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Honey bees infer source location from the dances of returning foragers

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Honeybees (*Apis mellifera carnica*) communicate the direction and distance to a food source by means of a waggle dance. We ask whether bees recruited by the dance use it only as a flying instruction, with the technical form of a polar vector, or also translate it into a location vector that enables them to set courses directed toward the food source from arbitrary locations within their familiar territory. The flights of recruits captured on exiting the hive and released at distant sites were tracked by radar. The recruits performed first a straight flight in approximately the compass direction indicated by the dance. However, this "vector" portion of their flights and the ensuing tortuous "search" portion were strongly and differentially affected by the release site. Searches were biased toward the true location of the food and away from the location specified by translating the origin for the danced polar vector to the release site. We conclude that by following the dance recruits get two messages, a polar flying instruction (bearing and range from the hive) and a location vector that enables them to approach the source from anywhere in their familiar territory. The dance communication is much richer than thought so far.

Apis mellifera | waggle dance | vector communication | landmark guidance | cognitive map

Significance

Whether even humans form mental maps has excited controversy for a century because it bears on the level of abstraction from sensory experience at which the computations underlying behavior operate. The dance of the returned honeybee forager conveys the direction and distance of the food source from the hive—on the surface, a simple flying instruction. However, a majority of recruits captured and released far from the hive gravitated eventually toward the true location of the food source, implying that they had inferred its map location. Map locations enable the setting of a course from one location to another within the same frame of reference, even when neither location has distinguishing sensory features nor previous motivational significance.

Honeybees (*Apis mellifera carnica*) are the only nonhuman animals that communicate navigational information by a symbolic form of information transfer, the waggle dance, which is performed by successful returning foragers to indicate the direction and distance of the food. The dance is performed on a vertical surface inside the hive out of sight of the sun and surrounding terrain. It takes the form of a figure 8 lying on its side. Where the two loops converge, the dancing forager makes a waggling run. The angle of that run—the tilt in the 8 relative to the horizontal—is the solar bearing of the food source from the hive. The number of waggles and the duration of the waggle run are proportional to the distance of the source.

Because the sun's compass direction may change by more than 40° within in an hour, the solar bearing rapidly becomes useless. In interpreting the dance, recruited foragers convert the solar bearing to a compass bearing by reference to a previously learned solar ephemeris function. The ephemeris function gives the location of the sun above the horizon panorama as a function of the time on the bee's circadian clock. It varies with both latitude and season. Thus, in conventional navigational terminology, the dance communicates the rhumb line to food from the hive (1, 2). Rhumb lines are origin-specific polar vectors. They are useless for navigation when the navigator is not at that origin. This analytic truth is the foundation of our experimental design: We displace recruits from the hive to release locations far from the hive in different compass directions, so their vector flight does not begin at the danced origin.

Dance-recruited bees also use previously acquired knowledge about the environment to navigate efficiently and adaptively between multiple locations (3–5). This knowledge consists of a memory of the outbound polar vectors between the hive and previously visited food sources, picture-like memories of the immediate surrounding of the nest and the places where food has previously been found, and memories of the sky-line profiles (panoramas). They also learn the olfactory, gustatory, and visual (color, geometric) features of the sources (6, 7). Thus, multiple features of the landscape and the properties of previously visited food sources are stored in memory.

Two questions arise from these findings: 1) Are the multiple components of navigational memory composed in their geometric relation, that is, in the form of a map constituted of location vectors? Location vectors enable the setting of a course to one location from any other location on the same map. 2) Do the memories that enable navigation within the familiar environment play a role in a recruit's interpretation of the dance? These two aspects have not been previously addressed together: The possibility that interpretation of the dance makes reference to stored terrain information has not been previously considered, let alone experimentally demonstrated.

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