A Summary of Spatial Representations in a Rat Brain

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This article was originally the "Read-me" file for a series of documents (referred as "this documentation" in this article). This series of documents is aimed to provide an overview of the major parts in rat brain involved in spatial representation, in terms of their connections, functions, and lateralisation.

The following regions of rat brain are covered in this documentation as they are shown to be essential to rat's spatial recognition and navigation abilities: Posterior Parietal Cortex (PPC), Retrosplenial Cortex (RSC), Entorhinal Cortex (EC), Dentate Gyrus (DG), Cornu Ammonis 3 (CA3), Cornu Ammonis 2 (CA2), Cornu Ammonis 1 (CA1) and Subicular Complex (SC), where EC and SB are parts of Parahippocampal Cortex, and DG, CA3, CA2 and CA1 form the Hippocampus Proper. The parts providing sensory inputs (e.g. the visual cortex areas such as V1-V5), or the parts sending behavioural outputs (e.g. the motor cortex areas) are not covered here, since the main goal of this documentation is not about understanding how a rat's sensory systems or motor systems work.

This article follows similar structure as the individual report in this series. Apart from summarising the information covered in this documentation, it is also a note on easy to be neglected points, which could be of significance in seeing the bigger picture.

1 Connection

The connections in brains are highly complex and not entirely mapped by humans yet. The summary below (Figure 1) is extremely simplified. However, it can give us a rough idea how different regions relate to each other, thus to aid the understanding of the spatial representation model in the brain. For a more detailed description of brain connectivity, please visit http://connectivity.brain-map.org/, which provides extensive experimental data on brain anatomy visualized interactively in 3D.

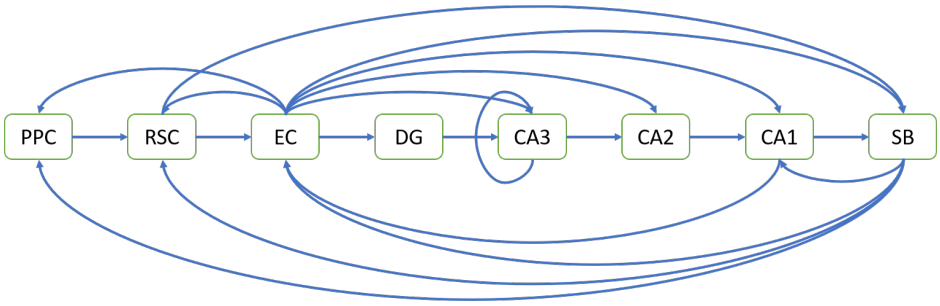

Figure 1: This is a schematic diagram of the simplified connections between the regions covered in this documentation. Inhibitory connections are not included. The inputs and outputs from/to other regions are not included.

In general, the sensory and motor inputs processed by PPC and RSC, flow to the hippocampal formation; the behaviour decisions output from CA1 to the subiculum and the EC region, and back to RSC and PPC to the motor neurons. However, each of the regions also receives/projects inputs/outputs from/to other areas apart from the ones mentioned here, e.g. EC also receives sensory input from postrhinal/perirhinal cortices, which connect to different areas in neocortex. These inputs/outputs are described in the individual documents for each area. Some of those inputs/outputs play important roles in spatial encoding and navigation, e.g. emotions can affect memory formation and decision making, but this documentation does not discuss them much as most studies of emotions focus on general functionality rather than specific relations to spatial recognition.

Moreover, reciprocal connections should not be neglected as they are very common across different areas of the brain. Except for the projections within the hippocampus proper (which are relatively unidirectional), most of the connections are bidirectional as shown in Figure 1. The properties of a certain reciprocal connection largely depend on whether it is the exact same subgroup of the neurons that is receiving the backward projections, as well as the strengths of the projections in each direction. Sometimes the strengths are quite different, which makes one of the directions major for the information flow and the other direction modulates this flow, e.g. between DG and CA3. In some cases, the projections in each direction may carry different types of information, e.g. the projection from RSC to EC carries mainly sensory information while the projection from EC to RSC mainly carries the output processed by the hippocampus.

Apart from the reciprocal connections, interneurons are also very common and important but easily be forgotten. There are around 20-30% of interneurons in the neocortex and hippocampus [1], which are the areas with the highest varieties of interneurons among central nerve systems [2]. Interneurons are primarily inhibitory, or have inhibitory effects in the target area (e.g. the neuron itself is excitatory but innervate an inhibitory neuron in the target area). Most of the interneurons predominantly connect to local principle cells, whereas some are long-range GABAergic cells (e.g. the ones across CA1-3 and DG areas). The major roles of interneurons are to stabilize brain activity levels, as well as to generate oscillations, e.g. theta/gamma rhythms. It is also shown that interneurons can directly encode spatial information. For example, the firing patterns of hippocampus interneurons are reported to be position modulated and obey phase precession dynamics [3, 4]. Also, the firing rates of CA1 interneurons exhibit an obvious decrease as the rat moves from familiar to novel environment, while the firing rates of DG interneurons increase [5, 6]. However, only few studies address the functional roles of interneurons in spatial representations apart from those discussing brain rhythms (the keywords "spatial representation cell interneuron" return 32,900 results in Google Scholar Search while "spatial representation cell" returns 840,000 results), so this documentation does not mention interneurons much as well.

The reciprocal projections and interneurons are two of the many factors that make the biological model really complicated, but at the same time make the brain so powerful. They allow different regions to "talk" to each other, synchronize brain activity, exchange information to enhance integration, or adjust firing patterns in a feedback/feedforward manner.

2 Function

Allo/Ego-centric	Encoded Information	PPC	RSC	EC	DG	CA3	CA2	CA1	SC
Allo & Ego	Cue (x Head direction)	Y							
Route (Allo & Ego)	Route	Y	Y						
Ego	Head Direction	Y	Y	Y					Y
Ego	Head Direction x Self-motion	Y	Y						
Ego	Self-motion	Y	Y						
Allo & Ego	Multiple Stimuli		Y						
Ego	Speed		Y	Y				Y	
Allo	Grid			Y					Y
Allo & Ego	Grid x Head Direction			Y					Y
Allo	Border			Y					Y
Allo & Ego	Boundary Vector								Y
Allo	Object x Place			Y					
Allo	Ordor x place			Y					
Allo	Place cells				Y	Y	Y	Y	
Allo	Social Information						Y		

Table 1: A summary table of the spatial representations in each region and the type of information encoded. "Y" means the information on the left has been found to be encoded by subgroups of neurons in that region. Blank cells in the table do not mean there is no representation of a certain information in that region, but only mean it has not been reported. "Allo" : allocentric information; "Ego": egocentric information; "Route": route-centric information.

In Table 1 the names of the spatial representation types follow the conventions in literature. Note that each region actually performs many more functions than mentioned here, but they are not the focus of the current work thus not discussed fully in this documentation.

It is not hard to notice from the Table 1 that PPC and RSC encode mostly egocentric information and the parahippocampal and hippocampus regions encode mostly allocentric information. However, it is hard to define any of them to be strictly egocentric or allocentric. Even in the allocentric encoding dominant region such as the hippocampus proper, speed encoding still exist as an example of the egocentric representation [7, 8], though the form of representation is different (in EC, the speed is represented by both the firing rates of neurons and the amplitude of theta oscillation, whereas in CA1 the speed is reported to modulate the rhythm frequency).

Both the allocentric and egocentric reference frames are essential since they aid the two main strategies in navigation: 1) the use of landmarks/cues and 2) the path integration strategy, respectively (the former one highly relies on allocentric information and the later one highly relies on egocentric information). It is proposed that PPC and RSC may play major roles in transforming and simultaneously representing two reference frames [9, 10]. However, the detailed mechanism of conversion between reference frames and the switching between the two navigation strategies is not well understood yet.

Another point to notice is that similar spatial representations in different regions do not necessarily mean causational relations (i.e. one region inherits the neuron activities from another). For example, both the cells in the entorhinal cortex and the pre/parasubiculum exhibit grid, border and head-direction firing patterns, but it is more likely that each region generates these representations locally, given the projection natures among them [11]. This leads to the following two questions. Why do different regions generate similar spatial representations independently? Is it more efficient than inheriting strategy or is it for "back-up" purpose? Unfortunately, we do not know yet.

Moreover, because brain research through history tends to focus on certain areas, not every region is well discovered, so that the Table 1 is expected to be proved quite incomplete as studies progress. For instance, CA2 had been neglected by most of the hippocampus researchers for a long time, only recently has CA2 been reported to participate in spatial recognition by encoding social and temporal information. Similarly, there is an increasing trend in the studies of the retrosplenial cortex. The history of neuroscience is continuing developing, thus many conclusions in this documentation are kept open.

Also, more research need to be done to better understand how different functional groups in different brain areas relate to each other, how these spatial representations are decoded by the network to aid decision making or encoding in other brain areas, and how brains develop such a network through maturity. All these questions are yet to be answered in the future, as described in a 2017 review paper [12].

3 Scales

3.1 Spatial Scales

Two strategies are adopted by the brain to cope with different scales of similar type spatial representations. The first one is to have different subgroups of neurons operate at different scales. A typical example is the consistent scale variation of firing fields of grid cells and place cells from the dorsal to ventral parts in both entorhinal cortex and hippocampus proper. Similarly, the speed cells in EC exhibit linear relationships between the firing rates and locomotion velocities with different gradients and intercepts, to encode different ranges of speed.

The second strategy to cope with different scales is the opposite of the first one: the representation scales up or down as the environment changes. The route cells in PPC are good examples here: their firing patterns can be compressed or expanded in size with the change in the scale of the route itself. By contrast, the firing patterns of route cells in the RSC cells use the first strategy: different subgroups encode the route at different scales, e.g. quarter scale, half scale, or full scale of the route.

3.2 Time Scales

In terms of temporal scales, it is more complicated as the representation of time is not well-understood yet (another not well understood mechanism). There are four types of mechanisms regarding time scales identified so far.

First, the time cells in the hippocampus register a sequence of time in a similar manner as the place cells register locations. They can undergo "re-timing" when the temporal structure is altered, similar to the "re-mapping" for place cells when part of the environment is changed (please see the review paper by Buzsaki and Eichenbaum groups for more details [13]). The similarity and overlap between the temporal map and spatial map in the hippocampus points to the possibility that the hippocampus may treat time just as another dimension in addition to the space, and it leaves us pondering whether there are other dimensions or other sorts of map in the hippocampus. However, the assemblies of the time cells can only register at scales of tens of seconds, which points to the second mechanism of time representation.

The second mechanism is more of a speculation so far, but it does work at longer time scales: the firing patterns of place cells in CA2 (some in CA1 and LEC) become dissimilar over hours or days, which may act as the "prerequisite" for encoding distinguishable memories over different periods [12].

The third type of time modulation is through different brain oscillations, such as theta rhythms (around 4-7Hz), and gamma rhythms (around 25-100Hz). As mentioned before, brain rhythms are mainly generated by interneurons and have inhibitory nature. The brain oscillations, e.g. the gamma rhythms, are proposed to refine the firing response and control the firing windows (the firings near the peak of the rhythm will be inhibited [14]). Also, there are quite a few studies about the theta phase precession of place cells (the hippocampus place cells fire in later phases of theta rhythms when the rat is entering the place field and fire at earlier phases when exiting) [15]. Some proposed that the interference of theta oscillations are the sources for the grid patterns in EC [16]. Besides, the functional differences between slow (around 25-55 Hz) and fast (around 60-100 Hz) gamma rhythms as shown in Table 2 may give us some hints about how brain oscillations modulate firing activities and affect the temporal encoding.

Reference	Slow Gamma Rhythms	Fast Gamma Rhythms	Implication
C. Zheng (2016) [17]	Associated with longer-path encoding on a compressed time scale, extending ahead of the current location; successive slow gamma phases can represent sequences of locations.	Associated with shorter paths and represent rat's current location; have not been observed to encode spatial sequences.	"Slow gamma promotes activation of temporally compressed representations of upcoming trajectories, whereas fast gamma supports coding of ongoing trajectories in real time"
K. Bieri (2014) [18]	The amplitude and phase-locking of spikes increases during prospective coding; the spikes occur earlier in place fields; encodes upcoming positions.	The amplitude and phase-locking of spikes increases during retrospective coding; the spikes occur later in place fields; encodes past positions.	"Alternating slow and fast gamma states allow the hippocampus to switch between prospective and retrospective modes, possibly to prevent interference between memory retrieval and encoding."
L. Colgin (2009) [19]	Synchronized between CA1 and CA3; appear at different phases and theta cycles of the CA1 theta rhythm from the fast gamma.	Synchronized between CA1 and MEC; appear at different phases and theta cycles of the CA1 theta rhythm from the slow gamma.	"These results point to routeing of information as a possible function of gamma frequency variations in the brain and provide a mechanism for temporal segregation of potentially interfering information from different sources."

Table 2: A list of studies about functional differences between slow (25-55 Hz) and fast (60-100 Hz) gamma rhythms.

The fourth possible mechanism for temporal encoding is embedded in the firing timing of certain subgroups of neurons. For example, a subpopulation of the PPC egocentric cue cells and the self motion cells fires before the actual movements, sometimes even 1s in advance [20, 21], which may contribute to the movement planning function in PPC. Also, the speed cells in MEC are reported to fire ahead of the actual acceleration, and their firing dynamics is 50-80 ms ahead of grid cells, which points to the mechanism where the speed cells actively update grid patterns [22].

4 Evidence of Lateralisation

The hippocampus region has generally been thought to be an unlateralized area. However, studies did find some differences between two hippocampi of different sides in memory forming/retrieval and

spatial recognition. A brief list of the studies is shown in Table 3. The list is not restricted to rodent research since there are too few papers on this topic. When analysing the experimental results of hippocampus lateralisation studies, one should be careful about what the results actually imply. For example, the right hippocampal activity decreases when retrieving more remote autobiographical memories, which does not necessarily imply that the "freshness" of the memory is the main factor here. In fact, the hippocampal laterality of autobiographical memories can be influenced by recollective qualities of the task and the age of the participants [23]. In short, it is still hard to summarise the lateralisation properties in the hippocampus, until we have a better understanding of the connections and coding/decoding mechanism of the hippocampus and related areas.

	left	right	Reference
Human	Less involved in short term memory of object-location associations	More involved in short term memory of object-location associations	[24]
	London taxi drivers have smaller left hippocampus comparing to the right side	London taxi drivers have larger right hippocampus	[25]
	More involved in egocentric sequential information encoding	More involved in allocentric spatial information encoding	[26]
	Smaller left EC volume is found in patients who are progressing to ALzheimer than just in a stable mild cognitive impairment state	No difference	[27]
	No difference	Activity decreased when retrieving more remote autobiographical memories, and more involved in recollective autobiographical memories retrieval	[28, 23]
Rodent	Left CA3 silencing impaired long-term memory	Right CA3 silencing does not impair long-term memory	[29]
	Microinjecting ANG II (a type of hormone) to the left hippocampus increased learning and memory performance more	Increased less in learning and memory performance when ANG is injected	[30]
	The left DG is more active during object exploration	The right DG is less active in object exploration comparing to the left side	[31]
Avian	Domestic chicks with damaged left hippocampus could still find the food buried in the center of the arena given geometric cues	Domestic chicks with damaged right hippocampus could not find the food buried in the center of the arena given geometric cues	[32]

Table 3: A list of studies on hippocampal lateralisation. The leftmost column indicates the animal hippocampus the study addresses.

5 Evidence of Building-blocks

After studying the forms of spatial representations in rat brains it seems highly likely that the building-block mechanism is used in rat navigation. The building-block mechanism is the ability to break down complex knowledge into simple blocks/attributes and utilise them to solve problems. We can find two types of building-blocks in the spatial recognition in rat brain. The integration and focus switching among different building-blocks enables the brain to perform spatial tasks.

The first type is relatively basic and rigid, such as the boundary knowledge, speed information, head-directions, etc. This type of building-blocks is usually environment independent, e.g. scale-independent or light-independent, which means no matter what kind of arena the rat is in, the rat can always recognize certain building-block properties of the environment thus perform similar responses based on that, e.g. whenever the rat encounter a border, it will generally turn to avoid crashing on it.

The second type of building-blocks is more complicated, more environment dependent, and usually mediated by the combination of knowledge of the first type. For example, a complex route can be divided it into building-blocks of sub-routes, and subgroups of PPC route cells log sub-routes with respect to headings and sequence of actions (e.g., turning left, turning right) [33]. This type of logging will expand or shrink in proportion to the change in the scale of the route as mentioned before [34, 33]. The place cell in hippocampus is another good example for this type of building-blocks. The place

cells register certain locations in an environment. When the environment is partially altered, the firing pattern of place cells will undergo partial remapping, either in terms of firing rates or firing fields [35, 36]. In addition, place cells in different regions are modulated by different environment cues, e.g. CA3 place cells are more sensitive to distal cues and CA1 place cells are more sensitive to local (proximal) cues.

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