

Opinion

Head direction and the evolutionary origins of spatial representation

Marcel E. Sayre^{1,*}, Ajay Narendra¹, Stanley Heinze², and Andrew B. Barron ¹

Spatial representations are a fundamental aspect of cognition. It remains largely unknown when and why the capacity to neurally represent space first evolved. In this opinion article, we argue that a strong candidate for the earliest such representation is the encoding of head direction. Dedicated circuits that compute head direction by integrating self-motion and external cues have been described in both vertebrates and insects and are likely to be ancestral in each lineage. This suggests a Cambrian or possibly Precambrian origin for head direction representation. In both lineages, head direction circuits occupy an evolutionarily and functionally foundational position. They occur in deeply conserved brain structures, sit upstream of other spatial representations, and can emerge from minimal neural architecture. In mammals, they also develop before other spatial systems. Together, these features suggest that head direction was the first neural representation of space, offering a window into the evolution of neural representation and spatial cognition more generally.

Neural representations of space

A central aspect of cognition is the internal representation of the external world. Views differ on what precisely should be considered a bona fide neural representation [1,2]. For this opinion article, we follow the definition of representation as a neural process that functionally substitutes for something else [3]. In this framework, for a neural process to qualify as a representation, it should meet three criteria: it should be able to stand in for an absent stimulus or internally recreate an external situation such that it can be used in its place to guide behavior; it should support predictive use [4]; and it should be capable of misrepresentation, such that discrepancies can be detected and corrected through direct sensing [3]. A counterexample would be a sensory neuron that responds directly to a stimulus. Although such a neuron may encode information about that stimulus, its activity depends on the stimulus being physically present. It does not persist in its absence, cannot stand in for it, and therefore does not function as a neural representation as defined here [3].

Canonical examples of neural representations come from mammalian spatial cognition [5]. The activity of 'grid' cells, for example, represents a hexagonally arranged lattice that functions as an internal spatial map, allowing distance and displacement to be computed directly from neural activity [6]. 'Place' cells fire in specific locations, even in the absence of external sensory input, thereby representing the animal's position [7]. Additionally, there are neural systems in mammals that represent features such as head direction, boundaries, and vector relationships to goals and objects, among others (reviewed in [5]). Not all forms of directed movement require internal representations of space, however. Consider a sea slug (*Aplysia vulgaris*) or an isopod (*Armadillidium vulgare*) turning away from bright light: negative phototaxis. Here, there is no requirement for the nervous system to represent the light stimulus (i.e., to create something to stand in for the light

Highlights

Head direction is a strong candidate for the first neural representation of space to evolve, marking an important step in the evolution of animal cognition.

Dedicated circuits that compute head direction by integrating self-motion and external cues have been described in both vertebrates and arthropods and are likely to be deeply conserved in each lineage.

Despite vast phylogenetic distances, head direction systems share core computational principles, including ring attractor dynamics and multimodal cue integration, with striking anatomical similarities recently reported between insects and fish.

Developmental, anatomical, and functional evidence points to head direction as foundational for other spatial representations.

¹School of Natural Sciences, Macquarie University, Sydney, New South Wales, Australia

²Lund Vision Group, Department of Biology, Lund University, Lund, Sweden

*Correspondence: marcel.sayre@mq.edu.au (M.E. Sayre).

stimulus). Rather, there is a sensorimotor transformation of the light stimulus into a motor turning response. Representation is therefore a special feature of some nervous systems rather than a universal feature of all nervous systems [3].

Neural representations are transformative because they free behavior from dependence on what is currently sensed. This allows animals to navigate toward goals even when those goals are not perceptually available. Spatial representations are not unique to humans or even vertebrates [8], but when and why the capacity to represent space evolved remains unclear. Here, we synthesize evidence from insects and vertebrates to argue that head direction, the neural representation of an animal's orientation in space, was the earliest neural representation of space to evolve. We highlight parallels across phylogenetically distant taxa, examine developmental and evolutionary evidence bearing on the foundational role of head direction representations in spatial cognition, and consider alternative candidate representations, outlining several findings that would challenge our proposal.

A head direction representation enables new behavioral capacities

The ability to represent head direction expands an animal's behavioral repertoire. Here, we use the term 'head direction representation' to refer specifically to a persistent internal representation of the animal's facing direction in allocentric coordinates—that is, a compass-like signal that provides a stable directional reference frame independent of the momentary presence of any single cue. Such representations integrate egocentric self-motion signals (e.g., vestibular, proprioceptive, or optic flow cues) with external landmarks or celestial cues to maintain a continuously updated estimate of heading. Animals that lack a head direction representation can still move adaptively, but their behavior is constrained to moment-to-moment transformations of sensory input into motor output. By contrast, a head direction representation enables an animal to maintain a heading in a flexible, cue-independent manner. For instance, straight-line movement over long distances can be achieved by holding a fixed arbitrary angle to a distant reference, which is essential for behaviors such as homing, dispersal, and migration [9–11]. Hardwired sensorimotor transformations can reproduce straight-line movement, but only while the guiding stimulus remains available and stable; once the cue is obscured or changes position (e.g., as the sun moves across the sky), orientation cannot be reliably maintained, and errors quickly accumulate. A persistent, multimodal head direction representation enables robust heading maintenance in complex environments [12], even when the main source of sensory input becomes unreliable. If, for example, a celestial cue like the sun becomes obscured, an animal with an internal head direction system can rely on alternative modalities such as an alternative celestial cue, mechanoreception, or proprioception to maintain its trajectory [13,14].

A representation of head direction is also a prerequisite for the emergence of a widespread navigational computation known as path integration [15]. Path integration allows an animal to monitor its position relative to a starting point (such as a nest or a foraging location) by continuously updating two variables: the direction of travel and the distance traveled along that direction [16]. The head direction system supplies the directional component, while temporal integration of odometry signals (e.g., optic flow, step-counting, or proprioceptive feedback [17,18]) indicates distance. To return home along the most efficient path, a path-integrating animal maintains a straight-line trajectory, often using external cues as references. Perturbations to the head direction system can disrupt straight-line orientation, as shown in flies [12,19–21], and, more generally, path integration, as shown in flies and rats [22–24].

More broadly, spatial representations underpin higher forms of cognition in vertebrates, and a head direction representation may have been a prerequisite for the emergence of these spatial

representations. In mammals, the neural systems that underlie spatial representations also provide a scaffold for episodic memory and support more abstract forms of reasoning, including conceptual and social inference, transitive reasoning, and flexible generalization across non-spatial domains [25]. If a head direction representation was indeed a prerequisite for the emergence of other spatial representations, as will be argued in the subsequent sections, then it also constituted a foundational evolutionary innovation upon which more elaborate cognitive functions could later be built. In this view, understanding the evolution of head direction networks is not only important for understanding the evolution of navigational behavior, but also for understanding the evolutionary trajectory of cognition itself.

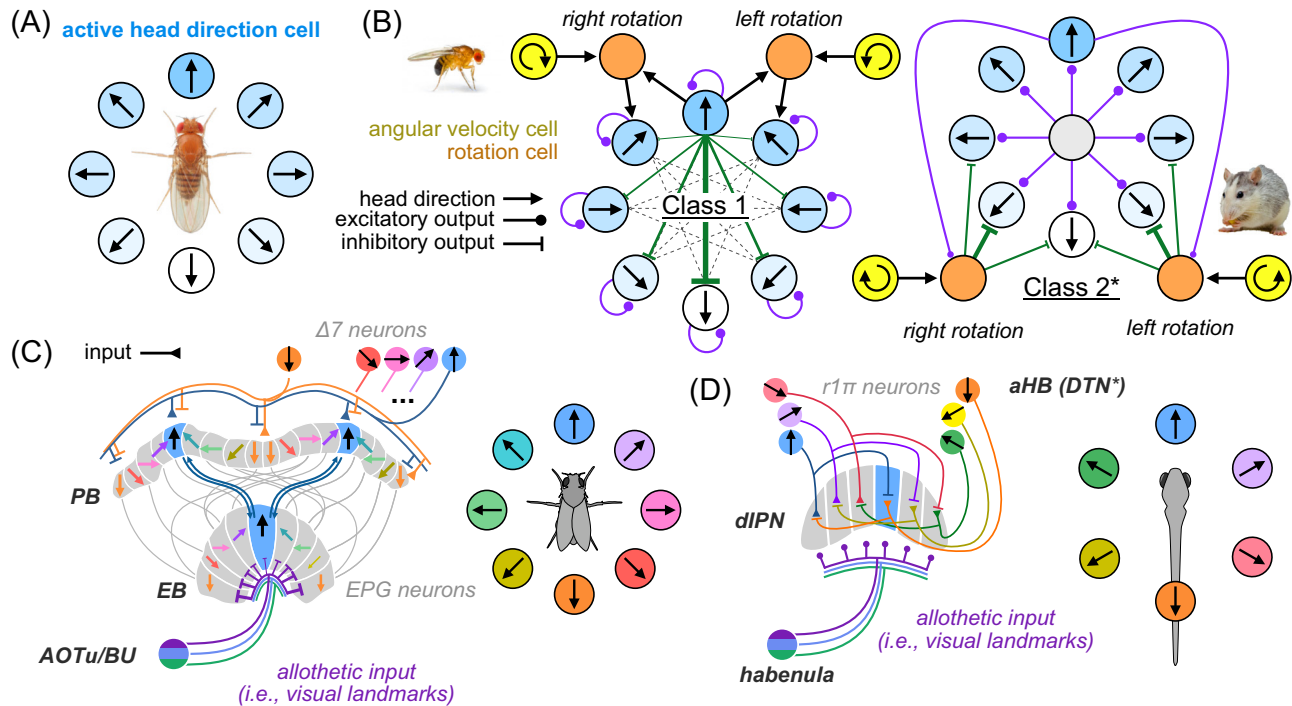
Head direction circuits

Neurons tuned to an animal's head direction (head direction cells) have been identified across diverse taxa, including mammals (primates [26], rodents [27], and bats [28,29]), birds [10,30], fish [31,32], and insects [33]. The collective activity of head direction neurons can be conceptualized as forming a circular map of 360° around the animal. Within this network, neural firing forms a localized 'activity bump' that shifts position as the animal turns, looping back to its starting point after a full rotation (Figure 1A). Within this loop, the angular position of the bump can be updated via self-motion cues and external sensory inputs. Although this property has only been adequately tested in a handful of organisms, a key feature of head direction systems is persistence: head direction neurons continue to signal a particular heading even when the animal stops moving or when external sensory cues are unavailable, such as in darkness [33,38–41]. In this way, head direction is not only dynamically encoded but persistently represented (for reviews, see [34,42,43]).

Following the discovery of head direction neurons in rats (reviewed in [44]), modeling studies predicted that such a representation could be implemented through a specific type of recurrent network known as a ring attractor [45–49]. A ring attractor is a continuous attractor network whose stable states form a 1D circular manifold. Importantly, this computational motif can be implemented through multiple circuit architectures (Figure 1B). Experimental work in fruit flies [50,51], rodents [23,52,53], and zebrafish [31] has provided evidence consistent with attractor dynamics in these systems, suggesting that shared computational principles may underlie diverse compass circuits, even if their mechanistic implementations differ (Figure 1B).

Just as ring attractor dynamics are a common computational solution, evidence from both insects and zebrafish points toward shared principles in the anatomical design of head direction circuits. Mechanistic understanding of the functioning of these circuits is particularly refined in the fruit fly [54]. The fly head direction circuit is a remarkable example of structure matching function. At the center of the fly brain lies the central complex, a set of four highly interconnected neuropils [55,56]. Within the central complex, head direction neurons are arranged in columnar domains that tile an ellipsoid structure, such that neural activity literally rotates around the ring of columns as the fly turns, akin to a compass (Figure 1C). The central complex is not unique to *Drosophila*; it is present in all insects examined thus far [57], and head direction neurons have been reported across insect species, including locusts [58], roaches [41], butterflies [59–61], moths [62], dung beetles [63], and bees [64–67].

Head direction circuits have also been widely reported in vertebrates, with some of the most detailed anatomical descriptions to date coming from larval zebrafish. By combining calcium imaging with comprehensive reconstruction of neuronal fiber projections, a recent study identified a population of zebrafish head direction neurons named 'rhombomere 1 pi' (or 'r1π' cells) [31].



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Figure 1. Features of head direction networks across species. (A) Conceptual representation of head direction cells, where each node represents a population of neurons that encode a specific azimuthal orientation. (B) Two ring attractor architectures: Class 1, where head direction cells (blue nodes) provide excitatory feedback through recurrent connectivity (purple edges), receive strongest inhibitory input from cells tuned to opposite directions (green edges), and shift their activity bump via angular velocity (yellow nodes) and rotation cells (orange nodes) that introduce local asymmetric excitation; and Class 2, where head direction cells receive directionally uniform excitatory input, and inhibition is provided by broadly tuned rotation cells that drive rotations of the bump around the ring [34] (for simplicity, only a single pair of rotation cells is illustrated). While there is strong empirical support for a Class 1 attractor network in insects, data supporting a Class 2 attractor in mammals are more limited (asterisk) [34]. (C) In insects, head direction neurons (EPG) in the central complex—specifically in the protocerebral bridge (PB) and the ellipsoid body (EB)—form a columnar representation of 360°. Their activity bump is anchored to allothetic cues (e.g., visual landmarks) via inputs from the anterior optic tubercle (AOTu) and bulb (BU), which can be remapped through rapid, experience-dependent synaptic plasticity [35,36]. (D) Zebrafish head direction neurons ($r1\pi$) in the anterior hindbrain (aHB; asterisk indicates proposed homology to the mammalian dorsal tegmental nucleus) display a strikingly comparable organization. Here, habenular inputs provide allothetic visual cues, aligning the internal compass with external landmarks. Furthermore, the circuits in both zebrafish and insects rely on reciprocal mutual inhibition (see also [37]). aHB: anterior hindbrain; dIPN: dorsal interpeduncular nucleus; DTN: dorsal tegmental nucleus; EPG: ellipsoid body-protocerebral bridge-gall neuron.

Each $r1\pi$ neuron extends branching projections that form two discrete columnar domains within the dorsal interpeduncular nucleus (Figure 1D). Although these neurons arborize within the dorsal interpeduncular nucleus neuropil, their somata are located outside this structure, in the anterior (prepontine) hindbrain, distinguishing them from intrinsic dorsal interpeduncular nucleus neurons. Additionally, both dendritic and axonal processes lie within the dorsal interpeduncular nucleus neuropil, giving these neurons a pseudounipolar organization reminiscent of typical arthropod neurons (Figure 1D). This study [31], along with subsequent work in zebrafish, has revealed several other intriguing parallels to the insect head direction circuit (Figure 1C–D): (i) in both zebrafish and insects, head direction neurons are organized into an array of adjacent domains that together represent 360° around the animal [31,33,64,68,69]; (ii) these domains are arranged in a topographically continuous manner; during rotation, head direction activity shifts sequentially between adjacent columns in antiphase to the animal's rotational movement [31,33,70,71]; (iii) the head direction representation is stabilized by reciprocal inhibitory connections, which send neural projections across columns to suppress neurons tuned to opposite directions [31,51,69,72]; and (iv) wide-branching input neurons innervate all columns, delivering allothetic visual

cues that anchor the compass to the external environment, and they exhibit rapid plasticity that allows remapping in novel environments [35,68,70,73–78].

The identification of head direction neurons in the goldfish dorsal pallium [32] (a telencephalic region developmentally homologous to components of the mammalian pallium, including the neocortex, hippocampus, and amygdala [36]) indicates that head direction representations in teleosts are present at both pallial and hindbrain levels, including within the habenula–interpeduncular system. In mammals, head direction signals are classically proposed to arise from reciprocal connectivity between the dorsal tegmental nucleus and the lateral mammillary nucleus, embedded within a broader loop that includes the anterodorsal thalamic nucleus and the postsubiculum [79]. Notably, the zebrafish anterior hindbrain head direction neurons share anatomical location and inhibitory identity with neurons of the mammalian dorsal tegmental nucleus, raising the possibility of a common evolutionary origin. However, whether mammalian dorsal tegmental nucleus head direction neurons project to the interpeduncular nucleus or receive comparable habenular inputs remains unresolved. It is therefore unclear whether a homologous habenulo–interpeduncular pathway contributes to head direction processing in mammals. Nonetheless, the parallels between insect and fish circuits point toward shared anatomical principles foundational for the formation and maintenance of head direction (i.e., ring attractor) networks—principles that remain to be fully uncovered in mammals (see also [80]).

Head direction networks are foundational for other internal representations

Head direction representations occupy a foundational hierarchical role in the formation of vertebrate spatial maps [43]. In mammals, head direction cells provide essential input to both grid cells of the medial entorhinal cortex and place cells of the hippocampus [81,82]. Lesion studies show that disrupting the head direction system destabilizes grid-cell activity and place-cell representations [23,83–85]. By contrast, head direction signals generally remain intact when grid cell or place cell function is compromised [83,86,87]. Head direction, therefore, provides a reference frame on which higher-dimensional maps of location and distance can be built (see also [88]).

Ontogenetic evidence mirrors this hierarchy [38,89–91]. Head direction cells have been recorded in rats as early as postnatal day 12—before the animals' eyes even open [92]. By postnatal day 16, just after eye opening, head direction activity shows near adult-like precision and stability, and within 24 h, a salient visual landmark is already sufficient to anchor and control the preferred firing directions of the cells. Other spatial representations emerge later: place and boundary cells appear around postnatal day 16, when pups begin active exploration, and grid cells only around weaning at postnatal day 20–21 [93]. The developmental trajectories of these cell groups also differ: head direction and grid cells display adult-like function almost immediately upon appearance, whereas the profile of place cells develops more gradually [94].

A comparable computational hierarchy is also observed in insects. In the fruit fly, the mechanisms for representing head direction and travel direction (the translational movement of the animal's body through space) are interconnected but implemented via distinct processes. The head direction signal—carried by 'EPG' neurons in the ellipsoid body (Figure 1C)—provides an upstream reference frame. Downstream, neuron populations in the central complex integrate this heading signal with egocentric translational velocity signals, resulting in an explicit allocentric travel-direction representation [24,95–97]. Silencing compass neurons abolishes accurate encoding of travel direction; by contrast, perturbing the translational velocity signals that contribute to computing travel direction does not disrupt head direction coding [95]. Thus, as in mammals, head direction in insects appears to function as a scaffold on which other spatial variables are

constructed [65], supporting the view that head direction is likely an evolutionary precursor to other types of spatial representations in the brain.

It remains to be determined whether, in insects, comparable developmental relationships exist at the functional level. Structural development of the central complex shows pronounced heterochrony across lineages: in most hemimetabolous insects, the central complex forms during embryogenesis, whereas in numerous holometabolous taxa, it is absent or only partially developed at hatching and differentiates later [98–100]. The delayed emergence of central complex neuropils in some holometabolous species may reflect the relatively simple locomotor and sensory demands of their larval stages, whereas the transition to articulated appendages, flight, and expanded sensory systems in the adult may require the later construction of more elaborate and precisely organized circuitry [101]. To our knowledge, no longitudinal recordings have examined at which developmental stage head direction, travel direction, or other spatial representations emerge during development in insect species.

The evolution of head direction networks

Head direction circuits exist in evolutionarily conserved brain regions. The habenula and interpeduncular nucleus are present across all vertebrates [102], while a central body neuropil is present in all major arthropod lineages, even in onychophorans (velvet worms), the sister group to arthropods [57, 103–106]. Assuming the head direction circuits described in fish and flies have been conserved across their respective clades, these systems have likely been maintained for hundreds of millions of years.

Computational modeling suggests that the minimal requirements for a stable head direction network are very modest: with appropriate tuning, continuous ring-attractor dynamics can, in principle, emerge with as few as four neurons [107]. If we imagine the earliest bilaterian animals possessing only simple sensorimotor control architectures, akin to a Braitenberg vehicle [108], that allowed them to turn in response to an external stimulus, then the evolution of a head direction circuit would involve adding only an angular integrator to continuously track orientation. The result of this evolutionary change would be to shift the animal from transforming sensory input directly into a turn to representing its own head direction when making a turn.

Once established, a head direction circuit has intrinsic flexibility. Head direction systems are agnostic to sensory modality, capable of integrating diverse inputs—including vision, proprioception, mechanosensation, efference copies, or even stereo olfaction [31, 109–112]. An ancestral nervous system could exploit whatever spatial cues were most reliable in its ecological niche and could evolve to exploit other cues or even other senses without changing the core head direction circuit. All that would be required is for the spatial component of an additional sense to become an input to the head direction circuit.

Other candidates for early representations

The head direction circuit we described provides only an internal representation of head direction. On its own, it is not sufficient for robust heading maintenance, representing travel direction, or monitoring current position relative to a starting position. However, without a head direction representation, all of these are impossible. We argue, therefore, that the head direction circuit evolved before these other capacities and, in doing so, enabled the subsequent evolution of these functions.

What kinds of evidence would falsify our proposal that head direction was the earliest neural representation of space? Several lines of evidence could, in principle, challenge our hypothesis:

(i) evidence of an animal that possesses another internal spatial representation without a corresponding head direction representation; (ii) evidence of a nervous system in which the computation of head direction is derived from or dependent on another spatial representation; (iii) developmental evidence showing that a head direction representation emerges only after (and especially if it is contingent on) the development of another spatial representation; and (iv) evidence that head direction and another spatial representation emerged together as part of an integrated circuit innovation, rather than in a sequential manner.

Are there any other candidates in the nervous systems of simple invertebrates that could be considered as an evolutionary earlier neural representation of space? One contender could be a representation of a 'goal direction' [19,97,113–115], defined as the direction toward some goal that cannot be detected by the animal in its immediate sensory environment. At first glance, this might seem more fundamental even than head direction. If navigation presupposes a target, might a representation of goal direction have preceded head-direction coding? But a goal direction has little behavioral value unless the organism can determine its orientation relative to that direction, and such a comparison would rely on a representation of current heading. In other words, a goal-direction vector presupposes a head-direction reference frame. Without a head-direction system, there is nothing against which a goal direction can be computed.

An alternative spatial system that does not require a head direction representation and could be implemented in an early nervous system is visual scene recognition [116]. In such a system, the animal can orient by matching the current view to a stored snapshot, steering to reduce the difference between the two. However, this does not require the learned visual scene to stand in for anything in the absence of direct sensory input. The stored view would function as a template, not as a representation. Given the dynamic interplay between the use of head direction (i.e., in path integration) and visual image recognition in insects [117–120], alongside the conserved nature of the brain areas involved [57,103,121], it is probable that these systems evolved in parallel, at least in arthropods.

We end by noting that neither functional dependency nor developmental precedence provides definitive evidence of evolutionary sequence. A circuit that is hierarchically upstream in computation need not have evolved earlier; components of an integrated navigation system could, in principle, have arisen together within a single evolutionary transition. Likewise, differences in ontogenetic timing may reflect developmental constraints or construction logic rather than phylogenetic order. Our interpretation, therefore, rests not on any single line of evidence but on the convergence of computational simplicity, anatomical distribution, hierarchical organization, and developmental precedence, which together make head direction a parsimonious candidate for an early-evolving spatial representation.

Concluding remarks

Head direction is a neural representation with origins that seem to extend to the Cambrian period, and evidence suggests that it is foundational to all other representations required for spatial navigation. For these reasons, we argue that head direction is a strong candidate for the first neural representation in animal brains—potentially marking the first occasion the animal nervous system represented a spatial component of the world.

A major question lies in whether head direction circuits in vertebrates and arthropods share a common origin or whether they arose independently (see [Outstanding questions](#)). This is important because, if these circuits are conserved, then by implication their common ancestor (perhaps the legendary urbilaterian) had a head direction circuit. Indeed, recent work suggests that the

Outstanding questions

Do head direction circuits in vertebrates and insects share a common evolutionary origin, or did they arise independently?

Do other major lineages with complex central brains, such as cephalopods and onychophorans, possess a head direction circuit, and, if so, how is it implemented?

What is the circuit architecture of the mammalian thalamo-hippocampal head direction network?

Do head direction neurons in the mammalian dorsal tegmental nucleus project to the interpeduncular nucleus and receive comparable habenular inputs, as described in zebrafish?

How do head direction circuits differ between animals that use different navigational strategies or inhabit different ecological contexts?

Head direction circuits are arguably relatively easy to evolve, yet they appear highly conserved across evolution. Are homologous circuits truly conserved in connectivity and function, or do they differ more than their anatomy suggests?

zebrafish ring attractor shares key computational and organizational features with that of the fly [31,68,70,71,76,122]. However, comparable circuit-level evidence is largely lacking for other vertebrates, particularly mammals. If the vertebrate head direction circuit ultimately proves to implement a different attractor class [34], this, along with differences in the neurochemical identities of head direction circuit cell types [31,51,72], may suggest that ring attractor circuits, as part of a head direction representation, have evolved more than once. Resolving the evolutionary origins of head direction representations will further require comparative analyses in early-diverging vertebrate lineages and in non-dipteran arthropods. Functional investigation of specific neuron populations will be essential but remains restricted to species in which genetic and circuit-level tools enable targeted manipulation and recording. Comparative connectomics [37] therefore provides a promising and broadly applicable starting point for tracing the evolution of head direction circuits across animal brains.

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Declaration of interests

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