Emergence of Iterated Function Systems in the Hippocampal CA1

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Abstract. In rat CA1 pyramidal cells, we previously observed hierarchical clusters of the distribution of membrane potentials, arranged according to the history of input sequences. In this study, we deal with the dynamical mechanism generating such a hierarchical distribution. The recording data were investigated using return map analysis. Each of the obtained return maps was well approximated by a set of contractive affine transformations. These findings provide direct evidence that the information of temporal sequences generated in CA3 can be self-similarly represented in the membrane potentials of CA1 pyramidal cells.

1 Introduction

By the clinical studies, it is established that the hippocampus is a necessary organ of the formation of episodic and semantic memories, especially for episodic memory. The hippocampus receives all kinds of sensory information via entorhinal cortex. One of the main components of hippocampus, CA3, is considered to function as a network for autoassociative memories via the framework of attractor dynamics, where memories can be stably stored as corresponding neuronal patterns and can be retrieved by partial cues. Since pyramidal cells in CA1 area have less recurrent connections compared with CA3, it may be thought that CA1 has different functional roles form CA3. One hypothesis is that CA1 would be involved in the information processing of spatiotemporal sequence from CA3. We have propose a scheme for encoding the temporal sequence of events in CA1, which we refer to as "Cantor coding" [1] and have discussed its significance for the formation of episodic memory in the hippocampus-cortex system [2][3]. Cantor coding enables the temporal pattern sequences generated in CA3 to be represented hierarchically in fractal subsets in state space of CA1. How can we verify the hypothesis of Cantor coding in CA1?

We conducted experiments using rat hippocampal slices to clarify how the spatiotemporal sequence delivered via Schaffer collaterals affects the postsynaptic membrane potentials of individual hippocampal CA1 pyramidal cells. We found that the membrane potentials of CA1 pyramidal cells were hierarchically

clustered according to the histories of input sequences up to two or three length [4]. However, the finding of such hierarchical clusters is still only indirect evidence of the presence of Cantor sets, because these sets are essentially infinite objects; observed sets are finite. A direct evidence of Cantor sets may be obtained by showing the existence of emergent rules such as iterated function systems (IFSs) which provide a deterministic framework for generating self-similar fractal patterns as their attractors. From this point of view, the experimental data was investigated using return map analysis [5]. We also deal with a collective behavior at population level, using a reconstructed multi-cell recording data set.

2 Materials and methods

Patch-clamp recordings were made from pyramidal cells of CA1 area in rat hippocampal slices (Fig. 1(a)). In order to generate spatiotemporal inputs to the pyramidal cell in CA1, two stimulus electrodes were set to the Schaffer collaterals, in sites proximal and distal to the soma, respectively. For each cell, a recording session consisted of 122 stimulus periods with an intervening rest period of 10s. In a stimulus period, ten successive inputs were applied with 30 ms intervals. Each input pattern was randomly selected among the four spatial input patterns of electrical stimulations: both electrodes ("**4**"), a electrode placed in the proximal site ("**3**"), or the distal site ("**2**"), and neither electrode placed ("**1**").

We analysed the recording data from eleven cells in six slices. The ten cells were classified into two groups, *sub-threshold* (cell1,. . . , cell5) and *supra-threshold* (cell6, . . . ,cell10), according to whether or not the continual stimulations induced spikes. For each stimulus-period, the baseline membrane potential was determined as mean amplitude during 2 s before the stimulus period. Hereafter, we express membrane potential as the difference between the measured voltage and the baseline membrane potential at each stimulus period.

A response at Δt to nth input was defined as the membrane potential at a fixed elapsed time Δt after the input, which is denoted by $V_{\Delta t}(n)$ (Fig. 1(b)). In particular, $V_{last}(n)$ denotes the value at $\Delta t = 28$ ms taken as the timing just before the next input. Responses for analysis were gathered from all stimulus periods for each cell using the same procedure. Return map analysis was used to examine the dynamics underlying the generation of responses to a spatiotemporal input sequence. For a response sequence $\{V_{last}(n)\}_n$, a return map was generated by plotting each response $V_{last}(n)$ against the previous response, $V_{last}(n-1)$.

3 Results and conclusions

At individual cell and population levels, a return map of the response sequence of CA1 pyramidal cells was well approximated by a set of contractive affine transformations (Fig.2). These finding strongly suggest that CA1 dynamics receiving spatiotemporal input from CA3 has a mode that is characterized by input-driven IFS consisting of a self-organized response rule for each spatial input pattern.

This dynamics ensures that the distribution of response is hierarchically clustered according to input histories, and also ensures that a spatial and retrospective code table can be automatically formed (Fig.3). Hence we obtain Cantor coding.

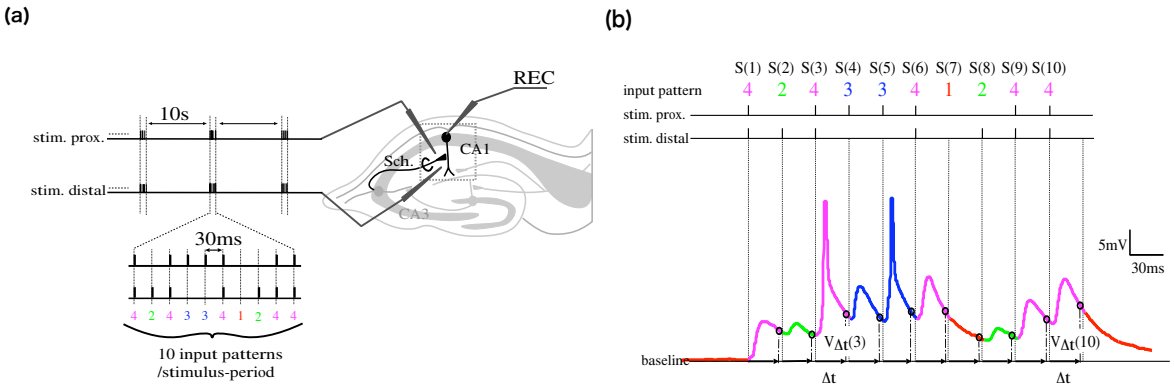
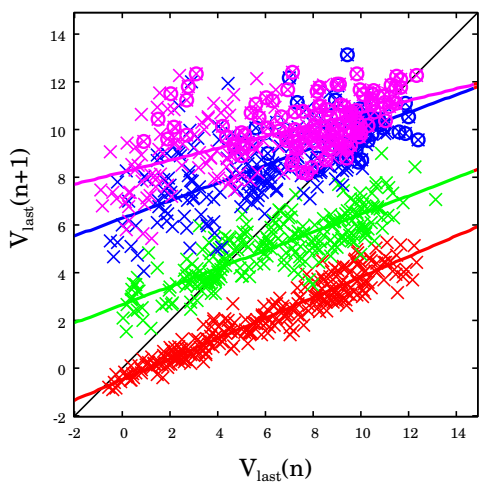


Fig.1 Experimental procedure and sample traces. (a) Schematic diagram of the experimental procedure. In each stimulus period, input patterns were randomly selected among four spatial input patterns of electrical stimulations: "**1**" (*red*), "**2**" (*green*), "**3**" (*blue*) and "**4**" (*magenta*). In the figures in this article, these input patterns are color-coded in the same way throughout. (b) Sample traces of membrane potentials and the neuronal responses in a stimulus period. The upper two samples show the timing of electrical stimulation and the lower sample shows the timing of responsive membrane potentials recorded from a cell in supra-threshold group, smoothed using a median filter to remove electrical stimulus artifacts. The membrane potentials are color-coded according to the kinds of their most recent input patterns.

Fig.2 Return map of response sequence $\{V_{last}\}$ at individual cell level. An example of a cell in supra-threshold group. $V_{last} := V_{\Delta t=28[\mathrm{ms}]}$. The return map consists of four parts, called *branches*, corresponding to four $n+1$st input patterns. The colors of the points indicate the kinds of $n+1$the input patterns. The points $(V_{last}(n), V_{last}(n+1))$ such that spikes occur in the $n+1$st input interval are enclosed by open circles. Superimposed on the branches are the fitting lines using major axis regression and the diagonal line $V_{last}(n+1) = V_{last}(n)$. Successive responses, $V_{last}(n)$ and $V_{last}(n+1)$, in each branch had a decent correlation coefficient, and all slopes of fitting lines for the branches were smaller than 1. These indicate the presence of contractive affine transformations.



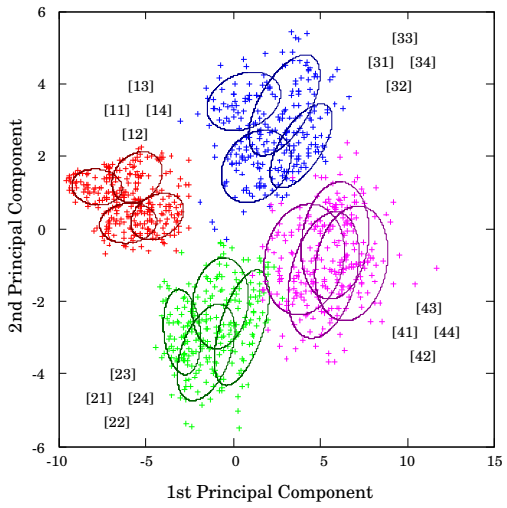


Fig.3 Conditional distribution of population response $\boldsymbol{V}_{last}$. The population response $\boldsymbol{V}_{last} = (V_{\Delta t}^{\mathrm{cell1}}, \cdots, V_{\Delta t}^{\mathrm{cell5}})$ in the sub-threshold group was projected on two-dimensional subspace spanned by the 1st and the 2nd principal components of the distribution. The colors of points indicate the kinds of the most recent input patterns. The location and shape of the conditional distribution $[i_1 i_2]$ for each input pattern sequence of length two $i_1 i_2$, where i_1 is the most recent pattern in the input, are depicted by an ellipsoid at the 63 percent probability level under an assumption that the population follows two-dimensional normal distributions. They show hierarchical clusterization in a self-similar manner, according to the similarity of the input pattern sequences.

References

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