J Comp Physiol A (2006) 192: 409–416
DOI 10.1007/s00359-005-0079-0

ORIGINAL PAPER

**Judith Reinhard · Mandyam V. Srinivasan
Shaowu Zhang**

Complex memories in honeybees: can there be more than two?

Received: 12 July 2005 / Revised: 22 November 2005 / Accepted: 25 November 2005 / Published online: 20 December 2005

Abstract Foraging honeybees are likely to learn visual and chemical cues associated with many different food sources. Here, we explore how many such sources can be memorized and recalled. Marked bees were trained to visit two (or three) sugar feeders, each placed at a different outdoor location and carrying a different scent. We then tested the ability of the bees to recall these locations and fly to them, when the training scents were blown into the hive, and the scents and food at the feeders were removed. When trained on two feeder locations, each associated with a different scent, the bees could correctly recall the location associated with each scent. However, this ability broke down when the number of scents and feeder locations was increased to three. Performance was partially restored when each of the three training feeders was endowed with an additional cue, namely, a distinct colour. Our results suggest that bees can recall a maximum of two locations when each is associated with a different scent. However, this number can be increased if the scent cues are augmented by visual cues. These findings have implications for the ways in which associations are established and laid down in honeybee memory.

Keywords Associative learning · Memory · Vision · Olfaction · Honeybee

Introduction

A honeybee colony's search for food is a well-coordinated process requiring precise orientation over distances of several kilometres (Gould 1993; von Frisch 1993). During foraging flights, honeybees learn navigational information about the location of a food source, in terms of its distance from the hive and its direction relative to the sun (Wehner and Rossel 1985; von Frisch 1993; Esch and Burns 1995; Srinivasan et al. 2000). Bees are also known to learn additional visual cues to aid the process of navigation, such as the landmarks expected en route and at the destination, or a flower's colour and shape, as well as olfactory cues associated with a food source, such as floral odours, or the taste and fragrance of the nectar (Wehner 1981; Collett 1992; Gould 1993; von Frisch 1993).

The honeybee's amazing capacity to learn environmental cues has been investigated extensively (e.g. Wehner 1981; Collett 1992; von Frisch 1993; Srinivasan 1994; Menzel and Mueller 1996; Srinivasan et al. 1998; Zhang et al. 1999, 2004; Menzel et al. 2000; Giurfa et al. 2001). Recent studies exploring learning and memory under natural conditions in the field demonstrated that honeybees form and recall associative memories of food sources across sensory modalities (Reinhard et al. 2004a, b). Bees that were previously trained to forage at differently scented feeders, each positioned 50 m away from the hive, could be induced in subsequent tests to visit a specific feeder location merely by blowing into the hive the scent that was associated with that location, even though the feeders were empty and unscented during the tests. Perceiving the scents in the hive triggered recall of visual and navigational memories of the feeders associated with the specific scents, guiding them to the correct locations.

Relying on scent-triggered recall of previously learnt information, honeybees navigated quickly and successfully to the appropriate feeders, irrespective of the scents used and regardless of whether the bees had to recall a specific location, or a specific colour (Reinhard et al. 2004b). But this was only true if the number of feeders was restricted to two. In a preliminary experiment using three feeders, injecting a scent into the hive did not cause the trained bees to return preferentially to the specific location that was associated with the scent during training. This raises the question of whether the

J. Reinhard (✉) · M. V. Srinivasan · S. Zhang
Visual Sciences Group, Research School of Biological Sciences,
The Australian National University, P.O. Box 475,
2601 Canberra, ACT, Australia
E-mail: judith.reinhard@anu.edu.au
Tel.: +61-2-61259701
Fax: +61-2-61253808

honeybee's capacity for complex memories is limited to two locations at any one time. In the present study, we therefore investigated the recall of two and three scent-associated locations in detail, in experiments involving larger feeder distances and greater angular bearings between the feeder locations, as well as additional visual cues on the feeders.

Materials and methods

The experiments were carried out from February to April 2004 in a field site with flower patches, bushes, and trees, ensuring ad lib food resources and providing a variety of naturally occurring landmarks for navigation. The experimental honeybee hive (*Apis mellifera* L.) was set up in a shed located at the edge of the area. Foraging bees entered and left the hive through a Perspex tube (length 20 cm, diameter 4 cm). The tube carried an arrangement, described in detail in Reinhard et al. (2004b), to blow scent into the hive entrance when desired. Three experiments were carried out in sequence, each involving training and testing. Experiment 1 used two feeders (described below) and served as benchmark for performance, against which the performance in Experiments 2 and 3 (which each used three feeders) was compared. The three experiments were performed sequentially, as it would have been impossible to simultaneously train three different groups of bees, from the same colony, to participate in three different experiments without bees from one experiment also interfering with the other experiments. Despite the sequential procedure, results were comparable as the environmental conditions were similar across all three experiments and the bees' general behaviour was consistent across the entire duration of the study.

Experiment 1: Association of two locations with two scents

Training

Honeybees were trained to forage at two artificial feeders, consisting of 500 ml bottles containing a 2 mol sugar solution with 3 ml scent per litre sugar solution. Each feeder was placed on top of a white PVC cylinder (1 m high, 30 cm dia), and carried a different scent. As scents we used Natural Flavouring Essences (Queen Fine Foods Pty Ltd., Australia): rosewater essence and lemon essence. Both scented training feeders were initially offered simultaneously and next to each other, 5 m from the hive until the bees had learnt and accepted the feeders as a food source. Ca. 30 bees visiting the feeders were marked individually with enamel paint on the thorax and/or abdomen. The feeders were then moved progressively away from the hive, in 10 m steps, always ensuring that enough bees had learnt the new locations before taking the next step, until the final feeder locations were reached, 120 m from the hive as shown in Fig. 1a. In this phase of the training, the feeders were offered alternately: we first offered the rose-scented feeder at location one for 20–30 min, until each marked bee had visited the feeder at least three times; then the lemon-scented feeder at location two for 20–30 min, until each marked bee had visited the feeder at least three times; then the rose feeder again at location one, and so on, thus ensuring that the same bees visited both feeder locations regularly and equally often. During the training, the scents were offered only at the feeders: they were not blown into the hive. The training was carried out over 2–3 consecutive days, and unmarked bees visiting the feeders were removed whenever possible. This was done in order to prevent unmarked bees from being trained, thus ensuring that a fresh, naïve group of bees was used for the subsequent experiments.

Tests

At least 2 h before starting a test, the training was interrupted and the feeders were removed to minimize random foraging around the feeder stations. During the tests, we offered empty, unscented feeders at the training locations. The scent was never offered at the feeders during the tests. Instead, it was blown into the hive, using a small fan connected to the hive entrance/exit. For a detailed description of the scent delivery device see Reinhard et al. (2004b). Using this device, we blew rose scent for 8 min into the hive, and then lemon scent for 8 min. During each scent interval, we registered the number and identity of the individually marked bees visiting the two test feeders, noting for each bee which feeder she visited first, the number of circlings (sightings of a bee flying around the feeder within a radius of 50 cm), the number of landings (touching down on the feeder), and the total number of visits to each feeder (sum of all circlings and landings, including first visits). Unmarked bees were not registered. The 8 min scent interval guaranteed sufficient numbers of visits while at the same time preventing bees from forming a lasting negative association, namely the lack of reward at the test feeders. The test was carried out five times. Between tests, training was resumed for short periods (ca. 1 h) to maintain the level of learning and motivation.

Experiment 2: Association of three locations with three scents

Experiment 2 was performed 2 weeks after concluding Experiment 1. In the interim period all previously marked bees were removed. This precaution, together with the procedure of removing unmarked bees visiting the feeders during training, ensured that the bees trained in the second experiment had no prior experience with the first experiment.

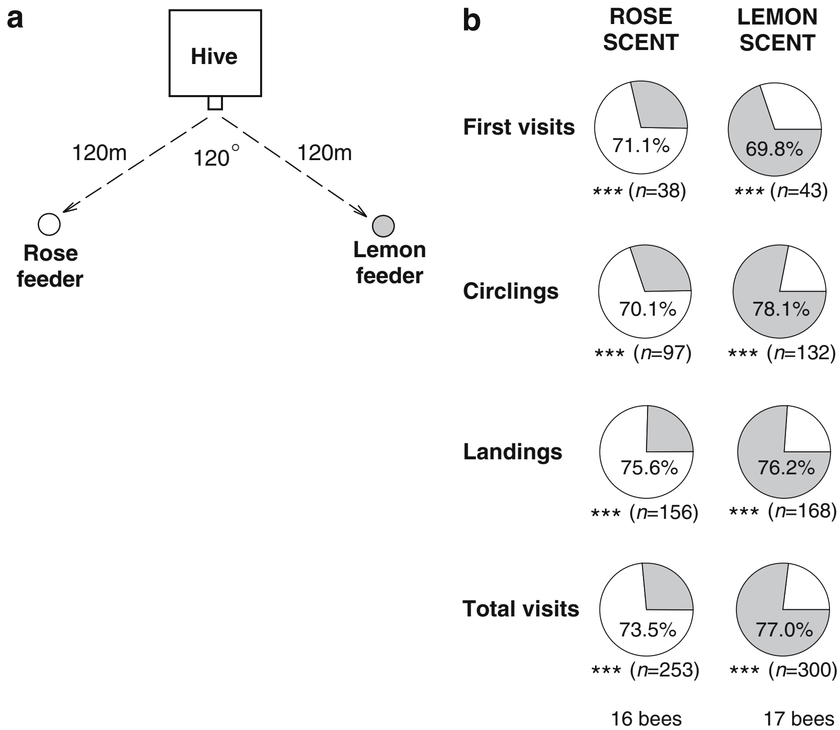

Fig. 1 Experiment 1: Scent-triggered navigation in individual bees, trained alternately to a rose-scented, and a lemon-scented feeder, each placed at a different location. **a** Experimental configuration, showing feeder locations relative to the hive. **b** Pie charts, showing the distribution of visits to two empty, unscented test feeders at the former training locations, when the respective scents were blown into the hive (*white* former rose feeder location; *light grey* former lemon feeder location). In each experiment data are accumulated from five tests for each scent, and are shown separately for first visits, circlings, landings, and total visits. The number of individually marked bees that visited the test feeders, the number of choices (n), and the result of the statistical analysis (observed vs. expected frequency Chi square test, *** indicates $P < 0.001$) are shown below the pie charts. The expected frequency, based on random choice among the two test feeders, was 50%

Training

Honeybees were trained in the same way as in Experiment 1, but this time we used three sugar water feeders, each placed at a different location. One carried rose-water essence, the other almond essence, and the third lemon essence (Fig. 2a). We used almond as additional scent, as earlier work (Reinhard et al. 2004a, b) had shown that bees could distinguish almond scent easily from rose and lemon, when the scents were offered in a pair-wise fashion, i.e. rose versus lemon, rose versus almond, and lemon versus almond. Using another scent should in itself not pose a problem to the bees, as learning performance in scent-triggered navigation is independent of the scents used (Reinhard et al. 2004b). Ca. 30 honeybees were marked individually and trained. The training was carried out as before, but the feeders were presented in a cyclic fashion: we first offered the rose-scented feeder at location one for 20–30 min, until each marked bee had visited at least three times, then the almond-scented feeder at location two for 20–30 min, then the lemon-scented feeder at location three for 20–30 min, then the rose feeder again etc., thus ensuring that the same bees visited all three feeder locations regularly and equally often. This way bees were trained to each location for the same duration of time in all experiments, and had the same number of training visits to each feeder, which is even more important for learning than the training time per se. The variation in training cycle time (Experiment 1: 40–60 min to complete a cycle with two feeders; Experiment 2: 60–90 min to complete a cycle with three feeders) did not seem to have an effect on learning performance. During the entire training period of 2–3 days, bees returned to the training feeders with the same frequency as in Experiment 1, i.e. irrespective of the number of feeders used.

Tests

The tests were carried out in the same way as described above, placing an empty, unscented test feeder at each of the three training locations. We blew rose scent for 8 min into the hive, then almond scent for 8 min, and finally lemon scent for 8 min. During each scent interval, the marked bees visiting the test feeders were registered, as described above. The test was carried out four times. Between tests, training was resumed for ca. 1 h. The number of tests conducted for Experiment 2 was less than for the other experiments, as fewer tests were

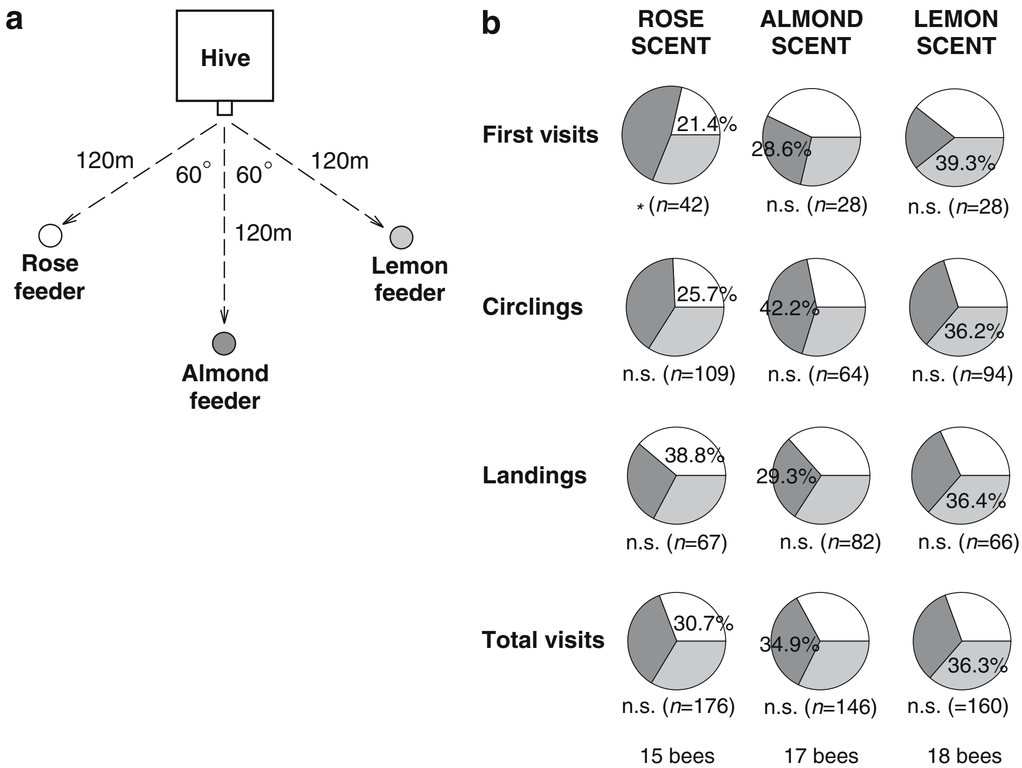

Fig. 2 Experiment 2: Scent-triggered navigation in individual bees, trained cyclically to a rose-scented, an almond-scented, and a lemon-scented feeder, each placed at a different location. **a** Experimental configuration, showing feeder locations relative to the hive. **b** Pie charts, showing the distribution of visits to three empty, unscented test feeders at the former training locations, when the respective scents were blown into the hive (*white* former rose feeder location; *dark grey* former almond feeder location; *light grey* former lemon feeder location). In each experiment data are accumulated from four tests for each scent, and are shown separately for first visits, circlings, landings, and total visits. The number of individually marked bees that visited the test feeders, the number of choices (n), and the result of the statistical analysis (Bonferroni corrected observed vs. expected frequency Chi square test, *n.s.* denotes $P > 0.05$, * indicates $P < 0.05$) are shown below the pie charts. The expected frequency, based on random choice among the three test feeders, was 33.3%

needed to obtain sufficient and comparable numbers of bees and visits.

Experiment 3: Association of three locations with three scents and three colours

Experiment 3 was performed 2 weeks after concluding Experiment 2, and again all previously marked bees were removed.

Training

Honeybees were trained in the same way as in the second experiment, but with one modification to the procedure. Here, the three training feeders offered not only scent cues, but also visual cues: each feeder was wrapped with a differently coloured piece of cardboard. Thus, bees were trained to a white rose-scented feeder, a blue almond-scented feeder, and a yellow lemon-scented feeder. The three colours were chosen based on preliminary training experiments showing that the bees could discriminate clearly between all three of them. The odour–colour combinations were chosen at random, as earlier experiments had shown that learning performance in scent-triggered navigation is independent of the combinations of scents and colours used (Reinhard et al. 2004b). There does not seem to be an innate bias towards certain combinations, bees can easily be trained to any odour–colour association including those which potentially contradict "natural" combinations, such as lemon–blue or rose–yellow. The coloured/scented training feeders were placed at the same locations as in Experiment 2 (Fig. 3a), with each scent representing the same location as before. Ca. 30 honeybees were marked individually and trained, as in Experiment 2.

Tests

The tests were carried out in the same way as described above, but the empty, unscented test feeders were in addition wrapped with coloured cardboard. Each test feeder carried the same colour that the bees had experienced at that particular location during training. Thus, a white test feeder was placed at the former rose feeder

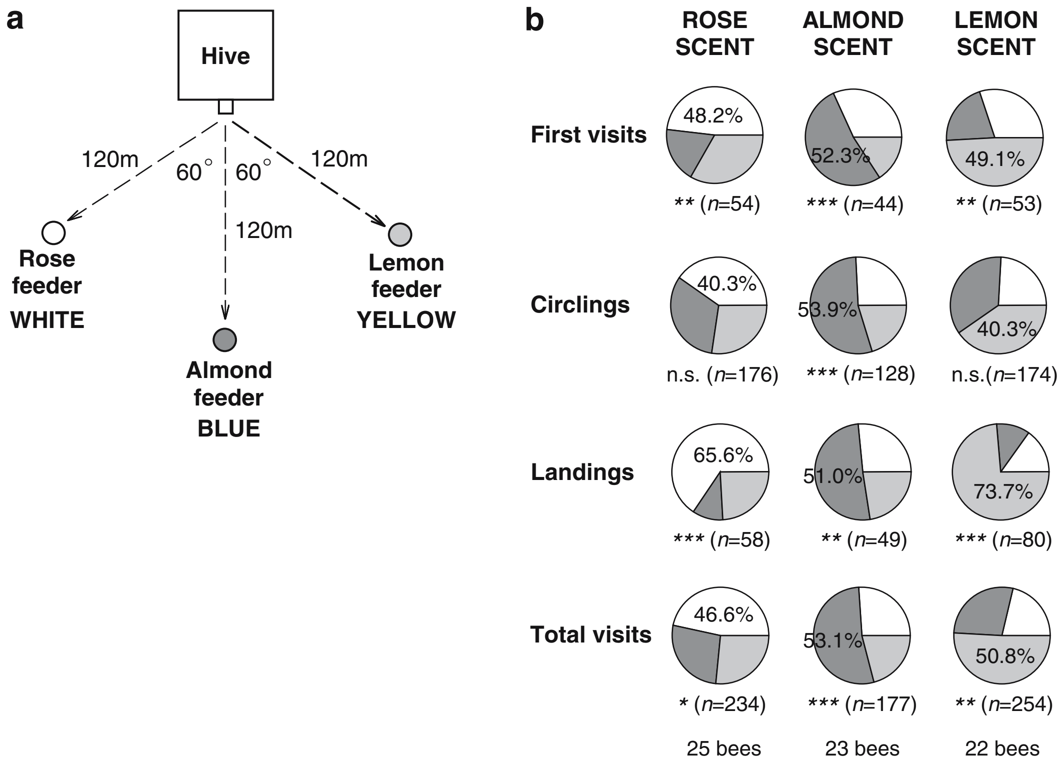

Fig. 3 Experiment 3: Scent-triggered navigation in individual bees, trained cyclically to a white rose-scented, a blue almond-scented, and a yellow lemon-scented feeder, each placed at a different location. **a** Experimental configuration, showing feeder locations relative to the hive. **b** Pie charts, showing the distribution of visits to a white, a blue, and a yellow test feeder (empty and unscented) at the former training locations, when the respective scents were blown into the hive (*white* former rose feeder location; *dark grey* former almond feeder location; *light grey* former lemon feeder location). In each experiment data are accumulated from five tests for each scent, and are shown separately for first visits, circlings, landings, and total visits. The number of individually marked bees that visited the test feeders, the number of choices (n), and the result of the statistical analysis (Bonferroni corrected observed vs. expected frequency Chi square test, *n.s.* denotes $P > 0.05$, * indicates $P < 0.05$, ** indicates $P < 0.01$, and *** $P < 0.001$) are shown below the pie charts. The expected frequency, based on random choice among the three test feeders, was 33.3%

location, a blue test feeder at the former almond feeder location, and a yellow test feeder at the former lemon feeder location. The three scents were blown into the hive in turn, for 8 min each and the marked bees visiting the coloured test feeders were registered, as described above. The test was carried out five times. Between tests, training was resumed for ca. 1 h.

Statistical analysis

For each experiment, the data collected for individual bees were added up, thus obtaining for each scent interval the overall number of first visits, circlings, landings, and total visits made to each feeder. Chi square tests, comparing observed versus expected frequency, were used to determine whether the relative preferences for the test feeders were significantly different from random-choice levels, and additional Bonferroni corrections were carried out for Experiments 2 and 3. Choice frequencies were evaluated separately for first visits, circlings, landings, and total visits.

Results

Experiment 1: Association of two locations with two scents

The aim of the first experiment was to investigate whether honeybees can learn to associate two different locations with two different scents, if the feeder locations are at a significant distance from the hive (120 m) and from each other (more than 200 m) (Fig. 1a). Owing to the large distances, the undulation of the terrain and the bushy vegetation, neither of the feeders could be seen from the hive, and neither feeder was visible from the other feeder. During the tests, when rose scent was blown into the hive, the overwhelming majority of individually marked bees visited the former rose feeder location (Fig. 1b). On the other hand, when lemon scent was blown, most of the same bees visited the former lemon feeder location (Fig. 1b). This was true regardless of how the bees' choices were measured: first visits, circlings, landings, or total visits. The trained bees performed very well in the tests: over 70%

of the total visits occurred at the location that corresponded with the injected scent. This experiment confirms our earlier findings (Reinhard et al. 2004a) and demonstrates that, even in challenging natural terrain, bees can easily learn to associate two different food locations with two different scents. The results of this experiment provided a benchmark for performance, against which we compared performances in Experiments 2 and 3.

Experiment 2: Association of three locations with three scents

The aim of the second experiment was to investigate whether individual honeybees can learn to associate three different locations with three different scents (Fig. 2a). During the tests, when each of the three scents was blown into the hive, in turn, the honeybees did not show any preference towards the feeder location associated with the scent, irrespective of the scent that was blown (Fig. 2b). This was true regardless of how the bees' choices were measured. In most cases, the locations of first visits, circlings, landings, and total visits were randomly distributed among the three feeders. The only significant preference registered was in the distribution of 'first visits' when rose scent was blown into the hive. However, the preference was not for the rose feeder, but for the almond feeder.

Experiment 3: Association of three locations with three scents and three colours

The aim of the third experiment was to investigate whether honeybees can learn to associate three different locations with three different scents, if a distinct colour cue is added to each of the locations (Fig. 3a). This time, the honeybees did show clear preferences when the scents were blown into the hive during the tests. Regardless of how the bees' choices were measured (first visits, circlings, landings, or total visits), the majority of trained bees visited the feeder location that carried the colour associated with the scent that was blown into the hive (Fig. 3b). Thus, when rose scent was blown, it was the white feeder that received the greatest proportion of visits. When the scent was almond, the bees showed a significant preference for the blue feeder, and when it was lemon, the bees significantly preferred the yellow feeder. With the rose and lemon scents, it was only the number of circlings that was statistically indistinguishable from a random distribution. However, even in these cases, the bees circled more often around the appropriate feeder, although the preference was not significant. Interestingly, the preferences were strongest for 'landings', reaching 65.6 and 73.7%, respectively, when rose and lemon scents were blown.

Discussion

Learning of two scent–location associations

The results of Experiment 1 confirm and extend earlier data (Reinhard et al. 2004a, b) demonstrating clearly that even under challenging natural conditions with undulating terrain and long distances between feeder locations, honeybees are able to associate two different locations with two different scents. When the training scents are blown into the hive, they trigger recall of specific visual and navigational memories in the trained bees, guiding them to locations that were previously associated with the respective scents.

Failure to learn three scent–location associations?

The results of Experiment 2 extend preliminary observations (Reinhard et al. 2004b) that bees seem to have difficulty in learning to associate three different scents with three different locations. In the present experimental situation the feeders were placed much further away from the hive than in the preliminary study (120 m as opposed to 50 m), and they were much further apart (120 m between neighbouring feeders, as opposed to 25 m). These large distances, together with the undulation of the terrain and the bushy vegetation meant that none of the feeders could be seen from the hive, and no feeder was visible from any other feeder. Despite the distinctness of the three locations, the bees behaved as if they were unable to distinguish between them. They visited all three locations equally often, irrespective of the scent blown into the hive. However, in the third experiment, when colour cues were added to the feeders, the honeybees showed a preference for the appropriate location. They preferentially visited the feeder associated with the scent blown into the hive.

The lack of discrimination in the second experiment cannot be due to the inability of the bees to discriminate the three scents, as bees are able to distinguish between the same scents when they are offered in pair-wise fashion, i.e. rose versus lemon, rose versus almond, and lemon versus almond (Reinhard et al. 2004a, b). The earlier studies as well as Experiment 1 clearly show that under the same natural conditions, bees are very good at learning to associate any two scents with two locations. Clearly, learning performance in scent-triggered navigation is independent of the scents used, and the drop in performance in Experiment 2 can neither be due to the particular scent combination that was used nor can the lack of discrimination be due to not having learnt all three of the feeder locations. Tests were only started once all marked bees visited all three feeders equally often during training, clearly demonstrating that they had learnt the locations. Also, the short flight durations between hive and feeders during the tests (15–20 s on average, J. Reinhard, unpublished observation) indicate that the results of Experiment 2 are not due to random foraging in the area, but that the test bees flew straight to the feeder—be it the correct one or not—on perceiving scent in the hive. Furthermore, given our earlier finding that bees can distinguish between feeder locations that are as closely separated as 30 m (Reinhard et al. 2004a, b), it is very unlikely that the bees would have difficulty in distinguishing between the feeder locations in Experiment 2, which were 120 m apart. It is also highly unlikely that the lack of performance in Experiment 2 compared to Experiment 1 is merely due to the slight methodological adjustments in the training and testing procedures, such as increased training cycle times and odour delivery cycle times, when using three feeders and three scents. If these adjustments would have a negative effect on learning performance, the results for Experiment 3 should have been the same as for Experiment 2, as the procedures were the same in those cases.

If bees can discriminate three different scents, and three different locations, why do they not learn three distinct scent–location associations? Possibly, three scent–location associations as presented in Experiment 2 involve too many complex or overlapping cues for the bees to recall reliably. Instead of learning to associate each specific scent with a particular location, the bees might in this context prefer to switch to the strategy of learning a simpler general rule, namely, 'scent in the hive equals food in one of the previously visited locations'. Scent would then trigger the bees to emerge from the hive and to inspect all three feeders in the area, leading to a random distribution of visits. It would be interesting to investigate whether the bees' capacity to form multiple scent–location associations improves if the angles between the feeders are larger (e.g. 120°, rather than 60°) or if the feeders are further away from the hive—although this possibility seems unlikely, as discussed above.

Effect of additional colour cues

The surprising effect of adding colour cues on the bees' performance, revealed in Experiment 3, can be explained in two ways. One possibility is that the addition of distinctive cues helps the bees to discriminate between and therefore remember the three locations. For example, the training scent could trigger recall of the associated colour, which could in turn trigger recall of the location, similar to using differently coloured dots on study cards while studying for an exam to improve recall of complex, inter-related facts. Another possibility might be that colours are less complex cues to learn than locations, thus causing the bees to form three scent–colour associations and to combine this with the general rule 'scent in the hive equals food in one of the previously visited locations'. Scent would then induce the bees to inspect all three feeders in the area, but to approach and land only on the feeder bearing the correct colour. Thus, the bees know all three locations, but in addition they are forming only the scent–colour associations, and not the scent–location associations. The second interpretation seems more likely, given that the number of circlings is not always significantly biased towards the correct feeder, whereas the number of landings always shows a highly significant preference for it (Fig. 3b). There could be ways to test between the two hypotheses, e.g. removing the colours during the tests to see if the bees continue to arrive at the correct feeder. If they do, it would mean that bees have learnt the complex odour–colour–location association. However, if the colours are removed during the test and the bees no longer perform, it would not necessarily mean that they have not learnt the odour–colour–location association. The bees might have learnt the association and flown towards the correct feeder when odour is blown into the hive, but on approach get confused by the lack of the expected colour. Lack of such a distinct visual signal might be interpreted as "wrong location" by the approaching bee, making her turn away. Another interesting option would be to use harmonic radar to track the bees' flights as they leave the hive when the scent is blown (Riley et al. 1996). Information on the directions and durations of flight could tell us whether the trained bees fly straight to the correct feeder in the tests, or whether they inspect each feeder from a distance, to determine its colour, before approaching the correct one.

Conclusion

Our study brings an important point to light, namely, that the honeybee's capacity for complex memories is not strictly limited to two. Rather, it is a plastic system in which multiple associative memories can be forged at the same time, depending on the types of cues that are available. For example, the number of associative memories that are formed could depend not only on the colours of flowers but also upon their shapes, as well as upon the layout and properties of the surrounding landmarks. Should the cues be insufficient with respect to number, distinctiveness, or salience, the honeybee might switch to learning a general rule. Menzel's early study (1969), showing that bees have difficulty in learning three colour–reward associations at the same time, could possibly also be explained in this way: The experimental colours and training paradigms used in that study might have induced the bees to switch to a general rule strategy. A recent study (Benard and Giurfa 2004) suggests that memory constraints preclude bees from solving more complex problems such as making transitive inferences (e.g. if $A > B$ and $B > C$ then $A > C$). However, our study suggests that seemingly 'hard' memory constraints can be overcome if the environment provides useful additional cues. Thus, the honeybee's cognitive capacities might be even richer than previously assumed. The ability to adapt memory strategies to the available cues may be the key to the honeybee's foraging success. But clearly, further experiments are required to fully understand how bees form complex foraging associations.

Acknowledgements We thank Regan Ashby, Emily Baird, Aung Si, and Hong Zhu for their help with the experiments. This work was partly supported by the Centre for Visual Sciences, ANU, and by grants DP0208683, DP0450535 and CE0348177 from the Australian Research Council. Our experiments comply with the current Australian law, as well as the NIH ''Principles of animal care'', 86–23, 1985.

References

Benard J, Giurfa M (2004) A test of transitive inferences in free-flying honeybees: unsuccessful perdormance due to memory constraints. Learn Mem 11:328–336

Collett TS (1992) Landmark learning guidance in insects. Phil Trans R Soc Lond B 337:295–303

Esch HE, Burns JE (1995) Honeybees use optic flow to measure the distance of a food source. Naturwissenschaften 82:38–40

von Frisch K (1993) The dance language and orientation of bees. Harvard University Press, London

Giurfa M, Zhang SW, Jenett A, Menzel R, Srinivasan MV (2001) The concepts of 'sameness' and 'difference' in an insect. Nature 410:930–933

Gould JL (1993) Ethological and comparative perspectives on honey bee learning. In: Papaj DR, Lewis AC (eds) Insect learning. Chapman Hall, New York, pp 18–50

Menzel R (1969) Das Gedaechtnis der Honigbiene fuer Spektralfarben II. Z vgl Physiol 63:290–309

Menzel R, Mueller U (1996) Learning and memory in honeybees: from behavior to neural substrates. Ann Rev Neurosci 19:379–404

Menzel R, Brandt R, Gumbert A, Komischke B, Kunze J (2000) Two spatial memories for honeybee navigation. Proc R Soc Lond B 267:961–968

Reinhard J, Srinivasan MV, Zhang SW (2004a) Scent-triggered navigation in honeybees. Nature 427:411

Reinhard J, Srinivasan MV, Guez D, Zhang SW (2004b) Floral scents induce recall of navigational and visual memories in honeybees. J Exp Biol 207:4371–4381

Riley JR, Smith AD, Reynolds DR, Edwards AS, Osborne JL, Williams IH, Carreck NL, Poppy GM (1996) Tracking bees with harmonic radar. Nature 379:29–30

Srinivasan MV (1994) Pattern recognition in the honeybee: recent progress. J Insect Physiol 40:183–194

Srinivasan MV, Zhang SW, Zhu H (1998) Honeybees link sights to smells. Nature 396:637–638

Srinivasan MV, Zhang SW, Altwein M, Tautz J (2000) Honeybee navigation: nature and calibration of the 'odometer'. Science 287:851–853

Wehner R (1981) Spatial vision in arthropods. In: Autrum H (eds) Handbook of sensory physiology 7. Springer, Berlin Heidelberg New York, pp 288–616

Wehner R, Rossel S (1985) The bee's celestial compass—a case study in behavioral neurobiology. Fortschr Zool 31:11–53

Zhang SW, Lehrer M, Srinivasan MV (1999) Honeybee memory: navigation by associative grouping and recall of visual stimuli. Neurobiol Learn Mem 72:180–201

Zhang SW, Srinivasan MV, Zhu H, Wong J (2004) Grouping of visual objects by honeybees. J Exp Biol 207:3289–3298