

Large-scale navigational map in a mammal

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AUTHOR SUMMARY

Navigation is critical for the survival of animals and has been extensively studied, mostly in nonmammalian species (1–4). The most advanced type of navigation is the ability to travel directly to a certain destination from any starting point in the environment, regardless of its direction and without relying on familiar routes. Evidence for the existence of such navigational map comes from field and laboratory experiments. In the field, homing experiments in translocated lobsters (3) and pigeons (1, 4), for example, showed an ability to navigate from an unfamiliar site to one or more goal locations. Typically, inferences from such homing experiments were based either on animals' vanishing bearing at the release site—that is, the direction in which the animal vanished after release—or based on animals' reappearance at the goal location. Only recently were translocated pigeons and honeybees tracked continuously (2, 4); yet, to date, no high-resolution movement tracks have been collected from free-ranging

mammals homing from translocation distances larger than a few kilometers—and the lack of such data severely limits our understanding of mammalian navigation mechanisms. In the laboratory, various experimental approaches have suggested the existence of a mental representation of space, or a “cognitive map” in rodents (5); yet, the inference of map-like navigation from laboratory experiments on such small spatial scale (i.e., meters) has been questioned. Thus, there is a gap in knowledge about mammalian navigation: most of our knowledge about large-scale navigation comes from studies in nonmammalian species, whereas detailed data on mammals' navigation in the field is scarce, certainly compared with data obtained from birds.

Here, we have set out to close this gap by examining whether a free-ranging mammal performs map-like navigation on large scales (~100 km). To this end, we developed a highly miniaturized global positioning system (GPS) datalogger device (Fig. P1A). We equipped cave-dwelling Egyptian fruit bats (*Rousettus aegyptiacus*) with these devices, which enabled high-resolution measurements of the bats' flight trajectories over several consecutive nights. We asked whether bats possess a cognitive map of their visually familiar environment, which would be manifested by their ability to perform novel short-cuts within this environment, and whether they are capable of homing back to



Fig. P1. (A) GPS device placed on the back of an Egyptian fruit bat. Photo credit: A. Tsoar. (B) Flight trajectory of a bat leaving the cave, flying locally (light gray line), then taking a long commuting flight to the feeding tree (black line) and then back to the cave (dark gray). Bats flew at very straight trajectories, and returned to the same favorite feeding-trees night after night. (C) Bat that was released in the Negev desert in Israel, inside a deep erosional crater that is surrounded by cliffs approximately 300-m high. Note the tortuous disoriented flight (green): this bat flew almost 34 km before it eventually left the crater and turned toward the familiar area. (D) Bats that were released from a high mountain at the crater edge have homed straight (blue line), in contrast to the disoriented flights of bats released inside the crater (green), suggesting an important role for vision in Egyptian fruit bat navigation. C, view from northeast; D, view from north-northeast.

their cave when translocated outside their visually familiar environment.

When bats were released at their cave, they undertook high, fast, and very straight commuting flights from their cave to remote fruit trees (Fig. P1B). Bats returned to the same individual trees night after night, from distances of tens of kilometers, demonstrating superb navigational abilities. When translocated 44 km south of their cave, bats homed directly to one of two goal locations—familiar fruit tree or cave—ruling out beaconing, route-following, or path-integration mechanisms. Bats released 84 km south of their cave, within a deep natural crater, were initially disoriented (Fig. P1 C and D, green line), but eventually left the crater and flew in the direction of their home; in contrast, bats released at the crater-edge top homed directly (Fig. P1D, blue line). Although it is possible that celestial, magnetic, or olfactory cues contribute to long-range navigation in bats, the most parsimonious explanation

for the dramatic behavioral differences between release at the crater edge (i.e., straight homing) and release inside the crater (i.e., disorientation) is visual, reflecting the availability of distal visual landmarks at the crater edge and the lack of familiar distal visual landmarks deep inside the crater. Thus, these data in Egyptian fruit bats suggest that navigation is primarily guided by self-triangulation based on distal visual landmarks.

Taken together, experimental releases at the roost as well as translocation studies suggest that (i) bats are capable of visual-based navigation within a familiar environment and

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(ii) bats can home from outside their visually familiar environment. Further, these data provide evidence for two kinds of navigational capacities in bats. The first is a cognitive map of their visually familiar environment, similar to the map-based mechanism proposed previously for rodent navigation in a water maze (1) but studied here in a free-ranging mammal at five orders of magnitude larger spatial scale. Second, these data demonstrate the ability of bats to home from outside their visually familiar environment. Our findings provide unique evidence for either of these navigational capacities in bats, as

well as evidence for large-scale navigation in a free-ranging wild mammal.

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