CA1

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1 Connection

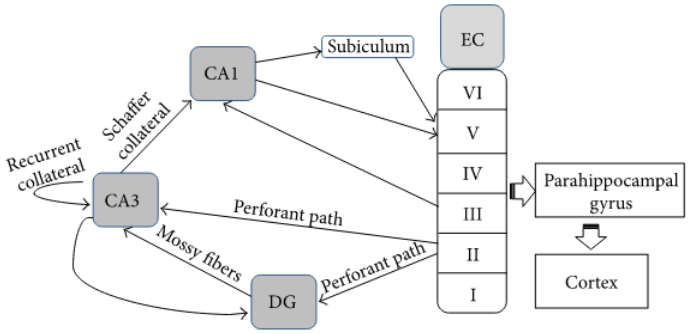

Figure 1: "The main input and output to CA1 regions. The diagram illustrates the monosynaptic and the trisynaptic pathways in the hippocampus. The monosynaptic pathway consists of a direct projection from the EC to CA1 or CA3, whereas the trisynaptic pathway consists of sequential projections from EC to DG, CA3, and then to CA1. Some of the backprojections are not shown in this figure. EC: entorhinal cortex; DG: dentate gyrus; CA: cornu ammonis." [1]

1.1 Input

- From CA3 and CA2 via schaffer collateral (SC): CA2-CA1 projections are heavily biased to be ipsilateral while the CA3-CA1 projection is dominated by the contralateral projection. (For more details, please see the 'output' session in CA2 discription.) CA3 input is shown to be "required for the precise temporal coordination of CA1 spiking; in its absence, theta sequences failed to emerge and spiking in low gamma periods coded space less accurately "[2].
- From medial and lateral entorhinal cortex (EC) layer III via temporoammonic (TA) pathway: some of the LEC cells connect to some dorsal CA1 pyramidal cells, while MEC cells uniformly project to all dorsal CA1 pyramidal cells [3] The trisynaptic pathways to CA1 is crucial in "forming and consolidating long-term spatial memory" [3]. The input from MEC is important for registering time-related events[4, 5], while the input from LEC is important for registering olfactory-related events [6].
- From subiculum: backprojectinos comprised of both excitatory and inhibitory elements [7], may give CA1 place fields the input of the head direction cells. This is not shown in Figure 1.
- Extrahippocampal inputs: excitatory input from the midline thalamic nucleus reuniens, passing on the trajectory-dependent firing from medial prefrontal cortex [8].

Note: The input from MEC or LEC is modulated by the frequency of CA1 gamma rhythms: low gamma frequencies mean the CA3 input is the dominant one at the moment and high gamma frequencies mean the EC is dominant [9].

1.2 Output

- To medial and lateral entorhinal cortex layer V: long-tern memory consolidation. And it was shown to be modulated with sharp-wave ripples (SWRs) [10].
- To subiculum: subiculum is the major target of the most CA1 cellsand it is "capable of undergoing both long-term potentiation (LTP) and paired-pulse facilitation (a short-term plastic effect)" [11]. The projections are not highly interconnected, which means the spatial input from a portion of CA1 is only transfered to a sub-population of subiculum neurons.
- To CA3: inhibitory backprojection [12], not shown in Figure 1.

1.3 Main Components

- Pyramidal cells: the firing of these cells are modulated by the locations and can undergo spatial remapping, rate remapping, and phase precession ("the progressive shift of spikes to earlier phases of the local field potential (LFP) theta oscillation as distance in the place field increases" [13].
- Interneurons: CA1 interneurons can be distinguished as local circuit cells (basket and others) and long range cells [14]. The inhibitory interneurons also exhibit firing fields modulated by position and phase precession dynamics [15].

2 Function

- Spacial encoding (place cells): the place cells in CA1 region can undergo both firing location remapping and rate remapping. Some of the place cells are shown to be tunned to local cues while other to distal cues. Generally, CA1 was shown to respond more to the distal cue changes while CA3 respond more to local cue changes [16]. The CA1 place firings are observed when either MEC or CA3 is damaged [17].
- Contextual encoding and retrieval (objective-vector-cells): it was reported that some CA1 cells fires when there are goal or certain landmarks in the environment, regardless of their positions in the environment. There are also "box-related cells" that activate when the rat is in the box or leaving/entering the box, no matter where the box is positioned in the environment.[18]. CA1 and CA3 both contribute to this context encoding, but only CA1 is shown to be mandatory for recalling the contextual memory [19]. Also, a small group of CA1 cells were shown to "encode direction and distance from one or a small number of discrete objects placed at different locations in the recording arena" [20]. It is postulated that the coordinate information of objects in CA1 is from MEC, and the contextual information is possibly from LEC [17].
- Goal-vector cells: some flying bat CA1 cells fires according to the relative direction between the bat head direction and the goal. The preferred firing directions distributed in 360 with a large percentage of the neurons fire when the head faces the goal, whose firing frequencies increase when the bat is close to the goal [21]. Aroud half of the goal vector cells are also shown to be place cells. Early studies has also shown neural firing of CA1 cells increased in the proximity of a goal [22, 23, 24, 25].
- Temporal encoding: the "time cells" or "episodic cells" fire successively and register the time flow in temporally structured experiences. It is shown to be independent of locations, behaviors and external events of the experience. It behaves very much like place cells - it can also 're-map' when the experiences changes, as illustrated in Figure 2 [26].

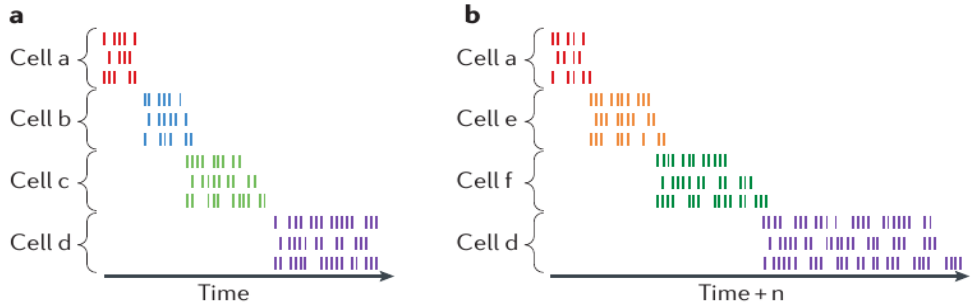

Figure 2: "Key features of time-cell firing sequences. a: A raster display of spiking activity from idealized, simultaneously recorded time cells (each shown in a different colour). For each cell, activity is shown as a raster of spikes for three example trials in which the cell fires for a brief period at approximately the same moment in each trial, with later-firing time cells being active for longer periods (indicating scalar coding of time). b: In the same recording session, when the time period is elongated (time + n), the cells shown at the top and bottom fire at the same moment relative to the beginning and end of the period, respectively (indicating that their activity is bound to those temporal boundaries), whereas the cells shown in the middle in part a have ceased firing and new cells (note the new colours in part b) fire to fill in the period, reflecting 're-timing' in these cells to represent the altered temporal dimension. These characteristics parallel those of place cells, which typically fire at adjacent locations in space and, when critical spatial cues are altered, either remain bound to cues still present or 're-map' to reflect the altered spatial dimensions".[26]

Note: Most of the functions are not proved to be restricted to CA1 area. However, experiments about hippocampus functions were mainly done in CA1 not other regions, and we have some ideas about how different subregions of hippocampus act differently but not very clearly. Also other functions not related to spatial recognition are not mentioned here.

2.1 Scales

- Spatial Scales: the place field of CA1 place cells are smaller in the dorsal CA1 and larger in ventral CA1 as in the grid patterns in EC.
- Temporal Scales: The fast gamma rhythm in CA1 and MEC are synchronized, and the slow gamma in CA1 and CA3 are synchronized. "The two types of gamma occurred at different phases of the CA1 theta rhythm and mostly on different theta cycles" [9]

2.2 Evidence of Building Blocks / Modularization

The neurons in CA1 can be divided into several groups(modules) performing different functions as mentioned before, or having conjunctive functions.

2.3 Evidence of Lateralization

- "The right hippocampus exhibited a temporal gradient correlated with the remoteness of autobiographical memories, whereas the left hippocampus showed a constant activation, implying a permanent contribution to remembering autobiographical episodes along the time axis" [27].

2.4 Empirical Lesion studies

Numerous lesion studies have been done to understand the importance of different input and out put to/from CA1 region. (I've seen a paper reviewing this but couldn't find it now....will add it here if I come across it again.)

3 Computational Model

There have been several computational models about the mechanisms of place cells but not restricted to CA1 region. See the last chapter of *Spatial representation in the hippocampal formation: a history [17] for a review*

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