Dentate Gyrus

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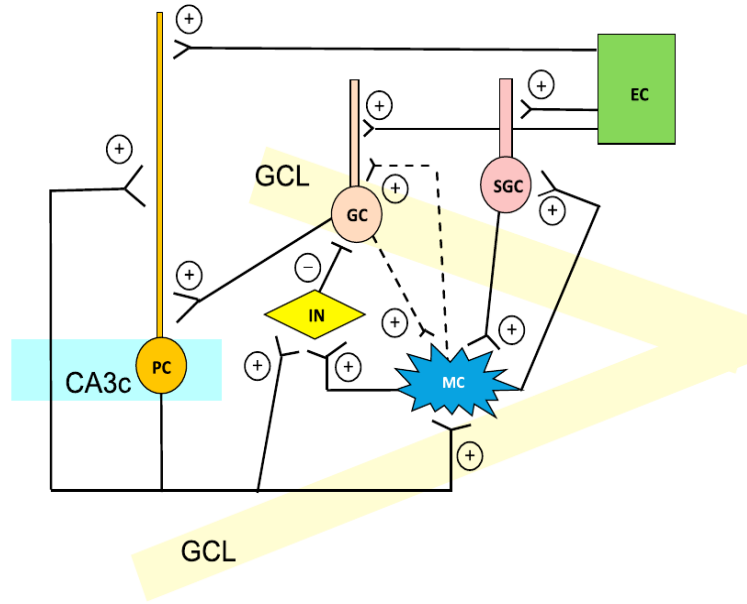April 29, 2018

1 Connection

Figure 1: "Despite the fact that mossy cells receive mossy fiber inputs from granule cells, projecting back to the granule cells, spatial representation between the two cell types appears to be independent (shown by dotted lines). Hypothetically, mossy cells may receive strong spatial information from CA3c pyramidal cells and/or semilunar granule cells, both of which also receive entorhinal inputs. EC, entorhinal cortex; GC, granule cell; MC, mossy cell; SGC, semilunar granule cell; IN, interneuron; PC, pyramidal cell; GCL, granule cell layer. GC, SGC ,IN and MC are all parts of a dentate gyrus." [1]

1.1 Input

- From Entorhinal Cortex (EC) layer II: "multiple sensory inputs, including vestibular, olfactory, visual, auditory, and somatosensory from the perirhinal and lateral entorhinal cortex", and inputs from grid cells in the MEC [2].

- From CA3c to DG mossy cells and interneurons: spatial information [1].

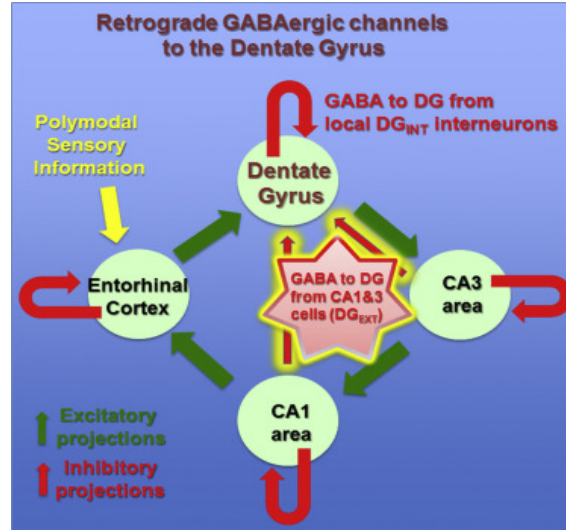- From CA3 and CA1 as shown in Figure 2: interneuron inhibitory input.

Figure 2: "Boundary-crossing interneurons with cell bodies in CA3 and CA1 constitute a numerically significant and diverse population that relays patterns of activity generated within the CA regions back to granule cells" [3].

1.2 Output

To CA3c pyramidal neuron: sparse encoded spatial representation from granule cells (GC) and multiple spatial representations from mossy cells (MC) [4].

1.3 Main Components

- Granule cells (GC): receive strong excitatory input from EC layer II (e.g. head direction, grid information)via the perforant path; send strong outputs to CA3c pyramidal neurons via the mossy fibers (not mossy cells), then to CA3b and CA1. Granule cells have low firing rate (peak firing rates around 6Hz [5], some could go to 47Hz, and the mean firing rates range from 0.17 to 1.12 Hz, the average mean firing rates are 0.5Hz [6]), sparse spatial coding. GoodSmith et al. (2017) reported only 9% are responsive in a given maze, with most of granule cells only have a single place field [5]. Senzai and Buzsaki (2017) reported 6.6% only has two or more place fields [7]. There are about 1.2×10^6 granule cells in total in a rat dentate gyrus [8].

- Mossy cells: mediate an intrinsic excitation loop of DG neurons, receiving strong input "from a relatively small number of granule cells and providing highly distributed excitatory output to a large number of granule cells"; may also receive spatial input from CA3c neurons [1]. Mossy cells have higher firing rates (about 12Hz?). It is reported 88% are active in a given environment, and mostly have multiple place fields [5]. Senzai and Buzsaki (2017) reported 58% has multiple firing field. The number of mossy cells is about one forth of the granule cells [5].

- Semilunar granule cells: receive projections from EC, and project to mossy cells [9].

- Interneurons: GABA neurons (basket cell) abundant in the dentate gyrus and have high concentration in the mossy cell hilus. [4, 8]. The ratio between basket cells and granule cells is on average around 1:150 [8].

2 Function

- Pattern separation: by sparse coding in granule cells, sparse connections between mossy fibers and CA3, and changes in the position of firings in mossy cells.

- Neurongenises: A very recent study showed that there could actually be no neurongenises in adults' DGs [10]. The neurongenises is believed to help with new memory formation and pattern separation (old DG cells help with pattern completion) [11].

- Object-place conjunctive encoding: The rats with DG lesions "did not differ from controls in recognition for a change within object feature configuration and object recognition tasks. In contrast, there was a deficit for the dDG lesioned rats relative to controls in recognition for a change within object-spatial feature configuration, complex object-place feature configuration and spatial recognition tasks". [2, 12].

- Temporal Association: can associate spatial events occurred within 3 min or 30s , may be mediated by neurongenises [2].

2.1 Scales

- Spatial Scales: the place field diameter for granule cells is about 50 cm, and varies for mossy cells [5].

- Temporal Scales: the location firing of granule cells are heavily theta modulated. If define the time of peak CA1 population activity as phase zero, most of the peak firing happened near phase 270 degree (about 90 degree in advance of CA1 pyramidal cells), and most of granule cells do not fire near phase zero. It is hypothesized that "the phase shift in CA1 could be inherited from the granule cells, and this requires that the synaptic integration time scale must be much shorter than the theta cycle" [6], (generally, the integration time in hippocampus is at least 10 times shorter than the theta cycle) [3]. Besides, "Extended interneuron system provides temporarily distributed inhibition to DG during sharp-wave rippls" [3].

2.2 Evidence of Building Blocks / Modularization

Granule cells remaps more to the change of distal cues, whereas mossy cells remaps more to the change of local cues. [1]

2.3 Evidence of Lateralization

Jordan (2017) reported that object exploration led to the expression of a specific protein in the left DG, suggesting that memories about novel objects may be mainly registered by the left side [13]

2.4 Empirical Lesion studies

- DG lesions impaired the animal to detect changes in the environment [12].

- Rats with damaged DG could not navigate through a familiar maze regardless of more trainings, which shows that DG damage impaired their working memories.

For more lesion studies, see the table in [14].

3 Computational Model

- Rolls et al., (2006) modeled the granule cells using a competitive learning network to "reduce redundancy and produce sparse, orthogonal outputs" [15, 16].

- Faghihi (2015) explored the pattern separation efficiency using simulations of different parameter values in the neural network of the entorhinal cortex and dentate gyrus [17].

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