A Complex Systems Approach to an Interpretation of Dynamic Brain Activity II: Does Cantor coding provide a dynamic model for the formation of episodic memory?

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Abstract. We here review the second lecture, in which we show that Cantor coding can be used to hierarchically embed temporal sequences produced by a chaotic or a random information source. We also propose a hypothesis on the possibility of Cantor coding for the formation of episodic memory in the hippocampus and also for the category formation of episodic memory. Smale's horseshoe map defines Cantor coding as a conjugacy of expanding dynamics embedded within the map. On the other hand, in the real world, this type of conjugacy does not always exist. We demonstrate the use of Cantor coding in a mathematical model of the hippocampus. The computational results suggest a dynamic mechanism for the formation of episodic memory and category formation of episodic memory.

1 The background of lecture II

The aim of the present lecture is to show how information of the time series generated by chaotic dynamical system is encoded in Cantor sets generated in a contracting subspace of chaos-driven contracting systems, and also to apply this idea to the construction of a mathematical model of episodic memory formation.

Episodic memory is defined by Tulving, as memory concerning the information of individual experiences [1]. It should be noted that an individual experience is not a series of events that one actually experiences in daily life, but, rather, can be identified with the reorganized structure of neural activity created internally, associated with the input information during such events. Furthermore, clinical reports on the subjects H. M. [2] and R. B. [3] have shown that the hippocampus, especially CA1, is indispensable for the formation of episodic memory.

With respect to mathematical modeling, it is important to note that the structure of CA3 is very similar to that of the neural network model of associative memory [4, 5]. The model studies since the work of Marr [6] are based on the idea that the hippocampus temporarily retains episodic memory as an associative memory, as reported by Treves and Rolls [7], and by McClelland *et al.* [8]. On the other hand, conventional neural network model of associative memory possess attractor dynamics only, and thus they cannot create temporal patterns that could represent episodic memory. Therefore, to prove the theory proposed by Marr, Treves and Rolls, McClelland and others, an additional mechanism to produce a temporal series of patterns is required.

The structural similarity of neocortical networks to the CA3 network is obvious. As demonstrated in lecture I, the recurrent networks of excitatory neurons with inhibitory interneurons forming a common architecture of neocortical subareas exhibit a temporal series of memory patterns that show chaotic itinerancy. Because CA3 mainly consists of excitatory recurrent networks and inhibitory interneurons, the activity of CA3 is expected not to generate stationary spatial patterns, but to produce a temporal series of spatial patterns.

The structure of CA1, on the other hand, lacks the recurrent connections of the pyramidal cells, thus the CA1 network may be stable as long as there are no synaptic modifications or inputs. Thus, it is possible to model the hippocampus as a chaos-driven contracting system.

It may also be worth considering that this mathematical model provides the dynamic characteristics for a reorganized hippocampal network driven by the other parts of the brain.

Let us briefly mention the related studies on Cantor coding. Coding on Cantor sets was first demonstrated in an iterated function system (IFS) [9–12] and later in a recurrent neural network (RNN) [13–15]. IFS was proposed to realize the coding of spatial patterns as fractals on Cantor sets. In particular, Karlin and Norman proposed a deterministic model of animal's stochastic behavior during reinforcement learning. A stochastic renewal of plural contacting systems led to the generation of Cantor sets. RNN was proposed to realize the Cantor set coding of temporal patterns, which were produced as a random series by the network.

Our problem was how to encode the information in the symbol sequences generated in a chaotic dynamical system into the system's contracting subspace. We investigated this issue in several chaos-driven contracting systems, where various Cantor sets appeared to encode various temporal patterns that the chaotic system produced [16–18] .

2 A computational model for the hippocampus

The model we propose is a computational one at the macroscopic network level. In other words, the concern here is with a basic network model exhibiting and encoding a temporal series of patterns. Thus, we do not deal with the details of the characteristics of single neurons or even with specificity of the layered structure of the network, but rather we try to model the basic network function related to the production and encoding of episodic memory. To construct such a model for the hippocampus, we first describe the physiological and anatomical facts at the network level. This description provides the basic architecture for the model, focusing on the network structure of the CA1 and CA3 regions and their interactions.

The detailed structure of hippocampus is quite different from the neocortex. Nevertheless, we would like to focus on the similarities between the two for the following reason. As mentioned in lecture I, the network consisting of the recurrent network of pyramidal cells and the inhibitory interneurons, which usually act as *destabilization by inhibitory cells*, produces a chaotic series of memory patterns. Finding a similar network in the hippocampus is the first step in modeling the formation and encoding of episodic memory.

In CA3, the axon-collaterals of pyramidal cells make synaptic contact with other pyramidal cells, and thus form a recurrent network. Furthermore, each pyramidal cell makes an excitatory synaptic contact with a neighboring inhibitory cell. Such a cell inhibits the neighboring pyramidal cells for at least 200 ms in all the physiological conditions studied so far. The other axon-collaterals of pyramidal cells, the Schaeffer collaterals, make synaptic contact with the apical dendrites of the pyramidal cells in CA1. Thus these connections establish a unidirectional coupling from the CA3 network to the CA1 network. Mathematically, this can be called a skew-product transformation of the dynamics in CA3 and CA1.

In CA1, on the other hand, recurrent connections between pyramidal cells have not been observed. Inhibitory cells also exist in CA1, each of which mainly receives the output of the nearest neighbor pyramidal cell and each in turn inhibits its neighboring pyramidal cells. The axon-collaterals of the CA1 pyramidal cells project to various other areas such as the subiculum, the entorhinal cortex, and other subcortical areas.

The inhibitory cells that project on CA3 and CA1 from other areas have relatively long axon-collaterals that form an interneuronal network [19, 20]. Both cholinergic and GABAergic afferents project from the septum to hippocampal CA3 and CA1. The cholinergic afferents contact both the pyramidal and inhibitory cells in the hippocampus. On the other hand, the GABAergic afferents make synaptic contacts mainly with inhibitory cells [21–23]. In fact, Toth *et al.* concluded from their experiments that the GABAergic septo-hippocampal afferents selectively inhibit the hippocampal inhibitory cells and consequently disinhibit the pyramidal cells.

Taking into account these anatomical and physiological facts, and also some additional hypotheses, the network model of the hippocampus was constructed [24].

One of the assumptions is that time is discrete that is not necessarily made in conventional model of neurodynamics. The reason that we made this assumption stems from both theories of cortical information processing based on rhythmic cortical activity and experimental facts describing the relation between θ and γ rhythms (see, for example, [25–28]). If θ rhythms are incorporated in the formation of episodic memory, each cycle requires approximately 200 ms for the transmission of the episodic signal from the hippocampus back to itself through the neocortical areas and the entorhinal cortex [19]. This suggests that a sequence of episodic events is generated during one cycle of the θ oscillations. On the other hand, the γ rhythms may be related to conscious experience, which is known to activate hippocampal neurons. If so, it is possible that the γ rhythms "filter" and *discretize* continuous signals accompanied by the θ oscillations. Thus, a few (4-8) discrete wave packets having the γ range frequency may represent a sequence of events during one cycle of this signal transmission. Lisman *et al* [27, 28] attempted to relate the appearance of such γ wave packets to the magic number 7 ± 2 [29] for short-term memory. As mentioned in lecture I, this magic number has also been discussed in relation to chaotic dynamical systems [30, 31]. The neural mechanism for the magic number is still an open question, because the magic number operates not only in remembering a sequence of numbers over a short period of time, but also for inferring the logical depth of a sentence that hierarchically contains other sentences, such as "A heard that B told C that D loves E", and also for classifying events and experiences into a number of categories. Although the neural mechanism for the magic number may be of interest, analysis of it is not our present purpose and we will not consider it further.

Let X and Y be N-dimensional vectors, with their ith components denoted by x_i and y_i, respectively, representing the activity of the ith pyramidal and inhibitory cells in CA3. For the reasons given above, we introduce a discrete time step n for the development of the neurodynamics. The following equation provides a $2N$- dimensional dynamical system in CA3 [24].

$$(X(n+1), Y(n+1)) = F(X(n), Y(n)), \tag{1}$$

where F is a $2N$-dimensional nonlinear transformation denoting the neurodynamics. Taking into account the effect of the stimulus-induced stochastic release of synaptic vesicles widely observed in the hippocampus, however, we interpret F as representing a *stochastic renewal of neurodynamics*, as in the case of Tsuda's model of successive association of memories [32–35].

The stochastic renewal of neurodynamics for the ith set of pyramidal and inhibitory cells is defined as follows.

$$x_i(n+1) = \begin{cases} H_x(\frac{1}{N}\sum_{j=1}^{N} w_{ij}x_j - d_i y_i) & \text{(with probability } p_x) \\ x_i(n) & \text{(otherwise)} \end{cases}, \tag{2}$$

$$y_i(n+1) = \begin{cases} H_y(\frac{1}{N}\sum_{j=1}^{N} e_{ij}x_j) & \text{(with probability } p_y) \\ 0 & \text{(otherwise),} \end{cases} \tag{3}$$

where $x_i \in [-1, 1] (i = 1, \cdots, N)$, $y_i \in [-1, 1] (i = 1, \cdots, N)$, w_{ij} denotes a synaptic weight from pyramidal cell j to i, $d_i \in [0, \beta]$ a synaptic weight from the inhibitory cell i to the pyramidal cell i, and $e_{ij} \in [0, \alpha]$ a synaptic weight from the pyramidal cell j to the inhibitory cell i. Furthermore, the neural transformation is given by the sigmoid function.

$$H_x(z) = H_y(z) = 2/(1 + exp(-\lambda_3 z)) - 1. \tag{4}$$

Here λ_3 is a steepness parameter.

Semantic memories encoded in the parahippocampal area are here represented by a vector, each component of which denotes the activity of pyramidal cell. The memories are assumed to be constructed in the recurrent network of pyramidal cells by the Hebbian learning algorithm;

$$w_{ij} = \frac{1}{N}\sum_{\mu} x_i^{\mu} x_j^{\mu}, \tag{5}$$

where x_i^{μ} is the ith component of the μth memory, $X^{\mu} = (x_1^{\mu}, \cdots, x_N^{\mu})$.

We first describe what could happen in the CA3 network in the case without the effects of the inhibitory neurons. This condition of the network, denoted by $d_i = 0$ for all i, can occur under the physiological conditions such that the inhibitory neurons in CA3 are inhibited by the GABAergic afferents coming from the septum. In this case, as in the conventional model of associative memory, the network dynamics become attractor dynamics. Some attractors are generated to represent semantic memories by the above Hebbian learning algorithm.

We next describe what could happen in the CA3 network in the case without the effects of GABAergic neurons from the septum, namely, with the effects of the inhibitory neurons of CA3 alone. This situation is similar to the one in the dynamic associative memory model [32–38]. As expected, the chaotic transitions between memories occur through *chaotic itinerancy* [39, 40, 33] between attractor ruins representing the memory traces (see also [41]). The chaotic sequence of memory patterns generated in such a way may be considered a representation of episodic memory.

Let us further describe our model for the skeleton of the CA1 network and its dynamics.

Let U and V be M-dimensional vectors of the space $[0,1]^M$, $U = (u_1, \cdots, u_M)$ and $V = (v_1, \cdots, v_M)$, where u_i and v_i denote the states of pyramidal cell i and stellate cell i, respectively. Here, M is the number of cells of each type.

$$u_i(n+1) = H_u(\epsilon \frac{1}{M}\sum_j T_{ij}\frac{(x'_j(n)+1)}{2} - \delta \sum_j c_{ij} v_j(n) + \theta), \tag{6}$$

$$v_i(n) = \sum_j b_{ij} u_j(n), \tag{7}$$

$$x'_j(n) = x_j(n) \quad (x_j(n) > 0), \tag{8}$$

$$x'_j(n) = -x_j(n) \quad (x_j(n) < 0) \tag{9}$$

Here, T_{ij} denotes the synaptic connection from the CA3 pyramidal cell j to the CA1 pyramidal cell i, and its value is fixed to a randomly chosen value from the uniform distribution on [0, 1]. In the simulation [24], we set $b_{ii} = 1.0$ and $b_{ij} = 0$ if $i \neq j$, and $c_{ii} = 1.0$ and $c_{ij} = 0$ if $i \neq j$. It would be worth studying network performance with different arrangements of connections, but here we review only the results in this restricted case. Because the Shaeffer collaterals of the CA3 pyramidal cells are excitatory, we introduced the terms x'_j. We also introduced the control term δ because GABAergic inhibitory neurons from the septum make synaptic contact with the stellate cells in CA1. We assumed $\delta << 1$ in the presence of GABAergic inhibitory inputs from the septum, and $\delta = O(1)$ in the absence of such disinhibitions.

The input-output transformation for the pyramidal cells is also the sigmoid function.

$$H_u(z) = 1/(1 + exp(-\lambda_1 z)), \tag{10}$$

where λ_1 is a steepness parameter.

3 Does Cantor coding provide a biologically plausibile representation of information in the hippocampus?

In the simulation of the CA1 model, we chose the parameter values that satisfied the inequality that establishes the contraction condition. We thus obtained a *chaotic dynamics-driven contracting system* as a computational model for the CA3-CA1 unidirectional couplings at the network level. We conducted computer experiments step by step in three separated stages, in each of which the inputs to CA1 pyramidal cells differed.

(1) Inputs of the random sequence of two temporal patterns, '100' and '10'

The symbol '1' indicates the presence of a pulse and '0' the absence of a pulse, so the random input sequence consists of two different pulse sequences. The randomness of the sequence was provided by a coin tossing algorithm. The computation results showed a hierarchical coding of such random temporal sequences on the Cantor set. In any two-dimensional space projected from the N-dimensional space of the membrane potential of pyramidal cells in CA1, say the space of $u_1 - u_2$, a nonoverlapping Cantor set is clearly seen (see Fig. 1). In Fig. 1, whenever the pulse denoted by '1' appears in input, the activity of u_1 and u_2 is plotted at the next time step. The plotted dots constitute a self-similar set, called a Cantor set, in the following way. The activity shown by the two subsets on the right upper part and on the left lower part of the figure indicate that the pulse sequences including the present pulse were '10*' and '100*', respectively. Here, the symbol '*' denotes arbitrary random sequences of '100' and '10', and the right hand side in the sequence indicates the past. The upper two subsets indicate that the sequences including the present pulse were '1010*' in the subsequent upper subset and '10100*' in the subsequent lower subset, respectively. In a similar way, the left lower two subsets indicate '100100*' and '10010*', respectively. This shows a hierarchical representation of the embedding of the random temporal series consisting of '100' and '10'.

(2) Inputs of random sequences of continuous spatial patterns

We define a continuous spatial pattern by a vector, with each component representing the activity of each pyramidal cell in CA3 that is sent to all pyramidal cells in CA1, via Shaeffer collaterals of the CA3 pyramidal cells. The activity is represented by a real number in the unit interval, $[0, 1]$. A random sequence consisting of different patterns acted as the temporal input to CA1, and the sequence is hierarchirally embedded in the N-dimensional space of pyramidal cell activity (see reference [24] for a concrete example of the embedding).

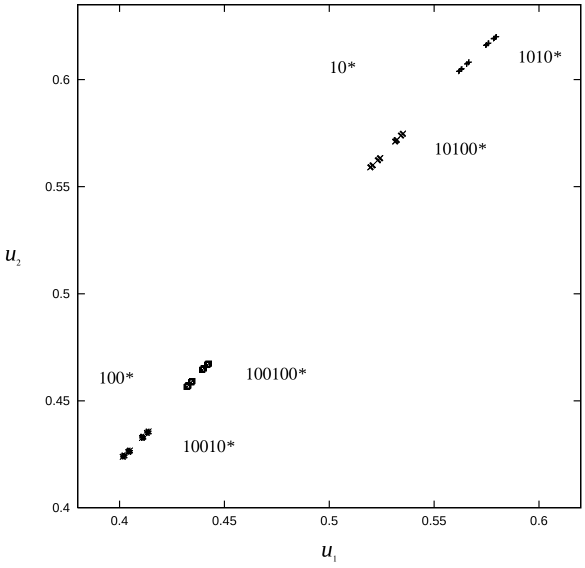

Fig. 1. A Cantor coding of random temporal series consisting of two pulse sequences, '10' and '100'. $N = 64$, $\lambda_1 = 50$, $\epsilon = 0.032$, $\delta = 0.06$, $\theta = 0$, $b_{ij} = 1(i = j)$ and $b_{ij} = 0$ (otherwise), and $c_{ij} = 1(i = j)$ and $c_{ij} = 0$ (otherwise).

(3) Inputs of the temporal output series from the pyramidal cells in CA3
This case corresponds to the actual physiological situation. Our model CA3 produces chaotic itinerancy of memory patterns, where a temporal series of memories represents an episode. Although the Cantor set is manifested in CA1 phase space, overlaps between subsets are generally observed. It is usually difficult to separate such overlapped subsets, so their appearance creates difficulties in decoding the embedded temporal patterns. Thus, the overlapping must be resolved so that the proposed algorithm will apply to the hippocampus. This important study will be published elsewhere.

In all of the three cases, the history of the temporal sequence is represented by the hierarchy of Cantor sets in phase space, hence the name Cantor coding.

4 summary and discussion

We proposed a computational model for the formation of episodic memory. The model was constructed to represent the basic network of the hippocampal CA3 and CA1, and their interactions. The main characteristic of CA3 dynamics is the generation of a temporal series that can be described as chaotic itinerancy [41]. It was shown that a certain kind of chaotic behavior provides a dynamic information channel, and hence such chaotic behavior should also be expected to work computationally in the brain [36, 41]. On the other hand, the main characteristic of CA1 dynamics is a contaracting dynamics if it is isolated so that there is less bombardment from CA3 changing the strength of connections. Thus, overall activity should follow chaos-driven contracting dynamics.

Generally, in chaos-driven contracting dynamics, the information read out by chaotic dynamics is written in the contracting space by the contracting dynamics, as is seen in the dissipative baker's transformation. In other words, a symbol sequence created by chaotic dynamics is represented as a subset of a Cantor set generated in the contracting subspace. *A code table can thus be dynamically formed on a Cantor set that is generated in the phase space in CA1 pyramidal cells.* This is what we would expect in CA1 with weak or no synaptic learning: the demonstration of a one-to-one correspondence between each symbol sequence generated by chaotic dynamics in CA3 and each position of a Cantor element in CA1, by virtue of unidirectional coupling from CA3 to CA1, i.e., CA3 → CA1.

The distance between (or the closeness of) semantic memories (or events experienced) represented by a spatial pattern of neuronal activity could be specified in CA3 by a scalar product between all the two patterns. On the other hand, the distance between the different temporal series may be defined in CA1 by the Euclidian norm between the corresponding two points in the Cantor set. In fact, it can be defined through the hierarchies of the Cantor set. Thus, the concept of distance between episodic memories could be realized in CA1. Therefore, the category formation for a variety of episodes may be expected to be realized in CA1 by the clustering of subsets of the Cantor set. This clustering will effectively be established via synaptic learning, i.e., LTP (see, for example, [42]). For such a categorization process for a temporal series of events, a Hausdorff metric between Cantor subsets can be used.

Our hypothesis on Cantor coding is depicted in Fig. 2.

In the formation of episodic memory, the relationship between the temporal series of spatial patterns in CA3 and the geometry with a Hausdorff metric of the Cantor set in CA1 may be flexibly altered, whereas in the cortices the alteration of the representation by structural changes will vary slowly. In this respect, the hippocampus may be likened to a *blackboard*. Writing and erasing on this hippocampus "blackboard" could be related to the θ -rhythms, thus taking about 200 ms. The timing between this writing and erasing and the slowly varying transition between symbols in the cortex is a key to the formation of episodic memory. This illustrates the necessity of a long period of time, from perhaps, a few years to a lifetime, for the complete formation of episodic memory. This can be understood by taking account of the existence of retrograde amnesia for one to three years as well as anterograde amnesia after hippocampal deprivation [2], and also after CA1 lesions [3].

Whether the Cantor coding actually occurs in CA1 can be examined in the laboratory experiments that must initially be conducted under a nonlearning condition, using a blocker for LTP, followed by experiments to observe alteration of the set structure in the absence of such a blocker. The three stages illustrated above will correspond to an actual procedure for the stages of experiments.

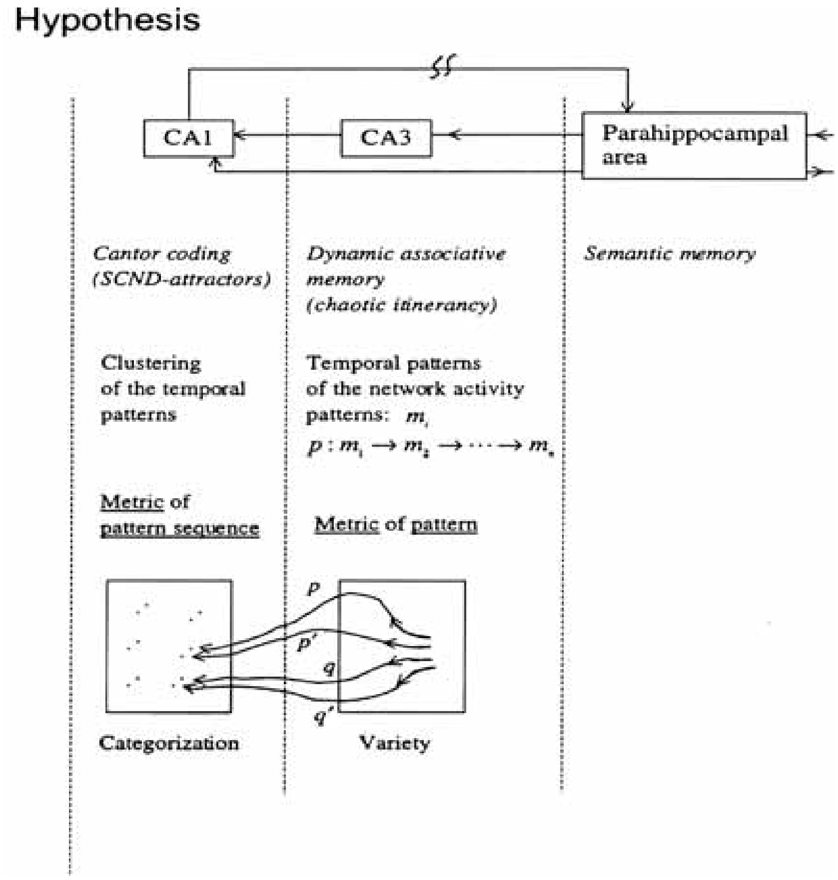

Fig. 2. Hypothesis on Cantor coding. See the text for details.

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