

Subicular Complex

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1 Connection

The subicular complex is the most inferior part of the hippocampal formation. It is located between the entorhinal cortex and CA1.

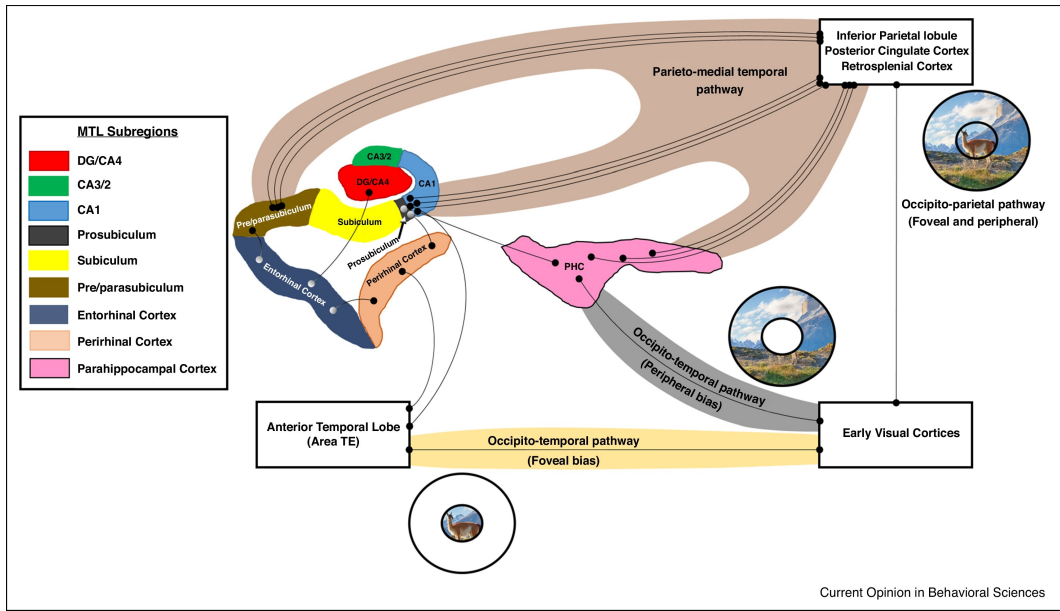


Figure 1: “Visual processing pathways into the hippocampus. This schematic diagram represents the major inputs into the hippocampus through the dorsal parieto-medial temporal visuospatial processing pathway and the ventral occipito-temporal visual processing pathway. Note the preferential connectivity of the pre/parasubiculum with regions of the dorsal pathway (light brown background) while the prosubiculum/CA1 region has a more distributed pattern of connectivity directly from the dorsal pathway and indirectly through portions of the ventral pathway which display foveal (ivory background) and peripheral (grey background) biases. For simplicity, the PHC is presented to the right of the hippocampus but in fact this region is located in a more posterior region of the medial temporal lobe.”[1]

1.1 Input

- Subiculum receives heavy projections from CA1 [2], and all parts of CA1 input to all regions of subiculum” [3]
- Subiculum receives reciprocal projection from the entorhinal cortex layer III.
- Subiculum receives projections from the perirhinal cortex and prefrontal cortex. [4]
- Subiculum also receives inputs from the medial frontal cortex, mostly inhibitory [5].
- The pre/para/prosubiculum mainly receives input from the parieto-medial temporal pathway (one of the three main visuospatial pathways). This pathway starts from caudal inferior parietal lobule (cIPL), then project to posterior cingulate cortex (PCC), retrosplenial cortex (RSC) and parahippocampal cortex (PHC), then send to pre/para/prosubiculum. [6, 1]
- The prosubiculum receives projections from RSC and PPC [1].

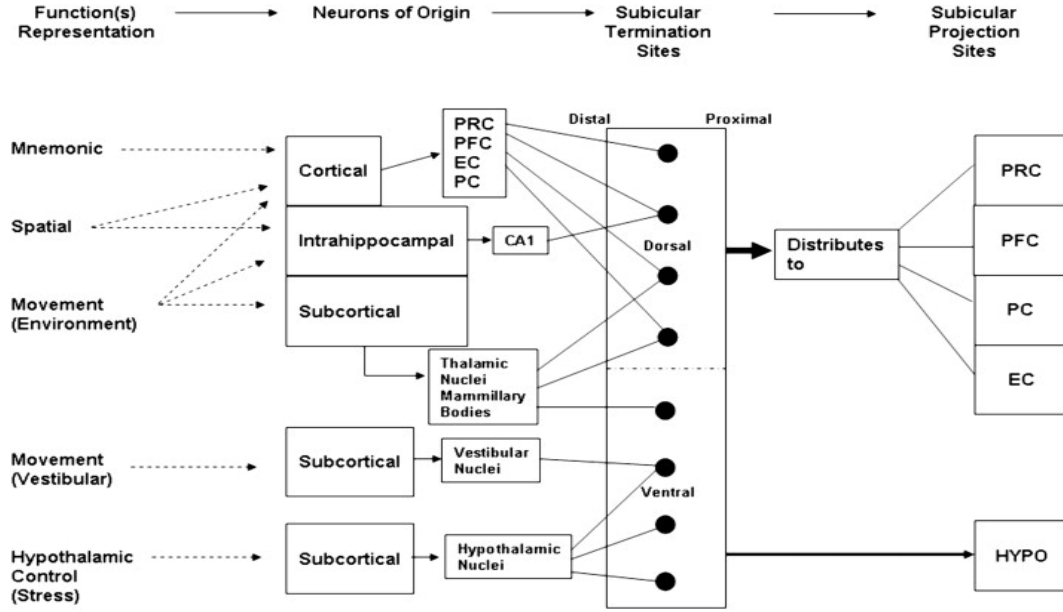


Figure 2: “A model of subicular functions and connections. Here, synaptic transmission and anatomical connectivity runs from left to right (a deliberate simplification); information of differing types (mnemonic, etc.) derives from various antecedent cortical and subcortical circuits, and is projected to the subiculum, converging in particular patterns, thereby giving rise to differing neuronal response types. EC: entorhinal cortex; Hypo: hypothalamus; PRC: perirhinal cortex; PFC: prefrontal cortex; PC: parietal cortex. For simplification no details of distalproximal distribution of fibres is provided (but these do vary); nor are there details of intrasubicular longitudinal associational fibres.” [4]

1.2 Output

- Subicular complex has strong both ipsi- and contralateral projection to entorhinal cortex. Presubicular projects more to EC layer III; parasubiculum more to layer II. Both pre- and para subiculum have weak projections to EC layers I and IV. [7, 8] Subiculum projects to all layers of the entorhinal cortex, especially at more ventral parts [8].
- Subiculum strongly output to regions between spatial and motor systems, also to septal nuclei, pre-frontal cortex, lateral hypothalamus, amygdala etc..
- Subiculum returns a small projection to CA1.[9]

1.3 Main Components

The names are a bit inconsistent among studies. See [10] for a detailed definition and description about different regions and their connections of the subicular complex.

- Subiculum: receive major input from CA1 and project to layer IV and V of entorhinal cortex and presubiculum, sometimes considered as part of the hippocampal formation but sometimes not. [4]
- Presubiculum: part of the Brodmann’s area 27 in posterior cortex.
- Parasubiculum: one of the longest and narrowest cortical structures.
- Postsubiculum: in the literature, the primate prosubiculum and rat postsubiculum are inconstantly identified [10]. Sometimes the dorsal part of the presubiculum is more commonly known as the postsubiculum [11].
- Prosubiculum: this term is often used in primates but rarely in rodents. It refers to the region between the CA1 and the subiculum, which has high cell density and small cell sizes. [10]

Note: Because of limitations in the resolution of neuroimaging techniques, most of the studies did not distinguish between pre/para-subiculum [1].

2 Function

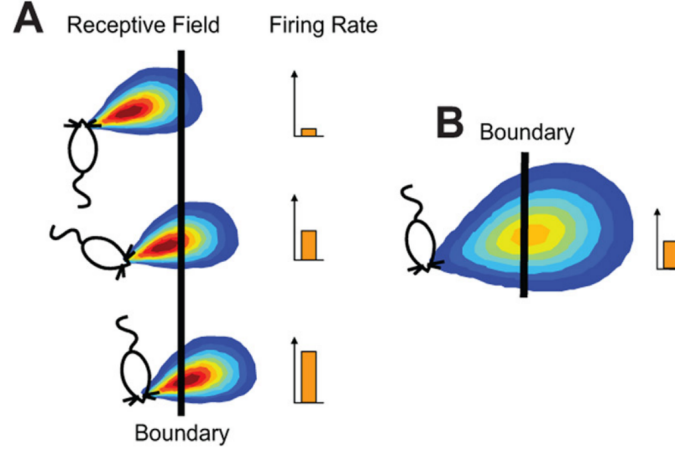


Figure 3: “A boundary vector cells (BVC) model. A, The receptive field of a BVC tuned to respond to a barrier at a short distance east-northeast from the animal. B, BVCs tuned to respond to barriers farther from the animal will have broader receptive fields.” [12]

Subiculum

- Boundary vector cells (BVC): register the allocentric direction of the boundary and the distance to the boundary at the same time, regardless of head directions. The firing field of a boundary cell is water-drop like, orientating to a boundary. The BVCs response preserves at short range without light, suggesting that the BVCs also using other sensory inputs apart from visual signals. These excitatory boundary cells is thought to be “likely provide input to place cells and could stabilize grid cells indirectly via the place cells, and/or could help to stabilize grids directly”. [13, 12].
- Boundary-off cells: fire in all the locations but stop firing when near a barrier. [13].

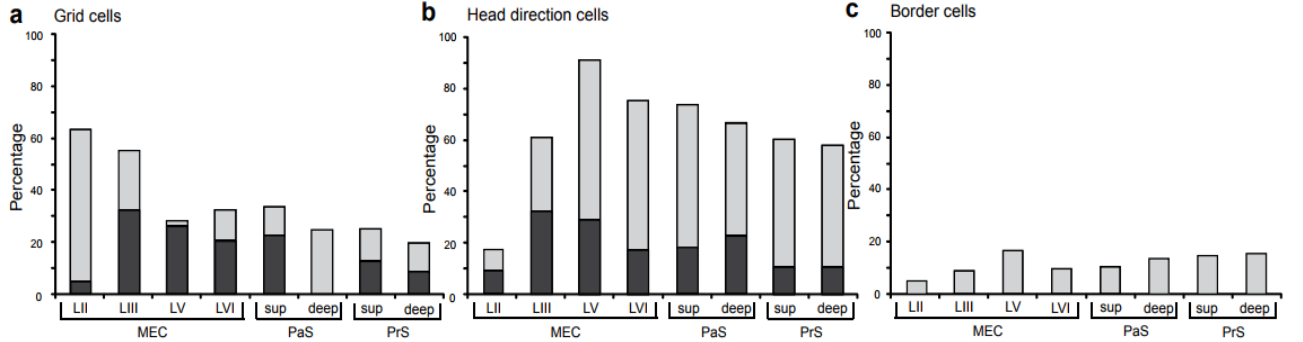


Figure 4: “Distribution of grid cells (a), head direction cells (b), and border cells (c) in the parahippocampal cortex. The figure shows the percentage of each cell type across layers of medial entorhinal cortex (MEC), parasubiculum (PaS) and presubiculum (PrS) (L = layer, sup = superficial layers). The proportions of cells with conjunctive grid head direction properties are indicated in dark grey.” [14]

Pre/parasubiculum

- Grid cells: mainly in dorsal pre/parasubiculum among subiculum complex, although, on average, the rotational symmetry of grid cells in pre/parasubiculum is weaker comparing to the entorhinal counterparts, as well as weaker correlation to theta oscillation, especially in presubiculum. However, the directional tuning is stronger in pre/parasubiculum: MEC layer II has the weakest directional modulation and presubiculum has the sharpest, suggesting the head direction representation may not be modulated by the theta oscillation. Pre/parasubiculum grid cells are co-localized with border cells and head-direction cells. Many grid cells are conjunctive with head directions. The scale and orientation are similar for the co-localized grid cells, similar as in MEC layers III-VI. Given the relatively weak output from MEC to pre/parasubiculum and the stronger projections in the opposite

direction, it is likely that the MEC functional cells inherit from pre/parasubiculum [15]. It is also likely that both regions generate the representations locally. [14]

- Head direction cells: they were actually firstly found in the primate pre-subiculum. See more descriptions in the notes of EC [16]
- Boarder cells: activate when the rat is close to boundaries. The proportion of border cells in pre/parasubiculum is similar to the one in MEC. They are different from boundary vector cells that they do not encoding boundary directions [14].
- The pre/parasubiculum may have "privileged access to holistic representations of the environment and be neuroanatomically determined to preferentially process scenes." [1]

Prosubiculum:

- It has similar input as the pre/parasubiculum, but it usually does not activate during scene processing under fMRI observation, while the pre/parasubiculum does. [1]

2.1 Scales

- Spatial Scales: the scale of the grid cells in the dorsal pre/para-subiculum is around 50cm [14]. The peak firing distance of the BVC in subiculum varies from around 7cm to 55cm, and length of the firing fields varies from around 12cm to around 50cm [12].
- Temporal Scales: 26.3% of presubiculum cells, 44.7% parasubiculum cells (comparing to 55.6% of MEC cells) are modulated by theta rhythm. [14]

2.2 Evidence of Building Blocks / Modularization

Similar to the entorhinal cortex, boundary vector cells, head direction cells etc. can be regarded as different modules.

2.3 Evidence of Lateralization

N/A

2.4 Empirical Lesion studies

Subiculum lesions of usually do not cause obvious or deficits that are easy to see. [4]

- Lesions of the pre/parasubiculum impaired working memory for spatial location information [17].

3 Computational Model

N/A

References

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