

## 1.18 Bat Navigation

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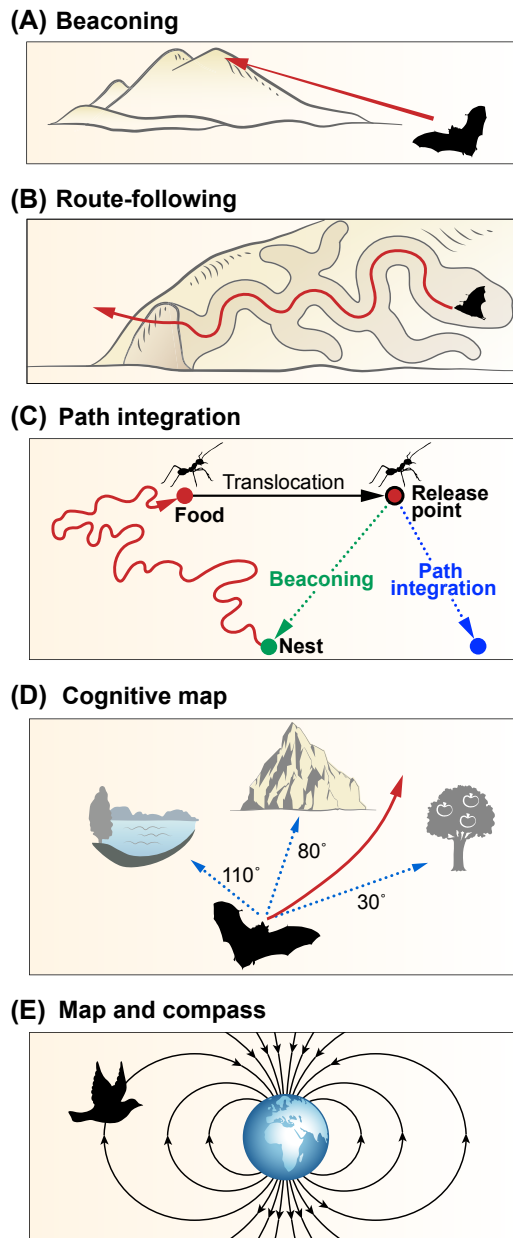
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Navigation, the capacity to plan and execute a goal-directed path (Gallistel, 1990), is crucial for almost any task an animal must perform, including foraging, roost finding, seasonal migration, and, sometimes even mating. Bats, the only mammals capable of self-propelled flight, show remarkable navigation capabilities on a wide range of spatial scales. Some bat species annually migrate over hundreds or thousands of kilometers, driven by food availability or heading toward better winter hibernacula (Griffin, 1970; Richter and Cumming, 2008; Bisson et al., 2009). Many bat species commute nightly over dozens to hundreds of kilometers, sometimes exhaustively searching for food in circuitous paths (Cvikel et al., 2015), while at other times returning to the exact same location in a remarkably straight line night after night (Tsoar et al., 2011; Sapir et al., 2014). Many bat species can orient themselves to an exact point in a small-scale space (meters) with a centimeter accuracy, based on proximal and distal landmarks (Neuweiler and Möhres, 1967; Jensen et al., 2005; Ulanovsky and Moss, 2008). Despite a dramatic increase in bat navigation research over recent years, our understanding is still sparse in comparison to that of bird navigation; and in particular, relatively little is known about the mechanisms and strategies underlying bat navigation.

In this chapter, we will summarize the current state of knowledge regarding bat navigation capacity. We will divide the chapter according to the commonly defined navigation strategies from the simplest one – beaconing, which requires sensing the ultimate goal or a landmark nearby the goal already from the starting point, to the most complex one – the “true map,” which allows the animal to freely move efficiently from any location to any destination including novel shortcuts. Navigation is tightly linked to sensing, and much of the study of navigation across species aims to reveal and understand the sensory systems involved in guiding navigation. We will therefore attempt to tie bat movement capabilities to the sensory abilities that might facilitate them. Finally, we will provide hypotheses about possible neural representations in the bat brain, which may underlie bat navigation in the wild; although highly speculative, we hope these ideas will help guide future experiments.

### 1.18.1 Beaconing

Beaconing is the simplest type of navigation, in which the navigator can sense directly its goal or a landmark near the goal, right from its starting point – and uses this direct sensory information to move toward that landmark (Fig. 1A). The use of beaconing by bats has never been proven completely, but several observations suggest that it is very likely used in some scenarios. For example, it has been suggested that phyllostomid bats in Trinidad rely on visual beaconing for navigation – using the view of the central mountain range of the island (Williams et al., 1966), but this has not been directly tested. A study on big brown bats suggested that they beacon toward the sounds of a frog chorus in a nearby swamp, as well as to the same sounds that were broadcasted by the experimenters – but only if the bats were hungry (Buchler and Childs, 1981). This study provided the most direct demonstration of beaconing in bats in outdoors navigation. Some recent surveys reported that *Nathusius' pipistrelle* bats, which are migrating over the North Sea, take rest during the day on oil-drilling rigs that are located many dozens of kilometers offshore



**Figure 1** Navigational strategies: schematic illustrations. (A) Beaconsing. (B) Route-following. (C) Path integration. (D) Cognitive map. (E) Map and compass. See (Gallistel, 1990; Geva-Sagiv et al., 2015) for more details. Adapted from Geva-Sagiv, Maya, Liora, Las, Yossi, Yovel, Nachum, Ulanovsky. 2015. Spatial cognition in bats and rats: from sensory acquisition to multiscale maps and navigation. *Nat. Rev. Neurosci.* 16 (2), 94–108. <http://dx.doi.org/10.1038/nrn3888>. Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved.

(sometimes more than 100 km; Boshamer and Bekker, 2008). The large size of these structures, which are lit in the middle of the dark sea at night, implies that the bats might be using visual beaconing to find them in this mostly cueless environment. While beaconing is a naïve strategy that is likely of limited utility for most long-distance navigation tasks, there is a more elaborate version of beaconing, namely: using a series of beaconing steps to move from one landmark to the next, thus creating a longer segmented trajectory, which could facilitate complex navigation. This navigation strategy is typically called route-following.

### 1.18.2 Route-Following

Navigation along a route, where the movement course changes at specific landmarks, is termed route-following (Fig. 1B). Such navigation necessitates recognition of specific landmarks, where the course of the movement changes, i.e., turning points or waypoints.

Strictly speaking, the animal may use certain landmarks as waypoints even without exhibiting an overt change in direction—but these cases are generally more difficult to study, in the absence of an overt behavioral response by the animal—except if one experimentally removes these landmarks (see later). Landmark recognition can be based on any sensory modality available to the animal. Route-following also requires straight-guided movement between turning points, and this movement can be maintained either using external sensory cues or by measurement of self-motion (idiothetic cues). Many bats fly along the same fixed routes when commuting from their roost to the hunting areas on a nightly basis. These routes, which have been termed flyways, stretch in many cases along linear landscape elements such as tree lines, bush hedges, river valleys, and natural or artificial walls (Racey and Swift, 1985; Verboom and Huiteema, 1997; Verboom et al., 1999; Schaub and Schnitzler, 2007). Bat flyways often do not stretch along the shortest (most direct) trajectory from the roost to the foraging areas, supporting the hypothesis that bats rely on route-following navigation when using flyways (Krull et al., 1991).

Flying along flyways is characteristic mostly for small bats, which forage relatively close to their roost (up to a few kilometers) (Racey and Swift, 1985). Many of the bats that exhibit this behavior do not excel in vision (Eklöf, 2003). In some cases there is no visual input available at all, as, for example, in bats that must fly several kilometers inside a cave, to reach its opening every night (Blatcheley, 1896). It is thus intriguing to hypothesize that some bats that use flyways, rely on acoustic echo-based landmarks to perform route-following navigation (although some bats that navigate along flyways might also rely on vision, olfaction, or other senses). Natural objects (e.g., plants) have acoustic signatures that can be recognized by an echolocating bat (Yovel et al., 2008, 2009), and can be used by it as landmarks for navigation (Jensen et al., 2005). Flying along linear landscape elements could provide orientation cues to guide the bat between landmarks. For example, the instructions for flying along a segment of the flyway could read: “fly along the hedge until detecting the echo of the pine-tree, and turn left at that point.”

Indirect evidence in support of this acoustic route-following hypothesis comes from reports that some bat species are able to return to their cave from up to 15 km when blindfolded but not when deafened (Stones and Branick, 1969). However, to date no one has systematically manipulated a bat flyway by adding, removing, or altering specific landmarks, while documenting the bats’ navigational response using precise tracking in a way that will prove route-following navigation. The route-following hypothesis is therefore only an educated guess. The primary reason for this lack of information is that, technologically, it is still very difficult to track small echolocating bats—many of which weigh under 15 g—with high accuracy over long distances (even tracking them over “only” a few hundred meters or several kilometers is difficult). Recent developments in technology should allow performing these crucial experiments in the near future.

Longitudinal elements such as hedges have the additional property that they generate acoustic flow (Müller and Schnitzler, 2000) – which could in theory allow a bat to estimate its flight distance similarly to how bees use optic flow to do so (Srinivasan et al., 2000). Reliance on acoustic flow could serve as an alternative explanation for the use of flyways by bats, without a need to recognize specific landmarks. The strategy of a bat could be: “fly 150 m (based on acoustic flow) and then turn right.” While beaconing and route-following navigation rely on constant acquisition of external sensory information, the next strategy that we will discuss—path integration—does not require any sensory input from external landmarks.

### 1.18.3 Path Integration

Navigating based on pure path integration enables an animal to compute its location and direction in the absence of any external landmarks, solely based on integration of self-motion (idiothetic) information. Pure path integration is very difficult to prove because it is almost impossible to deprive an animal from all sensory input and expect it to behave normally – except on very small spatial scales. Even if the animal can perform pure path integration, deprivation of all sensory input will most likely stress the animal, dramatically affecting its natural behavior. An alternative key paradigm used to test path integration—without depriving it of sensory inputs—is based on translocating an animal after it has moved a certain distance from a familiar location (e.g., its roost) and monitoring its return. The animal is considered to use path integration if it then moves in a straight vector (distance and direction) that would have led it to its target (e.g., its roost) had it not been translocated (Fig. 1C). A series of classical experiments of this kind have proven the use of path integration in the desert ant *Cataglyphis fortis* (Müller and Wehner, 1988; Andel and Wehner, 2004) – and were used as support for the idea that animals can maintain a “home vector” toward their goal (Muller and Wehner, 1988). However, such experiments have never been conducted in bats. Moreover, such translocation experiments are usually difficult to interpret in animals that may routinely use multiple navigation strategies simultaneously because even if they are capable of path integration, they might not exhibit the expected vectorial behavior described earlier, but choose a different strategy. For example, the animal might use various sensory cues to detect that it was translocated and then switch to using an alternative navigation strategy such as beaconing or map-based navigation – even if it path-integrated prior to the translocation (Menzel et al., 2005; Filanino et al., 2014; Finkelstein et al., 2016).

Several studies found that bats in the field and in the laboratory will orient in space based on their memory of the environment, ignoring new incoming sensory input. Three typical examples include bats crashing into a net at the location where a hole in the net was previously present (Jensen et al., 2005); bats searching for a nectar feeder at its previous location (Helvesen von and Winter, 2003); and bats flying into a door placed in the middle of a previously open flyway [even at the cost of losing their lives (Blatcheley, 1896; Griffin, 1958)]. Many other similar reports exist. They are usually correctly interpreted as examples for reliance on spatial memory – but they are often misinterpreted as evidence for path integration. The common assumption made is that because the bats ignored some new sensory information, they must have been moving based on internal, idiothetic information, ignoring

all external sensory cues. However, the bats' behavior could also be the result of relying on the many distal or proximal sensory cues that have *not* changed in the environment, other than the one specific landmark that has changed (e.g., the hole, feeder, or door in the examples described earlier). In all reported examples of spatial memory in bats, the environment has mostly remained the same, thus making it reasonable for the bat to maintain its previously used path. In humans, a visual phenomenon in which major changes in an image are ignored is well documented and termed change-blindness (e.g., O'Regan et al., 1999); something similar to change-blindness may have occurred in the aforementioned studies of bats. Importantly, none of the authors of these studies reported that bats stopped echolocating in these situations of change-blindness, suggesting that they were likely still actively collecting sensory information about their environment. In many of these examples, bats were reported to return to the same location in space with an accuracy of a few centimeters. This behavior might actually hint to an ability to map space with very fine accuracy rather than to an ability to fly based on purely internal path integration.

Although there is currently no demonstration of pure path integration in bats—with the possible exception of short flights of 1–2 m (Höller and Schmidt, 1996)—they can probably partially rely on path integration, in conjunction with other navigational strategies. Bats could estimate direction and speed of movement without external feedback, using, for example, information from their flow-sensitive hair cells (Sterbing-D'Angelo et al., 2011) and probably also from other sources such as their vestibular system or their wing-beats. However, flying long distances while relying only on pure path integration, without any external calibration, is prone to accumulate substantial navigational errors and is thus very unlikely (Cheung et al., 2007). A more realistic navigation strategy is a mixed approach combining internal idiothetic and external sensory cues. A bat could rely on different external cues to estimate its flight speed and direction. It could, for example, use acoustic flow for estimating distance (Müller and Schnitzler, 2000) and magnetic information for estimating direction (Holland, 2006; Wang et al., 2007; Holland et al., 2010). The bat's brain could then internally integrate its movement, which was measured based on this external information, to continuously assess its position in space within those "spatial gaps" where it does not encounter any familiar landmarks—for example, when it flies through clouds, fog, or behind hills (Finkelstein et al., 2016). By contrast, when external familiar landmarks are observable, the animal might use them to self-triangulate its position without using the path integration information. Self-triangulation is one of the mechanisms proposed for the most advanced type of navigation—map-based navigation—to which we turn next.

#### 1.18.4 Map-Based Navigation

The most sophisticated navigation strategy is map-based navigation, in which the animal holds a mental map of the environment in its brain (Tolman, 1948; O'Keefe and Nadel, 1978; Gallistel, 1990). This cognitive map enables flexible navigation without the need to pass through familiar waypoints. The hallmark of map-based navigation is the ability to move in an unfamiliar trajectory (i.e., a shortcut) between any two locations within the mapped area (Menzel et al., 2011). The navigation literature commonly distinguishes between a local cognitive map limited to some familiar area (Tolman, 1948) and a map-and-compass navigation strategy that allows map-based navigation over global geographical scales – even in unfamiliar areas (Kramer, 1953). We shall return to this difference later.

##### 1.18.4.1 Small-Scale Maps (Centimeters to Meters)

Many laboratory studies strongly imply that bats can create a map of a small-scale environment (several meters) with very high accuracy. Some examples include (1) bats repeatedly passing through the exact same hole in a grid composed of 70 identical holes (Neuweiler and Möhres, 1967) – where moving the hole by as little as 2 cm caused a drop in performance and (2) bats using the position of an acoustic landmark to precisely infer the location of a nearby hole in a net – moving the landmark resulted in crashing into the net next to the landmark's new position (Jensen et al., 2005). Bats have also been shown to adopt individual-specific highly stereotypical flight trajectories when flying through a confined space for several days: when released from different positions in the room, these bats immediately converged onto their typical flight trajectory, suggesting that they have mapped the room (Barchi et al., 2013). Finally, a field study of Brazilian free-tailed bats has shown that they can return to the exact same spot in the cave where they have left their pups while foraging (McCracken, 1993)—and they exhibited the same centimeter-scale accuracy even after the pup had been removed—suggesting that they possess a cognitive map of their cave system (or at least of that particular cavern), with a centimeter resolution.

To the best of our knowledge, however, no study has rigorously examined the ability of bats to perform shortcuts in an unfamiliar trajectory between any two arbitrary locations in a small-scale environment – which is the kind of experiment that would be required to strongly claim for the existence of a true cognitive map on such scales. The behaviors described earlier are suggestive of a detailed mapping of the environment – but they do not prove a cognitive map in the strict sense because they could potentially be explained otherwise, for example, by motor learning (example 1) or by beaconing (example 2).

##### 1.18.4.2 Large-Scale Maps (Kilometers to Hundreds of Kilometers)

Early studies showed that bats can find their way back to their roost after being translocated distances of dozens or even hundreds of kilometers, with the big brown bat holding the record of 720 km (see Davis, 1966 for a review). However, these experiments were based on capture–recapture techniques without any tracking of the bats, and oftentimes the bats were recaptured after 1 or 2 weeks,

or more – so until the recent emergence of new tracking technologies (e.g., miniature Global Positioning System [GPS]) it remained unclear whether the bats homed straight or found their home after circuitous searching (Davis, 1966; Griffin, 1970). Further, the lack of miniature accurate tracking technology did not allow studying the navigational mechanisms allowing the bats to do so. Nevertheless, it is quite clear that unlike small-scale maps, echolocation could not be the main sensory system used to construct such large-scale maps: The sensing range of echolocation is highly limited (no more than 100 m for very large objects [Stilz and Schnitzler, 2012]), making it highly unlikely that a bat could map a kilometer-sized area by solely relying on echoes.

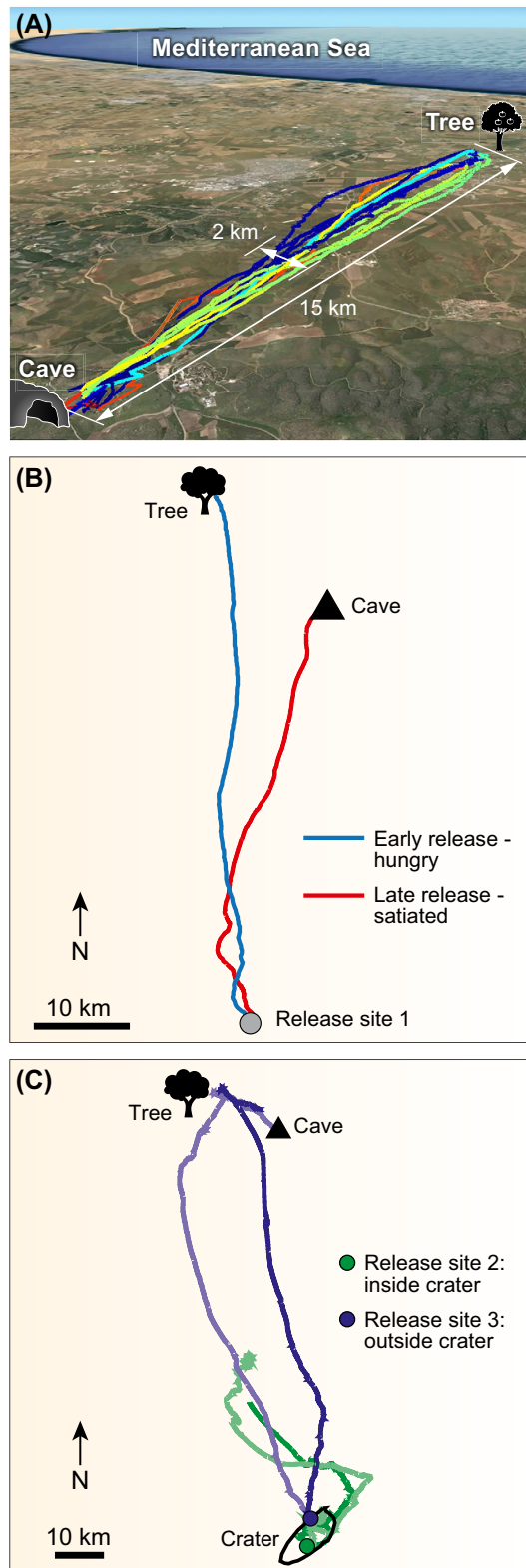
#### 1.18.4.3 A Visual-Based Large-Scale Cognitive Map

The miniaturization of GPS devices and other localization technology now allows studying the mechanisms of long-distance bat navigation for the first time. The first bat species to be investigated using GPS was the Egyptian fruit bat (*Rousettus aegyptiacus*) – a long-lived social bat roosting in colonies of dozens to thousands of conspecifics (Kwiecinski and Griffiths, 1999). These bats opportunistically feed on various fruit trees – oftentimes flying to the exact same tree night after night (Fig. 2A). Two translocation experiments provided strong evidence for the existence of a visual-based large-scale cognitive map in this species (Tsoar et al., 2011). Bats that were translocated 44 km from their cave chose to fly either back to the cave or to a familiar foraging tree (~30 km from their cave), depending on whether they were fed or not prior to the release (Fig. 2B: compare the trajectory of a hungry bat that was released early, in blue – vs. a satiated bat that was fed and released late, in red). GPS tracking revealed that bats used remarkably straight flight trajectories in both cases – despite the fact that both the cave and the trees were not visible to the bat and did not have any light sources near them (thus ruling out visual beaconing). This suggests an ability to move directly between locations within an area that was likely never visited before, but that was visually mapped from afar by these high-flying bats.

To elucidate the sensory mechanism underlying this long-distance navigation, the researchers translocated a second set of bats to a distant crater, located 84 km from the cave. This crater is located deep in the desert, far outside the home range of these animals, and was therefore with high likelihood completely unfamiliar to the bats. The bats were divided into two groups: one was released from the bottom of the crater, thus deprived of any possible terrestrial visual landmarks – but these visual landmarks were available to the other group, which was released from the top of a mountain at the crater rim. At least 75% of the bats found their way back to the cave, most of them doing so within a single night (the remaining 25% might have returned and lost their GPS-tags on the way). There was no difference in the probability of the two groups to home, but there were clear differences in their flight patterns, especially along the first kilometers of the flight. The visually deprived group exhibited initial disorientation and flew in trajectories with high tortuosity both inside the crater and after emerging from it (Fig. 2C, green lines) – whereas the control bats flew straight in the direction of the cave (Fig. 2C, blue lines). These results suggest that distal visual landmarks, such as mountains, the sea, or anthropogenic lights, are important for large-scale navigation in the Egyptian fruit bat and probably facilitate the maplike navigation capacity it exhibits. A reasonable hypothesis raised by the authors is that the bats performed self-triangulation based on multiple distal visual landmarks (Tsoar et al., 2011). That is, they localized themselves based on identifying distal landmarks whose locations they knew and they could then adopt a flight route that was relative to these landmarks (illustrated in Fig. 1D). Such a fully flexible self-triangulation representation can be considered as a kind of a cognitive map (Gallistel, 1990; Tsoar et al., 2011).

Reliance on vision in echolocating bats should not come as a surprise. All bats can see, and vision sometimes has clear advantages over echolocation, especially for long-range sensing (Rydell and Eklöf, 2003; Boonman et al., 2013; Bar et al., 2015). Several earlier studies have already demonstrated a role for vision in long-distance navigation by bats. Blindfolded bats showed dramatically reduced homing capabilities in comparison to controls in several homing studies, especially when testing long-distance homing >15 km (Smith and Goodpaster, 1958; Williams et al., 1966; Griffin, 1970; Davis and Barbour, 1970). Blindfolded bats were also shown to fly lower, perhaps trying to sense the ground using echolocation (Mueller, 1968), similar to how blindfolded humans move along walls.

The use of other sensory modalities such as olfaction or magnetic sensing, which are often suggested as important for large-scale navigation in birds, has not been overruled in this study of the Egyptian fruit bat: for example, the bats might have possibly smelled the odors of the Mediterranean Sea. Moreover, the bats released inside the crater always emerged from it oriented northward (Tsoar et al., 2011). This implies that another sensory system (besides vision) might have played a role in their initial choice of direction, although celestial (visual) cues might have also been available inside the crater to some extent. There is some evidence that certain bat species can visually detect stars (Childs and Buchler, 1981), and fruit bats have excellent vision relative to most bats (Neuweiler, 2000). Egyptian fruit bats are also renowned for using both echolocation and vision for short-range orientation (Griffin, 1958). They have been recently shown to modulate the acquisition of echolocation depending on the availability of visual input (Danilovich et al., 2015). Fruit bats thus might possess several cognitive maps at different scales, which are based on different sensory modalities. They could perform their nightly commute of dozens of kilometers from the roost to the fruit tree based on a visual cognitive map and then switch to an echo-acoustic cognitive map, which allows them to land on a specific branch once they arrive at the tree. Vision and echolocation could also be used to create maps at the same spatial scale: direct neuronal evidence for this come from a recent study of hippocampal “place cells”—the neurons that are thought to hold the cognitive map in the brain (see later)—in bats that flew in a laboratory setting where they had to rely either on vision or on echolocation; this study has found that the same space is represented by completely different (orthogonal) cognitive maps for the two different sensory modalities (Geva-Sagiv et al., 2016). This result may suggest that the brain of bats holds a “cognitive atlas,” with different maps for different sensory modalities – and these maps can be pulled up separately according to the animal’s needs (Geva-Sagiv et al., 2016).



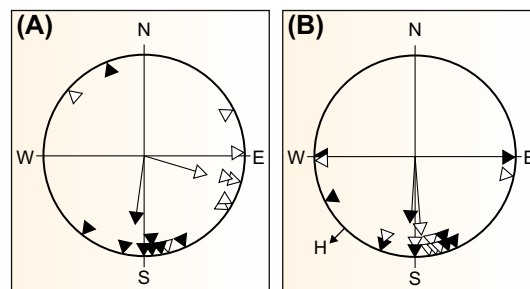
**Figure 2** Navigation in the Egyptian fruit bat. (A) Example of an individual bat that was tracked using a miniaturized GPS-datalogger, and commuted for 7 nights from its roosting cave to a specific fruit tree, to forage—exhibiting very straight flights. (B) Example trajectories of two bats that were translocated 44 km south of their cave and were released either early and hungry—in which case they flew straight to their favorite feeding tree (*blue line*); or were released late after having been fed and satiated—in which case they flew straight to their cave (*red line*). See (Tsoar et al., 2011) for further details. (C) Vision is important for navigation in Egyptian fruit bats. *Green lines*: example trajectories of two bats that were

#### 1.18.4.4 A Sun-Calibrated Magnetic Compass

Map-based navigation requires both a map to determine one's location in space and a compass, which then allows the animal to guide its movement in the correct direction. Self-triangulation, as has been suggested in the Egyptian fruit bat, may potentially allow map-based navigation without a separate compass mechanism – because the directional compass information can, in principle, be inferred from the distal landmarks, i.e., from the map itself. Alternatively, it can be useful to have a compass mechanism that is separate from the map mechanism (Wallraff, 2005). In another series of translocation experiments in bats, Holland and Siemers provided strong evidence for the existence of a magnetic sun-calibrated compass in insect-eating bats (Holland et al., 2010). They translocated greater mouse-eared bats (*Myotis myotis*) and released them at a distance of 25 km from their cave. The bats were divided into two treatment groups, both of which were allowed to observe the sunset before release. Half of the bats (the controls) sensed the natural geomagnetic field while observing the sunset, while the other half were exposed to a 90 degree (eastward)–rotated magnetic field, generated using a Helmholtz coil. The researchers monitored the vanishing directions of the bats using radiotelemetry and found a significant difference between the two groups: the experimental group was shifted eastward, flying on average 78 degrees eastward to the controls (Fig. 3A). The rotated magnetic field thus altered the navigational behavior of the bats. Similar results were reported for big brown bats (Holland et al., 2006). However, the role of the sun was not yet conclusively clarified.

To investigate the possible importance of the sun in this process, two new groups of bats were translocated to the same release site, but this time without seeing the sunset. As before, half of the bats experienced a rotated magnetic field and half were controls released at the same time—but none of them were exposed to the sunset or to any postsunset glow. This time there was no difference between the two groups, who both headed on average southward on release (Fig. 3B). The lack of an effect on the experimental group indicated that the exposure to some aspect of the setting sun was responsible for the shifted orientation in the first experiment. The authors concluded that bats use Earth's geomagnetic field as a compass, which they calibrate based on sunset cues.

Several previous studies suggested that bats can detect the Earth's geomagnetic field (Holland et al., 2006, 2008; Wang et al., 2007), but the mechanism of magnetic sensing in bats (and birds) is still under debate (Freake et al., 2006; Mouritsen et al., 2016). One immediate question that comes to mind is why should a magnetic compass be calibrated? An interesting hypothesis suggests that magnetic information could be used not only as a compass, but also as a map. Global latitude, for instance, can be roughly determined based on the intensity of the local magnetic field—but then another measurement is required for determining longitude. One option for estimating longitude is measuring declination—the deviation of the magnetic field from the geographical north—which varies substantially and systematically as function of longitude (this variation becomes larger in areas close to the poles). Declination could be assessed by observing the sunset to determine geographical north and calibrating the magnetic compass accordingly. In contrast to visual mapping—as has been suggested for Egyptian fruit bats—magnetic mapping



**Figure 3** A sun-calibrated magnetic compass. (A) Bats that were exposed to an east-shifted magnetic field at sunset (*empty triangles*) left the translocation site with an average bearing that was rotated 78 degrees eastward relative to controls (*filled triangles*). (B) When bats were not exposed to sunset while experiencing the shifted magnetic field, there was no difference between the experimental bats and the controls. Adapted with permission from Holland, Richard A., Ivailo, Borissov, Björn M. Siemers, 2010. A nocturnal mammal, the greater mouse-eared bat, calibrates a magnetic compass by the sun. *Proc. Natl. Acad. Sci. U.S.A.* 107 (15), 6941–6945. <http://dx.doi.org/10.1073/pnas.0912477107>.

translocated 84 km south and were released at the bottom of a deep crater, from which they could not see any familiar visual landmarks; these bats exhibited tortuous flights—but eventually found their way north, back to the cave. *Blue lines*: Example trajectories of two bats that were released on a high mountain at the crater edge, from which familiar visual landmarks were available, and have homed straight north. See Tsoar et al. (2011) for details. Panel (A) adapted from Geva-Sagiv, Maya, Liora, Las, Yossi, Yovel, Nachum, Ulanovsky. 2015. Spatial cognition in bats and rats: from sensory acquisition to multiscale maps and navigation. *Nat. Rev. Neurosci.* 16 (2), 94–108. <http://dx.doi.org/10.1038/nrn3888>. Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved; panel (B) shows data replotted from Tsoar, Asaf, Ran, Nathan, Yoav, Bartan, Alexei, Vyssotski, Giacomo, Dell’Omo, Nachum, Ulanovsky. 2011. Large-scale navigational map in a mammal. *Proc. Natl. Acad. Sci. U.S.A.* 108 (37), E718–E724. <http://dx.doi.org/10.1073/pnas.1107365108>; panel (C) adapted with permission from Tsoar, Asaf, Ran, Nathan, Yoav, Bartan, Alexei, Vyssotski, Giacomo, Dell’Omo, Nachum, Ulanovsky. 2011. Large-scale navigational map in a mammal. *Proc. Natl. Acad. Sci. U.S.A.* 108 (37), E718–E724. <http://dx.doi.org/10.1073/pnas.1107365108>.

(e.g., using field intensity and declination) could allow global navigation from unfamiliar locations because the animal can potentially determine its position anywhere on earth based on extrapolation of these magnetic gradients. This type of global navigation strategy is commonly termed “map-and-compass navigation” (Fig. 1E) – although we note that this terminology may be somewhat confusing because an internal compass (a sense of direction) is important also when navigating locally using a cognitive map (Geva-Sagiv et al., 2015; Finkelstein et al., 2015). It is highly debatable whether the mouse-eared bats in the aforementioned study (Holland et al., 2010) could rely on magnetic information to determine their location when translocated a short distance of ~25 km – because changes in magnetic intensity are very small (on the order of pico-tesla) at such short distances. Bats are more likely to use such a magnetic-based map-and-compass strategy when migrating over much longer distances, of thousands of kilometers – over which the magnetic intensity and declination gradients are much more substantial (Lohmann et al., 2007; Wiltschko and Wiltschko, 2013; Gould, 2015). An additional question that might be asked is how nocturnal creatures such as bats, which are often also cave dwellers, get access to the sunset to calibrate their compass. A possible answer is that many bat species typically fly in circles at the cave entrance prior to sunset, before emerging to forage, and thus may sense the sunset directly, and most bats emerge from their caves when postsunset glow is still visible.

A daily calibrated magnetic compass has been suggested in birds (Cochran et al., 2004). It has been proposed that in birds the magnetic compass is specifically calibrated by polarized light (Muheim et al., 2006). Therefore, to test whether bats also rely on polarized light, Greif and Holland conducted a complementary study to the magnetic compass study mentioned earlier in which they performed a similar translocation experiment and demonstrated that greater mouse-eared bats (*M. myotis*) also use polarization cues at sunset to calibrate their magnetic compass (Greif et al., 2014). They showed that rotating the polarization pattern of the sky at sunset by 90 degrees, results in an equivalently rotated flight direction of bats that were released after translocation – suggesting that at least part of the sun-based calibration process is done via polarization vision.

#### 1.18.4.5 The Missing Links I – Navigation Behavior

In our era of ever-increasing miniaturization, it becomes possible to develop small, lightweight, long-term, and accurate tracking devices – which will allow examining animal navigation in much more detail, possibly inferring also some of the sensory mechanisms and decision-making processes underlying navigation. This new avenue has the potential of dramatically increasing our understanding of bat navigation in upcoming years. Here are a few important directions that should be pursued.

##### 1.18.4.5.1 The Map

None of the numerous bat translocation studies has directly dealt with the map component of navigation, and specifically – how exactly do translocated bats recognize the location of the site they were translocated to? In one study, bats that were simultaneously translocated ~400 km in different directions showed dramatic differences in their probability of homing from different sites (16% from one release site vs. 67% from the other site), suggesting that maybe the familiarity with the translocation area affects the probability of return (Davis, 1966). Most studies settle for one or two translocation sites, thus overlooking such effects. Moreover, in most cases, researchers do not really know the home range or the familiar areas of the translocated species, thus making it difficult to examine the influence of familiarity. If one could track bats with tiny GPS devices over months or even years, before and after translocation experiments, these problems could potentially be addressed directly. Until then, mapping strategies are bound to be far less understood than compass mechanisms, due to the difficulty to probe them.

##### 1.18.4.5.2 Sensorimotor Navigation Strategies

A good part of navigation research focuses on the sensory basis for navigation. Because so little is known about real-world navigation, researchers are oftentimes content with revealing navigation-related sensory cues – thus neglecting the mechanism of *using* this sensory input, i.e., how is sensory input translated into motor commands leading to movement (Bar et al., 2015). For example, if the highly visual Egyptian fruit bats indeed use vision-based self-triangulation for navigation, which landmarks do they rely on and what is their triangulation algorithm? These and other questions could now be addressed by utilizing the modern ability to map the sensory landscape of the animal and to correlate it with its measured movement trajectories. The sensory landscape of a bat can be mapped using drones that carry a variety of sensors—such as three-dimensional (3D)-imaging technology, batlike sonar systems, and artificial noses—thus documenting in detail the sensory information available to the animal from the animal’s perspective, including taking into account its sensory acuity (Mann et al., 2014).

##### 1.18.4.5.3 Long-Term Spatial Mapping

Bats are extremely long-lived mammals, with some species living for >40 years. Many reports suggest that bats maintain a cognitive map of space over very long periods of time, even after they have been absent from the mapped environment for weeks, months, or years. For example, in the field, bats have been reported to return to the same (centimeter) location in the same cave year after year, or to the same exact tree holes (Griffin, 1970; Holland, 2006; Kerth et al., 2011) – even after having migrated for hundreds of kilometers in the interim (Gunier and Elder, 1971). In the lab, it was shown that bats can remember accurate flight trajectories even many weeks after training has stopped (Neuweiler and Möhres, 1967; Barchi et al., 2013) – and to remember the precise location of an escape-hole after being absent for several months from an experimental room (Hahn, 1908). The processes underlying long-lasting mapping and their limitations have never been scientifically examined. How many maps can a bat possess and for how long? These are some of the most intriguing questions.



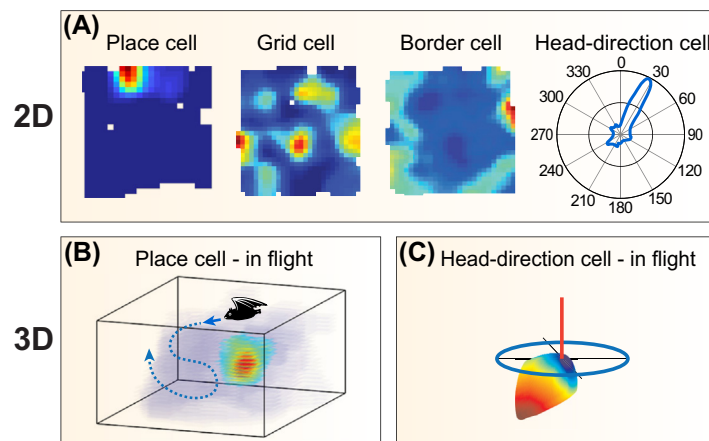
#### 1.18.4.5.4 Social Group Navigation

Many bats exhibit highly social behaviors, often roosting in large groups and emerging from their roosts together. Bats are commonly observed in aggregations in foraging sites, and there are some evidence that they actively search for food as a group (Dechmann et al., 2009; Cvikel et al., 2015). However there is currently very little research on whether and how bats navigate together. Do bats share navigational information when moving in a group and searching for food, or when migrating over long distances? Do bat pups learn from their mothers how to navigate in the environment? Are there leaders and followers in bat navigation, similar to some birds (Nagy et al., 2010; Pettit et al., 2015)? These are completely open questions.

### 1.18.5 Toward a Neurobiology of Natural Navigation in Bats

Practically nothing is known about the neural bases of natural navigation in bats. Similar to many other groups of animals (Krebs et al., 1989; Jacobs et al., 1990; Maguire et al., 2006), it was shown that hippocampal volume correlates with navigational load across bat species (Safi and Dechmann, 2005) – indicating that the hippocampal formation may be linked to large-scale navigation outdoors, similar to its proposed role for small-scale navigation in the laboratory (O’Keefe and Nadel, 1978; Morris et al., 1982). Several decades of research in rats and mice revealed that the rodent hippocampal formation contains several classes of spatially tuned neurons, including place cells that represent the animal’s position in space, grid cells that are thought to represent positions and distance traveled, border cells that encode the geometrical borders of the environment, and head-direction cells that encode the animal’s direction within the environment (Taube, 2007; Moser et al., 2008; Moser et al., 2014). These cell types were also found in bats, both in two-dimensional setups (Fig. 4A; Yartsev et al., 2011; Ulanovsky and Moss, 2007; Ulanovsky and Moss, 2011; Rubin et al., 2014) and—for place cells and head-direction cells—also in 3D flight setups (Fig. 4B; Yartsev and Ulanovsky, 2013; Finkelstein et al., 2015; Geva-Sagiv et al., 2016). However, the largest flight setups used to date for neural recordings in bats were only  $6 \times 5 \times 3 \text{ m}^3$  in size – reminiscent of some small bat caves, but certainly very different from long-distance navigation. Moreover, to date bats were not tested with electrophysiological recordings in naturalistic, complex navigation scenarios. We thus do not know whether, and to what degree, these cell types are relevant for natural navigation. In fact, this major gap exists also for rodents – we do not know, for any species, whether these spatial cell types are relevant at all for real-life natural navigation.

Given the complete gap in our knowledge, we can only speculate. Below, we list some open questions and raise some speculations – which we hope will help drive future experiments on the neural basis of natural navigation in bats (and other animals too).



**Figure 4** Navigation-related neurons on small spatial scales. (A) Spatial cell types recorded from the hippocampal formation of Egyptian fruit bats that were crawling on small two-dimensional (2D) surfaces, roughly  $1 \times 1 \text{ m}^2$  in size. From left to right: Examples of a place cell, a grid cell, a border cell, and a head-direction cell, all recorded from crawling Egyptian fruit bats. These cell types are very similar to those found in 2D in rodents (Moser et al., 2008). These cell types are thought to be used for the following functions in small-scale navigation: place cells, representing position (map); grid cells, representing positions or distances (odometer); border cells, representing the geometry of the environment; head-direction cells, representing absolute direction (compass). See further details in (Geva-Sagiv et al., 2015). (B) Example of a place cell recorded in an Egyptian fruit bat flying in three-dimensional (3D) volumetric space (Yartsev and Ulanovsky, 2013). (C) Example of a head-direction cell recorded in a bat flying in 3D (Finkelstein et al., 2015). The data in (B, C) were recorded in a large flight room, approximately  $6 \times 5 \times 3 \text{ m}^3$  in size—much larger than typical small laboratory boxes, but much smaller than real-life navigation distances in bats (e.g., Fig. 2). To date, it is unknown if these cell types are relevant for large-scale navigation, in either bats or rodents. Panel (A) adapted from Geva-Sagiv, Maya, Liora, Las, Yossi, Yovel, Nachum, Ulanovsky. 2015. Spatial cognition in bats and rats: from sensory acquisition to multiscale maps and navigation. *Nat. Rev. Neurosci.* 16 (2), 94–108. <http://dx.doi.org/10.1038/nrn3888>. Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved; Panels (B, C) were adapted from Finkelstein, A., Liora, Las, Nachum, Ulanovsky, 2016. 3D maps and compasses in the brain. *Annu. Rev. Neurosci.* 39, 171–196, with permission from the Annual Review of Neuroscience, Volume 39 ©2016 by Annual Reviews.

**1.18.5.1 The Missing Links II – Neural Mechanisms**

- How do place cells and grid cells represent large-scale spaces of a few hundred meters or kilometers? And are these cells involved at all in spatial coding of such large spaces? This remains experimentally unknown in any species. In a recent review we provided a detailed account of some of the theoretical possibilities (Geva-Sagiv et al., 2015) – so we will not elaborate on this further here. However, we wish to stress that there are good reasons to believe that the answer must be very different from the spatial codes found, for example, in rodents navigating in small boxes in the laboratory – which makes it vital to record from these neurons on large spatial scales (Geva-Sagiv et al., 2015). Bats provide a particularly good animal model to study these key questions because of their fast flight and ability to cover large distances.
- Are border cells relevant to navigation outdoors? Perhaps they may be relevant for navigating inside caves, or along hedgerows—where geometrical borders do exist—but are they relevant for bats navigating through open-spaces at high altitudes, where the nearest border may be some cliff a few hundreds of meters away, or further?
- How are spatial goals represented in the brain? When navigating from point A to point B, place cells and grid cells are thought to represent the animal's own position (point "A") – but what is the neural representation of the goal, and where in the brain it is stored (point "B")? One proposal is that by activating sequences of place cells, animals may "simulate" their future navigational trajectories (Pfeiffer and Foster, 2013) – but this mechanism could work only for familiar environments where place cells were already established; and additionally it is unclear how it would scale up to larger environments. An alternative possibility is that there might be neurons that represent the vector (direction and distance) to the goal – and could thus implement a neural mechanism for the "home vector" concept mentioned earlier. A recent study has indeed found such a vectorial representation of spatial goals in the hippocampus of bats (Sarel et al., 2017).
- How does the brain represent multiple spatial goals? And how does it choose between several possible goals? Namely, what are the neural bases of spatial decision making – in the context of navigation?
- What are the neural mechanisms underlying the ability of animals to exhibit reorientation – that is, to find their bearing again after the way was lost? This mysterious ability to lose one's way but then to reorient again, does not seem to be easily explained by the classical accounts of the various hippocampal-formation spatial cells – and may require more complex mechanisms.
- What is the neural mechanism of the long-term maintenance of spatial maps in the bat hippocampus, as well as long-term representation of goals – over months and years? Do fruit bats maintain episodic memory of food items, and if so, what is the neural basis of this capacity – namely, do fruit bats remember which fruit tree ("what") provides fruit at which location ("where") and at which season of the year ("when")? The combination of what–where–when constitutes an episode in episodic-like memory, and its neural-level elucidation could link the view that the hippocampus is involved in spatial mapping (O'Keefe and Nadel, 1978) with the view that the hippocampus is a memory circuit, in particular for episodic memories (Eichenbaum and Cohen, 2003).
- What are the neural mechanisms of transforming spatial representations from allocentric, absolute spatial coordinates to egocentric, body-referenced coordinates – which in turn could guide locomotion along a navigational trajectory? This question could be studied also in rodents (Wilber et al., 2014); however, bats provide a distinct experimental advantage here because in bats we can track how the animal scans the environment using its sensory gaze. Specifically, we can use an array of microphones to precisely measure the direction of the bat's sonar beam throughout its flight (Ghose and Moss, 2006; Yovel et al., 2010)—its egocentric "acoustic gaze"—while today it is still rather difficult to measure the eye gaze in freely moving rodents (but see Wallace et al., 2013).
- If bats do navigate in groups, as some evidence suggests: What are the neural bases of these capacities? How do bats track the position of one another? How do they transfer information to other individuals? How does their brain weigh and combine their own navigational knowledge with the behavior of the group – for example, does their hippocampal formation perform some sort of Bayesian combination of these two sources of navigational information (Angelaki et al., 2011)? And in particular, how do they decide which bat to follow and which not to?
- How do place cells, grid cells, and head-direction cells integrate information across different sensory modalities? Our recent study provided first glimpses into this issue (Geva-Sagiv et al., 2016), but when it comes to navigation outdoors, this becomes a much harder and more complex question because sensory information in real-life conditions varies over both space and time – so it is not entirely clear how it would be used to create a reliable large-scale spatial representation that could underlie real-life natural navigation.

These and many other open questions delineate an uncharted territory in the study of the neural bases of bat navigation—and animal navigation more generally. Beyond the border of this uncharted territory, there lie even more complex facets of navigation, and questions that we do not even know how to ask. This might sound as a grim state of affairs. However, the good news are that some dramatic technological advances over the last few years allow now, for the first time, to track the precise position and detailed behavior of animals in natural conditions (Tsoar et al., 2011; Cvikel et al., 2015a, 2015b); as well as to record the activity of single neurons over very large distances and in highly complex environments (Eliav et al., 2016). The next years will prove to be exciting indeed.

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See also: 1.14 Foraging. 1.15 Memory for Space, Time, and Episodes. 1.16 Spatial Memory in Food-Hoarding Animals. 1.20 Reconsolidation: Historical Perspective and Theoretical Aspects. 1.21 Navigation and Communication in Insects.

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