Reply to Cheung et al.: The cognitive map hypothesis remains the best interpretation of the data in honeybee navigation

Cheung et al. (1) criticize two points of our study, both of which are unfounded. The first is that general anesthesia is not shifting the clock controlling sun compass orientation in bees. This is clearly wrong. We show that sun compass orientation and food anticipatory behavior are systematically shifted by anesthesia. This effect results from anesthesia shifting the underlying molecular circadian clock of the bee (2).

Second, they claim that bees are using panorama-based orientation mechanisms. This is impossible in experiment 1 as the panorama is less than the visual acuity of bees (2°) (3, 4). Cheung et al. argue that subresolution brightness modulation at the level of single ommatidia may be used by insects for navigation. Their argument is based on the assumption that brightness modulation along a horizontal row of single ommatidia is sufficient for panorama matching. We do not know of any direct evidence for this assumption in any insect. Multiple studies speak against the assumption that bees are able to extract spatial information from the brightness modulation within a single ommatidium: Optomotor response data show a maximum 2° visual angle; a visual angle of 5° is necessary to resolve particular achromatic patterns (chromatic requires 15°), and at least seven ommatidia are required for spatial discrimination.

In the example Cheung et al. use with ants, the skyline is modulated between 22° and 43° above the horizon, and the rotational image difference function is calculated for 0°–22° above the horizon. Under these conditions, their ants behave similarly to our bees (experiment 2): they steer toward their tree from any direction using the local cues at their homing goal. Whether the ants use panorama matching is a matter of interpretation; they could use some form of steering toward a beacon at the goal. In our experiment 2, bees refer to an extended landmark (a row of trees and bushes) along which they were trained to fly between the hive and the feeder. They saw the learned extended landmark when released and used this information for homing. In our interpretation, these homing flights are guided by the learned and identified extended landmark and are not matching panorama. We discuss the arguments in favor of this interpretation in our paper (5).

The bees in our experiment 1 did not fly toward the hive at the release site but followed the sun compass-related flight vector, which they would have taken had they not been translocated, indicating they did not follow a panorama-matching strategy or beacon orientation as the ants did.

The argument for panorama-based orientation is predicated on data from walking insects rather than flying insects. The visual cues available to each are dramatically different. There are multiple lines of published evidence showing that ground-based extended landmark structures are far more dominant than panoramas for bee navigation. Bees look from above at the network of extended landmarks. It is well documented that these landmark structures are considered in relation to the sun compass and act as mutual backup systems for directionality (6).

The cognitive map hypothesis remains the best interpretation of the data in honeybee navigation.

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