

## Mechanisms of dance orientation in the Asian honey bee *Apis florea* L.

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Accepted May 10, 1985

**Summary.** Early studies of dance communication in *Apis florea* had shown that waggle dances are not performed on a vertical plane and oriented to gravity, as in the other species of *Apis*, but instead take place on the flattened top of the exposed comb and are oriented to celestial cues directly. More recent experiments showed that *A. florea* can dance in the absence of a view of the sun or blue sky, but did not establish what mechanism permitted this orientation. I now report that dances can be oriented directly to landmarks visible from the nest, the first evidence of an environmental feature other than celestial cues or gravity being involved in dance orientation. Landmarks near the nest are probably used to refer to celestial cues, in a fashion analogous to the use of broad features of the landscape by honeybees in order to learn the sun's course, which permits them to determine their flight angle on overcast days or at night, and to compensate accurately for solar movement. *Apis florea* may therefore be able to learn the sun's course with respect to two sets of landmarks.

In other experiments I have examined the influence of slope on *A. florea*'s dance orientation to visual references. In the first extensive observations of its dances on a vertical plane, I have amply confirmed that this species cannot transpose light and gravity in setting its dance angle, as the other species of *Apis* can. Nor do dancers orient so as to match visual information seen during the dance with that remembered from the flight. Patterns in the data when the same patch of sky was presented from different angles suggest instead that *A. florea* continues to orient to projections of celestial cues onto the horizontal plane even when dancing on

a steep slope. This compensation for slope may involve an ability to detect gravity and factor it out in aligning the dance to celestial cues.

These insights suggest that *A. florea*'s dance orientation system has been adapted to requirements imposed by its nesting behavior, and has diverged sharply from the system shared by the other species of *Apis*.

### Introduction

Since the 1940s it has been known that the waggle dances of the European honeybee *Apis mellifera* can be performed either on a horizontal surface and oriented to the sun and blue sky (von Frisch 1949) or on a vertical surface and oriented to gravity. In vertical dances the angle of flight relative to the sun's azimuth is transferred to an angle of dancing relative to the direction of gravity (von Frisch 1946). Whereas horizontal dances become disoriented when no light cue (natural celestial cues or artificial lights) is available, vertical dances normally proceed in the darkness of the hive. Lindauer's (1956) pioneering studies of the three Asian species of *Apis* showed that *A. cerana* and *A. dorsata* possess dance communication basically similar to that discovered in *A. mellifera*, but that the dance of *A. florea* seemed to involve a system of information processing that is somewhat restricted in its flexibility in comparison with *A. mellifera*, because dances are only seen on a horizontal surface, and seem to require a view of celestial cues. However, more recent studies by Koeniger et al. (1982), as well as my own preliminary observations, have indicated that *A. florea*'s dance might involve more complex processing than originally thought. This paper describes two sets of experi-

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ments which together reveal a dance orientation strategy in *A. florea* that diverges dramatically from that found in the other species, and is perhaps more complicated in some ways.

*Apis florea* builds its nest in the open rather than in cavities. A single comb is suspended from a slender twig in dense vegetation (Seeley et al. 1982), and wax surrounds the supporting branch so that a flattened surface is formed on top. On this surface the dancer signals the direction of the food in the fashion characteristic of *A. mellifera*'s horizontal dances – using celestial cues as a directional reference, she runs repeatedly in the direction she has flown to the food. (Even when the sun and sky patterns move during the day the bees continue to direct their dances toward the food, compensating for celestial rotation just as they do on successive flights.) On the other hand, when Lindauer forced *A. florea* dancers onto the vertical sides of the colony by denying them access to the top, they were usually disoriented, or at least did not adopt the angle relative to vertical that was expected if they could translate the horizontal angle of flight into a vertical dance relative to gravity, as the other species do.

It seems reasonable to interpret the horizontal dances of honey bees as representative of the earliest stage of dance communication, which may have begun as crudely oriented intention movements on a horizontal surface of an exposed colony, and to interpret the vertical dances of *A. mellifera*, *A. cerana*, and *A. dorsata* as a later modification (Lindauer 1956, 1960; von Frisch 1967). One presumed advantage of the use of gravity by the other species is that bees are freed from having to see celestial cues during the dance; in turn, this may have permitted the occupation of dark cavities by *A. mellifera* and *A. cerana* (von Frisch 1967), and of sheltered nest sites by *A. dorsata* (Koeniger and Koeniger 1980; Dyer unpubl.). This would also imply that *A. florea* is restricted to nesting in the open, and that its dance communication might suffer on cloudy days because its dependence on a view of the sky during the dance would render the dance language ineffective. These implications were supported by the discovery that, contrary to previous suggestions (von Frisch et al. 1960), the sun is probably hidden to *A. mellifera* and *A. cerana* (and presumably the other species) on most cloudy days, forcing the bees to rely upon a memory of the sun's position in relation to landmarks in order to determine their flight angle relative to the sun (Dyer and Gould 1981, 1983; Dyer 1984, in preparation). However, recently Koeniger et al. (1982) were able to induce *A. florea* workers

to dance without a view of the sky, raising the possibility that this species has evolved an ability to orient to an alternative cue. Koeniger et al. did not establish what references the oriented dancers employed; hence my first goal was to study this species in a controlled setting in which various possible cues could be tested against one another.

Based on the results of Koeniger et al. (1982), I could think of three mechanisms by which *A. florea* might orient its dances in the absence of celestial cues. One was suggested by Koeniger et al.: bees could orient to an earth-based reference that is perceived during both the flight and the dance. The earth's magnetic field is one candidate; sensitivity to the earth's field has been demonstrated in *A. mellifera* (Lindauer 1976; Martin and Lindauer 1977; Gould et al. 1978; DeJong 1982), and a magnetic compass plays an important role in the orientation of other animals. Second, dancers might use the topography of the upper surface of the comb, where the dances occur. The surface is vaulted rather than perfectly horizontal, often with some slopes over 45°. Moreover, bees tend to progress in successive waggle runs in the direction they are indicating, and those dancing to a given location end up crowded on the portion of the dancing surface closest to the food, which means all are dancing on approximately the same slope (Koeniger et al. 1982). If dancers could remember the slope on which they danced when the sky was visible, they might rely exclusively on this information when the sky becomes cloudy. Finally, bees faced with a cloudy sky might be able to remember their previous dancing orientation relative to non-celestial visual patterns. Since *A. florea* normally hides its nests in dense vegetation (Seeley et al. 1982), the typical colony would presumably be surrounded by conspicuous patterns to which dances could be referenced if the sky were overcast. The use of such patterns would be analogous to the 'canopy orientation' observed in certain forest-dwelling ants (Hölldobler 1980).

After performing experiments which pitted these hypotheses against one another, I sought to explore further the possible effects of slope on *A. florea*'s dance orientation. Apart from suggesting that might be used comb topography alone to set a dance angle, the tendency of bees to dance on sloped surfaces has an important implication for the processing of celestial information during the dance. Namely, bees standing on different slopes while dancing would see the same set of celestial cues from different perspectives, and so would be expected to align their bodies so as to compensate for slope. A priori the most reasonable hypothesis

is that the dancer orients so that celestial cues stimulate her eyes as nearly as possible as they did during the flight to the food. This 'matching' hypothesis explains dance orientation by all four species on a perfectly horizontal plane (von Frisch 1949; Lindauer 1956; Dyer 1984) as well as *A. mellifera*'s orientation on a vertical surface when it can see the sun (von Frisch 1962, 1967; Edrich 1977). On the other hand, some other mechanism for compensation might be involved.

To explore this question I emulated Lindauer's (1956) attempts to prevent bees from dancing on the horizontal surface. During pilot studies I often noticed dances on vertical or near-vertical surfaces, as described above, but their orientation was difficult to account for either by the transposition rule used by *A. mellifera* (a dance vertically upwards refers to the direction of the sun), or by the possibility that bees oriented to obtain the best match between cues seen during the dance and information stored on the flight. Thus, the plan of the second part of the study was to document thoroughly the actual orientation of vertical dances as compared with the orientation predicted by each of these hypotheses. Then, so as to probe further the rules by which vertical dances might be oriented, I performed a series of manipulations in which dancers were presented with the same patch of blue sky at different angles relative to the plane on which they were dancing.

## Methods

Colonies of *A. florea* were captured by cutting the branch to which the comb was attached, suspending the ends of the cut branch with a loop of twine, and gently swinging the colony while carrying it. The bees respond to this stimulus as they do to a strong breeze: they remain on the nest and cling tenaciously to the comb and to one another. Hence a colony can be transported long distances and resettled. With the help of an assistant I once carried an exposed colony 50 km by motorcycle without losing a single bee; the colony issued 5 reproductive swarms in its new location and remained for 2 months more. All experiments reported here were performed in Pune, India (Longitude 73° 41' E.; Latitude 18° 32' N.), in July, August, and September 1983. The four colonies that were used were captured in gardens and parks in the city of Pune.

To study mechanisms of dance orientation in the absence of celestial cues I installed a colony in a bamboo hut in which various possible cues could be controlled and manipulated (Fig. 1). The branch from which the comb was suspended was rested on a bamboo frame so that the colony could be lifted and rotated to any compass orientation with minimal disturbance to the bees. Bees on the dance floor (the top surface of the comb) initially could see a 20° patch of sky through an aperture in an arena (35 cm in diameter) formed by a cardboard wall around the colony. *Apis florea* can orient well to the polarized light of blue sky (Lindauer 1956; Koeniger et al. 1982). When the aperture was closed the bees could come and

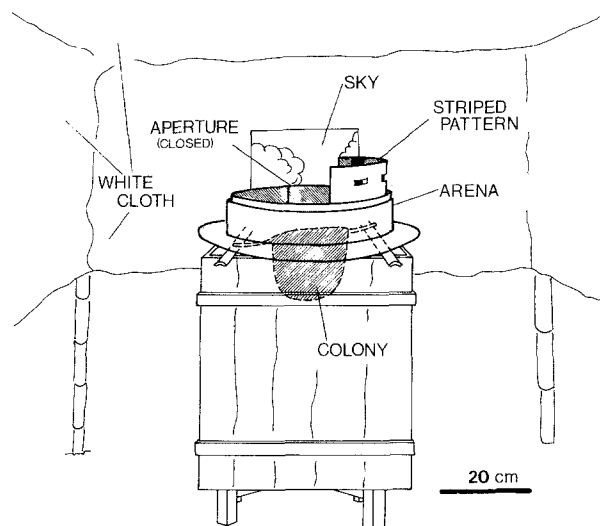
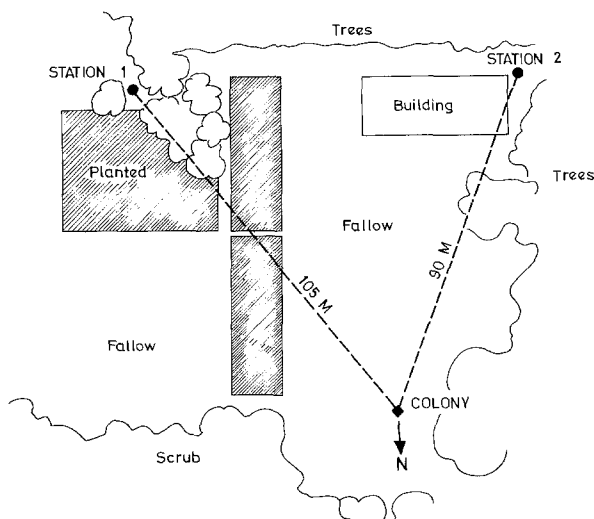


Fig. 1. View inside bamboo hut used for experiments with *A. florea*. A window to the outside offered a view of a patch of sky with a visual angle of about 20°, at the center of which was the sky point of azimuth 149° and elevation (above the horizon) 22°. The branch from which the colony was suspended was set upon a bamboo frame which could be lifted and rotated from its initial position on the open end of a wooden box. Also mounted on the frame were a horizontal protractor for measuring dance angles, and the cardboard arena around the colony, an aperture in which could be closed (as shown) to block the view of the sky seen by the dancers on top of the colony. The striped pattern was attached to the inside of the arena, and could be rotated independently of the orientation of the comb. Dancers were observed through slits in the striped pattern. Scale is approximate

go from top of the nest, but while dancing they could see only the wall of the arena (which rose 15 cm above the level of the dancers), the white cloth suspended from the ceiling of the hut (45 cm above them), and a conspicuous visual pattern located to one side of the colony and rising above the wall of the arena. The pattern, which subtended a horizontal angle of 135°, consisted of three evenly-spaced vertical blue stripes (each 5 cm wide) painted on a 42 × 30 cm rectangle of white cardboard that was fastened to the inside wall of the arena. The orientation of the striped pattern and the comb relative to the earth's magnetic field could be changed independently of one another, and by watching the effect of a change on the orientation of dancing bees I could isolate the cues to which they were oriented. The bees tolerated this home as long as local pollen sources were abundant; otherwise colonies tended to abscond (see also Lindauer 1956).

To train bees for an experiment, a feeder containing a solution of 2 mol/l sucrose with honey added for scent was placed near the nest. After the bees discovered it (usually quickly, but sometimes I assisted by transferring bees from the nest on a twig soaked in the solution), it was moved in steps to a position approximately 100 m away (map, Fig. 2). The bees at the feeding station were labeled individually with dots of colored paint applied in unique patterns on the thorax and abdomen. Usually 10–15 bees were visiting the feeder and dancing during a given experiment.

In a typical experiment these foragers were observed on their return to the colony as they danced first with a view of blue sky, then with no sky visible (aperture in arena closed),



**Fig. 2.** Site of all experiments on *A. florea* reported here; located on a sericulture research station in Pune, India. Hatched rectangles were planted with mulberry about 1.5 m in height. The trees to the west and south of the colony were about 15 m tall

and then with the striped pattern or the comb shifted. Bees orienting their dances to an earth-based reference such as the magnetic field would be expected to continue to aim their dances in the direction of the food, even when the comb and pattern were shifted. Bees orienting to the topography of the comb should maintain their dance angle relative to the comb axis, no matter what its compass orientation or the orientation of the pattern. Dancers orienting by means of non-celestial visual cues should only shift their dances to compensate for shifts in the orientation of the striped pattern.

I observed dancers through slits cut in the striped pattern so that my head did not provide bees an additional landmark. Because this restricted vantage point introduced a potential parallax error, I estimated dance angles only to the nearest 15°, referring to a large horizontal protractor that surrounded the colony and was level with the plane in which the dances occurred. This degree of resolution was sufficient for testing the hypotheses since the predicted dance angles based on the various possible orientation mechanisms could be separated by up to 180° when the corresponding cues were rotated with respect to one another. I dictated into a tape recorder the individual waggle runs (measuring angles clockwise from North, or 0°) of marked dancers that had flown to the feeding station, and transcribed the tapes later.

To study the orientation of bees dancing on a vertical surface, I removed the arena and the striped pattern and arranged cardboard baffles so that returning foragers could land easily only on one flank of the colony, which was aligned so that this side faced the open window. Though the bees could reach the other side of the nest by walking downward, the top of the comb was completely blocked. Hence the only place on the nest where dances could be performed with a view of the sky was the vertical curtain of bees on the side toward the window. After an initial period of adjustment during which bees tried to reach the top of the comb (Dyer 1984), foragers would commence dancing on this surface shortly after alighting. Although eventually it would be preferable to study vertical orientation to the sun, which is after all the primary orientational reference for bees, I assumed for these experiments that

the mechanisms of orientation to the blue sky would be closely linked to those involved in orientation to the sun, as is true of *A. mellifera* (reviewed by Wehner 1984; Wehner and Rosell 1985).

The dances I observed were those of foragers flying to Station 2 (Fig. 2). I recorded individual waggle runs of marked bees to the nearest 5°, measuring the angles relative to a plumb line with a protractor (clockwise from 0°, or straight up), and dictating them into a tape recorder. Because I kept the number of foragers at about 10, I could be assured of being able to measure almost all waggle runs performed during a given period of observation.

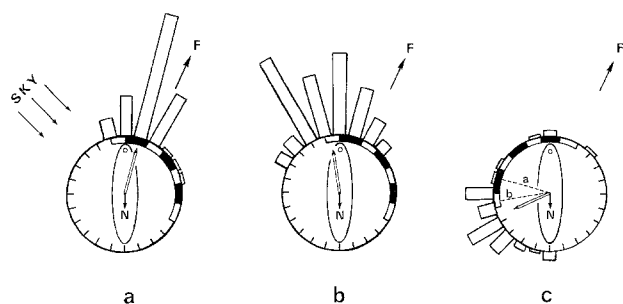
For both parts of the study the circular distributions of dance angles were analyzed by using Rayleigh statistics (Batschelet 1965, 1972). I calculated the mean angle ( $\theta$ ) of a set of waggle runs by vector addition, as well as the degree of clustering,  $r$ , where  $r=0$  for random orientation and  $r=1$  for identical orientation of all waggle runs. For analyzing significance the important tests were the  $z$ -test, which evaluates the significance of the clustering of orientation data, and the  $V$ -test, which evaluates the clustering relative to a predicted angle.

## Results

### *Orientation of horizontal dancers denied celestial cues*

My results amply confirmed the discovery by Koeniger et al. (1982) that *A. florea* can orient its dances when the sky is not visible from the dance floor, and furthermore established that non-celestial visual patterns provide the reference for this orientation. For example, on 9 August 1983 (Fig. 3), bees that had flown to Station 2 (205°) were oriented toward the food when the sky was visible (Fig. 3a;  $\theta=194^\circ$ ;  $r=0.97$ ;  $P \ll 0.0001$ ), and when the sky was blocked from view (Fig. 3b;  $\theta=171^\circ$ ;  $r=0.91$ ;  $P \ll 0.0001$ ). When the striped pattern was rotated 90° clockwise (Fig. 3c), the mean dance angle was shifted clockwise by 105°, to a direction ( $\theta=66^\circ$ ;  $r=0.79$ ) significantly different from the direction of the food, and from the prior orientation relative to either the earth's magnetic field or the comb axis.

In some trials the orientation was less accurate, and was often bimodal. Koeniger et al. (1982) observed a bimodal distribution of dance orientation when they denied bees a view of celestial cues, and speculated that perhaps the bees dancing in different directions were oriented to different cues. This was not the case in my experiments. Figure 4 shows dances observed on 19 July 1983, during an experiment in which the comb and the striped pattern were rotated to various positions with respect to one another and to the direction of flight. As before the dancers were well oriented toward the food when they could see the sky initially (Fig. 4a). After the sky was blocked most dances continued to point in that direction



**Fig. 3 a-c.** Experiment of 9 August 1983; unimodal landmark orientation. Bees were flying to Station 2 (vector F), bearing 205°. Dance orientation is shown relative to the orientation of the comb and striped pattern, as viewed from above. Mean angle of waggle runs and degree of clustering ( $r$ ) are indicated by the direction and length, respectively, of the open vector in each polar plot (length equal to radius of circle corresponds to  $r=1.0$ ). **a** Sky visible; mean orientation of 89 waggle runs (27 dances, a dance being the entire sequence of waggle runs measured for one bee between visits to the food) from 14:18 to 14:42 (all times local solar time) was 194° ( $r=0.97$ ). **b** Bees' view of sky blocked; mean orientation of 126 waggle runs (22 dances) from 14:26 to 14:42 was 171° ( $r=0.91$ ), and was not different from the direction of the food ( $V$ -test;  $P \ll 0.0001$ ). (For **a** and **b** the dancers were observed alternately with and without a view of the sky.) **c** Pattern rotated 90° counter-clockwise, and sky blocked from dancers; mean angle of 51 waggle runs (10 dances) from 14:43 to 14:56 was 66° ( $r=0.79$ ), and was significantly different from the direction of the food. The dashed radial lines labeled **a** and **b** show the orientation relative to the striped pattern of the dances in **a** and **b**, respectively. Scale: smallest bars indicate 1 waggle run

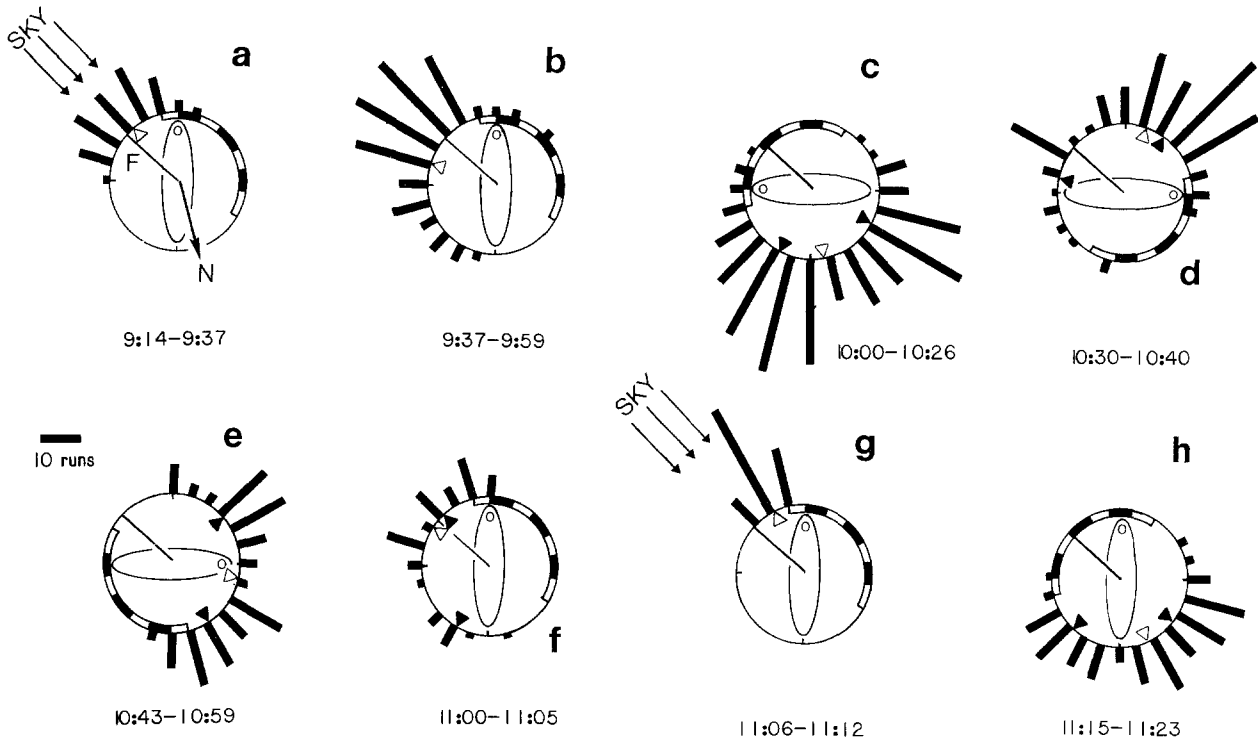
(Fig. 4 b), but several waggle runs also pointed in a direction counterclockwise of the main direction, producing a skew in the distribution. When I began to perform further manipulations this skew increased and became a second mode of the distribution of dances, oriented approximately 120° with respect to the orientation of the first mode. With various rotations of the striped pattern and the comb the two distributions of waggle runs maintained their angles relative to the striped pattern, and never remained faithful to a particular compass direction (such as the direction of the food) or to a particular slope of the comb (Fig. 4 c, d, e, f, h).

These experiments rule out any role for the earth's magnetic field or for slope (hence, gravity) in allowing bees to orient in the absence of celestial cues, at least in this experimental situation. Indeed, in all tests of the sort I have described above, performed on 4 different colonies, bees always shifted their dance angles when the striped pattern was shifted, even if it meant dancing in a different compass direction and at a different angle relative to the comb axis (hence on a different slope). As shown in Fig. 5 a, a summary of all 29 tests in which bees dancing without a view of the sky were

presented with a shift in the orientation of the striped pattern (e.g., Fig. 4b-f), there is a close correspondence between the degree of shift of the pattern and the degree of shift of the overall distribution of wagging angles. Furthermore, the evidence clearly indicates that the bimodal dances cannot be explained by invoking a different feature of the environment (such as the earth's magnetic field, slope, or even patterns of polarized skylight linked to the sun's position) to account for the orientation of one group of dancers. A summary of 18 tests (a subset of the 29 in Fig. 5 a) in which the overall distribution was divided into two obvious modes shows that both groups of dance angles were always affected in the same way by the shift in the pattern (Fig. 5 b).

Analyses of individual dancers revealed considerable variability in the tendency to perform bimodal orientation, or to remain faithful to one of the two directions, but provided no hints as to the specific causes of the bimodal distribution (Dyer 1984). Given my rather crude experimental apparatus, two possible explanations for bimodal orientation come to mind. First, changes produced in the pattern of illumination inside the hut when I blocked the bees' view of the sky sometimes could have influenced dancers as they tried to match their current view of the striped pattern with that remembered from previous dances. Second, the large angle subtended by the pattern (135°) could have produced an ambiguity by allowing bees to match their remembered image of the pattern with their current image in more than one way. Of course, the ambiguity could have been caused by a combination of these factors or by something else. It must be emphasized, however, that the bimodal response to the pattern does not detract from the conclusion that bees oriented their dances to landmarks when denied celestial cues. In fact, an interesting outcome of these observations is the implication that the rules by which *A. florea* orients to visual cues might be probed by specific alterations of the landmarks which produce responses such as bimodal orientation.

Once it became clear that all dances performed in the absence of the sky were oriented to the striped pattern, I removed the pattern and observed whether the dances continued to be oriented. For these experiments I used an arena with eight evenly spaced viewing slits, so that dances could be viewed from any side and yet my head would not be visible to the bees. Furthermore I screened with a white curtain the window through which the sky had been visible, so as to make the distribution of light inside the hut more uniform.



**Fig. 4 a-h.** Experiment of 19 July 1983; bimodal landmark orientation. Waggle runs performed by bees flying to Station 1 (vector F, labeled in a), bearing  $145^\circ$ . Sky visible to bees during dances in a and g, otherwise blocked from view. When the sky was blocked, the comb and striped pattern were set in various positions relative to each other and relative to North (also indicated in a). Dances were sometimes distributed bimodally when the sky was not visible, but the two modes were always oriented in the same way relative to the striped pattern. In each circular histogram the mean orientation of the overall distribution of waggle runs is shown by the open arrowhead at the perimeter of the circle. When the distribution could be divided (by eye) into two obvious modes, the mean orientation of the waggle runs in each mode is shown by the position of a filled arrowhead. The  $r$ -values for the overall mean angles (open arrowheads) are as follows: a 0.92; b 0.82; c 0.65; d 0.63; e 0.60; f 0.68; g 0.99; h 0.65. All distributions are significantly non-random in orientation ( $z$ -test;  $P \leq 0.0001$ ), but there is no consistent relationship to the actual compass bearing of the food, or to the alignment of the comb

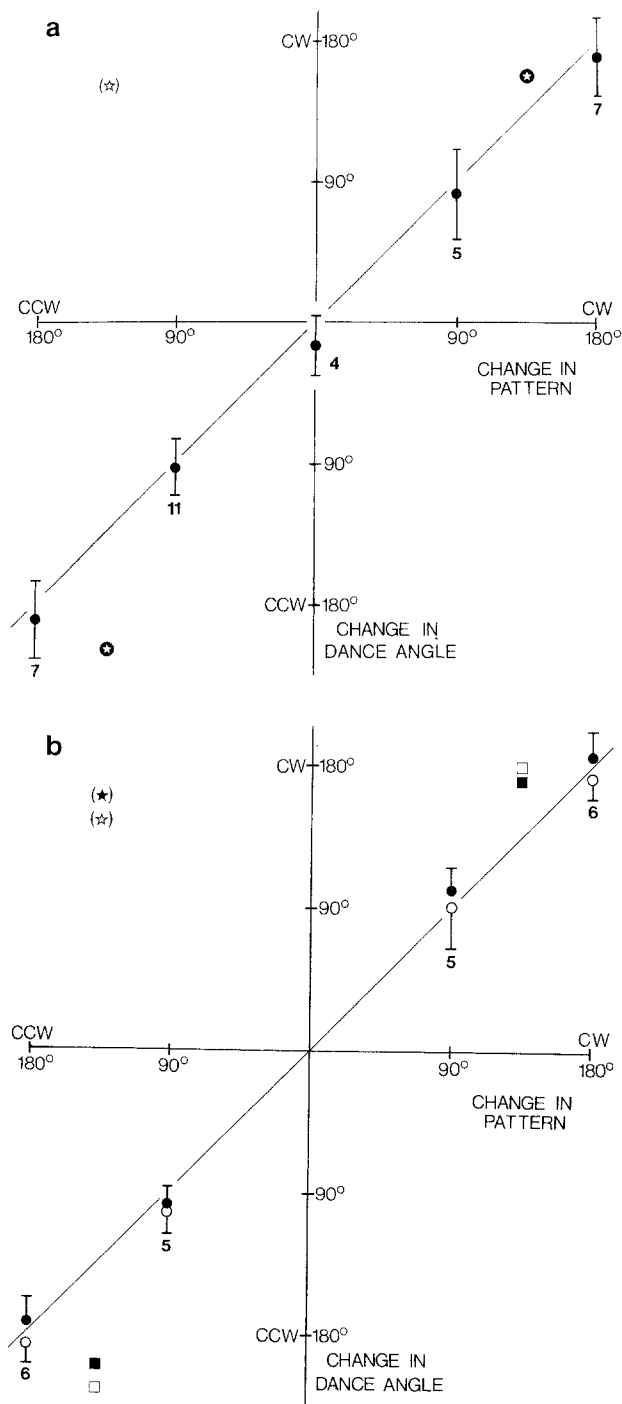
Also, I denied the bees on the colony a view of the sky for two days before observing their orientation without the pattern.

During one series of tests (Fig. 6), the bees tended to be oriented in one direction, about  $70^\circ$  clockwise of the direction of the food, albeit with considerable scatter. This orientation persisted when I changed my viewing angle, indicating that the bees were not cueing on me, and also when I changed the orientation of the comb, indicating that the part of the comb on which they were dancing had no influence on their orientation (Fig. 6 a-c). However, I was able to alter the distribution of dances by casting a shadow on the ceiling of the hut above the dancers. Though I had tried to make the light distribution uniform, a gradient of light still existed, so that the ceiling was brighter toward the window. When I disrupted this gradient by further reducing the light from the window, dances performed over the next 50 min were no longer oriented toward the direction of the food, though there was still a slightly non-random net

orientation ( $z$ -test;  $P < 0.01$ ). During another series of tests there was also a slightly non-random orientation over 1 h of observation, but it was actually in the direction *opposite* the food, hence eliminating geographical cues as a possible explanation for the orientation (Dyer 1984). The most reasonable interpretation of these observations is that the bees were oriented to the slight gradients of light that I could not eliminate, perhaps by matching asymmetries in the light distribution with visual patterns learned previously; the changes observed in the orientation can be attributed to changes in the patterns of illumination over the day. In any event these results reinforce the conclusion that dancing bees rely primarily upon non-celestial visual patterns for orientation when celestial information is unavailable.

#### *Orientation of vertical dancers to celestial cues*

My experiments have confirmed Lindauer's (1956) conclusion that *A. florea* does not transpose light

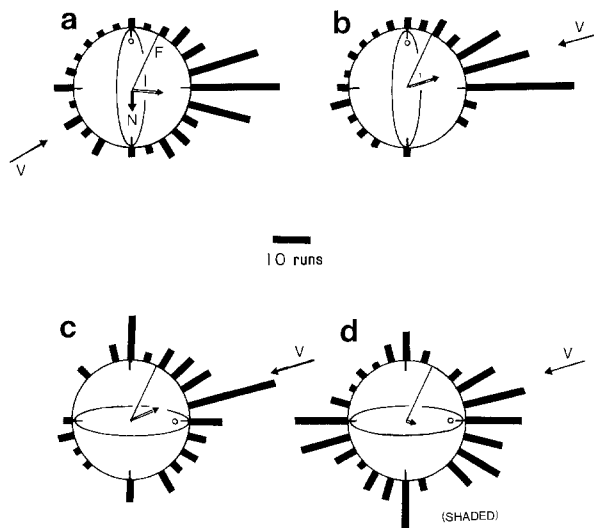


**Fig. 5 a, b.** Summary of landmark rotation experiments with *A. florea*. **a** Change in the mean dance angle in all 29 experiments in which bees dancing without a view of the sky were presented with a clockwise (CW) or counter-clockwise (CCW) rotation of the striped pattern. The diagonal line indicates the predicted shift of the dance angle if the dancers are oriented to the pattern. In a given experiment the overall mean dance orientation (measured waggle run by waggle run) was compared with the mean orientation in the most recent previous observation period. Each data point is the mean shift (error bar representing one standard angular deviation) recorded for all experiments in which the pattern was rotated to the same direction and degree. A total of 2902 waggle runs was recorded in the 29 experiments. The data points corresponding to 180° shifts of the pattern are identical, and can be read either as a 170° CW change in the dance angle or as a 190° CCW change. The star symbols are the means from two single experiments in which the pattern was shifted 135°, once CW and once CCW. The change in the dances in the latter of these experiments has been plotted twice, at 152° CW (symbol in parentheses) and at 218° CCW, which is closer to the predicted shift. **b** Change in the means of separate modes of bimodal distributions, the modes being plotted individually for the 18 experiments in which two could be easily discerned. Solid symbols represent the shift of the dance angle relative to the pattern that was oriented toward the food when the pattern was in its starting position. Open symbols represent the shift of the secondary mode in the distribution. Square symbols in **b** correspond to stars in **a**

and gravity to orient dances in a vertical plane, and have gone on to reveal consistent patterns of orientation which suggest that this species may possess a specialized system of information processing that is used for dances on non-horizontal planes. This system hints at a fundamental divergence within the genus *Apis* in the processing of celestial and gravitational cues.

In the initial experiments, when the plane of

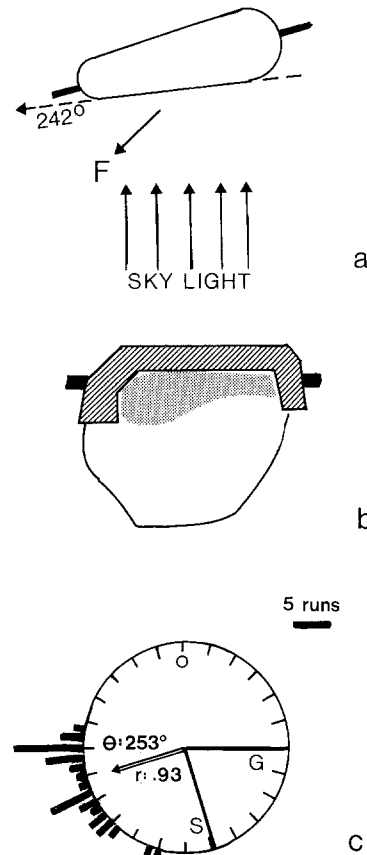
the vertical dance floor was oriented approximately parallel to the line of flight, dances were oriented so that the bees essentially 'pointed' at the food. The dances shown in Fig. 7 were performed on 3 September 1983 from 10:24–10:30 (solar time), when the comb was in this position. At this time the direction of flight to the food (205° clockwise of North) was 90° clockwise of the sun's azimuth. Dances that transferred to gravity the horizontal



**Fig. 6 a–d.** Experiment of 26 August 1983; neither sky nor striped pattern available. Arrow labeled 'V' indicates direction from which the dancers were viewed. Mean orientation and degree of clustering of the dances are shown by direction and length, respectively, of the arrow in each plot. Vector F (labeled in a) gives the direction of food (Station 2). **a** Mean orientation of 122 waggle runs (17 dances) from 11:16 to 11:33 was 70° clockwise of F ( $r=0.53$ ). **b** Viewing angle changed; mean of 101 runs (13 dances) from 11:34–11:48 was 48° CW of F ( $r=0.56$ ). **c** Comb rotated 90° CW; mean of 107 runs (18 dances) from 11:43 to 11:52 was 43° CW of F ( $r=0.54$ ). **d** Shade produced on ceiling above colony; mean of 167 runs (26 dances) from 11:59 to 12:51 was 122° CW of F ( $r=0.18$ ). Orientation in a, b, and c was significantly clustered in the direction of F ( $V$ -test;  $P \leq 0.0001$ ); in d there was no significant clustering toward F ( $V$ -test) but orientation was non-random ( $z$ -test;  $P < 0.01$ )

angle of flight relative to the sun, according to the formula used by *A. mellifera* and the other species, should have been oriented at a corresponding angle relative to gravity (vector G in Fig. 7), but instead the mean angle of the waggle runs was 107° counter-clockwise of vertically upwards.

Nor do *A. florea* dancers respond to celestial cues in the way that would be expected if they were to match their view of the sky during the waggle run with the view learned during the outward flight, which is what *A. mellifera* tends to do when dancing on a vertical surface with a view of the sun or blue sky. If the sun is visible, *A. mellifera* dancers seem to ignore gravity altogether, and instead set their angles according to the projection of the sun onto the vertical plane; as if on a horizontal plane, they align their dances so that the sun is seen from the same point of view as on the flight to the food (von Frisch 1962; Edrich 1977). If only blue sky is visible, dancers either continue to ignore gravity (Edrich 1977) or they adopt a dance angle intermediate between the angle that would be performed to gravity alone

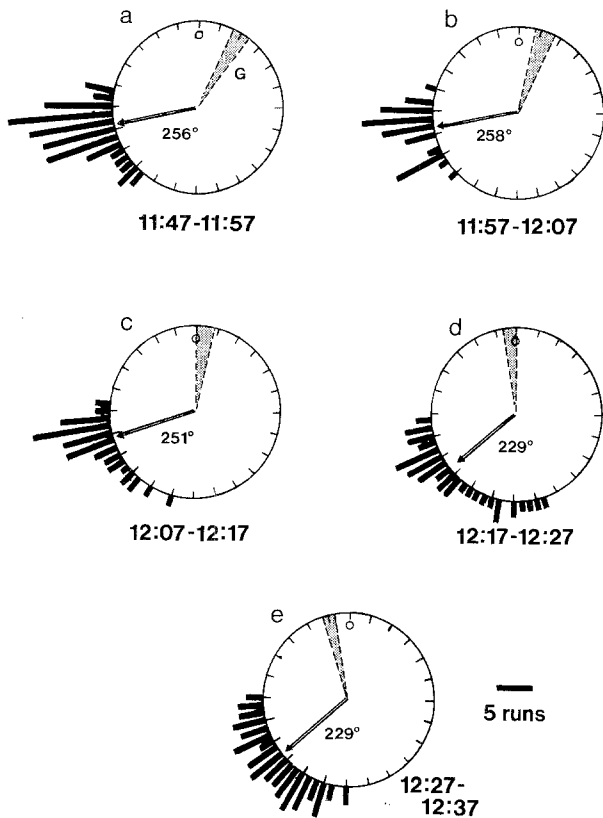


**Fig. 7 a–c.** Vertical dances on 3 September 1983 relative to sun and gravity. **a** Horizontal orientation of comb axis (seen from above) and direction of food, F (205°), shown relative to the patch of sky visible to the bees (azimuth 149°; elevation 22°). **b** View of the side of the colony, stippled region showing location of most of the dances. Hatched area represents a cardboard cap that excluded bees from the top of the comb. The black bar extending from the comb in a and b represents the twig from which the comb was suspended. Length of the colony along the twig was about 18 cm. **c** Polar histogram showing waggle runs of 7 dances relative to vertical (O) from 10:24 to 10:30. Vector G: dance angle expected if bees transferred the horizontal angle of flight relative to the sun's azimuth (115°) to a vertical angle relative to gravity. Vector S: angle expected if bees oriented to projection of the sun on the vertical surface so as to match the view on the flight. Scale bar: 5 waggle runs

and that that performed relative to the sun's projection (von Frisch 1962, 1967). *Apis florea* did not use the sky in this way, since the actual dance angles deviated considerably from the angle bees should adopt relative to the sun's projection onto the vertical plane (vector S in Fig. 7).

In addition, the dance angle for a given food source does not change much over the day, although a change would be predicted by both the sun-gravity transposition hypothesis and the matching hypothesis. The vertical dances of *A. mellifera*, *A. cerana*, and *A. dorsata* compensate





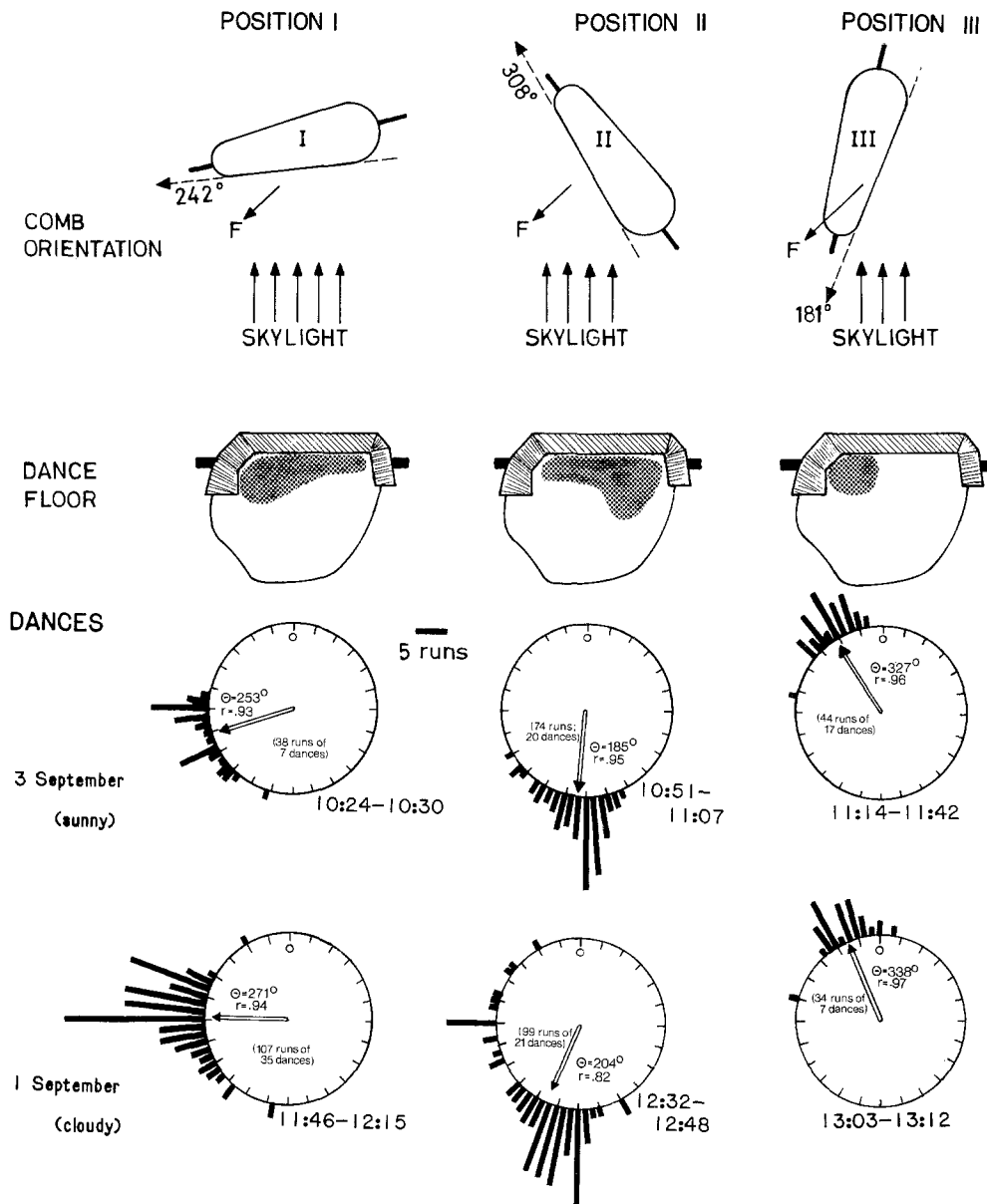
**Fig. 8 a–e.** Vertical dances on 3 September near noon. Comb in same position as in Fig. 7. Data are divided into 10-min intervals from 11:47 to 12:37. In each plot the stippled wedge (labeled ‘G’ in a) represents dance angles expected over the interval if *A. florea* transferred its flight angle to gravity as *A. mellifera* does. This predicted angle sweeps counter-clockwise as the sun moves. The  $r$ -values for the mean orientation in each interval are as follows: **a**  $r=0.97$ ; **b**  $r=0.97$ ; **c**  $r=0.96$ ; **d**  $r=0.89$ ; **e**  $r=0.91$

for the shift of solar azimuth relative to the fixed direction of flight by precessing to the same degree relative to the direction of gravity (or relative to the sun’s projection if the sky is visible to the dancers). The dances of *A. florea* did not change according to this prediction, although they did shift slightly. Figure 8 shows dances on 3 September over 5 consecutive 10-min periods around local noon, when the change in solar azimuth was most marked. At first the dance angle was approximately the same as it was earlier in the morning (cf. Fig. 7), and this angle was maintained over the next 30 min. Then, at 12:17 (Fig. 8 d) the mean angle of the dances shifted counter-clockwise by about 20°, and *this* angle was maintained for the next 20 min, and was seen also later in the afternoon. From the beginning of this 50-min period, however, the sun’s azimuth had shifted by 55°, and since 10:24 (Fig. 7) it had moved 108°. The foragers surely could have

witnessed solar movement on successive flights, but they did not shift their dances to a corresponding degree relative to gravity. Moreover, neither the actual dance angle nor the degree of shift seen corresponded to what would be predicted were the bees to match their view of celestial cues with what they remembered from the flight (predictions not shown).

The shift that did occur indicates that the bees might have been influenced in their orientation by some change in the patch of sky that they could see. However, I calculated the angle of the e-vector of the polarized light that would have been visible to them at that azimuth (149°) and elevation (22° above the horizon), and found that it rotated less than 2° – from –84° to –82° (the negative sign means the angle is counter-clockwise from vertical) – between 11:47 and 12:27. Although the mechanisms of orientation to polarized light in this species remain unexplored, the change in the e-vector hardly seems sufficient to account for the 20° shift of the dances. In fact, the change in the e-vector between 10:24 (+78°) and 12:25 (–84°) was much greater, and yet was accompanied by virtually no shift in the dance angle. Despite these difficulties, however, it seems safe to conclude that the orientation of vertical dances to a given source of food with the comb in one position will remain approximately constant despite the movement of the sun relative to the direction of flight.

The dancers whose behavior I have described so far all viewed the same patch of sky with the vertical plane in the same compass orientation. The relative stability of their dance angles over the day suggests that a given orientation on the dancing surface gives equivalent information at all times of day regarding the direction of a fixed source of food. The same holds true when *A. florea* (and any of the other species of *Apis*) dances on a horizontal surface – dances to one source of food maintain the same compass angle though the references for orientation (the sun and sky) rotate. To study further this parallel between *A. florea*’s horizontal and vertical orientation, I rotated the colony so that the same patch of sky was viewed at a different angle relative to the vertical plane. *Apis mellifera*’s dances that are oriented to gravity, or to the sun’s projection onto the vertical surface, are little affected by this manipulation. My preliminary observations had suggested that *A. florea*’s dance orientation would be greatly affected; since dances to the same food source presumably give equivalent information, different orientation on different vertical planes would be further evidence of a distinct strategy of information processing in the ver-



**Fig. 9.** Vertical dance orientation with comb rotated to different alignments. Top row shows the comb in three orientations, viewed from above (F indicates direction of food). Second row shows location of dances on the side of the colony in each of the three positions. Bottom two rows show orientation of waggle runs with the comb in each position on two different days, one sunny (3 September; third row) and one overcast (1 September; bottom row). When the bees viewed the same patch of sky from different perspectives they shifted the location of their dances on the nest and also shifted their dance angles relative to vertical

tical dances of *A. florea*, and could provide insights into the nature of the processing.

Figure 9 shows the dances performed when the comb was at three different orientations relative to the line of flight to the food (top row). In each case I began recording the dance angles (bottom two rows) immediately after shifting the colony from one alignment to another. The data confirm that there is no consistent correspondence between the dance angles that *A. florea* adopts on a vertical

surface and the dance angle expected either for matching of visual cues with information remembered from the flight or for light-gravity transposition. Instead of remaining oriented at an approximately constant angle relative to gravity, the bees shifted their dances dramatically when viewing the sky from differently aligned vertical planes. I have already discussed the orientation seen in the left column of Fig. 9, when the axis of the comb was in position I, approximately par-

allel to the line of flight. With the comb in position II (middle column), dances were performed on the same side of the comb as the food, which was in a direction nearly perpendicular to the plane in which the dances occurred; in this case the dances pointed downwards. This situation can be seen commonly in any *A. florea* colony. As discussed, dancers tend to cluster to the side of the vaulted top surface that is closest to the direction they are indicating, hence waggle runs often are performed on steep, even vertical, slopes, and are directed downwards. The situation in the right column (comb in position III), in which the dancers must indicate the direction of a food source on the opposite side of the nest, is probably rare in wild colonies. However, the dances were equally well clustered, and pointed upwards.

One perplexing fact is that the sky was overcast the very first time I forced bees to dance on the vertical side of the colony, and yet they performed just as I have described for the sunny day (Fig. 9, bottom row). A cloud cover usually depolarizes skylight completely (Brines and Gould 1982), but it is possible that openings in the clouds that I could not detect provided polarized light that the bees could use for orientation. Alternatively, because the colony had been in this site for 2 weeks, and had been used for other experiments in which sky cues were not available to the bees, it is also possible that the bees' memory of the location of the bright patch of sky could have provided an orientational reference in the same way that the striped pattern had previously.

## Discussion

The results of these experiments reveal a system of dance orientation in *A. florea* that is considerably more complicated than was originally assumed. Indeed, instead of possessing a system that is merely a simpler version of that exhibited by the other species of *Apis*, it now appears that *A. florea* has diverged from the others in fundamental ways, and depends upon information processing that is at least equally elaborate. Still, however, this divergence seems to be rooted in the dichotomy first described by Lindauer (1956): the tendency of *A. florea* to orient its dances to projections of celestial cues in the horizontal plane, whereas the other species mainly rely upon orientation to gravity in the vertical plane, with the 'option' of orienting to projections of celestial cues. In the following sections I discuss the insights into *A. florea*'s dance orientation that have emerged from this study.

## Landmark orientation of waggle dances

Ever since von Frisch first worked out the basic rules by which *A. mellifera* communicates the location of food, only gravity and celestial cues have been known to orient waggle dances (von Frisch 1946, 1949, reviewed 1967), and *A. florea* was thought only to use the latter (Lindauer 1956). (The earth's magnetic field can influence dance orientation, but is not known to serve as a reference for communication.) Now it appears that *A. florea* can orient its dances to a completely different feature of the environment, one that seems eminently suited to this bee's habit of nesting in thick vegetation (Seeley et al. 1982), where conspicuous visual patterns are likely to be visible immediately above and around the nest. Obviously more experiments need to be done to determine how precisely *A. florea* can orient to visual patterns like those which might actually exist around a typical nest in the wild. Moreover, the efficacy of this orientational strategy in recruitment must also be studied. (Recruits always appeared in large numbers during my experiments, and all were caught by an assistant, but I made little attempt to control for the possible role of odor in attracting these bees to the feeding station.) Still, it is reasonable to conclude that orientation to landmarks visible from the dance floor is distinct from orientation to celestial cues or to the direction of gravity.

Although several of the details remain to be worked out, it is possible to contrast the use of landmarks by *A. florea* in this context with other examples of orientation to landmarks by animals which forage from a central place. A number of ants have been reported to be able to learn their way to a food source and back home by landmarks visible en route (e.g., Jander 1957; see also Wehner 1981 for review), and at least one species can learn the patterns of canopy vegetation overhead (Hölldobler 1980), which are probably similar in complexity to the landmark patterns normally available to *A. florea* dancers. *Apis mellifera* also may rely heavily upon landmarks to find the food, even to the extent of ignoring sun compass information (von Frisch and Lindauer 1954; Dyer and Gould 1981). In each of these examples of 'piloting' the insect requires only landmarks in order to orient adaptively, although it might also be able to use other sets of cues when they are available. *Apis florea*'s use of landmarks in the dance is superficially similar, since the dancer adopts a consistent orientation relative to landmarks in indicating a given food source. However, it is not the landmarks that provide the actual reference for

dance communication, but rather it is the sun and blue sky. Dancers normally compensate for celestial rotation, adopting a consistent compass angle in successive dances to a given food source, and so fixed landmarks near the nest offer a reliable substitute when celestial cues are blocked from view. But whereas piloting ants may not even need the sky for orientation (Hölldobler 1980), *A. florea*'s dances in the presence of landmarks are meaningful only in reference to the sky. In turn, this implies that bees memorize the relationship between such landmarks and the sun's course.

Hence, nest site landmarks may play a role in *A. florea*'s dances that is analogous to the role that broad features of the landscape have been found to play in allowing *A. mellifera* and *A. cerana* foragers (Dyer and Gould 1981, 1983; Dyer 1984; ms. in preparation) to determine their direction of flight relative to the sun when overcast blocks celestial cues from view. These species can memorize the position of the sun in relation to landmarks which they use to fly to the food, and this memory is compensated for solar movement during the day (and perhaps into the night for the Asian bee *A. dorsata*, which may forage at night but still references its nocturnal dances to the sun; Dyer 1985). In fact, *A. florea* too must have a similar ability to memorize the sun's course in relation to features of the landscape. Such an ability probably plays a general role in sun compensation (Beier and Lindauer 1970; Dyer 1984), but in addition *A. florea* presumably relies upon this memory, as *A. mellifera* does, to determine the direction of flight relative to the sun in order to communicate this information after a flight under overcast (as I have often seen this species do). Then, of course, the forager might have to rely upon her ability to set a dance orientation relative to landmarks if celestial cues are still not available upon her return to the nest.

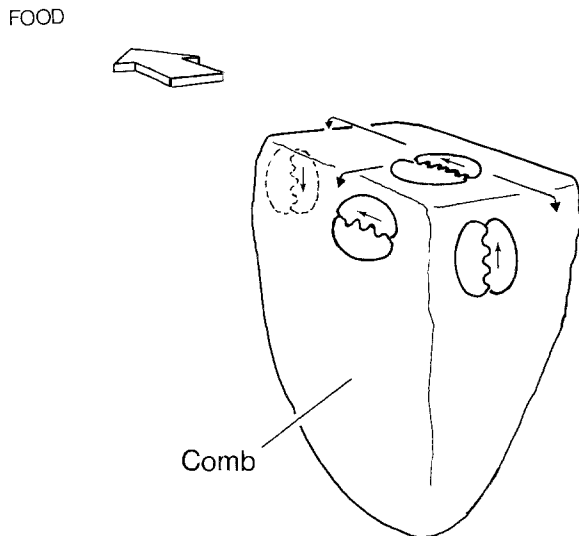
These considerations suggest one striking difference between *A. florea* and the other species (as the other three are understood mainly through work on *A. mellifera*) in the processing of orientational information on cloudy days. While foraging, *A. florea* probably determines its angle of flight relative to the sun as *A. mellifera* does, by referring to a time-linked memory of the sun's course relative to landmarks seen on the flight. Having determined the sun's location, however, *A. mellifera* needs process during its dance only information regarding its body position relative to gravity, employing the innately defined rule that a dance vertically upward means the food is toward the sun. *Apis florea*, by contrast, must rely

upon an additional learned relationship in each nest site – that between the direction of the food, the sun's azimuthal course, and landmarks visible from the dance floor, which would be different from those visible en route to the food. A given bee might live in only one site in her life, but the bees in each swarm that left the colony and settled elsewhere would have to learn both a new landscape and a new set of canopy patterns above and around the nest. Recruits face an equally formidable task, since to follow the dances on cloudy days they must have previously learned the sun's relationship both to the orientation of landmarks visible from the dance floor and to the orientation of landmarks that are visible once they fly from the colony.

Though it remains to be seen whether the three other species of *Apis* can orient their dances to landmarks under unusual circumstances, it now seems inappropriate to regard *A. florea*'s dance as handicapped in comparison to the other species with respect to the absence of celestial cues. Indeed, since the sun's course must be learned with respect to two sets of landmarks in any nesting site, *A. florea*'s system seems one step more sophisticated. On the other hand, *A. florea* is probably still constrained to nest where it has a view of the sky (whereas the other species, including *A. dorsata*, are not; Koeniger and Koeniger 1980), because the landmark system for dance orientation seems to require occasional reference to celestial cues. In any event, given the normal nesting habits of *A. florea*, it is clear that this modification of the information processing underlying the dance language could endow *A. florea* with the same sort of flexibility that *A. mellifera*, *A. cerana*, and *A. dorsata* possess in their ability to orient waggle dances when the sun is not visible during the dance.

#### *Orientation of waggle dances on a slope*

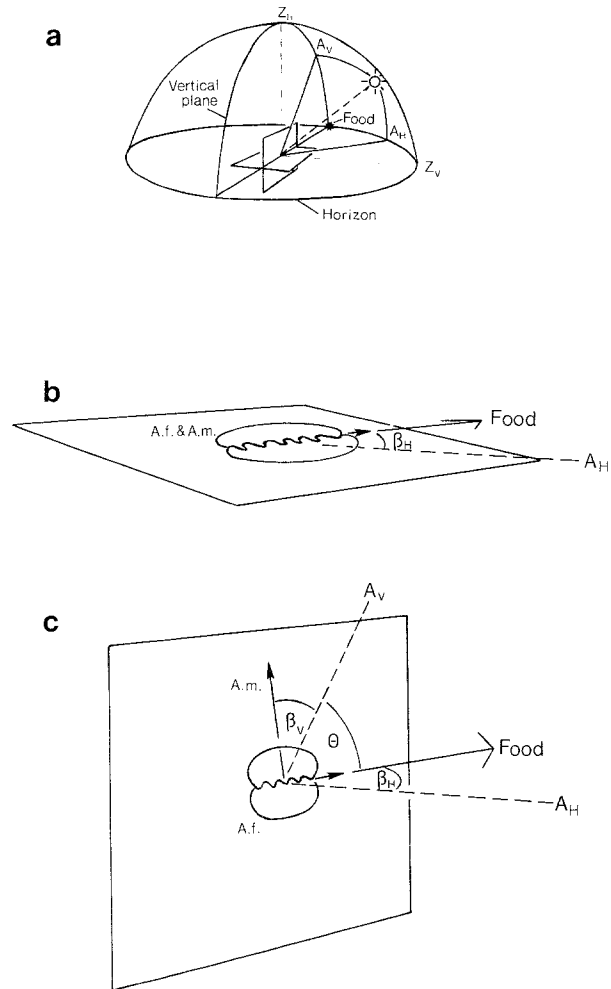
The patterns of dance orientation on vertical planes imply an even more fundamental divergence between *A. florea* and the rest of the genus. The patterns are summarized in Fig. 10, which is based on the data in Fig. 9 and shows a schematized comb to simplify the relationships between dances on horizontal and vertical surfaces. The dance orientations that I observed can be reproduced if one imagines a bee to be able to maintain her dance angle with respect to any given line on the dancing surface when the horizontal plane is rotated to a vertical position of any given orientation relative to the line of flight. Each figure-eight shape in Fig. 10 represents the form of the dance, with the



**Fig. 10.** Summary of horizontal and vertical dance orientation of *A. florea*. This schematic representation, based on the data in Fig. 9, suggests that dances on a vertical plane of a given compass alignment are related in a specific way to the angle of a dance on a horizontal surface to the same source of food. Short arrows represent orientation of the waggle run in the dance. If the horizontal plane is rotated in the direction indicated by each of the long arrows, the dance angle relative to the axis of rotation will remain the same. If the vertical plane is rotated to another alignment, the dance angle must change relative to the axis of rotation to give equivalent information

short arrow indicating the direction of the waggle run. If the horizontal plane is rotated around a horizontal axis to any of the three vertical orientations shown, or rotated back again, the dance angle relative to the axis of rotation (or relative to any line on the plane) will not change. By contrast, if, as in my experiments, a vertical plane is rotated around a vertical axis to a different compass alignment, the dance angle relative to the axis of rotation (hence, relative to gravity) must change. Therefore, although dances on differently aligned vertical planes give equivalent information about the direction of the food, the equivalence is apparent only through their common relationship to the horizontal plane.

The original angle on the horizontal surface is the same as the direction of flight, and is set by the dancer relative to the sun, blue sky, or non-celestial visual cues. However, my experiments showed that bees need not dance first on the horizontal plane in order to use such visual information to orient their dances on a vertical plane. Hence they apparently possess a mechanism that allows them to compensate automatically for slope. As I have argued, this mechanism must be very different from the mechanisms used by



**Fig. 11 a-c.** Comparison of horizontal and vertical dances of *A. mellifera* and *A. florea* when each is oriented to the sun. Top diagram (a) shows the geometry of the celestial sphere in relation to an observer (a bee dancing to a food source) on either a horizontal or a vertical plane at the central location. Actual zenith is indicated by  $Z_H$  and the apparent zenith to an observer on the vertical plane is  $Z_V$ . The diagrams below show dances on (b) horizontal and (c) vertical planes alone. Wagging form is shown with a short arrow pointing in the direction being communicated. The orientation attributed to *A. florea* is extrapolated from the results in Figs. 7-9. Though *A. mellifera* and *A. florea* should adopt an identical angle ( $\beta_H$ ) relative to the solar azimuth ( $A_H$ ) on the horizontal plane, they adopt very different angles ( $\beta_V$  for *A. mellifera* and  $\theta$  for *A. florea*) relative to the sun's projection onto the vertical plane. Situation in this figure is a simple one, with food located on a line formed by intersection of the two planes, but this analysis yields similar results for other locations of the food and for dance orientation to polarized skylight or to non-celestial visual patterns

*A. mellifera* when dancing on a vertical surface with a view of celestial cues. Figure 11, a hypothetical situation based on the patterns observed in this study, makes this difference more explicit.

When a honey bee of any species performs a

waggle dance on a horizontal surface, she adopts a body angle ( $\beta_H$ ) with respect to the sun's azimuth ( $A_H$ ), its projection onto the horizontal plane. On a vertical plane she obviously will see the sky from a different point of view, and the azimuth of the sun is now its projection onto the vertical surface ( $A_V$ ). If the bee is to adopt the same angle relative to the sun which she witnessed while flying to the food (or while dancing in the horizontal plane), she must orient to this transposed azimuth (body angle:  $\beta_V$ ). As I have discussed, this 'matching' is precisely what occurs when *A. mellifera* dancers on a vertical surface have a view of the sky; gravity is ignored and the sun's projection is used instead, sometimes even if only blue sky is available (von Frisch 1962, 1967; Edrich 1977). By contrast, the angle ( $\theta$ ) that an *A. florea* dancer would adopt relative to the projected azimuth of the sun with the comb, sun, and food positioned as shown in Fig. 11 would expose her to a completely different view of the sun from that which she would have seen during her flight or during a dance in the horizontal plane. Thus, it is difficult to explain *A. florea*'s orientation as sensory matching, whether one considers a bee's view of the sun, patterns of polarization, or even a landmark such as the bright patch of cloudy sky available to the dancers at one point in my experiments (Fig. 9 bottom row).

And yet it seems likely that *A. florea*'s orientation on a vertical surface is guided by visual cues. The dramatic shift in the mean dance angle when the vertical plane of the dance floor was rotated (Figs. 9 and 10) is most readily explained if the bees compensated for the different perspectives from which they had to view celestial (or landmark) cues during their dances. One means of compensating would be to take account of gravitational information in setting the dance angle relative to visual cues. The patterns in the vertical dances, as summarized in Fig. 10, suggest that *A. florea* dancers refer directly to the horizontal world even when on a slope. Perhaps the bees sense their body position relative to gravity, measuring slope, and then adjust their orientation relative to visual cues by an appropriate amount.

A striking correlation that supports the idea that gravity is involved in the vertical dances is apparent in Fig. 9. The angle of the dances relative to vertically downward is remarkably close in all cases to the angle between the food's direction and the direction perpendicular to the plane of the dancing surface. Hence, with the direction of the food perpendicular to the dance plane (position II), the dancers were oriented straight down;

with the comb in position I, 66° counter-clockwise of II, the mean dance angle was shifted relative to the dance orientation at position II by 68° on 3 September and 67° on 1 September; and with the comb in position III (127° from II), the mean dance angle differed from that in position II by 142° and 134° on the two days. This correlation could be construed as evidence of a 'convention' by which *A. florea* orients to gravity (e.g., 'down = perpendicular to the dance plane'), but it seems most prudent at this point simply to conclude that vertical dance orientation could involve an integration of visual and gravitational information. What needs to be established now is whether dancers and recruits can actually measure the compass alignment of the plane on which they are standing, and how they might measure the direction and degree of slope during the dance.

Two other considerations support the notion that *A. florea* could process gravitational information in setting its dance angles. In the first place, it can orient its body to gravity in other behavioral contexts. When forced to run on planes of varying slope, all four species of *Apis* show strong negative geotaxis, but *A. florea* differs from the other three in that the scatter around the mean uphill orientation of a group of bees decreases as the incline is increased, whereas there is no such change for *A. mellifera*, *A. cerana* and *A. dorsata* tested in the same way (Jander and Jander 1970; Horn 1973, 1975). Although the biological significance of the specific responses to varying slope is unclear, these results show that *A. florea* can process information about gravity, and that it responds to gravity in a manner that is qualitatively different from the responses of the other species in the genus. Perhaps it should not be a surprise if *A. florea* also employs gravity in the dance, but does so according to a set of rules completely different from that of the other species.

The second consideration concerns the topography of the dance floor. As I have discussed, the typical colony is usually rounded on top, and sometimes even undulates with saddles and knobs if the wax has been wrapped around the fork of a branch. Furthermore, dances take place on a layer of bees, which in the confusion of vigorous activity sometimes get piled into smaller mounds. As the dancer proceeds across this uneven surface, therefore, its body angle relative to the horizontal plane in which it has flown – and relative to the cues that orient the dance as well as the flight – may change dramatically even from one waggle run to the next. Recruits would face the same potential ambiguities as they followed the dance,

and their difficulties in extracting directional information would be compounded if they were standing on a slope different from that on which the dancer was standing. It would therefore seem essential to the efficacy of the dance for dancers and recruits alike to be able to factor out the slopes on which they are standing when measuring their body angles relative to visual cues. The required compensatory mechanism might be expected to result in a changing influence of increasing slope on simple geotaxis, such as is observed in *A. florea* (Jander and Jander 1970).

The influence of gravity on dance orientation could be tested directly and quickly by glueing small weights to the abdomens of foragers; this has been shown to skew *A. florea*'s geotactic response by altering the stresses on petiolar proprioceptive organs (Horn 1973, 1975). In addition, a systematic study of the interaction of light and gravity in orienting dances, such as Edrich (1977) performed on *A. mellifera*, would not only provide tests of the role of gravity in *A. florea*'s dances, but might also illuminate other mechanisms involved in the orientation of dances on slopes.

Whether or not gravity is involved in orienting *A. florea*'s dances, the existence of mechanisms allowing bees to orient to horizontal projections of celestial cues while on a non-horizontal plane raises additional questions about *A. florea*'s analysis of polarized skylight for orientation. Nearly all studies of this subject have been carried out on *A. mellifera*. The model that is best supported by the available evidence (reviewed by Wehner and Rosell 1985) proposes that the spatial arrangement of e-vector (polarization) analysers in the bee's eye corresponds to the spatial distribution of e-vectors in the blue sky, such that the sensory array is in register with the celestial one – and is maximally stimulated – when the bee is aligned with the solar meridian. The direction of the food is learned and communicated in the dance by reference to the meridian. Hence this model essentially proposes a 'matching' mechanism (albeit with a dynamic component since the solar meridian is presumed to be detected as a peak of stimulation when the bee turns, scanning the sky with her eyes), and explains *A. mellifera*'s horizontal dance orientation as well as the orientation of foraging desert ants, *Cataglyphis* sp. (reviews by Wehner 1982, 1984). But *A. florea* may require additions to this model. I have already discussed the limitations of matching as an explanation for *A. florea*'s orientation to visual cues when dancing on a vertical surface. Moreover, the model as described requires that the bee or ant oriented to horizontal projections of

polarization cues maintain her head at a fixed angle relative to the horizon, but *A. florea* is probably not able to do this on steep slopes. Thus, further study of *A. florea*'s orientation to celestial cues may reveal special mechanisms for the analysis of polarized light, and in any event would broaden our understanding of celestial orientation in insects.

### Conclusion

To conclude I would like to re-emphasize the apparent sophistication of the information processing in *A. florea*'s orientational system, as revealed by this study. Although this species has not been studied to the extent that *A. mellifera* has, we can assume that it is equipped with most of the same navigational abilities that *A. mellifera* employs to find its way afield on sunny and cloudy days. But *A. florea*'s dance, though superficially more 'primitive' because of the more direct reliance on the sky, actually incorporates two striking adaptations which may be unique to this species. With these insights we now have a more complete understanding of the orientation of *A. florea*, and by extension of dance orientation in general. First, *A. florea*'s dances in the horizontal plane are referenced to celestial cues even when such cues are not directly visible to the dancers and must be referred to via landmarks visible from the nest. The other species of *Apis* all can orient to celestial cues in the horizontal plane (Lindauer 1956; von Frisch 1967; see Dyer 1984 for a demonstration of *A. dorsata*'s ability), but are disoriented without a view of the sky unless a slope is available where gravity can provide a reference. Second, even when dancing on a vertical plane *A. florea* continues to use as a frame of reference the horizontal projections of celestial cues. This stands in sharp contrast with the other species, which shift their frame of reference so that the projections of celestial cues onto the vertical plane are employed when the sky is visible during vertical dances.

Apart from raising a host of new questions about the mechanisms underlying *A. florea*'s dance orientation, these results also suggest the necessity of looking anew at the adaptive reasons for the divergence in dance orientation mechanisms within the genus *Apis*. As mentioned, it seems logical that the earliest honeybees resembled *A. florea* in nesting and dancing behavior, orienting horizontal dances to celestial cues directly (Lindauer 1956, 1960; von Frisch 1967; Dyer 1984; see Koeniger 1976 for an alternative view). The evolution of dances that transpose light and gravity is usually

attributed to the presumed advantage of this system in allowing dance communication when celestial cues are not available to the dancer. Future speculation about the evolution of the dance language must take into account not only *A. florea* having apparently evolved a different solution to this contingency, but also the possibility that *A. florea*'s dance orientation strategy employs gravity in a way that is probably incompatible with the use of gravity seen in the other species of *Apis*.

*Acknowledgements.* This work was sponsored by a Fulbright Fellowship while the author was affiliated with the Center for Theoretical Studies, Indian Institute of Science, Bangalore. Pilot studies were supported by the Smithsonian Institution Foreign Currency Program. I thank Drs. Madhav Gadgil, Raghavendra Gadagkar, K.K. Kshirsagar, James L. Gould, Donald R. Griffin, William F. Towne, Rudolf Jander, and John B. Phillips for helpful comments; Mr. W.P. Mahindre, Mr. B.P. Singh, Mr. R.A. Badve, and Ms. E.P. Murdoch for technical help; and Ms. L.F. Jacobs for invaluable assistance in preparing the manuscript.

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