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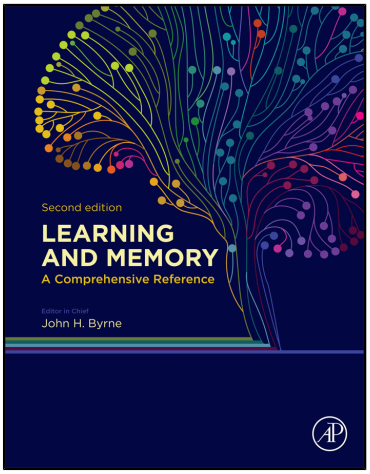

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3.13 Spatial Memory

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3.13.1	**Introduction**	209
3.13.2	**Historical Overview**	209
3.13.3	**Self-localization**	210
3.13.3.1	The Sense of Direction	210
3.13.3.1.1	Ethological and Behavioral Studies of the Direction Sense	210
3.13.3.1.2	The Head Direction Cells	211
3.13.3.2	The Sense of Place	212
3.13.3.2.1	The Cognitive Map	212
3.13.3.2.2	Landmarks and Geometry	214
3.13.3.2.3	The Place Cells	215
3.13.3.2.4	The Grid Cells	217
3.13.3.3	Path Integration	217
3.13.4	**Navigation**	219
3.13.4.1	Homing	219
3.13.4.2	Goal-Directed Navigation	219
3.13.4.3	Route Planning – Detours and Shortest Paths	220
3.13.4.4	Neurobiology of Spatial Inference and Planning	221
3.13.5	**Complex Space**	222
3.13.5.1	Large-Scale Space	222
3.13.5.2	Multicompartmented Space	223
3.13.5.3	Three-Dimensional Space	225
3.13.5.3.1	Moving Over a Surface	225
3.13.5.3.2	Moving Through a Multilevel Environment	226
3.13.5.3.3	Moving Through a Volume	226
3.13.6	**The Future**	227
References		227

3.13.1 Introduction

The study of spatial memory is deeply interwoven with the study of memory generally, but it has the added ingredient of space, which is a fundamental property of the universe and one which the brain is especially adapted to process. Space adds, over and above perception and memory, two properties of importance—one is *relatedness* (things can be between other things, or above and below them, etc.) and the other is *metricity*—it is possible to specify the distance, linearly or angularly, between things, either broadly (near vs. far) or precisely (number of meters/degrees, etc.). The relational and metric aspects of space are abstract properties that need to be deduced by combining incoming sensory signals, and it took psychologists a long time to accept that the brain can accomplish such high-level inference. What has finally convinced most researchers has been the discovery that the brain represents the metric properties of spatial relations to a high degree of precision: findings that have well and truly validated the so-called cognitive revolution. The task now is to uncover exactly *how* these properties of space are discovered, represented, and used by the brain. This chapter will review the previous and current states of the field of spatial processing, focusing mainly on mammals, and will explore how behavioral and neurobiological investigations have collaborated toward uncovering the mechanisms of spatial cognition.

3.13.2 Historical Overview

Space and memory go hand-in-hand, and even in ancient times it was recognized that space could be a useful organizing principle for memories, as with the renowned "method of loci" of the Greek and Roman orators (Yates, 1966). In the early years, scientific discoveries relating to spatial processing mainly involved observational research, categorizing the types of navigation that humans and animals are capable of. During this time, some remarkable feats of spatial performance were uncovered including the long-range migration (from—oddly—one pole to the other) of the Arctic tern (Austin, 1928), the ability of displaced animals to find their way home across sometimes hundreds of miles of unfamiliar terrain, and the ability of food-storing animals such as squirrels to retrieve thousands of cached seeds and nuts from their winter stores (Vander Wall, 1990).

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Toward the end of the 19th century, psychology slowly began to coalesce as a discipline and thinkers such as William James began to consider how knowledge, including spatial knowledge, might be processed by the brain. James is remarkable for his prescient and still-valuable insights about memory: in particular, he advanced one of the very first connectionist hypotheses. Connectionism is the doctrine that proposes storage of information in networks of neurons interlinked by modifiable connections. James wrote, "Memory being thus altogether conditioned on brain paths, its excellence in a given individual will depend partly on the number and partly on the persistence of these paths" (James, 1890). This idea was later developed by neuroscientists such as Pavlov, Cajal, Konorski, and Hebb (see Cooper, 2005 for review) into the formal proposition that memory occurs when networks of neurons change the strengths of their connections as a result of coactivation resulting from (usually repeated) experience. The so-called "Hebbian learning" has been central to many neural models of memory formation, and this is as true in the domain of spatial cognition as for other forms of cognition. Indeed, it was later discovered that the hippocampus is the foundation for both spatial representation *and* memory, and it thus became the principal focus for neuroscientific research into both of these domains.

In the early 20th century, psychology steadily gathered strength as a discipline and began to formalize the study of behavior. Owing to the crucial insights of Pavlov concerning association formation in the so-called conditioning paradigms (Pavlov, 1927), the framework for thinking about thinking, as it were, was for many years an associative one. By this view, learning and memory consist of new associations formed between stimuli and other stimuli, or stimuli and responses, and knowledge can thus be thought of as a complex but shallow network of input–output connections. The so-called behaviorist paradigm held sway for decades, and it successfully shifted psychology from the somewhat magical thinking of the late 19th century such as phrenology (Simpson, 2005) or introspection (Danzinger, 1980) to the very empirical, data-driven approach that characterizes it today. However, some experimental findings were not easily accommodated within a straightforward behaviorist framework because they seemed to suggest that animals might form internal representations that could be operated upon relatively independent of the animal's past experience, and sometimes without apparent changes in behavior (so-called "latent learning").

Spatial representation became the battleground for debate between the behaviorists and the so-called cognitivists, who maintained that the brain does indeed form internal representations of the world upon which it can perform what amount to simulations of possible actions. The catalyst for these debates was Tolman's work on maze learning in rats, detailed later, in which he showed that the animals can compute shortcuts and detours, which they should not be able to do if knowledge depends on experience alone. Tolman proposed that animals have an internal map of space, a "cognitive map," and thus laid down the initial framework for what we now call cognitive psychology.

The next major leap forward in spatial cognition research came toward the middle of last century when neurophysiology began to develop and to move from the in vitro preparations of Sherrington, Katz, Hodgkin, Huxley et al. (Berlucchi, 2010) to the in vivo study of whole animals. Hubel and Wiesel conducted pioneering research into the physiology of the visual cortex in cats, making the first links between neural activity and perception (Wurtz, 2009). A decade later, Ranck, O'Keefe and others began to apply similar techniques to other parts of the brain and to move from anesthetized animals to awake, freely moving ones. It was this advance in technology that led O'Keefe to discover that neurons in the hippocampus become active when the animal goes into particular locations in the environment, thus linking neural activity not just to perception but to something far more abstract. He and Nadel proposed that the hippocampus is the site of the mammalian cognitive map (O'Keefe and Nadel, 1978).

The notion of a "cognitive map" in the hippocampus was no more palatable to behaviorists than it was in Tolman's time, and the idea met with skepticism (Morris, 2015). However, in the ensuing decades, the idea that place cells are part of an internal representation of space has now reached general (if not universal) acceptance. The question now is how this representation is made and used; topics that are the focus of the remainder of this chapter.

3.13.3 Self-localization

Spatial behavior has two broad subcomponents: self-localization (working out one's current position and facing direction) and navigation (deciding where to go and how to get there). Although these faculties are obviously closely related, they can be distinguished, and so we will first look at research concerning self-localization, and then in the next section will look at navigation. Position and direction can be somewhat dissociated, and we will begin with direction as it is one-dimensional and arguably more fundamental.

3.13.3.1 The Sense of Direction

Knowing one's facing direction is a core navigational competence. It is often called "heading," but this term is sometimes also used to mean direction of travel, which is related but not quite the same thing (Raudies et al., 2015). On the horizontal plane, global head(ing) direction is also often called "azimuth," which is a term used by human navigators and astronomers. Here, we will use "head direction" or "direction" to refer to local direction, and "azimuth" to refer to global direction on the horizontal plane (used later in the discussion on three-dimensional (3-D) navigation).

3.13.3.1.1 Ethological and Behavioral Studies of the Direction Sense

As long ago as 1873, Darwin recognized that the brain probably has an innate ability to compute heading. In a *Nature* article entitled "Origin of certain instincts" he wrote, "The manner in which the sense of direction is sometimes suddenly disarranged in very old

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and feeble persons, and the feeling of strong distress which, as I know, has been experienced by persons when they have suddenly found out that they have been proceeding in a wholly unexpected and wrong direction, leads to the suspicion that some part of the brain is specialised for the function of direction" (Darwin, 1873). In the subsequent decades, many examples of the remarkable sense of direction of a variety of animal species were uncovered, most astonishing (due to the tiny size of their brains) being the directional abilities of insects. Von Frisch, for example, observed that honeybees (*Apis mellifera*) compute the direction between the hive and a food source, and in an elegant and ultimately Nobel-prizewinning series of experiments showed that they can convey both the distance and the direction (independently) of this source to their hive mates, via the remarkable waggle dance (von Frisch, 1974).

Initial studies of the sense of direction focused on the nature of the sensory information used by animals. In many spatially competent species from a variety of taxa, the Earth's magnetic field is an important cue to global direction (Wiltschko and Wiltschko, 2005). Animals can extract direction from the magnetic field in two ways – they can use its polarity (north vs. south) but they can also use inclination, since magnetic field lines angle toward the Earth's surface as one heads toward the poles and away from it heading toward the equator. Magnetoreception has been most extensively studied in birds but has also been seen in some mammals—for example, the blind, borrowing mole rat – also have the capacity to sense magnetic cues (Kimchi et al., 2004). It has not been convincingly demonstrated, however, in either rats or humans. As yet, the biological basis for processing of magnetic directional cues remains unknown and much-disputed, which has precluded lesion studies and other more traditional methods of biological investigation.

At least as important, if not more so, for geocentric (Earth-referenced) directional orientation are the celestial cues provided by the sun and stars. Many species use a "sun compass," for both local and long-range navigation (Schmidt-Koenig, 1990). A famous experiment by Santschi (1911) showed that ants would change the course of their journey of the apparent position of the sun was deflected by a mirror, and Kramer, using the same technique, showed that birds use a sun compass for migration (Kramer, 1950). Von Frisch showed that honeybees reference the direction of their waggle dance to the sun – the direction of the straight leg of the dance relative to gravity (i.e., vertical) matches the direction of the food patch relative to the sun. An important feature of celestial cues is that they change presence and direction throughout the day, and so an animal needs a "time-compensated compass" (Lindauer, 1960), although exactly how this might be achieved is still debated (Guilford and Taylor, 2014).

Many animals do not rely on global cues (geomagnetic or celestial) but rather on local cues provided by the immediately surrounding environment. These cues have broadly been divided into those that are focal (object-like) which are usually called "landmarks," and those that are more extensive and bound the environment—"boundaries"—and which confer a shape, or geometry, to the environment, which may or may not be directionally informative.

The majority of experiments studying local cue use have been conducted in rodents—mainly rats—and one reason for this has been the discovery of neurons in the rodent brain that encodes for direction, known as head direction cells. This extraordinary finding has opened up a critical window into the processes underlying spatial cognition. The next section describes the head direction cells and looks at how studies of these neurons under conditions of environmental manipulation have shed important light on the processes underlying directional orientation (at least in mammals).

3.13.3.1.2 The Head Direction Cells

The head direction cells were the second class of spatially responsive neuron to be discovered in rodents – place cells were the first, but we describe head direction cells first here because the sense of direction is both simpler and more fundamental, and the insights derived from this system have been informative for understanding the "sense of place" too. These neurons were first reported by Ranck, who was one of the first neuroscientists to successfully record single neurons from the brains of freely moving animals. Motivated by O'Keefe's recent discovery of place cells in the hippocampus, he was investigating the parts of the brain afferent to hippocampus and found, in the postsubiculum (also called dorsal presubiculum), a preponderance of neurons whose firing markedly increased when the animal faced in a particular direction (**Fig. 2A**). He published an abstract reporting their discovery in 1984 (Ranck, 1984) and set his then-postdoc Taube onto the task of characterizing these neurons. In 1990, they copublished a now-classic pair of papers, reporting the detailed physiology of the head direction neurons (Taube et al., 1990a), together with an investigation of their responsiveness to environmental manipulations (Taube et al., 1990b). In the years since, Taube and colleagues have traced the connections of the postsubicular head direction neurons and uncovered a wide-ranging and complex circuit that includes both low-level brainstem structures and high-level cortical ones (Taube, 2007).

Each head direction cell has its own preferred firing direction, and the population together encompasses (as it were) the entire 360 degrees of horizontal space (we will come to vertical later). One notable feature of the system is the fact that the signal, which is one of the sharpest tuning curves produced by neurons anywhere in the brain, is highly coherent – that is, neurons everywhere in the circuit seem to "agree" about which way the animal is facing at any one time (Yoganarasimha, 2006). Any manipulations to the environment or the animal itself that distort its processing of direction affects all the cells together, and it has not previously been possible to shift the firing direction of one cell without shifting those of all the others as well. This high degree of coherence has led to proposals that the network has interconnections, ensuring that a given cell is driven not only by incoming sensory signals but also by the activity of other head direction neurons in the circuit (Skaggs et al., 1995; Zhang, 1996). This type of network is called a "ring attractor," and in principle it provides a way to update the signal as the animal turns its head to face a different direction – all that is needed is some mechanism that couples a turn of a particular direction with a shift of activity of a particular amount "around" (in conceptual terms) the attractor network.

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Studies of how head direction neurons process information about direction yield important insights as to how the animal as a whole does so. The original papers showed the importance of visual landmarks in establishing the signal when the animal first enters a familiar environment, which in the behavioral literature is a process known as "reorientation." Soon afterward, it was shown that "internal" cues—those that are carried with the animal and track its movements—are also major contributors to the signal. This was first convincingly demonstrated by Taube and Burton (1995), who recorded head direction cells as rats exited a familiar environment, which was polarized by a landmark (a cue card), and proceeded along a short corridor to a novel room. Although there was no visual overlap between the rooms, the cells adopted the same orientation in the novel room (and also in the corridor) as they had in the familiar room, indicating that the rat's "sense of direction" was able to bridge the visual gap between the two rooms. If the signal was misaligned by rotating the cue card, it realigned again as soon as the animal entered the adjacent, previously novel, chamber, indicating that once the visual cues had been experienced, they could now control the direction signal. From this, two important conclusions about the sense of direction emerged: (1) internal cues can bridge periods of time when landmarks are unavailable and (2) landmarks are learned about quickly. The nature of the internal cues is currently being elucidated: a priori it was assumed that it would be some combination of vestibular cues to angular acceleration, optic and other sensory flow cues to angular velocity, proprioceptive cues to head and body turns, and motor efference copy signaling motor commands to head and body turns, that could forewarn the system about impending direction changes. These types of information are sometimes collectively called *idiothetic*, although "self-motion" is more common. So far, studies manipulating vestibular and optic flow cues have confirmed the use of these cues (Blair and Sharp, 1996); the others still remain hypothetical.

The head direction system provides a window into the animal's thoughts (or at least, its thoughts about which way it is facing), which is potentially useful to the psychological study of orientation. However, it has been relatively difficult to make links between head direction cell activity and behavior in the laboratory, with several instances of disjunction between behavior and the head direction signal (see Muir and Taube, 2002 for discussion and examples). This may be because animals can use several different strategies to solve a task, and in fact recording of neural activity as they navigate can shed light on the complexity of the underlying processes. For example, in the geometric reorientation paradigm of Cheng (1986) discussed later, animals might search in geometrically equivalent locations because they mistakenly think that food is found in two places, or because they know it is in only one location but are unsure which direction is which. Recording of head direction cells in these and other paradigms could answer this question (see Jeffery, 2010 for a fuller discussion of these issues). In this vein, a study of head direction cells in enclosures of different geometries found geometry to be only a weak cue, far less informative than focal cues (Knight et al., 2011), lending support to suggestions that the main contribution of geometry is by provision of visual snapshot information (Cheng, 2008). Future work recording head direction cells under conditions of cue manipulation can resolve ambiguities about how the animal thinks it is oriented versus where it thinks the goal is.

3.13.3.2 The Sense of Place

Knowing the direction to salient places in the environment can be useful to an animal, but as a representational mechanism it is limited because each new place that was encountered would need to be linked with all the other places. A better alternative, if the brain can manage it, is to make a map-like representation in which each place is encoded in some kind of coordinate system – then, each new place just acquires its coordinates. Navigation in this case would require consulting the map to determine the relative locations of the start and goal positions and then computing a vector between them. Much work in psychology in the past several decades has focused on the issue of whether the brain makes such a map, known as a cognitive map.

3.13.3.2.1 The Cognitive Map

The cognitive map concept has been highly contentious for many decades: part of the problem has been that the experiments on which it was originally based were not well conducted by the standards of today and have not been convincingly replicated. Despite this, the belief is now well ingrained that even animals like rats are able to consult a map-like representation to plan navigational behavior.

Tolman introduced the idea of the cognitive map following a set of experiments on maze learning in rats (**Fig. 1**), which he detailed in a renowned article with the (now-dated sounding) title "Cognitive maps in rats and men" (Tolman and Honzik, 1948). In it, he described problem solving that seemed to go beyond simple stimulus-response learning – indeed, Tolman and Honzik ascribed it to "insight" (Tolman and Honzik, 1930). In one experiment, Tolman and Honzik trained rats to take the shortest path to a goal and then blocked off the path, leaving two alternative routes, one of which would reach the goal and one of which would not: rats were more likely to take the route that would lead to the goal, suggesting they knew about the overall layout of the maze and could flexibly adapt their behavior when things changed. This type of inference could not be explained by stimulus-response learning. In the most famous experiment, the sunburst maze experiment (Tolman et al., 1946), Tolman trained rats to execute a dog-legged path to a goal and then blocked off the path and provided several alternatives: rats were more likely to choose the alternative that led toward the goal, again suggesting they knew about the location of the goal in the room, and were not just blindly executing a sequence of learned actions. These experiments led Tolman to conclude "We believe that in the course of learning something like a field map of the environment gets established in the brain." (Tolman and Honzik, 1948).

As noted earlier, Tolman's cognitive map theory met with resistance because it challenged the behaviorist view of learning as being experience-dependent and involving simple stimulus–stimulus relationships. However, when O'Keefe discovered place cells in the rat hippocampus, as described in section The Place Cells, Tolman's ideas were reawakened, and behavioral researchers began

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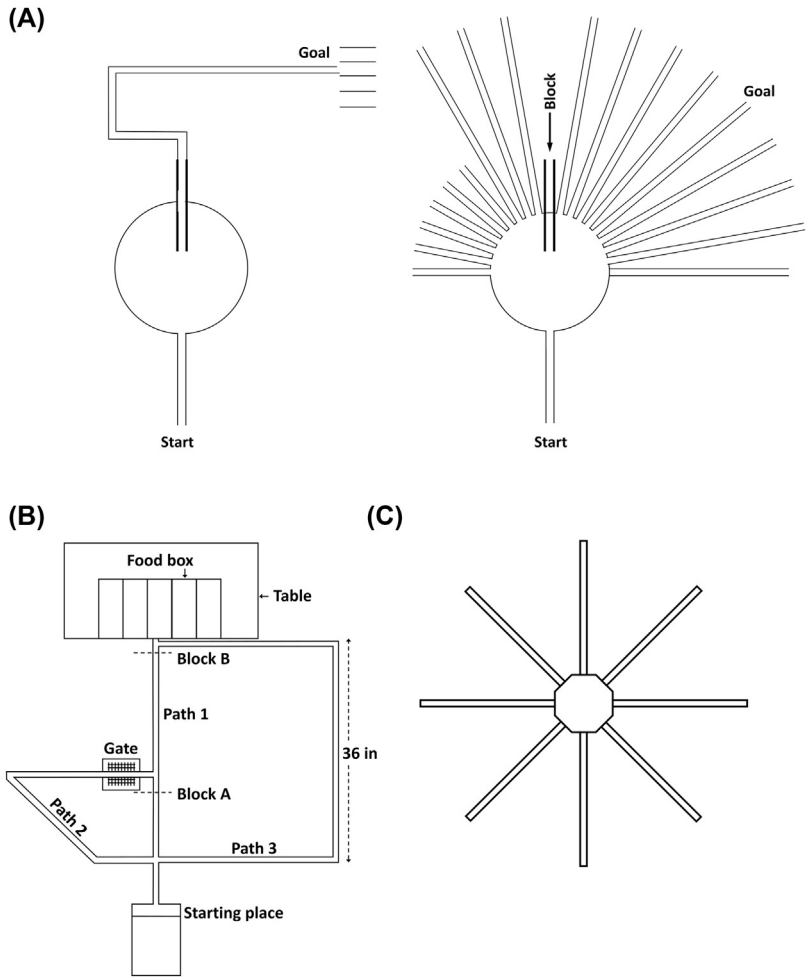

Figure 1 Linear maze–maze learning experiments. (A) The sunburst maze experiment of Tolman and Honzik (1948) – redrawn from the original. Rats were trained to take a circuitous route from the Start to the Goal. On the test trial, the training route was blocked and alternatives offered. Rats tended to take the direct arm toward the goal, suggesting knowledge of its spatial location. (B) The detour maze of Tolman and Honzik (1930) – redrawn from the original. Rats were trained along a direct route, Path 1, to a goal. When they subsequently encountered an obstacle to this route, at Block A, they tended to choose Path 2, the next-shortest route. However, when they encountered an obstacle at Block B, they chose Path 3, the only path that circumvented the obstacle. This suggested knowledge of the layout of the maze rather than trial-and-error learning. (C) The radial arm maze of Olton and Samuelson (1976) – redrawn from the original. Rats start on the central platform and retrieve food from each of the eight arms, having to keep continuous track of which they have visited and thus depleted, and which are still baited.

to take seriously once again the idea that animals might have an internal map of some sort. Decades of research and debate then followed, as the field struggled with the question of what a map is, and of whether evidence suggests that animals have one.

One thing that almost all researchers agree on is that a map encodes some kind of relational information between features in the environment – it is therefore "allocentric" (world-centered) rather than "egocentric" (self-centered). Whether these relations are metric (specified by distance and direction) or merely topological (adjacency relationships only) is open to debate and likely varies between species and situations (Geva-Sagiv et al., 2015). Also, two salient consequences of having a map have remained undisputed throughout this time: these were the ones that Tolman himself identified, namely shortcutting and detours. If animals have internal maps of space then they should be able to use these to recompute paths if they discover their usual route is obstructed, as, for example, in the Tolman and Honzik experiment. Indeed, it is this flexible usage that is the reason why a map is considered advantageous.

Some of the most impressive, and controversial, claims concerning cognitive mapping ability have come from the insect world and in particular from studies of honeybee navigation. In a famous example, which was never in fact published, honeybee foragers were trained to food on a boat in the middle of a lake (Gould, 1990) – the hive mates declined to follow the vector indicated by their dance, suggesting that they had an internal representation of the lake's location together with a representation of the low likelihood of finding food there. This experiment has been widely quoted in support of the notion of cognitive maps in insects, but the literature reporting such feats is sparse (Wehner and Menzel, 1990) and individual experiments can be refuted: for example, the lake

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experiment has not been replicated (Wray et al., 2008) – see Bennett (1996) for a detailed critique of some of the older cognitive mapping literature. The challenge for proponents of cognitive mapping is always to show that the animals could not have solved the task by a more straightforward stimulus-response method – for example, by smelling the food or following a learned olfactory gradient.

Nevertheless, the experiment was cleverly designed and has been very useful for illustrating the kinds of behavior that animals might be able to display if they do indeed have a map. Such experiments are hard to conduct, however. Finding appropriate controls is limited by the ability of human experimenters and their limited sensory capabilities to determine what to control *for* – researchers rarely appreciate, for example, the exquisite olfactory sense of animals like rats, pigeons, and dogs, nor that many animals are sensitive to ultrasound and infrasound, or electrical or geomagnetic cues.

To avoid the difficulties in controlling natural environments, researchers have relied heavily on laboratory experiments to try to discover the representational capabilities of navigating animals. For most of last century the standard protocols were linear mazes (**Fig. 1**), such as the detour and sunburst mazes of Tolman and colleagues, and the radial maze of Olton (Olton and Samuelson, 1976). The Olton maze (**Fig. 1C**) was developed to test the memory capabilities of animals, in pursuit of a task that might show the same sensitivity to hippocampal damage that the famous case of H.M. had recently revealed in humans (Scoville and Milner, 1957). It is a spoke-shaped maze, typically having 8 or 12 arms radiating from a central platform, and rats have to retrieve food from all or some subset of the arms, using experimenter-controlled cues to distinguish the arms. Olton et al. (1978) used it to demonstrate the requirement of the hippocampus for solving spatial tasks, but with linear mazes it is difficult to rule out the use of algorithmic solutions to the task, based on memory for cues and their associated actions. Indeed, Olton himself argued that the rats solved the task using working memory in a list-like fashion, without the need for spatial encoding (Olton and Samuelson, 1976). An important experiment by Suzuki et al. (1980) cast some doubt on this interpretation, however, by showing that although rats could perform the task equally well if the cues surrounding the maze were rotated *en bloc*, they could not do so if they were transposed, suggesting that the animals could not have been using the cues in a simple, list-like fashion.

However, it could be argued that the rats could instead have used lists of visual snapshots provided by *combinations* of the cues and that these snapshots were broken up by the cue transpositions. The critical solution to the list versus map debate was the introduction of a new kind of "maze" by Morris (1984), the water maze, in which rats have to swim to an unmarked escape platform hidden just beneath the water surface in a swimming pool. Morris (1981) used this task to show that rats could navigate to a specific location based only on distal cues, implying some kind of relational encoding of the cues. Hippocampal lesions were soon shown to induce a profound impairment on this task (Morris et al., 1982), providing the best support yet for the hippocampus/cognitive map hypothesis.

3.13.3.2.2 Landmarks and Geometry

How is the cognitive map (if there is one) constructed and from what information? In theory, one could make a map of completely featureless terrain, like the delightful "perfect and absolute blank" in Lewis Carroll's (1876) *Hunting of the Snark*, given only a source of directional information and a single fixed point. In reality, spatial representation in animals and humans makes use of arrays of landmarks in the environment. Considerable research has investigated *how* landmarks are used in navigation (see Tommasi et al., 2012 for review), but there is not a consensus, and in fact they are probably used in several different ways.

A single landmark can provide useful information provided, as mentioned earlier, there is also a source of directional information. Without a directional reference, places could be distinguished based only on their distance from the landmark, whereas with one, any point can be uniquely specified as being at a particular distance from the landmark in a given direction. This type of self-localization need not require a cognitive map: indeed, Pearce et al. (1998) found that rats with hippocampal lesions (and hence, supposedly, deprived of a cognitive map) could learn to swim to a point located at a fixed distance and direction from a landmark.

Although a single landmark can be informative, animals can also make use of arrays of landmarks, as shown by Tinbergen's classic demonstration that digger wasps used a landmark array to locate their nest (Tinbergen, 1951). With more than one landmark, additional factors come into play such as whether or not they can be identified based on visual and other sensory qualities. If there is a directional reference then the landmarks need not be discriminable, because they can be distinguished based on their relative locations and directions. With two identical landmarks, for example, positions can be specified relative to either or both. The literature on whether animals specify positions relative to either or both is somewhat mixed – a landmark (as it were) study of gerbils by Collett et al. (1986) found that when a pair of identical landmarks was separated, the animals searched at the two locations given by the vector of the original goal to each landmark independently, instead of halfway between the landmarks as in the original training condition. This shows that the animals encoded vectors to the individual landmarks but does not reveal whether they knew about the relationship between the landmarks. However, studies of search in situations where a landmark array has been expanded reveal a preference for search at absolute distances from landmarks (Gray and Spetch, 2006; Kelly et al., 2008; Potì et al., 2010; Marsh et al., 2011).

If landmarks are different from each other, which is usually the case in nature, then there is the additional problem of identifying them based on object processing. This is an ancient and widespread capability – even bees, for example, can remember the order of experienced landmarks and use these to estimate distance traveled (Chittka et al., 1995), showing a sophisticated discrimination ability, as well as a degree of spatial encoding. With nonidentical landmarks there is now in principle no need for a separate directional reference, because two distinguishable landmarks by themselves define a unique directional reference frame. It remains to be seen, however, whether even vertebrate brains can actually use this information, because head direction cells prefer distal landmarks to proximal ones (Zugaro et al., 2001), and in theoretical terms, the problem of extracting a stable directional reference from objects

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that can be walked around (and which therefore constantly change their relative direction) is complicated to solve. With more than two, distinguishable, landmarks there is the possibility for complex relational encoding of the locations of the landmarks with respect to each other – so-called allocentric encoding. Landmark recognition and the use of landmarks for spatial orientation can be functionally dissociated – patients with topographical amnesia, for example, frequently report intact landmark recognition in the face of a complete inability to use these landmarks for orientation (Aguirre and D'Esposito, 1999).

One thing that landmarks can help to do is define a geometric subdivision within a larger space. The simplest such area is the triangle formed by three noncollinear landmarks, and it has been suggested that such triangular regions, or "fragments," might form the units of a mosaic-like spatial representation (Worden, 1992). By this view, the line between two landmarks forms a virtual boundary – a related idea is that actual boundaries define environmental fragments, and the shape, or geometry, of these fragments can be used in navigating.

Considerable research has focused on the extent to which geometry—whether imposed by landmarks or boundaries—is a useful spatial cue for animals. The notion that animals—or at least rats—prioritize geometry when assessing environmental spatial cues first reached prominence following a report by Cheng (1986) that rats in a rectangular enclosure used geometric cues provided by the shape of the corners (i.e., whether long wall is left or right) in preference to the more informative but nongeometric cues that were provided by differentially colored walls and by patterned panels in the corners. This meant that they made errors, since there are two of each corner type but only one of each panel type. According to the associative accounts of learning prevalent at the time, this finding was hard to explain since the visual cues should have been rewarded more reliably and therefore learned about preferentially. Cheng postulated on the basis of these observations that geometry is a "module" in the brain. Modularity is a concept introduced by Fodor (1983), who proposed that cognitive architecture is composed of subsystems that are domain-specific (specialized, for example, in geometric processing) and "encapsulated" (operate independently and are impervious to other types of information). According to Cheng's proposal, geometry is a module in the spatial representation, used by the rats preferentially and impervious to the featural information that could have disambiguated the corners.

Cheng's (2008) geometrical module hypothesis stimulated a great deal of research, but he himself eventually abandoned the idea in a refreshingly humble review of the literature. While it is true that rats sometimes use geometry preferentially, sometimes they do not (Graham et al., 2006), and the parameters that influence cue use can be variable (see Cheng and Newcombe, 2005 for a detailed review). Also, geometry is a weak cue for head direction cells and only reorients them when no other cues are available (Knight et al., 2011). In humans, studies of children reveal that sometimes they prioritize geometry over featural cues (Hermer and Spelke, 1994), but under other conditions they do not (Learmonth et al., 2002). Thus, while geometry can be informative, it seems not to be obligatory in the way that the original modularity theory proposed. It is worth noting at this point that "geometry" is difficult (if not impossible) to examine independent of the specific cues that geometry also provides (e.g., unique snapshots of the environment from different positions, like narrow versus wide corners; McGregor et al., 2006). Thus, the question of a binary dissociation between geometry vs. local cues is slowly evolving into a question of *how* the sensory inputs coming into the brain are routed into different processing subsystems. In the next section, we look at what seems to be the final destination of these subsystems, the hippocampal place system.

3.13.3.2.3 The Place Cells

By the end of the 1960s, research had begun into the cellular basis of hippocampal function, motivated by the recently reported case of H.M. (Scoville and Milner, 1957) and the ensuing desire to understand how the hippocampus contributes to memory formation. Because the hippocampus is buried deep within the brain its neurons are not directly connected to any of the sense organs, but have been processed by at least two and usually many intermediate levels. Studies in anesthetized animals had previously found that hippocampal neurons seemed to respond to a heterogeneous vision and/or sound and/or odor, with variable reproducibility and no readily characterized sensory correlates (Green and Machne, 1955). The first studies of neural activity in unrestrained, freely moving animals began around the late 1960s and also found heterogeneity of hippocampal activity (Ranck, 1973), but then in a classic and ultimately Nobel-prizewinning study, O'Keefe and Dostrovsky reported that cells in the hippocampus fire most intensely when the rat is in a restricted region of the environment (**Fig. 2B**), suggesting that the hippocampus might be encoding "place," and they proposed that the hippocampus forms a spatial map (O'Keefe and Dostrovsky, 1971). Shortly afterward, O'Keefe and Nadel (1978) formalized this idea in a highly influential book, *The Hippocampus as a Cognitive Map*, proposing that the hippocampus is the site of Tolman's cognitive map. This idea, and indeed the notion that place cells code simply for place, created considerable controversy. Many investigators disputed that "place" is the sole correlate of activity, arguing that place encoding is part of a more general capability for "relational" or "conjunctive" encoding (Cohen and Eichenbaum, 1991). This argument persisted for many years, but recently the field seems to have settled on a compromise position in which space is fundamental to place cells but is used by the brain as an organizing principle for memory more generally (Buzsáki and Moser, 2013; Schiller et al., 2015).

The characteristic of place cells that first suggested that they respond to place, rather than to a complex combination of sensory inputs, is the fact that each cell fires in its preferred region in the environment, called the cell's "place field," regardless of the exact sensory stimuli impinging on the animal at that moment – for example, it does not matter which way the rat is facing (on the whole, although there are some situations in which place cells become directional; Battaglia et al., 2004), nor whether the room is lighted or in darkness (generally; but see Markus et al., 1994), or whether the animal is moving or standing still (with some qualifications). Thus, the neurons cannot be responding to a simple conjunction of sensory stimuli. The caveats are needed because although these other factors are not critical for place cells, they do sometimes play a role, and as time has gone on it has become apparent that the responsiveness of place cells is complex and extends beyond the mere physical location of a place.

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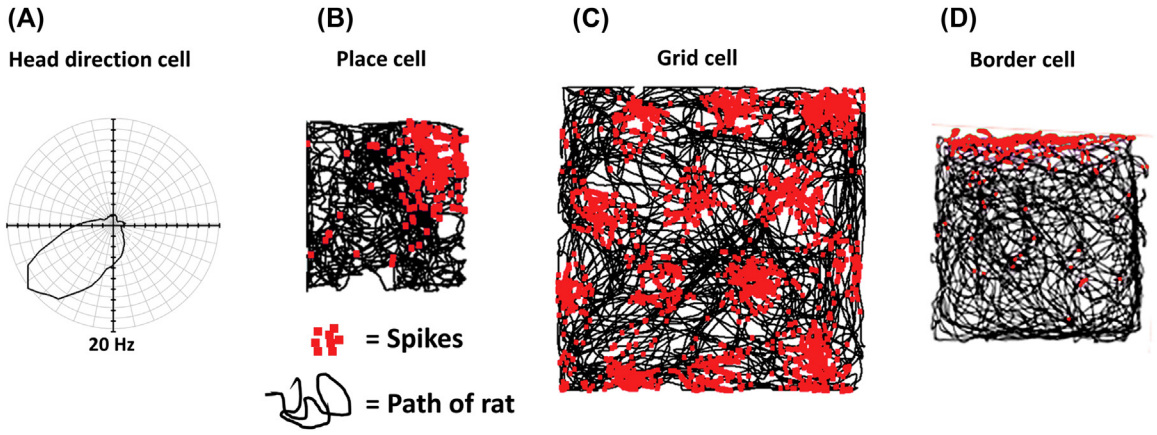

Figure 2 The four canonical spatial cell types. Adapted from Marozzi, E., Jeffery, K.J., 2012. Place, space and memory cells. Curr. Biol. 22, R939–R942.

A number of characteristics of place cells were somewhat surprising at first glance, although they have become less so as more is understood about how they operate. The first question that many people ask when they first learn of these cells is whether there is any topographical organization in the brain – do adjacent place cells have adjacent place fields, as in the visual cortex? It is an intuitively appealing notion that the map in the brain would have the same spatial organization as real space. However, the answer is no, adjacent place cells have apparently randomly distributed place fields (O'Keefe et al., 1998). While this seems odd at first, it becomes less so when one considers that the visual cortex has to deal with only one space—the retina—while the hippocampus has potentially to deal with anywhere on the planet, or even, these days, off it. Clearly, a different encoding scheme is needed for such an unconstrained domain, and it transpires that the brain has opted for a combinatorial, population coding scheme instead.

The second question is whether each cell has only one field in any environment, to which the answer is again no – each place cell will fire in many environments, and when a rat is removed from one environment and placed in a new one, about 50% of the cells active in the old environment will also be active in the new one. However, they fire in different relative locations, producing an apparently random redistribution of place fields (Muller and Kubie, 1987), a phenomenon which is called "remapping" on the assumption that the system has generated a new map for this new environment. Also, a place cell is not constrained only to have one field in an environment – they often have two or more, and as the environment increases in size the likelihood of additional fields increases (Fenton et al., 2008). As with the nontopographic distribution of place fields, it appears that the important factor is the *population* pattern of activity at a particular place.

The other surprising thing about the cells is that—at least in dorsal hippocampus where they have mostly been studied—they care relatively little about significant places in the environment such as goals. At first, it was thought they did not respond to goals at all, because an early experiment by Speakman and O'Keefe (1990) found that place cells did not follow goals on a four-arm maze when these were moved. However, as discussed in the section Goal-Directed Navigation, a slowly accumulating literature suggests there is *some* encoding of goal information, although whether the "goalness" of a goal is encoded, as opposed to the mere salience of that place, is still under investigation. Place cells also fire very intensely around doorways between subcompartments (Spiers et al., 2015), but again, it is not clear whether there is something special about the functional properties of doorways (their "affordance" for entering and leaving the place, in Gibsonian terminology), or whether it is just that doorways are rich in the type of environmental information that place cells like – particularly boundaries (see below). Place cells also often fire near objects (Rivard et al., 2004), but again, it may be a response purely to their spatial properties.

Supporting the place-encoding proposal, a significant aspect of place cell activity turned out to be its fundamentally metric nature. By this, it is meant that the cells are responsive to the relative distances and directions of environmental features, as well as to other sensory qualities. For example, if a place cell is recorded in a symmetrical environment such as a square or circular enclosure, its place field, or fields (there are often more than one), will typically be located off-center, often near one or other wall, or in a corner, but sometimes further toward the center. If the environment is symmetrical, then some kind of directional information must exist to tell the cell which wall is which. And if the field is not right next to a wall, how does it know how far from the wall the rat is? These observations lead us to the idea that there must be sources of distance and direction information carried by the inputs to the hippocampus. It was some years, however, before these sources began to be identified, beginning with the head direction cells, and followed a few years later by the grid cells. Grid cells are discussed in the next section.

An important finding to emerge from several decades of research is that, at least in rats, the boundaries of the environment are critical (the situation for animals that inhabit open spaces, such as whales and birds, is unknown at present). This was shown by O'Keefe and Burgess (1996) who parametrically adjusted the walls of an enclosure so that it "morphed" from a square to a rectangle. They found that place cells responded to these changes by morphing their fields, although not to such a large extent. Interestingly,

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different cells reacted differently to the changes, with cells tending to be most responsive to the walls nearest their fields, thus showing for the first time that place cells act as individuals rather than as a unified whole. However, subsequent tests of morphing behavior showed that under some circumstances they *do* react in a unified manner. When Wills et al. (2005) exposed rats to a square and circular environment, made sufficiently different to induce remapping, they found that when they then morphed the environment from one to the other, the cells switched suddenly from their "square" pattern to their "round" pattern and did so in unison. This, while under some circumstances place cells can dissociate from their neighbors, under other circumstances they show "attractor dynamics"—unitary behavior that suggests some kind of interconnection between them, as we saw earlier with head direction cells. Interestingly, a similar study that used a slightly different preexposure method did not reveal attractor dynamics (Leutgeb et al., 2005), testifying to the plasticity of this system and the delicate balance between learning environmental similarities (also called "pattern completion") versus environmental differences ("pattern separation").

Given the importance of boundaries to place cells, how do the cells get their boundary information? One possibility is that they receive inputs from a hypothetical class of neurons called "boundary vector cells" (Barry et al., 2006) which convey information about the distance and direction to the nearest walls. Another, related possibility is that they receive information from another class of boundary-responsive neurons – the grid cells.

3.13.3.2.4 The Grid Cells

As with head direction cells, the grid cells were discovered because researchers felt that the answer to how place cells know where to fire must lie in their inputs, and most likely the cortical inputs (subcortical inputs, as from medial septum, hypothalamus, etc., tending to be more diffuse). The largest cortical input to dorsal hippocampus is from medial entorhinal cortex, and so work in the 1990s and 2000s started to examine whether medial entorhinal neurons have spatial correlates: this work produced mixed findings (Quirk et al., 1992; Hargreaves et al., 2005). However, in two papers in 2004 and 2005, Fyhn and Hafting in the Moser lab reported finding cells with place fields somewhat like those of hippocampal cells, except multiple rather than single (Fyhn et al., 2004; Hafting et al., 2005). The second (2005) paper was particularly jaw-dropping to those in the field – by recording in very large (for a rat) environments, the researchers showed that these multiple fields were uniform in size and evenly spaced, producing an astonishing array of polka-dot-like blobs spread across the surface of the environment (**Fig. 2C**). They named these cells "grid cells" to reflect the organized hexagonal grid-like pattern and proposed that they could be a metric distance signal for place cells. Importantly, the grids have different scales as one moves from dorsal to ventral in the entorhinal cortex (Brun et al., 2008; Stensola et al., 2012), which may be important for computational reasons.

The effect of the grid cells discovery on the field of spatial coding was electrifying. These cells were indisputably spatial, inasmuch as the regular spacing between the fields had to reflect operation of an intrinsic distance-measuring process, and so grid cells laid to rest once and for all the lingering doubts about whether place cells were intrinsically spatial or merely "conjunctive." Also, the regularity of the pattern immediately demanded an explanation – what caused it? And what was it for?

The question of what causes the regular firing fields of grid cells is still unresolved, and it is beyond the scope of this chapter to review the arguments here. However, it is self-evident that at least one of the inputs to the system must be some kind of velocity or odometry (speed or distance) signal, but one that must be integrated with direction, since the interfield distance varies depending on direction of travel. Indeed, further investigation uncovered a population of head direction cells in medial entorhinal cortex (Giocomo et al., 2014), as well as a variety of other cell types including cells that fire along borders, the so-called border cells (Solstad et al., 2008; **Fig. 2D**), the latter similar to boundary vector cells discovered in the major output from the hippocampus, the subiculum (Lever et al., 2009). The discovery of this rich variety of spatially modulated cells in the hippocampal system has suggested that the brain uses the same building blocks for its spatial map as might be expected – information about distances, directions, environmental topography, and landmarks.

3.13.3.3 Path Integration

One of the reasons the discovery of grid cells was so important is that it seemed to provide strong evidence for a metric foundation to a process that had long been of interest in the spatial cognition world, which is path integration, the process of updating a representation of position based on self-motion information (Etienne and Jeffery, 2004). Grid cells, because of the regular distances between their firing fields, seem to be able to track distance moved – might they be a substrate for path integration? Later, we look at path integration studies, before examining whether grid cells might play a role in the computations.

Path integration is useful because it can take place in the absence of landmarks or other cues to position, needing only a directional reference and some way of measuring speed and time, or (alternatively) distance traveled. It has been used for centuries by human sailors to navigate over featureless oceans (Sobel, 1995), who refer to the process as "dead reckoning" (the "dead" is a corruption of "ded," short for "deduced"). The same principles discovered by sailors have also been discovered by nature, and research over the past century suggests that the majority of mobile animals use some form of self-motion tracking. Biologists have tended to prefer the term "path integration" for this process.

The operation of some kind of path integration process is evident in behavioral studies of both invertebrates and vertebrates. In the invertebrate world, the best known studies have involved the Tunisian desert ant *Cataglyphis fortis* (Müller and Wehner, 1988). In vertebrates, most work has been done on mammals, particularly hamsters, gerbils, rats, mice, and humans. These studies typically focus on homing, which is the tendency of a central place forager (an animal with a home base) to return to its nest, when it finds food or needs to escape to safety. A variant of homing that has been used in humans and dogs is triangle completion, in which

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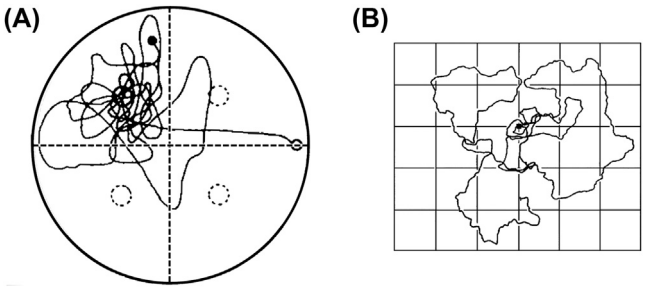

Figure 3 Looping goal-search paths for (A) a rat in a water maze and (B) a desert ant. (A) Adapted from Schenk, F., Morris, R.G., 1985. Dissociation between components of spatial memory in rats after recovery from the effects of retrohippocampal lesions. Exp. Brain Res. 58, 11–28. (B) Adapted from Müller, M., Wehner, R., 1994. The hidden spiral: systematic search and path integration in desert ants, *Cataglyphis fortis*. J. Comp. Physiol. A 175, 525–530.

a subject is led on a two-legged outward journey and then has to return to the start point. Homing studies reveal at least that the animal has a constantly updated representation of the direction home, but in some cases it has been possible to show that distance is also represented – the animal thus maintains a homing *vector* and not merely a homing direction. This has been shown most elegantly in the *Cataglyphis* studies in which displaced ants, having traveled the correct distance and direction, initiate a looping search indicating that they "know" they are in the expected region of the nest entrance (Müller and Wehner, 1994; **Fig. 3**).

An important question in path integration concerns what sensory information is required, and how it is processed. Early on, Barlow (1966) suggested a role for inertial signals, and soon afterward, behavioral studies of angular path integration strongly suggested use of a vestibular signal. The best known of these is an experiment on Mongolian gerbils by the Mittelstaedts (Mittelstaedt and Mittelstaedt, 1980), who displaced gerbil pups from the nest to a central cup in a circular arena. While the mother was retrieving the pups she was slowly rotated, at a speed below the vestibular threshold, and seen to subsequently set off for the nest in a direction that would have been correct without the rotation. A similar experiment with place cells, some years later, found that place fields would rotate if a rat was rotated at below vestibular threshold, showing that their asymmetric location in the symmetrical arena was not anchored by local cues, but rather by internal vestibular cues (Jeffery et al., 1997). Systematic studies of head direction cells that pitted vestibular against optic flow and landmark cues showed that the cells use all three information types (Blair and Sharp, 1996). Furthermore, vestibular disruption affects both place cells (Russell et al., 2003) and head direction cells (Stackman and Taube, 1997; Yoder and Taube, 2009), and indeed vestibular inputs have been suggested to have a widespread organizational function in spatial processing (Rancz et al., 2015).

Vision is another likely input into the angular component of path integration. The importance of vision is that it conveys information from the distant, static outside world, and so is able not just to update a position computation but also to reset it, if the animal becomes disorientated. Indeed, this resetting process may operate continually when landmarks are visible, with dependence on self-motion tracking only coming into play in unusual situations such as in a wide open space, or in the dark. Vision can also provide self-motion information, in the form of optic flow (Angelaki, 2014). The "flow field" is the pattern of movement (direction and speed of each part of the image) seen by different parts of the retina, and it can be used to derive egocentric heading direction (direction of travel relative to the facing direction). When a subject moves straight ahead then there is a zero point at the center of the retinal image, where the image of the world is motionless, and the rest of the image moves outward radially from this point as the subject moves. If the heading direction is displaced from the head direction then the zero point will be to one side, and so the brain can compute the difference between heading and facing direction and use this to work out direction of travel. For angular head turns, the vestibuloocular reflex, triggered by motion detection from the vestibular semicircular canals, actuates compensatory eye movements (Fetter, 2007) which the brain could in principle also use to help calculate the amount of turn.

The linear component of path integration involves calculation of distance traveled which is thought to involve the integration of velocity signals, coming from the visual and vestibular systems. Linear acceleration is detected by the otolith organs in the vestibular apparatus (Angelaki and Cullen, 2008), while optic (or other kinds of sensory) flow can add additional information about movement speed. An interesting recent line of inquiry has been to use virtual reality (VR) to dissociate these components, because it allows manipulation of landmarks and optic flow independently of vestibular cues. Studies of place and grid cells in VR environments, where the animal is held in one place (sometimes with its head fixed, sometimes with its body) and does not move relative to the Earth, show that the signals are altered – place cells have fewer fields (Chen et al., 2013), and grid cells have a larger scale (Aronov and Tank, 2014).

How are these signals integrate to yield a positional calculation? Path integration tracks movement in two dimensions (at least), and so to update position on a map, or a homing vector, it is necessary to track not just movement per se, but movement in a particular direction. The question of how this is achieved was an almost entirely open question until the discovery of grid cells—however, the two-dimensional nature of the grid cell immediately suggested a possible role in this integration, for several reasons. First, the cells clearly receive both directional and distance-related inputs, since the firing fields are aligned in specific and repeatable directions. Furthermore, subsequent studies revealed the coexistence, among the grid cells, of head direction cells and directionally modulated grid cells (Sargolini et al., 2006) and also "speed cells" – cells whose firing rate codes is linearly related to running speed

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(Kropff et al., 2015). Anatomical tracing shows projections to medial entorhinal cortex from several areas of the head direction system including postsubiculum, parasubiculum, and retrosplenial cortex (see Clark and Taube, 2012 for review). The preservation of firing relationships between grid cells independently of environment suggests, as with head direction cells, the operation of some kind of intrinsic attractor-like network organization (McNaughton et al., 2006), but one that allows for network movement in all (horizontal) directions rather than just one. Thus, it seems that the grid cells might act as a kind of "look-up table" for distance/direction combinations – a downstream structure could in effect achieve "path integration" by mapping individual grid fields onto specific points in space. Numerous computational models now exist to show how this could be achieved in practice (Giocomo et al., 2011). It should be noted, however, that place cells, downstream from the grid cells, can function effectively in the absence of grid cell input (Koenig et al., 2011; Brandon et al., 2014), so they clearly receive other forms of spatial information too. Currently, the most plausible working hypothesis is that grid cells function to drive place cells in the absence of more specific, landmark-based spatial information. In support of this idea, grid cells in baby rats come onstream at around the same developmental stage at which place fields are able to form stably in regions of the environment far from the walls (Muessig et al., 2015), suggesting that the grid cells help to bridge the gap, as it were, between the walls.

3.13.4 Navigation

Navigation is the process of deciding where to go and then planning and executing the actions to get there. It can be broadly subdivided into foraging (navigation without a specific goal, which covers a space efficiently) and goal-directed navigation (execution of a route to a specific point in space).

Goal-directed navigation has come to be subdivided into two kinds, often called model-free and model-based, where "model" may mean "map" (although it could apply more generally, beyond the spatial domain). Model-free navigation involves chains of actions leading to reward, whereas model-based navigation involves, as its name suggests, an internal representation of the environment onto which the goal is placed.

3.13.4.1 Homing

Much navigation, rather than being general and nondirected, involves computing a route to a specific, focal goal. For central place foragers such as rats and mice, or other animals with a home base (including humans), the "goal" might be the home base, in which case the navigation is called homing (Papi, 1992). As we saw earlier, homing is an important function of path integration and probably involves representation of a homing vector. Etienne et al. (2000) showed that this vector is not fixed but can be updated, if discovered to be inaccurate, by even a brief view of familiar landmarks. Having been guided back to the vicinity of home, most animals then execute a search strategy, which involves cross-crossing back and forth in the expected region of the target.

This is seen very clearly in animals performing the Morris water maze task, in which the goal platform is removed on probe trials – the animals search in a concentrated manner in the region of the expected target (**Fig. 3A**). In ants, Wehner et al. showed that the search pattern comprises loops and spirals that adapt the search profile to the probability density of the target (Müller and Wehner, 1994; **Fig. 3B**). The execution of these search patterns shows that animals can either recognize the goal location (as in the water maze – a faculty that depends on the hippocampus; Hollup et al., 2001a), or know the distance to it from the start of the homing trajectory, if in featureless terrain.

Other than homing, goal-directed navigation occurs toward a target that provides some kind of reward. It has been debated whether animals explicitly represent goals when navigating, because much apparently goal-directed behavior in laboratory tasks could be explained by the chaining of reinforced actions, without the need for a separate representation of the goal. However, accumulating evidence supports the notion that even animals like rats can represent a goal location independently of the actions required to get there, and also that they can represent the contents of the goal, as well as just its location. The best behavioral evidence for the former comes from studies like the water maze and the open-field place preference task (Rossier et al., 2000), in which the goal is specified relative to allocentric cues in the room. Evidence for the latter was first found in Spence and Lippitt's demonstration that hungry rats preferentially chose the arm of a Y-maze in which they had previously encountered food, and similarly for thirsty rats (see Tolman and Honzik, 1948), suggesting that animals may be able to link the contents of a place to the place itself. The idea garnered support from the demonstration by Clayton and colleagues that food-storing birds could remember the contents of food caches as well as their location (Clayton and Dickinson, 1999), and similar studies in rats showing that they can associate objects with specific places in the environment (Eacott and Norman, 2004).

3.13.4.2 Goal-Directed Navigation

The importance of goals in the navigational behavior of animals has led to expectations that the goal region(s) of space might be represented by place cells. Early support for this notion came from studies finding place cell firing in response to goal approach (Eichenbaum et al., 1987; Wiener, 1993) However, as mentioned earlier, a study of place encoding by O'Keefe and Speakman (1987), in which animals performed a four-arm radial (or "plus") maze task, found no evidence that place fields encode goals – there were no more fields on goal arms than on others during each block of trials, and when the goal arms were changed, firing did not follow. Similarly, other studies of place cells have failed to find evidence of frank overrepresentation of goals

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(Jeffery et al., 2003). However, in environments where the path of the animals is linearly constrained, several studies have found a subtle migration of fields toward the region of a goal. For example, Hollup et al. (2001b) found that place fields moved toward the goal zone of an annular water maze; a similar slow migration of place fields was reported in a shuttling task by Kobayashi et al. (2003), in a continuous T-maze task by Lee et al. (2006), and in a linear task on an open field by Dupret et al. (2010). In addition, in a study of navigation in an open field, Hok et al. (2007) found discharge of place cells that occurred while rats waited at an unmarked goal location.

This phenomenon, of place field migration toward goals, seems well established but its significance is not yet clear. Interpretation of goal-related activity is complicated by the problem that animals behave differently at goals – they stop running there, for a start, and place cells are sensitive to the locomotor state of the animal and fire in synchronous multiunit bursts when the animal is paused (Buzsaki et al., 1983). Also, attention to spatial cues is increased at goal locations, and attention is known to be a factor in driving place cell activity (Kentros et al., 2004). Thus, it is not clear just from goal-related firing that the "goalness" of the goal (in other words, its function as a rewarding and to-be-visited place) is important to place cells, over and above the associated spatially relevant characteristics of goals. However, manipulation of the rewarding properties of the place indicated by goal-associated place cells has been shown to increase their subsequent reactivation (McNamara et al., 2014) and also subsequent place-approach behavior (De Lavilléon et al., 2013), so it seems increasingly likely that such information does form part of the place code.

If place fields represent aspects of the goals, a problem that has long been recognized, when trying to relate place cell activity to goal navigation, is that the firing of place cells reflects where an animal *is* rather than where it wants to go (Poucet et al., 2004). An alternative, or perhaps additional, possibility is that goal representation lies outside the hippocampus itself, in areas such as prefrontal cortex (e.g., Koene et al., 2003). Two broad approaches to goal navigation have been explored theoretically in detail – stimulus–response learning and vector computation. In stimulus–response learning, a navigator learns a relationship between actions and rewards, and over time learns an efficient route to a goal. One formulation of this idea has been to use a reinforcement learning algorithm known as temporal difference learning (Barto et al., 1983) in which the outcome of an action is compared against the predicted outcome and then action–outcome connections adjusted accordingly so as to make rewarded actions more likely in future. Striking support for this idea in the nonspatial domain was provided by Schultz et al. (1997), who showed that dopamine neurons in the striatum of monkeys encode the error in reward prediction. Foster et al. (2000) applied a temporal difference learning algorithm to a model of hippocampal-dependent navigation and showed that it could learn a version of the water maze in which the goal was always in the same place, but failed when the goal was moved. This would be expected, as reinforcement learning algorithms have no flexibility to adapt to change.

Map-based goal navigation, on the other hand, involves computation of a vector to the goal. It has been suggested that the hippocampus encodes distance to the goal (Sherrill et al., 2013; Howard et al., 2014), while the entorhinal cortex encodes direction (Chadwick et al., 2015; Spiers and Barry, 2015). Exactly, how these computations could be undertaken is unknown, but the discovery of grid cells has led to suggestions that they may participate in the distance and/or direction calculations.

3.13.4.3 Route Planning – Detours and Shortest Paths

As discussed earlier, one of the most important claims made by the cognitive map theory has been that a map-like representation allows spatial inference such as the computing of detours and shortcuts, or the recall of what items might be encountered on a planned route. It has to be admitted, however, that the animal literature on route planning is somewhat mixed.

In detouring (see Spiers and Gilbert, 2015 for review), an animal faced with an obstruction to its usual route takes an alternative route, usually but not necessarily across familiar terrain. It is useful to distinguish visual detouring, when all parts of the route are visible from the start point, and hidden detouring when the route has to be planned entirely from memory. Visual detouring has been demonstrated even in spiders, who were able to plan a route to prey by surveying two circuitous walkways and choosing the one connected to the goal (Cross and Jackson, 2015). It relies on perception and likely also on simple visual snapshot memory but does not in principle require a cognitive map.

Hidden detouring, on the other hand, requires encoding of the relative location of the invisible goal. The simplest type of detour is to directly circumvent a barrier – the only demand on memory is the existence and general direction of the goal, and then the animal just needs to decide between going left versus right, usually based on which choice offers the vector closest to the goal vector. Detouring is sometimes regarded as one of the hallmarks of model-based navigation, but in fact it is possible to execute a detour using relatively simple algorithms, such as "execute vector toward goal where possible and if not, go left." However, to know whether to go left or right, an agent benefits from knowing something about what would be encountered after each of these choices: for example, one route might be much longer. Thus, model-based detouring may also take into account not just the vector to the goal but also the length of the path. Poucet et al. (1983), in a study of detouring in cats, found that when the goal was visible the animals would take the path having the closest vector to the goal even if this was longer, but when the goal was hidden behind a screen they used both path length and goal vector, prioritizing path length. The reverse, however, was observed in dogs (Chapuis, 1987). On a vertical wall, Jovalekic et al. (2011) found that rats chose the route around the barrier that presented the horizontal leg first; this preference persisted when the barrier was positioned asymmetrically until this route became considerably longer than the other but it eventually reversed, showing that the rats traded off their horizontal preference against path length/angle.

A more complex form of route length evaluation occurred in the detour experiment of Tolman and Honzik in which the direct versus detour paths were constrained on a linear-type maze – as mentioned earlier, Tolman and Honzik (1930) found that rats would take the shorter of two available detours if possible but quickly learned to take a longer detour if they knew (from previous

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exploration) that the shorter one would lead to a block too. This finding was replicated by Alvernhe et al. (2011), who found place cell remapping in the vicinity of the blockade, as well. However, in neither the Tolman and Honzik nor Alvernhe et al. studies were the rats completely naïve to the longer route, so the possibility that the choice reflects rapid one-trial learning cannot be completely ruled out – however, it seems unlikely, as rats are usually slow to learn new routes by trial and error.

The second navigational capability that is often regarded as indicative of model-based navigation is the computing of shortest paths to goals. As with detouring, computing of a shortest path suggests but does not prove the existence of an underlying model – sophisticated maze learning can be achieved with model-free algorithms. One of the most spectacular demonstrations of this was the report by Nakagaki et al. (2000) of complex maze learning by the slime mold *Physarum polycephalum*, which found the shortest path through the maze to a food source by the simple expedient of spreading out to fill every part of the maze and then retracting its dead ends.

Obviously, such a strategy is not available to vertebrates, or at least not physically, although the possibility remains that neural simulations might achieve the same result by a similar method. However, the question first arises as to whether animals like rodents *can* compute shortcuts in a complex environment, and if so, whether they do this by a model-free or model-based method. The sunburst maze is an example of shortcutting, but Tolman's interpretation of his experiment was disputed (e.g., by Bennett, 1996) on the grounds that he had placed a local cue over the goal arm, thus effectively turning this into a beacon task (a beacon is a landmark that is located *at* the site of a goal, so that a navigator merely needs to head directly toward it). The authors argued that the position of the light had changed by 50 degrees between the training and test trials and yet animals mostly preferred the correct arm, ruling out beacon-following, but this did not lay criticism to rest entirely. There has been a report of successful shortcutting in rats, in which a barrier on a hairpin maze was removed (Alvernhe et al., 2008): rats took the new shortest path to the goal, and there was a subtle shift in the pattern of place field firing, not only in the vicinity of the altered barrier as would be expected but also further away. However, reports of such behavior in the literature are limited. Subsequent efforts to replicate Tolman's findings, either directly or indirectly, met with some difficulty (Gentry et al., 1947; Muir and Taube, 2004; Grieves and Dudchenko, 2013), at least partly because when rats are faced with environmental change this tends to trigger exploration, which overrides the previous goal. Additionally, when animals are faced with stimuli that have been previously associated with actions, then these can dominate over more abstract map-like operations due to competition between hippocampal and striatal navigation systems (Packard and McGaugh, 1996). However, the sunburst maze finding was replicated in wild voles (Gaulin and Fitzgerald, 1986), and of course humans can do such tasks easily, so the ability of at least some vertebrate brains to compute shortcuts is indisputable.

3.13.4.4 Neurobiology of Spatial Inference and Planning

The question arises as to how the earlier processes of inference and planning might be implemented in the brain, at which point, attention naturally turns to the place cell system. The notion that the hippocampal place system might support such processes has received great impetus from the discovery that place cells "replay" sequences of activity in the period of time immediately after exploring a space. This phenomenon was first reported by Pavlides and Winson (1989), who found that hippocampal neurons that had been active during waking exploration increased their activity in the sleep period immediately afterward. Wilson and McNaughton (1994) then showed that correlations between pairs of neurons in these postactivation sleep periods increased in those place cell pairs that had shown correlated activity during waking, and subsequently showed that these "reactivation" phenomena could extend not just to pairs of neurons but to sequences (Lee and Wilson, 2002), sometimes quite long ones (Davidson et al., 2009). This suggested the idea that what was occurring during sleep—and, it later turned out, during wakeful quiet rest—consisted of "replay" of extended periods of waking experience. Reactivation and replay are consistent with an earlier idea, put forward by Marr (1971), that the hippocampus broadcasts newly learned information out to the neocortex for long-term storage and subsequent consolidation. However, this intuitively appealing idea has been somewhat challenged by the growing complexity of replay phenomena that have been accumulating over time. Foster and Wilson (2006), for example, found that replay could occur not just forwards but also in reverse, while Dragoi and Tonegawa (2012) suggested that it might occur even for places the animal had not yet experienced, raising questions about whether this phenomenon might just be an artifact of the connectivity of the network, rather than true memory replay.

Another line of enquiry supporting the replay/consolidation hypothesis of place cell reactivation has been the results of intervention studies in which the putative broadcast phenomenon is interfered with. Replay does not occur in real time but takes place very rapidly during bouts of multiunit activity known as sharp-wave ripples (Buzsaki et al., 1983), which occur when a rat is sitting quietly or is in the early, slow-wave stages of sleep. Investigators have used high-speed detection of these ripple events to trigger a burst of electrical stimulation to the hippocampus, disrupting the latter part of the ripple event and interrupting the replay sequence. This stimulation procedure was found to disrupt memory consolidation when applied during a ripple event, but not if applied in the period immediately afterward (Girardeau et al., 2009). Another intervention study involved stimulation of the reward pathways in the ventral tegmental area during the sleep period immediately after exploration of an open arena (De Lavilléon et al., 2013). Remarkably, when this stimulation was coupled to reactivation of a place cell, the animal upon waking would tend to make its way to the place associated with that cell, reinforcing the idea that sleep-associated replay reflects memory reactivation and suggesting also that these memories could be "edited" after the event.

The earlier studies support a role for place cell reactivation in memory consolidation, but what about spatial inference? Here, we would expect to see place cell activity "discover," independently of experience, spatial relationships corresponding to lawful relations in the real world. Increasing evidence links replay to places the animal is "thinking" about – it has been observed when

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rats are trying to decide between two choices on a T-maze (Johnson and Redish, 2007), when they are navigating to a goal in an open field (Pfeiffer and Foster, 2013), and when they are in a state of readiness to go to a not-yet-visited goal (Ólafsdóttir et al., 2015). However, the ultimate test of spatial inference is to observe evidence of detour planning and shortcutting in place cell sequences, independently of the animal's experience. These are difficult experiments to design because we have already seen that rats are disinclined to perform shortcuts and detours without exploring the altered space first, at which point, planning becomes confounded by experience. As mentioned in the previous section, a study of place cells in which a shortcut was opened up in a maze found that some of the cells changed their firing patterns (remapped), with greater changes occurring in cells with fields closer to the changed part of the maze (Alvernhe et al., 2008); however, sequences were not recorded in this study. Later, a phenomenon resembling shortcutting was seen by Gupta et al. (2010) in which place cells on a modified T-maze were observed to execute sequences that were valid combinations of previous sequences representing paths that the rat had never actually traversed.

However, phenomena such as detour calculating, shortest-path calculating, and journey optimization (such as in the so-called traveling salesman problem) have yet to be observed, and it is not a foregone conclusion that such processes would take place in the hippocampus itself.

Where else might they occur? As mentioned earlier, another likely candidate, if not *the* likeliest one, is prefrontal cortex, which is involved in many kinds of executive decision making and has access to widespread regions of the brain; for example, anterior cingulate cortex, which may have a role in processing the cost-benefit trade-offs of particular journeys (Hillman and Bilkey, 2010). Prefrontal cortex is connected to dorsal hippocampal CA1 via the nucleus reuniens of the thalamus, and neurons here have been reported to contain spatially responsive neurons including head direction cells (Jankowski et al., 2014) and place-like and border-like cells (Jankowski et al., 2015). Reuniens neurons are also modulated by the goal in a place-switching task, and inactivation of reuniens affects performance on this task (Ito et al., 2015). A neuroimaging study of humans in a VR detour-planning task by Viard et al. (2011) found activity in medial prefrontal cortex, precuneus, and left posterior parietal cortex. Neuroimaging studies in humans report prefrontal activation relative to goal distance (Spiers and Maguire, 2007), and a case study of a patient with a lesion of ventromedial prefrontal cortex revealed an inability to way find in familiar territory due to problems with retaining the goal in mind (Ciaramelli, 2008). Thus, prefrontal cortex seems a likely place to look for goal-related navigational computations.

The earlier studies raise many more questions than answers—it is clear that the next major step in spatial cognition research will be to understand how and where goals are represented and routes to them planned.

3.13.5 Complex Space

Although much research into spatial memory has taken place in the laboratory, using very simple environments, the real world is far larger and more complex. It is also frequently multicompartmented, and it is also, for most species, 3-D. How do animals and humans represent and make use of complex space?

3.13.5.1 Large-Scale Space

Little is yet known about how large-scale space is represented by animals, but there is no doubt that many species can navigate over enormous distances. Some of the behaviors may involve genetically encoded responses to global navigational cues—for example, monarch butterflies take several generations to complete their journey from Canada to Mexico and back (Flockhart et al., 2013).

Others may involve learning of large-scale navigational features, sometimes by social transmission of navigation routes, as in whooping cranes (Mueller et al., 2013).

The extraordinarily precise navigational abilities of many migratory species indicate that in addition to a compass, there is large-scale positioning information, but as with directional cues, the nature of positioning cues is not well elucidated. Over global scales, considerable evidence exists to suggest use of magnetic declination – that is, the angle made by the magnetic field lines as they intersect the earth's surface, mentioned earlier in the context of magnetic directional cues. By processing the magnitude as well as the direction of the intensity of the field and the steepness of the declination, an animal could in principle extract latitude (distance from the Equator/Poles), but longitude information is not provided by any geocentric cues and may instead involve long-range local information such as olfactory gradients. Tracking of homing pigeons over long distances has found evidence that they use large-scale features such as roads and mountains as guidance cues (Guilford and Biro, 2014) – these cues are not innate but must be learned about.

An open question is the extent to which long-range behavior makes use of a similar neurobiological substrate to more local navigation. A study of long-range migratory behavior in sparrows found that it was hippocampal independent (Bingman et al., 1999), as was orientation toward the home loft in hippocampal-lesioned homing pigeons (Gagliardo et al., 2004), suggesting that the role of the avian hippocampus might be for more local, familiar area navigation (Gagliardo et al., 2009). The question of how neurons encode large-scale space is almost entirely unaddressed at present, partly because of the practical difficulties of tracking position at the resolution needed to map out place fields, and also because place cells have not been found in nonmammalian species, while most migratory behavior has been studied in birds, amphibians, and insects. It is thus an open question as to whether place cells encode large-scale space, and if so, whether they do so with large firing fields or with multiple firing fields. Geva-Sagiv et al. (2015) have recently reviewed this issue and proposed that large-scale space is also represented by the hippocampus, but that across large empty spaces the fields may be larger and sparser. There is some neurobiological evidence to support this possibility. A study of rat

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place cells in a large arena found that fields were indeed larger, but not to scale, and they were also multiple (Fenton et al., 2008), and a study of grid cells in the ventral-most regions of medial entorhinal cortex found that grid cells can have very large-scale grids, sometimes of several meters (Brun et al., 2008). It will be interesting to see what happens over very large distances, and developing technology in position tracking and wireless recording may in due course enable answers to these questions from very long-range navigators like whales.

3.13.5.2 Multicompartmented Space

Natural spaces are often divided into subcompartments (or "rooms" in the case of humans) that are separated by boundaries and which do not share any spatial cues, but whose spatial relationships are important for wayfinding. Sometimes these subcompartments are hard to distinguish, as in the case of a row of similar-looking offices in a long corridor. Attention has recently begun to turn to how the brain achieves the task of both distinguishing and relating environmental subcompartments.

A large body of literature now exists to show that place cells can distinguish spatially identical environmental subcompartments by using other cues such as the color or the smell of the environments (Jeffery, 2007). The question of how the spatial and nonspatial cues interact has still not been resolved but may involve some kind of gating between the spatial and nonspatial cues (Anderson et al., 2003). However, when both spatial and nonspatial cues are identical then only spatial location distinguishes the subcompartments, and this can only be achieved by using path integration to work out the distance traveled between the compartments.

Several experiments to explore this issue have been conducted on place cells (**Fig. 4**). Skaggs and McNaughton (1998) found that two identical compartments connected by a corridor that ran along the outside of both (so that the interiors of the boxes looked identical) were distinguished by some place cells but were not distinguished by others, resulting in partial remapping of the place cell population. The firing pattern was influenced by which compartment the rat was placed in first, ruling out olfactory cue use and suggesting that discriminating cells used path integration to distinguish the boxes. Tanila (1999) also found discrimination between identical boxes – however, in this case the rats walked between the boxes through a central doorway, which—unlike the connecting external corridor of Skaggs and McNaughton—broke the symmetry and may also have allowed the head direction system to influence the spatial representation (as the doorway lay to, say, the East in one box and the West in the other). By contrast, Fuhs et al. (2005) found that place cells did not distinguish two identical compartments in which the corridor was configured in the same way as for the Skaggs and McNaughton experiment (running along the outside of the compartments). Similarly, Spiers et al. (2015) found that place cells failed to distinguish four repeated compartments connected by an external corridor. These experiments suggest a weak or nonexistent influence of linear path integration on place cell compartment discrimination, which seems slightly surprising given that previous work had shown an influence of linear path integration on place field positioning within a single environment (Gothard et al., 1996). However, it was recently replicated by Grieves et al. (2016), who also showed that rats did not behaviorally distinguish the compartments either.

Although the literature on discrimination of identical and similarly aligned compartments is slightly mixed but leans toward nondiscrimination, when identical compartments differ in their angular orientation then it seems clear that place cells readily discriminate compartments. For example, as mentioned earlier, the setup of Tanila (1999) introduced a reversal in intrabox cue orientation by virtue of the central doorway, and place cells readily discriminated the boxes. Paz-Villagrán et al. (2006) found that cells discriminated two identical segments of a three-compartment cylindrical apparatus in which the third had distinctive decoration (and hence uniquely oriented the environment). Fuhs et al. (2005) found discrimination (remapping) when the identical boxes had opposite instead of similar alignments, and Grieves et al. (2016) found that when their four identical compartments were splayed apart so that they had an angular difference, then both the place cells and the rats' behavior now discriminated the compartments. Putting this all together, it seems that while place cells use linear path integration for precise field positioning, they do not readily use it to disambiguate identical environmental subcompartments. It remains to be seen whether training rats to attend to the position of each compartment can induce the cells to discriminate them. By contrast, place cells do use angular information.

What about head direction cells? How do *they* respond when a rat moves between environment subcompartments? The issue of mediating between local (intracompartment) and global (large-scale) directional representations is an important one for spatial cognition, because navigation often involves moving between subcompartments of a space to get from one part of global space to another (think of moving through your house to get to the front door). To what extent does such between-compartment navigation require consistent directional alignment across the subspaces?

An early and important study, the Taube and Burton (1995) study mentioned earlier, found that when rats walk between connected subcompartments then head direction cells adopt the same alignment in the two compartments even though no visual cues are shared. It may be that the brain prefers to align directional representations across subcompartments to facilitate navigation across them. Some support for this notion was provided by Dudchenko and Zinyuk (2005), who familiarized rats independently to two diagonal compartments in a 2×2 array and then allowed them to walk between the compartments via the remaining two. In general, the head direction cells adopted different orientations in the first two compartments, the rats having been placed there by hand and presumably slightly disoriented in the process. However, when they walked under their own volition into the remaining two (novel) compartments, they carried with them the head direction cell orientation active in the just-visited compartment, switching where necessary when they reached the previously familiarized compartment. Occasionally, though the cells changed their orientation so as to be the same in all four compartments. Interestingly, these same cells regained their differing directions if the rat was again placed by hand into the original two compartments, suggesting a conflict between the representation retrieved by

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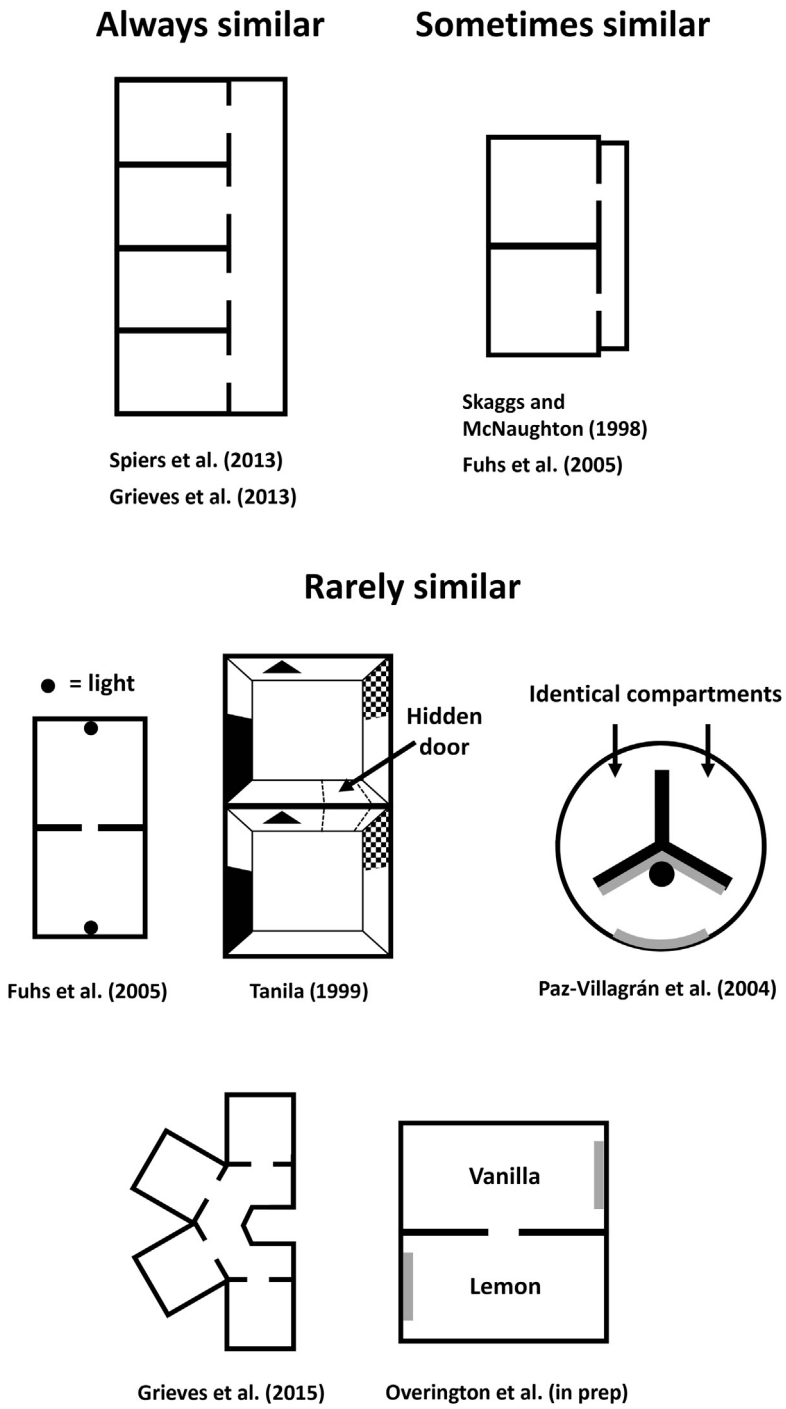

Figure 4 Multicompartment environments that place cells discriminate with difficulty (top: fields are always or sometimes similar in the compartments) and with ease (bottom: fields are rarely or never similar). Note that in the "difficult" cases the compartments have the same directional orientation, whereas in the easier cases, they do not: this suggests that direction may be an important discriminative cue for spatially ambiguous spaces. In the Tanila (1999) apparatus the door between compartments distinguishes them (being "north" in one and "south" in the other).

the visual cues and that elicited by self-locomotion. It seems likely that the strong influence of self-motion cues in establishing coherence across connected compartments has the adaptive advantage of allowing vector-based navigational planning across compartments.

The question of how and where the relationship between local and global spatial reference frames is mediated has not yet been resolved. A neuroimaging study of humans by Marchette et al. (2014) found that both retrosplenial cortex activation and behavioral priming were more similar when subjects imagined a certain heading within a local reference frame (one of four "museums" within

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a larger virtual park), irrespective of their global heading. Jacob et al. (2016) found that some neurons in dysgranular retrosplenial cortex were more strongly oriented by local than global directional cues, while standard head direction cells were globally oriented. It may be, therefore, that retrosplenial cortex is the place where local and global reference frames interact.

Overall, the question of whether navigation requires consistent directional alignment cross subspaces is still an open one. It is potentially important in, for example, urban design, such as when travelers need to be moved from a train to a station platform to a station concourse and then need to make their way outside. It could be that providing people with directional cues that are not only consistent between subspaces but also with global, aboveground space, will allow this process to occur more efficiently, and reduce milling, congestion, and confusion/stress among travelers.

3.13.5.3 Three-Dimensional Space

Although we have so far been considering only two dimensions of navigation, real space is 3-D, and so attention is starting to turn to the question of what additional problems occur with navigation in 3-D space. Two recent detailed reviews of this topic can be found by Jeffery et al. (2013) and Finkelstein et al. (2016); a synopsis of the issues is presented further.

The term "dimension" in mathematics refers to the number of coordinates needed to specify a position with reference to a fixed point (origin). A line is one-dimensional because a single number will uniquely pinpoint a place along it; a plane is two-dimensional because two numbers are needed to specify a place (x and y, in a Cartesian coordinate system, or distance and angle in a polar one), and a volumetric space is 3-D because one needs to specify height as well. Adding another dimension adds additional complexity due to the different properties of geometry in three dimensions – for example, rotations become order-dependent (noncommutative). However, it is also the case that the third dimension is the one that is aligned with gravity, so movement in this dimension has a different energetic cost compared with movement in the horizontal plane. Some animals move over a surface, in which case the third dimension supplies hills and valleys, some animals move through multilevel structures such as branches, burrow complexes, and (for humans) multi-storey buildings, and some animals move freely in volumetric space, which allows them to not only face in different directions but also to freely orient their body around its long axis in any of these directions. These three types of 3-D environment pose different navigational challenges.

3.13.5.3.1 Moving Over a Surface

The pattern of surface undulations in the natural world forms its topography, which may provide both constraints and advantages to navigation. One constraint is that topography might provide obstacles to locomotion, if the surface is steep or fissured. Walls or fissures seem to be considered "boundaries" by subicular and medial entorhinal boundary cells (Solstad et al., 2008; Lever et al., 2009), and so are clearly of interest to the brain (at least the rat brain): this may be because they help define the local space but may also be because of the constraints they place on navigation. An interesting way to distinguish these possibilities would be to impose a virtual boundary, such as a magnetic field or noise boundary (Hayman et al., 2008), to see if boundary cells form fields along these unmarked regions. Another constraint conferred by some kinds of topography is that energy cost that climbing hills or scaling walls entails. It seems very likely that animals take into account the energetic cost of hill climbing and weigh this in to their route calculations, although relatively little work has investigated how this trade-off is made. A study of detouring in rats on a climbing wall found that they tended to execute the horizontal leg of the journey first (Jovalekic et al., 2011), suggesting that they differentiated between the types of journey and also that they preferred the easier leg first, a strategy that makes adaptive sense for a prey animal (since their journeys are often interrupted). As mentioned earlier, anterior cingulate neurons have been found to encode effort in a spatial decision-making task (Hillman and Bilkey, 2010), so this seems likely to be at least one of the areas responsible for such evaluations.

In terms of advantages, topography can help by providing navigationally useful information. It is a commonplace experience that navigating in a hilly city is easier than in a flat one, because hills are useful landmarks and help anchor the sense of direction while moving around. Burgess and colleagues have shown that processing of hilly topography to define a spatial location requires the hippocampus, and indeed their "four mountains test" is a useful marker for early hippocampal degeneration (Bird et al., 2010). Another contribution from topography is the slope of the terrain, which does not provide localizing information in the same way that hilly arrays do, but which does provide directional information. Terrain slope has been shown to aid orientation in pigeons (Nardi and Bingman, 2009), and humans in a virtual environment (Restat et al., 2004) and also in a real one (Nardi et al., 2011), though interestingly the latter study found a considerable gender difference in slope use, with women using it much less. A study of place cells found that slope could reorient place fields in the absence of other polarizing information (Jeffery et al., 2006). These studies together suggest that slope of the terrain is a potentially useful navigational aid. Terrain slope is defined purely by gravity, so this is the first clue that gravity may be important for construction of a 3-D spatial map.

A slope may define a direction, but there is a particular problem for trying to update head direction computations while *on* a slope, which is how to extract azimuth from angular movements of the head, if these did not take place in a horizontal plane. This is complicated by the nonlinear relationship between head turns and azimuth, as a function of the slope of the surface (Wilson et al., 2016). For example, when standing on a flat surface facing north, a head turn of 45 degrees to the right now faces the head northeast; the same head turn on a 60-degree slope faces it closer to east–northeast, and on a vertical wall (for, say, a mouse or a gecko), azimuth is undefined. A compass would therefore have to compute a different azimuth update rule for every slope. One way around this problem is to define "azimuth" relative to the local surface instead of to the horizontal plane, but this introduces new problems about how to relate the different azimuth reference frames if moving from one surface to another, differently

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oriented one, because errors can accumulate in the head direction signal. There are two putative solutions to these difficulties – one is to maintain a locally referenced, planar map but to link local maps together by updating the azimuth computation not only for head turns but also for rotations of the whole animal around the gravity vector when moving from one local "map" to the next (Wilson et al., 2016). This strategy means that errors in the compass signal are prevented from accumulating. The other is to operate a fully volumetric, 3-D compass (see later), so that there is, so to speak, a head direction cell for every possible direction in 3-D space; this is computationally more expensive, and somewhat wasteful as many of the directional cells would rarely be used. Finkelstein et al. (2016) have suggested that the brain perhaps does both and can switch flexibly between 2-D and 3-D representations as needed. However, there is no evidence for such switching as yet; an alternative possibility is that animals use one or other mode of representation depending on their evolutionary and ecological characteristics. It should be noted that even bats showed relatively sparse directional coding of directions outside the horizontal plane (Finkelstein et al., 2015), suggesting that the brain concentrates representational resources on the most relevant and useful dimension.

As well as calculating direction on a slope, research has started to investigate how animals calculate distances. The basic question is, when on a slope, do animals track the distance they have traveled relative to the Earth's surface? or do they track distance traveled over the sloping surface? Both types of calculation could be useful in principle: ground distance is needed for computations across extended space, while surface distance traveled is necessary for energy calculations. A study of ants on undulating terrain suggested that they track Earth surface distance, meaning that they can compensate for undulations (Wohlgemuth et al., 2001); however, flying honeybees did not do this (Dacke and Srinivasan, 2007). It remains to be seen whether place and grid cells in mammals do so, although preliminary indications are that their odometry is tied to the locomotor surface (Knierim and McNaughton, 2001; Hayman et al., 2011, 2015): however, whether the scale is appropriate to the surface or to the corresponding ground distance has not yet been determined.

3.13.5.3.2 Moving Through a Multilevel Environment

A different kind of surface travel occurs when the surfaces are overlaid, as in a multistorey building or in a thickly branched tree, so that a given position in horizontal coordinates occurs more than once. There are three additional navigational problems to solve over and above traveling over a single surface; one is avoiding representational confusion between the levels (i.e., getting them mixed up), the second is having to encode the connecting points between levels, and the third is being able to relate places on one level to the other for the purposes of vector calculation to potential goals.

In the natural world, vertically repeated elements in the space could be easily differentiated by contextual cues – for example, by differences in the visual panorama at the different levels. There may in principle also be a contribution from path integration (self-motion tracking of the ascent) but this seems less likely, because (as discussed earlier) place cells do not distinguish horizontal repetition based on self-motion alone (Spiers et al., 2015), and grid cells—thought to be how place cells path integrates—do not appear to distinguish similar environments at different levels (Hayman et al., 2011). This suggests that while vertical levels might be discriminable, they may not be spatially related to each other precisely, in the brain.

Thus, mere differentiation does not suffice for navigation when it comes to route planning, short-cutting, etc., and so the next question concerns the extent to which places on the different levels can be spatially related. An early study by Montello and Pick (1993) found that college students who learned two routes through a hospital complex and were then shown how the routes were partially overlying, were able to derive the spatial relationships between landmarks both when these were within a route and when they were between routes. Thus, they could take into account the vertical as well as horizontal relationships. A study of wayfinding in a multilevel building found that participants who traveled to the correct floor first, before navigating to the goal's horizontal coordinates, did better—this may be because of the constraints provided by the staircases (Hoelscher et al., 2006). These studies aside, very little systematic study of navigation in multilevel environments has been undertaken, and the extent to which animals and humans are able to integrate and also separate the overlapping spaces remains to be explored.

3.13.5.3.3 Moving Through a Volume

The final type of 3-D environment that animals, including humans, frequently inhabit is a volumetric one, in which movement is possible in all three dimensions in an unconstrained way – either completely unconstrained, as in air or water, or partially unconstrained as in moving through a lattice of branches or a branching burrow system. On a surface, the surface itself provides a convenient reference plane for, for example, computing directional changes or distance traveled.

When moving through a volume, a local reference plane may not be so readily available, so an open question concerns how the brain conducts the processes of directional updating and odometry that we discussed earlier for 2-D navigation.

To help with spatial encoding, one organizing principle always exists in terrestrial 3-D space and that is the vertical axis defined by gravity. For land-dwelling animals, this is manifest as a constant downward pull on the organs, including the vestibular apparatus which is specialized for processing of the gravity signal (Angelaki and Cullen, 2008), while in aquatic animals it is manifest as hydrostatic pressure and/or buoyancy. Relatively, little work so far has investigated the role of gravity in global spatial orientation, although considerable research has investigated its role in postural adjustment and in calculation of the vertical direction (Carriot et al., 2008). As discussed earlier, gravity is the reference against which terrain slope is defined for slope-based orienting, but in volumetric space the role of gravity has been less well explored. Reports by astronauts in microgravity suggest that it normally helps define the reference plane—the "floor"—against which orientation can be referenced. The importance of this reference plane is most evident when absent, as evidenced by the unpleasant reorientation illusions that astronauts experience when they drift too

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far from the "floor" toward the "ceiling." Subjects report that the ceiling suddenly becomes the new floor, a switch that is accompanied by an unpleasant rotating sensation (Oman, 2007).

Given that gravity makes one dimension different from the other two, an interesting question concerns whether the brain's representation of volumetric space is also "anisotropic" – i.e., has different properties in different dimensions. That this might be the case was first proposed by Hayman et al. (2011) who found that place and grid cells showed firing fields that were elongated in the vertical dimension, in rats that climbed a spiral track or a pegboard-studded climbing wall. The possibility arises from this observation that grid cells do not encode travel in the direction orthogonal to the locomotor surface – which would make sense, since rats, being surface-dwelling animals, tend not to travel in this dimension. There are other possible explanations, however (Ulanovsky, n.d.), as the dimensions differed in structure as well as relation to gravity. A study of place cells in bats found, by contrast, that their firing fields were no more elongated in the vertical than in any other dimension (Yartsev and Ulanovsky, 2013). It may be that the spatial setting itself was more isotropic, or that bats differ from rats in their encoding capabilities (as we saw earlier in the case of head direction cells). It will be interesting to see whether grid cells in volumetric space will turn out to differ between the species.

3.13.6 The Future

As outlined in this chapter, the last century has seen enormous progress in our understanding of a fundamental behavioral competence, namely representation and navigation of the spatial world. Probably more than any other domain, the spatial cognition field has seen a close interplay between studies of behavior and studies of neural coding, and as a result we are much closer to understanding the foundations and biological underpinnings of spatial cognition. Much remains to be done, however. We still do not know how the basic building blocks of the spatial representation are established. For example, where is the place in the brain where our multiple maps are stored – are they all in hippocampus? This can be debated, since subjects with hippocampal damage can retrieve old spatial memories (Teng and Squire, 1999), but this may be because older memories are stored differently (Moscovitch et al., 2005). The brain has a tendency to make multiple representations for multiple purposes so it may well be that our maps of the world, too, are created in several different ways in different parts of the brain, depending on requirements, as suggested by recent surprising observations of "place cells" in thalamus (Jankowski et al., 2015) and claustrum (Jankowski and O'Mara, 2015), as well as the well-known distributed population of head direction cells described earlier.

As well as the cognitive map(s), we still know relatively little about the building blocks of these maps. Where is speed encoded, for example? How does landmark information reach the head direction system? Is the same pathway used for triangulating arrays of landmarks? How is a "boundary" discovered and processed by the brain? How are different parts of the world related to each other spatially?

Also, the issue of goal encoding and of computations that enable navigational planning is only just beginning and will probably form an important part of the next phase of investigation. Another big task for the future is to relate the findings from neurobiological studies, mostly of rodents, to other species and especially of course to humans. We have already seen evidence of species differences in spatial encoding, and of course spatial behaviors vary widely depending on ecological niche, so it is by no means certain that the cell types that have been found in rats and mice will be general phenomena. Preliminary studies of single neurons in humans have suggested, however, that there are certainly overlaps (Ekstrom et al., 2003; Jacobs et al., 2013), as described in this chapter, but the details of commonalities and differences remain to be discovered, and the matter will not be completely resolved until we can record single neurons from humans noninvasively, a technology that, while still some way off, will open many new doors.

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