

Responses to light under varying magnetic conditions in the honeybee, *Apis mellifica*

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Accepted April 11, 1984

Summary. In the dance of honeybees the indication of direction to a food source can be influenced by magnetic and photic stimuli. We have tested the behaviour of dancing honeybees illuminated with white light under varying magnetic conditions. The bees respond to the light stimulus with a maximum deviation from the correct dancing direction when they dance parallel to the inclination of the earth's magnetic field (EMF). The response to light drops to zero with increasing deviation from this 'zero-point' direction (see also Martin and Lindauer 1977). The time of total indifference to light varies with the magnetic conditions. In the natural EMF the reaction to light becomes zero 20.3° (i.e. 1 h) after the bees have passed the zero-point. In the compensated EMF this effect is delayed by 10° . The bees show nearly no reaction to light when the EMF is amplified to 2 Gauss.

The relative spectral sensitivity of dancing honeybees was tested in the compensated EMF. It is 1:1.63:2.64 for green-, blue-, and UV-light, respectively.

Introduction

Honeybees indicate the direction toward a food-source by transposing the angle between the goal and the sun with respect to gravity when dancing on a vertical comb inside the dark hive. The direction toward the sun is indicated by dances in an upward direction. According to the movement of the sun, the dance angle changes with time of day (von Frisch 1965). The dance angle is strongly affected by the earth's magnetic field (EMF) and its daily variations. As a result, regular deviations from the correct dancing direction, the misdirection, can be observed (Lindauer and Martin 1968).

Abbreviation: EMF earth's magnetic field

Yet, there are a few discrete points (zero-points) where the EMF does not influence the correct waggle angle (Martin and Lindauer 1977). Provided a north-south alignment of the comb, this happens, when the waggle direction corresponds with the inclination of the EMF. At an inclinational angle of 65° (for Würzburg, Germany) zero-points can be observed at 25° and 205° , when assuming 0° for the upward dancing direction and observing the dances on the eastern side of the honeycomb. Figure 1 illustrates the spatial arrangement of the comb with respect to the magnetic field and the position of the zero-points. – If the EMF is compensated, the dances subsequently exhibit no misdirection over the whole dancing circle. – Another behavioural component of the dance, the sounds

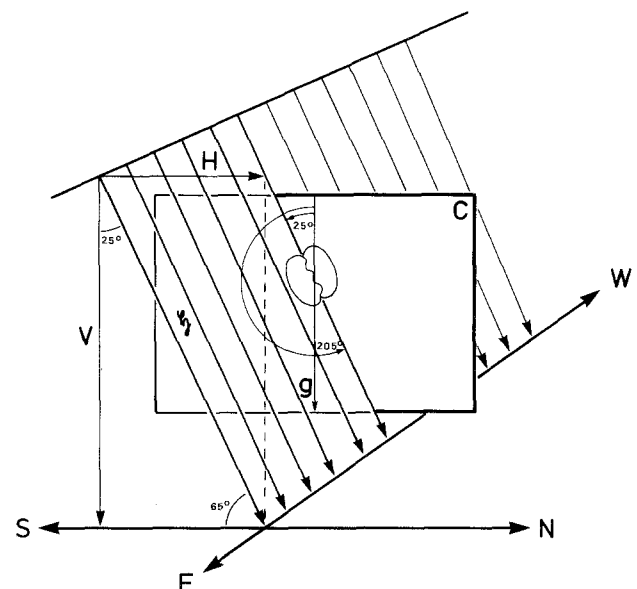


Fig. 1. Spatial arrangement of the comb relative to the EMF. N north; W west; S south; E east; V vertical component of the EMF; H horizontal component of the EMF; g total intensity of the EMF; g gravity; C comb. (Martin, unpublished)

produced by forager bees, is also strongly correlated with the daily variations of the EMF (Kilbert 1979).

Wagging bees illuminated with light react with a pronounced divergence from the correct dance angle in the zero-points. The reaction to light declines with increasing deviation from the zero-point (Martin and Lindauer 1977). To quantify the effects induced by the interaction of photic and magnetic stimuli, we have tested the behaviour of dancing bees under 'white' light illumination with respect to the length of the photosensitive period after the zero-point had been reached under varying magnetic conditions.

A second aspect of this paper is concerned with the spectral sensitivity of dancing bees in the zero-point region under compensated EMF conditions. Here the absence of magnetically induced misdirection allows a direct measurement of light sensitivity.

Material and methods

General. The experiments were performed with honeybees belonging to the race *Apis mellifica carnica*. The bees were housed in an observation hive containing two combs and having UV-transmitting quartz-glass as broadsides. For measurement of the dance angles, a protractor was attached to the glass window, allowing an accuracy of measurement up to 1°. Dance angles were determined by assuming 0° for the vertically upward direction and counting off through 360°. The bees danced on the east side of the vertical comb in the zero-point region of 25° and 205° (i.e. 15°–100° and 190°–245°, respectively). The hive was adjusted in north-south direction. A group of 20–25 individually marked foragers were trained to visit an artificial food source containing sugar water 700 m remote from the hive. An assistant caught away newcomers to prevent overcrowding of the feeding place. – All experiments were performed near Würzburg, Germany.

Variation of the EMF. Variation of the magnetic field was obtained by means of Helmholtz coils which were adjusted in the direction of the EMF's inclination. The current in the coils could be altered with an adjustable resistance. The experiments were conducted under three different magnetic conditions: EMF normal (total intensity about 0.5 Gauss), EMF amplified to 2 Gauss, and EMF compensated to less than 4% of total intensity. The magnetic stimuli were switched on 1 h before the start of measurements. The quality of the stimuli was repeatedly controlled during each experiment with a Gaussmeter (Bell 640) by placing the probe directly in the position of the dancing honeybee.

Light stimuli. The bees were illuminated with the light from a 100 W tungsten lamp with UV-transmitting quartz condensor, heat filter KG1 (Schott), neutral grey and interference filters (Spindler & Hoyer). The distance between lamp and dancing floor was 40 cm. The stimulus subtended an angle of 5° at the bee's eye. The bees were lit from beneath under an elevational angle of 45° with respect to the vertical comb and an azimuthal angle of 180°. In the experiments varying the magnetic field conditions, 'white' light with an intensity of $0.26 \times 10^2 \mu\text{W}/\text{cm}^2$ was used. – In the spectral sensitivity measurements, three interference filters were used with λ_{max} at 348 nm, 440 nm, and 548 nm. In the zero-point region at 25°,

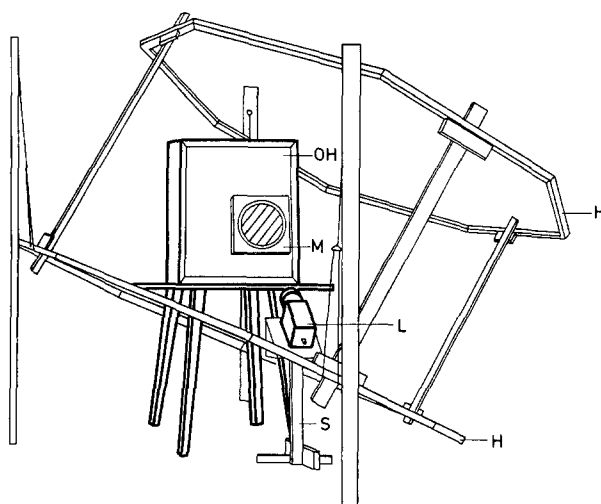


Fig. 2. Principle of experimental set up. OH observation hive; L lamp; M measuring wheel; H Helmholtz coil; S support

the irradiance values were tuned to equal energies as follows: 348 nm: 0.100×10^2 ; 440 nm: 0.125×10^2 ; 548 nm: $0.125 \times 10^2 \mu\text{W}/\text{cm}^2$. In the zero-point region at 205°, quantum densities were equalized: 348 nm: 0.110×10^2 ; 440 nm: 0.790×10^1 ; 548 nm: $0.640 \times 10^1 \mu\text{W}/\text{cm}^2$. Measurements of light intensities were conducted with an optometer (UDT 40 ×; United Detector Technology) in the laboratory simulating outdoor conditions. All spectral sensitivity experiments were performed under compensated EMF conditions. The whole experimental setup (Fig. 2) was placed inside a tent to achieve darkening of less than 4 Lux. Under these conditions dancing honeybees show no phototactically induced misdirection (Martin and Lindauer 1977).

Experimental procedure. Feeding of the marked foragers as well as compensation or amplification of the EMF started 1 h before the beginning of dance measurements. The measurement period started 15–20 min, i.e. 10°, before the zero-point and lasted at least 3 h. During this period 15 min of light stimulus alternated with a 15 min control-phase of diffuse illumination below 4 Lux. Before measuring the dance angle every bee had to perform at least 10 dances as 'tuning-in' phase. Only then the measurement was made.

Results

The present experimental results indicate that the sensitivity of dancing honeybees to light is directly influenced by magnetosensory inputs, or vice versa. Generally, a maximum light-induced misdirection is observed in the zero-point region at 205°, where the dancing direction corresponds with the inclination of the EMF when measuring the dances on the eastern side of the honeycomb. – A comparison of the curves obtained under the specified magnetic conditions reveals differences in absolute reactivity in the zero-point region as well as in the length of the phase, where dance errors can be induced by light. Figures 3 and 4 show examples. In the figures circles and triangles represent the mean values of those measurements that were ob-