; figure to scale; $\alpha = 0.80 \pm 0.04$ ($n = 89$, $P < 0.001$)

tures. Aligned contours can even lead to the perception of an illusory contour (see Fig. 4a): that is, the impression of a contour where none is physically present. Figure 4a shows a pair of illusory white rectangles, of the same size and orientation as the real ones in Fig. 4c. The illusion is based on the well-known Kanizsa triangle (Kanizsa 1955, see Petry and Meyer 1987 for a recent collection of articles on illusory contours). Figure 4b is a variation of Fig. 4a, with each of the black 'pacmen' rotated 90° clockwise; the illusory contours are now lacking. Although the number of edges in the two orientations is the same in both Fig. 4a and b, the presence of illusory contours in Fig. 4a gives an impression of orientation (as in Fig. 4c) that is absent in Fig. 4b.

When bees, trained on oriented random gratings as in Fig. 2c, were tested on these stimulus pairs, they were able to discriminate the patterns of Fig. 4a ($\alpha = 0.62 \pm 0.03$; $n = 275$, $P < 0.001$), but not those of Fig. 4b ($\alpha = 0.51 \pm 0.03$; $n = 241$, $P > 0.80$). These two performances were also significantly different from each other ($P < 0.025$). Figure 4c shows that the bees were well able to discriminate between two oriented white rectangles ($\alpha = 0.80 \pm 0.04$; $n = 89$, $P < 0.001$). The results of Fig. 4a and b suggest that similar processes might underlie edge detection in the visual system of bee and man, at least at a preperceptual level. We do not claim, of course, that bees actually perceive illusory contours in the way humans do. As the statistical difference between the tests of Fig. 4a and b is small, this experiment and its interpretation obviously need to be corroborated by further work.

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