or auditory beacons, the earth's magnetic field, or (as we have just learned) declination. It can be radial, or orthogonally bicoordinate, or have oblique axes. Worse, the cue choices and strategies often change with age or context [1].

Happily there are unifying trends. Most migrating birds travel singly and at night. The animals learn the layout of the night sky and update it regularly to take account of the changing seasons, and (while traveling) the dramatic effects of changing latitude. They must learn the declination so that they can orient magnetically under overcast, and recalibrate this value as often as possible during migration to adjust to the change. First-year birds (traveling toward the equator in their initial Fall) fly innately encoded vectors toward their winter grounds, gathering map information en route. Subsequent journeys are efficient map-based trips with relatively precise correction for drift. In at least some species, the target zone for that first trip is innately encoded with considerable precision, as demonstrated by particular populations of first-year Alaskan birds that fly 10,000 km to a remote set of Pacific islands [8,9]. The nearly pinpoint accuracy of the return journeys to the breeding grounds probably requires careful prior learning of the local map parameters in the first summer.

The ever-lengthening catalogue of opportunistic strategies and individual choices in migration should remind us that this life-or-death task demonstrates the power of natural selection to create ad hoc navigational solutions to supplement a basic orientational armory. But even as the dust begins to settle on the mechanistic 'how' questions, there remains an equally intriguing 'why' mystery connected with these annual redeployments that now deserves much more attention: what is the evolutionary logic that rewards the survivors of a life-threatening twice-yearly endurance test with much higher reproductive success compared to closely related species that remain in the tropics or the southern temperate zone all year? [1].

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Place Cells: Knowing Where You Are Depends on Knowing Where You're Heading

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Knowing where you are and knowing where you are heading are both necessary for navigation. Does knowing where you are depend on knowing where you are heading, or is it the other way around? A new study suggests that knowing where you are heading allows you to know where you are.

Understanding how motile animals navigate in large-scale environments is a significant intellectual challenge, with implications extending across many domains from biologically-inspired mobile robots to human dementia patients suffering from disorders of orientation and spatial knowledge. Navigation by animals and humans was posed by Tolman [1] as a psychological and behavioural question — do we possess flexible cognitive maps of space that drive our behaviour? — a view directly counterposed to Hull's theory [2] that we learn specific response sequences supporting navigation. The behavioural data favoured Tolman's cognitive map theory, as did supporting theoretical analyses by Hebb [3] and Lashley [4].

John O'Keefe's discovery of place cells [5], neurons in the hippocampal formation

which fire because of where you are, rather than their firing depending on what you are doing, inaugurated in large part the modern age of cognitive neuroscience. Here, in a tractable and accessible brain system (the hippocampal formation), were the elements of a major cognitive question: how we construct maps of our world in order to navigate, learn about, and remember, our world. Inscribing the cognitive map directly onto a brain structure was revolutionary, and remains so.

The subsequent discovery of head direction cells in the rat dorsal presubiculum, by James B. Ranck Jr. [6], showed that the brain codes for heading direction in a compass-like fashion, independent of positional information. The discovery of head direction cells led directly to the question of whether or not place coding by the brain depends on directional coding or *vice versa*, a question which to date has lacked an empirical answer. A new study by Harland *et al.* [7], reported in this issue of *Current Biology*, provides the likely answer. They show that input from the head-direction system is required by hippocampal place cells in order for place cells to discriminate between identical-looking rooms of differing orientations. Removing this directional input results in place cells not discriminating between locations. Directional information provided by the head direction system is the key input allowing place cells to resolve differences in visually-ambiguous locations in space.

One of the oldest approaches to study brain function is the lesion technique [8]. Combining circumscribed damage to defined brain structures or regions with careful behavioural analyses has yielded much regarding structure–function relations in the brain. Harland *et al.* [7] have combined the lesion technique with behavioural neurophysiology in a very promising way, resulting in new insights into how the place signal is generated in the hippocampal formation. In a previous paper [9], this group recorded place cells in freely-moving animals navigating between visually-identical chambers. When these chambers are laid out in a parallel fashion, with the same orientation in each chamber, place cells fire in much the same location in each chamber. No surprise there: the locations are visually identical. But when the visually-identical chambers are laid out at angles to each other, place cells can now discriminate between the boxes. The place cells now show a differential pattern of activity, depending on which box they are in. How do they do this? One potential answer lies in the head direction system, which might provide heading information that resolves the difference in the location of otherwise visually-identical places.

The logically necessary experiment is to remove the head direction input to the hippocampus, while simultaneously recording the activity of hippocampal neurons. Harland *et al.* [7] therefore employed a combination of lesions and recording of neuronal activity. Injections of the neurotoxin, ibotenic acid, were placed in the lateral mammillary nuclei bilaterally, giving rise to substantial destruction of neurons within these nuclei (while having no effect on fibres of passage that might traverse these nuclei). The lateral mammillary nuclei possess head direction cells, and these nuclei project directly to the hippocampal formation. These same animals also had recording electrodes implanted in hippocampal area CA1.

The question, then, is of the likely effect of removing a principal source of head direction information will have on the activity of place cells. Several predictions are possible, from a complete loss of place-related information, to more subtle changes in place coding by place cells. Harland *et al.* [7] disconfirmed the first prediction: place cells continued to fire normally, and showed the usual pattern of replicated firing in visually-identical, but parallel, boxes. But when recordings were made of place cells in identical boxes that were placed at angles to each other, place cells no longer distinguished between the differing boxes. They show instead a pattern of 'omnivorous' firing, where place cells are no longer able to discriminate identical chambers which differ only by a single dimension — their orientation in space. By contrast, place cells in sham-lesioned animals reliably disambiguate and differentiate between the visually-identical boxes laid out at angles to each other.

Notably, other brain regions are left intact after the lesions of the lateral mammillary nuclei. Entorhinal cortical grid cells [10], which are thought to provide a metric for extended space, are unaffected, and their inputs are seemingly unable to resolve the orientation-coding problem now encountered by hippocampal CA1 place cells. There is also a substantial population of head direction cells in nucleus reuniens of the thalamus [11]. Nucleus reuniens sends a substantial physiological and anatomical projection to hippocampal area CA1 [12]. It is not known if the nucleus reuniens head direction cells are affected by the lateral mammillary nuclei lesions. If they remain unaffected, the conclusion that nucleus reuniens head direction cells must not, therefore, participate in resolving the locational ambiguity follows, and the functional significance of reuniens head direction cells requires further investigation.

Head direction cells (see Grieves and Jeffery [13] for review) are found in at least nine brain regions, from the lateral mammillary nuclei, through the anterior thalamus and even the claustrum and neocortex. This contrasts markedly with place cells, which have so far been found in just two extra-hippocampal formation locations (the rostral thalamus and claustrum, both of which project to the hippocampal formation). Grid cells have been found in just two regions (medial entorhinal cortex and parasubiculum), both of which also project to the hippocampal formation. Head direction cells might also be found in other locations, yet to be explored. These await discovery by brave neural cartographers willing to explore beyond the usual hippocampal formation regions.

Why are so many brain regions concerned with coding head direction? One possibility is that head direction cells provide important, subtle, not yet understood but relatively ubiquitous contributions to cognition, especially where cognition is associated with imminent action selection. The form of action of selection might vary, but the position of the head must be central to the action to be performed. In the case of the rodent, this might be relatively simple aspects of behaviour involved in attending, selecting and locomoting down a maze arm. It might equally be the coding of mutual head direction trajectories during complex social behaviour (such as mutual nuzzling or fighting), where head position and direction is central to the behaviour. In both nuzzling and fighting, the rodent

must predict the head position and trajectory of the conspecific. During nuzzling, mutual comfort and nurturance is offered via directed head movements, whereas during fighting, head direction is central to biting and avoiding being bitten. The time-scales of these behaviours are sub-second; anticipation, selection, and action must take place rapidly and quickly in order to be behaviourally adaptive. Having head direction signals in close proximity to brain regions concerned with action allows this possibility.

A major challenge in brain science is relating the activity of ensembles causally to behaviour. Harland *et al.*'s [7] work makes a major, and to be tested, prediction: that the loss of the head direction system, in circumstances where animals are required to disambiguate visually-identically places in order to obtain reward, should leave their choice behaviour at chance. Establishing these causal chains will bring us closer to answering the question of how the brain supports behaviour.

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Centrosome Biology: Polymer-Based Centrosome Maturation

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The molecular mechanisms that control how the centrosome increases in size and microtubule nucleation capacity during mitosis have remained elusive. Recent work using *in vitro* assays provide exciting clues as to how this may occur.

Centrosomes play an important part in many cell processes, including the establishment of the mitotic spindle during cell division. They are formed when pericentriolar material (PCM) is recruited around the mother centriole [1,2]. Several hundred proteins are thought to be concentrated in the PCM, and these include major cell cycle regulators, signaling molecules and proteins involved in nucleating and organizing microtubules [2,3]. How the PCM is assembled so as to create a functional organelle remains a key question in centrosome biology.

During interphase, the centrioles in many cell types organize relatively small amounts of PCM, which is arranged as a ~200 nm toroid [4–7]. During mitosis, the PCM appears to retain some of its organizational properties [4] and undergoes a dramatic expansion to reach several microns in diameter, with a concomitant increase in microtubule nucleation capacity (termed centrosome maturation). Current models propose that the expansive mitotic PCM serves as a catalytic platform for γ-tubulin-containing complexes to induce microtubule nucleation [1,2,8].

How does the mitotic PCM scaffold form? The catalogue of PCM proteins in various organisms is diverse in number