Still no convincing evidence for cognitive map use by honeybees

Cheeseman et al. (1) claim that an ability of honey bees to travel home through a landscape with conflicting information from a celestial compass proves the bees' use of a cognitive map. Their claim involves a curious assumption about the visual information that can be extracted from the terrain: that there is sufficient information for a bee to identify where it is, but insufficient to guide its path without resorting to a cognitive map. We contend that the authors' claims are unfounded.

Proof that an animal uses a cognitive map requires, at the very least, results that cannot be explained by other known mechanisms. Cheeseman et al. consider only one alternative mechanism to the use of a cognitive map: the association of compass directions with visual scenes (as detailed in ref. 2). They thus neglect the extensive experimental and theoretical evidence that insects can also be guided purely by disparities between their memories of visual scenes and their current view of the world (3). It has long been known that this visual guidance in insects can operate independently of information from path integration and more generally with no celestial compass or with a conflicting celestial compass (4).

Image analysis and modeling show that the information contained in panoramic views of natural scenes can provide guidance across large areas, without the need of celestial compass information or a map-like representation (4, 5). For a flying bee, such a view would include both the skyline and the ground below. The authors have failed to do any image analysis of the visual information available to bees at their study site. However, based on what they supply, there is reason to expect that view-based guidance can also account for the bees' behavior at this site (Fig. 1).

With an understanding of how insects can use view-based guidance, we can go further and suggest an alternative explanation for the effect of anesthesia. Rather than acting to clock-shift the celestial compass, anesthesia may well have simply knocked out the path integration home vector. The authors claim that in one of the two conditions, the anesthetized bees follow a clock-shifted path integration home vector. This predicted direction, however, coincides with the direction of the trained feeder to which at least 8 of 24 bees in experiment 1 and 7 of 12 bees in experiment 2 indeed first fly. The initial flight directions of all of the anesthetized bees can thus be explained in terms of view-based guidance toward the trained feeders, toward the trained feeder nest routes, or toward dominant landscape features. Consequently, the authors' dismissal of a proposed association of compass directions with visual scenes (2) is also questionable.

Taking all these points, we believe that Cheeseman et al.'s claims are not substantiated and that their results do not add anything new to the debate surrounding cognitive maps in insects.

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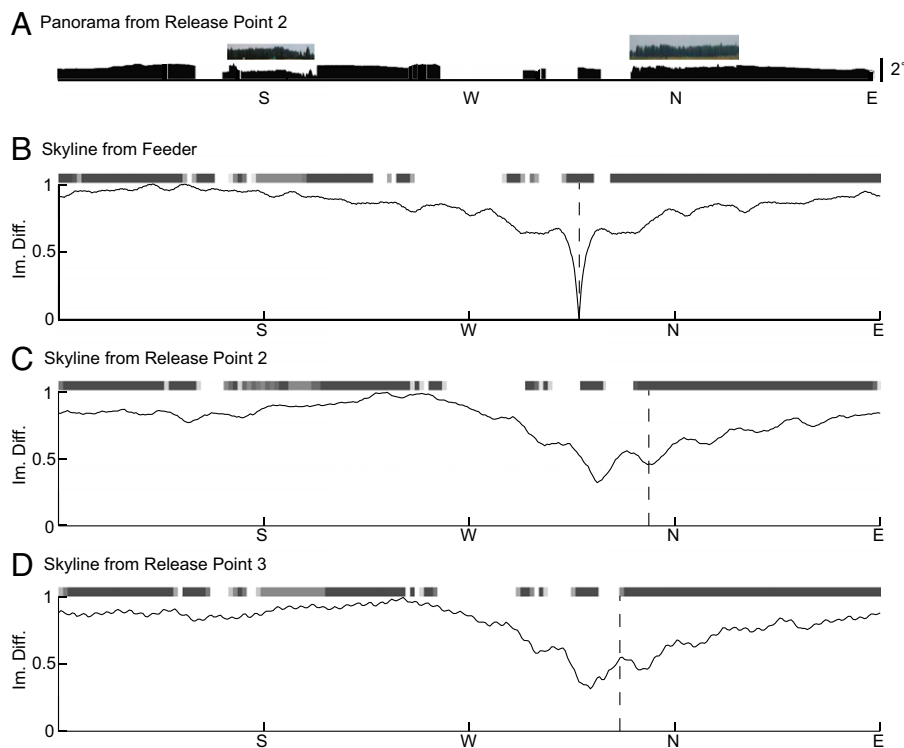
Fig. 1. Visual scenes from the experimental site are likely to supply visual guidance to navigating bees. Using the coordinates provided by Cheeseman et al., we used Google maps to estimate the distance of treelines and forest edges from the experimental area. Combining this landscape model with the landscape images (taken facing north and south) provided in their SI Materials and Methods, we estimated the typical height of trees in this area and created a 3D virtual reconstruction of the experimental site from which we could compute panoramic skylines from any of the experimental locations. (*A*) Recreated high-resolution skyline from release point 2, with the two photos provided in ref. 1 each showing ~45° of the skyline inserted above. The skyline and photos are magnified vertically for clarity. (*B–D, Upper*) Panoramic views of the skyline at a bee's 4° resolution from the feeder, release point 2, and release point 3, respectively. All views are centered on west. The gray level of each pixel represents how much of that pixel is covered by trees. Therefore, gray level is a proxy for skyline height. Pixels are magnified vertically for clarity. (*Lower*) Rotational image difference functions (rIDFs). An rIDF at a location compares the reconstructed panorama as perceived from that location with the reconstructed panorama as perceived from the feeder location. It is computed from the root-mean-square pixel differences obtained by horizontally sliding one panorama over the other in steps of 2° (for details, see ref. 4). Image differences are shown as a proportion of the maximum image difference. *B* shows an auto-rIDF of the reconstructed panorama from the feeder location compared with itself. The rIDF is zero when the panorama is aligned with itself and gradually rises with increasing shift of the panoramas relative to each other. In this case the reference panorama was centered on the hive direction (dashed line). *C* and *D* show rIDFs in which the view from each release point is compared with the view from the feeder toward the hive (i.e., *B*). In both cases, the minimum is near the hive direction (dashed lines). These comparisons show that a remembered direction can be obtained by matching a view stored at a location to the currently perceived view at that location (*B*) and, further, that homing directions can be obtained by comparing the stored view with the current view from other locations in the neighborhood (*C* and *D*). The general point that the terrain supplies visual information for view-based guidance is independent of the accuracy of this particular reconstruction. Indeed, bees will have a more complex set of stored views gathered during their exploration and orientation flights, including information below the horizon. These extra views would enhance the robustness of their view-based navigation.