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The representation of space in the brain

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ABSTRACT

Animals can navigate vast distances and often display behaviours or activities that indicate a detailed, internal spatial representation of their surrounding environment or a 'cognitive map'. Over a century of behavioural research on spatial navigation in humans and animals has greatly increased our understanding of how this highly complex feat is achieved. In turn this has inspired half a century of electrophysiological spatial navigation and memory research which has further advanced our understanding of the brain. In particular, three functional cell types have been suggested to underlie cognitive mapping processes; place cells, head direction cells and grid cells. However, there are numerous other spatially modulated neurons in the brain. For a more complete understanding of the electrophysiological systems and behavioural processes underlying spatial navigation we must also examine these lesser understood neurons. In this review we will briefly summarise the literature surrounding place cells, head direction cells, grid cells and the evidence that these cells collectively form the neural basis of a cognitive map. We will then review literature covering many other spatially modulated neurons in the brain that perhaps further augment this cognitive map.

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1. Spatial representations in the brain

The study of how organisms are able to navigate their environment is in many ways the study of survival; all animals must navigate to find mates, shelter, food and water. For wild animals this often means navigating large expanses of land, perhaps also with limited cues. For example, Peters (1978) reports that in wooded areas masked by snow, wolves often take long, complex, winding, unplanned paths when hunting – but they can still return directly to the distant location of their pups. Elephants have similarly been recorded navigating distances over roughly 100 km a month (Leggett, 2006); during these trips they frequently visit iso-

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lated and distant waterholes (Viljoen, 1989) despite navigating environments devoid of any stable landmarks. Navigating large distances is often not enough however, as animals must also be able to navigate flexibly and efficiently. Moustached tamarin (*Saguinus mystax*) and brown-mantled tamarin (*Saguinus fuscicollis*) living in the South American rainforest for instance, often move between foraging sites in such a way as to minimise the distance travelled between trees, even taking into account the timing that particular trees begin to fruit (Garber, 1988; Janson et al., 1981; Milton and Katharine, 1981). Efficient navigation also encompasses being able to take unplanned routes however. Powell (1977) for instance, reports that fishers (*Martes pennanti*) have a home range through which they have been observed taking novel, direct paths between the nesting sites of prey animals. Often animals are even expected to navigate in completely unknown territory. For example, captured Burmese pythons (*Python molurus bivittatus*) driven more than 30 kilometres into the everglades of South Florida have been tracked heading directly from their displacement site back to their home territory (Pittman et al., 2014). Similar results have also been observed in Egyptian fruit bats (*Rousettus aegyptiacus*), these animals frequently fly large distances to forage for food and when they are displaced from their territory by distances of over 80 km they are able to navigate directly back to their home cave (Tsoar et al., 2011).

The purpose of laboratory experimentation is not to replace ethological observations such as these, but to further advance our knowledge of how these processes may unfold and particularly, how they may be represented in the brain. These experiments are always in much smaller environments than those described above and almost always use rodents such as rats and mice. Despite some criticism (Geva-Sagiv et al., 2015), this approach is indeed informative about the processes at work in larger environments and rats do form a good basis for researching them. Experiments have shown that, like other animals, rats can navigate back to their home territory after being displaced (Innes et al., 2011), and radio tracking experiments have demonstrated that wild rats navigate considerable distances (over half a kilometre) in search of food and will also spend considerable time in open environments away from cover (Taylor, 1978). This is likely an underestimation of their navigation ability, though, as these animals were restricted to a small territory. In contrast, a rat released on an uninhabited island near New Zealand navigated the entire island before settling on a home territory spanning a hectare. Later, this same rat swam 100 m to a nearby island (Russell et al., 2005). Having observed these complex navigational feats in the wild, we are thus faced with the question of how these animals, and others, navigate such large trips: as it turns out, laboratory research suggests that the biological processes underpinning this spatial navigation can be very complex.

Early behaviourist psychological research into the behaviour of animals and humans, at the start of the last century, concentrated on the relationship between stimuli and the responses they evoke (Hull, 1950; Watson, 1919). It was not until forty years later that Edward Tolman (1948) suggested the idea that there might be an internal representation of space, which he called a 'cognitive map'. He based this proposal on a wealth of experimental evidence pertaining to studies of the processes underpinning spatial navigation in rats. A debate ensued between those researchers in support of this map hypothesis and those who instead embraced the stimulus-response interpretation of behaviour, culminating essentially in a combination of these two schools (Restle, 1957). Thirty years after Tolman's influential work, O'Keefe and Nadel (1978) revived Tolman's cognitive map hypothesis. This time it was built on a firmer bedrock of behavioural experiments, but also on tantalising electrophysiological work conducted over the preceding decade (O'Keefe and Dostrovsky, 1971).

This combination of behavioural and electrophysiological research began largely with John O'Keefe, who in 1971 demonstrated, together with Jonathan Dostrovsky, the existence of cells in the hippocampus of freely behaving rats that fired preferentially for specific spatial locations in the animal's environment (O'Keefe and Dostrovsky, 1971). Later, in 1978, O'Keefe published a highly-cited book with Lynn Nadel detailing how these 'place cells' could form the neural basis of a spatial representation in the brain, or a 'cognitive map,' and went on to elucidate the characteristics of these cells (O'Keefe and Nadel, 1978). A few years later a second class of cell, first reported by Ranck Jr. in 1984, and heavily researched since the 1990s by Jeffrey Taube and colleagues, was demonstrated to respond purely to the direction an animal is facing, in an almost compass-like manner (Taube et al., 1990a, 1990b). This seemed to further support O'Keefe and Nadel's proposal about a mapping function for the hippocampal system. Most recently, in 2005, May-Britt and Edvard Moser, together with Marianne Fyhn, Torkel Hafting and colleagues, published findings demonstrating the existence of cells that fire in a continually repeating hexagonal grid of fields across the surface of an animal's environment (Fyhn et al., 2004; Hafting et al., 2005). Many of the properties of these 'grid cells' have since been explored, and their relationship to place cells is a complex one (Rowland et al., 2016), but it seems likely that at least one of their functions is to provide metric information about how far the animal has been walking and in what direction. This confirmation of the truly spatial nature of the entorhinal-hippocampal system led to the award of the 2014 Nobel Prize in Physiology or Medicine to O'Keefe and the Mosers for their discovery of "a positioning system in the brain."

Thus, rather than fulfilling different niches, experimental psychology and cognitive neuroscience have always been intertwined, each building on the progress of the other. Now we know that many of the highly complex behavioural processes observed in humans and animals reflect an equally complex world of cellular processes, which have observable electrophysiological correlates. The three major spatial cell types described above appear to form the backbone of a complex system that we are only just beginning to understand. However, in the ensuing decades since place cells were discovered, a number of other cell types have been encountered, both cortically and subcortically, that may also contribute to spatial encoding. Many of these are less well described and less well known than the 'big three', but may be no less important. In this review we aim to concentrate on these, with the hope that illuminating them may provide insight into how the brain organizes its cognitive representation of space. We will focus largely on the functional aspects of these neurons, for a more detailed review of the anatomical aspects see Knierim (2006). First, however, we review the hippocampus and place, head direction and grid cells.

2. The hippocampus

Initial interest in the hippocampus was sparked by the observed impact of hippocampal damage, both accidental and intentional, on behaviour. One of the most influential cases in this respect was that of a patient, Henry Molaison, known for many years only as patient H.M., who suffered from epileptic seizures which were found to arise from structures in his medial temporal lobe. In 1953 surgeons removed, bilaterally, H.M.'s hippocampal formation and a number of adjacent structures (Corkin et al., 1997; Penfield and Wilder, 1958). Tragically, but of great interest to many researchers, after this surgery H.M. was afflicted with severe anterograde amnesia (Gabrieli et al., 1988; Scoville and Milner, 1957) which stayed with him until his death in 2008. During his life, H.M.'s long-term memory and language skills were largely unaffected (Kensinger et al., 2001), however, he was unable to form new episodic mem-

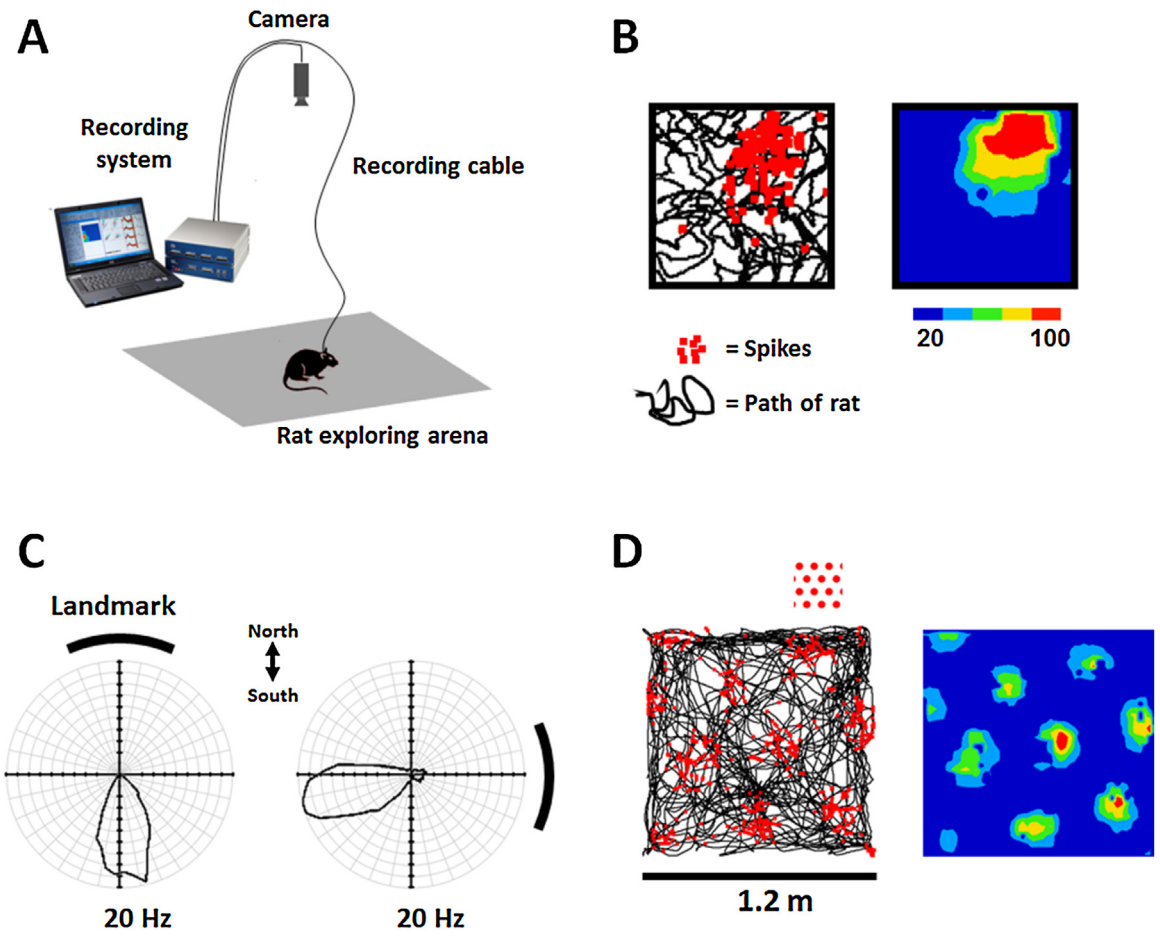

Fig. 1. Recording of the three first-discovered spatial cell types. ***A,*** A typical experimental setup for recording single neurons from freely exploring rats implanted with chronically indwelling electrodes. ***B,*** Data from a single hippocampal place cell in a single, 4-min recording trial. The left plot shows the action potentials ("spikes" – red squares) superimposed on the cumulative path of the rat across the 4 mins. Note that the spikes mostly occurred in the northeast part of the environment. The right plot shows the same data depicted, as it commonly is, as a heat plot of dwell-time-adjusted firing rate (see colour bar) between peak (100%) and 20% (peak). Action potentials and dwell time are binned, smoothed and divided to give a spatial map of the cell's firing rate as a function of spatial location. The patch of spatially localised firing is known as a place field, or firing field. ***C,*** Two trials recorded from a post-subicular head direction cell, in a symmetrical apparatus having a single polarising landmark. Each polar plot shows firing rate as a function of head direction. In the left plot, when the landmark is to the north, the cell fires maximally when the rat's head faces south. In the right plot, the landmark was rotated to the east when the rat was not in the compartment – now, when the rat returns, the cell fires to the west, maintaining the same relationship to the landmark. This shows that the cells are influenced by local cues and not by geocentric ones such as the Earth's magnetic field. ***D,*** Recording of an entorhinal grid cell, firing depicted as in ***A***. Note that instead of a single region of spiking, the cell spikes in multiple places that form a close-packed hexagonal array, like the one shown in the inset. The constant spacing between firing fields is characteristic of a given cell and is relatively constant in different environments, leading to suggestions that these cells function to encode distances. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ories. It was subsequently also discovered that he could not use a physical map to navigate in unfamiliar surroundings (Corkin, 2013, 1984) and was impaired on a number of spatial tasks (Corkin, 1979; Morris, 1999; Teuber and Weinstein, 1956) for a review see (Corkin, 1984, 2002, 2013). This finding implicated the hippocampus as a structure which is crucial for the formation of new memories, including (it later transpired) those that are spatial in nature. Subsequent to H.M.'s affliction, interest grew in whether the hippocampus is related to the formation, consolidation or retrieval of these memories, a question that is still not fully resolved.

Motivated by the findings of H.M. and other similar cases, animal researchers began to search for animal models of hippocampal amnesia, resulting in the development by Olton and colleagues of the radial maze, which was initially developed as a test of working memory (Olton et al., 1980). Using the radial maze, Olton and colleagues showed that the task is highly dependent on the hippocampus (Olton et al., 1978). While this could have suggested a role for working memory in episodic memory formation, in fact O'Keefe and Nadel, motivated by the findings described in the next section, suggested that the hippocampal dependence could be due to the spatial nature of the task (O'Keefe and Nadel, 1978). The debate between working-memory and spatial-map explanations for the effects of hippocampal lesions was finally settled when Richard Morris developed the water-maze (Morris, 1984), and used it to show that the hippocampus was necessary to solve the task even though it is mostly spatial and has no working memory component (Morris et al., 1982).

3. Place cells

The excitement generated by the case report of patient H.M. led researchers to embark upon electrophysiological investigations of the hippocampus. When O'Keefe and Dostrovsky (1971) took advantage of a newly developed technique to record single, complex spiking (Fox and Ranck, 1975; Ranck, 1973), pyramidal (Henze et al., 2000) neurons in the rat hippocampus (Fig. 1A and Fig. 2) they found that the firing rate of many of these cells was modulated purely by spatial location (Fig. 1B), and named them 'place cells'. Similar place-encoding neurons were subsequently found in several other species including mice (Rotenberg et al., 1996), bats

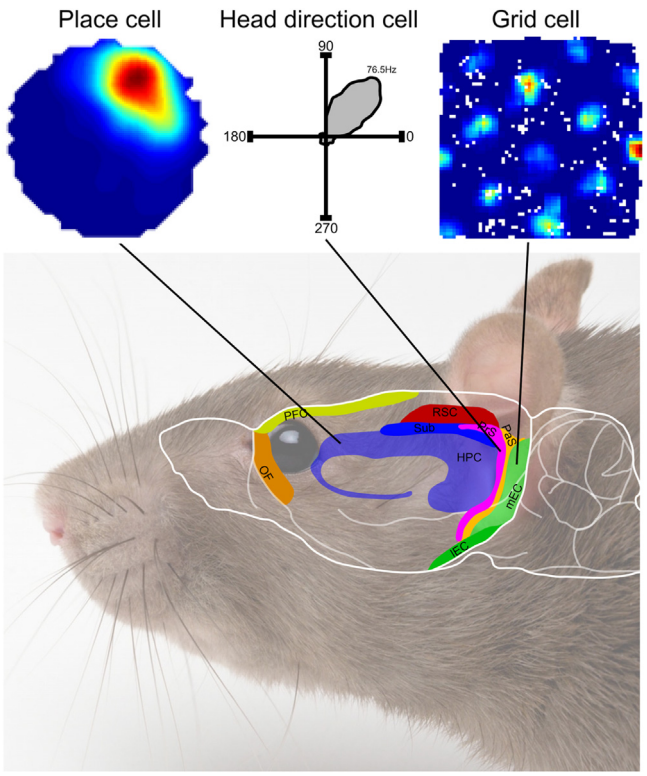

Fig. 2. Example cells and a graphic representation of their anatomical distribution in the rat brain. ***A,*** left, the firing rate heat map of a place cell (adapted from Grieves et al., 2016a) recorded as a rat explored a circular arena. **Middle**, an example head direction cell firing rate plot (adapted from Bjerknes et al., 2015). These 'polar' plots show the action potentials emitted by a cell, binned in terms of the animal's head direction at the time and divided by the amount of time spent facing that direction overall. This cell fires at a high rate when the animal is facing to the north east of the environment: this direction is the cell's 'preferred firing direction'. **Right**, an example firing rate map of a grid cell (Casali and Jeffery, 2015), this is produced using the same method as for the place cell. Multiple firing fields can be observed which form a triangular or hexagonal grid that spans the environment. ***B,*** a graphic representation of the location these cells occupy in the rat brain (white outline). Black lines highlight the region where each cell was discovered but they may be found in multiple regions. Brain regions are denoted by abbreviations, these are: HPC = hippocampus; Sub = subiculum, RSC = retrosplenial cortex; PrS = presubiculum; PaS = parasubiculum; mEC = medial entorhinal cortex; lEC = lateral entorhinal cortex; PFC = prefrontal cortex; OFC = orbitofrontal cortex.

(Ulanovsky and Moss, 2007), monkeys (Cahusac et al., 1989; Rolls et al., 1998) and humans (Ekstrom et al., 2003), suggesting a certain generality of the phenomenon, although place cells have not been reported yet in non-mammals.

Place cells were tremendously exciting because they revealed the formation, by the brain, of an abstract, cognitive representation. Their properties have led to a great deal of theorizing about how mammalian brains might construct a representation of space. Place cells recorded in exploring rats fire maximally when the rat's head is in one specific region of the environment, regardless of which way it is facing (and therefore what it can see). This area of high firing rate is known as the cell's 'place field' (O'Keefe, 1979; O'Keefe and Conway, 1978; O'Keefe and Nadel, 1978): typically, firing outside of the place field is absent. Place cells recorded simultaneously, and therefore near to each other in the brain, often have place fields in different areas of an environment, suggesting that the population of cells as a whole represent the entire surface of an environment (O'Keefe, 1976; Wilson and McNaughton, 1994). Furthermore, once the representation of an environment has formed it is stable across days (Hill, 1978; Muller et al., 1987) and even weeks (Thompson and Best, 1990), although recent evidence suggests that not all place cells are always stable (Mankin et al., 2015; Ziv et al., 2013) possibly for interesting reasons to do with charting the passage of time.

What makes place cells fire where they do? Visual information is important, as the location of a place cell's place field is often influenced by the distal cues or landmarks surrounding the environment (Muller and Kubie, 1987; O'Keefe and Conway, 1978; Yoganarasimha and Knierim, 2005). However, place cells still fire in the same locations in the dark provided the rat remains in the apparatus (Save et al., 2000; Zhang et al., 2014; Markus et al., 1994; Quirk et al., 1990) and blind rats also have relatively stable place fields (Save et al., 1998). This indicates that the place cell representation can be built in the total absence of visual information provided the availability of other sensory cues such as olfaction and tactility. We now know that these different sensory modalities are integrated both within and outside the hippocampus (Jeffery, 2007). Thus, place fields represent higher order constructs assembled from more primitive spatial ones such as direction, boundaries, and self-motion information (see below). If the environment is altered or completely novel, the cells may completely change their firing relationship and represent this environment in a unique way (Anderson and Jeffery, 2003; O'Keefe and Conway, 1978); this process of place field alteration between different environments is known as 'remapping' (Muller and Kubie, 1987). Together, these results further support the idea that place cells may underlie spatial navigation and memory

Although, as mentioned above, place cells have been found in several species, it remains unclear how much of what has been discovered in rats and mice is universal, even within mammals. Bats, whose ancestral lineage diverged from that of rodents around 65 million years ago, have well-formed place fields that resemble rodent ones in most important respects (Ulanovsky and Moss, 2007). However, the situation for primates appears to be slightly different. Humans and other primates primarily use visual cues, such as landmarks, when navigating (Ekstrom, 2015) and neuroimaging studies implicate the hippocampus and the parahippocampal region in human navigation (Aguirre et al., 1996; Maguire et al., 1998; Spiers and Barry, 2015). However, in humans and other primates, spatially modulated cells appear to make up the minority of cells in these structures. Initial reports suggested that cells in the primate hippocampus might instead respond to objects (Eifuku et al., 1995; Rolls, 2005; Rolls et al., 1989), whole-body motion (O'Mara et al., 1994) or relate to the direction of 'spatial view' – where the animal is looking, rather than where it is; (Rolls, 1999; Rolls et al., 1997; Rolls and O'Mara, 1995). In humans only around 11–25% of neurons in the hippocampus and parahippocampal regions appear to respond purely to spatial location, the majority of these being in the hippocampus (Ekstrom et al., 2003; Miller et al., 2013). However, most cells in that region of the temporal lobe encode many aspects of space conjunctively, combining features such as current location, current view, current spatial goal or heading direction (Ekstrom et al., 2003; Miller et al., 2013). Spatial view cells have not been observed in rodents (but see de Araujo et al., 2001) perhaps because rodents have particularly poor eyesight or because they explore environments directly rather than visually. Place cells in rats are unable to form a stable representation for an environment unless it has been directly explored (Rowland et al., 2011) which suggests that these animals may not have an inferred allocentric representation for remote space, although recent research suggests that observing a conspecific explore a novel environment can improve the stability of place cell representations when later exploring the same environment (Mou and Ji, 2016). Instead, rats may have the reverse representation; in the rodent superior colliculus (Cooper et al., 1998) and area V1 of the visual cortex (Haggerty and Ji, 2015) cells fire in spatial locations where visual cues appear the same. The firing of the latter cells seems to lead place cells temporally, suggesting that the

information from these may guide the activity of place cells. Thus, rats probably use remote visual cues to inform the spatial activity of place cells, whereas the activity of spatial view cells carries information about the remote visual cues being observed.

4. Head direction cells

The discovery of head direction (HD) cells came about in the aftermath of the original place cell report, when researchers were still trying to understand the source of their spatial firing. Ranck, (1985, 1984) reported finding, in the dorsal presubiculum of the rat, cells that were modulated by the facing direction of the head, and a detailed description of the activity of these 'head direction' cells was published shortly after (Taube et al., 1990a, 1990b, 1987). Head direction cells fire maximally when an animal's head faces a particular direction in the azimuthal (horizontal) plane (Fig. 1C and Fig. 2), this 'preferred direction' is independent of the animal's current behaviour or position. Different head direction cells have different preferred firing directions, equally distributed, such that as a population there is equal representation of all directions, and no overall preferred direction (Taube et al., 1990b). Like place cells, the firing of head direction cells has been shown to rely on the angular position of environmental cues (Goodridge and Taube, 1995; Taube, 1995a; Taube et al., 1990b; Zugaro et al., 2000) if these cues are stable (Knierim et al., 1995), but such cues are not necessary (Mizumori and Williams, 1993; Yoder et al., 2011a,b). As with place cells, if distal cues are rotated or if the animal is moved between environments then the preferred firing direction of all head direction cells realign or rotate (Fig. 1C), and they do this coherently (Skaggs et al., 1995; Yoganarasimha and Knierim, 2005).

Head direction cells are found in a comparatively greater number of brain regions than grid cells and place cells, and these structures seem to essentially comprise the classic Papez limbic circuit (Taube, 1998), originally thought to be an emotion circuit and then later a memory one. In rats the head direction 'signal' is thought to initially arise within the brainstem in the dorsal tegmental nuclei (DTN) and lateral mammillary nuclei (LMN), where neurons sensitive to angular head velocity can also be found. From here, the signal projects to the anterior dorsal thalamus (ADN) and then to a variety of regions in thalamus and cortex. Regions in the thalamus include antero-dorsal, lateral dorsal and reuniens nuclei, and cortical regions include postsubiculum, entorhinal and retrosplenial cortices, parasubiculum, posterior parietal cortex (see Fig. 8 for a schematic and Yoder et al., 2011a,b for a review). In other species, these cells have also been observed in the primate presubiculum (Robertson et al., 1999), drosophila central complex (Seelig and Jayaraman, 2015) and there is some evidence of directionally sensitive neurons in the human entorhinal cortex (Jacobs et al., 2010), retrosplenial cortex and thalamus (Shine et al., 2016).

5. Grid cells

Unlike place cells in the hippocampus, many cells in the mEC fire in multiple discrete and regularly spaced locations which form a triangular lattice or tessellated grid (Fig. 1D). These 'grid cells' are found close to the border between the mEC and postrhinal cortex (Fyhn et al., 2004; Hafting et al., 2005) and in the pre- and parasubiculum (Boccara et al., 2010)(Fig. 2). Like place cells, the firing of grid cells is partially dictated by external cues; when distal landmarks are rotated, grid cell firing fields rotate by a corresponding amount (Hafting et al., 2005), and deformation of the environment often causes partial deformation of the grid (Barry et al., 2007; Stensola et al., 2012). However, unlike with place cells, in new environments the firing of different grid cells remains coordinated, such that the grid patterns of grid cells rotate and move together, maintaining a stable relationship (Fyhn et al., 2007). This has led to suggestions that grid cells function cooperatively, by virtue of an interconnected matrix known as an attractor network (McNaughton et al., 2006).

Grid cells do not appear to depend on extramaze cues to maintain a stable firing pattern. In complete darkness the grid pattern persists undisturbed, provided (as with place cells) the rat has not been disoriented; this has led many to suggest that grid cells may be involved in the computations underlying self-motion calculation, also known as 'path integration' (Fuhs and Touretzky, 2006; Fyhn et al., 2007; Hafting et al., 2005; McNaughton et al., 2006). This idea is supported by the finding that lesions of the mEC result in path integration impairments (Allen et al., 2014; Van Cauter et al., 2013). Given their mathematical and geometric properties it is almost hard to believe these cells exist at all: however, they are not confined to the rat brain and are also found in mice (Fyhn et al., 2008) and have recently been observed in bats (Yartsev et al., 2011) and possibly also in humans (Jacobs et al., 2013). Evidence for their existence in humans has also been demonstrated using functional magnetic resonance imaging techniques (fMRI) (Doeller et al., 2010). The function and origin of these cells is still not greatly understood. However, their activity is likely informed by two other cell types found in the mEC; speed cells, which encode the movement velocity of the animal (Kropff et al., 2015), and a recent report of 'band cells' (Krupic et al., 2012 but see; Navratilova et al., 2016 and Krupic et al., 2015) which fire in discrete bands of activity and may aid in the formation of the hexagonal grids of grid cells.

Place, head direction and grid cells have turned out to be only the beginning of what promises to be a large array of diverse spatially modulated neurons, some of which have clear real-world correlates but many of whose properties are obscure, or 'conjunctive ' (combine several types of information). We turn next to some of these other cells, to see how their properties could contribute to the building of a cognitive map, but first we look at a class of neuron found throughout the brain, whose firing is more spatially diffuse, and yet seem to have a critical role to play in spatial computations: interneurons.

6. Interneurons

Interneurons are a morphologically diverse class of typically high firing-rate neurons that use the inhibitory transmitter gamma-Aminobutyric acid (GABA). They usually form local networks of neurons that mostly control their neighbours via short-range, inhibitory connections, and for a long time were thought only to have the relatively uninteresting role of modulating local network activity so as to prevent runaway excitation and epileptic seizures. It is now thought that some of them may have a much more computationally interesting role.

In each of the brain structures associated with spatial navigation there tend to be a minority (around 10% of all neurons, for example, in CA1 region of the hippocampus) of high firing neurons which are spatially insensitive (Freund and Buzsáki, 1998), and these are typically interneurons. When recording in the CA1 region of the hippocampus of awake animals, these cells are usually treated as a single class and are often ignored, on the basis that they are modulatory rather than signal-carrying. However, hippocampal interneurons have been suggested to consist of at least 21 distinct types (Klausberger and Somogyi, 2008; Somogyi and Klausberger, 2005), each having specific temporal relationships to the local field potential oscillatory signal known as theta rhythm, and so it seems increasingly likely that they have an important computational role. It has become clear that understanding or modelling neural networks will be impossible without an under-

standing of these intervening cell types (Sik et al., 1997).This has been examined in two domains – space and time.

We begin with spatial information. Although initial reports described interneurons as having no discernible spatial properties (Christian and Deadwyler, 1986), Kubie et al. (1990) showed that hippocampal interneurons do have a coarse but repeatable spatial specificity. This is relatively stable and even rotates with a visual cue like the place fields of place cells. Similar results were also reported in different apparatus (Ego-Stengel et al., 2007; Frank et al., 2001; McNaughton et al., 1983). Wilent and Nitz (2007) for example not only confirmed that the firing of interneurons is spatially modulated, but that this firing can be as informative as place cells. They also observed that some interneurons exhibit 'off fields', or an area of significantly lower firing, that resembles an inverted place field; indeed the authors suggest that this firing may result from interneuron and pyramidal cell interactions.

Is the information carried by interneuron firing more than might be expected from the combined input of multiple place cells? Marshall et al. (2002) found that stimulation of a place cell intracellularly can modulate the firing of monosynaptically connected interneurons and that the spatial specificity of these interneurons is often the result of place cell inputs, suggesting that this may not be the case. However, Hangya et al. (2010) simultaneously recorded pairs of interneurons and CA1 place cells and found that even monosynaptically connected neurons could have both similar and distinct spatial representations. These results provide evidence that the spatial specificity of hippocampal interneurons is greater than could be expected based purely on their inputs from place cells. It is the case however that in many correlated cell pairs, interneurons have an off field, as reported by Wilent and Nitz (2007), that corresponds to the location of a connected place cell's place field. This suggests that although interneurons may possess spatial specificity of their own, a subpopulation of these cells are probably involved with place cell firing in an inhibitory or excitatory way.

The other important domain in which interneurons have been extensively investigated is in control of the timing of activity in networks. Klausberger and Somogyi (2008) found fine-grained relationships between interneuron activity and theta rhythm, suggesting that the coordinated activity of spatial neurons might be regulated by an orchestra of interneurons, organised by a central conductor, the forebrain structure known as the medial septum. The medial septum probably controls the timing of theta rhythm via long-range inhibitory projections into hippocampus (Melzer et al., 2012). Timing is potentially important for spatial coding because space and time are linked by velocity, since travel at a certain velocity for a certain time translates a subject by a particular distance. It may be that one function of theta rhythm, which varies in frequency with running speed (Jeewajee et al., 2008; McFarland et al., 1975), is to convey a speed signal into the hippocampal formation. The question of whether this is due to explicit encoding of running speed or is a byproduct of the sensory drive associated with increased speed of movement through the sensory world has been debated. However, stimulation of the medial septum, which drives the theta rhythm in hippocampus (Vertes and Kocsis, 1997) directly affects running speed (Fuhrmann et al., 2015), and altering theta frequency artificially has been shown to lead to a change in the running speed of mice (Bender et al., 2015). These results suggest a specific locomotor role for theta, though whether this is on the sensory/encoding side as well as the motor side remains to be determined.

As well as the local field potential, cells that are modulated by running speed are common throughout the brain, but again, this might be due to the increased rate of sensory drive rather than a functional role in speed encoding per se. Place cells for example show a considerable amount of modulation by running speed (Czurkó et al., 1999; Kubie et al., 1990; McNaughton et al., 1996, 1983; O'Keefe et al., 1998; Rivas et al., 1996; Sharp et al., 1990; Whishaw, 1998; Wiener et al., 1989; Zhang et al., 1998); they oscillate at a higher frequency and emit more spikes per theta cycle (Geisler et al., 2007). In the medial entorhinal cortex, some of the grid cells in the deeper layers are modulated by speed as well as space – they are known as 'conjunctive' (Sargolini et al., 2006; Wills et al., 2012). Primary visual neurons are also – surprisingly – modulated by running speed (Niell and Stryker, 2010; Saleem et al., 2013). However, it has also been suspected that some cells in the brain might code more purely for speed. For example, O'Keefe reported an observation in hippocampus of a solitary 'speed cell' (O'Keefe et al., 1998) whose activity was linearly related to running speed and could be decoupled from effort, but attempts to find the source of this signal were not successful for many years. Recently, however, Kropff et al. reported that a large proportion of neurons in mEC are tuned solely for running speed (Kropff et al., 2015). These cells are thought to be interneurons. Putting this all together, a function for hippocampal interneurons in regulating spatial processing might be to provide a speed signal that the system can use to update the self-localization signal. One influential hypothesis for how this could be done is the oscillatory interference model first suggested by O'Keefe and Recce (1993) and subsequently elaborated by Burgess, O'Keefe and colleagues into a model that could also account for grid cell grids (Burgess et al., 2007).

The above ideas aside, the function of interneurons is still little understood, but it seems clear that the brain has not created such a vast array of neuronal cell types for trivial reasons. The next few years should see major advances in our understanding of these ubiquitous neurons.

7. Extrahippocampal place cells

This review is primarily concerned with spatial representations in the brain other than the 'big three' cell types, the simplest examples of which are perhaps neurons analogous to place cells in brain areas outside the hippocampus (HPC). For example; both Quirk et al. (1992) and Hargreaves et al. (2005) reported finding cells resembling hippocampal place cells in the medial entorhinal cortex (mEC): the same structure where grid cells can predominantly be found (Fig. 3). However, it is not known if these cells were truly place-specific units like those in the hippocampus or merely the isolated vertices of a grid cell's firing structure (Savelli et al., 2008). Indeed, Hargreaves et al. (2005) were also able to record a grid cell, suggesting that their electrodes were at least in a location where they can be found. Nonetheless, more recent studies have confirmed the existence of what appear to be spatially modulated non-grid cells which resemble hippocampal place cells in the mEC (Savelli et al., 2008) as well as spatially modulated cells with multiple firing fields that do not seem to conform to the traditional grid cell classification (Krupic et al., 2012; Latuske et al., 2015; Pérez-Escobar et al., 2016; Zhang et al., 2013), especially in the deeper layers of the structure (Tang et al., 2015).

Spatial correlates have also been observed in the striatum, a structure closely connected and compared to the hippocampus (discussed later). A small number of cells here appear to encode the head direction (Mizumori et al., 2000; Ragozzino et al., 2001; Wiener, 1993) or relative location of the animal (Wiener, 1993), but more recent studies have failed to find such spatial encoding (Berke et al., 2009) instead suggesting that neurons here encode specific motor responses or behaviours which may themselves occur in a specific spatial location. Nonetheless, the activity of proposed striatal location-sensitive neurons closely follows that of hippocampal cells (Yeshenko et al., 2004). Although, the striatum is thought to utilise contextual information differently to the hippocampus as cells there remap more when the lights are switched off during a navigation task (Mizumori et al., 2000). However, this is not the case

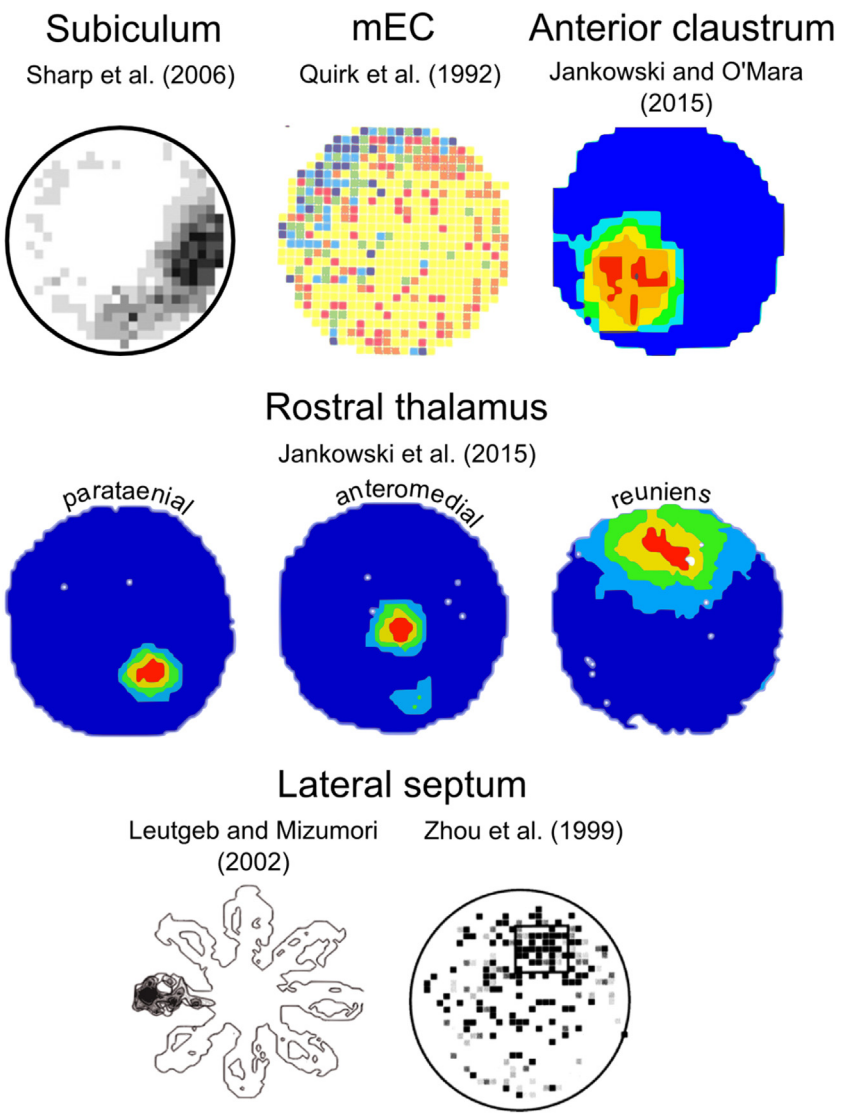

Fig. 3. Place cells outside the hippocampus. The plots show heatmaps, similar to the ones in Fig. 1, from various studies demonstrating the existence of highly spatially tuned cells outwith the hippocampus. **Top row:** Sharp et al. (2006 adapted from Fig. 3) reported observing cells with spatial characteristics very similar to hippocampal place cells in the subiculum, place cells have perhaps also been observed in the medial entorhinal cortex (Quirk et al., 1992 adapted from Fig. 2) and anterior claustrum (Jankowski and O'Mara, 2015 adapted from Fig. 1). **Middle row:** Jankowski and O'Mara (2015 adapted from Fig. 1) found evidence for spatially selective cells throughout the rostral thalamus (Jankowski et al., 2015 adapted from Fig. 2). **Bottom row:** Spatially selective cells have also been observed in the lateral septum (Leutgeb and Mizumori, 2002 adapted from Fig. 3; Zhou et al., 1999 adapted from Fig. 4).

when visual cues are simply reorganised, suggesting that these cells may integrate visual information or that they are more sensitive to the navigation strategy the animal is using (Shibata et al., 2001; Yeshenko et al., 2004). In any case, the evidence of true place encoding anywhere near the sensitivity of the hippocampus appears to be lacking in the striatum, this is compounded by the fact that the few reports of spatial activity there always involve a spatial task where animals execute specific responses for specific rewards, both of which we know are important correlates of striatal activity.

The medial septum has received considerable attention recently, mainly because inhibiting activity there disrupts entorhinal theta modulation (Jeffery et al., 1995) and grid cell firing (Brandon et al., 2011; Koenig et al., 2011). However, cells in the nearby lateral septum (LS) are reported to have spatial characteristics similar to those of place cells (Leutgeb and Mizumori, 2002; Ryoi et al., 1998; Zhou et al., 1999)(Fig. 3). In contrast to place cells however, these cells initially form orthogonal representations for different environments but later represent them similarly, perhaps indicating a role in pattern completion processes. Evidence suggests that spatially modulated neurons may also reside in the primate septal area (Kita et al., 1995; Nishijo et al., 1997). However, damage specifically to the LS does not seem to impact behaviour (Bland and Bland, 1986; Oddie et al., 1996) and so the function of these cells is still largely unknown.

Some cells in the subiculum have similarly been likened to hippocampal place cells (Sharp, 2006, 1997)(Fig. 3) but these seem to be more responsive to environment boundaries (Stewart et al., 2014), opening the possibility that these cells were boundary vector cells (discussed later). In any case, spatially modulated cells in the subiculum certainly seem to have much less spatial selectivity than hippocampal place cells (Anderson and O'Mara, 2004; Barnes et al., 1990; Martin and Ono, 2000) and may instead often encode a combination of positional, directional and speed information (Muller et al., 1991; Sharp and Green, 1994). This finding, coupled with the fact that the firing of these cells is relatively stable in complete darkness (Brotons-Mas et al., 2010), might mean that these cells

are more involved in path integration processes than the specific place representations of hippocampal place cells.

Jankowski et al. (2015), however, report the observation of much more spatially selective units, resembling hippocampal place cells, in the rostral thalamus (parataenial, anteromedial, and nucleus reuniens), an area associated with episodic memory in humans (Clarke et al., 1994; Mitchell et al., 2014; Van der Werf et al., 2003) and long term memory in rats (Loureiro et al., 2012)(Fig. 3). Mink et al. (1983) also previously reported individual neurons that seemingly responded to spatial correlates in the anteromedial thalamus. These cells are stable within a session, but it is unknown if they maintain a consistent representation over time or if they remap between environments or contexts. Further characterisation will be needed before these cells can be fully compared to hippocampal place units (Jankowski et al., 2015). Similarly, Jankowski and O'Mara (2015) report the existence of spatially modulated units resembling hippocampal place cells in the anterior claustrum (Fig. 3). However, these represent a low proportion of the cells recorded there (4.3%) and like many subicular cells some of them are directionally modulated, suggesting a different role to hippocampal place cells that is perhaps more closely related to visual processes.

Deshmukh and Knierim (2011) report the existence of units with spatial fields resembling those of place cells in the lateral entorhinal cortex (lEC): however, these cells require the presence of objects within the environment and are not well spatially modulated when objects are not present (Deshmukh and Knierim, 2011; Hargreaves et al., 2005; Yoganarasimha et al., 2010). These cells may thus provide hippocampal place cells with non-spatial information (Deshmukh and Knierim, 2013; Manns and Howard, 2006) rather than form a unique spatial representation outside the hippocampus. In rodents, the postrhinal cortex has been suggested to fulfil a similar role to the parahippocampal area in primates (Burwell et al., 1995) which is associated with processing spatial scenes (Epstein and Kanwisher, 1998). In rodents its connectivity supports processing both spatial and non-spatial information (Whitlock et al., 2008) and within the structure cells have been observed to fire in a spatially modulated manner. However, these representations are not stable (Fyhn et al., 2004) and do not rotate predictably when visual cues are rotated, but have instead been suggested to represent an initial step in the progression towards true place selectivity (Burwell and Hafeman, 2003). In another cortical structure, Lipton et al. (1999) report location-sensitive neurons in the orbitofrontal cortex (OFC). The firing of many of these cells (72% of recorded neurons) discriminated multiple odour ports based on their location. These cells did not usually encode purely location as many of them would also modulate their firing rate based on the behaviour of the rat or the phase of the task, suggesting that they may be integrating visuospatial processing and behaviour. Further results from Feierstein et al. (2006) suggest that pure location-dependent firing is unlikely in the OFC and that cells there may have a locomotor rather than a purely spatial representation. Thus we see that the precise spatial modulation of the hippocampal place cell may not be common outside the hippocampus.

8. Boundary/border cells

Perhaps the relatively unique spatial representation in the hippocampus is due to the variety of spatial inputs that project there. For example, another widely researched, but often overlooked cell type responds purely to environmental boundaries (Fig. 4) – these cells have a complex relationship with both place and grid cells that is still not greatly understood. Early observations demonstrated that hippocampal place cell firing often appears to be determined, at least partly, by the geometric constraints of an environment. By elongating a square environment into a rectangle, place fields which were previously small and round were seen to stretch in response to the wall changes, becoming long and distended in the same dimension, albeit by a smaller amount (O'Keefe and Burgess, 1996). This led a number of researchers to formulate a model of place cell firing which employed a class of cells known as Boundary Vector Cells (BVCs): these cells were predicted to fire in relation to environmental boundaries, with place cell firing arising as a result of a threshold sum activity of a subpopulation of these BVCs (Barry et al., 2006; Burgess et al., 1997; Hartley et al., 2000).

Initial reports suggested that cells in the subicular formation of the rat may be responsive to environment boundaries (Sharp, 1997; Sharp and Green, 1994) albeit with a weak overall spatial modulation. Later studies have since revealed cells which at least partially fit the description of the hypothesised BVCs, in areas as diverse as the subiculum (Barry et al., 2006), presubiculum and parasubiculum (Boccara et al., 2010), mEC (Bjerknes et al., 2014; Savelli et al., 2008; Solstad et al., 2008) and recently in the anterior claustrum (Jankowski and O'Mara, 2015) and rostral thalamus (Jankowski et al., 2015)(Fig. 4). These cells have a preferred firing direction, much like head direction cells, but instead of firing maximally when the animal's head is facing this direction a BVC will fire when the animal encounters an environmental boundary in that direction from the animal. This firing is driven by the memory of the boundary's position relative to the animal, based on self-motion information and not simply by perceptual cues (Lever et al., 2009; Raudies et al., 2012; Raudies and Hasselmo, 2012). This consistent firing is observed in every environment in which the cell is observed, if the animal's sense of direction remains the same in each (Lever et al., 2009; Sharp, 1997). Environmental boundaries which can drive BVC firing in this way may be walls, low ridges or vertical drops and the colour, texture or odour of these does not seem to influence the cell's firing (Lever et al., 2009).

Within this group of spatially modulated neurons there is a great diversity of different types. Initial models predicted that different cells would respond to different distances from boundaries. However, border cells in the mEC seem to respond to boundaries not more than 10 cm away (Bjerknes et al., 2014; Solstad et al., 2008); the same seems to be true of boundary cells in the claustrum (Jankowski and O'Mara, 2015). Subicular boundary vector cells, in contrast, can be observed to have fields distant from their preferred boundary (Lever et al., 2009) suggesting that these two types of cell may form discrete populations. Furthermore, Stewart et al. (2014) report the existence of 'boundary-off' cells in the subiculum. These cells fire in a way that resembles an inverted boundary cell, with activity covering an environment *except* for an area near one particular boundary. Stewart et al. (2014) propose that these cells may play a distinct role in navigation, suggesting that they may form another separate class of boundary cells. So far, all of these boundary and border cells do not direct their activity (or lack of activity) to all boundaries in all directions: they are selective only for those found at a specific distance from the animal and at a particular allocentric direction. However, so called 'perimeter' or 'annulus' cells in the rostral thalamus (nucleus reuniens and anteromedial thalamus)(Jankowski et al., 2015), anterior claustrum (Jankowski and O'Mara, 2015), mEC (Solstad et al., 2008) and mouse anterior cingulate cortex (Weible et al., 2012) break even this rule and fire along all environment boundaries (Fig. 4). These cells are also accompanied by corresponding boundary off counterparts that fire only in the centre of an apparatus (Weible et al., 2009). These cells may mark yet another distinct population, perhaps forming a precursor to boundary cells that is generally active near all boundaries.

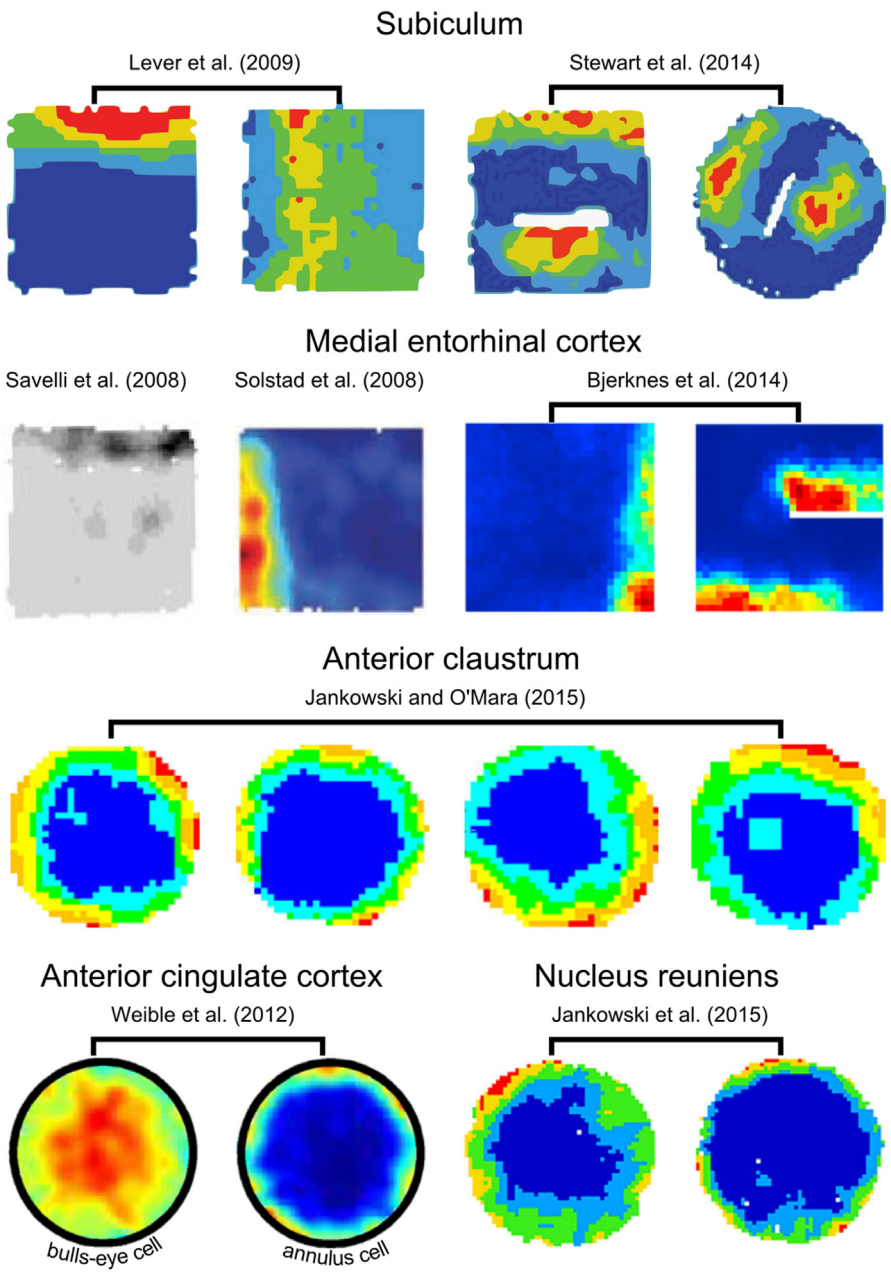

Fig. 4. Border/boundary cells. The plots show heatmaps, similar to the ones in Fig. 1, from various studies showing firing of cells concentrated near boundaries in the environment, irrespective of other contextual cues and of spatial location. **Top row:** boundary cells recorded in the subiculum by Lever et al. (2009 adapted from Fig. 2) and more recently by Stewart et al. (2014 adapted from Fig. 2). It is clear that cells in this region respond to boundaries, firing along them. This is best demonstrated using the classical 'barrier' test, as shown in the righthand plots. These cells can also fire at a distance to boundaries, as can be seen in the second plot from the left. **Second row:** border cells recorded in the medial entorhinal cortex by Savelli et al. (2008 adapted from Fig. 4), Solstad et al. (2008 adapted from Fig. 1) and more recently by Bjerknes et al. (2014 adapted from Fig. 1). As in the subiculum, these cells respond to boundaries, but few respond at a distance to them. **Third row:** boundary cells recorded by Jankowski and O'Mara (2015 adapted from Fig. 3) in the anterior claustrum. Unlike the more classical boundary cells, these seem to respond to all boundaries in the environment. **Bottom row:** Weible et al. (2012 adapted from Fig. 3) demonstrated that similar 'all-boundary' responses can be observed in the anterior cingulate cortex, they termed these cells 'annulus' or 'bulls-eye' depending on whether they fired along boundaries or away from them. Jankowski et al. (2015 adapted from Fig. 4) also observed annulus cells in the nucleus reuniens of the thalamus.

9. Object cells

Recognising if a stimulus is novel or familiar is often crucial to an animal's survival and this is true as much of object recognition as it is of recognising an immediate threat – confusing a slice of pizza for your hat may result in a short period of embarrassment but it's easy to see how faulty or non-existent object recognition such as this could escalate quickly to be a life or death matter, especially for animals. Furthermore, the recognition and memory of objects may underlie features of episodic and 'episodic like' memory in humans and animals: it would be difficult to forget the aforementioned pizza incident but it would likewise be impossible to remember without also having access to a memory for the associated objects. Indeed, a more recent view of the hippocampus is that it is involved in integrating a variety of stimuli in order to potentially lay the framework for the creation of episodic or episodic like memory. In this view, memory is comprised of spatial ('where') and nonspatial ('what') information (Knierim et al., 2014) of which objects comprise a small part. The hippocampus is known to be involved in processes far beyond purely spatial navigation (Eichenbaum et al.,

1999) including the discrimination of non-spatial cues such as objects (Clark et al., 2000; Fortin et al., 2004). For instance place cells in the hippocampus have been shown to respond to the spatial location of objects (Lenck-Santini et al., 2005) so this information is certainly being utilised by the hippocampus and thus possibly also in the formation of episodic memory. It likely originates in structures outside the hippocampus however; as nonspatial information is thought to progress through the perirhinal cortex and lateral entorhinal cortices before entering the hippocampus (Deshmukh et al., 2012; Witter et al., 2000; Witter and Amaral, 1991). We will review some electrophysiological evidence of object related activity outside the hippocampus, paying particular attention to those representations that are still spatial in nature.

It is important to remember that cells which are more active around or near specific objects are not necessarily spatially modulated, these neurons may be encoding visual or tactile information (Burke et al., 2012) or novelty (Wan et al., 1999; Zhu et al., 1995). Upon analysis this phenomenon may appear spatial, but this is merely because the objects occupy a specific spatial location (see O'Keefe, 1999 for a similar discussion) for an example see the dissociation between representations in the perirhinal and lateral entorhinal cortex (Deshmukh et al., 2012). However, a number of studies have highlighted cells that also possess spatial characteristics which we will discuss here. For instance, about 5.5% of cells in anterior claustrum show a sensitivity to objects: this firing begins immediately upon exploring the object and dissipates as soon as it is removed (Jankowski and O'Mara, 2015) (Fig. 5). Firing persists in darkness or if the object is replaced with a different one, meaning that it does not simply represent visual, texture or other sensory features. Rather, these cells seem to encode the spatial location of objects in the environment. In the absence of objects some of these cells are also spatially modulated and resemble hippocampal place cells suggesting that they are encoding spatial information about objects when they are present rather than their identity.

Similarly, lateral entorhinal cortex (lEC) cells are not well spatially modulated in a blank environment (Deshmukh and Knierim, 2011; Hargreaves et al., 2005) or even in an environment where many distal cues are provided (Yoganarasimha et al., 2010): however, when objects are placed inside the environment many cells show activity resembling the object-sensitive cells in the claustrum (Deshmukh and Knierim, 2011). In contrast to those cells though, units in the lEC often maintain their object-related firing when the object is removed, providing evidence of a spatial memory for the position of objects (Tsao et al., 2013)(Fig. 5). In support of this spatial view, some of these neurons are sensitive only to specific objects or fire in the position of a moved or missing object (Deshmukh and Knierim, 2011; Tsao et al., 2013): these object memory 'trace responses' were not seen in the claustrum cells. However, units which show the same trace response activity have been reported in lateral entorhinal cortex (Vandrey and Ainge, 2016) and can also be found in the mouse anterior cingulate cortex (ACC) where cells respond to the precise spatial location of a missing object for up to 30 days after initial exposure to the environment (Weible et al., 2012, 2009)(Fig. 5). One interpretation of these findings is that, as discussed above, these brain regions are involved in conveying object/place associations to the hippocampus. Certainly, lesions of the lEC result in object recognition impairments (Wilson et al., 2013).

10. Goal cells

Similar to object recognition, the representation of spatial and nonspatial goals is a fundamental requirement of survival. Rarely do we navigate without a specific goal in mind, even if it is only a subgoal on a longer journey or a simple place of regular interest such as the supermarket. Without a representation of the supermarket however you would need to walk aimlessly until randomly finding it every time you needed to buy milk. It is true that rats do not need to buy milk very often, but they do have to find food, potential mates and shelter. Thus, having a representation of these spatial goals can allow them to navigate quickly, efficiently, safely and flexibly whenever necessary. However, finding a representation of spatial goals in the brain has proven difficult and initial reports suggested that even the highly integrative spatial map provided by place cells does not encode this information (Hölscher et al., 2003; Siegel et al., 2008; Speakman and O'Keefe, 1990). Some studies suggested that the firing of place cells at the beginning of a complex maze may be related to the future goal of the animal and that this reflected the animal's anticipation of this location (Ferbinteanu et al., 2003; Frank et al., 2001; Wood et al., 2000), however, recent evidence suggests that this firing is actually related to the animal's future trajectory, not the goal (Grieves et al., 2016b). Other evidence suggests that place fields may subtly shift towards spatial goals causing an overrepresentation of that location (Hollup et al., 2001; Kobayashi et al., 2003; Dupret et al., 2010) or that some place cells may fire preferentially just before reward attainment (Eichenbaum et al., 1987). However, these goal representations are not as specific as one might expect or hope for. Early models actually predicted the existence of 'goal cells' which would modulate their firing rate based on an animal's distance from its current goal (Burgess et al., 1993; Burgess and O'Keefe, 1996; Pfeifer, 1998). These cells, which were thought to perhaps reside in the subiculum, could be used to navigate efficiently towards a goal location if the environment is not too complex. This seems like a much more attractive way to represent spatial goals and some cells in frontal-cortical regions may play a comparable role.

Despite direct hippocampal input (Jay and Witter, 1991), cells in the prelimbic area of the medial prefrontal cortex (mPFC) do not typically encode location (Gemmell et al., 2002; Ito et al., 2015; Jung et al., 1998; Poucet, 1997) though they may encode contextual information (Euston and McNaughton, 2006; Hyman et al., 2012; Ito et al., 2015; Jung et al., 1998). However, using a novel open field task where rats activate the availability of a food reward from a location separate to the one where they actually consume the reward (Rossier et al., 2000), Hok et al. (2005) found evidence of a quasi-spatial representation in the prelimbic/infralimbic areas of the mPFC (Poucet et al., 2004)(Fig. 6). Specifically, many units there increased their activity in the location of a spatial goal, despite this being spatially distinct from the location of the reward. This representation perhaps informs hippocampal activity – where similar goal related firing can also be observed in place cell firing (Hok et al., 2007; Poucet et al., 2004). Although inactivation of the mPFC does not disrupt goal firing in place cells (Hok et al., 2013), so the reverse flow of information may be true. These cells have very large firing fields located on or near the goal location, characteristics which are both important features of the aforementioned goal cells (Burgess and O'Keefe, 1996). However, further research will be needed to clarify whether mPFC cells do hold a spatial representation of the goal or if they are merely representing task-relevant stimuli (Hagler and Sereno, 2006) or goal-based action selection (Matsumoto, 2003) in a spatial task, thus just giving the appearance of a spatial response.

Looking at the nearby obitofrontal cortex (OFC); initial evidence from primates suggested that this structure may encode the economic significance of different behavioural outcomes (Padoa-Schioppa et al., 2006). Indeed, recent evidence in rats also suggests that the OFC may encode expectations or realisations about rewards (Steiner and Redish, 2012). In terms of a spatial representation, cells seem to simply modulate their firing in relation to spatial goals, perhaps giving the appearance of spatial coding (Steiner and Redish, 2012; Stott and Redish, 2014). However, cells in the OFC may be spa-

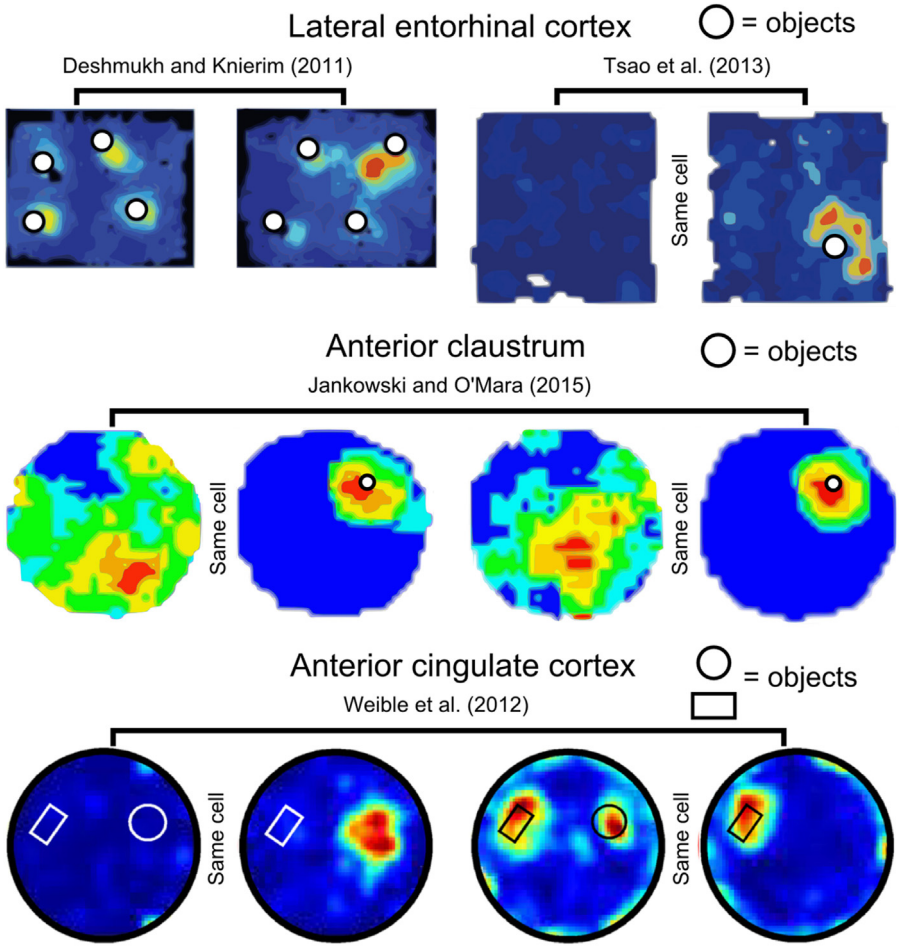

Fig. 5. Object cells. These plots show heatmaps, similar to the ones in Fig. 1, from various studies showing the firing of cells related to objects in the environment. **Top row:** object sensitive cells recorded in the lateral entorhinal cortex by Deshmukh and Knierim (2011 adapted from Fig. 3) and Tsao et al. (2013 adapted from Fig. 1). These cells fire near to objects placed in the environment, regardless of their identity. As can be seen in the right example, these cells do not typically show spatially selectivity in the absence of objects. **Middle row:** two example cells recorded by Jankowski and O'Mara (2015 adapted from Fig. 4) in the anterior claustrum. In the absence of objects these cells are somewhat spatially modulated, but when objects are added these cells show very specific firing around them. **Bottom row:** two cells recorded by Weible et al. (2012 adapted from Fig. 5) in the mouse anterior cingulate cortex. Cells in this brain region are also sensitive to the presence of objects, firing around them. However, some cells, as in the left example, instead fire in an area marking the *absence* of a previous object.

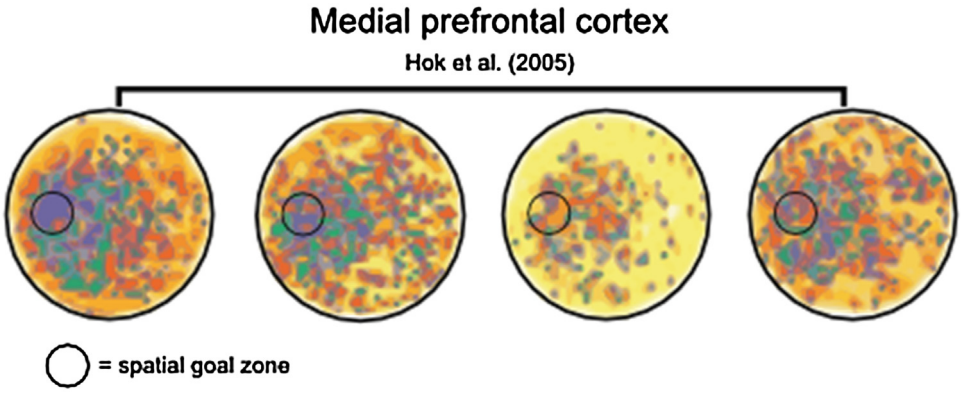

Fig. 6. Goal cells. These plots show heatmaps, similar to the ones in Fig. 1 but with a slightly different colormap that ranges from orange (no firing) to purple (maximum firing). These four medial prefrontal cortex cells were recorded by Hok et al. (2005 adapted from Fig. 3) and demonstrate a clear field of activity surrounding the goal zone. This zone was where rats had to wait to trigger the release of food and is thus dissociated from the location of actual food consumption. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

tially responsive to odour-place associations (Feierstein et al., 2006; Lipton et al., 1999) and their firing may also be related to future goal locations and response directions (Feierstein et al., 2006).

Another possibility is that already discovered cells actually fulfil this role. It has been proposed for instance that the firing of grid cells in the medial entorhinal cortex could be translated into a gradient signalling the distance to a spatial goal (Stemmler et al., 2015), but this signal may not be represented itself by a specific cell. Alternatively, we may not need to stray out into distal cortical regions in order to find a goal representation at all; more recent fMRI data suggest that there may be such a representation in the human hippocampus (Howard et al., 2014) but direct electrophysiological evidence in any animal of such a signal has remained elusive. Preliminary evidence from research on bats, however, may provide a concrete example of such a representation; these animals appear to have neurons that encode the precise spatial location and allocentric direction of a goal even when it is obscured (Sarel et al., 2015). How this representation is formed, utilised or adapted is still to be determined; likewise if a similar representation is to be found in the human or rat brain is still unknown

11. Conjunctive cells

So far we have seen examples of cells with specific representations of space, however, many cells in the brain do not form a pure representation such as this, especially those cells in structures associated with integrative processes. Many cells encode a number of environmental, spatial or behavioural features simultaneously and are thus termed 'conjunctive cells'. Concentrating on those cells that conjunctively encode spatial features, many of these are found in the medial entorhinal cortex, but there are also examples in other brain regions too. Theta-modulated place-by-direction (TPD) cells, for example, have been observed in the rat presubiculum and parasubiculum. These cells fire in specific spatial locations but only when the animal is facing in a particular direction (Cacucci et al., 2004)(Fig. 7). Similar cells have also been observed in the parasubiculum (Taube, 1995b) and retrosplenial cortex (Alexander and Nitz, 2015; Cho and Sharp, 2001; Vedder et al., 2016)(Fig. 7), there they are thought to integrate this information with self-motion information. Many cells in the medial entorhinal cortex (mEC) respond conjunctively to direction, location and running speed; for instance some grid cells may also exhibit head direction correlates (Sargolini et al., 2006) or head direction cells may exhibit strong spatial modulation (Tang et al., 2014)(Fig. 7). Indeed, these conjunctive cell types were being used in artificial navigation modules before they were discovered and may be necessary for efficiently computing current location (Milford et al., 2006, 2010) suggesting that these cells may fulfil an important role in spatial navigation processes.

12. Movement- or action-sensitive cells

So far in this review we have focused on those cells that encode an animal's spatial location: however, movement through space is a critical part of spatial processing, and many cells in the brain encode movement, or encode space conjunctively with movement. Self-motion information can be used to estimate spatial location through path integration processes if a known reference point is provided (Mittelstaedt and Mittelstaedt, 1980). As such, self-motion information is generally concerned with cues internally generated, which makes it a relatively simpler form of information. However, given the vast number of possible internal cues that these cells may encode and the fact that, as we saw earlier, many encode a conjunction of stimuli, these representations can be difficult to recognise or examine. Nevertheless, a number of brain structures and cells have been identified that reliably encode such features.

As mentioned above, early studies found that place cells conjunctively encode velocity as well as place (McNaughton et al., 1983), and studies of head direction cells have similarly found modulation by movements including angular head velocity (Chen et al., 1994; Sharp, 1996). Additionally, head direction cells in some regions show anticipatory firing that was originally suggested to reflect a motor efference signal (Blair et al., 1997; Blair and Sharp, 1995); however, it still occurs during passive movements (Bassett et al., 2005), and may reflect vestibular information about predicted head direction instead. Movement sensitivity is found in many other regions however. One such structure is the striatum, the activity of which is often compared and contrasted to that of the hippocampus. Whereas the hippocampus is thought to underlie the encoding of flexible, perhaps rare or unlikely experiences (Eichenbaum, 2004), the striatum appears to be more closely involved with repetitive experiences (Berke, 2009). In evidence of this, when animals are trained on a task that allows only the use of body-referenced (egocentric) or world-referenced (allocentric) information, inactivation of the striatum tends to increase the use of a hippocampal-dependent 'place' strategy, whereas inactivation of the hippocampus tends to increase the use of a striatum-dependent 'response' strategy (Packard and McGaugh, 1996). This makes the striatum an important structure for processing task-relevant action information which is often similar if not identical in repetitive tasks; it also implicates the striatum in the formation of automated responses or habits (Jog et al., 1999; for a review see Yin and Knowlton, 2006). Consistent with this, many studies reveal that the activity of striatal neurons is related to specific body movements in both primates (Alexander and DeLong, 1985; Schultz and Romo, 1988) and rats (Gardiner and Kitai, 1992; West et al., 1990). In behavioural tasks, striatal neurons also seem to encode task-relevant information such as rewards (van der Meer et al., 2010; van der Meer and Redish, 2009), task phase (Barnes et al., 2005; Kermadi and Joseph, 1995) or response sequences (Berke et al., 2009; Jin and Costa, 2010).

Strikingly, many striatal cells fire preferentially when the animal is making a particular movement at a particular location in an environment, such as turning left in a T-maze (Thorn et al., 2010). This is a pattern that has been seen elsewhere too: neurons which respond to specific response sequences can also be found in the posterior parietal cortex (PPC) (McNaughton et al., 1989; Chen et al., 1994). Neurons here are often modulated by head direction (Chen et al., 1994; Whitlock et al., 2008), but cells are also modulated by other factors, perhaps related to the time since the last response was made, distance to a goal or the animal's allocentric spatial location (Nitz, 2006; Nitz, 2012). More recent research suggests that these cells may represent a phase in the process required to transform egocentric information into an allocentric reference frame. By this view, they actually encode the egocentric position of a cue (Wilber et al., 2014). In support of this, previous studies identified that rats with posterior parietal cortex lesions suffered a strange inability to orient themselves towards a cue (Kolb et al., 1994) and rats are generally impaired in spatial tasks after lesions to this area – especially if those tasks require using proximal visual cues (Kolb et al., 1994, 1987; Save et al., 1992). A similar integrative process has been suggested to take place in retrosplenial cortex (RSC), where neurons can be found that encode both response sequence and spatial location (Alexander and Nitz, 2015). These cells were recorded in a stereotyped maze environment meaning that the location specificity may be due to similar visual scenes rather than location, however, in open field experiments conjunctive representations of spatial location and head direction have also been observed (Jacob et al., 2016) making this less likely. Recent reports also suggest that cells may reside in the retrosplenial cortex (Jacob et al., 2016, 2014)

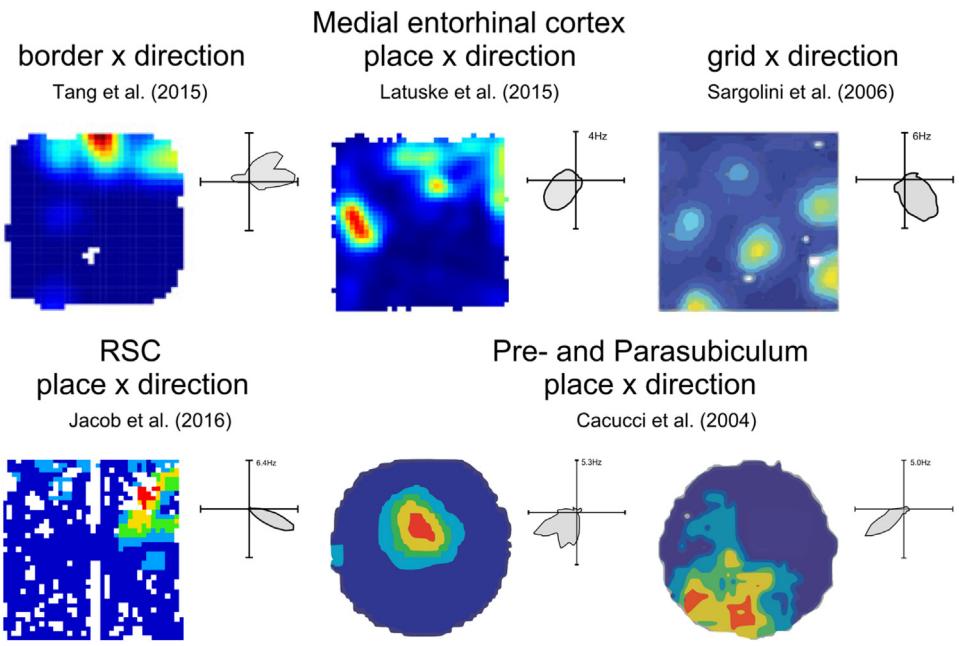

Fig. 7. Conjunctive cells. These plots show heatmaps, similar to the ones in Fig. 1, from various studies showing the multi-modal or conjunctive firing of different cells. Next to these are shown directional 'polar' plots as described in Fig. 1. **Top row:** conjunctive cells in the medial entorhinal cortex (mEC); Tang et al. (2015 adapted from Fig. S3) report that the activity of boundary cells may also be directional, like that of head direction cells. Latuske et al. (2015 adapted from Fig. 5) similarly report that some head direction cells can show a strong spatial modulation, much like place cells. Sargolini et al. (2006 adapted from Fig. 3 and S7) also demonstrated that many grid cells also show directional modulation similarly to head direction cells, further strengthening the view that these cells may be involved in processing self-motion information. **Bottom row:** spatially responsive cells can be observed in the retrosplenial cortex (RSC) and these cells often also have directional correlates (Cho and Sharp, 2001; adapted from Jacob et al., 2016). Cacucci et al. (2004 adapted from Fig. 2) observed cells in the pre- and parasubiculum that were sensitive to the heading direction of the animal but which also showed strong spatial selectivity.

and nearby subiculum (Olson et al., 2016) that encode a conjunction of visual and head direction information (Fig. 7), in the case of the subiculum these cells have been suggested to represent an animal's allocentric direction of travel.

13. Conclusion

The study of the neural encoding of space began with the discovery (albeit spread across 30 years) of a triumvirate of spatially modulated neurons: the place cells, head direction cells and grid cells. Studies of the network in which these neurons are embedded has revealed many more cells that have firing properties relevant to spatial encoding (See Fig. 8 for a summary "wiring diagram"). Some of the response profiles are conjunctive, making activity sometimes difficult to decipher, and it seems likely that the "big three" cell types represent nodes of unusually decipherable (by scientists at least) representatives of a diverse array of cell types, many of which will only be understood using complex analytical methods.

We have seen that spatial tuning outside of the hippocampus and medial entorhinal cortex is not particularly unusual. Why might these spatial representations exist in structures outside the hippocampus at all? Do they receive their spatial inputs from place cells in the hippocampus? Or are these representations independent of that signal? The answers to these questions are probably complex. We do know that the hippocampus represents a melting pot of spatial and non-spatial inputs, which in themselves must come from outside the structure. We know this because where other spatial signals such as that carried by the head direction system and grid cell system can be easily disrupted by lesions, the spatial representation of the hippocampus continues almost perpetually, even in the absence of both of these signals. This suggests that activity in the hippocampus is the result of multiple inputs and can adapt to a loss of a substantial amount before degrading. However, this fine-tuned spatial signal is likely also exported to other structures that are either associated with spatial navigation processes or involved in integrating it with other information. To compound the matter, many of these projections are likely to be reciprocal, so that the output of these structures will also be found in the hippocampus. Untangling this dense web of interconnections and shared spatial responses is a slow process that began almost forty years ago and will require still a great deal of sophisticated electrophysiology and concomitant behavioural investigation.

14. Future research

We have covered many different cell types so far discovered in a variety of different brain regions, but the question of how spatial cognition is supported is far from resolved. For instance, interneurons are spread throughout the brain and as we have seen here, may contribute significantly to the spatial modulation of many other cell types (Hangya et al., 2010). Neural network models, deep learning projects and major collaborative research such as the Human Brain Project all require data concerning the activity profiles of neurons in different brain regions. Yet, electrophysiology research has yet to tackle this large population of diverse neurons found throughout the brain, in part because it is often hard to find real-world correlates of neuronal activity, and we do not yet have a full suite of analytic tools with which to describe and interpret more complex firing patterns. Advanced brain research will require a fuller understanding of these neurons and the role they fulfil (Sik et al., 1997).

Even for cells that do have discernible real-world correlates, it is often unclear what inputs many spatial neurons are sensitive to. For instance, what constitutes an object, and why do object sensitive cells fire at or around certain items in the environment but not others? What makes these items different to walls or textures on the floor? For a better understanding of brain networks and how neurons process information we must know in greater detail what

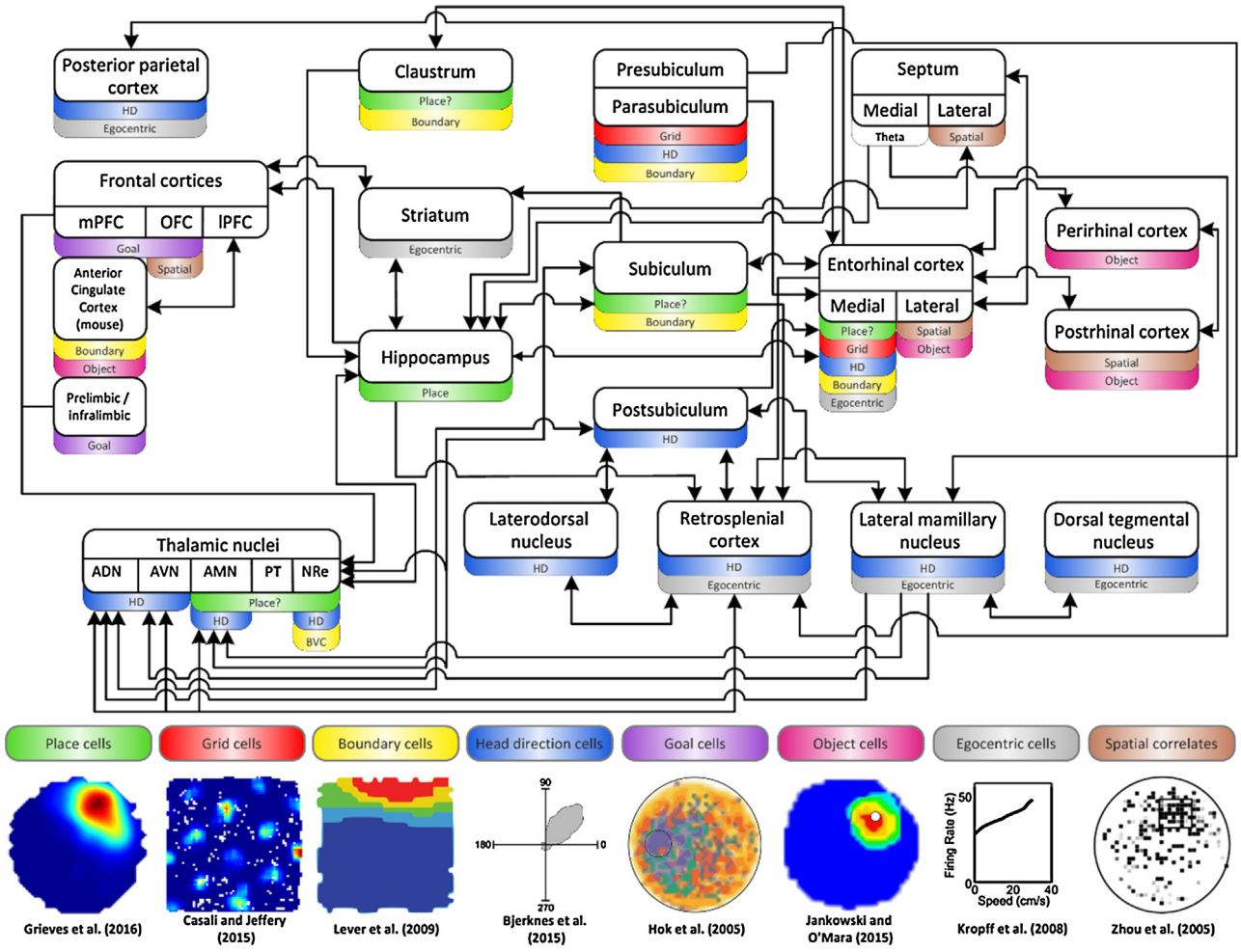

Fig. 8. Schematic diagram concentrating on the brain regions and cell types discussed in this review. Place cells can be found in the hippocampus, nucleus reuniens (NRe), parataenial nucleus (PT), anteromedial nucleus (AM), claustrum, medial entorhinal cortex and subiculum. Place correlates (i.e. weak spatial activity) can be found in the orbitofrontal cortex (OFC), postrhinal cortex, lateral entorhinal cortex and lateral septum. Grid cells can be found in the medial entorhinal cortex, pre- and parasubiculum. Head direction cells can be found in the lateral mamillary nuclei (LMN), anterodorsal nuclei (ADN), laterodorsal nuclei (LDN), retrosplenial cortex (RSC), postsubiculum, nucleus reuniens and anteromedial nucleus (AM). Boundary cells can be found in the parasubiculum, claustrum, subiculum, anterior cingulate cortex, pre- and parasubiculum and medial entorhinal cortex. Object sensitive cells can be found in the lateral entorhinal cortex, postrhinal cortex, orbitofrontal cortex (OFC) and the lateral septum. Goal cells can be found in the medial prefrontal cortex (mPFC) and prelimbic and infralimbic regions of the prefrontal cortex. Self-motion or egocentric cells such as those encoding running speed or angular head velocity can be found in the mEC, striatum, RSC, PPC, LMN and DTN. For a more in depth review of the connectivity of the anterior thalamic nuclei see Jankowski et al. (2013) or Aggleton and Nelson (2015). For the mammillary bodies see Dillingham et al. (2015). For the circuit between hippocampus, mPFC and NRe see Vertes et al. (2007) or Griffin (2015). For the entorhinal cortex see Canto et al. (2008). For hippocampal, subicular pre- and parasubicular connectivity see van Strien et al. (2009).

specific features these cells are attending to or if they represent a model of a more complex representation.

It is similarly unclear what constitutes a boundary. Are boundary sensitive neurons representing a physical barrier? Research suggests that they respond to vertical drops (Lever et al., 2009), which is an absence of support rather than the presence of a barrier, so perhaps boundary cells instead represent simple linear features of an environment? However the cells do not seem to be sensitive to patterns, textured flooring or changes in ground colour, suggesting that they instead represent something more meaningful to the animal such as impediments to locomotion (Stewart et al., 2014). Are boundary cells also sensitive to virtual or otherwise non-physical barriers, such as a purely acoustic boundary (e.g., Hayman et al., 2008)? Future research will be needed to clarify these relationships. It is also unknown whether the boundary cells found in the subiculum (Lever et al., 2009), mEC (Bjerknes et al., 2014), anterior claustrum (Jankowski and O'Mara, 2015), rostral thalamus (Jankowski et al., 2015) and anterior cingulate cortex (ACC)(Weible et al., 2012) are related or if they represent divergent features. Perimeter cells in some of these regions, which fire along all boundaries, and their 'boundary off' counterpart which fire away from all boundaries, certainly seem to satisfy a different function and perhaps precede the formation of traditional boundary cells, but this is unknown.

Another major, unsolved question concerns the representation of spatial goals in the brain. Research shows that in many cases animals plan what they want to do in terms of trajectories (Grieves et al., 2016a) and continuously recall entire trajectories through space (Pfeiffer and Foster, 2013). However, there is evidence of goal encoding in the prefrontal cortex (Hok et al., 2005) and the circuit this forms with the hippocampus (Ito et al., 2015). Recent data also suggest that some animals may possess a constantly updating goal vector that can be observed in the activity of single neurons (Sarel et al., 2015) or in the activity of whole brain regions (Howard et al., 2014). Finding out how goals are stored and retrieved, and the steps that lead to action planning, will be a major task for the coming period and will need to include areas of the brain outside the hippocampus, in addition to hippocampus itself. Indeed, one

conclusion that should be drawn from the examples described in this review is that many fascinating functions of the brain and of brain networks reside outside the most widely researched brain regions. The next generation of behaviourists and neuroscientists will certainly work together to better elucidate the form and function of different brain structures and the diverse neural specificity that awaits there.

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