Navigation and Compass Orientation by Insects According to the Polarization Pattern of the Sky

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A recent theory attempts to explain how bees take their compass orientation from the pattern of polarized light in the sky (S. Rossel and R. Wehner, Nature **323,** 128–131 (1986)). According to this theory, orientation can be erroneous and lead to the wrong course of a recruited bee in search of the foraging site whenever only a small patch of the blue sky is visible to the bee. It is shown that orientation under natural conditions is not erroneous, if the compass reference is variable in time but equally defined for both, scout bees and recruits.

Karl v. Frisch [1] discovered that honey bees derive compass information from the sun linked polarization pattern in the sky. Bees possess an advantage in that they can orient themselves by using this polarization pattern even if the sun is covered by clouds. A small patch of blue sky of a diameter of 10° or less will suffice for this orientation.

A recent theory by Rossel and Wehner attempts to explain how bees take their compass orientation from the pattern of polarized light in the sky. According to it orientation can be erroneous whenever only a small patch of sky is visible to the bee. The explanation of this "Mißweisung" can, in Rossel and Wehner's opinion, be derived from a specific alignment of the polarized light analysers located in the bees ommatidia of the "dorsal rim". These analyser alignments form a template ("map") of the polarization pattern of the sky. This map matches the celestial *e*-vector distribution in good approximation only at dawn and dusk. If the sun is more than 20° above horizon there will be a discrepancy between both maps, which, at the end, can be the reason of an orientational error as manifested in the wagging dance direction of a scout bee, dancing on a horizontal comb. Thus, when the bee applies a simple compass strategy, as suggested by Rossel and Wehner, it may arrive at an incorrect course to the foraging site [2]. Equivalent arguments hold for ants, navigating according to the polarization pattern in the sky.

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Rossel and Wehner considered this shortcoming not as a serious one because of two arguments: 1. Under normal circumstances the navigating bee has large polarization patterns at its disposal, and errors cancel each other out. 2. During free flight the navigating bee can resort to powerful backup systems such as the sun and land marks [2].

However, the navigational error encountered under natural conditions could be negligible for an entirely different reason as shown in Fig. 1.

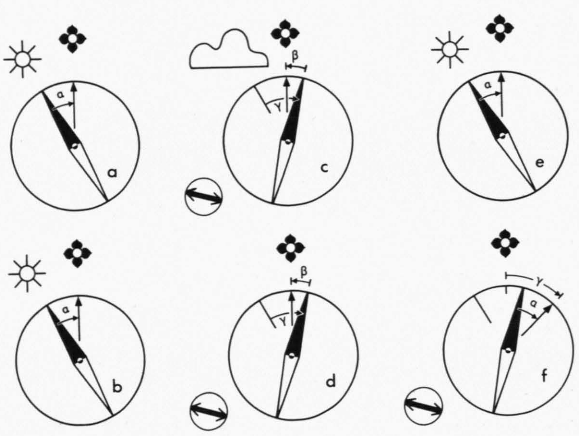

Fig. 1a, c, e. Schematic representation of the environment of a scout bee during foraging flight. In a and e the sun is seen and the flower indicates direction to the feeding station. In c the sun is covered by clouds and only a patch of sky is visible (*e*-vector direction of the polarized light is indicated by double arrow).
Fig. 1b, d, f. Conditions during the waggle dance on the horizontal honeycomb. In b the sun can be seen and in d and f there is an artificial or natural patch with polarized light. See explanation in text.

The top row in Fig. 1 represents the environmental surroundings of a bee during foraging, while the lower row depicts the test situation on a horizontal honeycomb as used by Rossel and Wehner. In Fig. 1a and 1b it is assumed that the sun can be seen directly during foraging by the scout bee as well as during her dance on a horizontal honeycomb. The reference direction of the "compass" of the dancing bee is therefore, as has been shown by von Frisch, directly pointing to the sun. The foraging site is at an angle α relative to the sun. If during performance of her dance on the horizontal honeycomb the bee can see the sun, the waggle runs are rotated by the angle α relative to the reference direction of the compass, and the waggle direction comes to point directly to the food source.

In Fig. 1c only a small patch of the sky is considered to be visible (with double arrow, indicating the *e*-vector direction). The reference direction of the scout bees' compass is rotated by the angle γ relative to the sun, because the bees' map does not exactly match the celestial map. During foraging the bee learns that the food source is located at an angle β to the left of her compass reference. If in the test situation (Fig. 1d) she sees the same patch of sky as during foraging she will dance β degrees to the left of their compass reference and therefore indicate the correct direction to the food source. The dance attenders *will follow the correct course,* provided that the same patch of sky as in Fig. 1c can be seen during the foraging flight (Fig. 1d)! This shows that there is no need for the compass reference of the scout bee to point at the sun. For correct orientation it is sufficient, if the recruits use the same compass reference as the scout bee, irrespective of whether it points to the sun or elsewhere.

The "mistakes" bees made in Rossel's and Wehner's experiments came up because the sky as seen by the bee during foraging and during the test was different (Fig. 1e and 1f). During foraging the bee learned that the feeding station was α degrees to the right of the compass reference point which, on the cloudless days at which the experiments were performed, was the sun. This angle was indicated in the waggle runs. Now, however, relative to the compass reference as defined by the *e*-vector direction in the patch of sky seen now. The consequence was an error angle γ, pointing into a wrong direction.

But even with such a waggle direction not pointing to the feeding station, recruits would still be able to follow the correct course: once on the wing, their compass reference on the blue sky is the sun again. They immediately adopt as new direction α degrees to the right of the original direction and are correct!

The concept that the bees' compass reference is variable and requires identical defining for scouts and recruits in order to enable correct orientation can only work if the sky parameters are sufficiently stable. Actually they need not be all that stable since, on entering the hive, scout bees immediately start dancing and do so for relatively short times (20–120 sec) as was shown by von Frisch [3]. He also showed that recruits arrive at the feeding station within a few minutes after their first contact with the dancing bee (Fig. 2). How stable sky parameters are depends upon specific weather conditions, such as wind velocity, height of clouds above ground, etc. We found the change in position of clouds in cases of moderate wind velocities is in the order of 2 to 4 degrees per minute (Fig. 3). This is not very much and does not lead to significant error angles.

The concept of a variable compass reference actually is not new: Von Frisch [1] used it in the context of other "Mißweisungen", and it has been discussed in a wider context by Brines and Gould [4]. Rossel and Wehner primarily used the orienting "errors" of the dancing bees in order to deduce the nature of the bees' internal representation of the celestial polarisation pattern. But they clearly discussed these "errors" also with respect to navigation, that is how bees find their way to the foraging site. They may have overlooked in earlier work that, according to this old concept, the mechanism they propose must not lead

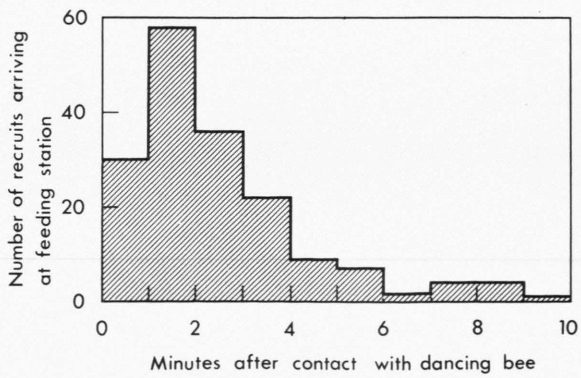

Fig. 2. Number of recruits arriving at feeding station as a function of time after first contact with dancing bee. Data from von Frisch [3].

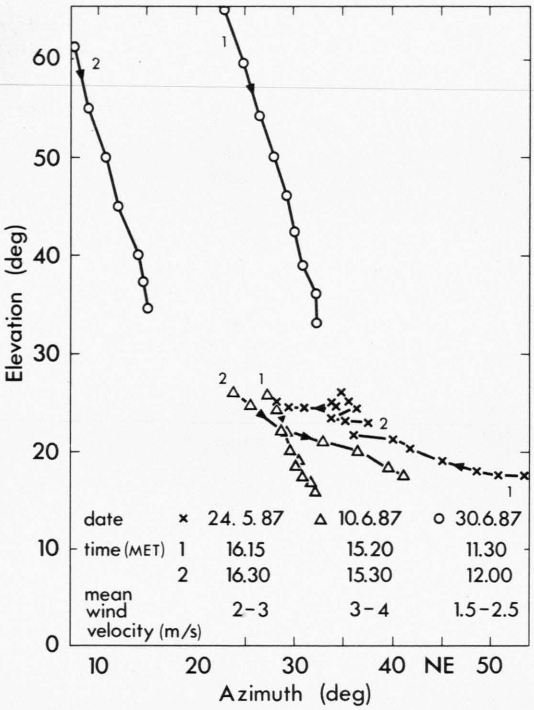

Fig. 3. Position of patches of blue sky or small clouds above horizon at Tübingen as a function of time. Points are separated by 1 min intervals and taken from photographs. Abscissa indicates angle relative to north. Inset gives data and wind velocity at 10 m above ground as communicated by the regional weather burreau at Stuttgart.

to navigational errors, even if the celestial map does not fit to the bees' internal map of the sky's polarization pattern. The argument holds also if bees dance not in a horizontal honeycomb but on a vertical one, as is usually the case. It also explains why there is no evolutionary pressure to improve the mechanism of *e*-vector determination in bees, since the errors as determined by Rossel and Wehner must not lead to erroneous orientation. This fact has been communicated in an early version of this manuscript and is, meanwhile, acknowledged in a recent paper of Wehner [5].

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