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The bee's map of the e-vector pattern in the sky

(polarized light/astronavigation)

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ABSTRACT It has long been known that bees can use the pattern of polarized light in the sky as a compass cue even if they can see only a small part of the whole pattern. How they solve this problem has remained enigmatic. Here we show that the bees rely on a generalized celestial map that is used invariably throughout the day. We reconstruct this map by analyzing the navigation errors made by bees to which single e-vectors are displayed. In addition, we demonstrate how the bee's celestial map can be derived from the e-vector patterns in the sky.

Even though it has been known for more than 30 years that bees use the pattern of polarized light in the sky (e-vector pattern) as a compass (1), the question of how they analyze the spatial and dynamic characteristics of this pattern still remains to be answered. Due to the general finding that the waggle dances performed by the bees on a horizontal comb are oriented rather exactly, even if the dancers can only view small patches of the polarized sky, it has generally been assumed that bees are able to exploit the e-vector pattern in all its spatial detail (2, 3). However, as already described (4), bees exhibit consistent orientation errors which depend not only on the direction of a given e-vector and the celestial altitude at which it is displayed but also on the time of the day—i.e., on the elevation of the sun. Obviously, the position assumed by the bees for a particular e-vector does not necessarily correspond to its actual position in the sky. From this we concluded that bees might use some generalized, rather than an accurate, map of the sky light pattern (4).

In the present account we reconstruct the bee's celestial map by analyzing the orientation errors made by the bees. Concomitantly, we demonstrate how the e-vector map used by the bees can be derived from the actual patterns realized in the sky. What we suggest is that the bees ignore the spatial details of the e-vector pattern and instead refer to a prominent intrinsic symmetry line of the pattern: the line of maximal polarization.

MATERIALS AND METHODS

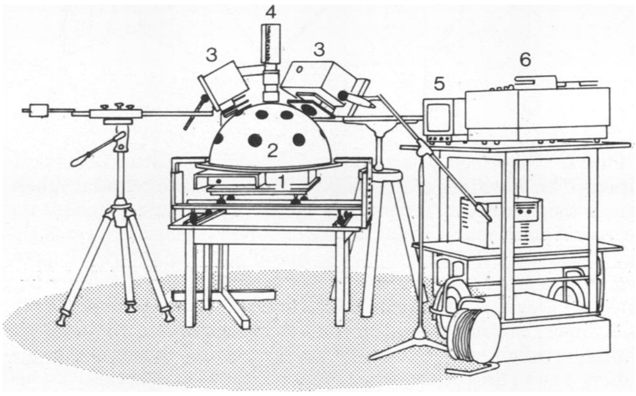

FIG. 1. Experimental setup. 1, Horizontally arranged hive containing a single comb. The hive can be moved in the *x* and *y* directions. 2, Translucent Plexiglas hemisphere (radius, 33 cm); if the apertures (black dots) are opened, either natural sky light or artificially polarized light can be presented to the bees. 3, Xenon arc lamps equipped with heat filters, diffusers, spectral filters, and polarizers. 4, TV camera. 5, Monitor. 6, Video recorder.

Individually marked bees (*Apis mellifera mellifera*) were trained to an artificial foraging station 400 m away from the hive. Having returned from the foraging station, they performed their waggle dances on a horizontal comb in the center of a translucent Plexiglas hemisphere (Fig. 1). This hemisphere depolarized the sky's light completely and thus provided the bees with a homogeneously lit visual surround. Under these conditions the waggle runs were oriented randomly unless the bees were allowed to view at least a single patch of naturally or artificially polarized light through one of the apertures of the hemisphere. When artificial stimuli were used, the light, provided by a xenon arc lamp (400 W), first had to pass through a heat-absorbing filter, a diffuser, a UV filter (UG 11; Schott), and a polarizer (HNP'B; Polaroid) before entering the aperture. The waggle dances were recorded by a video setup and were analyzed later by measuring the directions of the individual waggle runs. To ensure that, while foraging, the bees were exposed to the whole pattern of polarization, all experiments reported here were performed on cloudless days.

RESULTS

In order to understand the bee's celestial map, we first have to deal briefly with the geometry and the dynamics of the pattern of polarized light in the sky. Polarization of sky light results mainly from the scattering of sunlight in the earth's atmosphere. As a consequence, both direction and degree of polarization are strictly related to the position of the sun. Therefore, the e-vector pattern in the sky can be described most conveniently by referring to a sun-related system of coordinates, defined by the great circles that originate in the sun and converge toward the "antisun" (Fig. 2). Note that these great circles mark the planes in which the sunlight is scattered. It follows from the laws of Rayleigh (primary) scattering that the direction of polarization (e-vector direction) is oriented perpendicularly to the plane of scattering, and that the degree of polarization is proportional to some sine function of the angle the earthbound observer forms with the direction of the sun and the celestial point in question.

On the basis of these two rules, the general features of the e-vector pattern can be described as follows. The e-vector directions are arranged concentrically around the sun and the antisun. Originating from these two unpolarized points, the degree of polarization radially increases and reaches its maximum along the equator of the sun-related system of coordinates.

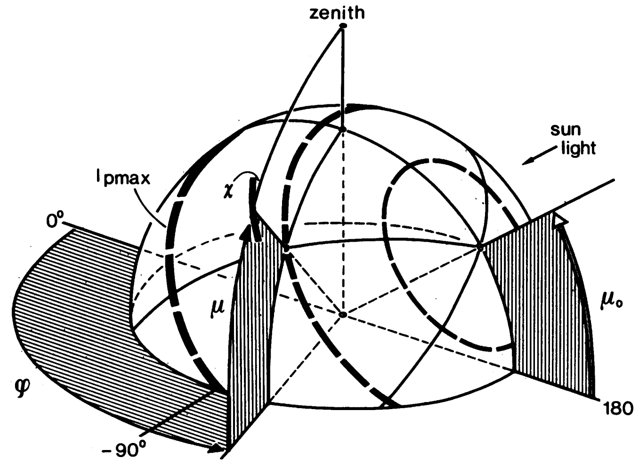

FIG. 2. Pattern of polarized sky light (e-vector pattern) and definitions. The directions of the bars plotted across the celestial sphere denote the e-vector directions; the widths of the bars symbolize the degrees of polarization. Note that the most highly polarized area of the sky occurs at 90° from the sun ($l_{P_{max}}$, line of maximal polarization representing a prominent intrinsic line of symmetry of the e-vector pattern). μ_0, Elevation of the sun. μ, Elevation of a given point in the sky. ϕ, Azimuth position of a given point as measured relative to the antisolar meridian. χ, e-vector direction as measured relative to the meridian. ϕ and χ are positive when counted clockwise and negative when counted counterclockwise.

This line of maximal polarization positioned 90° off the sun and the antisun forms a prominent line of symmetry of the e-vector pattern.

The situation becomes more complicated when the pattern of sky light is described in terms of the terrestrial system of coordinates, defined by meridians converging toward the zenith (Fig. 2). Within this system of coordinates a second line of symmetry is defined by the solar and the antisolar meridian. Because, during daytime, the more highly polarized part of the sky is subdivided by the antisolar meridian, its direction can be used as a reference direction ($\phi = 0°$) for defining the azimuth direction (ϕ) of any point in the sky presented at a given elevation μ. The directions of polarization (χ) are measured relative to the meridians. The directions of those e-vectors that lie along the line of maximal polarization are indicated by $\chi_{P_{max}}$. μ_0 defines the elevation of the sun.

Armed with this knowledge, let us emphasize some important spatial and dynamic characteristics of the e-vector pattern (compare Fig. 3). (*i*) Irrespective of the elevation of the sun, the horizontal e-vectors ($\chi = 90°$) are located exclusively along both the solar and the antisolar meridian (Fig. 3*a–c*). (*ii*) The positions of all other e-vector directions vary as a function of the elevation of the sun. (*iii*) Within the e-vector distribution realized at a given elevation (χ/ϕ function), any one e-vector direction usually occurs twice. The one that is farther from the sun is more strongly polarized than its counterpart closer to the sun (Fig. 3*c*). (*iv*) At least in the upper region of the sky ($\mu > 30°$), the azimuth position of any given e-vector direction lying along the line of maximal polarization ($\chi_{P_{max}}$) varies only slightly during the course of the day (Fig. 3*e*). (*v*) No ambiguities occur within the $\chi_{P_{max}}/\phi$ functions. As the only exception to this rule, the vertical e-vectors ($\chi_{P_{max}} = 0°$) occur twice (opposite to each other and at right angles to the antisolar meridian) (Fig. 3*f*).

Which of these characteristics of sky-light polarization are known to the bees? The question is answered by displaying to the bees single patches (diameter, 10°) of polarized UV light. If the bees were informed about the spatial distribution of the e-vectors in the sky, the waggle dances guided by any one e-vector should be oriented correctly—i.e., they should point toward the feeding station. However, such is not the case. Bees exhibit orientation errors that reflect the difference between the actual azimuth position of the given e-vectors in the sky and the corresponding azimuth position assumed by the bees.

In Fig. 4*a* some examples are given for an elevation of $\mu = 60°$ and elevations of the sun $60° \geq \mu_0 \geq 30°$. During the course of the experiment, different e-vector directions were displayed, including $\chi = 90°$, $+45°$, $-45°$, and 0°. No orientation errors occurred when horizontal e-vectors ($\chi = 90°$) were presented. The bees always interpreted them as lying along the antisolar meridian, as actually is the case in the natural sky (Fig. 4*a*, top row). As the sun decreases in elevation from $\mu_0 = 60°$ to $\mu_0 = 30°$, the actual azimuth positions of the e-vectors $\chi = +45°$ ($-45°$) as measured relative to the antisolar meridian ($\phi = 0°$) change from $\phi = -85°$ ($+85°$) to $\phi = -55°$ ($+55°$), but the bees invariably expect the $+45°$ ($-45°$) e-vectors to occur at $\phi = -50°$ ($+50°$) (Fig. 4*a*, middle row). The vertical e-vectors ($\chi = 0°$) are always assumed to lie at right angles to the antisolar meridian (and thus opposite to each other), even though in the natural sky they change their position continuously during the course of the day (Fig. 4*a*, bottom row). This stereotyped assignment of e-vector directions to azimuth positions also applies when a particular e-vector direction is not realized at a given elevation at a given time of the day (e.g., Fig. 4*a*; $\mu_0 = 60°$, $\chi = 0°$).

To assess the significance of these findings let us refer to the line of maximal polarization of the e-vector pattern (see Fig. 3*e*). In fact, the positions assigned by the bees to the e-vectors presented experimentally matched the positions of the e-vectors as they occurred along the line of maximal polarization [at the given elevation of $\mu = 60°$, $\chi_{P_{max}} = 90°$ occurs on the antisolar meridian ($\phi = 0°$), $\chi_{P_{max}} = +45°$ ($-45°$) occurs at $\phi = -48°$ ($+48°$), and $\chi_{P_{max}} = 0°$ occurs at $\phi = \pm 90°$].

Furthermore, the bees performed yet another remarkable generalization. Consider the azimuth position of $\chi_{P_{max}} = 0°$, $\pm 45°$, and 90° while proceeding from the zenith toward the horizon (Fig. 3*e*). Clearly, $\chi_{P_{max}} = 0°$ is 90° apart from $\chi_{P_{max}} = 90°$ over the whole celestial sphere, and this actually was expressed by the orientation of the dancing bees whenever they viewed a 0° e-vector. What the bee's behavior did not reflect was the variable position of $\chi_{P_{max}} = \pm 45°$. Irrespective of their elevation, the $\pm 45°$ e-vectors always were assumed by the bees to lie at $\phi = \mp 50°$. This corresponds to the average azimuth positions of $\chi_{P_{max}} = \pm 45°$ for all elevations $\mu > 30°$ (Fig. 5*a*). The same results held for any other e-vector direction. As a consequence, the χ/ϕ function as applied by the bees did not vary with the elevation above the horizon nor did it vary with the elevation of the sun (Fig. 5*b*). It was the average of the slightly variable $\chi_{P_{max}}/\phi$ functions as computed for $\mu > 30°$ (Fig. 3*f*).

In summary, we suggest that the bees use a celestial map that reflects the mean distribution of the maximally polarized e-vectors ($\chi_{P_{max}}$) as they occur across the sky during the course of the day. The result is a highly generalized version of the e-vector pattern which does not vary during the day.

Several additional findings support this hypothesis. First, in assigning e-vector directions to azimuth positions, the bee uses its generalized χ/ϕ function when confronted not only with an artificial e-vector but also with patches of the natural blue sky. Even when it views a rather large part of the sky, subtending a visual angle of 40°, it makes exactly the mistakes that can be predicted from its χ/ϕ function. Second, the bee's stereotyped χ/ϕ function also applies when, at a particular elevation, a given e-vector direction is realized twice (see Fig. 3*c*). In one example the bees viewed a patch of the blue sky (diameter, 40°)

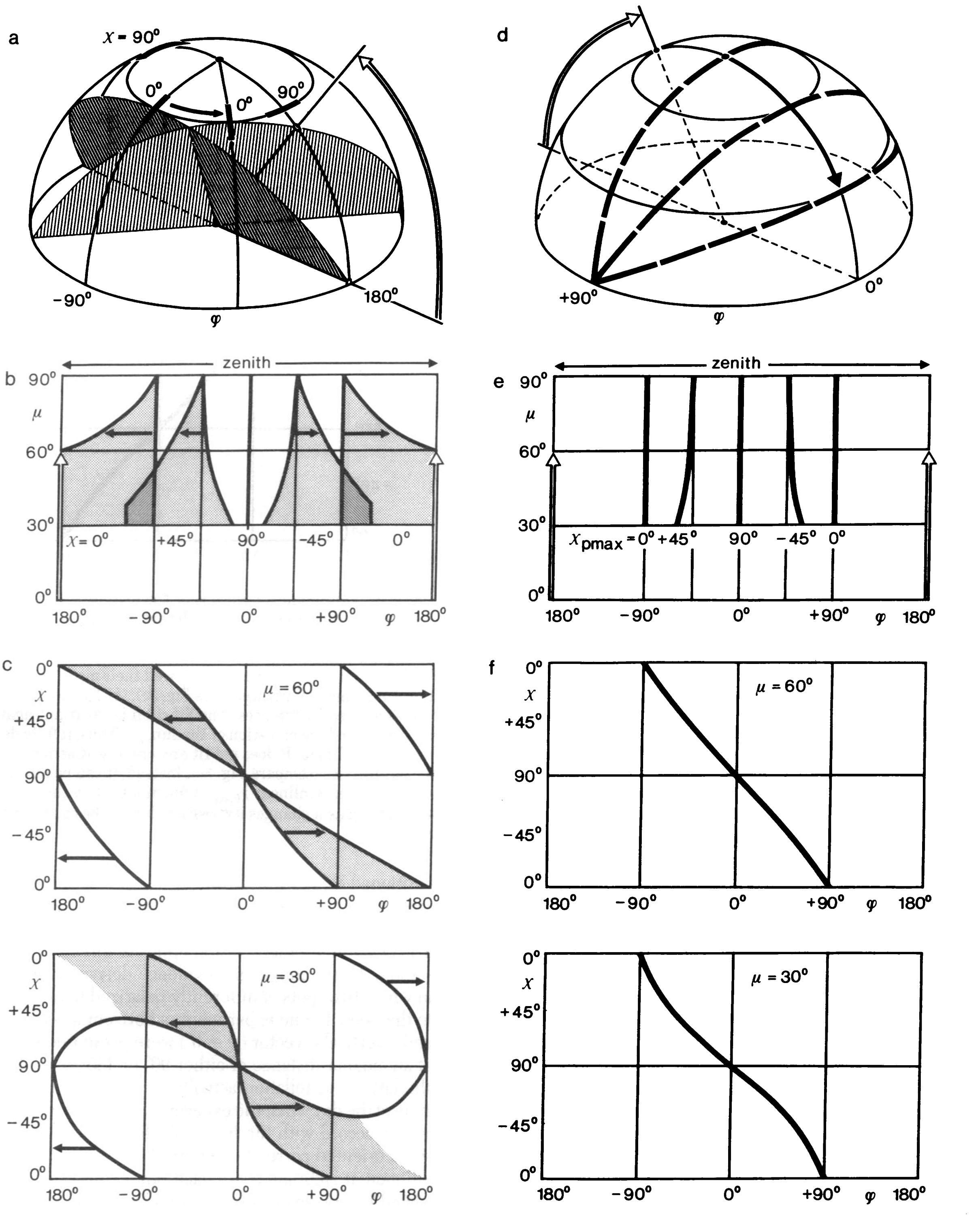

FIG. 3. Distribution of e-vector directions in the sky. (*a*) The e-vector directions are always perpendicular to the plane defined by the direction of the sun and the observed point in the sky. Consequently, with the sole exception of the horizontal e-vectors ($\chi = 90°$) that are positioned along the solar and the antisolar meridian, all e-vectors move toward the climbing sun. In the figure this is demonstrated for a vertical e-vector. The path of the sun is marked by the open arrow. (*b*) Celestial map (cylindrical equal-spaced projection) showing the azimuth positions of the e-vector directions $\chi = 90°, +45°, -45°$, and $0°$ (stippled areas) as they vary with the elevation of the sun ($0° \leq \mu_0 \leq 60°$). The solid arrows indicate the direction in which the e-vectors move when the sun moves up (open arrow). $\phi = 0°$ and $\mu = 0°$ mark the antisolar meridian and the horizon, respectively. (*c*) e-vector distribution for two elevations ($\mu = 60°$ and $\mu = 30°$) and different elevations of the sun ($0° \leq \mu_0 \leq 60°$). The solid arrows indicate the direction in which the e-vectors move when the sun moves up. Note that, at a given elevation, identical e-vector directions may occur twice (the stippled areas mark those e-vectors that are farther from the sun). In the text, these e-vector distributions are referred to as χ/ϕ functions. (*d*) When the sun moves up (open arrow), the line of maximal polarization tilts down. Thus, during the course of the day, all directions of polarization $0° \leq \chi \leq 90°$ get exposed along the line of maximal polarization. (*e*) Celestial map (cylindrical equal-spaced projection) showing the azimuth positions of $\chi_{P_{max}} = 90°, \pm 45°$, and $0°$, as set by the daily movement of the line of maximal polarization. It is important to note that this map does not represent any actual pattern in the sky but comprises the azimuth positions of $\chi_{P_{max}}$ as they occur during the course of the day (compare *d*). $\phi = 0°$ and $\mu = 0°$ mark the antisolar meridian and the horizon, respectively. (*f*) Distribution of the maximally polarized e-vectors for elevations $\mu = 60°$ and $\mu = 30°$ [($\chi_{P_{max}}/\phi$) functions]. The functions result from the daily movement of the line of maximal polarization.

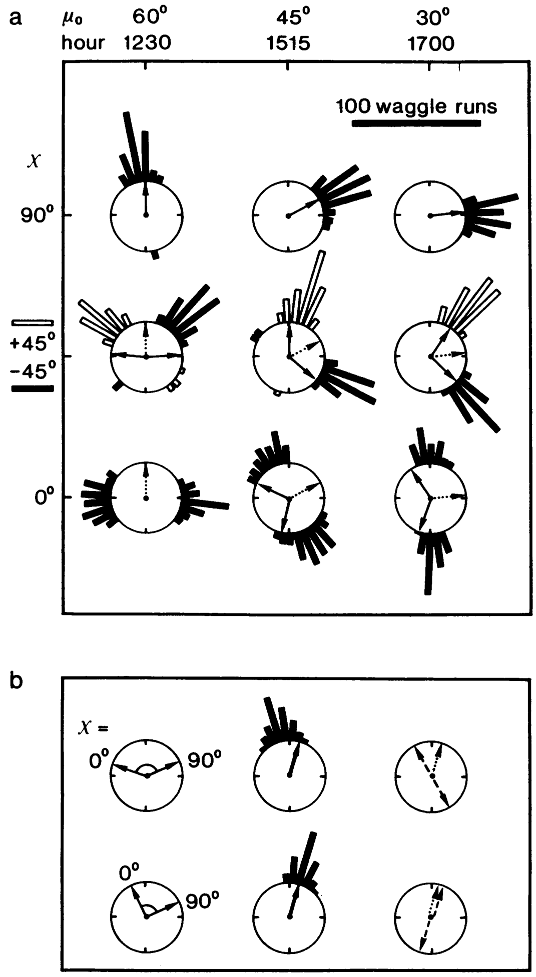

FIG. 4. (*a*) Angular distributions of the waggle runs indicating the azimuth positions (ϕ) at which the dancing bees assume the e-vector direction $\chi = 90°$, $+45°$, $-45°$, and 0° to occur. In each diagram the waggle dances of 10–15 individuals have been summarized. The e-vectors (artificially polarized UV light) are presented at elevation $\mu = 60°$ at different times of the day. The dotted arrows mark the position of the antisolar meridian ($\phi = 0°$) as measured relative to north (upward direction); the solid arrows indicate the positions of the e-vectors as they occur in the natural sky. Bees exhibit bimodal orientation (with preference directions 180° apart) when confronted with vertical e-vectors ($\chi = 0°$). Occasionally, a slightly bimodal orientation can be observed in the case of $\chi = 90°$ and $\chi = \pm 45°$ as well, but this observation is not considered here. Note that the mean positions assigned by the bees for the ±45° e-vectors and the 0° e-vectors deviate significantly from the actual e-vector positions in the sky ($P < 0.01$). However, no deviation occurs when the e-vectors are close to their position of maximal polarization ($\chi_{P_{max}}$). In the experiments described here this happened to be the case when ±45° e-vectors were presented at $\mu_0 = 30°$ (for positions of $\chi_{P_{max}}$ see Fig. 3*f*). (*b*) Orientation of the waggle runs performed by bees that viewed two spots of artificially polarized light. Upper row, left: one horizontal e-vector ($\chi = 90°$) and one vertical e-vector ($\chi = 0°$) are presented at an angular distance of 135°. [At this time of the experiment, this e-vector constellation actually was realized at the elevation considered ($\mu = 60°$) in the sky.] Upper row, middle: the angular distribution of the waggle runs deviated from the direction of the feeding station indicated by the arrow. Upper row, right: mean dance directions of the bees when either e-vector was presented alone (the dotted arrow, 90° e-vector; dashed arrow, 0° e-vector). Lower row, left: one horizontal and one vertical e-vector were presented at an angular distance of 90°. At the time of the experiment this e-vector constellation was not realized in the sky, but it is in accord with the bee's χ/ϕ function. Lower row, middle: angular distribution of the waggle runs; no orientation errors occurred. Lower row, right: dance directions when either e-vector was presented alone.

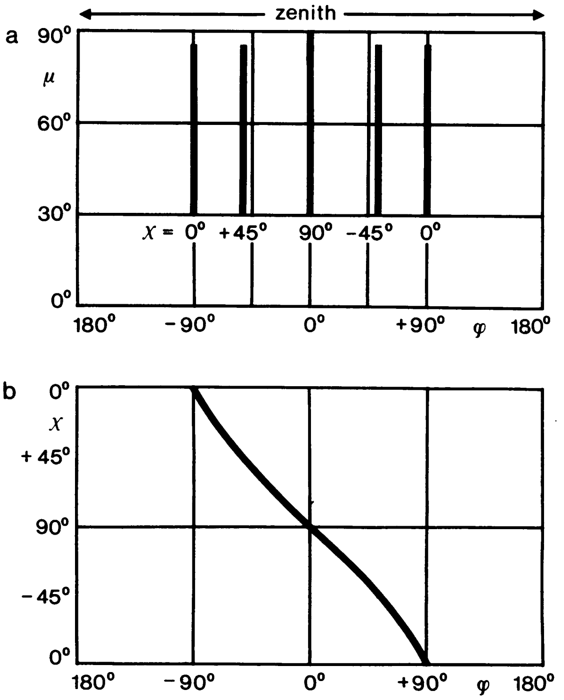

FIG. 5. (*a*) Azimuth positions of the e-vectors $\chi = 90°$, ±45°, and 0° as assumed by the bees for different elevations above horizon ($\mu > 30°$) and different times of the day. These azimuth positions do not correspond to the actual positions of the e-vectors in the sky (compare Fig. 3*b*). Instead, they match rather well their mean position along the line of maximal polarization (see Fig. 3*e*). (*b*) The nonlinear χ/ϕ function as applied by the bees. The function is invariant against the elevation, μ, and the elevation of the sun, μ_0. Thus, it fully describes the bee's celestial map. It does not fit any one χ/ϕ function as it occurs in the natural sky (compare Fig. 3c). Instead, it can be interpreted as an average of the nonlinear $\chi_{P_{max}}/\phi$ functions set by the line of maximal polarization as it changes its position during the course of the day (see Fig. 3*f*).

positioned along the solar meridian ($\chi = 90°$). Nevertheless, in accord with their χ/ϕ function, the bees interpreted these e-vectors as lying along the antisolar meridian, so that their waggle dances pointed exactly in the opposite direction of the feeding station. Third, convincing evidence derives from experiments in which two spots of differently polarized light were displayed to the bees. In one experiment, a horizontal e-vector ($\chi = 90°$) and a vertical e-vector ($\chi = 0°$) were presented simultaneously at an angular distance of either 90° or 135° (Fig. 4*b*). Whereas the latter constellation actually was realized in the sky at the time of the day when the experiment was performed, the former was in accord with the bee's χ/ϕ function. In fact, the dances were oriented correctly only when the two e-vectors were positioned at right angles to each other, but their directions deviated by approximately 25° from the correct course when the e-vectors were separated by 135°. The observed error exactly reflected the mean of the dance directions displayed by the bees when confronted with either e-vector alone.

DISCUSSION

The question of how bees use the pattern of polarized light in the sky as a compass has generally been answered by referring to some kind of visual spatial memory. According to this hypothesis, bees are supposed to memorize the e-vector pattern last seen, and later match the current image (i.e., the patches of the sky displayed to them during the experiment) with the memorized one (2, 3). Following this line of argument, bees should be able to orient correctly whenever they can view at least two e-vectors in the sky (two e-vectors are necessary when identical directions of polarization occur twice at the elevation concerned; see ref. 5 for full argument). However, even under such apparently unambiguous stimulus conditions, bees make mistakes. This holds true even if they have had the chance to view the full e-vector pattern during their preceding forays. Obviously, they do not know exactly where any particular e-vector occurs in the sky and thus cannot rely on memorized images of the e-vector patterns. What they seem to use instead is a celestial map that provides not correct but approximative compass information about the actual e-vector patterns in the sky.

What does this map look like? We have tried to answer this question by analyzing the orientation errors made by bees whose view of the sky was restricted to single (natural and artificial) e-vectors. The results can be summarized as follows. First, the map applied by the bee is fully described by just a single χ/ϕ function which does not vary with the elevation in the sky and the time of day but only rotates about the zenith when the sun moves across the sky (Fig. 5). Second, the map is confined to one-half of the celestial sphere (the one that is centered about the antisolar meridian). Because all e-vectors in the sky are interpreted as lying within this half of the sky (3, 4), it immediately follows that the bee's navigational errors become particularly large when the e-vectors are positioned close to the solar meridian.

There is one further point worth mentioning. Because in the bee's map the horizontal e-vectors are always positioned exactly opposite to the sun, one could surmise that the bees refer to the antisolar meridian as their decisive compass cue and use their generalized χ/ϕ function just to calculate the azimuth position of the horizontal e-vector from any one e-vector available to them. However, when any particular e-vector is presented in addition to a horizontal e-vector (two-point experiments), the bees do not refer selectively to the latter (Fig. 4*b*). It appears that all e-vectors are equally important. Their spatial arrangement forms what readily can be called the bee's celestial map.

The map can be derived not only experimentally as described above but also theoretically by referring to the line of maximal polarization in the sky. Then, the bee's map turns out to represent the mean distribution of the maximally polarized e-vectors as they occur at elevations >30° above horizon (compare Figs. 3 *d–f* and 5). Obviously, in perceiving the whole patterns of polarization the bees only use the e-vectors along the line of maximal polarization to calibrate their χ/ϕ function. What we do not know yet is the extent to which this function is genetically fixed or based on individual experience.

Finally, one wonders how strongly the bee's navigational abilities suffer from relying on a generalized rather than a correct map of the sky. Because the sun, positioned in the lowly polarized part of the sky, serves as an additional compass cue, there is in fact only one kind of situation in which the bee's orientation errors become really large—namely, when both the sun and the highly polarized half of the sky are covered completely by clouds and when small parts of sufficiently polarized sky light are available in the lowly polarized half of the sky. Most probably, this is not a common situation. However, when bees are exposed to such a situation experimentally, they make mistakes just as large as predicted. Their knowledge about e-vector patterns in the sky indeed seems to be confined to the celestial map described in this paper.

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