COGNITIVE MAPS

The ontogeny of a mammalian cognitive map in the real world

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How animals navigate over large-scale environments remains a riddle. Specifically, it is debated whether animals have cognitive maps. The hallmark of map-based navigation is the ability to perform shortcuts, i.e., to move in direct but novel routes. When tracking an animal in the wild, it is extremely difficult to determine whether a movement is truly novel because the animal’s past movement is unknown. We overcame this difficulty by continuously tracking wild fruit bat pups from their very first flight outdoors and over the first months of their lives. Bats performed truly original shortcuts, supporting the hypothesis that they can perform large-scale map-based navigation. We documented how young pups developed their visual-based map, exemplifying the importance of exploration and demonstrating interindividual differences.

Since the introduction of the idea of a cognitive map (1), there has been an ongoing debate regarding whether non-human animals have such a map (2-4).

It is widely accepted that the most essential characteristic of map-based navigation is the shortcut, i.e., the ability to navigate between familiar points but in a new and direct path (1, 5). When tracking an animal in the wild, one cannot know for certain that the animal has followed that path before the study period. That is, because we did not observe the first time the animal took this path, there is no way to know if it did so using cognitive map-based navigation or some other navigation strategy (Fig. 1A). In this study, we GPS tracked the full movement history of 22 Egyptian fruit bats (Rousettus aegyptiacus) pups from their first flight outside and over the first months of their lives.

The bats gradually increased their home range, which reached a mean of >60 km² after 70 days, similar to that of wild adult bats (6) (Fig. 1B and C). While increasing their home ranges, the bats detected new fruit trees to which they returned to forage on later nights. Individuals’ behavior typically included occasional exploratory nights that were spread between several nights of exploiting previously visited trees. On exploratory nights, the bats flew far beyond their home range and often detected new trees, whereas on exploitative nights, the bats foraged on familiar trees mostly near the colony (fig. SI).

All bats performed shortcuts (for examples, see Fig. 1D and figs. S2 and S3). To make sure that these shortcuts were truly novel, we used a set of conservative criteria, defining shortcuts as movements for which at least 50% of the trajectory was original, i.e., >100 m away from any location where the bat had been previously (see the supplementary text, section S1). Note that these criteria assume that locations where a bat passed before (even for a brief moment) are familiar to it. This conservative assumption substantially reduced the number of shortcuts, but it increased our confidence that shortcuts were truly novel (doubling this criterion to 200 m did not change the results).

Several analyses suggested that the shortcuts were intentional, new, and direct, supporting the conclusion that they were derived from a cognitive map. First, shortcuts were almost as straight as flights in previously used routes, which we defined as “commutes” (the straightness index (SI) quartiles were 0.64 to 0.92 in shortcuts versus 0.78 to 0.96 in commutes; Fig. 2B). Shortcuts were much straighter than exploration flights (i.e., events in which the bats moved to an unfamiliar location; the SI quartiles were 0.64 to 0.92 in shortcuts versus 0.04 to 0.80 in exploration; Fig. 2B and see Additional examples are shown in figs. S2 and S3. (E) A long-cut is depicted in green. The full movement of the bat on all previous nights is depicted in white. The movement on the same night before the shortcut is shown in pink. Additional examples are shown in figs. S4 and S5. (F) Three examples (different colors) of bats flying along a highway. Additional examples are shown in fig. S6.

Fig. 1. Bats gradually increase their home range while mapping their environment. (A) Tracking of an adult fruit bat for >80 days. Around night 60, after flying to points 1, 2, and 3 on the map, the bat performed what is supposedly a shortcut between points 2 and 3 (yellow trajectory). Because we do not know the history of this bat, we cannot be sure that this trajectory is truly novel. For example, the bat might have moved between these two points a year earlier using random search navigation. (B) Average home range size (black) and maximum distance from the colony (red) over time for all 22 bats. Means and SEs are presented. (C) All flown trajectories of one individual bat after 20, 60, and 90 nights of navigation. (D) A novel shortcut is depicted in blue. The full movement of the bat on all previous nights is depicted in white. The movement on the same night before the shortcut is shown in pink. Additional examples are shown in figs. S2 and S3.

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fig. bats headed toward their target from the beginning of the shortcuts, and take-off angles were centered around zero (i.e., they were significantly directional, $P < 10^{-6}$, Watson test, comparing with a uniform distribution between $-90^\circ$ and $90^\circ$; Fig. 2A). In the third analysis, the straightness of shortcuts could not be explained by a correlated random-walk model that was based on the bats’ actual step size and turning angles [but without any navigational goal, $P < 10^{-46}$, Kolmogorov-Smirnov test comparing the SI distributions for the model and the real shortcuts; see null models in (7)].

Because we knew the exact home range of the animals on any day, we describe shortcuts performed from outside the home range as “long-cuts,” and these typically occurred after long exploration flights. We make this distinction because long-cuts entail navigation in areas that were clearly unfamiliar to the bat, often many kilometers away from any location they had ever been before (see examples in Fig. 1E and figs. S4 and S5). Just as in the case of shortcuts, long-cuts were straight (fig. S4), and the bats embarked on them heading in the direction of the target (although this was not the case for exploration flights of similar range; Fig. 2, B and C, and fig. S8). Long-cuts were substantially straighter than exploration flights and only slightly less straight than shortcuts (SI quartiles were 0.52 to 0.81). Long-cut straightness could not be explained by a bat-like correlated random-walk model in which turning and step size were fit to the bats’ actual movement [$P < 10^{-51}$; see null models in (7)]. Long-cut take-off angles were centered around zero and were significantly directional ($P = 0.01$, Watson test, comparing with a uniform distribution between $-90^\circ$ and $90^\circ$; Fig. 2C). Long-cuts could not be explained by simply heading back in the direction of the home range [$P < 0.001$, permutation analysis (7); fig. S9]. Although this suggests that bats were heading directly to their target during long-cuts, we cannot fully exclude the possibility that they sometimes first headed in the direction of the home range and then switched to map-based navigation to home in on their target.

It is difficult to determine the intention of the bats, but many of the movements were performed at the end of the night while returning to the colony (~65% of the long-cuts and ~35% of the shortcuts). We thus ran the same analysis (i.e., straightness and take-off heading) for this subset of movements and the results were identical (Fig. 2 and fig. S10).

In total, we observed 125 shortcuts and 121 long-cuts with an average distance of 1500 and ~3300 m, respectively (fig. S11, A and B). We used a correlated random-walk model to test whether the frequency of performing long-cuts and shortcuts could be explained by a random-walk movement strategy. The model predicted fewer than one long-cut or shortcut compared with the 246 that we observed in reality [see null models in (7)]. Both shortcuts and long-cuts were performed in all possible directions (i.e., azimuths) without any directional preference ($P = 0.22$ and $P = 0.10$ for shortcuts and long-cuts, respectively, Rayleigh test; fig. S12). Bats performed both shortcuts and long-cuts from their first day outside, but it is noteworthy that the bats were at least 10 weeks old at this point (7). The rate of performing shortcuts and long-cuts did not increase over time, but their average distance increased substantially (fig. S13).

Our results suggest that the bats mostly relied on vision [the Egyptian fruit bat is extremely visual, whereas its echolocation can only sense up to a few dozens of meters ahead (8–11)]. First, bats flew significantly higher when performing shortcuts and long-cuts than when commuting in a familiar route [$P < 0.01$ and $P < 10^{-11}$ for the short- and long-cuts versus commute, respectively, generalized linear model (GLM), with altitude set as the explained variable and the type of navigation set as a fixed factor (7); Fig. 2D]. An increased flight altitude suggests the use of vision, especially in an urban environment, where the view is mostly blocked by nearby buildings. Second, the bats ascended just high enough to see beyond the buildings; there was a significant positive correlation between the maximum height of the buildings blocking the bats’ view and the maximum altitude to which they ascended ($P = 0.019$, GLM with building height set as a fixed factor; fig. S14). An analysis of the visual input available for the bats once they...
Fig. 3. Hypothetical schematic of bats’ navigation strategy. Prominent visual landmarks such as buildings are used to move in shortcuts within the home range (A), and to home to familiar points of interest from outside the home range (B). Green shaded area represents the bat’s home range. We propose that, when navigating, the bats set their heading relative to a spatial arrangement of familiar landmarks. The bats must have a map-like representation of these landmarks because they often see them from completely new angles and distances, e.g., when observing them from the south for the first time (inset, top) after only observing them from the north for many weeks (inset, bottom). Note how when observed from the south for the first time, both the right-left orientation of the landmarks and the relative distances between them on the retina change substantially.

ascended above the buildings using drone imaging confirmed that this behavior substantially increased the number of visible landmarks (see the supplementary text, section S2). Third, there was a positive correlation between the altitude above ground of the ascent and the distance of the shortcut or long-cut, as expected when orienting from a remote location while using vision (there was a significant positive correlation between the distance and the altitude, $P < 10^{-6}$ and $P < 10^{-8}$ for the shortcuts and long-cuts, respectively, GLM with the navigation strategy set as a fixed factor; Fig. 2E; also see supplementary text, section S2).

We performed several additional analyses to exclude the use of alternative, nonvisual input (fig. S15). First, to control for the potential use of an olfactory mosaic map (12, 13), we compared wind direction with the straightness of all shortcuts and long-cuts, assuming that if bats were using olfaction, then they should navigate more accurately when flying upward than when flying downward. There was no correlation between wind direction and navigation straightness ($P = 0.66$, $r = 0.04$ and $P = 0.051$, $r = 0.18$ for the shortcuts and long-cuts, respectively, Pearson’s correlation test; fig. S15D). The olfaction-gradient navigation hypothesis is probably not relevant for our bats because this navigation strategy has been shown to be relevant only when homing from long distances (beyond ~5 km), and most of our navigations were shorter (14). We do not entirely exclude the possibility that olfaction plays some role in fruit bat navigation but argue that it is probably used for short-distance orientation when searching for a tree with ripe fruit. Second, to control for use of sound cues, we analyzed continuous audio recordings performed onboard nine bats [see (7) and fig. S16]. Third, the use of echolocation for performing long-cuts or shortcuts is unlikely because echolocation is a short-ranged modality and bats can detect a large tree from a distance of no more than 50 m (15). Moreover, Egyptian fruit bats usually do not echolocate during their commute (10), a fact that we also confirmed in our audio recordings.

Although bats may use additional senses during foraging and navigation, our data suggest that vision is their main sense in map-based navigation (see the supplementary text, section S8). Our data also suggest that the bats had to represent navigational information in a viewpoint-invariant fashion (Fig. 3) to assess their location and desired heading, an ability that is considered to be a key feature of a cognitive map (16). We therefore suggest that the bats used the spatial arrangement of distal visual landmarks (e.g., using triangulation) before embarking on a navigation flight to determine their desired heading, and to some extent also distance (an analysis of their flight speed at the beginning of shortcuts and long-cuts suggested that they had some estimate of the distance; see the supplementary text, section S4). It is very unlikely that our bats followed other bats when performing shortcuts or long-cuts (see the supplementary text, section S5).

Individual bats varied in their degree of exploration (Fig. 4, A and B). As has been shown in other species (17, 18), we hypothesized that bats that explored more would build a more complete cognitive map, thus allowing better navigation. Indeed, bats translocated to unfamiliar locations (7) showed more direct paths home when they had been more exploratory previously (Fig. 4, C and D).

Moreover, bats that flew higher on the nights preceding the translocation also homed in significantly straighter trajectories, supporting the vision-based navigation hypothesis ($P = 0.004$, GLM with altitude set as a fixed factor; Fig. 4E). Bats that were closer to the translocation release point before the translocation night did not necessarily navigate home better, once again contradicting the template-matching hypothesis ($P = 0.66$, GLM with the previous distance to translocation point set as a fixed factor; Fig. 4F). In other words, a bat that was near the translocation point on the previous night was not necessarily able to home back directly, whereas a bat that was never near this point but tended to fly high on previous nights homed in a straighter trajectory, supporting the use of map-like navigation. There was also no significant correlation between the day of the translocation or the age of the bat and the straightness of the return ($P = 0.9$, $r = 0.04$ and $P = 0.8$, $r = 0.05$, respectively, GLM), suggesting that it is not experience per se but specifically exploratory experience that is important for navigation (19).

In one of the most critical reviews, Bennet (1996) raised three main limitations that led him to conclude that no study had shown a cognitive map in a wild animal under natural conditions (20). In brief, Bennet claimed that (i) because the animal’s history is unknown, reported novel shortcuts might not truly be novel; (ii) some studies did not rule out the use of path integration when performing the supposed shortcuts; and (iii) some studies can be explained by non-map-based, simpler navigation strategies (21) that could explain the animals’ movement (e.g., beaconing or route following).

Our study allows us to exclude all of these possibilities. First, we tracked the animals’ full
Fig. 4. Translocation experiments reveal individual navigation capabilities. (A) Different individuals (x-axis) tended to be more or less exploratory. The y-axis depicts the bat’s home range on day 60. “Koral,” “Suki,” and “Nature” are bat names. (B and C) Three examples of translocations for a weak explorer (left column), an intermediate explorer (middle column), and an extreme explorer (right column). (B) Movements of the three bats before the translocation. (C) Return flights of the same three bats from the translocation point. (D and E) The straightness of homing back from the translocation point significantly correlated with: (D) the tendency to explore (depicted by the home range) and (E) the altitude flown by the bats on the nights before the translocation. (F) The straightness of homing back did not correlate with the nearest distance of previous trajectories to the point of translocation (i.e., how close the bat was to the translocation point on previous nights).

hypotheses and were thus able to determine where a shortcut was truly novel. Second, we ruled out the use of path integration. Specifically, path integration, which does not require external sensory input, is notorious for its accumulation of error (22), and this is true in bats (23). If the animals were using path integration, then we would expect an increase in error when they flew farther from their starting point and when they turned more (22, 24, 25). We found no correlation between the straightness of the long-cuts and any of these parameters: accumulated flight duration, flight distance, or turning before the return (fig. S17). In addition, the animals’ ability to return from the translocation sites (in straight trajectories) could not be explained by path integration.

Taken together, our results satisfy the requirements of demonstrating visual map–based navigation. That said, some caveats are in order. First, we do not claim that the map is Euclidean or that the distances are accurately represented in the bat’s brain. Second, navigation is a complex behavior that probably does not always rely on a single strategy (2, 26). Bats occasionally switched from using map-based navigation to alternative strategies like flying along landscape elements such as highways (Fig. 1F, fig. S6, and supplementary text, section S6), but our data demonstrate that they have a map-like representation of their environment and can navigate according to this cognitive map when necessary.

ACKNOWLEDGMENTS

We thank N. Ulanoynsky, T. Elav, and M. Geva for reading and commenting on the manuscript and M. Taub for assistance with graphics. Funding: This research was partially supported by the European Research Council (ERC–GPSBAT). Author contributions: L.H. and Y.Y. designed the experiment. Y.Y., A.K., and A.G. conducted the experiment. A.G. performed drone imaging and analysis. Y.Y. wrote the manuscript. L.H., A.K., and A.G. reviewed the manuscript. Competing interests: The authors declare no competing interests. Data and materials availability: All datasets included in the paper are available on Mendeley (27).

SUPPLEMENTAL MATERIALS

science.sciencemag.org/content/369/6500/194/suppl/DC1

Materials and Methods: Supplementary Text, Sections S1 to S6 Figs. S1 to S25
Captions for Movies S1 to S4
References (28–38) Movies S1 to S4
GPS Tracking Data
11 June 2019; accepted 29 May 2020
10.1126/science.aay3354
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Science 369 (6500), 194-197,
DOI: 10.1126/science.aay3354

Knowing their way around
The presence of a cognitive map is essential to our ability to navigate through areas we know because it facilitates the use of spatial knowledge to derive new routes. Whether such maps exist in nonhuman animals has been debated, largely because of the difficulty of demonstrating qualifying components of the map outside of a laboratory. In two studies on Egyptian fruit bats, Harten et al. and Toledo et al. together show that this species’s navigational strategies meet the requirements for the use of a cognitive map of their environment, confirming that this skill occurs outside of humans (see the Perspective by Fenton).

Science, this issue p. 194, p. 188; see also p. 142

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