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Mechanisms Underlying the Neural Computation of Head Direction

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Keywords

ring attractor, head-direction cells, navigation, central complex, path integration, angular velocity

Abstract

Many animals use an internal sense of direction to guide their movements through the world. Neurons selective to head direction are thought to support this directional sense and have been found in a diverse range of species, from insects to primates, highlighting their evolutionary importance. Across species, most head-direction networks share four key properties: a unique representation of direction at all times, persistent activity in the absence of movement, integration of angular velocity to update the representation, and the use of directional cues to correct drift. The dynamics of theorized network structures called ring attractors elegantly account for these properties, but their relationship to brain circuits is unclear. Here, we review experiments in rodents and flies that offer insights into potential neural implementations of ring attractor networks. We suggest that a theory-guided search across model systems for biological mechanisms that enable such dynamics would uncover general principles underlying head-direction circuit function.

Contents

1. INTRODUCTION	32
2. RING ATTRACTOR NETWORKS	34
3. EVIDENCE FOR HD REPRESENTATIONS IN MAMMALS AND INSECTS	36
3.1. Mammalian HD Cells	36
3.2. Insect HD Cells	36
4. NEURAL MECHANISMS UNDERLYING HD FUNCTION IN MAMMALS	38
4.1. Hierarchical Structure and Function Point to a Subcortical Ring Attractor ...	38
4.2. Cell Types and Circuits	39
4.3. Updating the HD Representation by Integrating Angular Velocity	40
4.4. Tethering the HD Representation to Allothetic Sensory Cues	40
4.5. Evidence for Attractor Dynamics	41
5. NEURAL MECHANISMS UNDERLYING HD FUNCTION IN INSECTS ..	41
5.1. Updating the HD Representation by Integrating Angular Velocity	43
5.2. Mechanisms of Persistent Activity	43
5.3. Inhibitory Feedback Pathways	44
5.4. Tethering the HD Representation to Allothetic Sensory Cues	44
5.5. Evidence for Attractor Dynamics	45
6. OPEN QUESTIONS AND FUTURE DIRECTIONS	45
6.1. Cognitive Maps and Vector Navigation	45
6.2. Synaptic Weight Calibration	46
6.3. Coordination Across Structures	46
6.4. Angular Velocity Signal	46
6.5. Added Complexity	47
6.6. Future Work in Insects	47
6.7. Future Work in Mammals	47
6.8. The Comparative Advantage	47

1. INTRODUCTION

To survive and reproduce, animals move about the world in search of food, mates, and safety, displaying a remarkable ability to navigate in the process. Long-distance navigators like Egyptian fruit bats, for example, return to their home cave even after being displaced by over 40 km (Tsoar et al. 2011), and foraging honeybees communicate the distance and direction of a newly discovered food source to conspecifics through their waggle dance (von Frisch 1967). Underlying these flexible behaviors are neural networks that form internal representations of information used to support different navigational strategies. One critical internal representation that most navigational strategies rely on is a sense of direction.

The neurons thought to underlie an animal's sense of direction are known as head-direction (HD) cells. First discovered in rats, individual HD cells fire when an animal's head is facing a particular azimuthal direction in its environment, independent of where the animal is located and whether or not it is moving (Ranck 1984, Taube et al. 1990a). Across the population of HD cells, the range of preferred firing directions effectively spans all orientations, motivating a view of the

Head-direction (HD) cell: neuron tuned to an animal's head direction. Their population activity functions as a local neural compass that tethers to sensory cues in the animal's surroundings

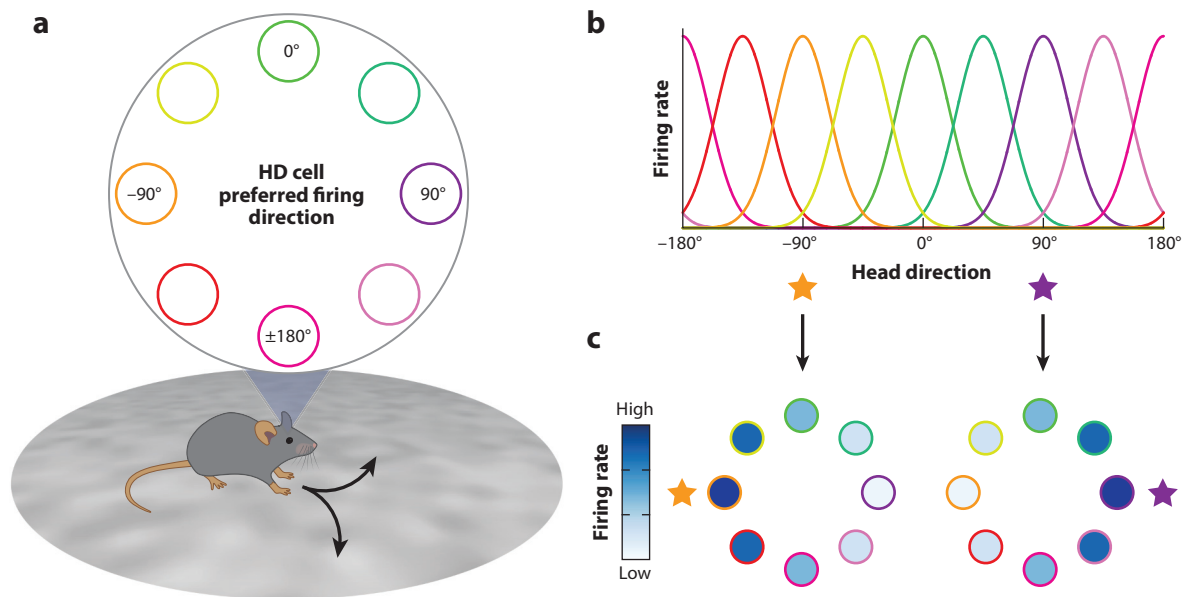


Figure 1

Head-direction (HD) cells and the neural compass of insects and mammals. (a) Illustration of how, as an animal navigates a two-dimensional environment, a population of HD cells in its brain maintains an internal representation of head direction. (Top) Diagram showing a population of schematized HD cells, each colored according to its preferred firing direction and together covering 360°. (b) Schematic of firing rate as a function of head direction for the HD cells shown in panel a. Each HD cell has an approximately triangular or Gaussian-shaped tuning curve, which peaks at its preferred firing direction. (c) Diagram of how, at the population level, head direction is encoded by a bump of activity formed by coactive HD cells. Here, the same HD cells as in panels a and b are filled in with color intensities according to their firing rate when the animal is facing -90° (left ring) and 90° (right ring). The colored stars mark the animal's head direction.

network as a neural analog of a compass (Skaggs et al. 1995) (**Figure 1a,b**). Cells with HD-like responses have since been found in a diverse range of species, from cockroaches and fruit flies to mice, monkeys, and bats, highlighting their evolutionary importance (Finkelstein et al. 2016, Laurens et al. 2016, Seelig & Jayaraman 2015, Taube 2007, Varga & Ritzmann 2016). Across species, most HD networks share four key properties. First, the population activity of these networks encodes a single, unique representation of direction at every moment in time, consistent with the head facing a single direction at a time (Peyrache et al. 2015, Seelig & Jayaraman 2015). Conceptually, when HD cells are arranged around a ring according to their preferred firing direction, head direction is encoded by the angular position of a traveling bump of activity (**Figure 1c**). That is, at the population level, the angular position of the activity bump serves as a one-dimensional representation of direction. The ring architecture ensures that the directional representation is circular, returning the bump to the same angular position after a 360° rotation of the head. Second, HD-cell networks display persistent activity, which maintains the activity bump at a particular position during periods when the animal is not turning (Taube & Bassett 2003, Taube et al. 1990a). Third, to update the position of the bump, these networks are able to use idiothetic information regarding self-motion to perform angular path integration (Goodridge et al. 1998, Green et al. 2017, Mittelstaedt & Mittelstaedt 1980, Taube et al. 1996, Turner-Evans et al. 2017). This process ensures that the bump's position gets updated when external sensory landmarks are lacking, such as in darkness. However, imperfect integration or biased angular velocity signals can lead to error accumulation, causing the bump's angular position in the ring

Angular path integration: process by which information regarding angular velocity is integrated to update internal representations of head direction

Allothetic cue:

external signal such as a prominent visual landmark

Angular velocity cell:

neuron tuned to rotational velocity. Neurons tuned to rightward (CW) and leftward (CCW) rotation speeds are often treated as two distinct populations

Rotation cell:

neuron tuned to head direction and angular velocity that functions to update the position of the HD cell activity bump

Landmark cell:

neuron that responds to the presence of prominent allothetic cues and dictates the bump's precise position in the ring

to drift from the animal's true head direction. Fourth, to mitigate this error, HD-cell networks can use prominent allothetic cues, when present, to provide an absolute measure of direction and dictate the bump's precise position in the ring (Seelig & Jayaraman 2015, Taube et al. 1990b). This landmark-based system is thought to operate in parallel with angular path integration mechanisms (Savelli & Knierim 2019). How brains implement these computations has been the subject of decades of study, but many open questions remain. Here, we review the neural mechanisms underlying these computations, focusing primarily on work from rodents and flies.

Section 2 describes how hypothesized ring attractor networks compute head direction and identifies experimental data required to discriminate between competing implementations of such models. Section 3 describes phenomenological evidence for HD representations in mammals and insects. Subsequent sections review key findings from experiments in mammals (Section 4) and insects (Section 5) that constrain the space of possible neural implementations. Finally, Section 6 lists gaps in our understanding, highlights interesting research avenues, and proposes a path forward.

2. RING ATTRACTOR NETWORKS

Neural networks that represent an animal's head direction should satisfy the same computational requirements: uniqueness, persistence, integration, and drift correction. Inspired by experimental work in mammals (Taube et al. 1990a,b), a series of theoretical studies described how these requirements are elegantly met by network structures called ring attractors (reviewed in Knierim & Zhang 2012). While many different flavors of ring attractors have been proposed, here we focus on two biophysically plausible classes: one that contains recurrent excitatory connections between HD cells and one that does not (Amari 1977, Ben-Yishai et al. 1995, Blair 1996, Boucheny et al. 2005, Compte et al. 2000, Goodridge & Touretzky 2000, Hartmann & Wehner 1995, Kim et al. 2017, McNaughton et al. 1991, Page et al. 2018a, Redish et al. 1996, Rubin et al. 2001, Sharp et al. 2001a, Skaggs et al. 1995, Song & Wang 2005, Touretzky et al. 1993, Tsodyks & Sejnowski 1995, Xie et al. 2002, Zhang 1996).

In most ring attractor models of HD networks, which we refer to as Class 1 (**Figure 2a**), nodes are arranged in a ring with location-dependent connection strengths, such that neighboring nodes excite one another more strongly than distant nodes (Skaggs et al. 1995, Zhang 1996). The different nodes represent HD cells with different preferred firing directions. The nodes receive either uniform feedback inhibition or inhibition that increases with the distance between nodes. With appropriately balanced excitation and inhibition, network activity localizes into a single unique bump, which serves as a one-dimensional representation of direction, thus meeting the first computational challenge. Assuming symmetric recurrent excitatory connections between similarly tuned HD cells, the bump's position is stable during periods devoid of movement, thus fulfilling the second computational challenge. To update the position of the bump using biophysically plausible mechanisms, several additional cell types were theorized (see Skaggs et al. 1995) (**Figure 2b**). First, angular velocity cells were theorized, because the directional representation must be updated by integrating angular velocity. Second, in order to perform this integration, an additional layer of neurons is added, known as rotation cells, which conjunctively encode direction and angular velocity. These neurons send excitatory projections to HD cells in either the clockwise (CW) or counterclockwise (CCW) direction, depending on whether they receive CCW or CW angular velocity input, respectively. Therefore, these neurons overcome the third computational challenge, allowing angular velocity information to update the directional representation by moving the bump around the ring. Finally, neurons carrying information about allothetic cues, known as landmark cells, provide localized input that, when sufficiently strong, can dictate the bump's position in the ring (**Figure 2c**). This mapping of sensory stimulus to HD representation

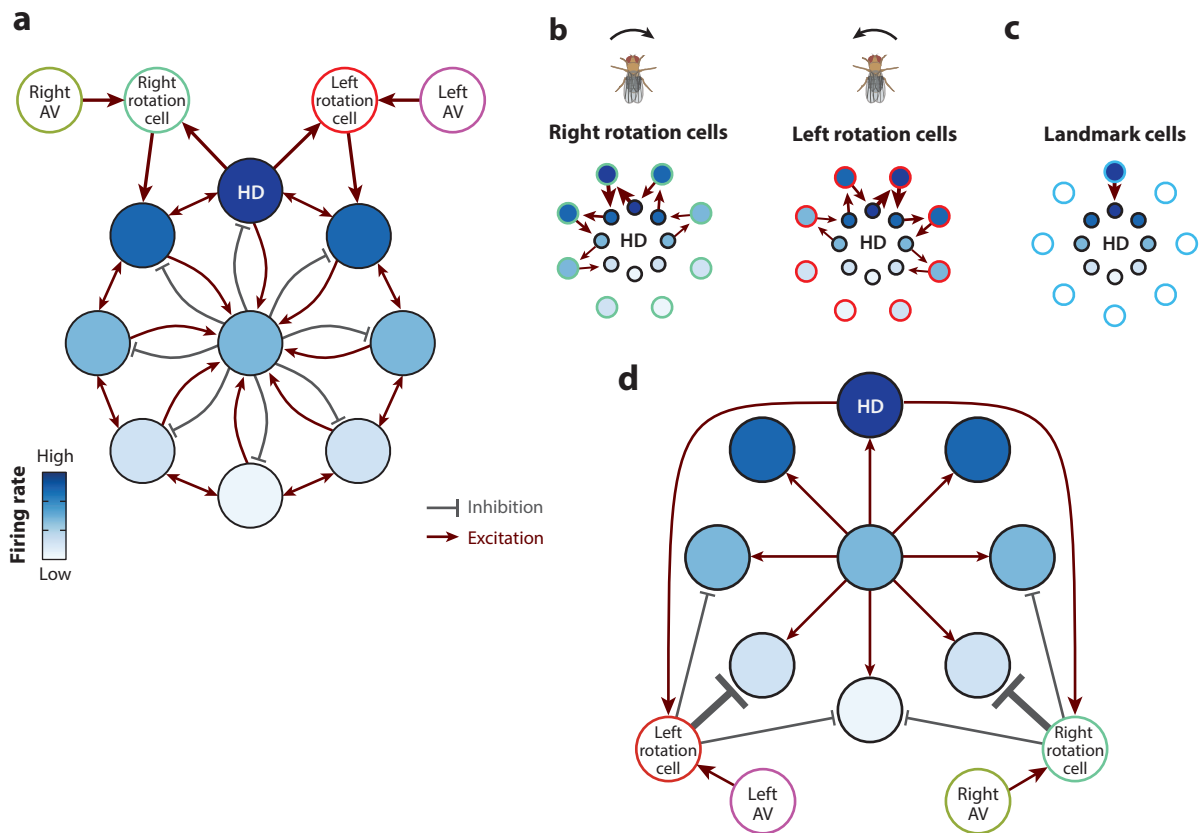


Figure 2

Two classes of ring attractor networks for computing head direction. (a) Example of a Class 1 ring attractor network, which contains recurrent excitatory connections between similarly tuned head-direction (HD) cells and excitatory rotation cells for moving the bump around the ring. Borders of each cell indicate cell type. Cells are filled in with color intensities according to their firing rate. The HD network is shown in the static state, with persistent activity maintaining the bump's position near the top of the ring. Only one left and one right rotation cell are shown for simplicity, but there are as many left and right rotation cells as HD cells, as shown in panel *b*. Rotation cells are driven by angular velocity (AV) cells signaling right or left turns. (b, left) When the animal turns clockwise (CW), the population of right rotation cells (*outer ring*) is active and moves the HD cell (*inner ring*) bump counterclockwise (CCW) due to their asymmetric connectivity. (b, right) Similarly, when the animal turns CCW, left rotation cells (*outer ring*) are active and move the bump CW in the ring. (c) When present, landmark cells (*outer ring*) can dictate the bump's position in the HD-cell network (*inner ring*). (d) Example of a Class 2 ring attractor network, which contains a directionally uniform excitatory input to HD cells, endowing them with persistent activity, and broadly tuned inhibitory rotation cells for moving the bump around the ring. Only one left and one right rotation cell are shown for simplicity. Similar to panel *a*, the network is shown in the static state. During turns, differential activity between the population of left and right rotation cells moves the bump around the ring using mechanisms analogous to those in panel *b*, but with inhibition instead of excitation.

serves to correct any drift that might accumulate from errors in angular velocity integration, thus meeting the fourth challenge (Cope et al. 2017, Knierim et al. 1995, McNaughton et al. 1991, Ocko et al. 2018, Page et al. 2018b, Skaggs et al. 1995, Tsodyks & Sejnowski 1995, Zhang 1996).

A second group of ring attractor models function similarly but do not require the presence of recurrent excitatory connections between HD cells (Boucheny et al. 2005, Hartmann & Wehner 1995, Song & Wang 2005). We refer to these models as Class 2 (Figure 2d). Due to the lack of recurrent excitatory connections in these models, HD cells are required to be spontaneously active

due to either cell-intrinsic conductances or a directionally uniform excitatory input. In addition, inhibitory rotation cells provide a broad, offset inhibition to HD cells, and their differential activity moves the bump around the ring during turns. Similar to Class 1 networks, landmark cells provide input to HD cells, thereby dictating the bump's position. Both classes of ring attractors require structured connectivity between four key neuron types: angular velocity cells, rotation cells, HD cells, and landmark cells. In the sections that follow, we assess the experimental support for the key assumptions and predictions of ring attractor models. We also rely on this computational perspective to describe the still-evolving picture of how HD networks might function in the evolutionarily distant brains of mammals and insects.

3. EVIDENCE FOR HD REPRESENTATIONS IN MAMMALS AND INSECTS

3.1. Mammalian HD Cells

In the three decades since their discovery (Ranck 1984; Taube et al. 1990a,b), numerous studies have investigated the function of mammalian HD cells at many levels, from their general firing properties and anatomical distribution to their role in navigational behaviors. Here we provide a brief overview of HD cell properties in rodents navigating two-dimensional environments, where most experiments have been performed. For simplicity, we refer to this work as mammalian. For a more in-depth treatment, we refer the reader to many excellent reviews (Clark & Taube 2012; Cullen & Taube 2017; Dumont & Taube 2015; Finkelstein et al. 2016; Sharp et al. 2001a; Shinder & Taube 2014; Taube 2007, 2011; Taube & Bassett 2003; Taube et al. 1996; Wiener & Taube 2005; Yoder & Taube 2014).

HD cells are found in many brain regions, composing an extended network that runs from brainstem nuclei that receive angular velocity input all the way to the cortical structures involved in navigation. Unlike schematized ring attractor networks, mammalian HD cells are not topographically arranged in space but are scattered throughout each of the brain regions in which they are found. The population dynamics of these cells exhibit the four key properties described above. First, simultaneous recordings from populations of HD cells reveal that the activity of these neurons is effectively organized as a single, unique bump, whose position encodes the animal's head direction (Bassett et al. 2018, Peyrache et al. 2015) (**Figure 3a–c**). Second, during periods of immobility, HD cells display persistent activity (Taube et al. 1990a). Third, the HD network can integrate self-motion cues encoding angular velocity to update its directional representation, although with gradual error accumulation over time (Valerio & Taube 2012). And fourth, familiar visual landmarks can control HD cells' preferred firing direction (Taube et al. 1990b).

Identified neuron:

genetically determined cell type with stereotyped morphology, connectivity, gene expression, and function. In *Drosophila*, identified neurons can be genetically targeted using highly specific driver lines

3.2. Insect HD Cells

In contrast to the prominent role that neurophysiology has played in our understanding of rodent navigation and HD cells, the first suggestions that insect brains use internal representations of directional information came from ethologically grounded behavioral studies (see sidebar titled Behavioral Evidence for HD from Insects). More recently, recordings of neural activity have firmly established that insects indeed do possess an HD-like network, which resides in a highly recurrent, evolutionarily conserved brain region called the central complex (reviewed in el Jundi et al. 2019, Green & Maimon 2018, Honkanen et al. 2019, Pfeiffer & Homberg 2014, Strauss 2002, Turner-Evans & Jayaraman 2016, Webb 2019). Intracellular recordings from identified neurons in the central complex of a wide variety of insects, including locusts, butterflies, and dung beetles, have uncovered well-organized visual responses suggestive of a neural compass that uses celestial

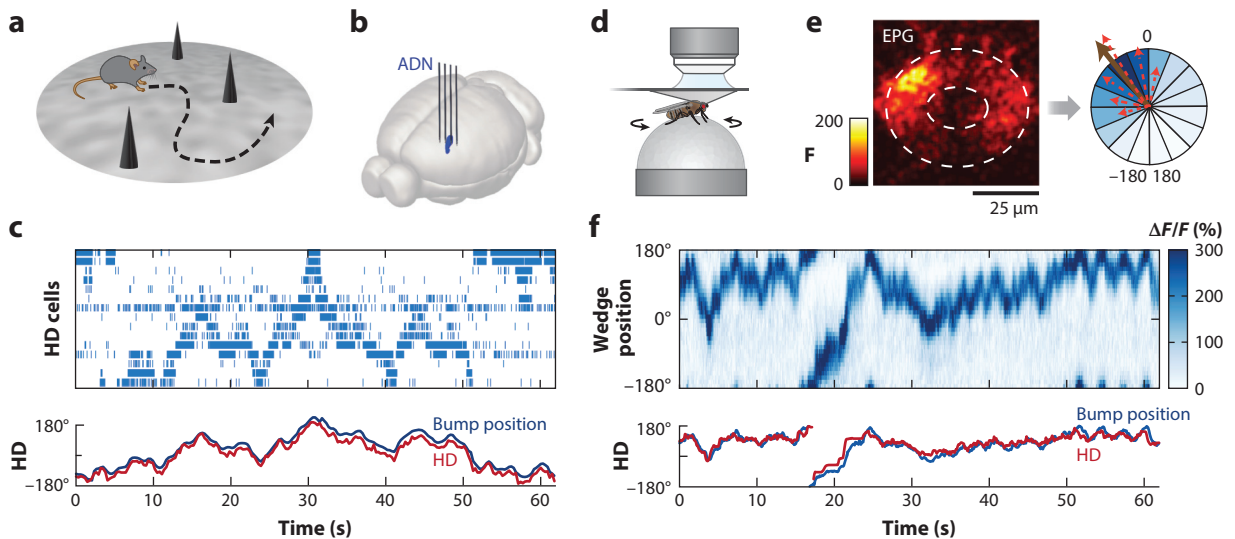


Figure 3

Head-direction (HD) cell activity in rodents and *Drosophila*. (a) Illustration of a mouse navigating a two-dimensional environment. Panel *a* adapted with permission from Haberkern et al. (2019). (b) Schematic of the mouse brain with multisite probes targeting the thalamic anterior dorsal nucleus, one region where HD cells are found. (c) HD-cell population activity forming a single bump that tracks the mouse's head direction across time. (Top) Raster plot showing the spike times from 15 simultaneously recorded thalamic HD cells. Cells were sorted according to their preferred firing direction. (Bottom) The mouse's head direction is accurately tracked by the HD cell activity bump. Panels *b* and *c* adapted with permission from Peyrache et al. (2015). (d) Schematic of a head-fixed fly walking on a spherical treadmill during two-photon calcium imaging. (e, left) EPG calcium activity in the ellipsoid body (EB) at one moment in time, showing a single, unique bump of activity. (e, right) The EB is segmented into wedge-shaped regions of interest (ROIs), and the $\Delta F/F$ is computed for each ROI. A population vector average (brown arrow) of $\Delta F/F$ across ROIs (red arrows) tracks the angular position of the bump in the EB. Panels *d* and *e* adapted with permission from Turner-Evans et al. (2017). (f) EPG population activity across time revealing a traveling bump of activity that encodes the fly's head direction. (Top) EPG population activity, as in panel *b*, but unwrapped from -180° to 180° . (Bottom) The bump's angular position in the EB (blue) tracking the fly's angular orientation (red).

cues (el Jundi et al. 2014, 2015; Heinze & Homberg 2007; Heinze & Reppert 2011), and extra-cellular recordings in the cockroach have revealed neurons tuned to visual and mechanosensory cues for direction (Ritzmann et al. 2008, Varga & Ritzmann 2016) as well as to the animal's voluntary movements (Bender et al. 2010, Guo & Ritzmann 2013, Martin et al. 2015). More directly, a population of HD-like neurons known as EPGs in *Drosophila melanogaster* were found to represent the fly's angular orientation as a bump of activity that travels around a toroidal structure called the ellipsoid body (EB) (Seelig & Jayaraman 2015) (Figure 3d–f). That is, the arbors of HD cells in *Drosophila* together tile a ring-like structure, with neighboring cells showing similar HD tuning. Although this topographical arrangement of HD cells resembles schematics for ring attractor networks—a remarkable example of biological structure suggesting function—it is the fly network's topological similarity to these theorized networks that is more functionally relevant, as discussed below (Green et al. 2017, Turner-Evans et al. 2017). Importantly, the four computational abilities described above—uniqueness, persistence, integration, and drift correction—are also shared by the HD network of *Drosophila* (Seelig & Jayaraman 2015) and likely of other insects, too. It is currently unknown whether these neurons encode the orientation of the head or body, or whether they represent global orientation or orientation relative to local cues, but we use the term HD cell throughout for simplicity—importantly, all the computations we describe below are relevant regardless of this distinction. With the identification of insect HD cells, the invertebrate

BEHAVIORAL EVIDENCE FOR HD FROM INSECTS

Despite their small brains, insects are remarkable navigators. Wasps (Tinbergen & Kruyt 1938), bees (Cartwright & Collett 1983), and ants (Collett 2010) rely on stored visual information to return to their nests and hives after foraging, potentially matching patches of visual scenes with internal templates during return routes (Sturzl et al. 2016). *Drosophila* learn to use visual cues to locate a cool region within an uncomfortably warm environment (Ofstad et al. 2011). Honeybees even communicate the distance and direction of a food source to their hive mates through their waggle dance (Frisch 1967). Insects rely not just on visual features on the ground but also on celestial objects and the polarization pattern of skylight (el Jundi et al. 2015; Reppert et al. 2004; Warrant & Dacke 2016; Warren et al. 2018, 2019; Wehner & Srinivasan 1981; Weir & Dickinson 2012). Migrating insects maintain a stable heading for extended periods of time, potentially using a time-compensated sun compass (Kennedy 1945, Reppert et al. 2010). In addition to allothetic cues such as visual landmarks, some insects utilize idiothetic information about self-motion to perform path integration (Collett 2019, Muller & Wehner 1988). *Drosophila*, for example, orient toward recent landmarks after they vanish (Neuser et al. 2008) and loop back to sites associated with food in total darkness (Brockmann et al. 2018, Corfas et al. 2019, Kim & Dickinson 2017, Murata et al. 2017).

field is beginning to link navigational behaviors to their neural underpinnings. Indeed, recent studies have demonstrated that HD neurons in *Drosophila* are necessary for menotaxis (Giraldo et al. 2018, Green et al. 2019), where flies maintain a constant but arbitrary heading relative to a visual landmark, a good strategy for ensuring straight trajectories during long-range navigation. More generally, the discovery of HD representations in identified neurons of small-brained animals that perform complex navigational feats offers the promise of mechanistic insights that may generalize to larger animals. We now take a closer look at HD networks in mammals and insects and evaluate experimental evidence for the implementation of ring attractor networks.

4. NEURAL MECHANISMS UNDERLYING HD FUNCTION IN MAMMALS

4.1. Hierarchical Structure and Function Point to a Subcortical Ring Attractor

Based on anatomical and functional considerations, the mammalian HD network is thought to function in a hierarchical fashion, with a subcortical ring attractor that passes HD information to cortical areas (Figure 4). Indeed, a large body of anatomical evidence indicates that the mammalian HD network is structured in a hierarchical fashion (see Taube 2007, table 1). HD cells are thought to first arise in the dorsal tegmental nucleus (DTN) and lateral mammillary nucleus (LMN), but they are found in their largest proportion downstream, in the thalamic anterior dorsal nucleus (ADN). Angular velocity cells have been reported in vestibular-related brainstem nuclei upstream of HD cells (Bassett & Taube 2001, Cullen & Taube 2017, Sharp et al. 2001b), but the two cell types co-occur in several structures. Similarly, HD cells in downstream cortical regions are intermingled with other spatial cells such as grid cells (Boccaro et al. 2010).

Support for the idea that the mammalian HD network functions hierarchically has come from converging lines of physiological evidence. First, and most importantly, a consistent finding across many studies is that lesions to a particular region in the hierarchy will disrupt HD representations in downstream but not upstream structures (see Clark & Taube 2012, table 1). A second line of evidence comes from careful analysis of the temporal delay between changes in a cell's firing rate and head orientation (Sharp et al. 2001a). HD cells in the LMN anticipate future head movements by ~40–95 ms, a quantity known as the anticipatory time interval (Blair et al. 1998, Stackman

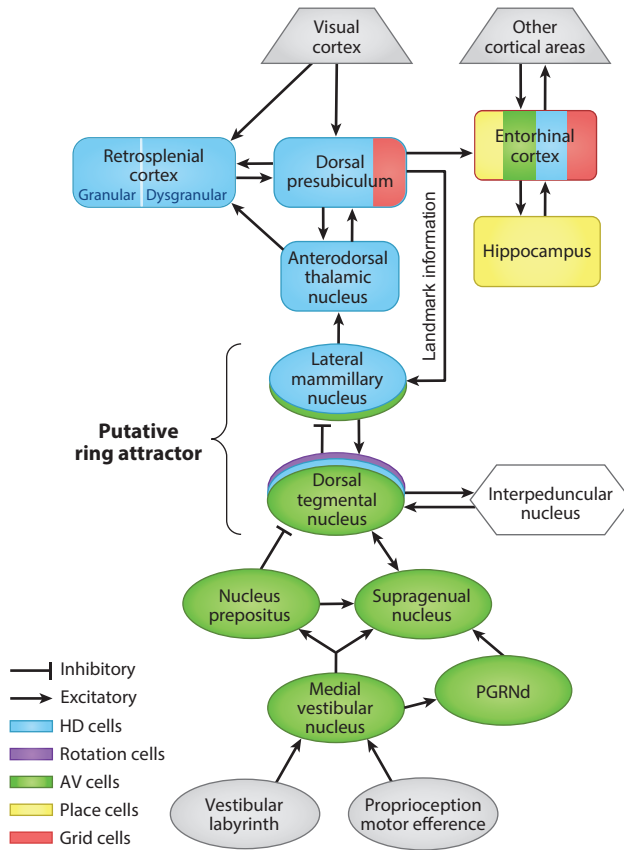


Figure 4

Schematic of the extended mammalian head-direction (HD) network, illustrating relevant brain regions and their major connections. The color of each box indicates some of the major cell types present and their relative abundance. HD cells have been found in a distributed network running from brainstem nuclei that receive vestibular input to cortical structures thought to house cognitive maps. The putative ring attractor is thought to function through reciprocal interactions between the dorsal tegmental nucleus and the lateral mammillary nucleus. Figure adapted with permission from Cullen & Taube (2017).

& Taube 1998). In contrast, in the downstream dorsal presubiculum, HD cell firing lags head movements by ~ 10 ms (Blair & Sharp 1995, Blair et al. 1997). Third, HD cell directional tuning width decreases from the DTN to downstream ADN (Bassett & Taube 2001, Stackman & Taube 1998). Finally, the percentage of HD cells increases and the percentage of angular velocity cells decreases from the DTN to ADN (Sharp et al. 2001b, Stackman & Taube 1998, Taube 1995). For these reasons, the mammalian ring attractor is thought to reside at the bottom of the hierarchy and function through reciprocal interactions between the DTN and LMN (Taube et al. 1996).

4.2. Cell Types and Circuits

Despite the importance of the DTN and LMN in generating the HD representation, relatively few studies have focused on how HD correlates emerge in these areas (Bassett & Taube 2001, Blair et al. 1998, Sharp et al. 2001b, Stackman & Taube 1998). This is likely due to the difficulty

Idiothetic cue:

internal signal such as proprioceptive feedback, motor efference copy, and vestibular input used to estimate self-motion

of recording from these deep structures. Nevertheless, these studies indicate that three major cell types required to build a ring attractor—angular velocity cells, rotation cells, and HD cells—may be present in both areas. Two classes of neurons tuned to angular velocity have been described. First, symmetric angular velocity cells modulate their firing rate with angular velocity regardless of turning direction, giving rise to symmetric tuning curves that encode angular speed. Second, asymmetric angular velocity cells increase their firing rate when the head turns in one direction and decrease or do not modulate their firing rate when the head turns in the other, as predicted by ring attractor models (Bassett & Taube 2001, Sharp et al. 2001b, Stackman & Taube 1998). Both types of cells are present in the DTN and LMN, but the DTN contains a higher proportion of neurons with angular velocity correlates (~75%) compared to the LMN (~35%). In addition, about 10% of DTN neurons display HD cell-like properties. Unlike classic HD cells, however, these neurons show very broad direction tuning and, more importantly, fire at higher rates during head turns in one direction compared to the other (Bassett & Taube 2001, Sharp et al. 2001b). This conjunctive tuning to head direction and angular velocity suggests that these neurons, which are thought to be inhibitory, may function as rotation cells. The LMN contains HD cells and potentially rotation cells, which together constitute ~25% of the population (Blair et al. 1998, Stackman & Taube 1998).

How might these cell types be connected to form a ring attractor? DTN is thought to send primarily inhibitory projections to the ipsilateral LMN, while the LMN is thought to send primarily excitatory projections back to the DTN (Allen & Hopkins 1988, 1989; Hayakawa & Zyo 1989, 1990; Wirtshafter & Stratford 1993). In addition, the majority of LMN neurons project to both DTN and ADN (Takeuchi et al. 1985). Importantly, at present, there is no evidence for recurrent excitatory connections between LMN neurons. The apparent lack of recurrent excitatory connections between LMN HD cells and the presence of putative inhibitory rotation cells in the DTN that show broad directional tuning suggest that the mammalian HD network may function as a Class 2 ring attractor.

4.3. Updating the HD Representation by Integrating Angular Velocity

Mammals are thought to continually rely on idiothetic information to perform path integration (Savelli & Knierim 2019), a strategy that operates regardless of whether landmarks are present or not. Indeed, an important finding is that lesions or inactivation of the peripheral vestibular system—one important source of idiothetic angular velocity information—abolishes the HD representation (Muir et al. 2009, Stackman & Taube 1997, Stackman et al. 2002, Valerio & Taube 2016). Vestibular information cannot be the only idiothetic cue, however, since passively transporting rats from a familiar environment to a novel one leads to considerable drift in the HD representation, despite intact vestibular inputs. In contrast, if blindfolded rats are allowed to navigate between the two environments, the HD representation is maintained with little drift (Taube & Burton 1995). Indeed, information regarding motor efference copy and proprioception is thought to be conveyed to the DTN (Dumont & Taube 2015).

4.4. Tethering the HD Representation to Allothetic Sensory Cues

Several studies have found that, in familiar environments, a well-learned visual landmark can dictate activity in the HD cell network (Blair & Sharp 1996; Goodridge & Taube 1995; Knierim et al. 1995, 1998; Zugaro et al. 2001, 2000). These visual signals are thought to be carried by projections from the postsubiculum and retrosplenial cortex to the thalamic ADN and the LMN (Chen et al. 1994, Goodridge & Taube 1997, Jacob et al. 2017, Yoder et al. 2011). Indeed, visual landmarks

appear to gain control of the HD representation at the level of the LMN (Yoder et al. 2015). Interestingly, a recent study found neurons in the retrosplenial cortex, intermingled with classic HD cells, that are tuned to two directions in a bilaterally symmetric environment, suggesting a system for integrating landmark information with the HD network (Jacob et al. 2017). Together, these studies indicate that vestibular input is critical for generating the HD representation, but under normal conditions, visual cues and proprioceptive/motor signals play a prominent role in updating the current HD representation.

4.5. Evidence for Attractor Dynamics

While its exact circuit architecture remains poorly understood, key experimental observations are consistent with the hypothesis that mammalian HD networks may be organized as a ring attractor (Knierim & Zhang 2012). Most importantly, when the preferred firing directions of HD cells change, the cells shift their tuning in concert so that pairwise differences between the preferred firing directions of individual HD cells are preserved. This has been observed under several experimental manipulations. For example, moving a prominent visual cue by 180° causes pairs of simultaneously recorded HD cells to rotate their preferred firing directions by approximately 180° as well, while maintaining a stable pairwise offset (Taube et al. 1990b), although this could be explained by HD cells that are each driven by the visual cue. More convincing is the demonstration that the HD population can break free from landmarks and other external sensory cues while maintaining their internal consistency (Hargreaves et al. 2007, Yoganarasimha et al. 2006). Similar effects are observed during slow drift in the preferred firing direction induced optogenetically (Butler et al. 2017) and during a so-called bursty firing pattern produced through lesions of the vestibular system (Clark & Taube 2012, Muir et al. 2009). In addition, consistent with ring attractor models, HD cell population activity is strongly influenced by internal network dynamics, with activity patterns during periods of sleep that resemble those recorded during awake behavior, despite relative isolation from sensory inputs (Chaudhuri et al. 2019, Peyrache et al. 2015).

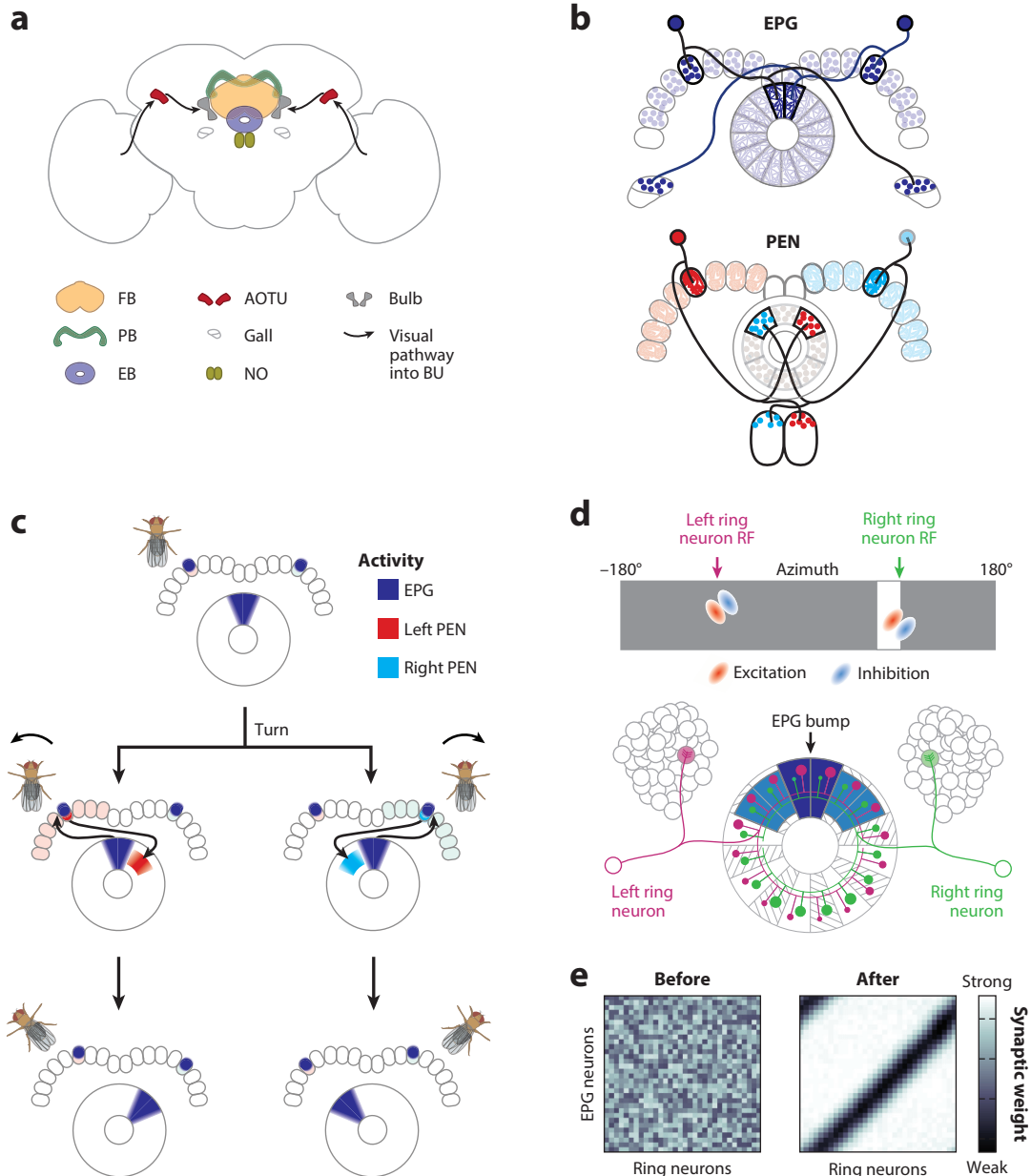
5. NEURAL MECHANISMS UNDERLYING HD FUNCTION IN INSECTS

The brain region that hosts the insect HD network, the central complex, consists of four mid-line neuropils: the protocerebral bridge (PB), the ellipsoid body (EB, or central body lower), the fan-shaped body (FB, or central body upper), and the paired noduli (NO) (Hanesch et al. 1989, Heinze & Homberg 2008, Pfeiffer & Homberg 2014, Power 1943, Strausfeld 1976, Turner-Evans & Jayaraman 2016, Young & Armstrong 2010b) (**Figure 5a**). Each neuropil can be further subdivided based on the compartmentalized arbors of neurons that innervate them. In addition to the PB, EB, FB and NO, a large number of accessory neuropils carry sensorimotor information to and from the central complex. Unlike mammals, the brains of insects are mostly composed of identified neurons, which can be recognized between individuals of the same species and even across species when conserved. Recently, the powerful genetic tools available in fruit flies have been used to characterize central complex circuits in unprecedented detail (Lin et al. 2013, Wolff & Rubin 2018, Wolff et al. 2015).

The structure and function of EB columnar neurons, which innervate single compartments within both the PB and the EB, suggest the implementation of a Class 1 ring attractor network. As mentioned above, EPG neurons appear to function as HD cells: Their population activity in the EB is organized as a single bump whose angular position is maintained through periods of immobility, gets updated by the integration of angular velocity, and is tethered to visual landmarks (Seelig & Jayaraman 2015). Individual EPG neurons innervate one of 16 wedges of

EPG neuron: insect HD cell. Also known as CL1a, wedge neuron, or compass cell. Columnar neuron named after structures it innervates: ellipsoid body, protocerebral bridge, and gall

the EB and send axonal projections to a corresponding single glomerulus in either the left or right PB (**Figure 5b**). As a population, they innervate all 16 wedges in the EB and the medial eight glomeruli in the left and right PB (Wolff et al. 2015). Due to this structured connectivity, the bump of activity in the EB gets transmitted to both the left and right PB, generating two bilaterally symmetric bumps, which both encode the same head direction but whose amplitudes can be differentially tuned to support angular velocity integration, as discussed below.



(Caption appears on following page)

Figure 5 (Figure appears on preceding page)

Structure and function of the insect HD network. (a) Illustration of the insect central complex, associated neuropil, and visual input pathways. (b) Schematic showing the morphology of individual EPG and PEN neurons. (Top) Individual EPGs innervate a single wedge in the EB, a single glomerulus in the left or right PB, and the left or right gall. (Bottom) Similarly, PENs innervate a single tile in the EB, a single glomerulus in the left or right PB, and the left or right noduli. Compartments with predominantly presynaptic sites are marked with circles. (c) Diagram showing the mechanism by which PENs update the EPG bump position in the EB. (Top) To start, a single bump of activity exists in the EB, which is conveyed to the left and right PB in a topographic fashion by EPG neurons. (Middle) When the fly turns left, PENs innervating the left PB are activated and move the EPG bump clockwise. Similarly, when the fly turns right, PENs innervating the right PB are activated and move the EPG bump counterclockwise. (Bottom) The EPG bump has an updated position after left or right turns. (d, top) Individual visually responsive ring neurons have spatiotemporal receptive fields centered at particular locations in the fly's visual field. Two example ring neurons are shown. The ring neuron on the right is being driven by the presence of a vertical bar that overlaps with the excitatory portion of its receptive field. (Bottom) Visual ring neurons innervate individual glomeruli in the left or right bulb and project to the entire EB, where they synapse onto the population of EPG neurons. The strength of ring neuron to EPG synapses is proportional to the size of the circles in each EB wedge. Anti-Hebbian plasticity between ring neurons and EPGs functions to map a visual scene onto bump positions in the EB. For example, here the bump is located at the top of the EB, and the right ring neuron (green) is being driven by a visual stimulus. This leads to a selective reduction in right ring neuron to EPG synaptic strength, but only in regions of the EB where the bump is located, schematized as a reduction in the size of the green circles at the top of the EB. Because the left ring neuron (pink) is not being driven by a visual stimulus, its synapses with EPG neurons at the top of the EB remain strong (large circles). If the fly were to turn $\sim 180^\circ$, the bump would move to the bottom of the ring, and the visual stimulus would now be driving the left ring neuron, leading to synaptic depression between it and EPGs innervating the bottom of the ring, consistent with small pink circles at the bottom of the ring. (e) Illustration of the synaptic connectivity matrix between visual ring neurons and EPGs before (left) and after (right) visuomotor experience. (Left) Initially, a visual ring neuron's synaptic strength is distributed randomly across the EPG population. (Right) After visuomotor experience, anti-Hebbian plasticity has structured the connectivity matrix such that individual ring neurons show reduced synaptic strength onto particular neighboring EPG neurons. Since ring neurons inhibit EPGs, this diagonal trough in ring-neuron output strength allows a visual stimulus to localize the bump's position to regions in the EB where inhibition is weakest. Abbreviations: AOTU, anterior optic tubercle; EB, ellipsoid body; FB, fan-shaped body; HD, head direction; NO, noduli; PB, protocerebral bridge. Panels b and c adapted with permission from Turner-Evans et al. (2017); panels a, d, and e adapted with permission from Kim et al. (2019).

5.1. Updating the HD Representation by Integrating Angular Velocity

A second group of EB columnar neurons, known as PENs, function as rotation cells. This was first suggested by their innervation patterns relative to EPG neurons (Wolff et al. 2015) and confirmed through physiology (Green et al. 2017, Turner-Evans et al. 2017). PEN neurons innervate a single glomerulus in the left or right PB and project to one of eight tiles in the EB (**Figure 5b**). Importantly, individual PENs receive input from EPGs in a PB glomerulus but project back to the EB with a CW or CCW offset, depending on whether they innervate the left or right PB, respectively. This is precisely the connectivity expected from putative excitatory rotation cells (Skaggs et al. 1995). In addition to this offset connectivity, PENs should also conjunctively encode direction and angular velocity if they are to function as rotation cells. Indeed, recordings of neural activity have demonstrated that the population of PENs that innervate the left or right PB shows a single bump of activity whose amplitude is larger during CCW or CW turns, respectively (**Figure 5c**). While this basic layout corresponds remarkably well with those predicted by ring attractor networks, the PEN-EPG circuit appears considerably more complex. For example, PEN neurons come in two types, PEN1s and PEN2s, with distinct connectivity, spatial activity profiles, and dynamics (Green et al. 2017; Turner-Evans et al. 2019). In addition, the amplitude of the EPG bump is modulated by the fly's angular speed and behavioral state, typically decreasing during periods of prolonged immobility (Turner-Evans et al. 2017).

5.2. Mechanisms of Persistent Activity

Importantly, although EPG activity often decreases during periods of immobility, it resumes with the bump in the correct position when the animal begins moving again, even in darkness (Seelig & Jayaraman 2015). Several pathways potentially contribute to this persistent activity in the insect

PEN neuron: insect rotation cell. Also known as CL2 or tile neuron. Columnar neuron that innervates the protocerebral bridge, ellipsoid body, and paired noduli

HD network. First, the anatomy of a final class of EB columnar cells, known as PEGs, suggests that they may play a role in generating persistent activity. Individual PEGs receive input in single glomeruli in the PB and project back to the same EB region that provides their input. That is, their connectivity is similar to PENs, but without the spatial offset in their projection patterns. This creates a potential excitatory feedback loop involving EB-PB-EB connections, which could be one mechanism supporting persistent activity. Second, an excitatory feedback loop involving PENs could function similarly (Turner-Evans et al. 2017). Third, EM data confirm the existence of local connections between different EPG neurons and between EPG neurons and other columnar neurons in the EB, which could potentially sustain a bump of activity through local interactions (Turner-Evans et al. 2019). Such local interactions may allow for a subthreshold activity bump, which need not engage the EB-PB-EB feedback loop. Which of these and other potential cellular and circuit mechanisms support persistent activity and why the network might contain multiple potential mechanisms remain open questions.

5.3. Inhibitory Feedback Pathways

Similar to persistent activity, multiple pathways likely generate the feedback inhibition required by ring attractor models (Franconville et al. 2018). First, a population of cells known as $\Delta 7$ neurons seem to contribute to passing the bump from EPGs to PENs and other neurons in the PB (Turner-Evans et al. 2019). The stereotyped morphology of $\Delta 7$ neurons ensures strong output to regions of the PB opposite the EPG bump's location, effectively generating an antibump, which could sculpt PEN and EPG activity (Turner-Evans et al. 2019). In addition to $\Delta 7$ s, neurons projecting from the gall to the EB likely provide uniform inhibition to the circuit. These neurons receive strong excitatory input from EPGs in the gall and provide strong inhibition back to EPGs in the EB, distributed throughout the ring (Franconville et al. 2018). Unlike $\Delta 7$ s, these ring neurons likely provide direct feedback inhibition and may provide gain control to the circuit. Finally, as discussed below, visually responsive ring neurons provide sculpted inhibition to EPGs (Omoto et al. 2017, Seelig & Jayaraman 2013, Shiozaki & Kazama 2017, Sun et al. 2017, Turner-Evans et al. 2019). Together, the anatomy, connectivity, and physiology of the neurons innervating the EB and PB directly suggest the implementation of a ring attractor network that uses multiple feedback pathways and local recurrent connections to support persistence and provide the requisite inhibition.

5.4. Tethering the HD Representation to Allothetic Sensory Cues

When present, prominent allothetic cues such as visual landmarks can provide a reliable indication of one's direction. How might landmark information dictate an animal's internal representation of head direction? In *Drosophila*, a population of visually responsive ring neurons likely function as landmark cells. These neurons receive input in a structure known as the bulb, where their dendrites innervate individual glomeruli. These glomeruli are arranged retinotopically, respond to oriented visual features, and are well-characterized by center-surround receptive fields, although glomerular responses also depend on stimulus history and context (Omoto et al. 2017, Seelig & Jayaraman 2013, Shiozaki & Kazama 2017, Sun et al. 2017). Each visual ring neuron sends axonal projections throughout the EB, making synapses onto all EPG neurons (Turner-Evans et al. 2019) (**Figure 5d**), suggesting that the retinotopy present in the bulb is lost in the EB. Consistent with this, when flies walk in closed loop with a single vertical feature, there is an effectively arbitrary angular offset between the position of the bump in the EB and the position of the vertical feature (Seelig & Jayaraman 2015). Across flies, all offsets are observed and with approximately equal probability. These data suggest that the circuit is able to map visual scenes to an abstract

HD representation, but that retinotopy is indeed lost in the EPG population. How might this mapping of visual feature location to EB bump position occur? Previous work has proposed that the synapses between visual feature detectors and HD cells are likely plastic, which could enable the correlated activity of ring neurons and EPGs to map different panoramic views onto distinct bump positions (Cope et al. 2017, Knierim et al. 1995, McNaughton et al. 1991, Ocko et al. 2018, Page & Jeffery 2018, Skaggs et al. 1995, Zhang 1996). Indeed, the idea of plasticity reconciling angular velocity–driven bump movements with visual cue–driven displacement of the bump, first proposed in models (Cope et al. 2017, Ocko et al. 2018, Page & Jeffery 2018), has since found experimental support in the fly (Kim 2019, Fisher et al. 2019) (**Figure 5d,e**). The mechanisms underlying such plasticity are as yet unknown, although nitric oxide signaling may be involved (Kuntz et al. 2017).

Cognitive map: an internal representation of the two- or three-dimensional structure of the environment in the brains of many animals

5.5. Evidence for Attractor Dynamics

A recent experiment combining two-photon calcium imaging and optogenetic activation of EPG neurons in tethered, flying flies provided direct support for ring attractor dynamics (Kim et al. 2017). In these experiments, optogenetic stimulation of EPGs was used to generate an artificial bump in the EB. Critically, the formation of this new bump was accompanied by the disappearance of the original bump, consistent with ring attractors enforcing a single bump of activity at a time. This phenomenon is thought to be mediated by a winner-take-all process acting through lateral inhibition between EPG neurons. Interestingly, the necessary stimulation strength was found to be independent of distance from the original bump, supporting a model involving uniform inhibition that acts on all EPGs equally rather than scaling with distance between EPGs. How this uniform inhibition is generated by the combination of inhibitory neurons mentioned above remains unknown.

6. OPEN QUESTIONS AND FUTURE DIRECTIONS

As we described above, HD networks in insects and mammals share key properties consistent with the implementation of ring attractor networks: uniqueness, persistence, integration, and drift correction. Thus, incorporating insights from different model systems should accelerate the search for mechanisms underlying the function of neural compasses. However, it is also important to keep in mind that compass systems likely differ in their circuit architecture and in aspects of their function. We discuss these issues in the subsections below.

6.1. Cognitive Maps and Vector Navigation

HD networks are thought to support both map-based and vector-based navigational strategies that help animals navigate in two or more dimensions. In map-based strategies, internal representations of the animal's location, direction of travel (i.e., heading direction), and goal are combined with a cognitive map of the environment, allowing the animal to calculate trajectories and plan novel routes through space (Tolman 1948). Indeed, the mammalian hippocampal formation and related structures contain neurons that represent location, environmental boundaries, and a host of other variables that are both important for navigation and strongly imply the existence of a cognitive map (Grieves & Jeffery 2017, O'Keefe & Nadel 1978) (**Figure 4**). By contrast, in vector-based strategies, an animal keeps track of a homing vector that points toward important locations such as a food source or nest. While insects are thought to lack a cognitive map, considerable behavioral work has strongly implied the existence of neural representations for homing vectors (Collett et al. 2013). For both map-based and vector-based strategies to work, an animal must know its

heading direction. Yet, head direction and heading direction can be dissociated, and mammalian work shows that head direction cannot be used as a proxy for heading direction (Raudies et al. 2015). How HD information gets transformed to heading information that can be used to support navigation in two or more dimensions is an important question for future research.

6.2. Synaptic Weight Calibration

To function properly, ring attractors require the presence of precisely tuned synapses between many cells (Itskov et al. 2011, Renart et al. 2003). Given the large parameter space and the requirement for precise parameter tuning, it is unlikely that connection strengths are entirely hardwired through genetics alone. Instead, these networks are likely approximately set up during development and calibrated through spontaneous activity or early experience. How these steps occur remains poorly understood, but theoretical and experimental work is beginning to address this issue (Bjerknes et al. 2015, Page et al. 2018a, Stringer & Rolls 2006, Stringer et al. 2002, Tan et al. 2015). Here, *Drosophila* may lead the way with its powerful genetics tools for studying development (Andrade et al. 2019, Boyan & Reichert 2011, Sullivan et al. 2019, Young & Armstrong 2010a). Similarly, these networks must remain in the appropriate parameter regime throughout adulthood. Mammals are able to calibrate their path integration system well into adulthood (Jayakumar et al. 2019). Whether insects can manage similar feats remains unclear (Seelig & Jayaraman 2015).

6.3. Coordination Across Structures

HD networks consist of hundreds to thousands of neurons distributed across several brain structures. How might the dynamics of these networks, subject to noisy synapses, conduction delays, and other biological constraints, be coordinated within and between structures? Recent studies reported that synchronous spiking, organized as a 130–160-Hz oscillation, coordinates activity in the mammalian HD network (Butler & Taube 2017, Peyrache et al. 2015). Such synchronous activity may function to increase the impact of spiking on downstream brain regions by grouping outputs within the time constant of downstream neurons. Whether similar processes, or others serving similar functions, are needed in the insect ring attractor is unknown.

6.4. Angular Velocity Signal

What is the nature of the angular velocity signal? Recent conceptual work in mammals has suggested that the angular velocity signal may be the output of a Kalman filter (Finkelstein et al. 2016, Laurens & Angelaki 2018). This would predict that the system contains an internal model of its sensors, sensory-prediction errors, and a way to combine the two. Whether and how these systems combine various sources of angular velocity information are unclear. In addition, experimental work in mammals has shown that, with an angular velocity signal that takes into account rotations about the axis defined by gravity, HD networks can patch together surfaces arranged in three dimensions in a parsimonious way (Page et al. 2018b, Shinder & Taube 2019). Interestingly, bats have HD cells that are tuned to all three axes of rotation, and the properties of azimuthal-tuned HD cells during inversions suggest the use of a toroidal coordinate scheme (Finkelstein et al. 2015). This work raises the possibility of angular velocity signals for each axis of rotation. Similarly, during two-dimensional navigation, neurons in the bat postsubiculum are tuned to angular velocity, head direction, and combinations of the two, including putative rotation cells (Finkelstein et al. 2019). The firing properties of these neurons could be accounted for by an extended ring attractor network that may use visual information from the cortex to update the HD representation. Such

results in nonmodel organisms further illustrate the importance of work in a diversity of species to gain broad insights into circuit function.

6.5. Added Complexity

The putative insect and mammalian ring attractor networks appear considerably more complex than those suggested by theoretical work, but the functions enabled by this added complexity remain mysterious. For example, mammalian HD cells and angular velocity cells show considerable variability in peak firing rates and tuning properties from cell to cell. And insects, whose HD network anatomy directly suggests a ring attractor implementation, contain several local and long-range loops that could support persistent activity. With these examples and countless others, it is tempting to speculate that the additional complexity may increase the robustness or stability of HD network dynamics, but a grounded theoretical account for these functions is lacking.

6.6. Future Work in Insects

Much work remains on the insect HD network. First, there are many neurons that provide input to EB columnar neurons whose activity remains to be characterized. Neurons conveying angular velocity information, neuromodulatory tone, and internal states such as hunger and sleep drive likely converge on this circuit, but how these sources of information are combined is unknown (Dus et al. 2013, Liu et al. 2016). Second, the bump of activity in the EB is conveyed to an intriguingly complex structure known as the fan-shaped body (Franconville et al. 2018). Here, HD information can be combined with a large number of potential sources of information to support successful navigation in two or more dimensions (Martin et al. 2015, Stone et al. 2017, Weir et al. 2014). Insect researchers can take inspiration from their mammalian counterparts, whose efforts have focused extensively on how HD information gets integrated into downstream brain regions to support more complex navigational abilities. Third, most work on insects has been performed in immobilized or head-fixed preparations walking in closed loop with simple, one-dimensional environments. This both limits the behaviors available for study and constrains the circuit to operate in situations that it did not evolve to handle. For example, how the insect ring attractor might function in two or three dimensions remains entirely unexplored, although work in freely behaving cockroaches and head-fixed flies navigating two-dimensional virtual reality is beginning to address this (Haberkern et al. 2019, Varga & Ritzmann 2016).

6.7. Future Work in Mammals

A key aspect of future work in mammals should be to refocus on the subcortical structures implementing the putative ring attractor: the DTN and LMN. Previous studies have recorded from a relatively small number of neurons in these areas, and modern analytical approaches are needed to more fully characterize their tuning properties. Similarly, how homogeneous are the neurons composing these areas? Do HD and rotation cells correspond to morphologically and biophysically distinct cell types? If so, electrical and optical recordings from defined cell types could advance our understanding of these important structures tremendously. Similarly, if distinct cell types do exist, light and targeted electron-level microscopy studies could begin to dissect the connectivity between elements of the circuit.

6.8. The Comparative Advantage

Our understanding of navigation has benefited enormously from the wide range of species whose navigational behaviors have been carefully studied (Collett & Graham 2004, Finkelstein et al.

2016, Mouritsen 2018, Zeil 2012). However, the animal kingdom's best navigators do not necessarily offer the best tools for the detailed neural circuit analysis work required to understand how navigational computations are implemented by neuronal networks. Similarly, although important insights into the neural basis of navigation have been uncovered in model organisms, there are few examples of causal links between these mechanisms and specific deficits in meaningful navigational tasks. Thus, it remains vital to study navigation in a combination of species, each with its own experimental advantages, behavioral specializations, and ethological niches (Krogh 1929). Furthermore, if the ultimate goal of the field is to extract general principles, it seems essential to understand how different animal brains may have evolved convergent solutions to some of the same fundamental navigational problems.

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