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Cognitive maps and the magnetic sense in vertebrates

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Abstract

Navigation requires a network of neurons processing inputs from internally generated cues and external landmarks. Most studies on the neuronal basis of navigation in vertebrates have focused on rats and mice and the canonical senses vision, hearing, olfaction, and somatosensation. Some animals have evolved the ability to sense the Earth's magnetic field and use it for orientation. It can be expected that in these animals magnetic cues are integrated with other sensory cues in the cognitive map. We provide an overview of the behavioral evidence and brain regions involved in magnetic sensing in support of this idea, hoping that this will guide future experiments.

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Introduction

Spatial navigation depends on a complex underlying network of neurons that encode a map of the environment. Initially hypothesized by Tolman in 1948 [1], the first direct evidence of a cognitive map came in 1971, with the discovery of neurons in the brains of rats that increased their firing rate when the animal visited a specific location in the environment, hence, termed place cells [2]. Many other spatial cell types were discovered in the following years, including grid cells that fire at regularly spaced distances, head direction cells that fire at specific head orientation angles, and border cells that fire at the edges of the environment [3]. The ensemble activity of spatially tuned neurons represents the neural correlate of a map of the external space: a cognitive map.

Forming and maintaining a cognitive map requires sensory and motor cue inputs. Internal self-motion cues (idiothetic cues) like vestibular signals, sensory flow, proprioception, and motor efference copies keep track of travelled distances and directions. Over time, however, these accumulate errors, which are minimized by consulting external environmental cues (allothetic cues) [4]. The predominantly studied organisms for cognitive maps are rats and mice, which effectively navigate with external cues perceived by the canonical senses - vision, olfaction, hearing, and somatosensation - used flexibly depending on availability and task requirements (Figure 1). However, within the diverse animal kingdom some species have evolved sensory specializations to navigate in their unique habitats, such as the ability to detect the Earth's magnetic field [5]. Do magnetic cues integrate into the cognitive map in these animals?

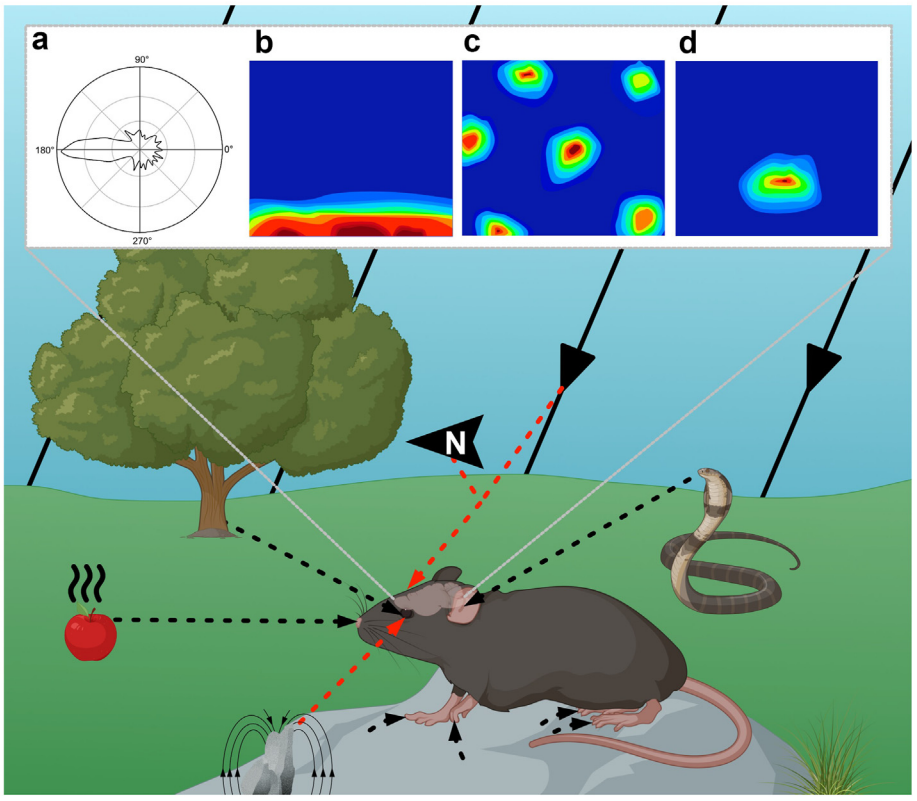
The geomagnetic field

The Earth's magnetic field provides an omnipresent set of allothetic cues to any navigator able to sense it (Figure 2): The polarity (direction), inclination (tilt), declination (angle between magnetic and geographic north) and intensity (density) of the field lines. In addition to directional (compass) information, inclination, declination and intensity gradients potentially provide positional (map) information [6,7]. Moreover, magnetic anomalies created by magnetic minerals in the Earth's crust could serve as local landmarks [7].

The magnetic compass sense

Many organisms use the direction of the Earth's magnetic field for orientation [8]. An intensively studied model organism is the European robin, a long-distance migratory bird that uses a magnetic inclination compass on its biannual migrations [9,10]. Fishes, amphibians, and turtles also possess a magnetic compass sense. Even among mammals a magnetic compass has been demonstrated in species that inhabit aphotic habitats, such as bats and subterranean mole-rats [11]. Mole-rats use their compass to navigate through mazes of tunnels [12], bats to return to their home roost after nightly foraging bouts [13], and presumably for long-distance migration [14].

Figure 1

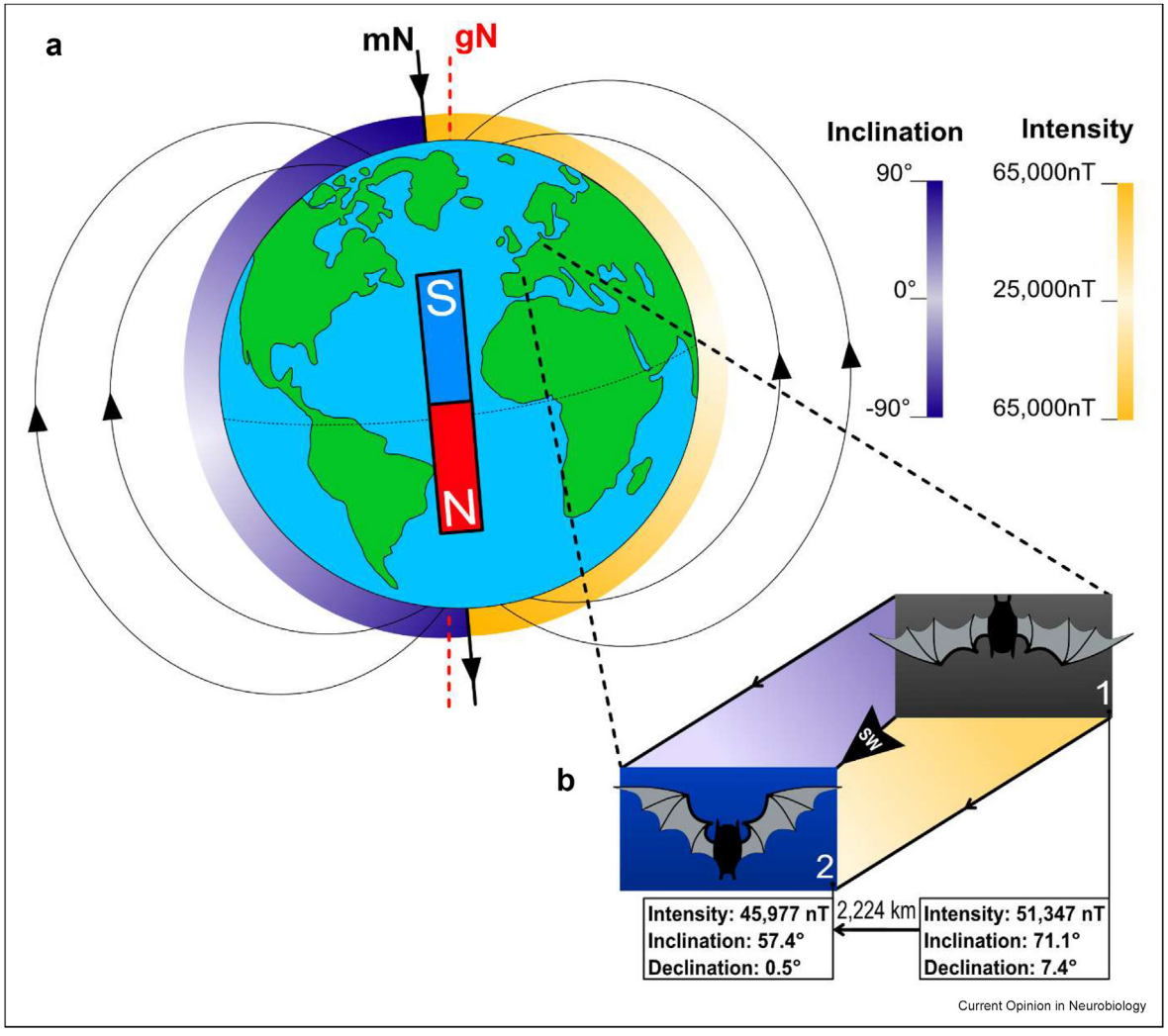


Sensory cues used by an animal orienting in space: The environment offers visual, olfactory, auditory, tactile, and possibly magnetic cues from the geomagnetic field or local anomalies that can aid navigation of an animal able to sense these cues. Together with idiothetic information such as vestibular signals, optic flow and proprioreception, a cognitive map in the brain is formed, consisting of spatially firing neurons such as **a.** Head direction cells **b.** Border cells **c.** Grid cells **d.** Place cells. a: Example polar plot of firing rate of a cell at different angles in the environment, b–d: Example firing rate maps of respective cell types in an animal exploring a rectangular environment, with warmer colors denoting the location encoded by the cell.

The magnetic map sense

In addition to the magnetic compass, evidence from long-distance migrants supports the use of geomagnetic cues for true navigation, i.e. to determine position based on magnetic parameters [6,7]. The global gradients of geomagnetic field intensity, inclination and declination often form grids that provide information for a bi-coordinate map. Virtual displacement experiments in which animals displayed compensatory reorientation behavior after sole exposure to the magnetic field parameters of a remote location (without being physically displaced) provide the strongest evidence. For example, reed warblers exposed to the magnetic field parameters of a location ∼2700 km northeast from their southern migratory route displayed a corresponding southwest deflection of their directional preference in a laboratory orientation assay [15]. Similarly, hatchling green turtles use magnetic signatures to identify critical locations along their migratory route, where they must change their swimming direction to stay in the Atlantic gyre and prevent drifting into colder waters [7]. Migratory fishes such as eel and salmon also possess a magnetic map sense [16,17]. It is important to note, however, that the geomagnetic field gradients are very shallow, rendering a magnetic map most feasible for long-distance migrants. Intensity and inclination change ∼3–5 nT and ∼0.009° per km, respectively, corresponding to a relative change of 0.01% per km [18,19]. Absolute sensitivities and discrimination thresholds of the magnetic sense are not well studied, but published thresholds for the inclination compass of 2–5° for birds [19] and 0.5° for newts [18] suggest that the use of magnetic maps over distances <50–200 km is unlikely (others have suggested a lower limit of >10 km [6]). The lower threshold might be determined by receptor properties [20] or background noise, such as the daily fluctuations of the geomagnetic field, which are regularly of the same magnitude as the field would change over a distance of 10 km. Indeed, even in homing pigeons which home from distances of up to several hundreds of kilometers,

Figure 2



The geomagnetic field as an allocentric cue for navigation. a. Magnetic cues from the Earth's magnetic field can be used to derive directional information by using polarity, inclination or declination angle (angle between magnetic north' mN and geographic north' gN) or positional information by using declination changes or the gradients of inclination angle or intensity of the field. **b.** Example of a bat migrating a distance of 2,224 km in southwest direction from Pape, Latvia to Pitillas, Spain [14]. The bat could either follow a magnetic direction over a specified distance or follow magnetic field gradients until the parameter of the local magnetic field matches the desired location (which the animal remembered or interpolated).

there is no strong evidence for the use of a magnetic map sense [21]. Similarly, magnetic manipulations did not impede homing success in shearwaters that were displaced 400 km [22]. Accordingly, geomagnetic gradients are likely not helpful for animals orienting over short distances (<2 km), such as rodents. However, local magnetic anomalies caused by magnetic minerals in the Earth's crust could steepen gradients and serve as landmarks [7].

Sensory basis of the magnetic sense

The cellular and molecular basis of the magnetic sense remains obscure [23], but several physically plausible sensory mechanisms have been suggested [24]. The radical pair hypothesis describes a quantum mechanism based on the influence of weak magnetic fields on the recombination of radicals [25]. There is evidence for magnetic field effects on radicals produced in photoexcited cryptochromes in the retina [26]. A second proposed mechanism is based on magnetic nanocrystals (e.g. magnetite), but such particles are still awaiting their discovery in a sensory cell of any vertebrate [23]. Finally, recent evidence from pigeons supports a compass mechanism based on electromagnetic induction in the semicircular canals of the inner ear [27]. It is conceivable that an animal species possesses two magnetic sensors tuned to fulfil different functions (e.g. compass + map).

Brain regions involved in the magnetic sense

Our understanding of the neuronal circuits responsible for processing magnetic information remains incomplete. Various species appear to engage different circuits for this task, although direct neurophysiological recordings supporting this assertion are scarce [28]. Instead, in many experiments animals were exposed to magnetic stimuli and immediate early genes (IEGs such as c-fos, ZENK/EGR-1, pERK) served as proxies for neuronal activity [29]. The IEG expression was compared to sham-exposed control animals to identify activated brain regions. Stimulus-response properties of magnetosensory systems are unknown, thus often complex changing magnetic fields served as stimuli to maximize the likelihood of activating the receptors. Based on such studies, brainstem trigeminal and/or vestibular nuclei are likely primary processing centers for magnetic information in rodents, birds, and fishes [30–32]. From the primary brainstem areas, magnetic information distributes across many brain areas, including the thalamus, superior colliculus, hippocampal formation, and cortical/hyperpallial areas. A separate thalamofugal pathway from the retina to a forebrain region termed Cluster N appears to process magnetic compass information coming from the retina in night-migratory birds [33]. Cluster N densely connects with the hippocampal formation [34], a key brain region for spatial navigation and cognitive maps.

Brain regions involved in navigation (cognitive maps)

The formation of a cognitive map requires integration of multiple sensory cues, both internally generated and external landmarks, distributed across several brain regions [35,36]. Information from these sensory systems is first encoded in an egocentric reference frame, i.e. with respect to the animal's position and orientation in space. This is then transformed into allocentric information to form a coherent cognitive map of the external space, independent of the animal's head and body position [37].

Upstream brain regions like the medial vestibular nucleus, nucleus prepositus, dorsal tegmental nucleus, lateral habenula and the lateral mammillary nucleus encode angular head velocity using inputs from self-motion cues [38,39]. This idiothetic information on speed and direction of head turning is integrated with allothetic sensory cues, leading to the directional firing of head direction cells that are found in many brain regions, including the dorsal tegmental nucleus, lateral mammillary nuclei, anterodorsal thalamic nucleus, laterodorsal thalamic nucleus, postsubiculum, postrhinal-retrosplenial-, and medial entorhinal cortex (MEC) [39]. Edges of the environment are encoded in border cells, also called boundary vector cells, in the subiculum, postrhinal cortex, retrosplenial cortex and MEC [40–42]. Moreover, object vector cells in the MEC encode information on the distance to objects in the environment [43]. Cells that encode the speed of movement are also found in the MEC [44]. The combination of movement speed, distance and direction leads to the formation of multiple hexagonally arranged periodically firing fields characteristic of grid cells in the MEC [44] and the pre- and parasubiculum [45]. These cells likely provide metrics for navigation by laying a grid on the external space which acts as a reference for measuring distances. Ultimately, inputs from this distance metric together with spatial information from other cell types feed into place cells in the hippocampus CA1, CA3, and dentate gyrus [46,47]. Apart from the animal's location in space, the hippocampus also encodes the position of objects in landmark cells and their sensory features in object recognition cells [48]. Moreover, spatially selective neurons resembling place cells were also discovered outside the hippocampus, e.g. in the visual cortex [49], somatosensory cortex [50], the subiculum [47], and superior colliculus [51], suggesting a wide distribution of spatial signals in the brain with the hippocampus playing the role of a central hub [52].

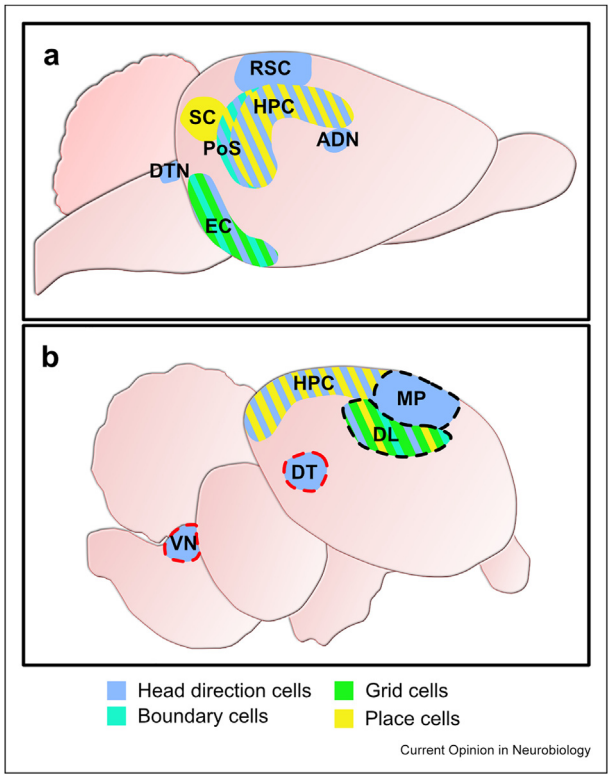
Possible integration of magnetic information into the cognitive map

Animals with a magnetic sense likely use directional (compass) and perhaps positional (map) information of the geomagnetic field together with other sensory inputs when forming a cognitive map. It is conceivable that they possess neurons that respond to specific values or combinations of magnetic field parameters, but where could these neurons be located?

In birds and mammals, several brain regions have been identified to exhibit both spatially firing cells and responses to magnetic fields (Figure 3). An early step in the formation of a cognitive map requires the integration of head position and movements using input from brainstem vestibular nuclei [53]. Interestingly, in head-fixed pigeons these nuclei are also activated by magnetic field rotations [27,54] and electrophysiological recordings in head-fixed pigeons revealed vestibular brainstem neurons tuned to specific magnetic field directions [55]. Interestingly, the cells appeared to be tuned to the intensity of the Earth's magnetic field, as their response increased from 20 μT to 50 μT, but did not increase further at 100 μT or 150 μT [55]. These results are consistent with a population of magnetic head direction cells that transmit allocentric directional information to downstream spatial brain areas. Where and how this information is integrated is currently unknown.

A study in mole-rats reported a reduction in c-fos expression in the anterodorsal (AD) and laterodorsal (LD) thalamic nuclei, the dorsal tegmental nucleus, the postsubiculum, the retrosplenial and entorhinal cortices, and the hippocampus when the ambient magnetic field was perturbed. While this does not prove that all these areas process magnetic information, it suggests a

Figure 3



Brain regions that contain spatially firing neurons and are involved in magnetic sensing. a. Schematic rodent brain with functional overlaps in RSC = retrosplenial cortex [56,94], ADN = anterodorsal thalamic nucleus [56,95], HPC = hippocampus [2,56,96], PoS = postsubiculum [42,47,56], SC = superior colliculus [32,51], EC = entorhinal cortex [44,56], DTN = dorsal tegmental nucleus [56,97]. **b.** Schematic bird brain with functional overlaps in MP* = medial pallium [77], HPC = hippocampus [54,61], DL* = dorsolateral hippocampus [98]. DT† = dorsal thalamus [49] and VN† = vestibular nucleus [55]. *Magnetic responsive cells are yet to be discovered in MP where head direction cells were discovered in shear water chicks and DL where grid-like cells along with other spatially selective cells were very recently found in the tufted titmouse in a region lateral to the dorsal hippocampus seen as a functional homolog to the mammalian MEC (dashed black lines). †DT and VN were found to have a magnetic response. The vestibular nucleus contains angular head velocity (AHV) cells while the dorsal thalamus contains head direction cells in mammals. However, presence of these directionally selective cells is yet to be established in the two brain regions in bird brains (dashed red lines).

correlation between stable magnetic fields and the cognitive map in these subterranean rodents [56]. It is known from other rodents that spatially tuned cells often stop firing when their sensory anchors are unreliable [57] and the expression of c-fos has been linked to their activity in a given environment [58]. The reported magnetic responses in the anterior thalamus in mole-rats are particularly noteworthy, as recently the firing of head direction cells in the anterior thalamus of mice were found to increase their average firing rate in response to auditory and somatosensory stimulation [59]. This demonstrates that multimodal information from external cues already enters the head direction network at the level of the thalamus. Furthermore, magnetic field effects on c-fos expression in the dorsal thalamus were also found in head-fixed pigeons [54]. It would be interesting to test if magnetic stimuli modulate the activity of head direction cells in this brain region. Consistent with the notion that magnetic cues are integrated with other modalities to form a multisensory representation of space, magnetic responses were also found in the superior colliculus of mole-rats [32].

Further downstream, the retrosplenial cortex which contains head direction cells and border cells is centrally involved in egocentric to allocentric transformation [37]. Irrespective of the upstream magnetic information processing brain regions, we postulate that this hub for transformation of external sensory information into the spatial navigation circuitry could integrate magnetic information into the cognitive map. Once incorporated into the allocentric map, the spatial representations in downstream brain regions like the MEC and the hippocampus can also be expected to exhibit activity modulation by magnetic cues.

Finally, the hippocampal formation, which harbors place and head direction cells in bats, birds and rodents is an especially intriguing brain region [60–63]. Magnetic field effects on hippocampal c-fos expression were found in birds and mammals. In freely hopping zebra finches, a changing magnetic field increased c-fos expression in the dorsomedial anterior hippocampus [64], and a similar effect has been reported for the hippocampus in head-fixed pigeons [54]. The pigeon hippocampus is involved in spatial navigation [65,66] and contains place cells [67], as does the anterior hippocampus of zebra finches [61]. Overall, these findings are consistent with the integration of magnetic cues in the hippocampal formation.

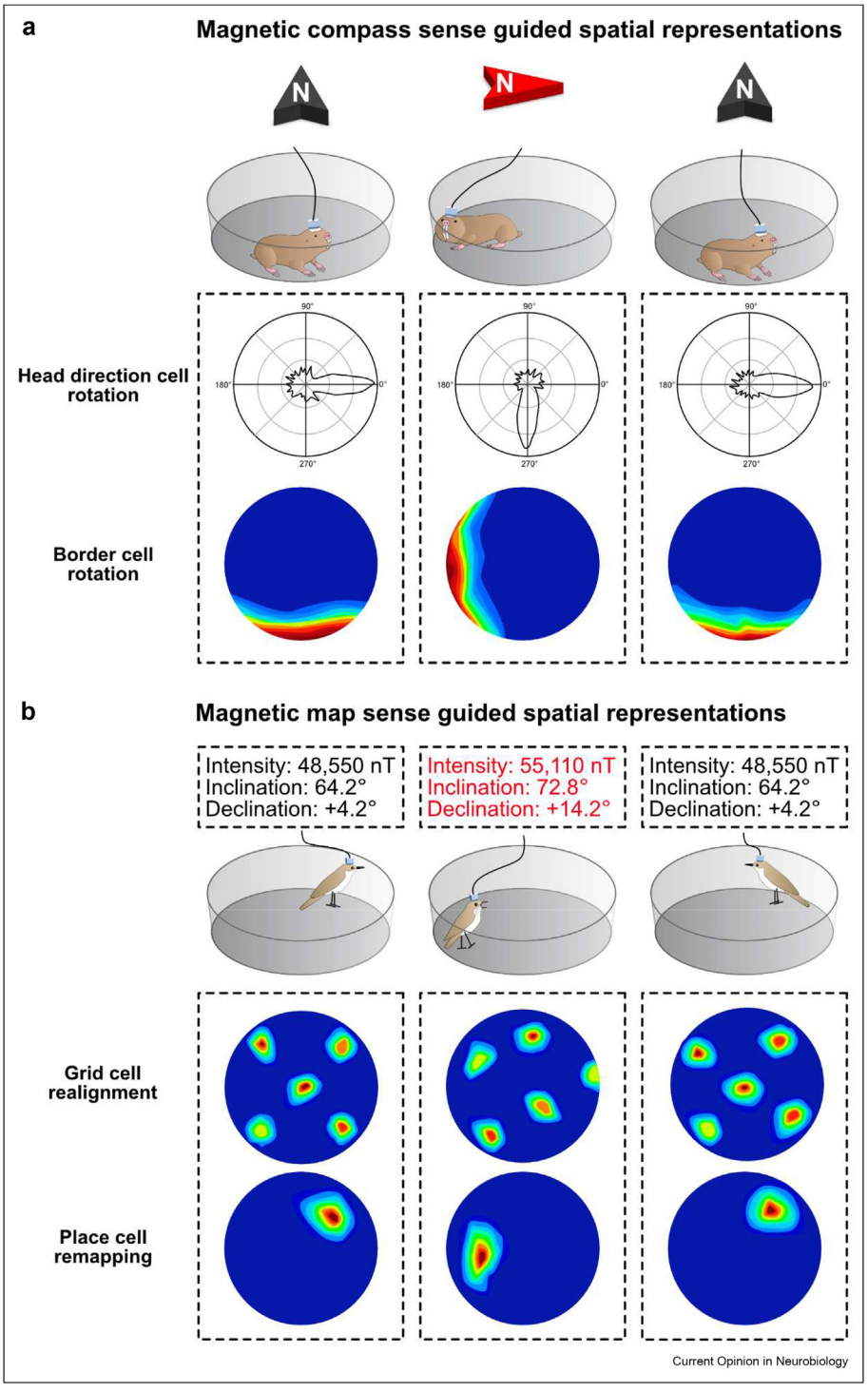
Possible encoding of magnetic landmarks

The hippocampus, MEC, and LEC [68] store information on both the spatial location and non-spatial sensory features of objects in the environment. Interestingly, mole-rats inspect magnetic objects longer than similar non-magnetic ones [69]. We speculate that magnetosensitive animals encode the magnetic properties of objects in object tuned cells to map them as magnetic landmarks (anomalies) during navigation, comparable to the use of acoustic landmarks in bats [70].

Feasibility of recording brain activity in animals with a magnetic sense

Although there is some evidence for a magnetic sense in standard laboratory rodents [71–73], there is a lack of evidence for the use of magnetic cues in navigation in these animals [74]. It is, therefore, advisable to study sensory specialists. These are primarily non-model organisms inhabiting specific niches, but recent advances in recording technology enable freely moving electrophysiological recordings in any animals able to carry a

Figure 4



Putative magnetic cue effects on neural representations of space. Schematic representations of predicted outcomes of spatial tuning patterns of hypothetical cells anchoring to different parameters of magnetic cues. **a.** Magnetic compass guided spatial representations in head direction cells and border cells of mole-rats exploring a circular arena: A 90° clockwise rotation of the magnetic field is expected to rotate the preferred firing direction of a head direction cell (depicted in the polar plots) and the firing field of a border cell (depicted in the firing rate map) by corresponding angles in the same direction. **b.** Magnetic map sense guided spatial representations in grid cells and place cells of reed warblers virtually magnetically displaced from Illmitz, Austria to Neftekamsk, Russia [15]: Each location on Earth has distinctive magnetic field parameters like field intensity, inclination angle, and declination angle. Spatial representations in grid cells and place cells (both depicted as firing rate maps) could anchor to these external parameters to form a unique map of the respective locations. Grid fields of a grid cell could realign in new environments whereas place cells could remap their firing fields.

few grams on their head. Wireless transmission or logging of acquired neural data has made it possible to record from freely flying bats [62] and barn owls [60], swimming goldfish [75], freely moving quails [76] and migratory seabirds [77]. High-density silicon probes enable the acquisition of stable neural data from hundreds to thousands of neurons over months and in deep brain regions [78]. In addition to advances in electrophysiology, modern imaging technologies such as functional ultrasound imaging [79] and multi-photon quantification of calcium reporters enable functional assessment of large neuronal populations in freely moving animals [80].

Considerations for studies on the role of magnetic cues in cognitive maps

When studying magnetic orientation behavior, the stimuli should mimic natural situations, i.e. they should have Earth's field strength and be spatially homogeneous. Furthermore, when integrating magnetic stimuli into electrophysiological experiments, one needs to be aware of artefacts due to electromagnetic induction [81]. Controlling for other artefacts, such as heating or vibrations, by using double-wrapped coils is crucial [82]. Moreover, as the compass of birds and possibly some mammals is sensitive to interfering radiofrequencies [71,83,84], minimizing and characterizing the electromagnetic fields in the recording setup is imperative.

Attention states and task requirements influence the dynamics of spatial representations [85]. Hence, it is crucial to study the contribution of magnetic cues to the cognitive map when the magnetic information is relevant to the task [77]. Long-distance migrants rely on their magnetic sense primarily during the migratory seasons and in specific migration phases [10]. Furthermore, some animals might use their magnetic sense only during certain times of the day, e.g. around sunset, either to calibrate a sun compass [86] or because the magnetic field fluctuations are minimal during this time [87]. A key challenge is, therefore, to find a species and behavior with a robust magnetic response at a spatial (<1–2 m arena) and temporal scale (<30–60 min per session) suitable for freely moving neural recordings inside a magnetic coil system.

An exciting example are streaked shearwater chicks just before their first migration, in which HDCs were found to fire preferentially towards the seasonally appropriate northern direction [77]. The recordings were made during 10 min sessions in a small arena (diameter 120 cm), providing an ideal opportunity to study the effect of magnetic field manipulations on HDC firing. Other magnetosensitive species in which spatial cell recordings have been achieved include bats [62], fishes [75], pigeons [67], and zebra finches [61]. To screen for magnetic compass information in spatial brain regions of these species, several sessions could be recorded from an animal inside a magnetic coil system that changes magnetic directions between the sessions (Figure 4a). Rotations of spatial representations (e.g. the preferred firing direction of a head direction cell) would indicate a compass response, similar to the response observed in rats when a prominent visual cue has been rotated [88].

It is currently technically impossible to study the cognitive map at the scale relevant for the magnetic map sense. It could be addressed, however, by recording from long-distance migrants before and after a virtual displacement. Place cells and grid cells are known to exhibit environment-specific firing patterns that can be stable over several months [90]. In different environments, however, the cells reorganize their firing activity [91] in form of global remapping by place cells wherein the place fields of place cells change their respective firing locations, and in the form of grid realignment wherein the entire grid pattern of a grid cell moves and rotates. If an animal indeed perceives an environment as novel after a magnetic virtual displacement (with all cues except magnetic cues unchanged), one would expect to observe global rearrangement of activity in these cells (Figure 4b).

To promote the use of magnetic cues, other available cues should be minimized [20], although presenting the magnetic field along with additional visual cues as a reference could yield insights in cue conflicts induced by magnetic field rotations as demonstrated in bogong moths [89]. Finally, global remapping has also been demonstrated to occur in the hippocampus and subiculum of bats when they were forced to switch from one sensory modality (vision) to another one (echolocation) within the same environment [92]. It is therefore conceivable that remapping takes place in magnetosensitive animals when the magnetic field is not present.

Conclusion

In recent decades, our understanding of cognitive maps and the magnetic sense has evolved substantially, albeit independently. At the same time, neuroscience has undergone a technological revolution that begins to relax the restriction to a handful of standard model organisms. Novel tools allow bridging both fields to record neural activity in animals exploring naturalistic environments [93] and investigate the role of the Earth's magnetic field in the cognitive map of sensory specialists. We anticipate that as technology progresses, the number of recordings of spatial cells across diverse species will increase and simultaneously advance our understanding of the cognitive map and the role that magnetic cues might play in it.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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** of outstanding interest

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The spatial navigation circuitry in mammals has so far focused on a subset of spatially selective cells in the hippocampal formation. However, space was predicted to be an a priori to overlay experiences and hence was expected to have representations distributed in multiple brain regions. Long & Zhang provide evidence for the prevalence of the spatial code by demonstrating the presence of the entire subset of spatially tuned cells like place cells, grid cells, border cells, and head direction cells in the somatosensory cortex wherein the spatial map could enable representation of body in space.

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Wu & Dickman exposed head-fixed pigeons to a rotating magnetic field stimulus and mapped c-fos expression across the brain. They identified a set of brain regions with increased c-fos compared to controls kept in a zero magnetic field, including the hippocampus, dorsal thalamus, lateral hyperpallium and vestibular brainstem nuclei. Interestingly, the response was reduced to baseline levels after ablation of the inner ear lagena in all regions but the hyperpallium. These findings suggests that the lagena plays a critical role, but that a second magnetoreceptor exists which might be trigeminally innervated as they also found increased c-fos in the principal sensory nucleus of the trigeminal system.

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Wu & Dickman exposed head-fixed pigeons to a rotating magnetic stimulus and recorded single units in the vestibular brainstem. They discovered neurons tuned to the different components of the magnetic field, direction, intensity and polarity. Sensitivity to polarity is in line with magnetoreceptors based on ferrimagnetic particles or an induction based mechanism, while it contradicts a mechanism based on radical pairs.

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