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Review

Neural circuits for goal-directed navigation across species

Jayeeta Basu[1,2,3,4,*] and Katherine Nagel[1,2,4,*]

Across species, navigation is crucial for finding both resources and shelter. In vertebrates, the hippocampus supports memory-guided goal-directed navigation, whereas in arthropods the central complex supports similar functions. A growing literature is revealing similarities and differences in the organization and function of these brain regions. We review current knowledge about how each structure supports goal-directed navigation by building internal representations of the position or orientation of an animal in space, and of the location or direction of potential goals. We describe input pathways to each structure – medial and lateral entorhinal cortex in vertebrates, and columnar and tangential neurons in insects – that primarily encode spatial and non-spatial information, respectively. Finally, we highlight similarities and differences in spatial encoding across clades and suggest experimental approaches to compare coding principles and behavioral capabilities across species. Such a comparative approach can provide new insights into the neural basis of spatial navigation and neural computation.

Highlights

The hippocampus of vertebrates and the central complex of insects are both engaged by navigational tasks that require spatial memory or inference.

The hippocampus builds flexible place maps of both real and abstract spaces.

The insect central complex comprises ordered arrays of cells that are well suited to encode and compute with vectors.

Both the hippocampus and central complex feature heading-direction signals based on ring attractor networks, and both structures receive input from partially segregated 'where' and 'what' pathways.

Current understanding of the differences between vertebrate and invertebrate navigational systems might reflect ecological, historical, and methodological differences. Future comparative approaches will help to reveal fundamental relationships between brain circuits and navigational and cognitive abilities across species.

Towards a comparative neuroscience of spatial navigation

Navigation is a fundamental and crucial function for survival and sustenance across species. From foraging for food, to escaping from prey, to finding shelter or a mate, all animals need to navigate towards goals in their environment. Studying how brains perform these behaviors has yielded considerable insight into the logic of neuronal computation and the format of internal representations across species. However, direct comparisons between navigation systems across vertebrates and invertebrates have been relatively rare.

When sensory cues directly signal a goal location, navigation can often be accomplished through feedforward sensorimotor pathways. For example, hunting zebrafish can locate their prey using simple retinotectal circuits that transform visual signals into directional movements [1]. Similarly, during courtship, male flies chase female flies using direct visuomotor pathways [2]. In contrast, when the location of a goal is hidden, is related indirectly to sensory cues, or must be remembered or inferred, more complex computations are required. Two ancient structures have been implicated in these spatial computations: (i) the hippocampus/entorhinal cortex of vertebrates, and (ii) the central complex of arthropods. In recent years technological developments such as closed-loop virtual reality, *in vivo* imaging, targeted circuit manipulations, and connectomics have revealed new principles of how information is encoded and processed in both structures, how this information guides behavior, and how learning and plasticity allow each structure to adapt to new environments and contexts. These discoveries suggest both similarities and differences in how vertebrate and invertebrate brains encode space.

In this Review we summarize both classical and recent studies on how the hippocampus and central complex represent information that is crucial for goal-directed navigation. We show how each structure builds representations of the location or orientation of the animal in space and of the

[1]Neuroscience Institute, New York University Langone Health, New York, NY 10016, USA
[2]Department of Neuroscience and Physiology, New York University Grossman School of Medicine, New York, NY 10016, USA
[3]Department of Psychiatry, New York University Grossman School of Medicine, New York, NY 10016, USA
[4]Center for Neural Science, New York University, New York, NY 10003, USA

*Correspondence:
jayeeta.basu@nyulangone.org (J. Basu) and
katherine.nagel@nyumc.org (K. Nagel).

location or direction of potential goals. Intriguingly, both structures build representations of global heading by combining external sensory cues with ideothetic self-motion information, through computations consistent with a ring attractor network. Furthermore, both structures receive input from pathways in which 'where' information about the position and movement of the animal through space is at least partially segregated from 'what' information about objects in space and the nature and value of potential goals, rewards, or threats. These similarities, as well as differences in spatial coding, suggest both common solutions and divergent implementations that may allow different types of spatial and cognitive computations across species. Finally, we consider how differences in experimental approaches across organisms might bias our observations and propose more direct experimental and behavioral comparisons across species. We argue that such comparisons can potentially reveal new relationships between neural circuit structure and cognitive capacities.

In the forest of place cells: flexible maps of locations and goals in the hippocampus and entorhinal cortex

The hippocampus has long been considered the epicenter of the spatial navigation system of the mammalian brain. Foundational work in the 1970s capitalized on the technological feat of recording extracellularly from the hippocampus in freely moving rats to reveal the presence of place cells (Figure 1) [3]. Place cells increase their firing at distinct locations of space the rat has explored – called their place fields. The population of place cells has long been hypothesized to form a 'cognitive map' that can be used as a Cartesian reference frame to plan trajectories and solve navigational tasks [4]. One such task is the widely used Morris water maze, in which a swimming rat

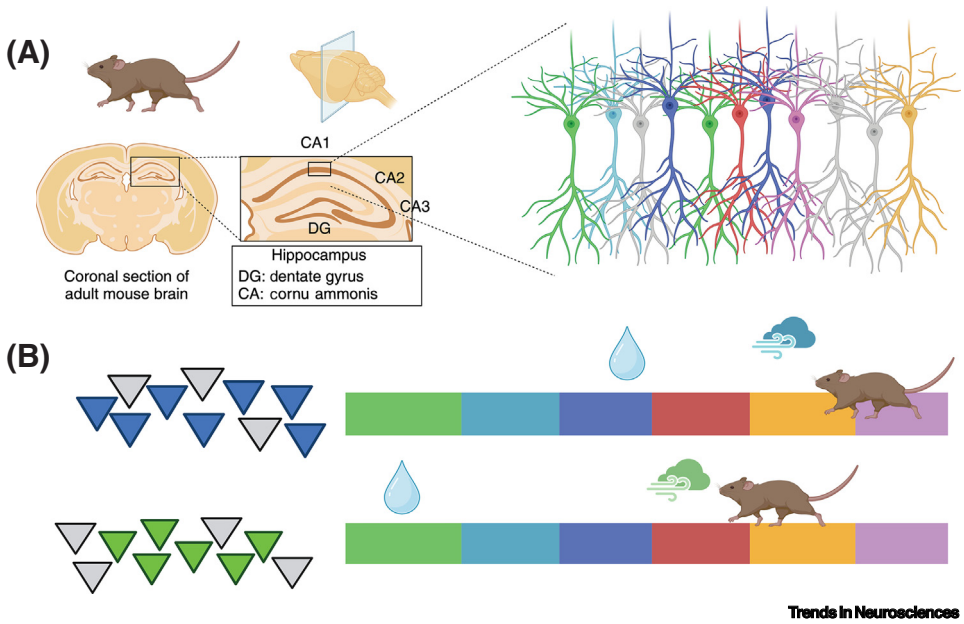

Figure 1. Place cells of the hippocampal formation. (A) Schematic overview showing the mouse hippocampal place cell system. The hippocampus and its subdivisions (DG, CA1, CA2, and CA3) are indicated in a coronal cross-section of the adult mouse brain. CA1 pyramidal neurons show spatially tuned activity characterized by an increase in firing rate as the mouse navigates across distinct locations in space (place fields). In the schematic on the right, the CA1 place cells are color-coded as per their place field locations on the linear track in panel (B). (B) Task-selective place maps emerge to orthogonally represent goal-oriented spatial navigation learning rules and contexts. In the illustrated spatial navigation task, the mouse probes two distinct odor cues and learns to navigate on the same textured belt to distinct reward locations and operantly lick for sugar water rewards (task design and observations adapted from [26]). Distinct place cell ensembles are activated for the different odor trial types, showing task selective place map representations and remapping based on the reward context. Figure created with BioRender.com.

must find the hidden location of a submerged platform [5]. The finding that lesions to the hippocampus, entorhinal cortex, and subiculum impair learning in this task [5] has lent support to the idea that this system of interconnected areas allows the animal to learn and plan trajectories to remember spatial locations.

Place cells have been observed across many vertebrate species spanning rodents [3], fish [6], birds [7–9], bats [10], monkeys [11,12], and humans [13,14], and are fundamental to how the hippocampus represents spatial information. During free exploration, place cells typically tile the environment evenly, in principle allowing the animal to compute its location from the population of place fields firing at any given time. In freely flying and swimming animals such as birds [15], bats [16,17], and fish [6], 3D space is isotropically encoded to represent both position and heading, but in landbound animals such as rats, place and grid cells show anisotropic encoding of 3D space [18].

Initially, place maps were often considered to be static and devoid of behavioral contexts or goals. Indeed, place maps appear very early in development, when animals have limited experience in their environment [19]. However, substantial evidence now suggests that place cell activity is experience-dependent [20,21], and serves as a neural correlate for the encoding of spatial memories [22,23]. Place ensembles can be reorganized to generate distinct maps for distinct places [24,25]. Task contexts imposed within the same physical space can also produce distinct place maps. Task-selective place maps representing task context or trial choices, or episodic sequences within the task, emerge as animals learn a multidimensional behavioral task [26–29]. Finally, recent advances in longitudinal imaging in mice have revealed that hippocampal place cell representations in CA1 and CA3 show a large degree of drift over days. On a given day, 70–80% of place cells participating in the spatial representation lose their place tuning, and new cells take their 'place' [30,31]. Imposing behavioral, attentional, or memory demands upon animals by engaging them in structured goal-oriented tasks increases the stability of place maps. This effect of task demands on stability has been observed in bats [32], rats [33], mice [26,34], and humans [23], in support of the cognitive map hypothesis [3].

Although place maps clearly encode the location of the animal in its environment, how the hippocampus represents the location of potential goals is less clear. When a rodent is allowed to forage for a food or water reward, either in an open environment or in virtual reality, the abundance/propensity of place cells in hippocampal area CA1 increases around the reward zones – a phenomenon referred to as over-representation of reward locations [35]. Novel place fields can be formed through the coincidence of reward information with locomotion through a given environment, and these place fields predict the location of the upcoming reward [35–42]. More recently, using a clever honeycomb platform that allowed the experimenters to separate goal computation directly from the trajectory towards the goal, hippocampal place cells were shown to develop 'consinks' – directionally tuned arrays of place fields that collectively point towards the goal location, and move their focus when the goal location changes [43]. Goals might also be encoded outside the hippocampus. For example, recent studies have shown important roles for prefrontal cortex and orbitofrontal cortex in encoding navigational goals [44,45]. Thus, emerging evidence in rodents suggests that neuronal vectors encode goal locations and landmarks within the hippocampus and beyond [46–48]. However, how this information is read out to produce goal-directed movement is currently unclear.

Representations of navigational goals have also been described in vertebrates beyond rodents. In freely flying bats navigating towards a hidden landing platform, a subset of hippocampal neurons developed angular and distance tuning towards the goal, suggesting a type of vector representation of the goal location [49]. Electrophysiology in the hippocampus of homing pigeons freely navigating in a radial arm maze in search of food at different goal locations revealed increased firing in cells at specific

goal locations (goal cells) or on the path between goal locations (path cells) [7,50], as well as lateralization of spatial versus goal coding to neurons in the left versus right hemispheres [51]. Wireless unit recordings from the hippocampus of barn owls, either flying freely between two targets or engaged in a search task to find food among four perches, revealed a variety of spatially modulated neurons, including place cells tuned to in-flight position, trajectory direction, and perching goal locations [8]. High-density electrophysiology recordings from the larger hippocampi of food-caching tufted titmice [9] and chickadees [52] revealed superior place coding with increased sparsity of place activity, as well as specific cache events in barcode-like firing patterns that may allow these birds to meet the specialized ethological demands of food caching. In humans, evidence for goal coding comes from electrophysiology and fMRI studies in the hippocampus and entorhinal cortex during virtual reality navigation [40,53,54]. Although representations of location have been observed in non-human primates during free movement [11,55], more complex codes involving eye and head movements [12], and features of gaze direction and target [56], have also been observed, perhaps reflecting the centrality of visual search in primate navigation.

To build these neuronal representations of places and goals, the hippocampus interacts closely and bidirectionally with the entorhinal cortex (Figure 2). The entorhinal cortex is anatomically and functionally divided into medial and lateral parts. The medial entorhinal cortex (MEC) is well established to encode spatial features of the environment. Populated with grid cells [57–62], head-direction cells [63–65], border cells [66], and speed cells [67–69], the MEC produces a flexible code for space that is also shaped by reward locations [70], and can even represent visual space [71]. The MEC receives and integrates multi-sensory information from various sensory cortices, including visual, auditory, and somatosensory cortices [72]. Other cortical areas that are also involved in spatial processing, namely retrosplenial [73–75], orbitofrontal [45,76,77], parietal [78], prefrontal [79], and postrhinal [80,81] cortices, as well as pre- and parasubiculum [82], are connected to the MEC [83,84], Importantly, MEC receives direct input from the hippocampus (CA1 and subiculum), as well as from the thalamus, medial septum, claustrum, and amygdala – allowing MEC spatial activity to be modulated by mnemonic feedback and brain state-related information.

By contrast, the lateral entorhinal cortex (LEC) [85] appears to specialize in non-spatial information such as odors [86–88], objects [89–92], traces of objects [93], task timing and sequence [94], and novelty [89,90], although this region may also be associated with spatial coding and its modulation [95–97]. Rodent studies have shown that the LEC can code for reward approach, departure, and consumption [98,99], punishments [90,100], associative learning [100–102], and contextual salience [90]. In rats, LEC disruptions impair behavioral performance in novel object recognition memory [89,92] and in an object-based cheeseboard maze spatial learning task, where LEC–dentate gyrus (DG)/CA3 are coupled in slow gamma synchrony [103]. Consistent with these responses, the LEC receives strong input from the olfactory areas, especially the olfactory bulb and piriform cortex [84,104]. The LEC is connected with the emotion-processing and decision-making centers of the brain, namely the amygdala [105] and prefrontal cortex [106]. Thus, although the segregation is not complete, MEC and LEC encode complementary features of the environment, with MEC specializing in spatial information derived from self-motion, and LEC specializing in non-spatial information about potential goals or objects in the environment – a principle that is also observed in the organization of the central complex.

In addition to this segregation, several studies also highlight functional interactions between these two systems. Some activities demand integration of MEC and LEC input and association of spatial and contextual information to render multisensory memory representations. For example, LEC lesions impair rate remapping in CA3 place cells [96] and may help to drive context-dependent remapping [60,91]. By contrast, MEC lesions or input manipulations disrupt place cell precision

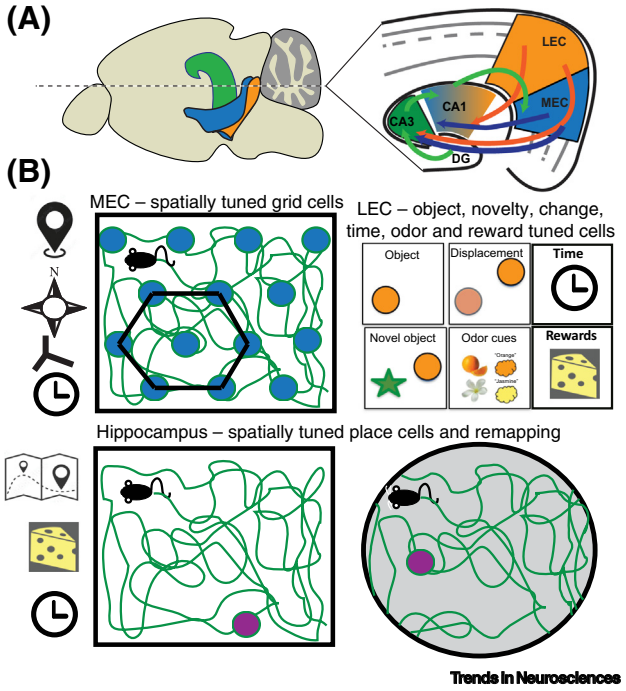

Figure 2. Information flow in the vertebrate navigation system. (A) Information flow. (Left) Schematic of the mouse brain showing the topographical relationship between entorhinal cortex, subdivided into medial (blue) and lateral (orange) entorhinal cortices (MEC and LEC, respectively), and the hippocampus (green) in the temporal lobe. (Right) Horizontal cross-section showing direct and indirect information pathways. Direct inputs from the MEC and LEC convey multisensory spatial and context information to each of the hippocampal subfields. MEC and LEC inputs are anatomically segregated along the proximal–distal axis in CA1, but are integrated by the same neurons in CA3 and dentate gyrus (DG). The indirect trisynaptic pathway routes EC information through the DG via the mossy fiber inputs to CA3, and then from CA3 to CA1 via Schaffer collateral inputs. CA1 serves as the major output region of the hippocampus and projects mnemonic spatial and contextual 'feedback' information to several cortical areas including the entorhinal cortices. (B) Functional separation between the LEC and MEC showing distinct feature-selective tuning. MEC neurons code for spatial features including grid position, Cartesian position, boundaries, head angle, and speed. LEC neurons respond robustly to objects, particularly novel objects and their displaced locations, salient cues such as odors or rewards (and punishments), and the temporal structure of tasks. The hippocampal place cell system builds a map of space in which each cell shows selectivity for a particular spatial location (a place field). Whereas grid cells have multiple firing fields, most CA1 neurons show only one. CA1 neurons also show selectivity for rewards, episodic sequences, and learning rules. Changes in context, such as the shape of a room in which navigation occurs, lead to changes in place cell tuning. Such remapping results in reorganization at the ensemble level and the emergence of a new place map.

and stability [36,107], as well as place memory, although only partially [108,109], without significantly affecting the number of place cells *per se*. LEC has also been proposed to encode egocentric information, whereas MEC encodes allocentric information [91].

Building representations of places and goals requires plasticity within the complex circuitry of the hippocampus and entorhinal cortices. Coordinated activity and integration of entorhinal cortex and CA3 inputs to CA1 pyramidal neurons can result in dendritic spikes [90,110] that have been implicated in context-discrimination behavior [90] and context-dependent place cell formation and remapping [37]. Remapping and place cell formation during the learning phases of goal-directed navigation are thought to require non-Hebbian plasticity mechanisms such as input timing-dependent plasticity (ITDP) [90,111,112] and behavioral timescale-dependent plasticity (BTSP) [37,113]. Conversely, Hebbian plasticity such as theta-modulated postsynaptic burst firing [114,115] and experience-dependent strengthening of coincident spatially tuned synaptic inputs [116] have been proposed to drive long-term stabilization of ensemble coding. The clustering of hippocampal place fields near start and goal locations in a virtual water maze has been shown to be consistent with Hebbian plasticity, correlated with task performance and impaired by NMDA receptor blockers [117]. Intracellular recordings from mouse CA1 neurons during a cued two-choice virtual T-maze suggest a model in which trial type-specific inputs are rapidly potentiated by Ca^{2+} plateau potentials to induce task-selective place cells [118]. Thus, multiple forms of plasticity allow the internal representations of the hippocampus and entorhinal cortices to be flexibly linked to external places and sensory inputs.

A head for math: allocentric vector coding in the central complex

In insects, the brain area most closely associated with spatial navigation is the central complex (Figure 3A) – a highly conserved set of interconnected structures in the center of all arthropod brains. Early studies of mutant flies with disrupted central complex morphology showed deficits in visually guided navigation [119]. Whereas normal flies will readily walk back and forth between a pair of stripes, central complex mutants instead showed wandering, looping trajectories, suggesting a high-level deficit in navigation. Genetic silencing of visual neurons in an input pathway to the central complex was shown to disrupt a behavior modeled on the Morris water maze in which flies used distal visual cues to navigate towards a safe location in a heated floor [120]. A role in spatial navigation was further supported by intracellular recordings in locusts, which revealed a 'sky-compass' map of light polarization that could be used for celestial navigation [121]. More recently, 'virtual reality' systems in head-fixed flies have enabled major advances in understanding the functions of the central complex. These systems allow functional imaging and intracellular recording during closed-loop behavior [122–124]. Connectomic reconstructions of these circuits in multiple species have also greatly advanced our understanding of their organization and function [125–127].

The ordered arrays of genetically related and morphologically similar cells that make up the layers of the central complex appear to be particularly well suited for encoding vectors (Figure 3B) [126,128,129]. In these representations, a bump of calcium activity across the array can represent a vector angle, while

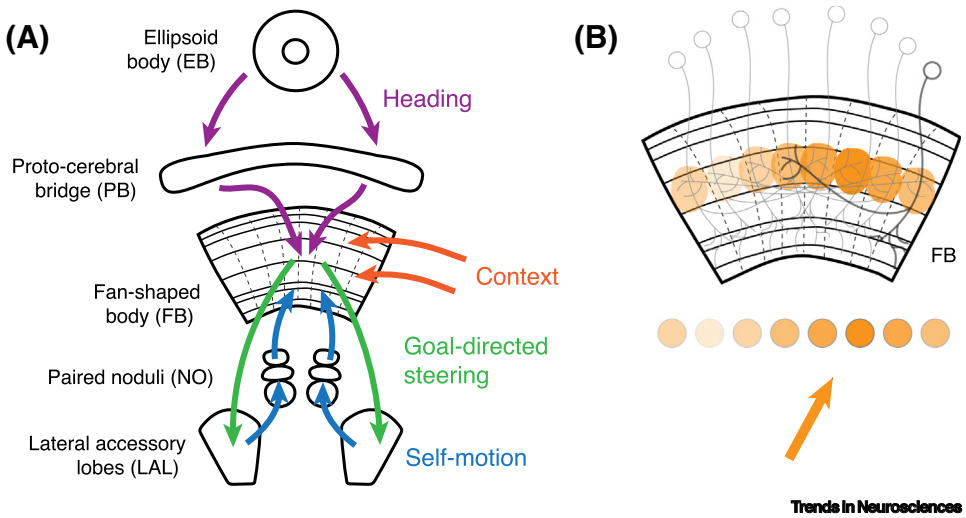

Figure 3. Overview of the insect central complex. (A) Structure of the insect central complex. The ellipsoid body (EB) houses a heading representation that is broadcast to the protocerebral bridge (PB), and then to the fan-shaped body (FB). The fan-shaped body also received self-motion information via the lateral accessory lobe (LAL) and paired noduli (NO). Contextual information enters the fan-shaped body through a separate pathway. The fan-shaped body is thought to generate representations of goals in allocentric coordinates which are read out by neurons projecting back to the lateral accessory lobe to drive goal-directed steering. (B) Vector representations in the central complex. The neuropils of the central complex, such as the fan-shaped body shown here, are composed of ordered arrays of developmentally related neurons that can represent vectors through calcium activity in their processes. The schematic depicts a class of h -type local neurons that arborize in two different columns of the fan-shaped body, with a separation of half the fan-shaped body (one neuron is shown in dark bold to clarify its anatomical projections). Like all insect neurons, these have their cell bodies at the exterior of the brain and make arborizations within the structured neuropil of the central complex. Most such populations exhibit sinusoidal patterns of calcium activity (orange) that are restricted to rows of processes. The location of the peak of the sinusoid corresponds to a vector angle, while the intensity of the activity can correspond to vector length (arrow at bottom). Ordered projection patterns across the rows of the fan-shaped body can allow vector summation and rotation.

the intensity of the activity can represent vector length. Connectivity motifs across layers then allow mathematical operations such as vector addition and rotation that directly support spatial computations. The best-understood representation in the central complex is in so-called 'compass neurons' of the ellipsoid body (Figure 4A). This donut-shaped ring of neurons produces a bump of calcium activity whose location on the ring corresponds to the heading of the fly in space [122], similar to head-direction cells that were first described in vertebrates [63,64,130]. Although the bump can lock onto visual landmarks [124,131] or wind direction [132], it can persist in the absence of sensory cues, and also rotates in the dark using proprioception [123]. This global and persistent heading representation is thought to rely on the presence of a ring attractor network [133,134] similar to the ring attractor that was proposed to underlie head-direction encoding in vertebrates [135]. In insects, an anatomical substrate for such a ring attractor has been identified using connectomic reconstruction of the complete connectivity of the ellisoid body [126,134]. A similar head-direction network has recently been described in the brainstem of zebrafish [136], suggesting that this form of internal representation is a widely shared feature of navigation systems across species.

The global heading signal in the ellipsoid body is then broadcast to a grid-like region called the fan-shaped body (Figure 3A) through a system of columnar neurons [126,128,129,137]. Columnar neurons integrate heading information with optic flow and airflow cues about self-motion to form a vector representation of the movement of the animal through space [125,128,129,137,138]. By summing these vectors, a pair of recent studies showed that the fly can translate egocentric sensory cues into an allocentric representation of its traveling direction in a 2D plane [128,129]. In principle, this traveling direction signal could be integrated [125] to produce a homing vector that would allow an insect to return directly to its nest, as has been observed in desert ants [139]. A recent theoretical study proposed a model in which two vectors – one pointing towards a 'home' point and one towards a goal – could be used to encode not only direction but also the location of a goal in 2D space using a highly

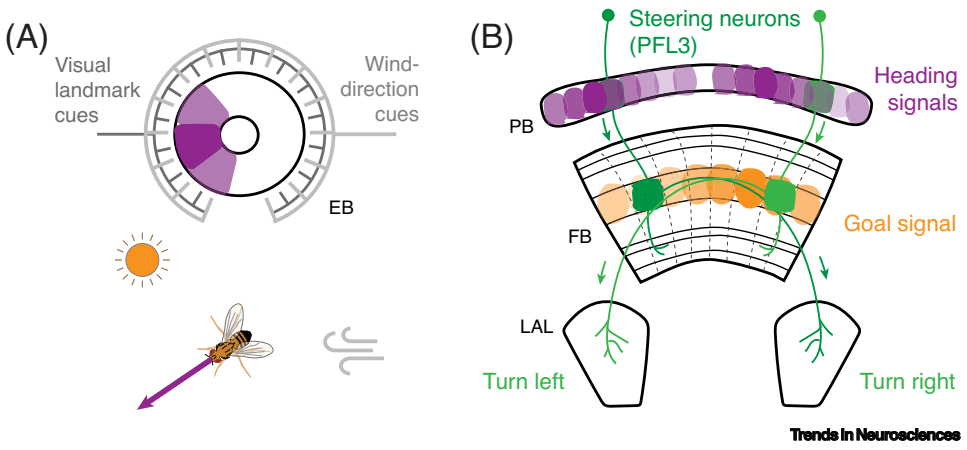

Figure 4. Heading and steering systems of the central complex. (A) The compass system of the ellipsoid body. Compass neurons (also known as EPG neurons, top) arborize in tiles of the ellipsoid body. A bump of calcium activity across this array represents the heading of the fly relative to visual and mechanosensory landmarks (bottom) and rotates when the fly rotates. Inhibitory ring neurons (gray, top) carry sensory information about visual landmarks and wind direction to the compass system. Anti-Hebbian plasticity between ring neurons and compass neurons that is gated by rotational movement allows the fly to learn new mappings between sensory cues and heading direction. Two copies of the ellipsoid body heading signal are transmitted to the protocerebral bridge, one to each side (see panel B). (B) Steering system of the central complex. PFL3 neurons (green) receive input from both the protocerebral bridge and the fan-shaped body and output to descending neurons in the lateral accessory lobe that can drive left or right turns. The anatomy of these neurons allows them to compare the heading representation in the protocerebral bridge (purple) with a goal signal in the fan-shaped body (orange) and drive turning until these two are aligned. Abbreviations: EB, ellipsoid body; FB, fan-shaped body; LAL, lateral accessory lobe; PB, protocerebral bridge.

efficient vector code [140]. Thus, representations of space in the central complex appear to be built around allocentric movement direction vectors rather than more flexible place maps, although both insect and rodent navigation systems allow for the computation of navigational direction vectors [43,49,141,142].

Like the hippocampus, the central complex also appears to generate internal representations of goals (Figure 4B). This idea was first proposed theoretically, based on connectomic studies [125]. Noting the structured connectivity pattern of one set of columnar output neurons, it was suggested that these neurons could compare the compass neuron heading signal to a second bump of activity that represents an allocentric goal. Through their precise connectivity and projection patterns to the left and right steering centers, these neurons could translate this allocentric comparison into an egocentric steering signal to drive the animal toward a goal. Two recent studies have made recordings from these output neurons – known as PFL3 neurons – and found strong support for this theory [143,144]. In addition, a second population of columnar neurons called PFL2 was shown to have 'anti-goal' activity that drives the fly to turn when it faces opposite to its intended goal [143]. Several recent studies have found evidence supporting goal representations in the fan-shaped body. One study using extracellular recording in monarch butterflies found a population of neurons whose preferred direction rotated when the butterfly was trained to adopt a new goal direction with respect to the sun, but not when the animal rotated its heading [145]. In another study, sparse activation of a set of local neurons in the fan-shaped body was shown to produce a reproducible heading with respect to a wind direction cue [146]. Most recently, elegant two-photon laser activation of a bump in a different set of fan-shaped body local neurons was shown to drive orientation in specific allocentric directions depending on the location of the bump [144]. Thus, rapidly emerging evidence in insects suggests that goal directions can be stored as bumps of activity in local neurons of the fan-shaped body. A diversity of different local neuron types provides a potential substrate for computing, storing, and selecting between multiple goals [147].

A striking similarity between the organization of the central complex and the hippocampus, is the presence of distinct 'where' and 'what' pathways. The fan-shaped body can be thought of as a grid composed of vertical columnar neurons and horizontal tangential neurons. Columnar neurons of the fan-shaped body, called PFN neurons (Figure 5A), encode spatial features such as heading and self-movement [125,128,129,137,138,148]. PFNs receive a heading input in the protocerebral bridge and a sensory input from a region called the noduli. The noduli relay different types of self-motion cues – optic flow, airflow, and proprioception – from a premotor center called the lateral accessory lobe [125,126,128,129,137,138]. This self-motion information has been proposed to provide the input to hypothesized path-integration circuitry in the fan-shaped body [125,128,129,140]. Thus, the columnar neuron pathway, that receives both heading input from the protocerebral bridge and self-motion information from the noduli and lateral accessory lobe, might be thought of as analogous to the MEC which likewise carries a diverse range of self-motion cues, derived from multiple modalities, to the navigation center [149,150].

By contrast, tangential neurons of the fan-shaped body (Figure 5B) map nearly all regions of the fly brain onto different horizontal layers of the fan-shaped body [151]. Although recording data from these neurons remain sparse, the available evidence suggests that these primarily encode non-spatial information such as odorants [146], tastants [152], and behavioral states [152–155], although optic flow information has been observed in a few tangential neurons [156]. Activation of tangential neurons can drive navigational behaviors such as upwind running [146], whereas silencing of tangential neurons can bias flies between exploration and exploitation of a food source [154]. Thus, tangential neurons may allow flies to select the most appropriate goals based both on external sensory cues such as food odor and on internal states such as hunger.

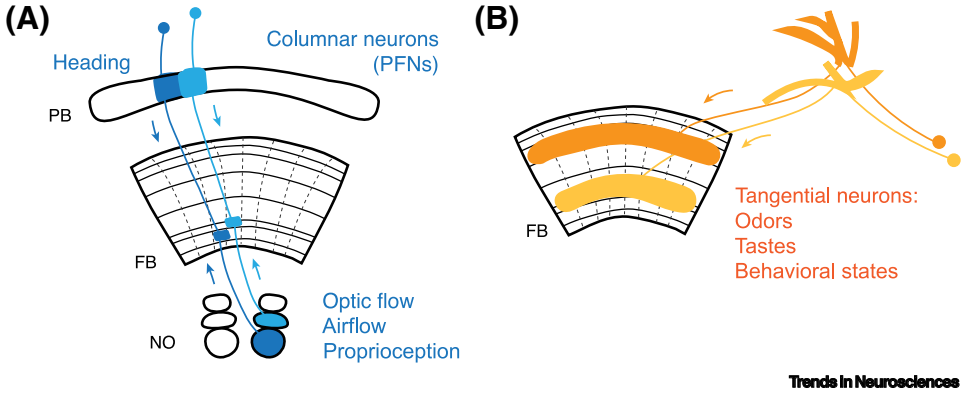

Figure 5. Input pathways to the fan-shaped body. (A) Columnar input neurons of the fan-shaped body (PFN neurons) carry heading and self-motion information. Each neuron receives a heading signal from the protocerebral bridge and one or more sensory inputs from the paired noduli related to self-motion: optic flow, airflow, or proprioception. Fan-shaped body columnar neurons form a vector representation of self-motion that can be used to compute allocentric traveling direction within the fan-shaped body through vector summation. (B) Tangential neurons of the fan-shaped body carry predominantly non-spatial context cues such as odorants, tastants, and behavioral states. Activation of tangential neurons can alter navigation behavior, presumably by regulating the activity of different goal-encoding local neurons. Abbreviations: FB, fan-shaped body; NO, paired noduli; PB, protocerebral bridge.

Many fan-shaped body tangential neurons are anatomically downstream of the mushroom body [157,158] – an associative learning center with a well-established role in learning the valence of olfactory stimuli through the sequential activation of odor-encoding Kenyon cells and reward- or punishment-encoding dopamine neurons [159]. This same valence-learning circuitry has been proposed to subserve visual route learning by allowing an insect to associate a visual pattern encoded by visual Kenyon cells with a dopaminergic reward signal related to being on track toward a goal [160–162]. Consistent with this model, mushroom body lesions have been shown to impair visually guided navigation in several insect species [163–165]. Emerging models thus suggest that the mushroom body and the central complex may work together to support navigation, with the mushroom body providing information about which sensory cues (odors or visual panoramas) are attractive or aversive, and the central complex translating these valence signals into spatially oriented steering commands [166–168]. Distinct neural pathways also carry information directly from the mushroom body to premotor centers such as the lateral accessory lobe and might subserve direct translation of valence information into egocentric navigational commands [169–170].

As in the hippocampus and entorhinal cortex, diverse forms of plasticity appear to be crucial for tethering the representations in the central complex to changing features of the outside world. Plasticity in the central complex has been most closely investigated in the compass neuron system where the heading bump can flexibly tether to different visual or mechanosensory features of the external world (Figure 4A). Recording and imaging studies suggest that inputs to the compass system represent a rich array of visual features and synapse uniformly onto the entire array of compass neurons [124,126,131,171,172]. Anti-Hebbian plasticity between these neurons allows the fly to learn a stable mapping between environmental features and the location of the heading bump [124,131]. Intriguingly, this plasticity is itself gated by the behavior of the fly. A specific dopamine neuron monitors angular velocity and gates plasticity when the fly is actively rotating [173]. This system allows the compass system to learn a reliable mapping without drifting during periods of straight walking. Thus, similar to the hippocampal place-field system, the fly compass system combines both intrinsic dynamics that enforce a 'bump' structure and plasticity that allows this representation to flexibly tether to features of the outside world. Understanding the diversity of

such plasticity mechanisms will help to explain how brains are able to so rapidly learn and deploy new information in the service of goal-directed behavior.

Concluding remarks

Experiments to date suggest that the hippocampus and central complex contribute to similar behaviors. Both are engaged when the animal must make a spatial inference about the location of a goal. For example, hippocampal place fields aggregate near reward sites when rats learn the location of hidden rewards in a cheeseboard maze, but not when those sites are marked by prominent visual cues [35]. Similarly, the fly compass system is required for a fly to adopt a fixed offset orientation from the sun, but is not necessary for orienting directly to a visual landmark [123,174]. These observations suggest that both structures play an important role in spatial inference – allowing the animal to estimate the location of a goal that it cannot perceive directly and continuously. However, representational differences between the hippocampus and the central complex suggest that vertebrates and invertebrates adopt distinct computational strategies to perform this type of inference. In the hippocampus, a highly flexible place code allows the animal to rapidly learn new locations even in abstract 'spaces' such as those of auditory or olfactory features [175,176]. Thus, the hippocampal coding scheme may underlie many higher cognitive abilities observed in humans and other vertebrates. By contrast, the simpler vector code in the insect central complex may allow sophisticated spatial computations – such as path integration [139] and inferring new routes between rewards [177] – with very small numbers of neurons [178,179]. Studies directly comparing spatial representations across diverse species, and linking these to species-specific behavioral capabilities [9,145,180], as well as computational investigations of the relationship between internal spatial representations and navigation task performance [181,182], will provide deeper insight into the relationship between neural representations, neural circuit architecture, and behavior (see Outstanding questions).

One challenge in interpreting differences across species is that rodents and insects have generally been studied in different paradigms using different tools. Like the proverbial elephant, differences in hippocampal and central complex coding might reflect to some extent the different tools that scientists have used to look at them, and not real differences in these complex 'beasts'. In rodents, spatial navigation and learning were initially studied in freely moving animals equipped with head-mounted electronics for extracellular recordings. The small enclosures they explored may have facilitated the discovery of a place code as the animal often crosses the same location via different paths. Such freely moving recordings are currently not possible in the fruit fly *Drosophila*, but can be performed in many larger insects such as cockroaches [183] and butterflies [145]. Extracellular recording studies in larger insects might complement current work in the fruit fly to provide insights into spatial coding during natural movement through complex 3D environments. In parallel, connectomic reconstruction of tiny insect brains has revealed exquisite and largely unanticipated precision of the connections between groups of neurons [125–127]. Models and findings for how the central complex translates egocentric to allocentric coordinates and back have been largely driven by connectomic data [128,129,143,144]. Extending these approaches to larger vertebrate tissues [136,184] will undoubtedly lead to new discoveries.

Outstanding questions

To what extent do the differences in spatial representations between the hippocampus and central complex reflect different experimental approaches rather than different biologies?

Can navigational abilities be directly compared across diverse species? How do these abilities relate to the underlying circuit structures? Do different spatial representations in the hippocampus and central complex support different behavioral capabilities?

Do invertebrates show place-like representations? Where might these be encoded, and are they similar to or different from those described in vertebrates?

How are goals represented in vertebrate and invertebrate navigation systems? How many different types of goal representation are there? Are these representations similar or different across these two systems? Are the circuits that translate goals into actions similar or different across species?

To what extent are spatial and non-spatial representations segregated or integrated in the input streams to vertebrate and invertebrate navigation centers? What is the function of segregating spatial and non-spatial representations?

How is movement through 3D space encoded in both vertebrate and invertebrate systems?

What are the cellular and plasticity mechanisms underlying goal coding and learning of goal-directed behaviors in vertebrates and invertebrates?

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Declaration of interests

The authors declare no competing interests.

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