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Cognitive representations of spatial location

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Abstract

Spatial memory has fascinated psychologists ever since the discipline began, but a series of findings beginning in the middle of last century propelled its study into the domain of neuroscience and helped bring about the cognitive revolution in psychology. Starting with the discovery that the hippocampus plays a central role in memory, particularly spatial memory, studies of the mammalian hippocampus and related regions over the latter half of the century slowly uncovered an extensive neural system involved in processing place, head direction, objects, speed and other spatially informative parameters. Meanwhile, the concurrent discovery of hippocampal synaptic plasticity allowed theoreticians and experimentalists to collaborate in linking spatial perception and memory, and genetic techniques developed towards the end of the century opened the door to circuit dissections of these processes. Building on these discoveries, spatial cognition and episodic memory may be the first cognitive competences understood across all levels from molecules to behaviour.

Keywords

Cognitive maps, hippocampus, neurobiology, path integration, reference frames, rat, spatial memory

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For the first half of last century, behavioural neuroscience was dominated by associative explanations of learning and memory. These had begun with William James' (1890) insights that memory depends on 'brain paths', followed by Pavlov's (1927) seminal experiments on conditioned association formation, which together led over the next few decades to Behaviourism (Watson, 1958) and related associative learning theories. By the 1940s the first neural network models were emerging, formed from simple elements such as the McCulloch-Pitts neuron (McCulloch and Pitts, 1943), after which it was discovered that by endowing neural networks with the capacity for re-wiring according to simple rules like Hebb's co-activation rule (Cooper, 2005; Hebb, 1949), networks could store and retrieve patterns of activation in a memory-like way. Two decades later, a physiological correlate of Hebb's rule was discovered, in the form of the electrically induced phenomenon of 'long-term potentiation' (LTP; Bliss and Gardner-Medwin, 1973; Bliss and Lømo, 1973), shown to be dependent on a new type of neurotransmitter receptor, the coincidence-detecting *N*-methyl-D-aspartate (NMDA) receptor (Collingridge and Bliss, 1995; Collingridge et al., 1983). Thus, the earlier part of the 20th century saw steady recruitment of both theoretical and experimental evidence to support Behaviourism's idea that learning is formed from associations between neurons, stemming from associations occurring in the real world.

The cognitive map

At around the middle of the 20th century, a quiet revolution against Behaviourism began. The start of this revolution is often attributed to Tolman (1948), who identified that some types of learning, such as the computing of novel short-cuts by rats in a maze, could not easily be explained with simple associative models but seem instead to require the existence of an internal representation of space. Although the 'cognitivist' models of Tolman and others did also assume association formation as a critical component of memory, these models also proposed that the brain constructs internal models of the world and operates on these independently of external experience, thus generating something akin to insight (Tolman and Honzik, 1930). In the case of spatial learning, Tolman and Honzik wrote 'We believe that in the course of learning something like a field map of the environment gets established in the rat's brain' (Tolman, 1948), an idea that is generally called the 'cognitive map' theory of spatial learning. Such an internal representation, or map, could potentially account for flexible spatial responses such as short-cutting and detour-taking.

The proposal that there might be a map in the brain was not well received, possibly because in the popular conception of a map the terrain is viewed from above, and there is a one-to-one

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mapping (as it were) between points on the map and points in the world. The idea that a rat brain can make a map of this kind was quite reasonably dismissed. However, this is not what Tolman and Honzik meant. They elaborated as follows:

> The stimuli, which are allowed in, are not connected by just simple one-to-one switches to the outgoing responses. Rather, the incoming impulses are usually worked over and elaborated in the central control room into a tentative, cognitive-like map of the environment. And it is this tentative map, indicating routes and paths and environmental relationships, which finally determines what responses, if any, the animal will finally release.

Thus, in their formulation, the representation in the brain is essentially associative *except that* internal processes also operate on the incoming signals so that spatial relations such as sequences of places (i.e., routes) can be inferred and represented. This prescient idea took many years to be accepted and it was not until single neuron studies began that unequivocal evidence for purely internal spatial processes, operating independently of external stimuli, finally emerged.

Place cells and head direction cells

The single-neuron discovery that helped cause the tide to start turning against Behaviourist explanations of spatial learning was O'Keefe's discovery of the hippocampal place cells. Neuroscientific interest in the hippocampus had been growing since the report of Scoville and Milner (1957) that bilateral hippocampal damage in humans causes a profound anterograde amnesia. O'Keefe began recording neurons from the dorsal hippocampus of freely exploring rats (equivalent to the posterior hippocampus of humans) and found that single neurons from this region would become selectively active when the animal visited a particular region of the environment (O'Keefe and Dostrovsky, 1971), irrespective of exact sensory conditions (direction of entry to the place, etc.). He called these cells 'place cells' and suggested, together with the neuropsychologist Nadel, that the hippocampus might be the site of Tolman's cognitive map (O'Keefe and Nadel, 1978).

The suggestion that the hippocampus might be for space, rather than memory, was not immediately accepted, but it was rapidly supported by evidence that hippocampally lesioned animals could not solve a radial maze task (Olton and Samuelson, 1976) or other spatial tasks (reviewed in O'Keefe and Nadel, 1978). Nor could lesioned animals learn to find a hidden platform in a tank of water, a task developed by Morris (1981) that lacks local cues to location and thus requires integration of environmental 'allocentric' cues for its solution. Hippocampal lesions proved devastating to this task (Morris et al., 1982), particularly when made to the dorsal region – ventral lesions left spatial processing much more intact (Moser et al., 1995), suggesting some other role for this region, perhaps in emotional processing and anxiety (Bannerman et al., 2004). Spatial tasks were also found to be severely disrupted by administration of pharmacologic agents that block synaptic plasticity, particularly those blocking the then-newly-discovered NMDA receptor (Morris et al., 1986), providing important support for the emerging synaptic-plasticity theory of memory formation. Studies of humans followed, and it was found that humans with unilateral medial temporal lobe damage (with spared memory) show subtle spatial mapping impairments (Maguire et al., 1996), and furthermore, that humans navigating virtual environments show functional magnetic resonance imaging (fMRI) activation of the hippocampus (Maguire et al., 1998). Most notably, Maguire et al. (2000) showed that London taxi drivers, who navigate all day long, show enlargement of the posterior hippocampus (homologous to the spatial dorsal pole of rodents), a report that won Maguire a coveted Ig Nobel Prize (Lenzer, 2003). Eventually, place cells were also found in humans too (Ekstrom et al., 2003). It is now generally accepted that the hippocampus is critical for large-scale spatial cognition (small-scale, local space being more the purview of the parietal cortex).

The study of place cells soon began to yield a number of findings of importance to understanding how animals represent space. It was rapidly determined that the representation is not a pixel map so much as a population code, inasmuch as a given place cell may have firing locations (place fields) in many environments (Alme et al., 2014), apparently randomly distributed. It was also soon discovered that although the cells use specifics of the sensory environment to establish their firing locations (Muller and Kubie, 1987), their activity is independent of exact sensory input (e.g., as O'Keefe noted, it does not depend on the direction through which the field is traversed) and seems to form an abstract representation of 'place' that uses sensory information in a flexible manner that seems more constructive than reflective. Another revealing early observation was that firing can be sustained in the dark (Quirk et al., 1990) and influenced by self-motion or 'path integration' information (Gothard et al., 1996; Jeffery et al., 1997), indicating an interaction between external environmental inputs and intrinsic processes (McNaughton et al., 2006; Samsonovich and McNaughton, 1997). The finding that place cells can switch between static, environmental cues (landmarks) and dynamic, movement information provides unequivocal evidence for Tolman and Honzik's proposal that 'the incoming impulses are usually worked over and elaborated' – that is, the systems form a superordinate representation that is independent of exact sensory information. Thus, the place cell map is cognitive rather than simply associative (though it is associative *as well*).

The developing spatial view of the hippocampal system soon afterwards received additional support in the 1980s and 1990s from Ranck and colleagues, who reported the discovery of a new type of spatially sensitive neuron in the dorsal part of the presubiculum (Ranck, 1984; Taube et al., 1990a, 1990b). These 'head direction cells' did not seem to produce place fields (the localised patches of activity characteristic of place cells) but they would fire only when the rat faced in a particular direction. The head direction (HD) system was subsequently elaborated by Taube and others and found to be remarkably extensive, involving both cortical and subcortical structures (see Taube, 2007 for review), and it steadily became apparent that a directional signal likely forms the core of the spatial representation. An important insight that emerged from work on head direction cells is that activity across the cell population is highly coherent, inasmuch as the relative firing directions of the neurons seems to be the same in every environment. This observation led to proposals that the neurons are interconnected in a so-called attractor network (Skaggs et al., 1995; Zhang, 1996), a concept that was soon after recruited to explain why place cells often show collective responses (Samsonovich and McNaughton, 1997) and indeed,

why our subjective sense of place and facing direction tends to be unitary (we never feel as though we are in two places at once).

Use of the place cell map

Following the discovery of place cells, intensive investigations began into how the map is configured and used. The 1990s were a fertile decade in this regard. An important discovery from this time was that during periods of restfulness or early (slow-wave) sleep, local field potential activity would switch from a rhythmic movement-related pattern known as theta to the more sporadic and abrupt, high frequency sharp-wave ripple pattern (Buzsáki et al., 1983), during which ensembles of place cells would reactivate (Pavlides and Winson, 1989; Wilson and McNaughton, 1994), often in the same sequence in which they had been active during waking (Lee and Wilson, 2002). This 'replay' activity was suggested to underlie memory consolidation, in line with Marr's (1971) early suggestion that hippocampal memories are consolidated during offline states in neocortex, and this notion was supported by subsequent observations of neocortical 'replay' occurring in tandem with hippocampal replay (Ji and Wilson, 2007). Subsequently, Foster and Wilson (2006) found that replay could occur in reverse when a rat pauses at a goal location, suggesting a possible role for 'reverse replay' in learning the recent action sequences that led to reward (Foster et al., 2000). In addition, forward replay, or 'preplay', has been seen in animals deciding where to go next (Johnson and Redish, 2007; Ólafsdóttir et al., 2015; Pfeiffer and Foster, 2013), consistent with internal simulation of possible routes. Such observations add to the growing weight of evidence that animals not only form but also actively use internal representations of the world.

Although the place cells seem to form a 'you are here' signal, it was, and remains, unclear how the system is used in navigational planning, because little evidence has been seen of a goal signal hidden among place cell activity (Poucet et al., 2004). Indeed, place cells seemed rather uninterested in goals (Speakman and O'Keefe, 1990), although more recent studies have suggested a slight and unexplained tendency for place fields to creep towards goals (Dupret et al., 2010; Hollup et al., 2001; Lee et al., 2006). The replay studies discussed above suggest a potential role for place cells in learning rewarded versus unrewarded routes, but the weight of behavioural evidence suggests that animals are able to navigate more flexibly than simply by rote learning of routes. Although Tolman's experiment has not been successfully replicated (Gentry et al., 1947; Grieves and Dudchenko, 2013; Muir and Taube, 2004), it is generally assumed that even rodents can likely execute simple forms of spatial inference such as short-cutting and detour planning, and of course, it is well accepted that humans can do this with ease. A challenge for the future then is to understand how the brain represents goals, how it computes optimal paths between them given the constraints of the environmental layout, and how it distinguishes perceived from remembered space.

The start of a new century, grid cells, and the way forward

By the end of the 20th century, it was well accepted that the hippocampal place cells form the core of a spatial cognition system (which most would call a cognitive map, despite a degree of remaining controversy – see Bennett, 1996), but the question of how this system contributes to cognition was only just beginning to find answers. One outstanding issue was whether the place cell map is metric – that is, has explicit information about distance and direction – or whether it is merely associative. The question of direction had seemed settled by the finding of head direction cells, but distance representation was not confirmed until the discovery of grid cells, first reported in 2005, which express multiple, regularly spaced place fields (Hafting et al., 2005). The first sight of the iconic 'grid cell' firing pattern was a flashbulb memory moment for many of us – that such a regular pattern could arise from the messy and unpredictable activity of neurons was truly amazing, and the finding electrified the field, being recognised fairly soon after by the award of the 2014 Nobel Prize in Physiology or Medicine to O'Keefe and the Mosers, 'for their discoveries of cells that constitute a positioning system in the brain'. Intensive investigations of entorhinal cortex soon followed, and a large collection of spatial cell types (cells encoding combinations of direction, objects, borders, context, etc.) was eventually unearthed (Grieves and Jeffery, 2017; Hardcastle et al., 2017), the functions of which are just beginning to be understood.

Grid cell 'grids' are apparent from the animal's first entry into a novel environment, and since there is nothing about most environments that could impart either the sixfold rotational symmetry or the even spacing between firing fields, two hypotheses immediately suggested themselves. The first is that as well as a direction signal, grid cells must be in receipt of intrinsic self-motion information, which as noted earlier is often called 'path integration' (although this term is more properly reserved for the spatial computations such as self-localisation, or computation of a homing vector, that arise *from* use of self-motion signals; Etienne and Jeffery, 2004). This means they can produce regular grids even when the environment is unfamiliar to the animal, which is potentially useful for remaining oriented while exploring a new environment. The second is that the grid cell signal might be how place cells make these computations – for example, positioning a firing field at some distance away from the environment walls, even in the dark. Grid cells have thus been considered to either receive or compute a path integration signal (McNaughton et al., 2006), and more recent work in humans has suggested that there may even be a grid-like system for representing non-spatial cognitive structures (Constantinescu et al., 2016).

The question of what grid cells are actually for is far from solved, and has been confounded by accumulating evidence that place cells can function quite well without a clear grid input (Brandon et al., 2014). Indeed, the question of what place cells are for has not been answered either. Studies of primates (human and non-human) find activity of both place and grid cells that seems to be influenced by visual scene as well as location (Ekstrom et al., 2003; Killian et al., 2012; Rolls, 1999), while much evidence now suggests that the cells encode not just current location but also other aspects of the animal's situation including its intentions (Wood et al., 2000), recent and future navigational paths (see preceding section) and in some species, vectors to goals (Sarel et al., 2017) or information about items a subject has learned about (Ison et al., 2015).

Increasingly, it is being suggested that the entorhinal-hippocampal system is for more than just place, and that it may be

part of a broader memory system, of which place is the fundamental organising principle (Buzsáki and Moser, 2013; Eichenbaum, 2017; Marr, 1971). The remainder of the 21st century will see the deployment of sophisticated new tools including genetic manipulation and new methods for recording neurons, as well as new behavioural methods for making cognitive processing explicit and measurable. These techniques will allow us to not just peer into the brain and observe Tolman's cognitive map in operation, but to reach in and tweak it so that we can fully understand not just where it is but how it works, and why Nature has seen fit to make it the core of our entire autobiographical memory store.

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