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A painful conversation

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Navigation strategies on multiple
scales

Spatial cognition in bats and rats: from sensory acquisition to multiscale maps and navigation

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Abstract | Spatial orientation and navigation rely on the acquisition of several types of sensory information. This information is then transformed into a neural code for space in the hippocampal formation through the activity of place cells, grid cells and head-direction cells. These spatial representations, in turn, are thought to guide long-range navigation. But how the representations encoded by these different cell types are integrated in the brain to form a neural ‘map and compass’ is largely unknown. Here, we discuss this problem in the context of spatial navigation by bats and rats. We review the experimental findings and theoretical models that provide insight into the mechanisms that link sensory systems to spatial representations and to large-scale natural navigation.

Place cells

Hippocampal neurons that become active whenever the animal traverses a specific location in the environment, called the ‘place field’. The dimensions of the place field govern the spatial resolution of a single place cell; and together, multiple place cells are thought to represent a mental map of absolute (allocentric) space.

“A journey of a thousand miles must begin with a single step.” Lao Tzu

Many animals (including humans) can navigate over thousands of miles, and yet research into the neural basis of navigation has been conducted almost exclusively in the confined spaces of laboratories. How do we find our way to far-away destinations? What are the neural mechanisms underlying our mental maps of complex, natural environments? No definitive answers to these questions exist, in part because spatial navigation and the neural encoding of space in the brain have been studied by two very different research traditions over the past century.

Research originating from the fields of ethology and ecology has examined animal navigation in the wild over large spatial scales (from tens of metres to thousands of kilometres). This approach has focused on non-mammalian species — including birds^{1–3}, lobsters⁴, ants^{5–7}, honeybees⁸ and sea turtles⁹ — and has been limited mostly to behavioural studies, with relatively few studies of the underlying brain mechanisms^{10–12}. This research tradition is dominated by the ‘map-and-compass’ theory of navigation^{1–4,8,9,13}.

In a second approach, psychologists and neuroscientists have studied the navigation of mammals — mostly rats — in mazes and small experimental arenas, and characterized the activity of neurons that might underlie their navigation. The brain area that has been most extensively studied is the hippocampal formation, which contains place cells^{14–23}, grid cells^{24–30} and head-direction cells^{28–34}.

However, the link between these spatial cell types and the map-and-compass navigation strategy remains conjectural. It is unknown whether the activity of place, grid and head-direction cells, as recorded in laboratory-sized environments, is relevant to large-scale navigation and spatial memory in the real world (over kilometres). Thus, there is a fundamental conceptual gap between these two parallel approaches. This gap encompasses different experimental methodologies, different species studied, and an emphasis on natural behaviours versus highly controlled set-ups, as well as a major gap in the spatial scales studied by each approach.

Here we propose a synthesis between the two research approaches. We focus on an animal with extraordinary navigation abilities — the bat — and make comparisons with findings from laboratory rats. Bats are the only mammals that have been studied extensively using both of the research approaches described above. We consider how the bat’s ‘active sensing’ systems (echolocation, vision, olfaction and somatosensation) shape the spatial information available to the animal, and translate this into a neural representation of space via hippocampal spatial cells. In particular, we discuss evidence that the spatial resolution of these cells is determined by the resolution of the sensory information available. We suggest that the need to orient and navigate across multiscaled natural environments^{35–41} must be reflected in multiscale neural codes for space, and argue that the neural representation of large-scale space is unlikely to be a simple scaled-up

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version of laboratory-sized environments. We review recent theoretical models of multiscale neural coding^{42–46} and describe the limited experimental evidence that is available to support these unconventional neural coding schemes.

Sensory perception in bats

Active sensing systems, in which an animal actively interacts with the environment to control sensory information acquisition, are widespread in the animal kingdom. Primate vision, for example, is influenced strongly by eye movements⁴⁷; olfactory perception in both rats and humans is influenced strongly by sniffing^{48–50}; and neural activity in the rat somatosensory system is influenced by whisker movements⁵¹. Bat echolocation (or ‘biosonar’) is another classical example of a mammalian active sensing system⁵⁵ (FIG. 1; BOX 1).

Echolocating bats emit brief sound pulses through their mouth or nostrils, and use the returning echoes to forage and navigate^{55,52,53}. Bats compute target direction with a resolution of 2° to 3° by comparing the sounds arriving at each of their two ears^{54–56}. They compute the distance-to-object by measuring the time delay between the emitted pulse and returning echo (FIG. 1a), with an accuracy of ~10 mm (REF. 57) (and can sometimes reach a super-resolution of <1 mm (REF. 58)). Several bat species use the Doppler effect to measure target velocity⁵⁹ and even to detect wing movements that enable them to identify an insect species^{60,61}. Furthermore, bats use the structure of returning echoes to infer the detailed shape and texture of an object^{62–66}, which allows them to use trees and rocks as acoustic landmarks for navigation. Thus, echolocation provides the bat with a rich and detailed three-dimensional image of the world.

When approaching an object, bats dramatically change their echolocation pulses, in order to control the acquired image of the world (BOX 1): they decrease pulse duration and increase pulse bandwidth^{67,68}, which improves the accuracy of range measurements⁶⁹; concurrently, they increase the pulse emission rate (sensory-update rate)^{53,67–69}. Interestingly, many other mammalian sensory systems exhibit similar dynamics when approaching objects of interest. For example, rats increase their whisking rate when approaching an object^{70–73} (BOX 1), and humans increase the rate of eye saccades when examining objects of interest⁷⁴. In these active sensing systems, the increase in sensory update rate is thought to allow faster behavioural responses and finer object identification^{53,67,68,70–74}.

There are many other variables in echolocation that the bat can tightly control (BOX 1). Of particular importance for spatial perception is the bat’s ability to change the sonar beam’s shape and angular width, and to steer the spatial direction in which it emits the beam, both of which are used to optimize object detection or object localization^{55,56,75,76} (BOX 1, see the figure part c).

Although echolocation is a primary sensory modality in most bats, it is not the only one. Indeed, because ultrasonic sounds quickly attenuate in air⁷⁷, echolocation has a limited maximal range of a few metres for small insects^{78,79}, and up to 100 metres for large landscape

objects^{78,80} (landmarks). Therefore, bats rely on other senses, such as vision, for longer-range orientation and navigation^{79,81,82,83}. Indeed, many bat species have excellent vision, much better than that of rats or mice^{35,84,85}. Old-world fruit bats, for example, have visual acuity that is better than that of humans at light levels equivalent to an overcast night (FIG. 1b). Moreover, in several bat species, vision provides a better angular resolution than echolocation^{56,84}. These differences in sensory resolution are important when considering sensory contributions to hippocampal place cells and navigation (see below, and BOX 2).

Four additional sensory systems contribute to long-range bat navigation: olfaction⁸⁶ (FIG. 1c), somatosensation⁸⁷ (FIG. 1d), the vestibular sense⁸⁸, and magnetosensation^{89–91}. Olfaction is particularly important in fruit bats, which can detect fruit-associated odours at very low concentrations⁹² (FIG. 1c). Somatosensation was recently suggested to contribute to flight control, as well as to the self-speed measurement that may support ‘path integration’⁸⁷ (FIG. 1d; BOX 3). The vestibular sense is crucial for intact directional coding by head-direction cells in rodents⁹³, and probably has a similar role in bats. Magnetosensation also contributes to bat spatial orientation and navigation^{89–91}. Thus, bats possess a suite of superb sensory systems that enable them to negotiate the challenging nocturnal environment.

From perception to spatial codes

Most sensory modalities for bats and rats — vision, olfaction, echolocation (bats) and whisking (rats) — are represented in the coordinate frame of the head (egocentric coordinates); that is, sensory perception rotates with the animal’s head and eyes. By contrast, spatial representation in the hippocampal formation is coded in absolute-space coordinates (allocentric coordinates). How do bats and rats transform the incoming sensory information into spatial representation, spatial memory and navigation?

Building blocks of spatial codes in the brain. The hippocampus, entorhinal cortex and surrounding regions contain four types of spatial cells thought to underlie absolute-space representation: place cells, grid cells, border cells and head-direction cells^{34,94,95} (FIG. 2a).

Place cells^{14,96} are hippocampal neurons that become active whenever the animal passes through a specific location in the environment, called the place field. A population of several-dozen place cells can be used to precisely read out the animal’s location^{15,97}. Moreover, the hippocampal circuit can store multiple maps in parallel. Thus, although a given place cell may be active in several different environments, its place field will often differ from one setting to another^{98,99}. Even subtle changes in sensory input may induce remapping⁹⁹ (a change in the mental map represented by the population of place cells). Thus, hippocampal place cells can be thought of as storing a dynamic map of the external environment¹⁰⁰.

Grid cells, found in the medial entorhinal cortex and the pre- and parasubiculum^{24,28}, become active whenever the animal traverses one of the vertices of a periodic hexagonal or triangular lattice that tiles the

Grid cells

Neurons in the medial entorhinal cortex (and some adjacent regions) that become active whenever the animal traverses one of the vertices of a periodic hexagonal or triangular lattice that tiles the environment.

Head-direction cells

Neurons found in multiple brain areas, which become active whenever the animal’s head points to a specific absolute (allocentric) direction, thus providing a compass signal.

Doppler effect

The change in wave frequency for an observer that is moving relative to the wave source. For example, when an ambulance with a siren approaches an observer, a high-pitched sound (high frequency) is heard, but the perceived frequency drops when the ambulance passes and drives away. Bats know their own emitted frequency, and thus can use the perceived shifted frequency of the echo (Doppler shift) to compute the relative velocity of the target.

Magnetosensation

The ability to detect the Earth’s magnetic field and use it to compute direction or spatial position. Utilizing magnetosensation for navigation purposes has been described in many animals, including some rodents and bats.

Egocentric coordinates

Coordinates that are given relative to the body axis; for example, ‘1 km to your left’.

Allocentric coordinates

Coordinates that are independent of the observer’s orientation; for example, ‘1 km North of Tel Aviv’. Also known as absolute-space coordinates.

Border cells

(Also known as boundary cells.) Neurons that become active when the animal is close to a salient border of the environment, thus signalling the environmental geometry.

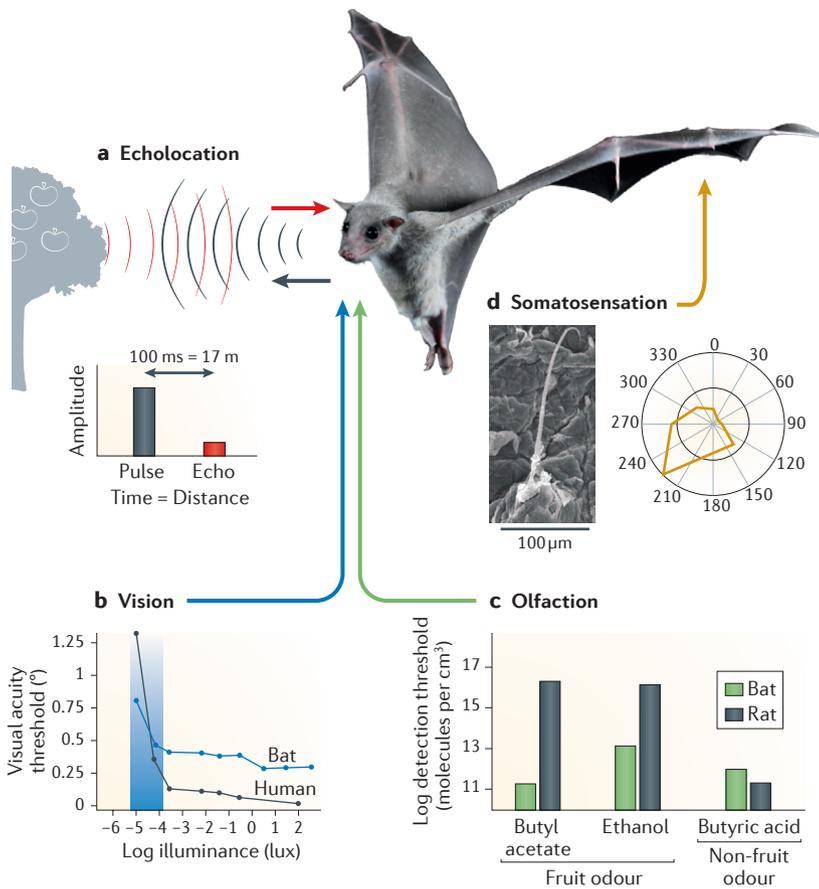


Figure 1 | Sensory modalities of bats. Bats use a variety of sensory modalities to orient and navigate in the environment. **a** | Echolocation provides detailed information about the distance (range), velocity, size, shape and texture of nearby objects. Target range is determined by measuring the time difference between the pulse and echo (multiplied by the speed of sound). For example, the 100-ms pulse–echo delay shown here indicates a range of 17 m (REF. 83). **b** | Vision provides information for long-range sensing and navigation⁷⁹. The graph shows that the visual acuity of the greater Indian fruit bat exceeds human acuity at ecologically relevant low light levels equivalent to an overcast night sky (blue shaded area). Data from REFS 188, 189. **c** | Excellent olfactory abilities are exhibited by fruit-eating bats, such as Seba’s short-tailed bat: as shown in the graph, the olfactory detection thresholds for some fruit-related odours are up to 100,000 times better in these bats than in rats (data from REFS 92, 190, 191). **d** | Somatosensory abilities in bats have been neglected for many years, but recent findings demonstrate that thousands of micro-hair cells covering the bat’s wings (shown in the scanning electron microscope image) enable it to detect changes in air flow, which in turn may be translated into information about its movement (air speed)⁸⁷. Graph shows normalized directional tuning to different directions of air flow for a multi-neuron cluster in the wing area of the bat’s somatosensory cortex⁸⁷. The angle of air flow (in degrees) is indicated along the periphery and the firing rate is indicated by the distance from the centre. The image of an Egyptian fruit bat is reprinted with permission from Haim Ziv, Weizmann Institute of Science, Israel. Part **d** is adapted with permission from Sterbing-D’Angelo, S. *et al.* Bat wing sensors support flight control. *Proc. Natl Acad. Sci. USA* **108**, 11291–11296 (2011).

environment (FIG. 2a). The spatial scale of the grid can differ between grid cells: therefore, combining multiple grid cells with different scales could allow accurate decoding of the animal’s position^{42–45, 101, 102}. Thus, the mammalian brain employs two fundamentally different neural codes for representing the animal’s position in the environment; the ‘place code’ and the ‘grid code’^{242–45}.

Border cells, found in medial entorhinal cortex and subiculum^{27, 103, 104}, fire when the animal is located along one or several borders of the environment (FIG. 2a). These neurons may thus represent the environmental geometry and could anchor the spatial map to the surrounding borders.

Head-direction cells, found in dorsal presubiculum^{31, 34}, anterodorsal thalamus^{32, 105} and multiple additional brain regions³⁴, become active whenever the animal’s head points in a specific absolute direction relative to its environment (FIG. 2a). Head-direction cells are thought to underlie the animal’s mental compass^{34, 106}, allowing it to maintain an internal sense of direction. A directional signal is also carried by a subset of grid cells²⁵ and by hippocampal CA1 place cells¹⁰⁷.

These four spatial cell types may implement navigation mechanisms. Two of the main theories of animal navigation — the cognitive map theory^{14, 108} and the map-and-compass theory^{2, 13} — require neural mechanisms for a map and a compass (BOX 3). Place cells, grid cells and border cells may implement the neural map, while head-direction cells may function as a neural compass.

Although these four cell types (FIG. 2a) were discovered and mainly studied in rats and mice^{96, 109}, subsequent studies established their existence in other mammalian species^{110–114}, and all four cell types are found in bats^{23, 30, 114} (FIG. 2a, bottom).

Transforming sensory inputs to spatial maps. How are hippocampal spatial maps formed? Two types of information can underlie the tuning properties of hippocampal spatial neurons. The first are external sensory inputs (FIG. 1), which can be further subdivided into distal senses (such as vision and biosonar) that provide information about remote landmarks, and proximal senses (such as somatosensation) that provide information about nearby cues. The second type of information is provided by self-motion cues (for example, proprioceptive and vestibular). The integration of self-motion information (known as path integration) enables animals to compute location and direction in the absence of external cues, at least over short distances^{102, 115}. The contribution of path integration to short-range navigation and small-scale spatial maps in the brain has been reviewed elsewhere¹⁰². Over long distances, however, path integration accumulates noise and produces large positional errors^{116–118} (BOX 3). Therefore, we focus here on the contributions of external sensory inputs to long-range navigation.

Most studies on the influence of sensory input on place-cell tuning have emphasized the contribution of vision. For example, rotation of prominent distal landmarks causes place fields to rotate accordingly^{18, 99}. Likewise, when a rectangular arena is stretched, many place fields also stretch¹⁶. These and similar results have led to the development of several theoretical models that describe the formation of place-tuned activity from distal sensory inputs, and make some key predictions about the transformation of sensory inputs into a cognitive map. In particular, the models have been used to consider the mechanisms that determine the location of place fields and the resolution of the map.

Box 1 | **Echolocation in bats**

Bat echolocation pulses can be classified into frequency-modulated pulses, constant-frequency pulses, and ultra-short clicks (see the figure, part a). Each pulse design provides specific signal-processing advantages that match the bat's foraging strategy and habitat^{53,165}. Bats can rapidly change their pulse design to optimize sensory acquisition^{35,53,166,167}. Researchers have defined three phases of bat echolocation (see the figure, part b): the 'search phase' (which in the absence of targets, optimizes detection); the 'approach phase' (which localizes a target, enabling approach); and the 'attack phase' (or 'terminal phase'; which occurs just before reaching the target). The transitions between phases are characterized by a dramatic increase in the pulse emission rate (thus providing a higher temporal resolution when manoeuvring towards a target), an increase in the pulse bandwidth (which improves the resolution of range measurement⁶⁹), and a decrease in pulse duration (which avoids temporal overlap between emitted pulse and received echo, thus preventing auditory masking^{53,165}). This transition illustrates a classical trade-off. The long, low-bandwidth pulses of the search phase provide more energy for the auditory system's narrow-frequency filters and are thus ideal for target detection at longer distances^{53,165}. By contrast, the high-bandwidth approach pulses are ideal for target localization, at the expense of detection range. Thus, bats rapidly change their perception of the world from a blurry long-range acoustic image to a sharp yet short-range image.

There are several parallels between the active-sensing systems of bats, rats and other mammals. Many of these sensory systems, including bat echolocation, rodent whisking and sniffing, and primate eye saccades, are rhythmic^{48-50,70-73,168}, and these sensory-acquisition rhythms occur broadly around the 'theta' frequency band (4–11 Hz)^{48-50,53,67,70-73,78,168}. Similarly, many active-sensing systems exhibit an increase in sensory update rate (such as an increase in rat sniffing or whisking rate) near objects of interest⁷⁰ (see the figure, part b). Moreover, rats change the dynamics of individual whisks⁷¹⁻⁷³, perhaps analogous to the changes in pulse shape exhibited by bats^{53,67,68}.

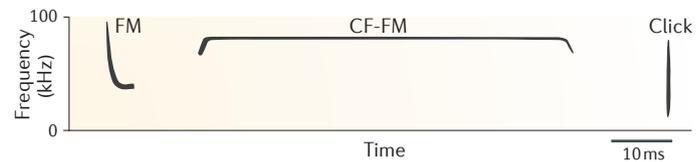
Bats can also alter pulse intensity and spectrotemporal shape, each with its own sensory trade-offs^{35,53}. In addition, they widen their sonar beam when approaching a target⁷⁵, which may prevent them from losing sight of a rapidly manoeuvring insect. Several bat species also exhibit sophisticated strategies of steering their sound beams to optimize sensory acquisition^{55,56,76}. For example, Egyptian fruit bats that need to detect a target under low signal-to-noise conditions direct the part of their beam containing the maximal energy towards the target, thus optimizing detection⁵⁶ (see the figure, part c, left). However, when localizing a target under high signal-to-noise conditions, they instead aim the edge of their beam towards the target⁵⁶ (see the figure, part c, right). At the edge (maximal slope) of the beam, the beam intensity changes fastest as a function of the angle to target: thus, every change in the angle to target results in the largest possible change in echo intensity, which optimizes localization (see the figure, part c, right);

and REF. 56). The ability to switch on-the-fly between optimal detection and optimal localization provides yet another example of the bat's sensory flexibility.

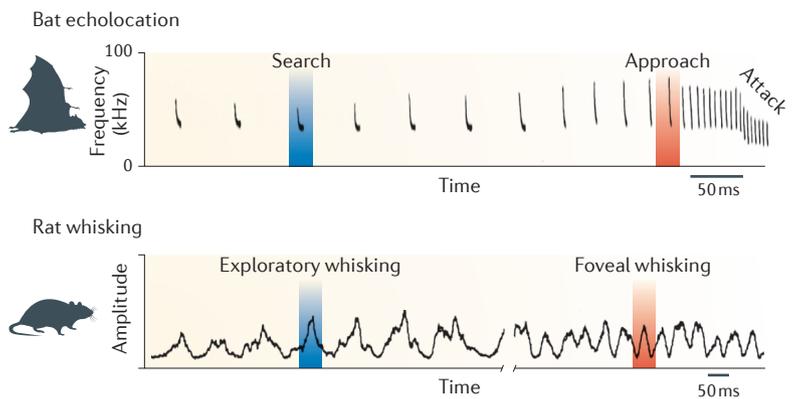
The extensive literature on the mathematical theory of sonar and radar^{69,169} provides a theoretical understanding of why bats change their sonar pulses. This theoretical background, together with the experimenter's ability to monitor and manipulate the dynamics of echolocation^{56,58,63,76}, make the bat an ideal animal model for studying spatial perception via active sensing.

In the figure, part a, the click is adapted with permission from Ulanovsky, N. and Moss, C. F. What the bat's voice tells the bat's brain. *Proc. Natl Acad. Sci. USA* 105, 8491–8498 copyright (2008) National Academy of Sciences, U.S.A.; and the frequency-modulated (FM) and constant-frequency frequency-modulated (CF-FM) calls are reprinted from *Curr. Biol.* 15, Jones, G. Echolocation R484–R488 copyright (2005) with permission from Elsevier. The figure part b, top, is reprinted from *Trends Ecol. Evolut.* 18, Schnitzler, H.-U., Moss, C. F. and Denzinger, A. From spatial orientation to food acquisition in echolocating bats 386–394 copyright (2003) with permission from Elsevier. The figure part b, bottom, is adapted with permission, from Berg, R. W. and Kleinfeld, D. Rhythmic whisking by rat: retraction as well as protraction of the vibrissae is under active muscular control. *J. Neurophysiol.* 89, 104–117 (2003).

a Echolocation pulse types



b Sensory acquisition modes



c Spatial scanning modes



One sensory-based model of place-field formation is the boundary vector cell (BVC) model, which posits that place fields are created by summing inputs from a population of boundary-sensitive cells. The firing fields of these boundary-sensitive cells create bands in the

environment^{16,104,119,120} (FIG. 2b), akin to those of the border (boundary) cells that were discovered later experimentally^{27,103,104} (FIG. 2a). However, it is important to note that most of these experimentally identified cells fire along walls and very few actually fire at a distance from

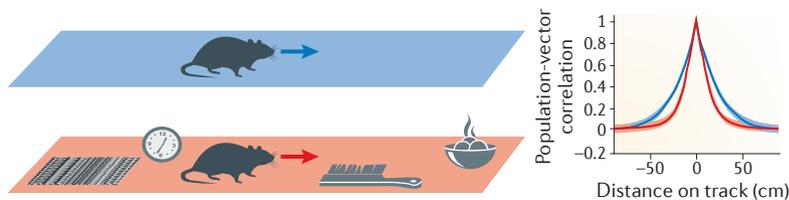
Box 2 | Sensory resolution affects spatial-map resolution

Although it is commonly thought that hippocampal place-field sizes are relatively uniform in a given environment (possibly reflecting path-integration processes that are largely independent of external sensory cues¹⁰²), two theoretical sensory-based models for place-cell generation — the boundary vector cell (BVC) model (FIG. 2b) and the view-based model (FIG. 2c) — predict that changes in sensory resolution should affect the size of hippocampal place fields. This prediction is supported by several experimental findings in rats and bats. Two recent studies showed that rat place fields were significantly smaller when visual landmarks were present than when they were absent^{171,172}. In a different experiment, rats were tested on a smooth featureless running track or on a track that contained a rich set of somatosensory and olfactory cues. Place fields were significantly smaller in the latter condition¹⁷³ (see the figure, part a; in the right panel, the width of place fields is indicated by the width of the population-vector decorrelation). In addition, place fields in rats tend to be smaller for locations near the walls of the arena during open-field exploration¹⁷⁴, which may result from the higher whisking rate near the walls⁷⁰ (BOX 1). Finally, in big brown bats, place fields are small when tested immediately after each echolocation pulse, when the animal receives rich echoic sensory information, but rapidly diffuse within a few hundred milliseconds¹⁷⁵ (see the figure, part b, for an example (left panels) and for population data (right panel) showing place-field widening after each sonar pulse). The place fields then shrink back upon arrival of a new pulse carrying sensory information¹⁷⁵. All of these results are consistent with the notion that sensory resolution determines spatial resolution.

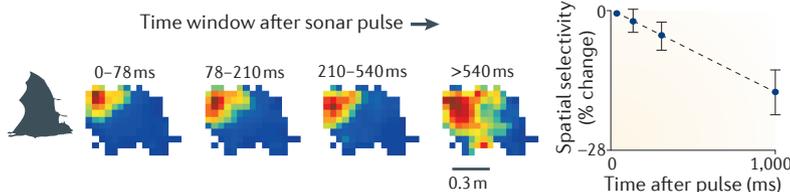
Several additional experiments in bats could test this prediction more directly. First, the sonar signal-to-noise ratio could be reduced by parametrically varying the levels of background acoustic noise. According to the BVC and view-based models, this should increase the place-field size. Second, place-field size could be examined near walls and goals, where bats use high-bandwidth sonar pulses (BOX 1), and we might therefore expect^{53,69,176} smaller place-field size. Third, place-field sizes could be compared under conditions in which the bat uses pure vision versus pure echolocation. Vision in Egyptian fruit bats provides a better angular sensory resolution than echolocation^{56,84}. We would therefore predict that in these bats, place fields will be systematically smaller when using vision than when using echolocation. These three proposed experiments may cleanly isolate the effects of variations in sensory resolution, and how it translates to hippocampal spatial resolution.

The figure, part a, right, is adapted with permission from REF. 173, Society for Neuroscience; part b is adapted with permission from REF. 175, © Wiley-Liss, Inc.

a Spatial coding sharpens in cue-rich versus cue-poor environments



b Place fields broaden with time after each sonar pulse



a wall. The BVC model further assumes that distances to geometrical boundaries are continuously available to the animal; an assumption that could perhaps hold true for indoor laboratory experiments, but seems less likely for rats navigating through borderless agricultural fields¹²¹, or for bats flying at a height of 500 m (REF. 82).

A very different model — the view-based model^{122,123} — takes as its input a realistic full retinal image (along with path-integration information). This, via several interconnected populations of neurons, eventually drives the firing of place cells and head-direction cells (FIG. 2c). In this model, positional and directional information are derived directly from the raw retinal image, without using any abstract geometric or landmark information or an external compass input. The model utilizes the rich information available in natural panoramic visual scenes: this makes the model relatively insensitive to specific details of the image, and thus allows robust spatial representation and navigation even in the absence of prominent landmarks^{122,124}. This highlights the need to examine more closely the level of abstraction that animals use for real-life navigation: for example, one question is whether mammals use the full retinal image, as was proposed for some insects¹²⁴. In the case of bats, could they use an analogous mechanism based on the full echoic soundscape? Or perhaps animals primarily use abstracted geometric borders or isolated landmarks?

Many animals dynamically change their sensory sampling rate (BOX 1, see the figure part b), thus altering the resolution of the incoming sensory information. Therefore, for both of these models, one question is how changes in sensory resolution would affect the size of place fields (BOX 2). This question has been addressed in the BVC model by simulations in which the sensory tuning was degraded, which led to wider BVC activity bands and, in turn, increased place-field size (FIG. 2b). For the view-based model, place-field size has been compared for high-resolution visual input versus visual input with degraded angular resolution: these simulations showed that the average place-field size increases substantially when the visual input is blurred (FIG. 2c). Thus, both of these sensory-based models predict that sensory resolution affects the size of hippocampal place fields, which in turn determines the resolution of the spatial map. This prediction is indeed supported by several experimental studies (BOX 2).

Finally, we note that spatial resolution can be improved by pooling information across neurons¹⁵. Thus, if specific spatial locations are over-represented by a larger number of neurons, the ensemble resolution at that location will be higher even if individual place-field sizes are constant across the arena. Non-uniform densities of place fields near ‘important’ locations (such as the location of hidden food rewards or the hidden platform in a water maze) were indeed found in several laboratory studies^{17,125}. This might imply that navigational accuracy is improved at such over-represented locations; this prediction awaits experimental testing.

From maps to real-world navigation

So far, the spatial cells described above have been tested only in small-scale, artificial laboratory environments that are also impoverished in sensory cues compared to the natural environment. Are these cell types relevant to real-life navigation (BOX 3)?

Box 3 | Theories of animal navigation

Egyptian fruit bats navigate dozens of kilometres to a specific fruit tree, and return night after night to forage in the same individual tree⁸². The figure, part a, shows global position system (GPS) tracking of a single bat over 7 consecutive nights (flight tracks of this bat on different nights are shown in different colours; data collected using methods similar to those described in REF. 82). How do animals accomplish such navigational feats? Five main types of (not necessarily mutually exclusive) navigational strategies have been proposed^{2,14,177}.

Beaconing: navigation directly towards a distant sensory cue, such as a visual object, a sound, or an odour. Visual beaconing was proposed for greater spear-nosed bats in Trinidad, which use the central mountain range of the island as a beacon⁸¹ (see the figure, part b). Auditory beaconing was demonstrated in big brown bats, which beacon toward the sounds of a swamp frog chorus¹⁷⁸.

Route following (route guidance): Navigation along a complex physical route, where movement course changes at specific landmarks. This is how humans navigate when driving in cars, turning left and right at specific intersections. Bats also exhibit route-following along forest paths¹⁶⁵, or through complex kilometre-long underground passageways¹⁷⁹ (see the figure, part c).

Path integration: navigation based on an online computation of the present location from the past trajectory^{115,180}. Path integration (also known as ‘dead reckoning’ (REF. 177)) does not require any external landmarks and relies only on integrating the animal’s own movements. Path integration over short distances is tested by letting an animal wander away from its nest, and then translocating the animal: if it uses path integration, the animal will move directly to where the nest should have been (see the figure, part d, rightmost dashed line), as indeed was found in desert ants^{181,182}. Notably, path integration is unreliable because it accumulates noise and produces extremely large errors within a few seconds^{117,118}; behavioural studies demonstrated that when rodents forage in an arena, their path-integration may deteriorate after one 360° rotation^{116,183}, and fails completely after more than three full rotations¹¹⁶. Bats can path-integrate over very short distances (1–2 m)^{184,185}, but it is unlikely that they (or any mammal) could path-integrate over ethologically relevant large distances.

Cognitive map: a navigation strategy that relies on a mental map of the environment, which allows flexible navigation without the need to pass through familiar waypoints. This is the most sophisticated navigational strategy and seems to require the highest cognitive abilities. Cognitive map theory^{14,108}, originating from laboratory studies in psychology, emphasizes the need to combine self-motion (path-integration) cues with sensory information arising from multiple distal landmarks, to yield self-triangulation¹⁴ (see the figure, part e). Although there have been intense debates on whether animals possess fully detailed cognitive maps^{14,177,186}, it is noteworthy that some of the navigational abilities of bats are consistent with a map, or a map-like mechanism over a 100-km scale. For example, Egyptian fruit bats⁸² that were displaced to several release sites at different directions and distances from their cave nearly always navigated straight back to their cave or favourite fruit tree (see REF. 82 for details).

Map and compass: a navigation strategy that allows animals to return from unfamiliar release points, using either self-triangulation or stimulus–place associations that are based on universal gradients of olfactory odorants or magnetic fields^{2,9,86,187} (see the figure, part f). The map-and-compass theory^{2,13} originated from studies of bird ethology¹³, and was later applied to study navigation in a variety of species^{2,4,9}. Although map-and-compass and cognitive-map theories differ in the proposed sensory stimuli used, they share substantial similarities in navigational processes: in particular, both theories utilize self-triangulation, and both allow flexible navigation without the need to pass

through familiar waypoints. Interestingly, homing pigeons, whose ability to return from unfamiliar areas has provided much of the experimental support for the map-and-compass theory², were also shown to use cognitive-map-like navigation within familiar environments².

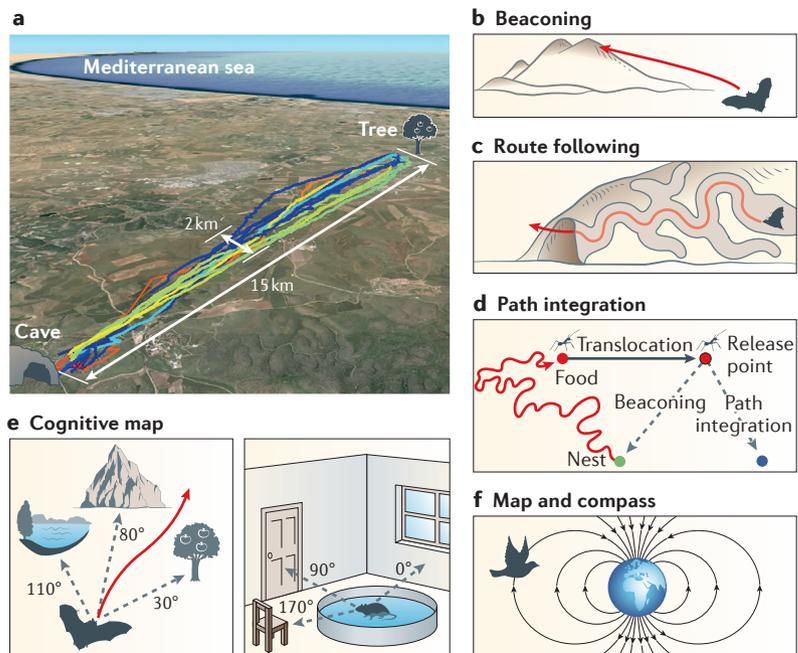
Animals often use different navigational strategies in different circumstances, or even switch strategies while navigating. It remains unknown what the implications of such navigational switches are for our understanding of the neural basis of navigation.

Distal senses

Senses that provide long-range information to the animal. For rats, vision is the primary distal sense. Bats have two distal senses, echolocation and vision, when considering a small environment like a cave or a room. However, echolocation range is limited to < 100 m, so on a scale of kilometres, echolocation may be classified as proximal, while vision remains a truly distal sense. In both species, olfaction is a proximal sense in enclosed spaces (cave, burrow), but may serve as a distal sense outdoors where winds can carry odours from afar.

Proximal senses

Senses that are restricted to a short range. For rats, somatosensation (whisking) and olfaction are the primary proximal senses.



Bats possess outstanding spatial memory and navigational abilities³⁵. At long ranges, some bat species migrate annually up to 2,500 km, returning year after year to the same roosting location^{35–39}. At medium ranges, Egyptian fruit bats navigate dozens of kilometres to forage at the same individual fruit tree night after night⁸² (BOX 3, see the figure part a); and moreover, these bats can return straight back to their cave after a 100-km translocation⁸², suggesting that they possess a detailed spatial map of their environment over a 100-km range. There is evidence that Egyptian fruit bats use ultra-distal visual landmarks (such as mountains, sea, cities and factories) to visually guide this precise navigation⁸². At short ranges (metres), bats rely on spatial memory of echo-based landmarks¹²⁶, and can even remember the three-dimensional position of objects with an accuracy of 1 to 2 cm (REF. 35). Thus, bats seem to have multiple mental maps of their environment on different spatial scales.

Wild rodents also have excellent navigational abilities: they can find goals with 1-cm accuracy^{127,128}, and some species routinely navigate distances of several kilometres^{121,129}. For example, Norway rats and jerboas have been shown to navigate every night up to 2 km away from their burrow, and back^{121,129}. This suggests that some wild rodents possess a detailed mental map of their environment, and this map represents spatial scales from ~1 cm to several kilometres^{121,127–129}.

The question of how the brain supports this large-scale navigation remains largely unanswered. Are the principles and spatial cell types discovered in small-scale navigation applicable to large-scale navigation, or is the neural basis of natural navigation entirely different? In particular, is the hippocampal formation involved in large-scale navigation? Several studies showed that homing pigeons with hippocampal lesions exhibit deficits in homing performance over kilometres¹², and other studies reported correlations between hippocampal volume and large-scale navigational load in birds¹³⁰, rodents¹³¹, bats¹³² and humans¹³³. Therefore, our working hypothesis is that the hippocampus is indeed involved in large-scale navigation. This leads to two additional questions. The first concerns the encoding of spatial information on multiple scales. Is there one mega-map of the environment, or are there many fragmented maps for different regions of space, possibly at different resolutions? That is, does the hippocampal formation contain detailed high-resolution representations for important locations but sparser representations for less important locations (FIG. 3a)? Second, how does the mammalian brain represent spatial information on very large scales (kilometres)? Laboratory-sized place fields increase with the size of the experimental environment^{16,19}, but can place fields scale up to 1 km or even 1,000 km, to support a real-world cognitive map? If not, what are the alternative possibilities for neural coding of very large spaces?

Spatial representation on multiple scales. Consider a bat in its cave, or a rat in its burrow. These confined environments are highly important to both animals, and hence they pay close attention to the abundant sensory cues, such as tree roots, rocks and crevices. Therefore, place fields are expected to be comparable in size to those

recorded in small laboratories. Place fields recorded in ~1 × 1 m laboratory setups have a typical diameter of ~20 cm for rats⁹⁴ and bats^{23,30} in one- or two-dimensional environments (FIG. 3b). However, three-dimensional place fields recorded in bats flying in a 5.8 × 4.6 × 2.7 m flight room had a ~1-m diameter¹³⁴ (FIG. 3c, top). At some point after sunset, the bat and rat will exit their roost to forage⁸² (FIG. 3a). Should we expect the place fields along the bat's flyway to have the same size as the tiny place fields in the cave? This is unlikely, for several reasons.

First, it is important to consider the total number of neurons needed to tile a typical 20-km flyway (BOX 3, see the figure part a), which (at 2 km width and 500 m height⁸²) has a total volume of 20,000,000,000 m³. To cover this flyway with laboratory-sized 1-m³ place fields¹³⁴, with a few tens of neurons overlapping at each location^{15,97}, would require ~1,000,000,000,000 place cells; a million times more neurons than the total cell count in the hippocampus^{42,135}. This discrepancy can be fully accounted for if place fields in the middle of the flyway have a millionfold larger volume (that is, a diameter 100 times larger) than place fields within the cave: that is, a place-field diameter of 100 metres, or more.

Second, it can be argued that the bat's cave needs to be encoded at high resolution, whereas there is no behavioural need for such high resolution if a bat is flying at a ~500 m altitude with speeds of 40 to 60 km per hour⁸². In such a 'mid-air void', we might expect place fields with a size of a few hundred metres simply because the bat does not need any better resolution. Thus, different locations in the environment may be represented at very different spatial resolutions, depending on their behavioural relevance to the animal.

Third, if we consider the sensory resolution of the view-based model of place fields^{122,123} (FIG. 2c) and assume a certain angular visual acuity that is determined by properties of the eye's lens and retina, then the sensory resolution is proportional to the flight altitude above ground. For example, when a fruit bat flies at an altitude of 500 m above ground⁸², its visual resolution (in metres) is 100 times poorer than that obtained when flying at an altitude of 5 m. This suggests that place-field volumes at 500 m altitude should be larger by ~100³ than when flying at 5 m altitude, which would resolve the millionfold discrepancy discussed above.

We therefore reason that the natural habitat of bats and rats is encoded by a multiscale spatial representation (FIG. 3a), reflecting both the behavioural demands and the sensory inputs available to the animal. To experimentally demonstrate such a multiscale representation would require recording hippocampal neurons in a bat or a rat moving in a very large (kilometre scale) environment that has multiple compartments of varying physical scale and/or importance to the animal. This has not been done, to date; however, some laboratory studies lend experimental support for this hypothesis. FIGURE 3b shows place-field sizes for several neurons recorded in the dorsal hippocampus of rats in different arena sizes, demonstrating that — at least in small-scale laboratory environments — place-field size scales up (somewhat sublinearly) with environment size^{16,19,136,137} (FIG. 3b, right).

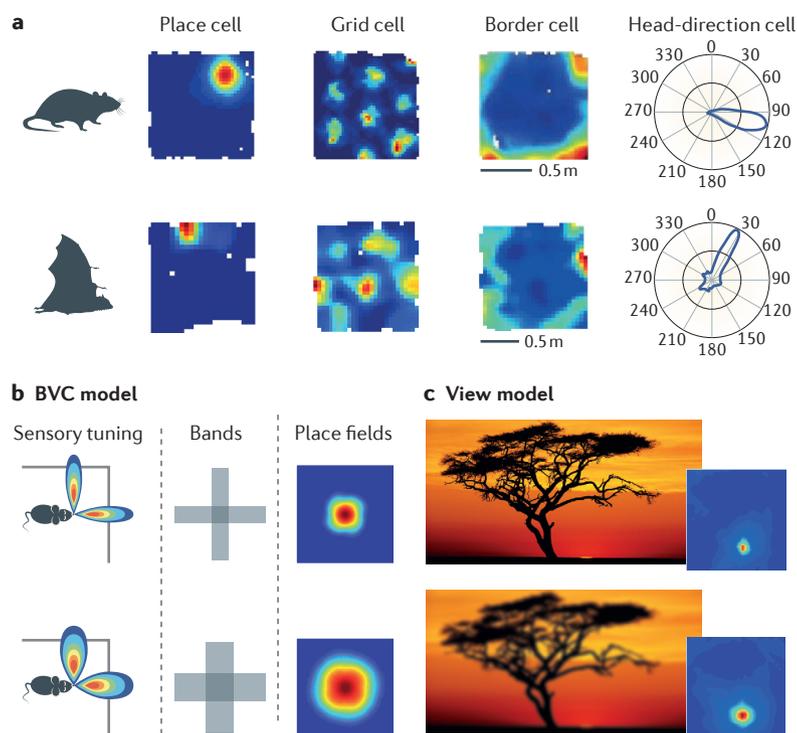


Figure 2 | Effects of sensory input on spatial representation. **a** | Properties of spatial cell types in the hippocampal formation of rats and bats. Recordings were made from neurons in animals exploring a square 1 m × 1 m box. Left panels show the firing rate (colour-coded from zero (blue) to maximal rate (red)) of the neuron as function of the animal's position within the box. Right-most panels show the directional tuning curve of a head-direction cell: direction (in degrees) is indicated on the periphery and firing rate is indicated by the distance from the centre. **b, c** | Two sensory-based models of place cells predict that degrading the resolution of the sensory input would increase place-field size (BOX 2). **b** | The boundary vector cell (BVC) model^{116,119,120}. In this model each boundary cell is tuned to a specific preferred distance and direction from a boundary (left column), and the intersection of the activity bands of several boundary cells forms a place field (middle and right columns). Right panels show simulated place fields for two different sensory resolutions. These simulations used parameters as in REF. 119 but varied the values of the distance resolution and angular resolution. The place-field size for the same neuron increases substantially when the sensory resolution of the input BVC population is degraded. **c** | The view-based model^{122,123}. Two images that simulate a retinal image were used as the visual input to the model: the top (sharp) image had a resolution of 500 × 180 pixels, whereas the bottom image was blurred with a 5 × 5 pixel Gaussian filter. Photographs show an example of the type of images used (other examples were used in the simulations) and inset panels show the place fields that were computed. The place-field size for the same neuron increases substantially when the sensory input is blurred. Part **a**, top, grid-cell data were adapted with permission from REF. 28, Nature Publishing Group; the border-cell and head-direction-cell data were reprinted from Solstad, T., Boccara, C. N., Kropff, E., Moser, M.-B. and Moser, E. I. Representation of geometric borders in the entorhinal cortex. *Science* **322**, 1865–1868 (2008) with permission from AAAS; and the place-cell data were adapted with permission from Whitlock, J. R., Sutherland, R. J., Witter, M. P., Moser, M.-B. and Moser, E. I. Navigating from hippocampus to parietal cortex. *Proc. Natl Acad. Sci. USA* **105**, 14755–14762 copyright (2008) National Academy of Sciences, U.S.A. Part **a**, bottom row, adapted with permission from REF. 30, Nature Publishing Group. Simulation results in part **c** reproduced with permission from D. Sheynikhovich, University Pierre and Marie Curie, Paris, France. Photographs in part **c** courtesy of © Royalty-Free/Corbis.

In addition to the scaling of place-field size according to the arena dimensions (FIG. 3b,c), there is evidence that spatial representations with different scales exist simultaneously along the anatomical dorsoventral axis of the hippocampus^{19,21,138–140} (FIG. 3d). One study, conducted

in rats running on an 18-m track, showed a ~10-fold increase in place-field sizes along the dorsoventral axis of the hippocampus: from ~1-m fields at the dorsal pole to ~10-m fields at the ventral pole¹⁹ (FIG. 3d, blue dots). A somewhat smaller range of place-field sizes was found along the dorsoventral axis of the hippocampus in other studies^{21,138} (FIG. 3d, green and orange dots), perhaps owing to the small apparatus sizes used in these studies and the fact that most did not record at the very ventral tip of the hippocampus^{138,139}. Combining this dorsoventral 10-fold scaling with the finding that dorsal place-field sizes scale with arena size, we propose that all neurons along the dorsoventral axis scale their place-field sizes together if the environmental size changes (FIG. 3d, ellipses).

The situation with regard to grid cells seems to differ from that of place cells. On one hand, the spacing (wavelength) of grid cells in rats was shown to scale up along the dorsoventral axis of the entorhinal cortex by a factor of ~10-fold¹⁴¹, with grid spacing increasing in a stepwise manner^{26,142}. However, based on experiments conducted so far, the grid scale seems quite resistant to environmental changes: when the arena size is increased, grid spacing also increases²⁶ (possibly signalling novelty¹⁴³) but then returns to baseline^{26,143}. Thus, although grid cells exhibit multiscale representation along the dorsoventral anatomical axis¹⁴², they are quite different from place cells in that their spatial scale seems relatively rigid and does not adapt to environmental changes, other than in a transient manner^{26,143}. Therefore, grid cells might have a particularly important role in stably encoding large-scale environments.

As discussed above, over-representation of a specific region by a large number of neurons may improve the ensemble resolution at that location¹⁵. Therefore, we predict that in natural environments, important locations such as the environs of the bat cave or rat burrow may be represented by many more neurons than locations in mid-air or mid-agricultural-field.

Thus, multiple scales of spatial representation can be obtained by several mechanisms, or a combination of these: an anatomical gradient of spatial scales along the dorsoventral axis of the hippocampus (FIG. 3d); dynamic scaling with changes in environment size (FIG. 3d, different ellipses); and population scaling by increasing the density of place fields for important spatial locations (FIG. 3a).

Finally, another important question is how different maps are pieced together to allow smooth navigation^{100,144,145}. Natural habitats contain multiple compartments, which may have different spatial scales, often without a direct line of sight between the compartments¹⁴⁵ (FIG. 3a), requiring some mechanism for coalescing the compartmentalized maps. One answer to this question comes from human navigation studies, which proposed that navigational strategies differ for different spatial scales^{145,146}, and that small spaces are navigated using independent maps, which are connected to each other through a graph^{145,147}. For example, a city might be encoded as a set of cognitive maps that represent open vista spaces, such as town squares

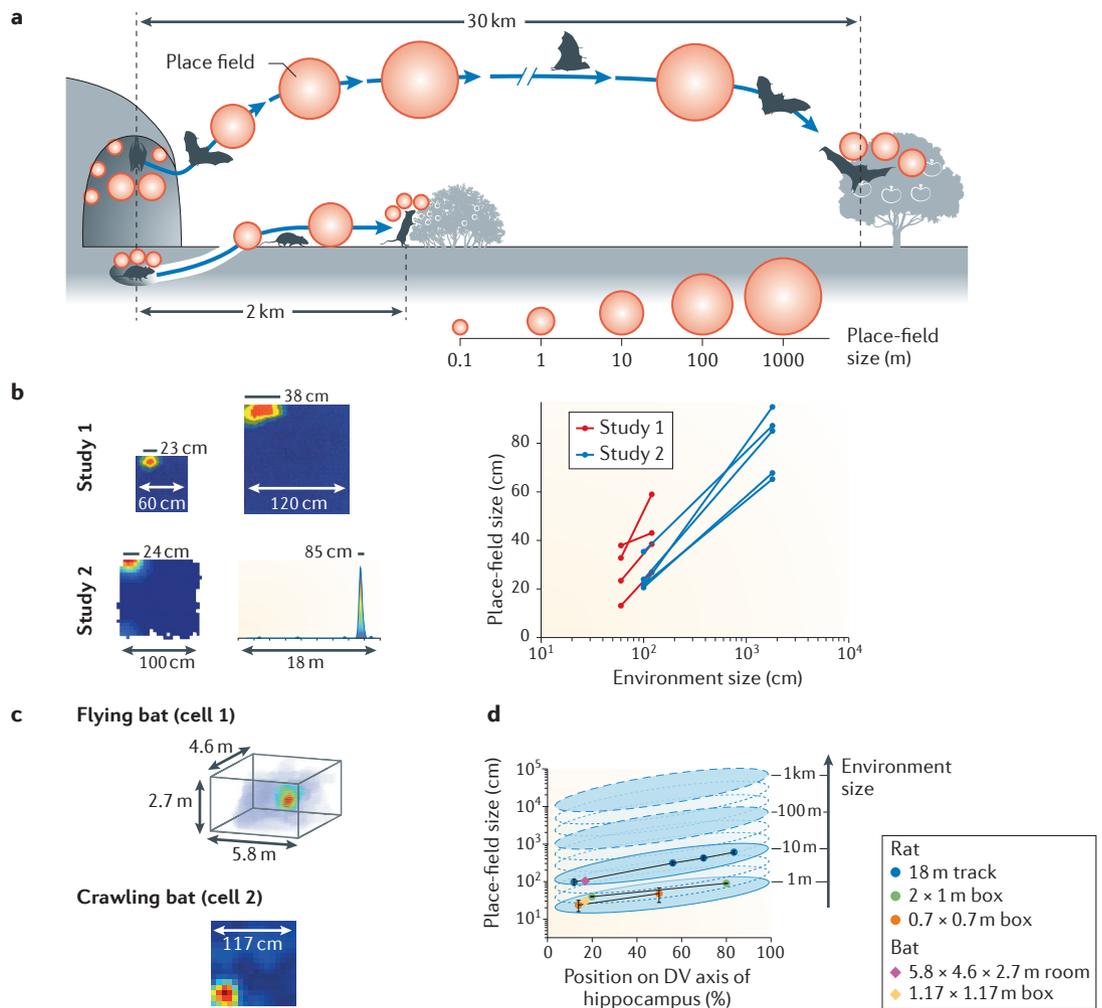


Figure 3 | Spatial representations on multiple scales. **a** | Hypothetical schematic showing how the home range of a bat or a rat may be represented on multiple spatial scales. We propose that there may be a higher-resolution representation (smaller place fields) for more important locations such as the cave or burrow, or the feeding tree, and a lower-resolution representation (larger place fields) at less important locations such as at a 500-m altitude in mid-flyway. **b, c** | Experimental data from rats and bats showing that place-field sizes of individual neurons increase when the environment's dimensions are enlarged. **b** | Left, place-field sizes of two rat cells, each recorded in two different environments: in study 1 the cell was recorded in a 60 × 60 cm box and a 120 × 120 cm box¹⁶; in study 2 the cell was recorded in a 100 × 100 cm box and on an 18-m linear track¹⁹. Right, changes in place-field size in all individual cells for which data are available in each study^{16,19}. **c** | Examples of place fields in bats. Top panel, example of a three-dimensional place cell recorded from dorsal hippocampal area CA1 of a flying bat¹³⁴. Bottom panel, example of a two-dimensional place cell recorded in a crawling bat^{30,107}. **d** | The spatial scale of the hippocampal representation increases along the anatomical longitudinal axis of the hippocampus. Data shown are population average place-field sizes from a variety of published hippocampal recordings in rats and bats, taken from various dorsoventral (DV) positions; error bars depict mean ± SEM (except the green dots, in which case medians are shown; for two- or three-dimensional place fields, the field size was averaged across dimensions). Data are from REFS 19,21,30,134,138. Neurons near the ventral (temporal) pole of the hippocampus have larger place fields than neurons near the dorsal (septal) pole; the increase in spatial scale along the dorsoventral axis is approximately 10-fold. This anatomical gradient of spatial scales is illustrated by the ellipses, depicting the place-field size versus the dorsoventral position. In addition, the place field of the same neuron also increases with environment size, illustrated by the vertical shift between the different ellipses, with each ellipse corresponding to the larger place fields in the larger environment. We speculate that these relations, as encapsulated by the two bottom coloured ellipses (solid lines), will hold over a continuum of environmental sizes (dotted ellipses), including for very large-scale environments, for which no experiments have been conducted to date (see the uppermost two coloured ellipses with dashed lines). Part **b**, top place-cell example is adapted from REF. 16, Nature Publishing Group; and bottom place-cell example is from Kjelstrup, K. B. *et al.* Finite scale of spatial representation in the hippocampus. *Science* **321**, 140–143 (2008). Reprinted with permission from AAAS. Part **c**, top place-cell example is from Yartsev, M. M. and Ulanovsky, N. Representation of three-dimensional space in the hippocampus of flying bats. *Science* **340**, 367–372 (2013). Reprinted with permission from AAAS. Part **c**, bottom place-cell example is adapted from REF. 107, Society for Neuroscience.

Dorsoventral axis of the hippocampus
 The hippocampus of rats and bats is an elongated, banana-shaped structure, and its long axis is referred to as the dorsoventral axis (or septotemporal axis). Place fields increase in size approximately 10-fold along this axis.

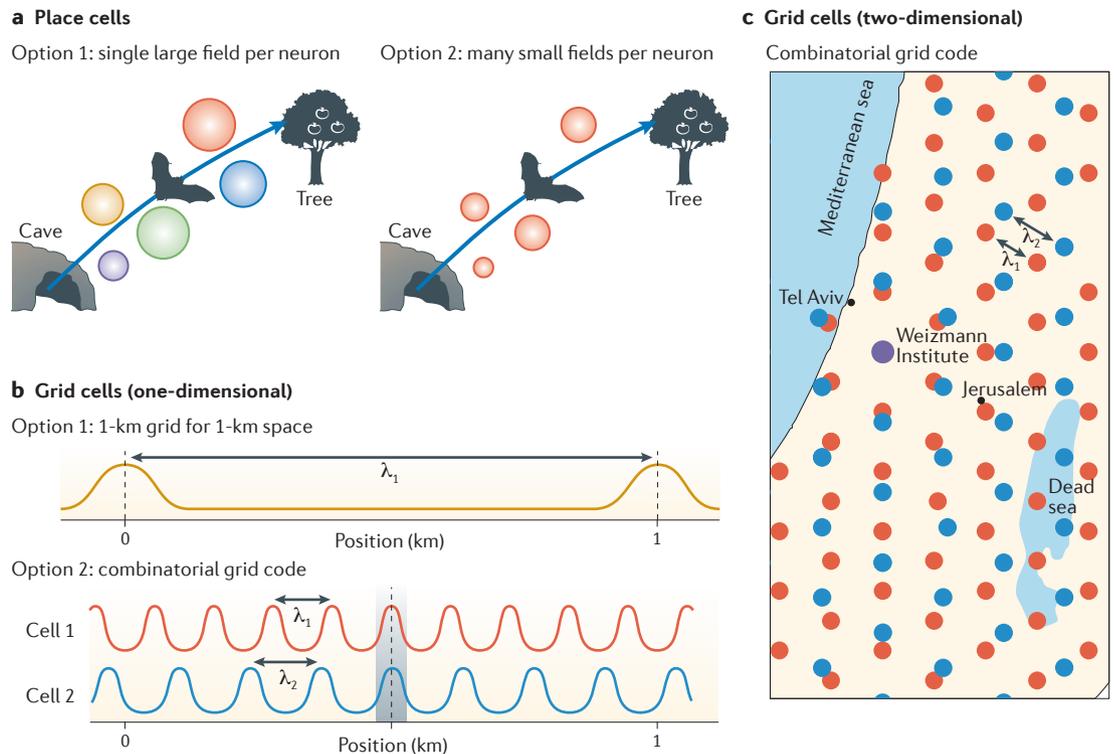


Figure 4 | Models of large-scale spatial codes. **a** | Schematic depiction of two options for the representation of a 1-km space by hippocampal place cells. Option 1 is based on scaling up results from the laboratory: it proposes that each neuron might have one large place field (represented by coloured spheres), with field size scaled up to match the environment size. Option 2 is based on laboratory experiments¹³⁶ and on a recent theoretical study⁴⁶; the latter study suggested that it may be beneficial, from a decoding perspective, to have dozens of small place fields for each neuron, in order to have more neurons covering each spatial position. This is indicated by all place fields being shown in the same colour (belonging to the same neuron). Combinations of options 1 and 2 are also possible (for example, multiple fields per neuron, with each field having a different size, according to the importance of each location). **b** | Schematic depiction of two options for the representation of a 1-km space by entorhinal grid cells. Option 1 is based on dorsoventral scaling results from the laboratory, suggesting that grid sizes up to 1 km will exist in a 1-km environment. Option 2, as suggested by several recent theoretical studies^{42–45}, suggests that the animal’s position could be encoded by combining grids with different scales, allowing the brain to encode very large spaces using much smaller grid scales^{42–45}. In the illustrated example, the two periodic functions represent two grid cells with periods λ_1 and λ_2 slightly larger than 100 m; and these functions coincide only at position = 0.5 km (grey shading): that is, their unambiguous coding range is >1 km (REFS 43,44). **c** | Schematic of a grid code in two dimensions. This illustrates the same concept as in part **b** (option 2) but adapted to two dimensions. The activity of two hypothetical grid cells (red and blue hexagonal grids, with periods λ_1 and λ_2) is shown here overlaid on a map of Israel. The two grids coincide only at one location: The Weizmann Institute of Science, Israel.

and large intersections, which in turn are connected to each other by a network of streets that create a cognitive graph^{145–147}. It would be of great interest to search in the hippocampal formation of bats and rats for a neural correlate of such a ‘cognitive graph of cognitive maps.’

Computational models of large-scale spatial codes. Spatial scales in the real world span 8 orders of magnitude for a bat — from 1 cm to over 1,000 km — whereas the dorsoventral gradient of place-field sizes in the hippocampus covers only 1 order of magnitude. Similarly, for wild rats, which can navigate several kilometres¹²¹, the dorsoventral gradient is also four to five orders of magnitude too small to support the huge dynamic range of spatial scales that are behaviourally relevant for rats. How does the brain cope with these extreme gaps?

For hippocampal place cells, there are two possibilities (FIG. 4a). First, in very large environments, each neuron might have a single large place field. Second, as proposed in a recent theoretical study⁴⁶, place cells in very large environments may have dozens of small place fields per neuron. This would increase substantially the number of neurons that are active at each spatial location and hence encode the animal’s position much more precisely⁴⁶. In contrast to the common view, which suggests that one place cell typically has one to two fields⁹⁴, this ‘multiple fields hypothesis’ offers a radically different neural coding scheme: it requires downstream decoders to be much more sophisticated than currently thought. This is akin to proposing that, under natural conditions, V1 visual neurons should have dozens of receptive fields, rather than just one.

Combinations of these two options are also possible. For example, a single place cell may have dozens of place fields, which may vary in size according to the availability of sensory inputs and the importance of different locations. Thus, all of the place fields depicted along the bat's flyway or rat's runway in FIG. 3a may in fact belong to a single hippocampal place cell.

Place-cell recordings are yet to be conducted in kilometre-sized environments, but data from multiscale laboratory experiments so far support both of these possibilities. In one experiment, in rats running on an 18-m linear track, very large place fields of 6 to 10 m were recorded in ventral hippocampus, but each neuron typically had a single field¹⁹. In another experiment, when an open-field arena was suddenly increased in size, neurons exhibited multiple place fields in the larger arena^{136,137}. Multiple fields were found also in rats running on a 48-m zig-zagging track¹⁴⁸ (although the number of fields in that experiment may have been boosted up by the large number of sharp corners on the track, eliciting multiple remappings¹⁴⁹). In a fourth experiment, conducted in bats (FIG. 3c, top), three-dimensional hippocampal neurons recorded in a larger environment tended to exhibit both a slightly larger number of fields and a larger field-size than those recorded in a smaller three-dimensional environment¹³⁴; consistent with both options. It remains to be seen which of these possibilities holds true in kilometre-sized environments.

In terms of grid cells, there have also been two main proposals (FIG. 4b). First, the largest grids could match the environment size, that is, a 1-km environment will have grids with a 1-km wavelength. A second, very different possibility was recently proposed by several computational studies^{42–45}, which suggested that two grids with different scales could combinatorially represent a coding range that is much larger than the individual grid wavelengths^{42–45} (FIG. 4b, bottom). Although a single grid cell encodes space with a cyclical ambiguity, the combination of two or more grids with different wavelengths — through readout of cells from different grid modules, for example¹⁴² — allows for the coding of space unambiguously within the coding range^{42,43}. Furthermore, these theoretical studies demonstrated that this 'combinatorial grid code' produces a highly precise estimate of position, which is exponentially efficient in terms of the number of neurons involved^{44,45}; the first example of an exponential neural code proposed for any brain function^{44,45}.

The combinatorial grid code could be potentially extended to two dimensions, and to very large environments. FIGURE 4c shows how combining two two-dimensional grids with wavelengths that are much smaller than the state of Israel can unambiguously represent a coding range the size of the entire state of Israel. Whether such combinatorial grid codes exist in real brains remains an open question. Although a common view is that grid cells are used primarily for path integration¹⁰², the combinatorial grid code hypothesis proposes that the function of grid cells is to efficiently encode very large environments^{42–45} (FIG. 4c). A major challenge for

behavioural neuroscience in coming years will be to determine which of these possibilities (or both) captures best the basic function of grid cells.

The need for a neural theory of real-world navigation.

We described above the need for mental spatial maps on multiple scales, and discussed experimental results from small environments and theoretical ideas about how these maps may generalize to larger spatial scales. A major open question is how such maps might be used in the process of navigation. The key problem is that place cells, grid cells and head-direction cells (FIG. 2a) may represent a neural map and compass (BOX 3) but are insufficient to navigate from point A to point B. Navigation requires much more than knowing where you are and where North lies: it entails trajectory planning, motor coordination, and decision making at navigational choice points. How does the brain accomplish this? One mechanism that was proposed involves route cells and goal-directed cells, found in the posterior parietal cortex^{150–153}. Some of these cells fire along most of the route as a rat navigates in a complex laboratory maze¹⁵⁰. Route-related codes also exist in the hippocampus itself, where some place cells encode also the future path of the animal¹⁵⁴. Moreover, ensembles of hippocampal neurons can accurately preplay future trajectories of the animal over distances of 1 to 2 m (REFS 97,155). These studies have been reviewed elsewhere^{95,156,157}, and may form the starting point for constructing a comprehensive neural theory of real-world navigation (BOX 3).

Future directions

In this Review, we have discussed the neural basis of real-world navigation, focusing on bats and rats as key models. We described some ideas that were proposed for the transformation of incoming sensory information into hippocampal spatial maps, which are used in turn for navigation. We highlighted two key problems. First, there is a requirement to represent very large environments in order to perform real-life navigation. As discussed above, some recent models have proposed fundamentally different views on how very large outdoor environments may be represented in the brain's navigation system. Second, there is a need for multiscale spatial maps that can dynamically adjust their scale to match the variable size of the environment and the changes in behavioural needs. This 'dynamic matching' process seems to be implemented by place cells, but not by grid cells (at least according to the data available to date).

Two further issues are noteworthy here. First, it is possible that laboratory-born animals, which have never experienced 1-km environments, may not display 1-km place fields. Therefore, experiments that aim to test large-scale (kilometre-sized) spatial representations in the mammalian brain should use wild-born rodents, bats or other mammals that have experienced large-scale environments during ontogeny. Indeed, comparing kilometre-scale representations in laboratory-born versus wild-born animals, may illuminate the role of experience in shaping the neural codes for space. Second, the neural matching of place fields to the world's spatial

statistics may be similar to the mechanisms by which vertebrate and invertebrate sensory systems adapt their neural responses to match natural stimulus statistics, as was demonstrated, for example, in the visual system^{158,159} and auditory system^{160–162}.

A word of caution is due here: it may be that the neural bases of large-scale representation and navigation are profoundly different from small-scale navigation, with differences much greater than those depicted in FIGS 3,4. For example, it could be that grid cells, which were proposed to result from path-integration processes^{24,102,163}, will lose their spatial periodicity on large spatial scales, because of the inability to path-integrate over long distances. However, real environments contain a multitude of local landmarks and visual cues¹²⁴, including trees, boulders and a variety of textures and strong odour sources, all of which can serve to anchor the path integrator and stabilize the grid; therefore, the richness of real landscapes might be fundamentally different from the emptiness of experimental boxes used to study grid cells in the laboratory. In a similar vein, one may ask whether head-direction cells would convey a similar kind of information in the field as they do indoors; and the same question applies to border cells. For head-direction cells, the answer is probably yes, because these cells encode cyclical variables, either 360° of azimuth³⁴ or three-dimensional directions in space¹⁶⁴ (360° azimuth × 360° pitch), both of which are independent of spatial scale. For border cells, the answer is less clear, because on the one hand it seems

unlikely that animals could measure distances to very distal boundaries such as mountain ranges, but on the other hand, natural landscapes contain also rich sets of elongated local features, such as rock ledges or hedgerows, which could activate border cells similar to their activity in small boxes. Nevertheless, all these classes of cells might also operate completely differently on large scales, or might perhaps not even be involved in real-life navigation; this caveat reinforces the urgent need to conduct electrophysiological studies of the neural basis of long-distance navigation.

Finally, we note that — even if we assume that the same spatial cell types in the hippocampal formation underlie both small-scale and large-scale navigation — we still have a very limited understanding of how the process of long-range navigation may be supported by these neurons. As discussed above, route cells and route preplays might possibly be relevant also for long-range route-following. However, real-world navigation requires much more than that. It requires, for example, the ability to optimize travel distance and/or effort; the ability to perform novel unplanned shortcuts; and the ability to re-orient oneself if the path is lost, or when an unexpected obstacle is encountered. Current models of brain function come short of explaining these complex facets of navigation. A major challenge for future work will be to determine how brain circuits support these feats. Furthermore, pursuing this challenge may help to bridge the gap between the major scientific disciplines of neuroscience and ecology.

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Competing interests statement

The authors declare no competing interests.