

## ORIGINAL PAPER

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**Eye-specific learning of routes and “signposts” by walking honeybees**

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**Abstract** This study investigates the honeybee's ability to learn routes based on visual stimuli presented to a single eye, and to then navigate these routes using the other (naïve) eye. Bees were trained to walk through a narrow tunnel carrying visual stimuli on the two walls. At the end of the tunnel the bees had to choose between two arms, one of which led to a feeder. In a first experiment, bees had to learn to choose the left arm to get a reward when the right wall carried a yellow grating, but the right arm when the left wall carried a blue grating. The bees learned this task well, indicating that stimuli encountered by different eyes could be associated with different routes. In a second experiment, bees had to turn left when the right eye saw a blue grating, but to the right when the same eye saw a yellow grating. They also learned this task well. In subsequent tests, they chose the correct arm even when these gratings were presented to the untrained eye. These results suggest that there is interocular transfer of route-specific learning with respect to visual stimuli that function as navigational “signposts”.

**Key words** Honeybee · Vision · Navigation · Learning · Interocular transfer

**Introduction**

Over the past 15 years, evidence has been accumulating that ants and bees can learn to carry out tasks based on visual stimuli presented to a single eye (e.g. Wehner and Müller 1985; Lehrer 1990, 1994; Giger and Srinivasan 1997). In some cases, a task learned by visual input to one eye can also be carried out when this input is presented to the naïve eye. For example, the desert ant *Cataglyphis* learns to navigate back to its nest by using visual information based on a celestial compass and on landmarks encountered on the way – and it can do so even when one eye is covered (Wehner and Müller 1985). When *Cataglyphis* is trained to “home” with one eye occluded, and is subsequently tested by covering the trained eye and uncovering the naïve one, it exhibits interocular transfer if the task requires use of the celestial compass, but not if the task involves the use of earthbound landmarks (Wehner and Müller 1985). Bees with one eye occluded can learn the colour of a food source using a single eye, but they are unable to recognise the same colour when it is presented to the untrained eye (V. Pelzer, unpublished observations). Similarly, bees can learn to distinguish between two different sites based on colour or pattern information presented to a single eye, but they are unable to distinguish these sites when the same visual information is presented to the naïve eye (Giger and Srinivasan 1997). Bees can learn to use the position of a spatial feature (such as an edge) presented to the lateral visual field of a single eye, to pin-point the location of a frontally positioned target; but, they cannot locate the target when the feature is presented to the untrained eye (Lehrer 1994). However, when detection of this feature involves the use of motion cues, bees exhibit interocular transfer of learning (Lehrer 1990, 1994). Thus, whilst hymenopterans can clearly learn to perform a variety of tasks using one eye, their ability to transfer this learning to the naïve eye depends upon the nature of the task at hand.

This paper is dedicated to Professor Adrian Horridge on the occasion of his seventieth birthday

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Relatively few studies have addressed the question of whether the two eyes can simultaneously learn different tasks. Here, we ask whether bees can learn to navigate through a Y-maze by using route information in an eye-specific way: that is, can they learn to associate one particular route with a stimulus presented primarily to one eye, and another route when a different stimulus is presented primarily to the other eye? We also examine whether bees that have learned to navigate through the maze by using information presented to one eye can transfer this learning to the other eye. An unusual aspect of this investigation is that, unlike most earlier studies of honeybee learning using Y-mazes, the stimuli that are presented to the eyes do not represent the bee's destination; rather, they act as "signposts" which specify the future route through the maze.

## Materials and methods

The experiments were conducted at the Australian National University's Centre for Visual Sciences in Canberra during the (Australian) summers of 1995 and 1996. The experimental apparatus, as well as the bee hive used for the experiments, were located in a large indoor flight room with translucent walls and roof. The experiments were thus carried out under nearly natural daylight conditions, except for the fact that the illumination was deficient in the ultraviolet and not polarised. A computer-controlled air-conditioning system maintained the internal temperature of the facility at  $24 \pm 5^\circ\text{C}$  during the day and  $17^\circ\text{C}$  at night.

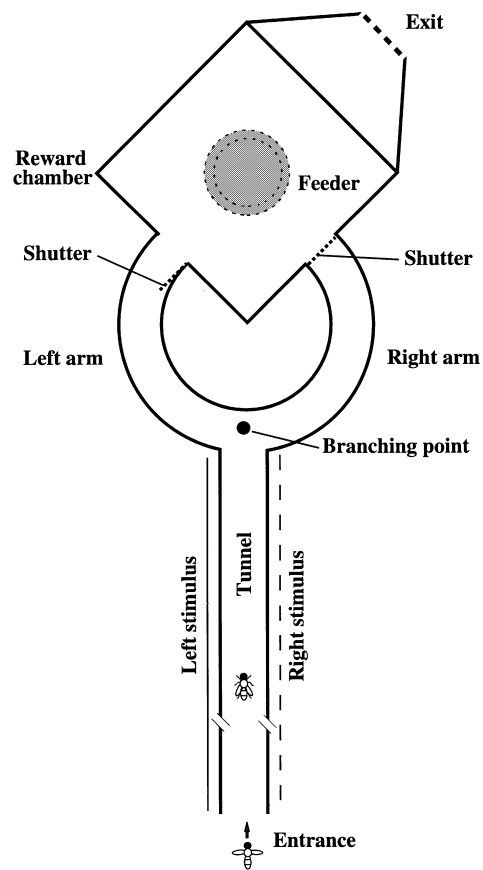
### Experimental setup

For each experiment, a group of six to ten bees was individually marked and trained to collect a food reward at a Y-maze apparatus (Fig. 1). Bees entered the apparatus through a tunnel 20 cm long, 2 cm wide and 1.5 cm high, constructed of transparent Perspex. Although the bees flew freely between the apparatus and the hive, once they entered the apparatus they could only walk because of the restricted cross-sectional dimensions of the tunnel. Whilst walking along the tunnel, they encountered visual stimuli on the side walls as they proceeded toward the branch point of the Y-maze. From this point, they could reach a reward chamber through the right or the left arm, depending upon the stimuli displayed in the entrance tunnel. The reward chamber contained a feeder which offered sugar water. Shutters were used to control access to the reward chamber. The reward chamber was almost completely dark. The back of the chamber led to an exit, which was an opening covered by a transparent flap. Light entering the chamber through this opening encouraged the bees to leave the chamber via the exit after they had collected the reward. The flap had a one-way action which prevented bees from entering the reward chamber directly from the outside: the only way they could collect the reward was by walking through the entrance tunnel and choosing one of the two arms.

The bees were trained to walk through the tunnel and the Y-branch by placing a long wick of tissue, soaked in sugar solution, in the tunnel and pulling it slowly toward the feeder in the reward chamber.

### Stimuli

On their 20-cm-long path through the tunnel the bees viewed a coloured, vertical grating placed on one of the lateral walls. In accordance with the dimensions of the tunnel, the grating was presented on a 20-cm-long, 2-cm-high piece of cardboard which could easily be removed or replaced. Three different gratings were



**Fig. 1** Y-maze apparatus used for eye-specific route training of walking honeybees. Details in Materials and methods. The illustration is not to scale

used: one was constructed using yellow and white papers, another using blue and white papers, and a third using black and white papers. In the following we shall refer to these stimuli as "yellow grating", "blue grating" and "black/white" (B/W) grating, respectively. All of the gratings had a spatial period of 4 cm. We used gratings, rather than spatially homogeneous colours because we assumed that gratings would be more "noticeable" (i.e. have a greater visual impact) for the bees. The floor of the tunnel was homogeneously white. The tunnel was narrow enough to discourage bees from turning around mid-way and leaving the apparatus through the entrance. After 1 day of training, none of the visiting bees ever turned back in the tunnel. Thus, trained bees rarely saw the left wall of the tunnel with the right eye, and vice versa.

The relative excitations produced by each of the papers in the bee's UV, blue and green receptors under the actual experimental conditions are given in Table 1. These excitations are expressed as a percentage of the maximum excitation, which was that experienced by the green receptor whilst viewing the white paper. The contrasts produced by each of the gratings in the UV, blue, green and luminance channels are shown in Table 2. Owing to the lack of ultraviolet in the ambient illumination, the contrasts in the UV channel are not meaningful. For definitions of contrast and details of the measurements and calculations, see Srinivasan and Lehrer (1988) or Lehrer and Bischof (1995).

### The experiments

Two experiments were conducted. In Experiment I, bees had to learn to choose the left arm when the yellow grating was present on the right wall of the tunnel (i.e. to the right eye), and the right arm

**Table 1** Relative receptor excitations

Paper	UV receptor	Blue receptor	Green receptor
“Blue” paper	1.8%	31.4%	61.1%
“Yellow” paper	1.9%	12.4%	71.9%
“White” paper	2.0%	40.3%	100.0%
“Black” paper	0.2%	2.5%	5.7%

**Table 2** Channel contrasts

Grating	UV channel	Blue channel	Green channel	Luminance channel
Blue grating	5.3%	12.1%	24.1%	20.3%
Yellow grating	2.6%	52.9%	16.3%	24.6%
B/W grating	81.8%	86.9%	89.2%	88.9%

when the blue grating was present on the left wall. The other wall of the tunnel was lined with homogeneous white paper. In Experiment II, bees had to choose the left arm when the blue grating was presented to the right eye, but the right arm when the yellow grating was presented to the same eye. In this experiment, the left wall of the tunnel carried a vertical B/W grating.

#### Experimental procedure and data evaluation

In each experiment, the bees were trained for a full day (representing an average of ca. 40 rewarded visits per bee) before testing was commenced. During training, the two training situations encountered by the bees in the entrance tunnel were alternated after every 3–4 rewarded visits per bee, on average. At the branch point, each bee was free to enter either the “correct” arm or the “wrong” one. When a bee entered the correct arm, she found the entrance to the reward chamber open and had access to the feeder. When she entered the wrong arm, she found the entrance to the reward chamber blocked; she then had to turn back and follow the route to the correct arm past the branch point.

In the tests, the bees’ choices in the Y-maze were determined by allowing them to enter the apparatus one at a time. A bee that had made a wrong decision was allowed to return to the branch point and make a new choice. However, only her first decision was recorded on each visit to the apparatus. A bee entering the correct arm scored a “plus” point, and a bee entering the wrong arm a “minus” point. Thus, each visit by a bee to the apparatus generated either one plus or one minus point. The percentage of correct choices (choice frequency) was calculated as the ratio between the total number of plus points and the total number of visits. A  $\chi^2$  statistical test was used to determine whether the measured choice frequencies were significantly different from the random choice level of 50%. This test assumes that the bee’s choices can be characterised by a binomial distribution and yields a *P* value which specifies the level of confidence with which the measured choice frequency is different from the 50% level. Details of this statistical procedure can be found in van Hateren et al. (1990).

After the bees’ learning performance had been measured as described above, we carried out a number of “transfer” tests in which the bees were presented with several novel situations to test for the occurrence of interocular transfer, as well as for other possible cues that might have been responsible for the bees’ choice behaviour observed in the training situations. Since the outcome of these transfer tests could not be predicted, the “positive” arm was defined arbitrarily.

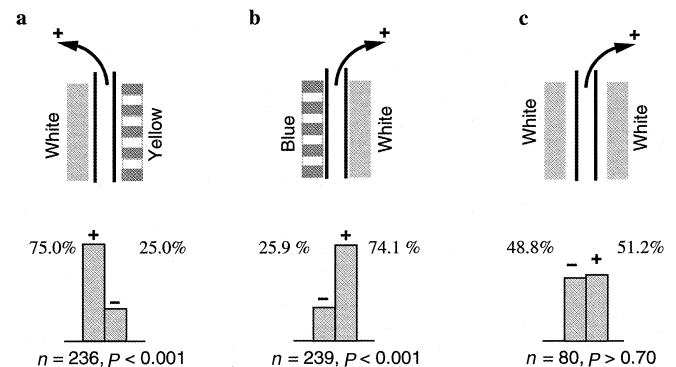
During a transfer test, a bee entering the arm defined as “positive” was rewarded as she reached the feeder. The reward continued to be present during these tests. This was necessary in order to maintain the bees’ motivation to visit the apparatus despite the tedious nature of the task. To prevent the bees from learning to

associate the new stimulus with the reward, each transfer test was performed for only a short period of time, typically encompassing two visits per bee on average. This method has been employed many times in the past when using Y-mazes (e.g. van Hateren et al. 1990; Zhang and Srinivasan 1994). Between transfer tests the bees were further trained using the training stimuli for a period encompassing at least eight rewarded visits per bee, on average, to maintain their level of learning. Since the transfer tests were brief, each type of transfer test was repeated several times in order to accumulate sufficient data (numbers of bee decisions). Inspection of the results of successive transfer tests of a given type showed no systematic increase in the preference for the rewarded arm, indicating that the bees were not exhibiting any significant learning during these tests.

## Results

### Experiment I

This experiment investigated whether bees can learn to choose different routes through the maze, depending upon which eye receives a stimulus. Specifically, we asked whether bees can be trained to choose the left arm when the right eye sees a yellow grating, and the right arm when the left eye sees a blue grating. The results of the learning tests (Fig. 2a, b) reveal that bees indeed learn this task well. When the trained bees are subjected to control tests in which both walls are homogeneously white, they choose the two arms randomly (Fig. 2c). This indicates that the bee’s performance in the learning tests is not influenced by extraneous (e.g. olfactory) cues.



**Fig. 2a–c** Performance of bees trained in Experiment I. Nine bees were trained to choose the left arm when a yellow grating was presented to the right eye **a**, and the right arm when a blue grating was presented to the left eye **b**. **a** and **b** show the results of learning tests representing the two training situations. The arrow labelled “+” denotes the “correct” arm. The histograms show the choice frequencies that the trained bees displayed in favour of the two arms. Also shown for each test are the number of choices analysed (*n*), and the *P* value obtained in a statistical test examining whether the choice frequencies are significantly different from random choice (details in Materials and methods). These notations also apply to Figs. 3–5. **c** Results of a control test in which both walls of the tunnel were homogeneously white, to check for the influence of extraneous cues. In **c** the direction of the “+” arrow is defined arbitrarily, as explained in Materials and methods. The mean and standard deviation of the choice frequencies displayed by the nine individual bees is  $76.4\% \pm 15.7\%$  in **a** and  $73.7\% \pm 15.4\%$  in **b**

Before we can conclude from these results that the bees have learned two different routes through the maze, each associated with a stimulus to a different eye, we must make sure that they did not simply learn to choose the side on which the homogenous white stimulus was present. In the above training paradigm, the homogeneous white stimulus was always on the side of the rewarded arm, i.e. opposite to the coloured grating. We therefore subjected the trained bees to two transfer tests in which the white wall was replaced by a B/W grating, leaving the yellow and blue gratings, respectively, on their usual side. In these tests (Fig. 3a, b), the bees preferred the arm opposite to the coloured grating, just as they did in the training situation (see Fig. 2a, b). Consequently, the position of the homogeneous white stimulus was not the cue that the bees had learned for coping with the task. This result suggests that the bees had indeed learned two different routes, each based on chromatic information acquired by a different eye.

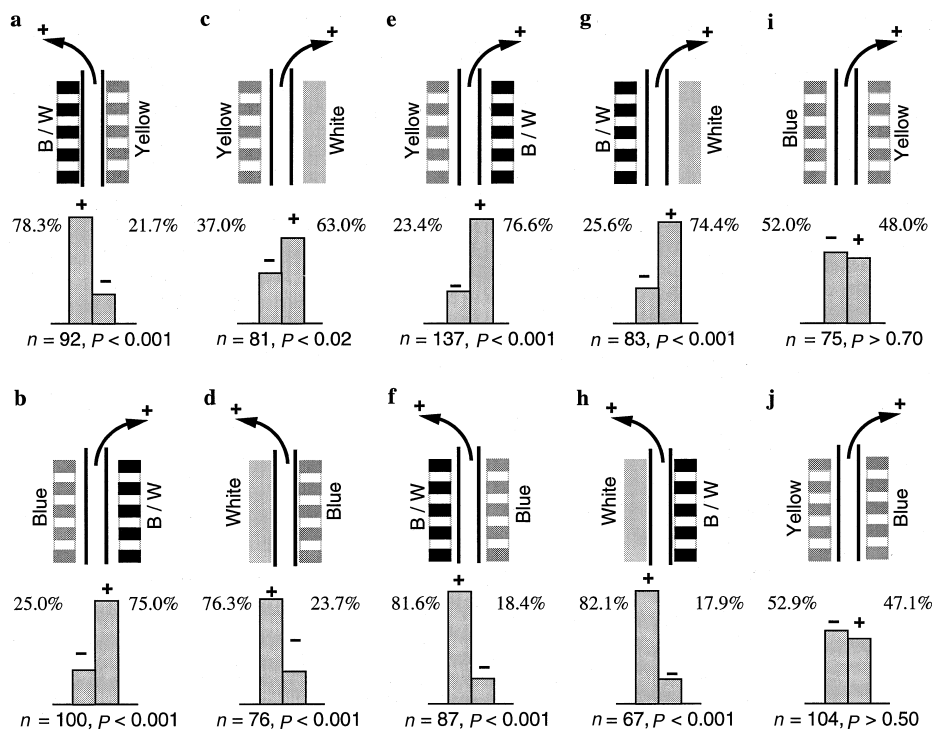
We were now ready to examine whether the trained bees could exhibit interocular transfer of the task that they had learned. In the next two transfer tests (Fig. 3c, d), we interchanged the sides of the coloured grating and the homogeneously white stimulus. If there was interocular transfer, then the bees would be expected to choose the left arm even when the yellow grating was presented to the left eye, and the right arm even when the blue grating was presented to the right eye. However, this is not what happened: the bees again preferred the arm opposite to the coloured grating (Fig. 3c, d), although in these tests the grating was of the “wrong” colour. Evidently, the bees had learned to turn left when a coloured grating (any colour) was viewed by

the right eye, and right when a coloured grating (any colour) was viewed by the left eye. Thus, in hindsight, interocular transfer of learning cannot be examined using the training paradigm of Experiment I because in such a training the bees do not distinguish between the differently coloured gratings: rather, they treat both of them as belonging to a single category (“coloured”) and only distinguish between “coloured” and “uncoloured” gratings.

In two further transfer tests (Fig. 3e, f), the coloured gratings were again presented to the wrong eyes, but, in addition, the homogeneous white stimulus on the opposite side was replaced by a B/W grating. Even in these tests, the bees preferred the arm opposite to the coloured grating. Thus, the position of the coloured grating is the cue that determines which arm the bees choose, but the colour of the grating per se is, again, unimportant.

In the next two transfer tests the colour cue was removed. Instead, B/W was presented either on the left wall (Fig. 3g) or on the right wall (Fig. 3h), and homogeneous white was presented on the opposite side. In these tests, the bees preferred the arm opposite to B/W. Since we already know from the tests shown in Fig. 3a, b that “homogeneous white” does not serve as a cue, we must conclude that the bees’ decisions in the tests in Fig. 3g, h depended on which eye was stimulated by a grating. In other words, stimulation of the left eye by a grating indicates to the bee “turn right”, and stimulation of the right eye indicates “turn left”. Thus, although “colour”, when present, dominates over “pattern” (Fig. 3a, b, e, f), “pattern” is used as a cue when colour cues are no longer present.

**Fig. 3a–j** Results of transfer tests performed with the bees trained in Experiment I. In these figures the direction of the “+” arrow is defined arbitrarily, as explained in Materials and methods”. Notation as in Fig. 2; details in text



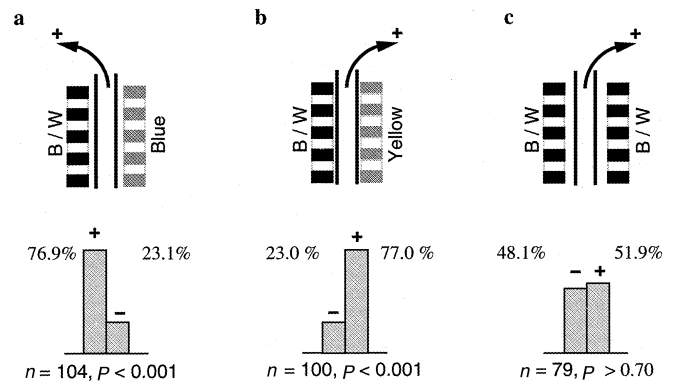
These conclusions were confirmed by two further tests in which both walls carried gratings, but of different colours: a blue grating on the left wall and a yellow grating on the right (Fig. 3i) or vice versa (Fig. 3j). In each test the bees chose randomly between the two arms, indicating that when both walls carry coloured gratings, the turning tendencies triggered by the two stimuli neutralise one another. The finding that both arms are chosen equally frequently in these tests also suggests that, for the purposes of the task on which they have been trained, the bees perceive the gratings on the two walls as being equally “coloured”.

## Experiment II

In Experiment II we trained bees with the yellow grating and the blue grating presented alternately on the right wall of the entrance tunnel, thus stimulating only the right eye. Access to the reward was through the left arm when the blue grating was present, and through the right arm when the yellow grating was present. To encourage the bees to pay particular attention to the colour of the grating, the left wall displayed the achromatic B/W grating throughout the training.

The results of the learning tests (Fig. 4a, b) show that bees learn this task well. Since the left eye always viewed B/W, it is clear that the only cue that signalled the correct route was the colour of the grating viewed by the right eye. Thus, in this experiment, bees have learned to take two different routes through the Y-maze by using two different colour signals available to one and the same eye, blue indicating “go left”, and yellow “go right”. In a control test using B/W gratings on both sides (Fig. 4c) the bees chose randomly between the two arms, indicating that they were not being influenced by extraneous cues.

The trained bees were then tested for interocular transfer by presenting each of the two coloured gratings, in turn, to the left (untrained) eye, and B/W to the right eye. The results (Fig. 5a, b) show that, in this situation, the blue grating made the bees turn left, whereas the yellow grating made them turn right. We conclude that colour-based information acquired by one eye to learn a



**Fig. 4a–c** Performance of bees trained in Experiment II. Eight bees were trained to choose the left arm when a blue grating was presented to the right eye **a**, but the right arm when a yellow grating was presented to the same eye **b**. The arrow labelled “+” denotes the “correct” arm. **c** Results of a test in which both walls of the tunnel were B/W to control for the influence of extraneous cues. In **c** the direction of the “+” arrow is defined arbitrarily, as explained in Materials and methods. The mean and standard deviation of the choice frequencies displayed by the eight individual bees is  $76.7\% \pm 9.2\%$  in **a** and  $79.1\% \pm 9.5\%$  in **b**. Notation as in Fig. 2; details in text

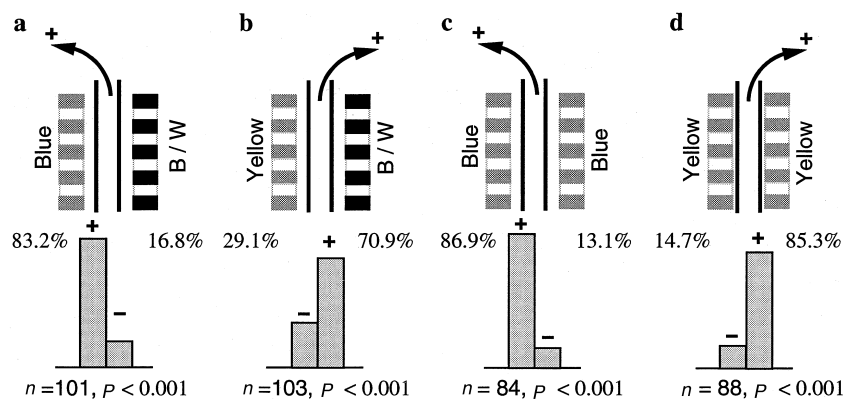
navigational task can be used by the other (naive) eye to perform the same task. In other words, there is interocular transfer of colour-based “signpost” information.

This conclusion is corroborated by the finding that the bees’ preference for a specific arm of the tunnel was even stronger than in the training situation (though the difference is not statistically significant) when gratings of the same colour were presented to *both* eyes. When this colour was blue, the bees exhibited a strong tendency to turn left; when it was yellow, they showed a strong tendency to turn right (Fig. 5c, d).

## Discussion

A bee walking along the entrance tunnel of our Y-maze would view the right wall primarily with the right eye, and the left wall primarily with the left eye. We say “primarily” and not “exclusively”, because the stimulus on a given wall may be partly visible to the contralateral

**Fig. 5a–d** Results of transfer tests performed with the bees trained in Experiment II. In these figures the direction of the “+” arrow is defined arbitrarily, as explained in Materials and methods. Notation as in Fig. 2; details in text



eye as well. In the bee, as in most insects, the visual fields of the two eyes overlap to some extent in the dorsal, ventral and frontal regions (Seidl and Kaiser 1981). In our experiments, the overlap in the ventral region is not relevant because this region of each eye views only the floor of the tunnel, which is homogeneously white. The overlap in the dorsal eye region is unlikely to be important because firstly this region is specialised to analyse the patterns of polarised light in the sky (e.g. Labhart 1980) and not spatial parameters or image motion, and secondly in our experiments, this region of the bee's eye does not view the stimuli on the walls; rather, it views the ceiling of the laboratory through the transparent Perspex roof of the tunnel, and therefore receives no useful information with regard to navigating the maze. The overlap in the frontal eye region, however, may be important as this means that a stimulus on, say, the right-hand wall, could be partially visible to the left eye, particularly when the bee first enters the tunnel. Some contralateral stimulation can occur even if there is no overlap in the frontal visual fields, since bees do not always walk with their long axes strictly parallel to the tunnel axis. However, if there were excessive binocular stimulation, the bees would not have exhibited the strong reversals in choice preference when the stimuli on the two walls were swapped in the transfer tests shown in Fig. 3: compare the results of the tests in Figs. 3a and 3e, Figs. 3g and 3h, and Figs. 3b and 3f. We must conclude, therefore, that in our experiments, the stimulus on each wall was viewed primarily by the corresponding ipsilateral eye. When a trained bee chose the wrong arm of the Y-maze and returned to the branch point, she never went into the entrance tunnel, but simply proceeded along the curved corridor to the correct arm. On her way, one of her eyes would have obtained a brief glimpse of both walls from the back end of the entrance tunnel, but it is difficult to imagine how this could have had any influence on her decisions. In any case, we counted only the first decision of each bee after she entered the maze, and disregarded subsequent choices (see Materials and methods).

Taking the above considerations into account, we can make the following tentative conclusions. The results of Experiment I suggest that bees can learn navigational tasks in an eye-specific way: they can be trained to take different routes through a Y-maze, depending upon which eye is stimulated. Specifically, bees can learn to turn left when the right eye sees a yellow grating, and right when the left eye sees a blue grating. Interocular transfer of learning could not be demonstrated using this training paradigm, because the bees "chose" not to distinguish between the two colours in tackling the task that was presented to them: they behaved as though they simply determined which wall of the tunnel was "coloured", and turned in the opposite direction. This finding, however, calls attention to the possibility that bees can determine whether an object or stimulus is "coloured"; that is, the possibility that they categorize all levels of grey (including black and white) as "col-

ourless" and distinguish them from all other "coloured" stimuli, the way humans do. While it is true that a stimulus which is "colourless" (e.g. white) for humans need not also be "colourless" for bees, it is likely that the bees perceived the "coloured" papers that were used in the experiments as being more colour-saturated than the "white" paper (compare the "blue", "yellow" and "white" papers in terms of the relative excitations that they produce in the UV, blue and green receptors, Table 1).

It is important to note that the bee's visual system is indeed capable of distinguishing between the blue and the yellow papers that we used: if not, they would not have learned the discrimination required of them in Experiment II (see Fig. 4a, b) or performed the appropriate discriminations in the associated transfer tests (see Fig. 5). It has also been shown that bees can directly be trained to distinguish between precisely these two coloured papers, by associating one of them with a food reward (see Zhang et al. 1996). Thus, the reason why the bees treat the blue and yellow gratings as being "equivalent" in Experiment I is not because they *cannot* distinguish them visually. Rather, the bees behave as though they are categorising both stimuli as "coloured". More transfer tests of the kind shown in Fig. 3, but using a range of different colours and patterns, are needed to establish with certainty that the bees are indeed performing colour generalisation in Experiment I. Further work is obviously needed to explore fully the ability of bees to generalise across stimuli in colour space.

The ability of bees to generalise across stimuli has already been demonstrated in the orientational domain, where it has been shown that bees can be trained to treat a number of different patterns – which they can distinguish visually – as belonging to the same category (Wehner 1971; van Hateren et al. 1990; Srinivasan et al. 1994). The transfer tests in Experiment I in which colour cues were removed (Fig. 3g, h) suggest that bees also possess the capacity to categorise stimuli as being "textured" or "not textured": in these tests, the trained bees always turned away from the wall that carried the grating. The capacity of bees to generalise texture is another aspect of bee perception that merits further study.

It might be argued that the bees learned the task in Experiment I by using cues that relied on image motion. For example, when a bee walks along the tunnel in the training paradigm of Experiment 1, she experiences image motion only in the right eye when she is supposed to turn left, and only in the left eye when she is supposed to turn right. This is because, in each situation, only one of the walls of the tunnel carries a grating, the other wall being homogeneously white (see Fig. 2a, b). Therefore, a bee could, in principle, perform the task by learning to turn away from the eye that experiences image motion. However, the transfer tests in Fig. 3a, b rule out this possibility: when the bees encounter a coloured grating on one wall and a B/W grating on the other, they turn

away from the coloured grating as often as in the training situation, despite the fact that the coloured grating possesses a lower contrast and therefore provides a weaker motion signal than the B/W grating. It is well established that motion detection in the honeybee is mediated by a single receptor channel: green (reviews in Kaiser 1975; Lehrer 1991, 1994; Srinivasan 1993). Each of the coloured gratings provides a lower green contrast to the movement-detecting system than does the B/W grating (see Table 2). We conclude, therefore, that in the training paradigm of Experiment I, the bees chose the correct arm by learning to turn away from the wall that was *coloured*, not the wall that provided image motion.

The results of Experiment II demonstrate that bees which have used one eye to learn a navigational “signpost” signal can recognise and respond to this signal appropriately even when it is offered to the untrained eye. The observation that bees can learn a “signpost” signal to navigate through a maze is not new: this was demonstrated recently by Zhang et al. (1996). The novelty of the present finding, however, is the observation that such signals can be learned via a single eye, and then transferred to the naive eye.

It is important to compare the results of Experiment II, which demonstrate interocular transfer of a learned “signpost” signal, with the recent findings of Giger and Srinivasan (1997) who found no interocular transfer in another experimental paradigm which, at first sight, appears similar to ours. In their study, bees were trained to fly into a Y-maze and distinguish between two stimuli, one presented at the end of each arm of the maze. The apparatus was designed such that, in each case, only the right eye saw the stimulus, which was one colour in the arm that carried the reward and another colour in the arm that offered no reward. After the bees had learned the task, they were tested for their ability to discriminate the two colours when they were offered to the naive eye. In this transfer test, the bees behaved as though they recognised neither colour (Fig. 7 in Giger and Srinivasan (1997)). In other words, there was no interocular transfer of the learned colours, a result which appears to contradict the present findings. There is, however, an important difference between the two experimental paradigms which may be crucial to understanding why they led to different results. In the experiment of Giger and Srinivasan the stimuli defined the bee’s *ultimate* destination: the stimulus associated with the reward (the positive stimulus) defined the correct destination, while the stimulus in the other arm (the negative stimulus) defined the wrong destination. In such a situation, the bees evidently learn the stimuli in an “eidetic” fashion, i.e. as photographic images (reviews in Wehner 1981; Collett and Cartwright 1983), thus making interocular transfer impossible. This absence of interocular transfer is in agreement with other studies in which the stimuli defined the target, e.g. the spatial position of a feature (Lehrer 1994); the spatial configuration of landmarks (Wehner and Müller 1985); or the presence of a particular colour (Giger and Srinivasan 1997; V. Pelzer, un-

published results). In the present experiment (Experiment II), however, the stimuli that the bees encountered in the maze did not represent the destination: rather, they acted as abstract “signposts” that pointed the correct way to the destination. Here, there was no such thing as a “positive” and a “negative” stimulus, because neither stimulus was associated with the reward (or its absence). Each stimulus merely signalled the correct route to the destination. Evidently, bees seem to treat such “signpost” stimuli more flexibly than stimuli which define the destination per se. Further investigation is necessary to discover why this is so, and what advantage it confers. One advantage may be added robustness in navigation: for example, if getting to a food patch requires that a right turn be made after passing a specific landmark, interocular transfer of signpost information would enable this manoeuvre to be carried out reliably regardless of whether the bee flies to the left or the right of the landmark.

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