

## Field repetition and local mapping in the hippocampus and medial entorhinal cortex

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## 1 **Abstract**

2           Hippocampal place cells support spatial cognition and are thought to form the neural  
3 substrate of a global 'cognitive map'. A widely held view is that parts of the hippocampus also  
4 underlie the ability to separate patterns, or to provide different neural codes for distinct  
5 environments. However, a number of studies have shown that in environments composed of  
6 multiple, repeating compartments, place cells and other spatially modulated neurons show the  
7 same activity in each local area. This repetition of firing fields may reflect pattern completion,  
8 and may make it difficult for animals to distinguish similar local environments. In this review we  
9 will (a) highlight some of the navigation difficulties encountered by humans in repetitive  
10 environments, (b) summarise literature demonstrating that place and grid cells represent local  
11 and not global space, and (c) attempt to explain the origin of these phenomena. We argue that  
12 the repetition of firing fields can be a useful tool for understanding of the relationship between  
13 grid cells in the entorhinal cortex and place cells in the hippocampus, the spatial inputs shared  
14 by these cells, and the propagation of spatially-related signals through these structures.

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25           How locations in the outside world are represented in the brain has been a topic of  
26 intense research interest for almost 50 years, since the discovery of neurons in the rodent  
27 hippocampus - place cells - which fire in individual places in an environment (O'Keefe and  
28 Dostrovsky 1971). Following O'Keefe and Nadel's (1976) conceptualisation of the hippocampus  
29 as a cognitive map, much of the ensuing work has assumed that place cells comprise a  
30 representation of the entire environment in which the animal finds itself (though different  
31 reference frames are possible within this map, e.g. Poucet 1993; Gothard et al. 1996; Zinyuk et  
32 al. 2000). In the current review, we challenge this assumption of a global map in light of data  
33 indicating that many spatial cells are driven by local boundaries and a directional input. These  
34 influences provide an allocentric encoding of local spaces, which is only incidentally global.

35           Space is traditionally defined from two reference points. In the first, location within an  
36 environment is defined using 'self-relative' directions, such as "on my left" or "20 feet in front of  
37 me". This is egocentric space. In the second, locations are identified independent of the  
38 observer, for "halfway between the window and the door" or "behind the chair and towards the  
39 painting". This is allocentric space. In the current review we are primarily concerned with how  
40 the latter is represented in the brain.

41           In humans, representations of space likely vary in terms of their scale and detail. For  
42 instance, a person can recognise their location within a given room of their house, but also,  
43 simultaneously, where they are within a geographical region. Thus, different types of spatial  
44 representations may operate, depending on the task at hand (Burgess 2006; Ekstrom et al.  
45 2014). In the present review, we restrict our consideration to allocentric space as it is  
46 represented by (or as it correlates with) the firing fields of spatially tuned neurons in the rodent  
47 brain. Identifying the rules by which these operate may allow us to understand the interplay  
48 between location recognition and longer-range navigation.

49 Whether the mammalian brain maps space in local or global coordinates is an important  
50 issue because it likely constrains spatial cognition. From this perspective, there is evidence that  
51 certain types of spaces, such as repetitive local geometries, are more challenging than others  
52 for wayfinding. For example, city planners are discouraged from using repetitive street designs  
53 as they are considered disorienting (Rumbarger and Vitullo 2003). This effect is embodied in the  
54 repetitive streets of Brasília, which are challenging to navigate (Scott 1998). Difficulties in  
55 distinguishing locations can also be problematic for patients suffering from dementia. Such  
56 individuals can find long corridors confusing, especially those with repetitive elements (Netten  
57 1989; van der Voordt 1993). There is also evidence that patients prefer 'L' shaped corridors to  
58 long straight ones (Elmståhl et al. 1997; Marquardt 2011; Passini et al. 2000; Rainville et al.  
59 2002). As we will consider below, such observations are consistent with the responses of  
60 spatially tuned neurons in the rodent brain to repetitive local environments.

## 61 Place and grid field repetition

62 In the traditional view of place cells, each cell exhibits a unique firing field and together  
63 these place fields represent the animal's entire environment (e.g., Barnes et al. 1997; see  
64 Figure 1). One approach to studying place cells and other types of spatially-tuned neurons has  
65 been to manipulate the animal's environment and see how this affects firing fields (e.g., Muller  
66 and Kubie, 1987; Bostock et al. 1991; O'Keefe and Burgess 1996; Lever et al. 2002; Leutgeb et  
67 al. 2004; 2005; Barry et al. 2007; Chen et al. 2013; Krupic et al. 2015; Acharya et al. 2016). A  
68 second approach has looked at these cells during purposeful behavior. This work has shown  
69 that place cell firing is modulated by task demands (e.g., Markus et al. 1995; Wood et al. 2000;  
70 Moita et al. 2004; Hok et al. 2007), and by the internal state of the animal (Kennedy and Shapiro  
71 2004; 2009; for review see Schiller et al. 2015). From the perspective of the hippocampus at  
72 least, the latter approach has indicated a function beyond the representation of space. In the

73 ensuing discussion, however, we limit our consideration to studies focussing on the changes to  
74 the animal's environment, though we acknowledge that the addition of task demands also  
75 influences place cell firing correlates.

76         Within this domain, several findings suggests that when rats move between two or more  
77 similar maze rooms, a given place cell produces the same field in each room. For instance,  
78 Skaggs and McNaughton (1998) recorded dCA1 place cells while rats explored an environment  
79 composed of two identical compartments joined by a corridor. They found that place cells often  
80 showed similar firing fields in each of the two compartments (Figure 2A; see also Fuhs et al.  
81 2005). Thus, instead of having unique representations of each compartment, as one would  
82 predict for a mapping of the entire environment, many place cells showed similar fields across  
83 compartments. The lack of remapping observed between compartments suggests that place  
84 cells are partly driven by local views.

85         In an elegant extension of the Skaggs and McNaughton study, Spiers et al. (2015)  
86 recorded dCA1 place cells as rats moved between four parallel maze compartments connected  
87 with an alleyway. They found that individual place cells tended to show similar place fields in all  
88 four compartments (Figure 2B). Cells only formed a distinct representation for a specific box  
89 when its size or colour was changed, and even in this case repetition of fields was found in the  
90 remaining three boxes. These findings were replicated by Grieves et al. (2016), as will be  
91 described below.

92         A similar phenomenon has been observed in grid cells - neurones from the entorhinal  
93 cortex, pre-, and post-subiculum which exhibit multiple, regularly arranged fields within an  
94 environment (Hafting et al. 2005; Figure 1). For example, Derdikman et al. (2009) recorded  
95 from grid cells and place cells in a zigzag alleyway, or 'hairpin' maze and found that both types  
96 of cell showed firing fields that repeated across alleyways facing the same direction (Figure 2C).  
97 These fields did not repeat across alleyways that the animal entered in the opposite direction.

98 Repeating, local representations persisted regardless of the large number of alleyways (five in  
99 each direction), suggesting that self-motion information, such as distance travelled, did not  
100 inform the activity of these cells. The authors refer to this phenomenon as a ‘fragmentation’ of  
101 the firing fields.

## 102 Repetition/fragmentation of firing fields depends on direction

103 An important finding from Derdikman et al.’s (2009) hairpin maze experiment was that  
104 place and grid cell fields were modulated by the heading direction of the animal. Cells  
105 differentiated North facing compared to South facing alleyways and the position of fields was  
106 also dependent on the direction with which the rat ran through the maze (Figure 2C). As the zig-  
107 zag route through the maze was continuous, the most parsimonious explanation for this finding  
108 is that the spatial cells were sensitive to the animal’s allocentric direction (e.g., McNaughton et  
109 al. 1983; Muller et al. 1994), as opposed to alternating between different motivational states  
110 (Smith and Mizumori 2006).

111 Supporting this interpretation, Whitlock and Derdikman (2012) recorded from mEC  
112 layers II, III and V and showed that head direction cells, neurones in an interconnected series of  
113 brain regions that are tuned to individual allocentric directions (Taube et al., 1990a), maintained  
114 a stable firing direction throughout this apparatus. The head direction system is a defining input  
115 to both place cells and grid cells (Leutgeb et al. 2000; Zhang et al. 2013; Acharya et al. 2016;  
116 Peyrache et al. 2016; Winter et al. 2015; see also Rubin et al. 2014), one possibility is that such  
117 a directional input provides an invariant directional reference which contributes to repetition of  
118 spatial fields when an animal repeatedly faces the same direction across maze compartments.  
119 In this view, the head direction system provides a global reference frame across maze  
120 compartments (e.g., Taube and Burton 1995). This maintenance of orientation across

121 compartments likely requires self-movement of the animal between compartments; when a rat is  
122 passively moved between different compartments or local features, the preferred firing direction  
123 of its head direction cells can switch from room to local cue anchors (Stackman et al. 2003;  
124 Taube et al. 2013)

125         The notion that a directional input to place cells is also supported by findings from Nitz  
126 (2011), who recorded dCA1 place cells in an alleyway which spirals inwards to a point. The cells  
127 had multiple fields in coils of the spiral that have the same angular relation to the centre and  
128 which face the same direction (Figure 3B). Furthermore, as in Derdikman et al.'s (2009) hairpin  
129 maze, cells fired differently depending on the direction of travel through the alleyway. This is  
130 consistent with the finding of Fuhs et al. (2005) in a multicompartiment environment. They  
131 replicated the two box apparatus of Skaggs and McNaughton (1998), but also recorded dCA1  
132 place cells in the same two compartments joined end to end and connected directly by a  
133 doorway (Figure 3A). When the compartments were connected by a corridor, place cells  
134 showed the same activity in each. However, when the compartments were connected directly to  
135 one another, the cells formed a different representation for each compartment. Importantly, in  
136 the latter, the doorways are in different relative positions (South in one compartment, North in  
137 the other), whereas in the corridor situation the doorways are in the same position for both (e.g.,  
138 West).

139         The results of Tanila (1999) are consistent with these findings. Tanila recorded dCA3  
140 place cells in a similar apparatus – two compartments connected directly by a doorway. Similar  
141 to the results with CA1 cells, 91% of the place fields in CA3 cells differed between  
142 compartments. Again, as the rats actively moved between the compartments, it is likely that the  
143 doorway between the two served as a distinguishing landmark.

144         To directly assess the impact of compartment orientation as a distinguishing cue,  
145 Grieves et al. (2016) recorded place cells in a four compartment apparatus similar to the one

146 used by Spiers et al. (2015). In addition to this 'parallel' configuration, an alternative maze was  
147 used where a 60° angle was introduced between the compartments (Figure 3C). The same  
148 actual compartments were used in both situations, and they differed only in their orientation and  
149 the shape of the connecting alleyway for each. In the parallel configuration, dCA1 place cells  
150 fired similarly in every compartment, as observed by Spiers et al. (2015). However, similar to the  
151 results of Fuhs et al. (2005), when compartments were at a 60° angle to one another, place field  
152 repetition was not observed. These results again suggest that directional reference allows place  
153 cells to disambiguate otherwise visually and geometrically identical local environments.

### 154 Repetition of spatial fields may constrain spatial learning

155 As noted earlier, human navigation performance decreases as directional and geometric  
156 cues become invariant, such as in long repetitive corridors or streets (Marquardt 2011). Might  
157 repetition of the activity of spatial cells underlie such difficulties in navigation? To test this,  
158 Grieves et al. (2016) trained naïve animals on a conditional odor discrimination task in either the  
159 parallel or radial version of their four compartment maze (Figure 3C). In this task, an identical  
160 set of four odorised sand wells was present in each box and a different odor was rewarded in  
161 each one. Thus, rats had to discriminate between the compartments to find the food efficiently.  
162 In the parallel configuration, where field repetition was found, animals were significantly  
163 impaired in learning compared to the group trained in the radial configuration where field  
164 repetition was absent. These results suggest that local environments in which place field  
165 repetition is observed are more difficult for animals to discriminate compared to those in which  
166 place field repetition is not observed. Although it was not examined in the Grieves et al.  
167 experiments (where separate rats were used in the recording and behavioral experiments), it is  
168 also possible that learning to discriminate maze compartments yields more unique place cell



169 fields across compartments.

170 Can a bias towards local mapping be overcome with experience? Although rats in the  
171 Grieves et al. (2016) study were impaired in parallel compartments, some did eventually learn  
172 the task. Thus it is possible that with repeated experience of connected environments, a global  
173 representation replaces local maps. A recent study by Carpenter et al. (2015) provides evidence  
174 for this. They recorded grid cells in the mEC as rats explored two parallel, connected  
175 compartments similar to those of Skaggs and McNaughton (1998) although larger (90cm  
176 instead of 60cm square) in order to reveal the grid firing structure. During initial exposure to this  
177 environment, grid cells often fired similarly in both compartments. However, after multiple  
178 exposures to the environment, cells tended to possess fields that formed a continuous grid  
179 across the two compartments (Figure 4A). This suggests that, with experience, the encoding of  
180 local compartments gives way to a representation of the entire enclosure. Whether this slow  
181 change in grid firing is accompanied by a change in place cell activity is not known, although  
182 such a relationship has been observed in other experiments (Fyhn et al. 2007; Jeffery 2011). If  
183 grid and place cells behave similarly, it might also be predicted that grid fields are less local in  
184 compartments that face different directions.

185 In contrast to the spatial deficits reported by Grieves et al. (2016) and the gradual  
186 transformation towards a global map reported by Carpenter et al. (2015), some research  
187 suggests that a form of place field repetition increases with spatial learning. This evidence  
188 comes from studies by Frank et al. (2000, 2001) and Singer et al. (2010), where the activity of  
189 spatial cells while animals navigated mazes composed of multiple, parallel alleyways. As in  
190 Derdikman et al.'s (2009) hairpin maze, dCA1 and dCA3 place cells and neurons in the  
191 entorhinal cortex (superficial and deep layers of mEC) fired similarly in multiple alleyways  
192 (Figure 4B). Furthermore, these representations were also dependent on the direction of the  
193 animal's movement. In agreement with the view of the hippocampus as a pattern separator, this

194 field repetition was observed more in EC neurons than in hippocampal place cells. Frank et al.  
195 (2000, 2001) and Singer et al. (2010) termed this field repetition ‘path equivalence’ and  
196 suggested that it represents encoding of the relationship between behaviour and location. In  
197 support of this, the frequency of path equivalence appeared to increase as animals learned a  
198 task (Figure 4B). To account for this, it may be speculated that in well learned tasks, spatial  
199 cells also begin to reflect common elements of different paths, perhaps via inputs from regions  
200 such as the retrosplenial cortex (e.g., Alexander and Nitz 2017).

## 201 Visual, geometric, and directional inputs to spatial cells

202 Due to the strong control the geometry of the environment has over place cell activity  
203 (O’Keefe and Burgess 1996; Barry and Burgess 2007; Lever et al. 2002; see Figures 2D, 5A  
204 and 5B), it has been proposed that place fields arise from the activity of cells sensitive to  
205 boundaries, termed “Boundary Vector Cells” (BVCs) (Barry et al. 2006; Hartley et al. 2000).  
206 These cells were originally predicted to be sensitive to boundaries at a specific direction and  
207 distance from the animal (Figure 5C). Actual cells resembling BVCs were subsequently  
208 observed in the subiculum (Barry et al. 2006; Lever et al. 2009; Solstad et al. 2008; Broton-Mas  
209 et al., 2017) (Figure 1 and 5D), the presubiculum and parasubiculum (Boccaro et al. 2010), the  
210 mEC (Bjerknes et al. 2014; Savelli et al. 2008; Solstad et al. 2008) and recently in the anterior  
211 claustrum (Jankowski and O’Mara 2015) and the rostral thalamus (Jankowski et al. 2015).  
212 These ‘boundary cells’ are sensitive to walls, low ridges or even vertical drops (Figure 5C and  
213 D) (Lever et al. 2009). The directional component of boundary cells is presumably informed by  
214 the head direction system (Peyrache et al. 2016 but see Burgess et al. 2001; Byrne et al. 2007;  
215 Julian et al. 2015). Importantly, in multiple, geometrically identical, similarly oriented  
216 compartments the firing of a single boundary cell is expected to be identical (Carpenter et al.

217 2015; Lever et al. 2009). If place cells are driven by local borders (e.g., Zhang et al. 2014),  
218 identical place fields would be observed in each compartment. In this view, as the angle  
219 between identical compartments or alleyways increases, boundary cell firing should  
220 correspondingly start to differentiate them. It is also possible, however, that other types of  
221 spatially tuned neurons represent the shape of local environments (e.g., Broton-Mas et al.  
222 2017), and thereby contribute to repetition of spatial firing fields.

223         As an alternative, visual inputs could account for spatial field repetition. If the corners of  
224 a compartment or alleyway can function as visual cues, then parallel compartments or  
225 alleyways may fall on the retina in similar patterns at the same head direction. If the angle  
226 between these compartments is increased, however, this relationship will decrease. Thus, place  
227 field repetition could arise from the congruence of visual and directional inputs. As with  
228 boundary cells, neurons that are sensitive to a conjunction of head direction and position can  
229 also be found in the retrosplenial cortex (Cho and Sharp 2001). Grid cells are also sensitive to  
230 visual and olfactory contextual changes (Marozzi et al. 2015; Chen et al. 2016; Pérez-Escobar  
231 et al., 2016) and changes in grid fields are correlated with remapping in place cells (Fyhn et al.  
232 2007; Jeffery 2011; Monaco and Abbott 2011; Miao et al. 2015).

233         Are these inputs functionally different? Research suggests that there are differences in  
234 how visual information and boundaries are used. Field repetition can be observed in  
235 environments whether or not a distal visual cue is provided (Grieves et al. 2016; Derdikman et  
236 al. 2009), if proximal cues are provided (Fuhs et al. 2005) and even in the dark (Grieves 2015).  
237 This striking perseveration suggests that perhaps only local visual cues such as those utilised  
238 by Spiers et al. (2015) are enough to drive pattern separation and overcome field repetition,  
239 which would be suggestive of a contextual input, such as that from the entorhinal cortex. This is  
240 supported by the finding that in many environments humans and animals primarily utilise  
241 geometric information to orient themselves while ignoring contextual visual information (Cheng

242 1986; Hermer and Spelke 1994; Krupic et al. 2016; but see Learmonth et al. 2002; Hupback and  
243 Nadel 2005). Furthermore, mice have been observed to utilise contextual visual cues to  
244 recognise an environment, whilst continuing to make systematic heading errors, suggesting that  
245 contextual and geometric information may be processed and utilised by two separate systems  
246 (Julian et al. 2015). One possibility is that place cell firing is largely and primarily dictated by  
247 geometric inputs from boundary cells, but that this input is mediated by a contextual input from  
248 entorhinal cortex, similar to the contextual gating model proposed by Hayman and Jeffery  
249 (2008).

250         The view proposed here is that on initial exposure to an environment, a rapid process is  
251 initiated which relies heavily on geometric inputs from boundary cells to orient and arrange both  
252 place and grid fields. In a repetitive environment these inputs are identical in each local area  
253 and hippocampal pattern separation fails, resulting in repeating place fields. However, with  
254 greater exposure to an environment, information accumulated through path integration drives  
255 the repeating grid fields towards a global representation with low levels of field repetition  
256 (Carpenter et al. 2015) and this development in turn could potentially drive increasingly global  
257 (spatially unique) place fields. Evidence for rapid mapping based on geometry can be seen  
258 when comparing the time scales at which spatial cells develop their firing patterns. In novel  
259 environments boundary and head direction cells develop stable firing patterns instantaneously  
260 (Jankowski et al. 2015; Taube and Burton 1995; Taube et al. 1990b), whereas hippocampal  
261 place cells require 5-10 minutes to form stable place fields (Bostock et al. 1991; Frank et al.  
262 2004; Hill 1978; Wilson and McNaughton 1993) and grid cells require a number of hours to  
263 stabilise (Barry et al. 2012). Visual inputs also play an important role within this framework. For  
264 instance, when large contextual changes occur within an environment, like the colour change of  
265 a subcompartment, EC cells locally remap which allows for greater pattern separation in the  
266 hippocampus in the altered compartment.

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## Remaining challenges

269 A central theme of this review is that place cells, and to an extent grid cells, are driven  
270 by local boundaries and a directional input. If these are congruent across maze compartments,  
271 repetition of firing fields is observed. This suggests that, at least initially, the mapping of  
272 external, allocentric space in the mammalian brain is local, and not global.

273 Grid cell field fragmentation and place field repetition are strikingly similar, and would  
274 appear to represent the same phenomenon. However, several questions remain. First, as place  
275 fields are still present after grid cell firing is abolished (Brun et al. 2008; Hales et al. 2014), does  
276 inactivation of the mEC affects hippocampal field repetition (or vice-versa)? Second, do inputs  
277 from the subiculum, where many boundary cells reside, affect firing in either the mEC or the  
278 hippocampus? Indirect evidence for this is found in work showing that grid cells may be  
279 sensitive to border cell inputs (Hardcastle et al. 2015) and that lesions of the subiculum  
280 contribute to spatial navigation deficits (Morris et al. 1990). Third, what effects does disruption of  
281 the head direction system have on border/boundary cells (Burgess et al. 2001; Byrne et al.  
282 2007)? Finally, does disruption of the head direction system affect place field repetition?

283 Given the framework of this review, without head direction input place cells should be  
284 reduced to relying purely on visual inputs, assuming boundary cells require the head direction  
285 system. Do grid cells immediately form a global representation in radial compartments as place  
286 cells do and how do contextual changes in local compartments influence grid cells? One  
287 prediction is that grid cells remap immediately following a compartment context change and that  
288 this is accompanied by remapping in place cells, but this has yet to be shown in a  
289 multicompartment environment. With a better understanding of these relationships we should  
290 gain insight into processing between the hippocampus, the entorhinal cortex and the

291 surrounding structures. Ultimately, this may inform the design of repetitive environments to  
292 minimize spatial ambiguity.

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## 572 **Figure Legends**

573

574 **Figure 1** Spatially modulated cell types in the mammalian brain. **Top left:** The firing rate map of  
575 a dCA1 (hippocampus) place cell. Action potentials and dwell time are binned, smoothed and  
576 divided to give a spatial map of the cell's firing rate. Generally, hot colours represent high firing  
577 rates, cold colours represent low firing rates, and white represents unvisited locations. This cell  
578 has an area of high firing located to the Northeast of the environment, and this area is known as  
579 this cell's 'place field'. **Top middle:** An example of a medial entorhinal cortex (mEC) head  
580 direction cell. These 'polar' plots show the action potentials of the cell, binned in terms of the  
581 animal's head direction at the time and divided by the amount of time spent facing that direction  
582 overall. This cell fires at a high rate when the animal is facing to the North (90°) within the  
583 environment, and this is referred to as the cell's preferred firing direction. **Top right:** The firing  
584 rate map of an mEC grid cell. This is produced using the same method as for the place cell.  
585 Multiple firing fields can be observed which form a triangular or hexagonal grid that spans the  
586 environment. **Middle:** Firing rate maps of a single subicular boundary cell recorded in three  
587 different environments, a circle, a diamond, and a square, placed in the same room. Note that

588 the cell continues to fire along walls that subtend the rat at the same angle (North-easterly  
589 boundaries) even when the environment changes (adapted from Lever et al., 2009; Figure 3,  
590 cell 2d). **Bottom left:** The firing rate map of a border cell recorded in the mEC. **Bottom right:**  
591 An example of a modelled boundary vector cell, generated in the same way as in Hartley et al.  
592 (2000).

593  
594 **Figure 2** Examples of local encoding by place cells. Firing rate maps utilise the colour axis  
595 given below **B**. **A**, an example dCA1 place cell recorded in the maze used by Skaggs and  
596 McNaughton (1998). **B**, dCA1 place field repetition in the four compartment apparatus used by  
597 Spiers et al. (2015). **C**, Derdikman et al.'s (2009) hairpin maze. An example of mEC grid field  
598 repetition is shown in the top row of firing rate maps, recorded when the animal moved through  
599 the maze from left to right (left map) and right to left (right map). A similar example of dCA1  
600 place field repetition is shown in the rate maps below these. **D**, Two example dCA1 place cells  
601 recorded by Lever et al. (2002) in a circular and square environment of the same size.

602  
603 **Figure 3** Place field repetition depends on direction. In the top rows, the maze schematics are  
604 shown, and in the bottom rows examples of the corresponding firing activity maps are provided.  
605 The colour bar next to **A** corresponds to **C** also. **A**, The maze used by Fuhs et al. (2005); left:  
606 example of dCA1 place field repetition when compartments were parallel and connected by a  
607 corridor (corridor data are ignored); right: the same cell showed a lack of repetition when the  
608 compartments were rotated 90°, and abutted each other. **B**, The mazes used by Nitz et al.  
609 (2011) and Cowen and Nitz (2014). Rats ran along a spiral path of either a square (left) or  
610 circular (right) maze. In both, linearised rate maps revealed that dCA1 place cells have multiple  
611 fields which occur when the animal is facing the same direction. **C**, The mazes used by Grieves  
612 et al. (2016). Two example dCA1 place cells are shown, one per row. Left column: place field

613 repetition when animals navigate four parallel compartments connected by a corridor; right  
614 column: absence of place field repetition when the same compartments are arranged in a radial  
615 formation.

616

617 **Figure 4** Mixed evidence for pattern repetition changes with learning. **A**, Top diagram shows a  
618 floor plan of the maze used by Carpenter et al. (2015). The second row shows representative  
619 rate maps from one mEC grid cell for the two compartments in an early session (session 4)  
620 where it fires similarly in two compartments. The third row shows maps for the same cell in a  
621 later session (session 19). Here it fires with a global representation - the grid pattern extends  
622 between the environments as if the wall between them was not present. The bottom scatter plot  
623 shows the result of subtracting the measure of local encoding from one of global encoding for all  
624 grid cells that were recorded at differing session intervals of exposure. As animals were  
625 exposed for more sessions their representation became more global, and thus the line  
626 corresponds to a linear increase. **B**, Top diagram shows a floor plan of the maze used by Singer  
627 et al. (2010). The second row shows the firing rate map of a dCA1 place cell which shows  
628 pattern repetition, and the row below this shows the same data when the color map is capped at  
629 3Hz. The bottom bar graph shows the normalised overlap or similarity of place cell firing (when  
630 linearised) for cells recorded by Singer et al. (2010) in their multi-arm maze. Greater overlap  
631 here is suggestive of pattern repetition in the maze arms and this seems to increase with  
632 training. **C**, The top diagram shows a schematic of the maze used by Grieves et al. (2016). The  
633 plot below this shows the average level of correlation between compartments as a function of  
634 recording session. Correlations between compartments in the parallel version of the task were  
635 consistently higher than those in the radial version. Moreover, the level of correlation in either  
636 configuration did not change significantly over the course of the experiment. **D**, Top diagram  
637 shows a mock firing rate map for a cell recorded in the maze used by Spiers et al. (2015). The

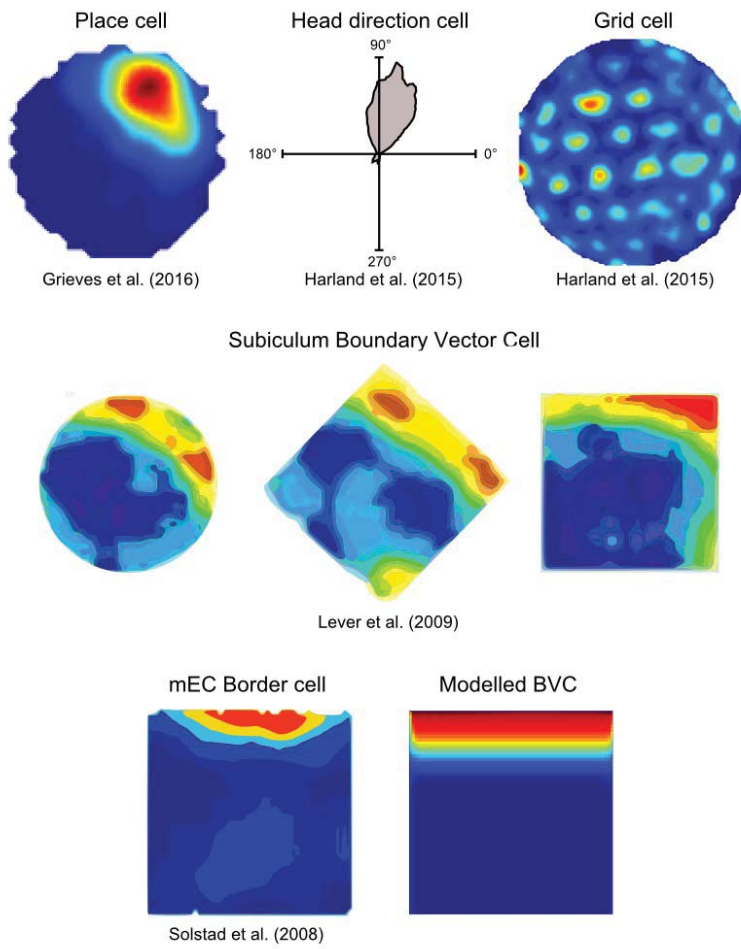
638 numbers show the distance of each compartment (in compartments) from the one with the  
639 highest firing rate. The plot below this shows the highest compartment firing rate (compartment  
640 0) and firing rates of every other compartment ranked in order of their distance from this  
641 (compartments 1-3) found by Spiers et al. (2015). This relationship is shown for the first day of  
642 recording and the last. Because this analysis selects the highest firing rates for compartment 0,  
643 this value is significantly higher. If some form of rate coding or remapping was present the other  
644 compartment distances would also be distinguishable in terms of firing rate. However, this is not  
645 the case and this effect does not develop with training.

646

647 **Figure 5** Pattern repetition likely reflects environmental geometry. The color bar below **A**  
648 applies to **A**, **B** and **D**, and the color bar below **C** applies to **C** and **E**. **A**, Example adapted from  
649 O'Keefe and Burgess (1996) of a dCA1 place cell recorded in an environment where the walls  
650 could be moved to change its size. In the small square the cell has a field in the top left corner.  
651 When the square's length was extended (bottom left plot) the cell's firing remains unchanged.  
652 However, when the square's width was extended (top right plot) the place cell's field extended  
653 proportionally. When the environment was extended isometrically the cell's field faintly extends  
654 equally in all directions (bottom right plot). These results show that place cell firing is at least  
655 partly dictated by boundaries in the animal's environment and that some boundaries exert more  
656 control over a given cell than others. **B**, Middle plot shows the firing rate map of a dCA1 place  
657 cell recorded in a square environment with a bisecting wall. Note that the cell has two fields, one  
658 on each side of the barrier. The plot below this is of a modelled place cell generated using BVC  
659 inputs and shows the same pattern of firing (figure adapted from Barry and Burgess 2007). **C**,  
660 The firing rate maps of an example, modelled, boundary vector cell in four different shaped  
661 environments. This cell maintains the same preferred firing direction (roughly North West) and  
662 distance in all environments (modelled using the Boundary Vector Cell model, Barry et al.

663 2006). Note that in the top right plot, where a barrier bisects the environment the BVC's firing is  
664 also bisected and takes on a repetitive appearance. **D**, Example boundary cell recorded from  
665 the rat subiculum in a three platform environment, adapted from Stewart et al. 2014. The cell  
666 fires along the West boundary of each platform, which in this case is a vertical drop. **E**, A dCA1  
667 place cell recorded in an elevated platform maze composed of four parallel alleyways. In this  
668 maze we can see that vertical drops are also sufficient to drive pattern repetition in place cells  
669 (Grieves 2015). This cell does not fire in the far right arm of the maze, and this is consistent with  
670 the findings of Spiers et al. (2015) and Grieves et al. (2016) which suggest that place field  
671 repetition is a continuous phenomenon. In repetitive environments, many place cells exhibit  
672 repeating fields in every sub-compartment, but some only exhibit them in a minority of  
673 compartments and some do not exhibit repeating fields at all. This suggests that the strength of  
674 different inputs (e.g., geometry, self-motion) may vary for different place cells.

675



**Figure 1**

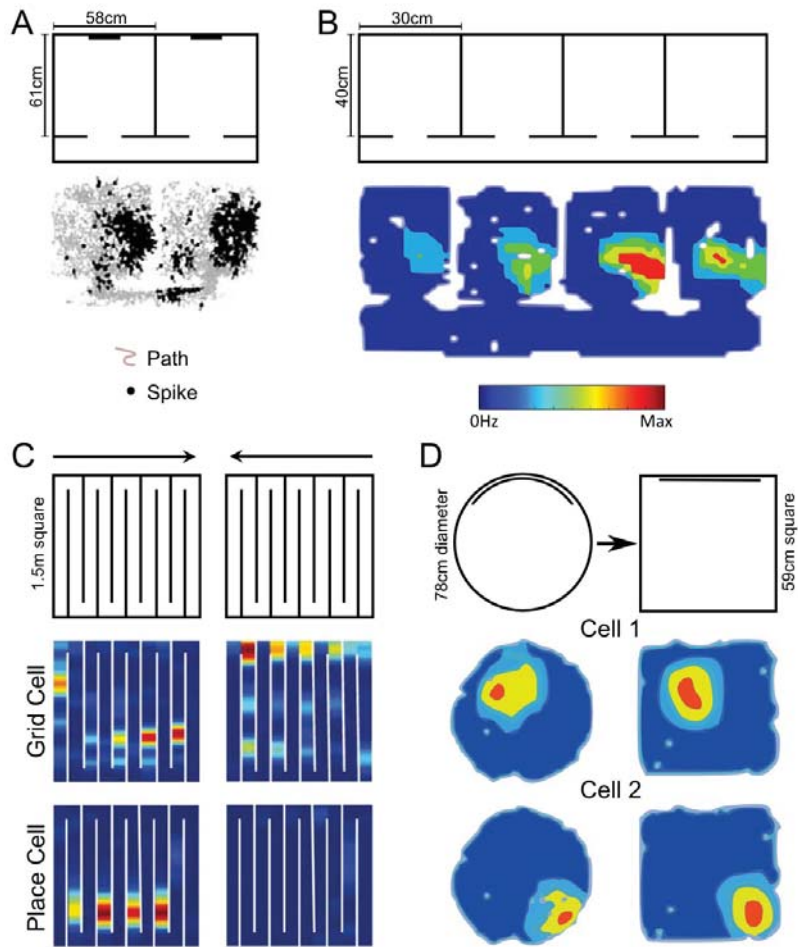


Figure 2



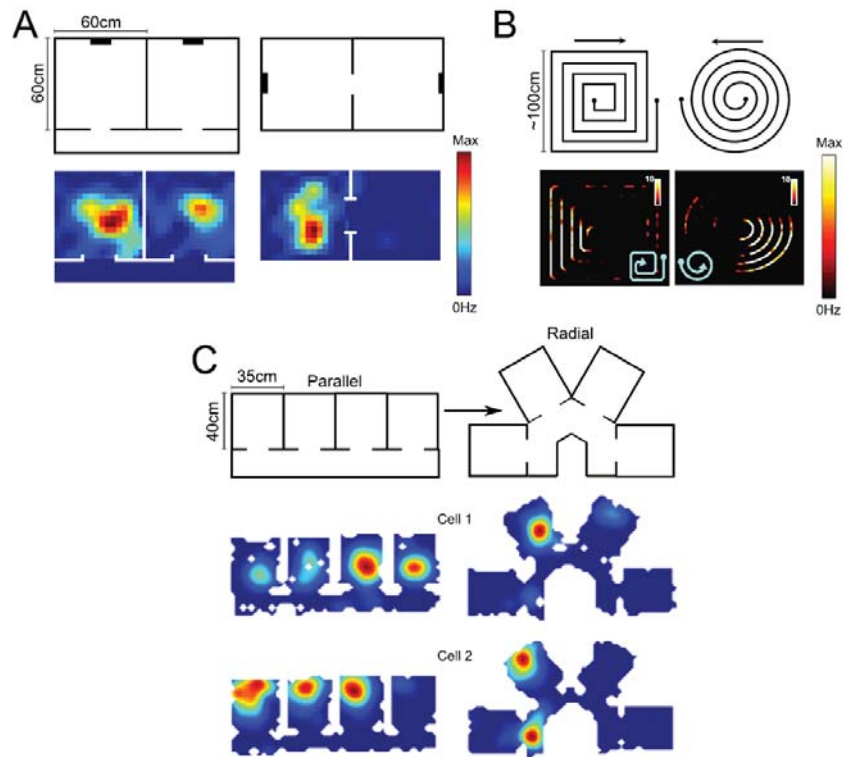
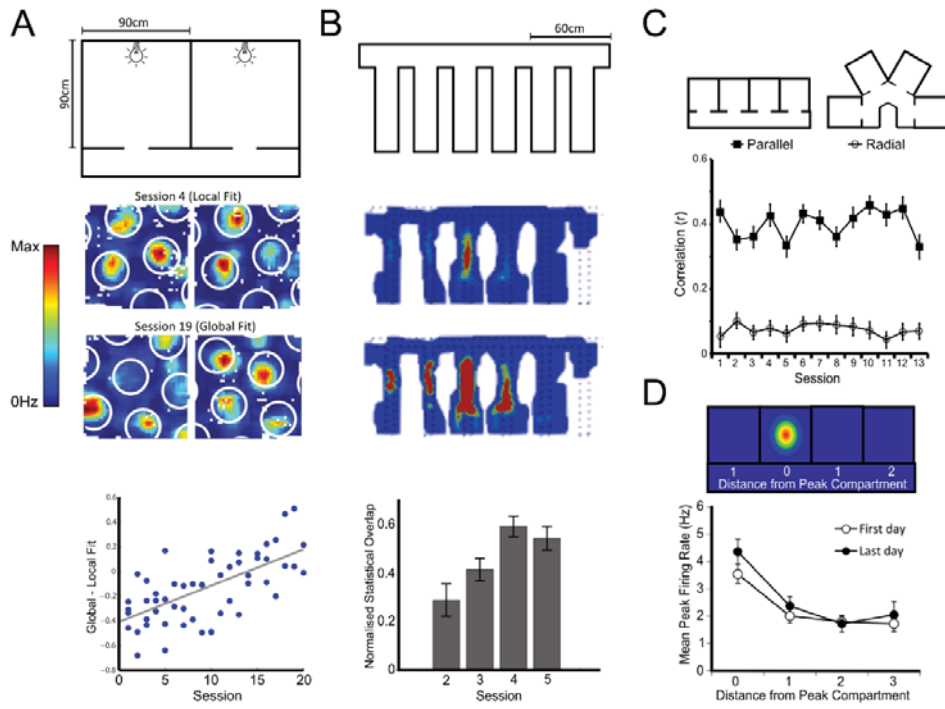


Figure 3



**Figure 4**

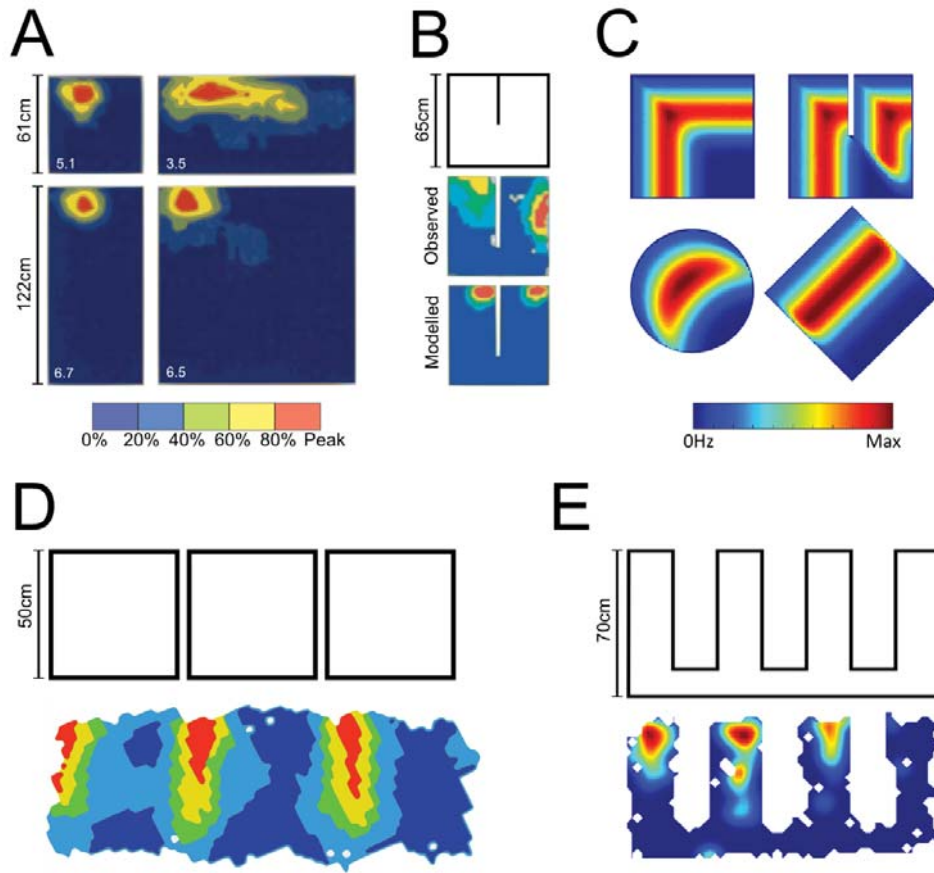


Figure 5