



Taking shortcuts in the study of cognitive maps

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Summary

Harten, Katz, Goldshtein, Handel, and Yovel (*Science*, 369, 194–197, 2020) tracked fruit bats from their first flight and demonstrate that they can perform novel shortcuts both within and from outside their home ranges, fulfilling an important criterion of a cognitive map. Their richly detailed data set could be used to explore more key aspects of spatial cognition.

Keywords Fruit bat · Navigation · Cognitive map · Shortcut

The debate over cognitive maps (CM) in nonhuman animals is in its eighth decade, yet our most common question is still whether or not they exist. As noted by Mackintosh (2002) nearly 20 years ago, whether or not animals possess CM is far less interesting than detailing the mechanisms that underlie their spatial abilities. Do animals have unitary maps or multiple representations that combine at the output level to guide navigation? What are the contents of spatial representations? How are they acquired? What happens when guidances based on different cues conflict? Despite reams of published research on all these questions, and a growing understanding of many aspects of spatial cognition, the search for a definitive marker of CM continues, frequently centered on one candidate: the ability to traverse a novel route between two familiar locations, commonly referred to as a shortcut.

The key to identifying CM lies in distinguishing them from other types of representations that animals could be using to guide their movement. The characteristics a representation must have to qualify as a CM depend on the definition used, which has varied between authors and across time. However, three criteria have gained broad acceptance (O’Keefe & Nadel, 1978): CM represent the metric properties of a space (independent of any objects in it); they are unitary and connected—integrating several types of spatial information into a single representation; and they are allocentric—they do not depend on the animal’s current position on the map.

Importantly, CM that fulfil these criteria will enable flexible navigation, from any point on the map to any other point.

Just as definitions of CM have matured over time, so have the alternatives they are compared with. Tolman (1948), who first coined the term CM, contrasted them with the idea that rats’ navigation of a maze was guided by a chain of stimulus–response–stimulus associations (i.e., the rat sees a cue, performs a learned response, which leads to detecting the next cue, and so on). Using the now-famous “sunburst maze,” Tolman and colleagues demonstrated that such associations were not sufficient to explain rats’ behaviors in the maze. We would not today consider their data evidence for a CM, since a beacon (a cue colocated with a destination, detectable from a distance) was visible above the target. Later CM definitions also explicitly excluded navigating by beacons or chains of beacons (O’Keefe & Nadel’s, 1978, “routes”), using path integration and image matching.

As noted above, the most commonly cited behavioral test for the presence of a CM is the ability to take novel shortcuts. As long as no beacon at the destination (nor any of a chain of beacons culminating at the destination) is visible from the starting point, and the animal is not retracing its outward path, the ability to navigate a new direct route between two points serves as a marker for all the desiderata of a CM listed above. First, both locations must be part of a single representation that respects the metric properties of the space between them. Second, this representation must allow for calculating movement vectors between the two points, independent of the animal’s current location. However, throughout the chequered history of claims regarding shortcutting in a range of species, from bees to ferrets, one final criterion has proven especially resistant to empirical verification—that the shortcut taken is truly novel.

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Harten, Katz, Goldshtein, Handel, and Yovel (2020) have brilliantly overcome this difficulty by tracking young Egyptian fruit bats (*Rousettus aegyptiacus*) from before they left their roost for the first time. The authors placed light-weight GPS devices on 22 young bats and tracked every foraging flight they made for several months, accumulating an impressively fine-grained and detailed data set. The authors also mapped the locations of all the fruit trees in the area, and made valiant efforts to determine what global visual cues the bats would have had access to (by taking drone footage of the panoramas visible at several points along the bats' routes and at the maximal heights they commonly ascended to).

The data thus collected reveal numerous cases of bats moving in a straight line between two parts of their home range along a route they had never previously traversed—truly novel shortcuts. Many of these neither originated nor terminated at the roost, suggesting they were probably not guided by path integration. The authors also observed bats performing “long-cuts”: direct flights back to a specific destination in their home range from a location outside it (which they reached while exploring new areas). Finally, the authors performed translocation experiments, releasing bats in completely novel locations, from which they frequently homed in straight lines.

These data are compelling. Though it is certainly possible, I think, for the bats to have been utilizing specific beacons visible from large distances to perform some of their navigational feats, the results presented leave little doubt that these bats have a complex, detailed, and flexible representation of their home ranges. In combination with some of the cutting-edge neuroscience produced in recent years by the same research group on the neural underpinnings of bat spatial representations, these data give us a more detailed picture of airborne spatial cognition than I think we have ever had. In this respect, there is also a missed opportunity here.

Instead of focusing on the single question of whether or not bats can perform novel shortcuts, a more detailed investigation of Harten et al.'s (2020) rich dataset might reveal important facts about the ontogeny of spatial representations and how they vary between individuals. For example, Fig. S1 of the paper appears to show that young bats' home-range sizes are constant for long periods and then increase in discrete and abrupt leaps on “exploratory nights,” as if the bats engage in a Piagetian cycle of assimilation (navigating within the bounds of an existing map) and infrequent accommodation (exploring and learning new areas). I am aware of no comparable data on any other vertebrate species, including humans. Ontogenetic investigations of bee foraging show no such sudden changes in maximal range. The same figure also shows extreme differences between two bats in the size and development of their home ranges. These findings, in my opinion, if explored further, could teach us a lot about the nature of mammalian spatial representations and how they are actually used in the wild.

The current results could also help resolve questions about navigation raised by data from other species. Pigeons, for example, may rely on different sensory modalities over the course of their development to acquire and then use their spatial map. Is the same true for flying mammals? Chimps and elephants have been shown to use fixed, learned routes when in the periphery of their ranges and navigate more flexibly—in a more map-like manner—when in the core areas where they spend the majority of their time (Presotto, Fayrer-Hosken, Curry, & Madden, 2019). These results seem counterintuitive: Learning fixed routes requires experience, yet they seem to be used more often where experience is lacking. The level of detail in Harten et al.'s (2020) bat data could shed some much-needed light on this and similar questions about the mechanisms of spatial cognition.

CM and other spatial representations are inherently relational. In other words, they express the (metric) relationships of environmental features to each other (of course, animals also represent nonspatial features of objects in their environments). The most interesting questions on spatial skills are therefore about which relationships are represented and how animals acquire and manipulate those representations. As Tolman (1948) took pains to note, data from his sunburst maze experiments served only to set limits on the “breadth” of rats' “cognitive-like” maps (his terms). Shortcutting abilities set a lower bound on the complexity of a spatial representation, but leave open many fascinating questions about the mechanisms of navigation. As students of language and consciousness are increasingly discovering, complex skills often decompose into sets of interrelated cognitive processes that different species may embody to different degrees. Focusing exclusively on yes or no questions about the existence of such skills is, like a lost bat, fruitless.

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