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Uniform discrimination of pattern orientation by honeybees

B. C. SATHEES CHANDRA*, L. GEETHA†, V. A. ABRAHAM*, PRAVEEN KARANTH*, KENAZ THOMAS†, MANDYAM V. SRINIVASAN‡ & RAGHAVENDRA GADAGKAR†
*Centre for Ecological Sciences, Indian Institute of Science, Bangalore
†Behavioural Ecology Laboratory, Evolutionary & Organismic Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research, Bangalore
‡Centre for Visual Sciences, Research School of Biological Sciences, Australian National University

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ABSTRACT

To explore how honeybees, *Apis cerana*, discriminate the orientation of patterns, we trained workers to discriminate between a black stripe of a certain orientation on a white disc and a pure white disc. We tested trained bees for their ability to discriminate between the trained orientation and deviations from it. This was done either in a dual choice situation where the bees had to choose between the trained orientation and one deviation from it at a time, or in a multiple choice situation where bees had to choose simultaneously between the trained orientation and 11 successive deviations from it. In the dual choice situation, bees did not discriminate behaviourally between the trained orientation and deviations up to 25°, whereas in a multiple choice situation, they discriminated between the trained orientation and a deviation of 15° or more. Thus, orientation can be analysed more precisely in multiple choice experiments. The response of the bees was independent of the orientation of the trained orientation; the 12 different trained orientations all yielded identical results. This finding, considered together with a model that we present for orientation discrimination, suggests that at least three orientation-sensitive channels (a neuron or a set of neurons that respond maximally to a particular orientation) participate in the analysis of pattern orientation.

Insects, and especially honeybees, have long been known to discriminate between a variety of spatial patterns in their visual field. Like humans, honeybees can learn the orientation of stripes in their visual field and recognize the learned orientation even in other patterns they have never encountered before (Wehner 1971, 1985; van Hateren et al. 1990). A commonly held view is that bees accomplish this task by perceiving the directional movement signals that a pattern generates owing to the movement of the bee itself. Indeed, insect vision is often thought to depend entirely on such motion cues (Exner 1876; Lehrer et al. 1988; Srinivasan & Lehrer 1988; Horridge 1991).

Recent behavioural experiments by Srinivasan et al. (1993), however, strongly suggest that honeybees, even in the absence of motion cues, can perceive specific spatial features of the patterns encountered and detect their orientation. Insects, like mammals, may analyse orientation by a system of orientation-sensitive 'channels' (Srinivasan et al. 1993, 1994). According to this model, each channel consists of a neuron (or set of neurons) which responds maximally to a particular orientation. The orientation of the pattern is represented in terms of the responses of an assembly of neurons tuned to different orientations.

This idea is supported by recent neurophysiological investigations on dragonflies, *Hemicordulia tau* (O'Carroll 1993) and honeybees, *Apis mellifera* (Yang & Maddess 1997) which report the existence of neurons that respond specifically to bars or stripes with particular orientations. It is not known whether bees and other insects have orientation channels that perform a similar function as the orientation channels in the mammalian cortex. Since bees are known to discriminate between vertical and

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Correspondence: R. Gadagkar, Centre for Ecologial Sciences, Indian Institute of Science, Bangalore 560012, India (email: ragh@ces.iisc.ernet.in). L. Geetha is now at the Department of Physiology, School of Medicine, Hokkaido University, North 15, West 7, Sapporo 060 8638, Japan. V. A. Abraham is now at 26/4, Sirur Park Road, Seshadripuram, Bangalore 560 020, India. K. Thomas is now at the Department of Microbiology, The University of Oklahoma, Norman, U.S.A. P. Karanth is now at the Department of Biological Sciences, SUNY, University of Albany, Albany, New York 12222, U.S.A. M. V. Srinivasan is at the Centre for Visual Sciences, Research School of Biological Sciences, Australian National University, Canberra, ACT 2601, Australia.

horizontal stripes as well as between stripes at +45° or −45°, it has been argued that if they have orientation channels, they must have at least three (Collett 1993; Srinivasan et al. 1994). However, the predictions and consequences of this hypothesis have not been tested rigorously. Here we systematically investigated the ability of the honeybee *Apis cerana* to learn the orientation of a pattern, and to discriminate this orientation from others. Furthermore, in a series of experiments we examined whether the capacity to discriminate orientation depends upon the trained orientation. The data afford a rigorous test of the three-channel hypothesis, and in addition provide new information on the processes underlying the analysis of pattern orientation by the visual system of the honeybee.

METHODS

Dual Choice Experiments

We marked 20–25 *A. cerana* workers with quick-drying coloured paint and trained them to discriminate between two discs, each 10 cm in diameter, presented in a vertical plane. One disc, termed the positive stimulus, was white, with a black stripe 2 cm wide running along the diameter and oriented along a particular direction. This disc carried a black tube (1 cm diameter) in the centre, which led to a feeder with 70% sucrose solution. The other disc, termed the negative stimulus, was plain white. It carried an identical tube which was blocked at the rear end and did not lead to a food reward. During training, the relative positions of the positive and negative stimuli were interchanged every 10 min so that bees did not associate the reward with the relative position of the stimulus. Training was continued for 4–5 days by which time the percentage of bees going directly to the positive stimulus (without searching at the negative stimulus) reached a high plateau.

During a test, fresh discs and tubes were used and the tubes in both discs were open and led to a feeder with water but no sugar solution. We counted the number of bees landing on each disc or flying through each tube. Once again the two discs were interchanged every 10 min. While one disc was identical to the positive stimulus used during the training, the other was either plain white or had a black stripe, whose orientation deviated from the trained orientation. With intervening periods of training (lasting 30 min each) as described above, the same marked bees were tested (as described above) for their ability to discriminate between the trained orientation and successive deviations (one at a time) from this orientation. We repeated the whole experiment for 12 different trained orientations, by training a fresh group of 20–25 bees for each trained orientation. Only the first landing by each bee since it last returned from the hive was counted. The percentage of landings on the pattern representing the trained orientation (as opposed to the pattern representing a different orientation) was taken as a measure of the bees' capacity to discriminate orientation.

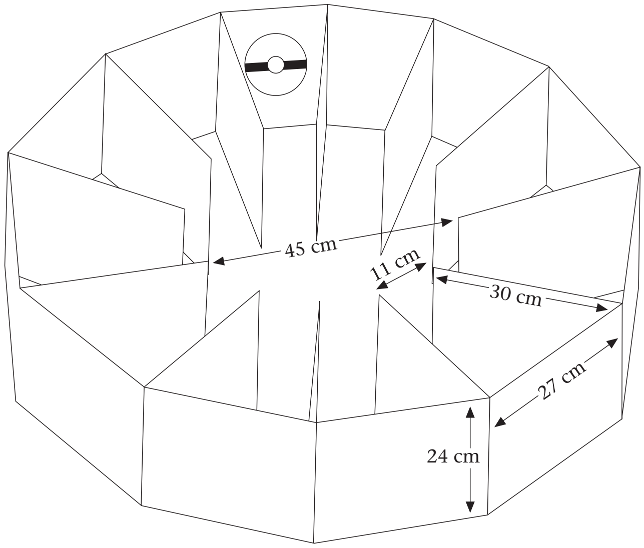

Figure 1. A view of the 12-chamber apparatus used for the multiple choice experiments.

Multiple Choice Experiments

As in the dual choice experiments, we trained marked worker bees to discriminate between a white disc with a black stripe (positive stimulus) and 11 pure white discs (negative stimuli). During the test, the trained bees were simultaneously presented with a disc with a black stripe of the trained orientation and 11 other discs with stripes differing successively in orientations from the trained orientation in steps of 15°. We used an apparatus (Fig. 1) consisting of 12 compartments opening upon a central circular arena as described by Lehrer et al. (1995). The trained orientation and the 11 deviations from it were all randomly assigned to the 12 compartments. In this case, we prevented bees from learning the absolute position of the positive stimulus (during training) and the correct stimulus (during testing) by rotating the apparatus periodically. As in the dual choice experiments, all tubes were kept open during the test period but the bees were not given any reward and we merely counted the number of entries into each chamber. Only the first choice of each bee returning from the hive was recorded. The criterion for a bee's choice was her crossing an imaginary line at the entrance to the compartment at a distance of 30 cm from the pattern. As in the dual choice experiments, the multiple choice experiment was repeated for 12 different training orientations.

In a third set of experiments, we used the multiple choice apparatus to test the bees in a dual choice situation by blocking entry to 10 of the 12 chambers. This set of experiments was repeated for three trained orientations, namely 90° (horizontal), 0° (vertical) and 45° (right diagonal). In contrast to the original dual choice set-up and as in the multiple choice experiments, here the bees had to make their choice at about 30 cm from the disc.

After the bees had made about 200 choices, we compared the number of landings of the bees on the two discs in the dual choice experiments, and the number of bees entering each of the 12 chambers in the multiple choice

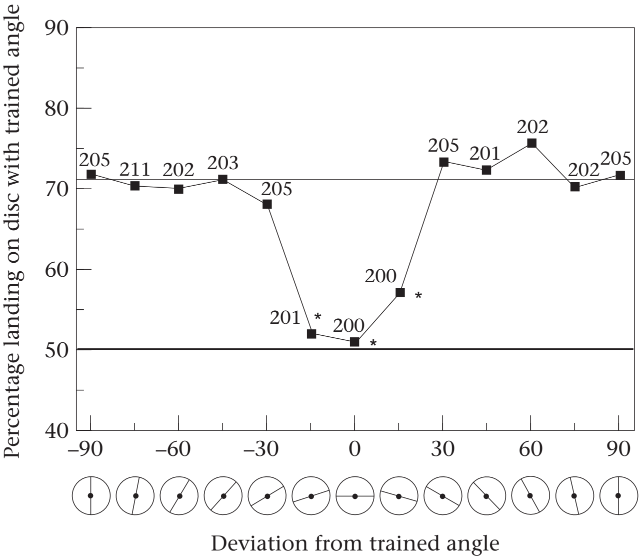

Figure 2. Results of a typical dual choice experiment. Bees were trained to discriminate between a white disc with a horizontal black stripe (arbitrarily designated as 90°) and a plain white disc and tested for their ability to discriminate between the trained orientation and orientations deviating from it in steps of 15° one at a time. The horizontal line at 71% represents the results of the learning test (disc with trained orientation versus plain white disc). Discs representing novel orientations differing from the trained orientation are shown below the *X* axis. The solid line at 50% represents random choice. Asterisks denote responses that are not significantly different from the 50% level. The number of choices for each orientation is also shown.

experiments, by a normal approximation of the binomial distribution (Feller 1968). The probability of landing on each disc by chance alone in the dual choice experiment was considered to be 0.5 and the probability of entering any of the 12 chambers in the multiple choice experiment by chance alone was considered to be 1/12. In the dual choice experiments, the proportion of bees landing on the correct disc when the alternative was a 0° deviation (identical to the correct disc) was compared to the proportion of bees doing so when the alternative was a deviation of 15°. In the multiple choice experiments, the number of bees entering the correct chamber (the one representing the trained orientation) was compared with the numbers of bees entering chambers that represented a deviation of 15° (+ and −) from the trained orientation.

RESULTS

Bees trained to discriminate between a disc carrying a horizontally oriented stripe (designated arbitrarily as 90°) and a plain white disc were able to learn this task well: the learning tests indicated a choice frequency of 71% for the positive stimulus, a level significantly above that corresponding to random choice (Fig. 2; $P<0.05$).

In the tests involving a disc with a stripe at 90° and discs bearing stripes with successive 15° deviations from the trained orientation (Fig. 2), when the unfamiliar orientation deviated from the trained orientation by less than 30° the number of choices for the trained orientation did not differ significantly from that expected by random choice of the two discs ($P>0.05$). However, when the trained and novel orientations deviated by 30° or more the number of choices for the trained orientation was significantly greater than that expected by random choice ($P<0.05$). Thus, bees trained as described above can discriminate orientations that differ by 30° or more, but not those that differ by less than 30°. This finding raises two questions.

(1) What is the critical deviation, between 15 and 30°, at which the bees can just discriminate between the trained and the novel orientation?

(2) Do these results hold only for bees trained to a horizontal stripe (90°) or do they hold for bees trained to any orientation? When we repeated the experiment for 12 different training orientations, each time with a fresh set of bees and each time using deviations of 0, 15, 20, 25 and 30° from the trained orientation, the bees were unable to discriminate deviations that were less than or equal to 25° from the trained orientation. A novel orientation was distinguished from the trained orientation only when the two orientations differed by more than 25° (Fig. 3). This discrimination capacity was identical for all 12 orientations that were used (Fig. 3).

In the multiple-choice experiments (Fig. 4), bees visited the chamber representing the trained orientation (0° deviation) and chambers with deviations of 15° from the trained orientation at a rate significantly higher than expected by chance alone. Bees visited all other chambers (with one exception out of 108 cases) with discs deviating by 30° or more from the trained orientation with probabilities equal to or less than expected by chance alone. While we did not test deviations of 20 and 25° in the multiple choice experiment, we repeated this experiment for all 12 trained orientations as in the dual choice experiment and the results are identical (Fig. 5). The behaviour of the bees was thus again identical for all the 12 trained orientations. However, in 22 out of 24 cases, the bees visited the chambers with orientations deviating by +15° and − 15° significantly less often ($P<0.05$) than they did the chamber with the trained orientation (although they visited all three chambers more often than expected by chance alone). This suggests that, in the multiple choice experiments, bees were able to discriminate deviations as low as 15°. This performance is clearly better than in the dual choice experiments described above.

The discrepancy between the results of the dual choice and multiple choice experiments may be related to (1) the fact that bees had simultaneous access to all the orientations in the multiple choice experiment but not in the dual choice experiment or (2) that in the multiple choice experiment, bees were forced to make their choice at about 30 cm from the disc (and thus with a global view of the disc), whereas in the dual choice experiment they could make their choice even after approaching the disc very closely and thus losing a global view of the stimulus constellation. The results of the third set of experiments, in which the bees were trained and tested in a dual choice mode, but were forced to make their choice 30 cm from

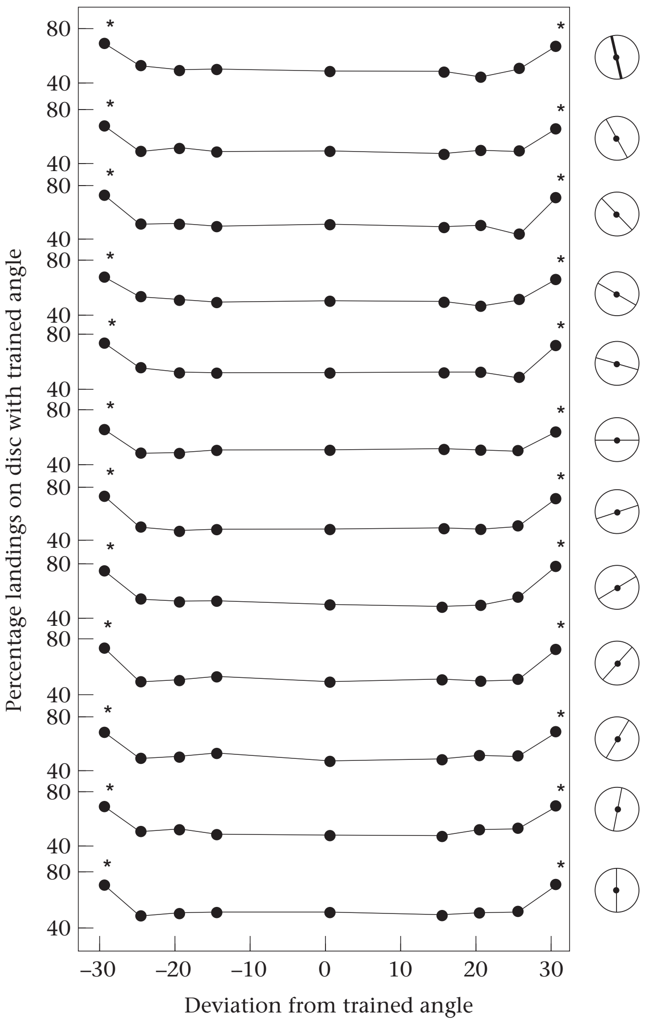

Figure 3. The percentage of bees landing on the disc with the trained angle in the dual choice experiments for all 12 trained orientations. Asterisks indicate orientations chosen significantly more often than expected by chance alone (*P*<0.05).

the discs, were identical to those of the original dual choice experiment and differed from those of the multiple choice experiments, however. It was clear therefore, that in a dual choice experiment, bees could not discriminate orientational deviations of less than 30° (Fig. 6), despite being forced to make their decision 30 cm from the discs.

DISCUSSION

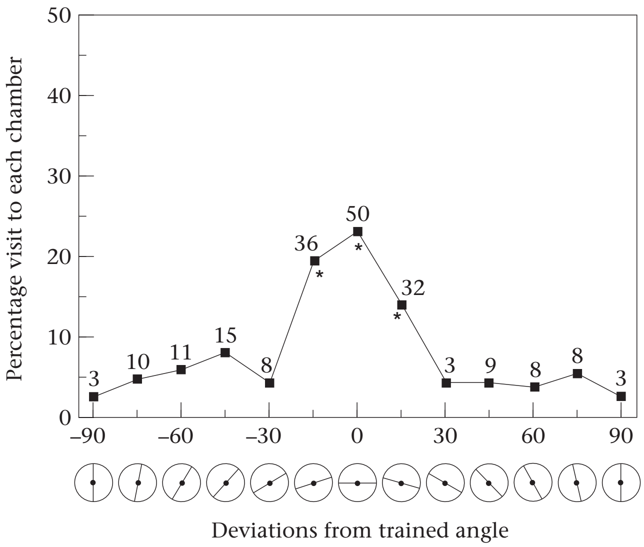

Figure 4. Results of a typical multiple choice experiment. Bees were trained to discriminate between a white disc with a horizontal black stripe (arbitrarily designated as 90°) and 11 plain white discs and tested for their ability to discriminate between the trained orientation and orientations deviating from it in steps of 15°, all presented simultaneously. Deviations from the trained orientation are shown below the *X* axis. Asterisks denote chambers chosen significantly more often than expected by chance alone (*P*<0.05). The number of choices for each orientation is shown.

Our experiments show that bees can discriminate orientation differences as small as 15° when trained in a multiple choice situation. However, the smallest discriminated orientation was greater (ca. 25°) when bees were trained in a dual choice task. One reason why the dual choice training yielded poorer discrimination performance could be that in such a training, the consequences of choosing the wrong stimulus are less severe: the bee simply has to move to the other stimulus to get the reward. In a multiple choice situation, however, an incorrect choice does not provide much information about where the reward is located: it can be at any of the 11 remaining stimuli. The more imprecise the bee's discrimination, the more time and energy that she will waste in visiting incorrect stimuli. Hence, the multiple choice experiment might motivate the bee to discriminate the stimuli more precisely. Further work is needed to examine whether this is indeed why the bees perform better under multiple choice conditions. It would also be interesting to investigate the effects of multiple choice training and testing in other sensory discrimination tasks.

Our main finding is that the ability of the bees to learn the orientation of a pattern and to discriminate this from other orientations is independent of the orientation of the training pattern. This is in contrast to orientation discrimination in human vision, where discrimination is substantially poorer at oblique orientations than at those close to the vertical and horizontal (Heeley & Timney 1988; Davey & Zanker 1998). It is also different from the situation in the octopus, which can discriminate a vertical bar from a horizontal one, but not bars oriented at +45° and − 45° (Sutherland 1957). As we discuss below, our results for the bee could have important implications for the neural mechanisms that are thought to underlie the analysis of pattern orientation in this animal.

Earlier work has suggested that, in the honeybee (and possibly in other insects), pattern orientation is analysed by a number of orientation-sensitive channels, in a manner somewhat analogous to that prevailing in the mammalian cortex (O'Carroll 1993; Srinivasan et al. 1993, 1994; Giger & Srinivasan 1995). There is also evidence to indicate that, in the insect visual system,

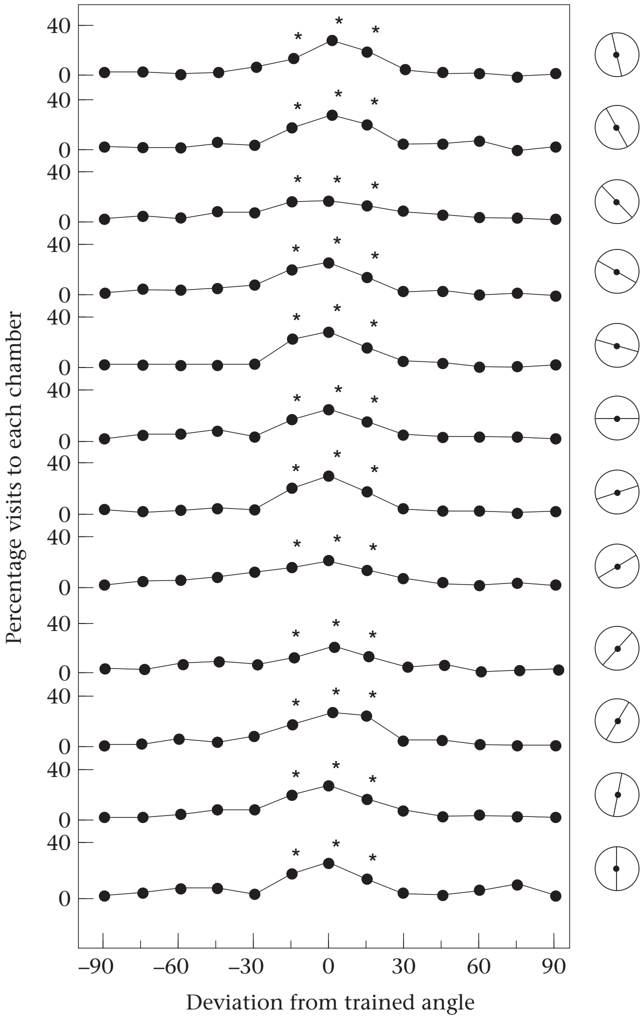

Figure 5. The percentage of bees visiting each chamber in the multiple choice experiments for all 12 trained orientations. Asterisks denote orientations chosen significantly more often than expected by chance alone ($P<0.05$).

these channels are rather broadly tuned for orientation, with a tuning half-width of ca. 90° (O'Carroll 1993; Srinivasan et al. 1994; Yang & Maddess 1997). The number of participating channels is not known, however. We believe that the present findings will shed some light on this question. If the ability to discriminate deviations in the orientation of a pattern is to be independent of the original orientation (as our experiments indicate), then it is clear that the visual system must possess an adequate number of channels to cover the range of possible orientations uniformly, without any 'gaps' in orientation sensitivity. How many channels are necessary to achieve this? We attempt to answer this question by modelling the process of orientation discrimination as follows.

Assume that the orientation tuning of a channel can be described by the function

$$r(\theta)=1+\cos[2(\theta-\theta_O)]$$

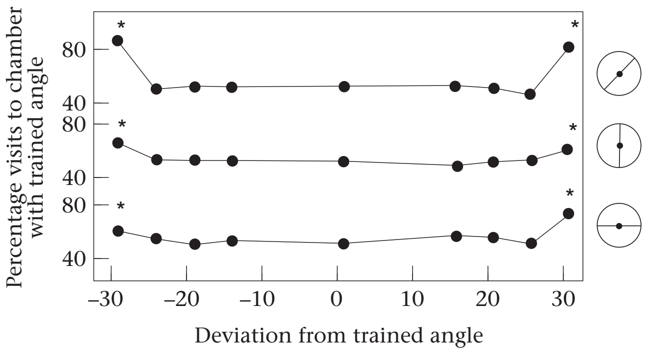

Figure 6. Results of the dual choice experiments where bees had to make their choice 30 cm away from the disc. Three trained orientations, 0, 90 and 45° and deviations of 0, 15, 20, 25 and 30° from each of them were used. Asterisks denote orientations chosen significantly more often than expected by chance alone ($P<0.05$).

Here θ denotes pattern orientation (measured anticlockwise relative to the rightward horizontal direction), θ_O denotes the preferred orientation of the channel, and $r(\theta)$ denotes the orientation-dependent response of the channel. Such a channel has an orientation tuning half-width of 90° (Fig. 7a). There is evidence that the tuning of orientation-sensitive channels in the insect visual system can be adequately described by such a function (O'Carroll 1993; Yang & Maddess 1997).

Consider first a system comprising two channels, with horizontal and vertical preferred directions, respectively, as shown in Fig. 7a. The responses of the two channels to a training pattern oriented at an angle α relative to the rightward horizontal direction would be

$$r_1(\alpha)=1+\cos[2\alpha]$$

and

$$r_2(\alpha)=1+\cos[2(\alpha-\pi/2)]$$

The responses of these channels to a test pattern oriented at an angle θ would similarly be

$$r_1(\theta)=1+\cos[2\theta]$$

and

$$r_2(\theta)=1+\cos[2(\theta-\pi/2)]$$

From the above equations, it is clear that a two-channel system, comprising a horizontally sensitive and a vertically sensitive channel, will not distinguish between stimuli oriented at +45° and −45°. Each of these stimuli would produce the same pattern of responses in the two channels: the response of both channels would be equal to 1.0 for each stimulus. Thus, a two-channel system will not account for the experimental results. Nevertheless, we shall complete the analysis of the two-channel system below, before considering a three-channel system.

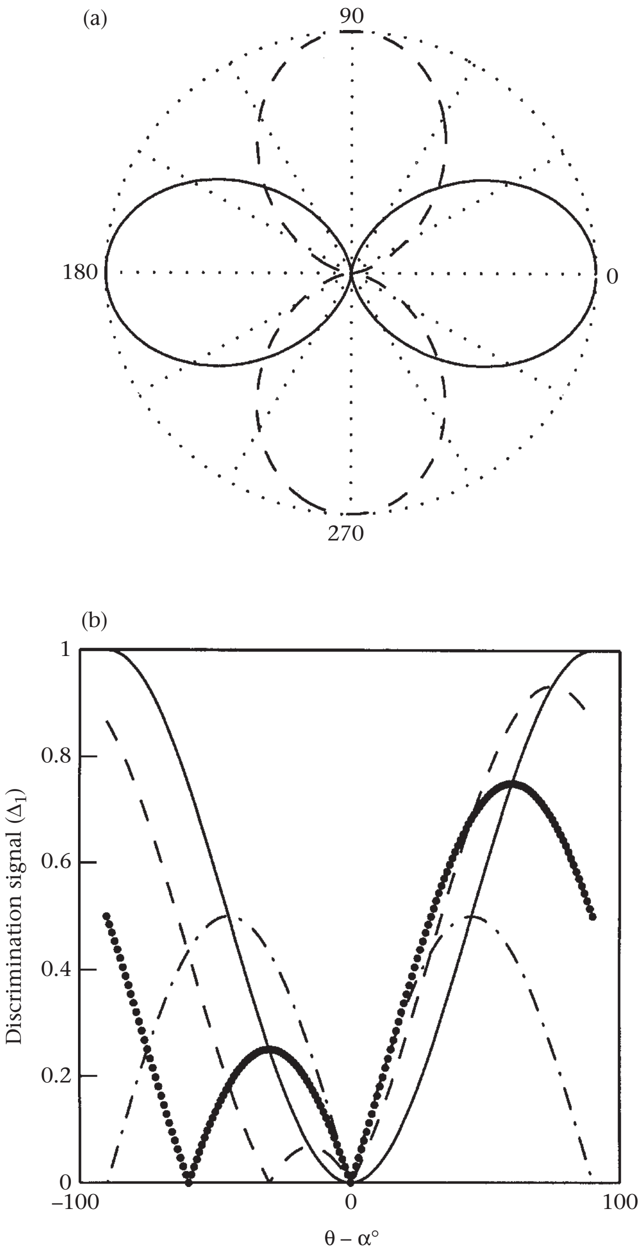

Figure 7. (a) Model of orientation analysis using two orientation-sensitive channels, each with a tuning half-width of 90°, and with horizontal and vertical preferred directions, respectively. See text for details. (b) Discrimination signal (Δ_1) as predicted by this model (see text), plotted as a function of the differences between training and test orientations ($\theta-\alpha$) for various training orientations (——: $\alpha=0°$; – – –: $\alpha=15°$; · · ·: $\alpha=30°$; – · – .: $\alpha=45°$).

We assume that the ability to discriminate the test orientation from the training orientation is proportional to the sum of the absolute differences in the signals that are created in the individual channels by the two orientations. That is, we assume that the discrimination signal, Δ_1, is given by

$$\Delta_1=|r_1(\theta)-r_1(\alpha)|+|r_2(\theta)-r_2(\alpha)|$$

Figure 7b shows how this discrimination signal varies as a function of the differences between the test and training orientations ($\theta-\alpha$) for various training orientations, α. The discrimination signal is zero when $\theta=\alpha$. For $\alpha=0°$, the discrimination signal increases symmetrically on either side as θ moves away from α. We note, however, that as α is varied, the shape of the predicted discrimination curve changes substantially: the curve is no longer symmetrical about $\theta=\alpha$. Furthermore, when α is not zero, the discrimination curve always has a second null point, in addition to that at $\theta=\alpha$. That is, there is always one test orientation that cannot be discriminated from the training orientation. For $\alpha=15$, 30 and 45°, the second null occurs at $\theta=-15°$, $-30°$ and $-45°$, respectively. These properties persist even when the form of the discrimination signal is changed. For example, if we define a different discrimination signal, Δ_2, as the sum of the squares of the differences between the responses to the training and test orientations in the individual channels, that is,

$$\Delta_2=[r_1(\theta)-r_1(\alpha)]^2+[r_2(\theta)-r_2(\alpha)]^2,$$

then the resulting theoretical discrimination curves are as shown in Fig. 8a. These curves again have the property that they vary dramatically in shape as the training orientation α is changed. Furthermore, they display secondary nulls at the same test orientations as the curves in Fig. 7b.

The bees showed neither of the above properties, the experimentally measured discrimination curves displaying the same shape at all training orientations. Furthermore, the bees never confused a training orientation with any other orientation. Therefore, we conclude that the experimentally observed orientation discrimination performance cannot be explained in terms of an orientation-analysing system with two channels.

Consider now a system comprising three channels, with preferred orientations of 0, 120 and 240° respectively, as shown in Fig. 9a. The responses of these channels to a training pattern oriented at an angle α relative to the rightward horizontal direction would be

$$r_1(\alpha)=1+\cos[2\alpha],$$

$$r_2(\alpha)=1+\cos[2(\alpha-\pi/3)]$$

and

$$r_3(\alpha)=1+\cos[2(\alpha-2\pi/3)]$$

The responses of these channels to a test pattern oriented at an angle θ would similarly be

$$r_1(\theta)=1+\cos[2\theta],$$

$$r_2(\theta)=1+\cos[2(\theta-\pi/3)]$$

and

$$r_3(\theta)=1+\cos[2(\theta-2\pi/3)]$$

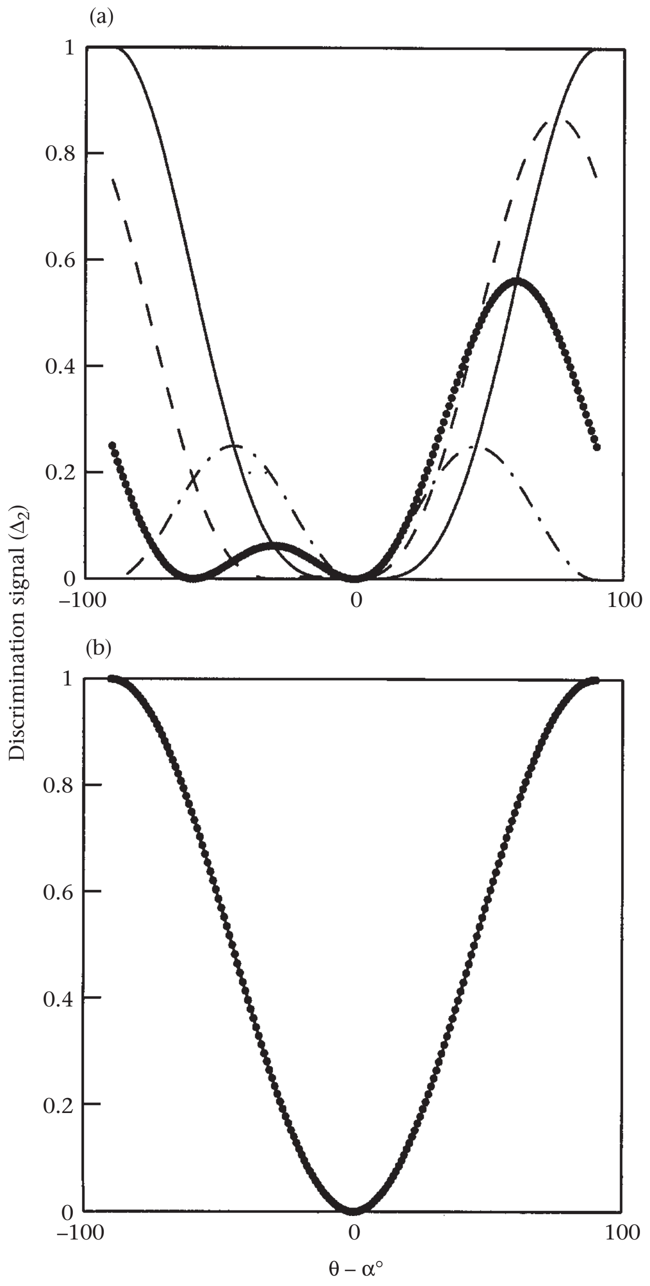

Figure 8. (a) Discrimination signal (Δ_2) as predicted by a two-channel model (see text), plotted as a function of difference between training and test orientations (θ−α) for various training orientations (——: α=0°; – – –: α=15°; · · ·: α=30°; – · –: α=45°). (b) Discrimination signal (Δ_2) as predicted by a three-channel model (see text) plotted as a function of difference between training and test orientations (θ−α) for various training orientations (——: α=0°; – – –: α=10°; · · ·: α=20°; – · –: α=30°; all curves overlap).

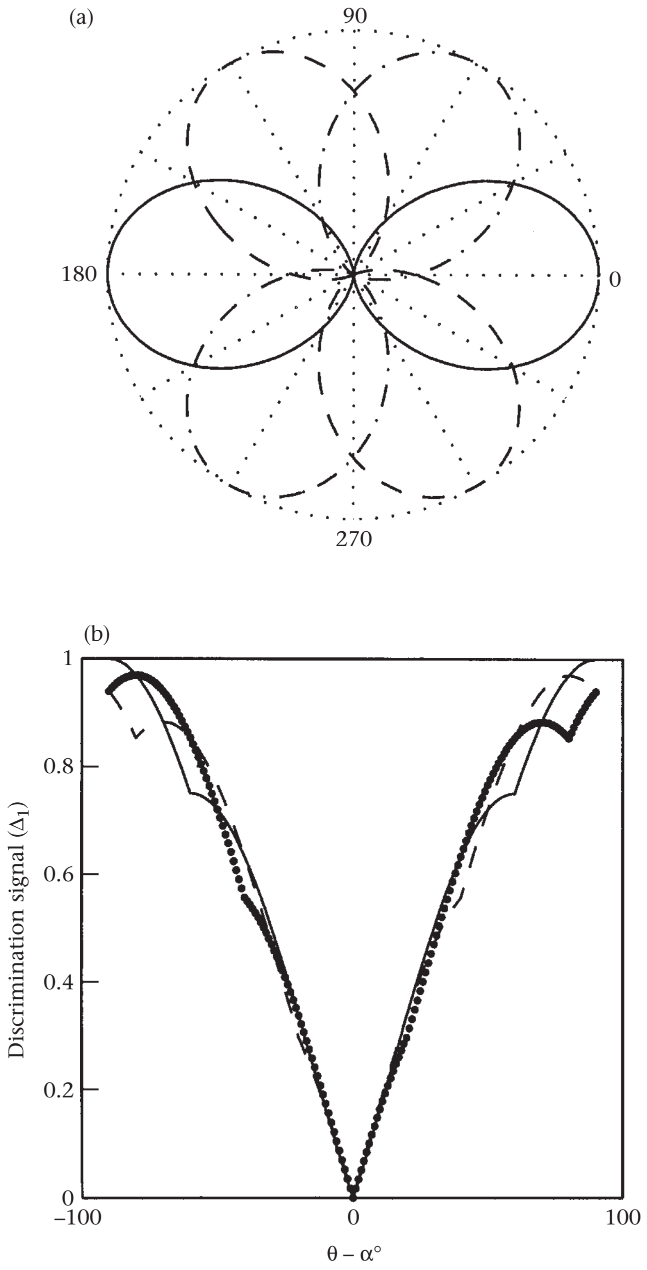

Figure 9. (a) Model of orientation analysis using three orientation-sensitive channels, each with a tuning half-width of 90°, and with preferred directions separated by 120°. See text for details. (b) Discrimination signal (Δ_1) as predicted by this model (see text), plotted as a function of difference between training and test orientations (θ−α) for various training orientations (——: α=0°, 30°; – – –: α=10°; · · ·: α=20°; – · –: α=30° (overlaps with solid curve)).

Figure 9b shows the discrimination signals, defined as

$$\Delta_1 = |r_1(\theta) - r_1(\alpha)| + |r_2(\theta) - r_2(\alpha)| + |r_3(\theta) - r_3(\alpha)|$$

plotted as a function of the difference between the training and test orientations, and Fig. 8b shows discrimination curves plotted using

$$\Delta_2 = [r_1(\theta) - r_1(\alpha)]^2 + [r_2(\theta) - r_2(\alpha)]^2 + [r_3(\theta) - r_3(\alpha)]^2$$

as the discrimination signal.

With three channels, the shape of the discrimination curve is virtually independent of the training orientation. This is true regardless of whether the discrimination signal is defined as Δ_1 (see Fig. 9b) or Δ_2 (see Fig. 8b). Furthermore, the discrimination curves do not have spurious nulls; that is, no matter what the training orientation, no other orientation is confused with it. The tuning curves of Fig. 8b and Fig. 9b are similar to those experimentally observed (compare with Figs 2–6). The exact shape of the theoretical discrimination curve near the trained orientation depends upon the particular functional form that is chosen for the discrimination signal (e.g. Δ_1 or Δ_2) and upon the nature and magnitude of thresholds in the sensory nervous system. However, the qualitative properties of the discrimination curve are not affected by these factors.

Increasing the number of channels to six, with preferred orientations separated by 60°, also produces very similar discrimination curves (results not illustrated). With six channels, discrimination performance comparable to that experimentally observed is predicted even when the half-width of the orientation tuning curves is reduced to 45°. However, we have not pursued this possibility, since earlier studies suggest that the individual channels possess a tuning half-width of 90° (O'Carroll 1993; Srinivasan et al. 1994; Yang & Maddess 1997).

On the basis of these simulations, we conclude that a minimum of three orientation-sensitive channels, each with a tuning half-width of 90°, and with preferred orientations separated by 120°, is sufficient to account for the orientation discrimination performance that we have observed experimentally. Further investigation is needed to determine whether the bee's visual system uses more orientation-sensitive channels than the minimum required number of three.

Giurfa et al. (1996) showed that bees are better at learning patterns that are symmetrical about the vertical axis, than at learning asymmetrical patterns. Our stimuli varied in the extent of symmetry about the vertical axis, the vertical and horizontal bars being perfectly symmetrical, and the other stimuli being asymmetrical to varying extents. One may then ask why bees did not differ in the ability to learn and discriminate the variously oriented bars in our experiments. However, each of the stimuli that we used does possess an axis of symmetry, even if the axis is oblique, and there is evidence that bees can recognize symmetry about any axis (Horridge 1996). The reason why orientation discrimination was independent of orientation in our experiments may be (1) that all of the stimuli used were perceived as being equally 'symmetrical' by the bees, or, more likely, (2) since the single bars used in our experiments were rather simple patterns compared with the elaborate symmetrical patterns used in the aforementioned studies, they probably stimulated predominantly the orientation analysis system and not the symmetry detection system.

Acknowledgments

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