MAGNETIC COMPASS CUES AND VISUAL PATTERN LEARNING IN HONEYBEES

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Summary

We show that honeybees can learn to distinguish between two 360 ° panoramic patterns that are identical except for their compass orientation; in this case, the difference was a 90 ° rotation about the vertical axis. To solve this task, bees must learn the patterns with respect to a directional framework. The most powerful cue to direction comes from the sky, but discrimination between patterns is possible in the absence of celestial information. Under some conditions, when other potential directional cues have been disrupted, we show that bees can use a magnetic direction to discriminate between the patterns.

Key words: honeybee, visual pattern learning, magnetic compass, orientation.

Introduction

Under some conditions, insects learn visual patterns retinotopically (Wehner, 1981; Dill *et al.* 1993), recognising a pattern only if it falls on the same region of retina with which it was viewed during learning. If retinotopically stored patterns are to be used in tasks such as locating a familiar foraging site or recognising a flower, the insect needs to adopt a standard viewing position during learning and recall. Wehner and Flatt (1977) showed that honeybees hovered in a stereotyped posture in front of a horizontal tube leading to a sucrose reward. From here, the bees were able to tell whether a pattern behind the tube corresponded to the one that they had associated with the presence of food. The orientation was determined in this case by the arrangement of objects in the immediate environment, as also happens naturally when a bee turns to face a flower.

Sometimes the viewing orientation is not specified by the spatial layout of the pattern and its surroundings, but this lack of local directional information does not prevent bees from recognising a pattern. For example, Lindauer (1960) was able to train bees to feed at the southern corner of a black square painted on a round table. Training was restricted to the afternoon with the table to the east of the hive. After several afternoons of training, the hive and table were transported one morning to an unfamiliar area, with the table positioned to the south of the hive and with empty feeding dishes placed at each corner of the square. Even though the sun and hive were in different positions with respect to the table, the bees chose overwhelmingly to visit the southern feeder, revealing that they had identified the relative bearings of the corners of the pattern. This experiment shows that patterns can be learnt with respect to Earth-based compass coordinates.

One simple means of keeping retinotopic and Earth-based coordinates in register is to view the world from a particular compass orientation. Collett and Baron (1994) showed that bees that were trained to feed at a site located at a constant distance and direction from a nearby cylindrical landmark tended to search for the feeder while facing in a constant compass direction. Dickinson (1994) showed that directional information in a similar task can come from the solar compass. He trained bees to forage within a circular arena. A single cylindrical landmark was placed in the centre of the arena and four identical feeders were placed at cardinal bearings from the cylinder, with only one filled. Bees rapidly learned to choose correctly between the four feeders; a problem that could only be solved by knowing the compass direction of the correct feeder from the cylinder. The choices were random on cloudy days, indicating that the bees relied on the sun and sky for directional information.

Magnetic cues also contribute to providing a 'coordinate frame' for visual landmark learning (Collett and Baron, 1994). When bees were trained to feed at a site defined by a single landmark in an artificial magnetic field in the absence of celestial cues, their heading seemed to be dictated by the field direction. However, once the bees were well trained, their orientation remained the same when the artificial magnetic field was removed on subsequent visits. Thus, magnetic cues can clearly influence the viewing direction while bees learn the relationship between food and landmarks, but it is not clear whether they have any effect on the orientation of experienced bees. In Dickinson's experiment, magnetic cues seem to be ignored altogether.

In the present paper, we ask whether bees can be influenced by magnetic fields when learning and recognising 360 ° panoramic patterns. Bees were trained to distinguish between two panoramic patterns that were identical except for a rotation

about the vertical axis, so that discrimination required the continuous presence of a directional cue. We then tested under what circumstances pattern discrimination is determined by magnetic cues.

Materials and methods
Pattern presentation

Panoramic patterns were displayed around the inside of two plastic dustbins (Fig. 1A) that stood side by side on various areas of grass near the Biology building. The bins were 55 cm high and circular in cross section with a 46 cm radius at the top and a 38 cm radius at the bottom. The patterns were composed of four vertical coloured or striped elements, each 14 cm×50 cm, spaced equidistantly on a white paper background that reflected well into the ultraviolet end of the spectrum. The coloured panels were made from 'yellow' or 'blue' card. The yellow reflected predominantly above a wavelength of 500 nm (so exciting the long-wavelength receptor of the bee) and the blue reflected maximally at 450 nm, exciting mainly the medium-wavelength, but to some extent the long-wavelength, receptor. The striped patterns were made from 4 cm wide strips of black paper glued 4 cm apart, oriented at either 45 ° or 135 ° from the vertical, on a white background. The pattern elements were glued onto thick board.

A horizontal plastic tube, with an internal diameter of 1.6 cm, ran from the centre of the bin through a hole in the bin wall between two of the pattern elements at a height of 30 cm from the base and entered a feeding box supported on the outside of the dustbin. The end in the centre of the bin was made conspicuous by wrapping a strip of blue tape around the tube. The feeding box attached to one bin (the 'positive' or rewarded bin) contained a jar of sugar solution, whereas the box attached to the other bin was empty. For the pattern discrimination experiments, the tubes in the two bins were arranged in the same direction.

Training procedure

Foraging bees were enticed to a feeder inside one of the bins. After they had returned several times, tissue soaked with sugar
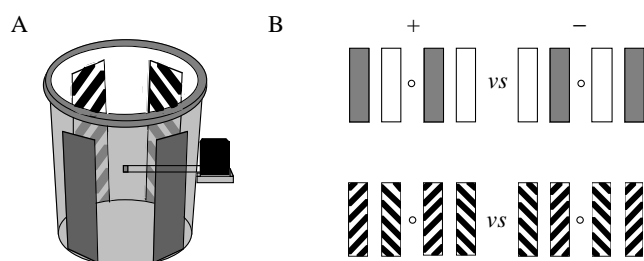

Fig. 1. (A) Plastic bin displaying a panoramic pattern. The positions of the four striped pattern elements and the feeding tube and box are shown. In the experiments, two bins were placed side by side, with patterns and tubes arranged as shown in Figs 3–5. (B) Positive and negative patterns shown 'unrolled' with a circle representing the tube position.

solution was placed in the tube entrance and then gradually moved along the tube until the bees had learned to crawl into the feeding box. Bees foraging from the box were marked with a paint dot on the thorax or abdomen. Roughly 40 bees were marked at the start of each experiment. At this stage in the training, the pattern elements were introduced. Both bins had alternating yellow and blue panels or alternating 45 ° and 135 ° stripes. Rewarded and unrewarded patterns were the same except for a 90 ° rotation (Fig. 1B).

In experiments with magnetic coils, the bins were moved around each other every 5–10 min so that the axis of the bins did not provide a directional cue. In all experiments the pattern elements in each bin were rearranged and the feeder switched from one bin to the other every 10–20 min, so that the bees could not simply return to one bin or side, but had to associate a particular pattern with the sugar reward.

The strength of the sugar solution was varied to attract as many marked bees back as possible without encouraging the trained bees to recruit others. Any bees that were recruited were caught.

Celestial cues

One of the main compass cues used by bees is the position of the sun and the pattern of polarized light that it produces (Wehner and Rossel, 1985). When tests required us to prevent the use of this cue, a 'tent' was built over the experimental site. Two thicknesses of white woven polyethylene sheeting were used, which depolarized the light falling on the bins. Tests were carried out on overcast days, during which the light intensity measured towards the edges of the tent varied by roughly 10 % of the maximum value, but the variations were patchy and did not form any pattern of intensity gradients that might have provided a directional cue. The tent also removed the view of distant landmarks that would have been learned on journeying to and from the test site.

Magnetic stimuli

In initial experiments, the magnetic field under each bin was manipulated by two rows of bar magnets placed on a steel base-plate, 60 cm square. The magnetic fields from the two rows interacted to give a field as shown in Fig. 2A, of up to 7.4 times Earth strength at tube height, decreasing to roughly 2.4 times at the top of the bin, measured with a portable Hall-effect instrument (Heme International TB2 fluxmeter). The bins were raised about 7 cm above the metal sheet beyond the region where the rows did not interact, and the field still controlled a compass needle roughly 60 cm above the bins. In later experiments, a set of wire coils was built following a design by Merritt et al. (1983). Four 1.5 m diameter square coils were arranged in series (Fig. 2B), the outer two having 52 turns of wire and the inner two 22 turns. The coils were electrostatically shielded with earthed aluminium foil. A direct current of approximately 0.4 A was sufficient to produce an Earth-strength magnetic field in the central region of the coils. The arrangement is said to give the best field uniformity over a large volume of space (Kirschvink, 1992). The bins were
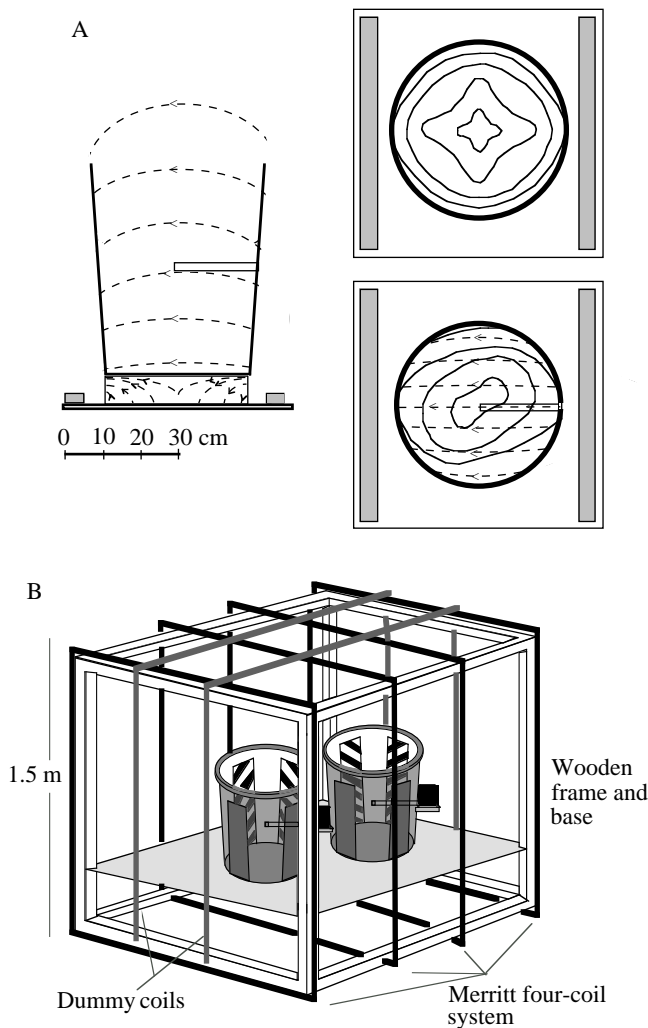
Fig. 2. The two magnetic stimuli used. (A) Two rows of ferrite magnets (shaded) placed one at each end of a square steel base-plate gave a field direction indicated by the broken lines. Plots of the intensity gradients are given at the top of the bin (upper right) with contours at 0.02 mT intervals decreasing outwards from roughly three times Earth strength in the centre, and at tube height (lower right) with contours at 0.05 mT intervals decreasing outwards from roughly seven times Earth strength in the centre. The bins were raised slightly into the more uniform field. (B) The coil system based on the design by Merritt *et al.* (1983) (see text). Four 1.5 m diameter coils of 2.5 mm^2 multi-stranded insulated copper wire (tri-rated switchgear cable) were wired in series, the outer two coils having 52 turns and the inner two 22 turns of wire. The coils were wrapped in plastic trunking, shielded by earthed aluminium foil, and suspended on a wooden frame with a wooden shelf to hold the bins in the centre of field. A d.c. power supply (Thurlby Thander), adjusted to 0.4 A and 8 V, produced an Earth-strength field in the centre of the coils. A dummy set of coils (made from empty plastic trunking) was added to reduce the obvious visual direction cues provided by the coils. Conspicuous visual cues made bees less likely to follow the magnetic field. A square Helmholtz pair (not shown) was added for dip experiments only. These were 1.6 m diameter coils, with 50 turns of wire each, and were placed horizontally 87 cm apart centred at the height of the feeding tube.

placed on a wooden platform positioned so that the tube entrances were in the centre of the magnetic field. Striped patterns were used for training and testing in experiments using artificial magnetic fields, as such patterns were more difficult to discriminate from above or at a distance from the bins when the bees were outside the influence of the artificial magnetic field. The apparatus was placed roughly 15 m from the nearest building, away from prominent visual cues.

Testing procedure

To determine whether bees had learnt to find the correct pattern, the food was removed for a test period, generally of 4 min. The patterns and bins were moved around so that the bees could not simply return to the previously rewarded position. The pattern elements were rearranged so that the previously rewarded bin contained the negative pattern and the unrewarded the positive pattern, thus eliminating the possibility that bees choosing correctly were returning to the most recently scented location. In tests with coils, the patterns were rotated by 90° after 2 min, so that any spontaneous bin preference was cancelled, and again the previously rewarded bin was set up with the negative pattern for the first 2 min period. The number of bees preferring each pattern was scored in one of two ways. In preliminary tests, we simply counted the number of bees that entered each tube during the test period. Either the test period was recorded on video tape using a camera that looked down on the bins, or the number of bees entering each tube was counted during the tests by two observers. One entry was scored when the abdomen disappeared inside the tube. A further entry from that bee was only counted after it had flown away from the tube. Both feeding boxes were left open to reduce congestion in the tube. Most tests, however, were carried out with both tubes removed and the hole covered, by moving the cardboard pattern elements round by 45° (and, if necessary, counter-rotating the dustbin). Bees flying in and out of the two bins were video-taped for 4 min and the number of bees hovering in each bin was scored afterwards. This was done by pausing the video tape every 10 s of the test and counting the number of bees present in each bin. The accumulated count from 25 frames within 4 min gives an indication of how many and for how long bees hovered in each bin. The bin attracting the larger count was termed the winner. Each test thus provided one data point (as the choice of any one bee could not be considered to be independent of that of other bees), and the sign test (Segal and Castellan, 1988) was used to determine whether one pattern was preferred in significantly more tests than the other.

Viewing orientation

Tests were also performed to discover whether bees learnt the direction of the tube and oriented preferentially in that direction. Striped patterns were arranged as before, but during training the tubes were oriented perpendicularly to each other so that the patterns had the same relationship to the tube in both bins. This procedure was adopted to

maximise the chance that bees would orient in the direction of the positive tube. Four groups of bees were trained. Each had the tube in the positive bin aligned with a different cardinal compass point. In tests, the tube was removed from the feeding box and placed upright in the bin where the blue taped end provided a radially symmetrical target towards which bees flew and on which they landed. The hole in the bin wall was covered on the inside with thick white paper, which matched the background and extended between the flanking pattern elements, and on the outside with a sheet of aluminium. The flights were video-taped, and the horizontal orientation of the bees just before they first contacted the tube was measured from the video tapes. The mean of these orientations for each training regime was determined as described by Batschelet (1981). The mean orientation during whole approach flights inside the bins was also measured for two group of bees trained with striped patterns and south- or west-facing tubes.

Results

Bees learn to distinguish between the 'positive' and 'negative' patterns

Preliminary tests with all of the natural visual and magnetic cues available showed that bees could discriminate easily between the positive and negative bins after about 4 h of training, both when the patterns were striped and when they were coloured. Bees preferred to enter the feeding tube of the bin containing the rewarded pattern (Fig. 3A,B; $P \leqslant 0.004$, sign test). Taking the average across tests, 71.5 % of entries were into the tube associated with the positive pattern.

External directional cues are used to distinguish between the patterns

When the tubes were removed, bees hovered for significantly more of the time in the positive than in the negative bin (Fig. 3A,C; $P < 0.0005$, sign test; mean preference 74.9 %). Bees can therefore distinguish between the patterns in the absence of the tubes, demonstrating that the pattern is not simply learnt by linking the pattern elements to the tube position. This is shown directly by the observation that the patterns can still be distinguished when the tubes are 90 ° apart so that the patterns in each bin are identical in their relationship with the tube orientation (Fig. 3D; mean preference 73.6 %, $P \leqslant 0.062$ for four out of four correct choices, sign test).

If the axis between the two bins is constant, then the bees might use this axis to discriminate between the patterns. However, bees continue to hover in the correct bin when the bins are rotated with respect to each other during training and testing, showing that this axis is not a required directional cue (Fig. 3E; mean preference 68.7 %, $P \leqslant 0.004$, sign test). Directional information must come from external cues such as biological compasses, distant landmarks or dead reckoning. Shadows on the bin wall might also provide helpful information. The following experiments show that bees are
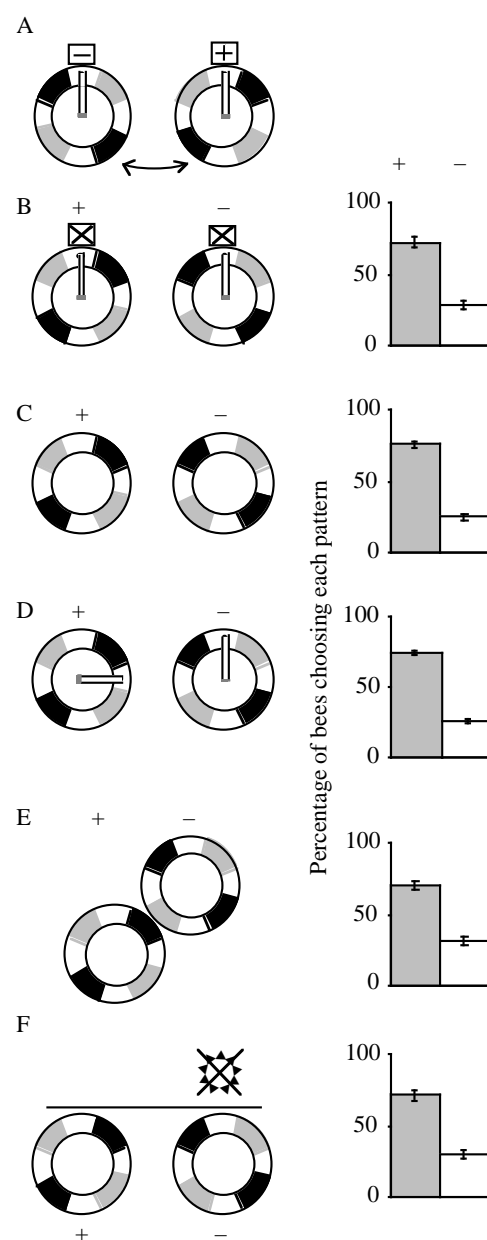

Fig. 3. Plans of the training and testing arrangements for pattern learning experiments, the two bins being represented from above. Tubes and feeding boxes are shown where present. Histograms show the mean percentage (± S.E.M.) of bees choosing each pattern (see text for scoring methods) averaged over the number of tests indicated below. (A) Training position for the majority of tests; + represents the food reward. The patterns and reward are swapped from side to side periodically. (B) Number of bees entering each tube during eight unrewarded tests. (C) Hovering scores with tubes removed; 20 tests. (D) Training and testing with tubes perpendicular, so that pattern elements have the same relationship with the tube in each bin; four tests. (E) Bins are moved around each other during training and tests to prevent the long axis from providing a directional cue; eight tests. (F) Training and testing in the tent; seven tests.

flexible in their use of compass information and rely on different directional cues under different circumstances.

A view of the sky is not essential for learning or recognition

Bees trained and tested in the tent were able to distinguish between the patterns (Fig. 3F; $P \leq 0.008$, sign test; mean preference 70.3%). Learning was a little slower, but this could have been due to the difficulty of escaping from the tent after feeding. We conclude that neither a solar compass nor shadows on the bin walls are essential for discriminating the patterns.

An imposed magnetic field can supply a directional cue

Initially, bees were trained and tested with magnets underneath the bins and with a view of the sky (Fig. 4A). During training, the magnets were oriented so that the applied and natural magnetic fields were aligned. After bees had learnt to distinguish the patterns (Fig. 4B; mean preference 72.8%, $P \leq 0.002$, sign test), several types of tests were given in which the direction of the imposed field was changed. The different types of tests described in Fig. 4 were interleaved. For the first type, bins and magnets were rotated clockwise or anticlockwise through 45° (Fig. 4C). By this manipulation, both positive and negative patterns were equally misaligned with the solar compass, with the surrounding panorama and with the Earth's magnetic field. Under these conditions, the bees preferred the pattern that was correct with respect to the imposed magnetic field ($P \leq 0.004$, sign test; mean preference 63.1%). Thus, magnetic cues can give orientational information when the patterns cannot be matched with directional information available from sky or landmark cues.

Tests were also performed with magnets and patterns rotated through 135° (Fig. 4D). Bees preferred the positive pattern in five out of eight tests. This is not a significant preference according to the sign test. The sample size can be increased on the assumption that counts made every 30 s are independent of their neighbours. If a winner is determined for counts separated by 30 s, there are 41 positive winners out of 63 non-tied counts. Using this procedure, the preference for the positive pattern is just significant ($z=2.27$, sign test for large samples, $P=0.0116$, mean preference 60%).

More rigorous tests of this type were carried out using coils, producing roughly Earth-strength fields. Using this apparatus, we could create a more uniform field and control for the possibility that intensity gradients rather than field direction governed the choices made by the bees. The axis of the coils was placed in an east–west orientation. The coils were switched off during the training periods, so that learning of the patterns took place with all the natural cues available, including a good view of the sun and blue sky throughout almost all experimental days. When preliminary tests had
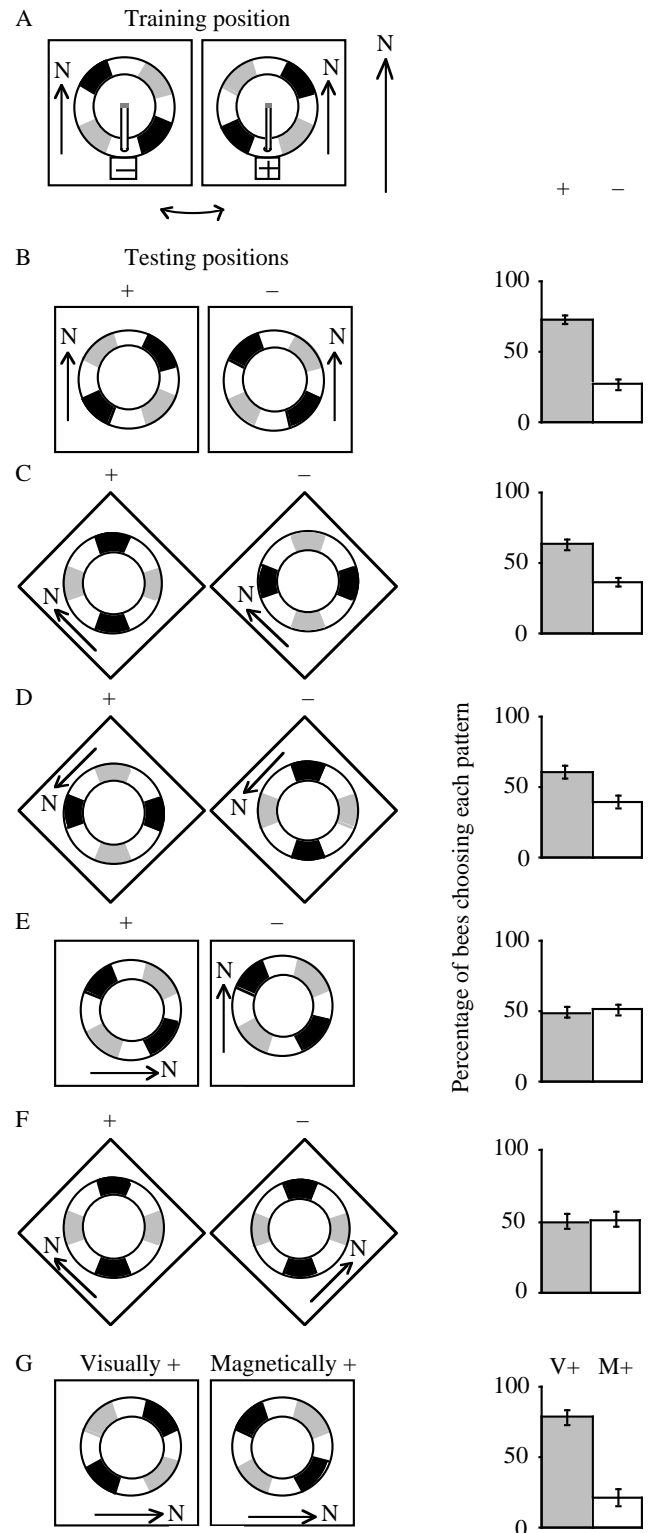

Fig. 4. Arrangement of apparatus during bar magnet experiments. Histograms show mean per cent preferences ± S.E.M. (A) Training position for all of the following tests. Magnets were aligned with the Earth's field and patterns were swapped from side to side as described in the Materials and methods section. Earth north is indicated by the arrow to the right, and the field directions of the bar magnets are indicated by the arrows inside the squares. (B) Hovering tests in the training position, with the tubes removed. + and − indicate the relationship of the pattern to the magnetic field; nine tests. (C) Testing position with magnets and bins rotated by 45°; eight tests. (D) As C, but with 135° rotation of apparatus; eight tests. (E,F) When tests were performed with fields perpendicular, there were no preferences; eight and seven tests, respectively. (G) With magnets and patterns turned through 90°, visual (V+) and magnetic (M+) cues give conflicting answers. The visual cues are followed; two tests.
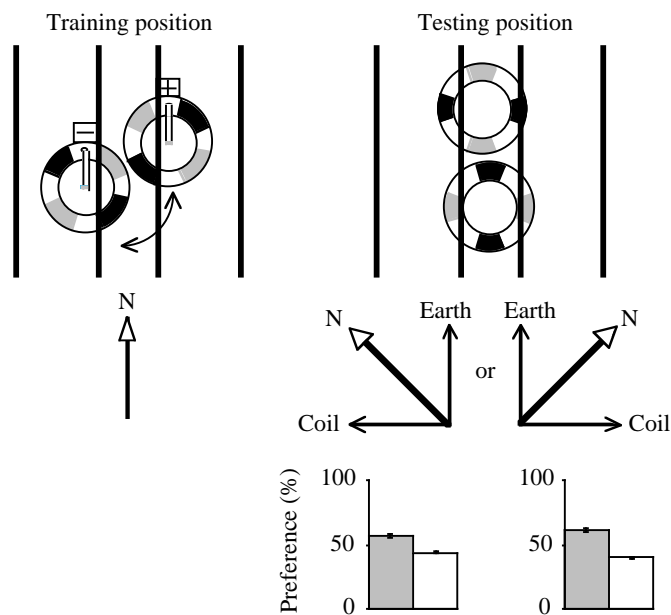
Fig. 5. Plan of the procedure for experiments with coils. Heavy lines show the position of the four coils from above. Training was carried out with the coils turned off, and the bins were moved around each other. In addition, patterns and reward were swapped periodically between bins. The tubes were removed for tests and the bins rotated by 45° in either direction. A corresponding 45° rotation of the field in either direction was produced as the resultant of the Earth's field and the coil field, as indicated below the diagram of the apparatus. The direction was selected arbitrarily and was the only factor determining which bin was termed 'positive' (for example, a clockwise field rotation means that the top bin contains the positive pattern). Histograms of a total of 24 tests split into two groups according to whether the field was rotated anticlockwise or clockwise (mean per cent preference ± s.e.m.) are shown below.

shown that the patterns had been learnt in the training position, tests with altered magnetic fields were performed (Fig. 5). Again the bins and patterns were rotated through 45°, the tube being removed and the hole covered by moving the pattern elements. The coils were switched on and the current raised until the resultant north deviated 45° from Earth north. This produced a field of roughly 1.4 times Earth strength, with a slightly reduced inclination. The current could be reversed to rotate the field in the opposite direction. Half of the tests were run in each direction, with the choice of direction being selected to avoid alternation. Again solar, landmark or vector cues could not help to identify which pattern might be correct. Only the field direction was a useful predictive cue. The patterns were rotated after 2 min of testing so that the opposite bin became the correct choice for the final 2 min of the test (to control for spontaneous preferences). In 24 such tests, the correct pattern was weakly preferred 22 times ($P<0.0005$, sign test). The average preference in the positive tests was only 57.9% (56.2% over all tests), but this small preference was consistently in the direction dictated by the magnetic field direction. Because training took place with the coils off, we conclude that the bees could not learn to associate the patterns

with other cues that might be associated with the coils, such as field intensity gradients or anomalies, and therefore must be able to use the field to provide a compass cue. The preference for the magnetically correct stimulus was perhaps so small because of the disturbance caused by the disruption of all other directional references that the bees had associated with the pattern during learning.

Bees do not discriminate patterns when imposed magnetic fields in the two bins are perpendicular

Using the bar magnets (but not the coils), it was possible to impose a different field direction in each of the bins. When one bin and its magnet were rotated through 90° (Fig. 4E), or the two bins and associated magnets were rotated 45° in opposite directions (Fig. 4F), the patterns in both bins were aligned in the same direction with respect to external coordinates, although the horizontal components of the magnetic fields beneath the two bins were perpendicular to each other. Bees did not distinguish between the two patterns in either arrangement (mean preferences 48.9%, Fig. 4E; 50.7%, Fig. 4F; not significant). It is possible that there was an anomalous magnetic field near the bins because the two magnetic plates were not aligned, but the direction of the field inside the bin (as shown by a compass) was normal.

We also found that bees could not be trained to distinguish patterns under these conditions. Four separate attempts were made to train bees to discriminate between bins arranged so that the positive and negative patterns were in the same orientation relative to Earth north, but with the applied magnetic fields perpendicular to each other (as in the test shown in Fig. 4F). Mean choices for the positive pattern after periods of such training were: 51.7% (six tests), 52.2% (14 tests), 43.2% (six tests) and 47.5% (nine tests). In the last of these experiments, bees underwent pretraining with the magnets aligned and the positive and negative patterns rotated by 90° with respect to each other (as in Fig. 4A) until they were able to find the correct pattern.

Role of field inclination

A square Helmholtz pair was added to the coil system to provide a vertical field with which the inclination or dip could be manipulated. A dip compass was used to set the current to such a level that the field dip was nulled as accurately as possible. Bees were trained as in the other coil experiments, with no current running through either set of coils. In tests, the horizontal field was again rotated by 45°, and the field inclination was cancelled. In all of eight such tests the bees still chose the correct pattern ($P<0.004$, sign test, average preference 58.5%). Because the sensitivity of bees to dip may be extremely high, we can only conclude that reducing the inclination to extremely small values did not make the task appreciably more difficult.

Sky or landmark cues dominate magnetic ones

When both bins and sets of magnets are rotated through 90°, the bin that is positive with respect to magnetic cues is negative

with respect to Earth coordinates and *vice versa*. In two tests, bees strongly preferred the pattern that was correct with respect to Earth coordinates, seemingly unperturbed by the conflicting magnetic cue (Fig. 4G; mean preference 78 %). The sample size was increased to allow statistical analysis by taking the preference scores at 30 s intervals (as described for the 135° rotation tests) and the two tests yielded 18 out of 18 positive scores ($P<0.0005$). The choice of pattern can thus be determined independently by visual or by magnetic cues.

Landing and flight direction

The approach flights of bees trained with the positive tube entrance in one of four directions were filmed with the tube placed vertically in the bin. For each flight in the positive bin, the orientation of the bee was measured just before it touched the tube. Circular distributions of these 'landing' orientations (Fig. 6A,B,D,E) show that bees orient preferentially in the direction that the tube entrance had faced. In Fig. 6G, the data from the four groups have been pooled and normalised with respect to the tube entrance. The mean vector of the combined data is 17° anticlockwise of the tube direction and is significantly oriented ($P \leqslant 0.001$).

For one group of bees trained with a south-facing entrance and another with a west-facing entrance, the orientation was measured throughout the approach, from the point when the bee entered the bin until it landed on the vertical tube. The mean direction was computed for each of 60 recorded flights in the 'south' group and 40 in the 'west' group. The distribution of these vectors is plotted in Fig. 6C,F.

Overall, these results show that the preferred orientation reflects the direction of the horizontal tube. Bees fly and land at this preferred orientation when the tube is vertical. We conclude, therefore, that bees have learnt the horizontal direction of the tube with respect to other cues. As the pattern has 180° symmetry, it cannot specify direction unambiguously, so bees must use additional information to help control their orientation. However, the pattern may play some role in specifying orientation, as the landing orientations in the negative bin are much more erratic, showing no significant orientation when data are normalised with respect to either the positive (Fig. 6H) or negative (Fig. 6I) tube position.

Discussion

These experiments have shown that honeybees can learn to distinguish between panoramic patterns that are identical except for their orientation; in this case a 90° horizontal rotation. Discrimination is possible when the patterns can be distinguished only by means of external directional cues. These external cues include sky cues (as in the experiments of Dickinson, 1994) and/or distant landmarks. However, sky cues are not essential and we find that under some conditions experienced bees can discriminate the patterns by means of magnetic cues.

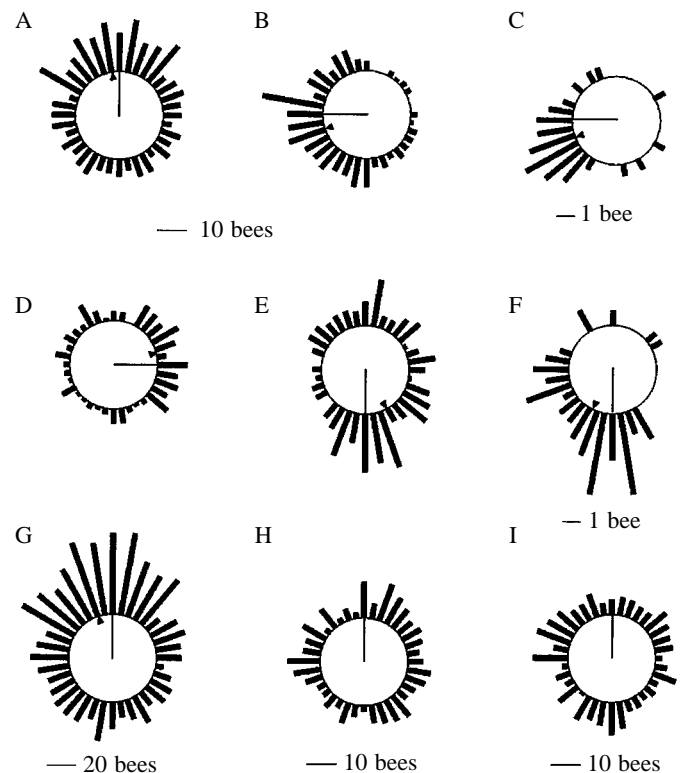The influence of magnetic cues only surfaced when magnets

Fig. 6. Circular histograms showing results of orientation experiments. (A,B,D,E) Mean vectors are plotted of the landing orientations of bees on a vertical tube in the centre of the positive bin for four groups of tests. Scale bar below A applies to the four groups. Bees were trained with the positive tubes pointing north (A) (mean vector 352°, length 0.25, $N=298$ landings), west (B) (253°, 0.48, $N=179$), east (D) (74°, 0.28, $N=148$) or south (E) (151°, 0.21, $N=259$). The tube orientation is indicated by a line and the orientation of the mean vector by an arrowhead. Each distribution is significantly different from random orientation (Rayleigh test, $P<0.001$ in each case). (C,F) Second-order distributions of mean vectors of whole flights, from entry to the bin until landing. Training was with a west-pointing (C) or a south-pointing (E) tube. Only flights that were significantly oriented are included ['south' group, 52 of 60 recorded flights, vector length 0.80±0.03 (mean ± S.E.M.), second-order mean vector 209°, length 0.648; 'west' group, 33 of 40 recorded flights, length 0.60±0.04, second-order mean vector 248°, length 0.71; vector lengths significantly differed from random according to Rayleigh test $P<0.001$]. (G) Data from A, B, D and E normalised with respect to tube orientation (vertical line indicates normalised tube position) show that tube orientation during training influences landing bearings during tests (mean vector 343°, length 0.29, $N=884$, significantly different from random $P \leqslant 0.001$). (H,I) Tests with bees in the bin containing the negative pattern. Data are normalised with respect to the training orientation of the tube in the positive (H) or negative (I) bin. Normalised tube orientations are again shown by vertical lines.

and patterns were rotated so that the patterns were ambiguous with respect to directional signals from the sky and from distant landmarks. In bees, as in birds (for a review, see Able, 1994), celestial and landmark compasses dominate magnetic cues, so that the latter only come into play when visual cues are unavailable or unhelpful. Such a hierarchy can account for

the preferences expressed in Fig. 4C,D,G, but the results shown in Fig. 4E,F are puzzling. In these tests, bees showed no preferences. The patterns were oriented identically relative to visual directional cues, but the local fields in the two bins were perpendicular. One possibility is that the bees ignored magnetic cues because the two patterns could not be discriminated visually. Another possibility is that as bees fly from bin to bin they repeatedly encounter a change in the relationship between the magnetic and visual compasses. This change could disrupt the choice of viewing orientation, but so far we do not really understand the failure of the bees in these tests.

The behaviour described here shows that bees are able to extract a directional cue from magnetic fields of Earth strength and higher, providing an example of a potential compass response in freely flying bees to be added to evidence for magnetic orientation in landmark learning (Collett and Baron, 1994), in dancing bees (Lindauer and Martin, 1972), in bees walking in the hive (Schmitt and Esch, 1993) and in comb-building (DeJong, 1982). Our experiments by themselves do not, however, show that bees have a true polar compass sense. In principle, the correct pattern could be identified even if bees could not distinguish magnetic north from magnetic south. We tried unsuccessfully to test whether bees can exploit magnetic polarity in visual discrimination tests. To do this, bees were trained to panoramic patterns, with the positive and negative exemplars differing by a $180\,°$ rotation. In tests, bees chose randomly when the magnetic fields and patterns were rotated through $90\,°$ (results not shown). Either the $90\,°$ conflict between visual and magnetic directional cues disrupted the behaviour of the bees or they do not distinguish between poles. However, with all directional cues available, the orientation of the bees is unimodal, despite the twofold symmetry of the visual pattern (Fig. 6), and we know from earlier experiments (Schmitt and Esch, 1993; Collett and Baron, 1994) that bees can orient unimodally in an artificial magnetic field. Thus, taken together, the current and earlier findings make it very probable that bees do possess a directional magnetic compass.

It is most unlikely that bees distinguished the visual patterns through information from spatial variations or gradients in the intensity of the magnetic field. Training was with the coils off, but bees were influenced 'correctly' by the direction of the magnetic field when current was passed through the coils. The coil design provides a field with a large volume of uniform intensity, and any imperfections were experienced solely during tests and could not have provided useful learning cues. It is also unlikely that the inclination of the field, or the dip angle, is used in this task, although the field may not have been nulled accurately enough to exclude this cue completely. It did seem, however, that cancelling the dip of the field did not noticeably impair the choice behaviour, whereas if bees relied on an inclination compass as used by birds (Wiltschko and Wiltschko, 1972) and sea turtles (Light et al. 1993), we might expect that the move from the normal Earth's field inclined at nearly $70\,°$ during training to a degree or so during the tests

would cause some disruption. Bees seem to be highly sensitive to the presence of magnetic field anomalies and to small differences in intensity (Walker and Bitterman, 1989; Kirschvink et al. 1992) but, even with this degree of sensitivity to vertical field information, it would be unlikely that bees could extract map information from the variation in dip angle with latitude (see discussion in Able, 1994) over their relatively small foraging range. It seems most likely that directional information is obtained from the horizontal field component, as seen in lobsters (Lohmann et al. 1995).

The simplest account of the ability of the bees to choose between patterns that differ solely in their orientation with respect to compass cues is that bees learn and distinguish between patterns when facing in particular learned directions. The data presented in Fig. 6 give some support to this hypothesis in that bees flying and landing in the positive bin tend to orient in the direction that the tube entrance faced during training, even during tests in which the tube was placed vertically. Zeil (1993a,b) observed an analogous phenomenon in the orientation and return flights of solitary wasps. In this case, their viewing direction in both orientation and return flights was determined by the compass bearing of a landmark relative to the nest entrance. Wasps, on return flights, continued to orient in the same preferred direction when the landmark was moved away from its habitual position.

Our data suggest that the preferred viewing direction can be learned and recalled by the opportunistic use of several different directional cues. Visual cues dominate, but magnetic information is exploited when other directional information is disrupted. The accuracy of the directional information gained from magnetic fields may be much better than we have demonstrated. Under normal conditions, magnetic cues are likely to become significant when other cues are unavailable. In our experiments, magnetic and visual cues were rotated with respect to each other so that bees obtained conflicting directional signals. Although our experiments were limited to small-scale panoramic patterns, we conjecture that bees generally simplify the learning and recognition of natural scenes by adopting preferred viewing directions.

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