Synchronization in the Hippocampus as a Neural Principle Representing Contextual Information

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ABSTRACT

The contexts in cognition and behavioral situation are required for the establishment of the synthetic logic. In this paper, we show that the hippocampus represents the contextual information as spatio-temporal pattern of neural activities generated by synchronization. The information structure in the brain to enable the operation of synthetic logic is elucidated based on the concept of Gestalt cycle and it relevance to hippocampal function. It is concluded that the circulation loop in the brain including the hippocampus and cortices provides the structure necessary for synthetic logic. Synchronization in multi-hierarchical system is proposed to be an important neural principle to evaluate the consistency of the circulation loop in such a hierarchical system,

Keywords: synthetic logic, Gestalt cycle, cortico-hippocampal interaction, theta rhythm, phase precession.

1. INTRODUCTION

Logic is classified into two types, analytic logic and synthetic logic in philosophical concept. This classification is found in Critique of Pure Reason by Kant and discussed by Miller [1] in relevance with the function of the hippocampus. The function of the hippocampus is mostly studied with respect to the contribution to the declarative memory or episodic memory, in humans [2]. Another hippocampal function is known as the cognitive map theory by O'Keefe and Nadel [3] It is developed in rodents. Although these two are independent, they are consistent with each other from the viewpoint of "context". Present paper is devoted to the elucidation of the information structure of the contextual information by focusing on the neural dynamics of synchronization in the hippocampus.

2. COGNITIVE FUNCTION OF THE HIPPOCAMPUS

The episodic memory is characterized by the context dependence and distinguished from the semantic memory that is independent of the context. Since the definition of episodic memory comes from verbal communication between the subject and observer on the personal history, it inevitably covers various time scales, the neural, behavioral, cognitive and also the progressive change during the lifetime. It seems to be difficult to catch the neural mechanism of episodic memory in humans.

On the other hand, the concept of cognitive map was proposed by Tolman [4], as an idea opposing to the behaviorism based on stimulus – response relation. Tolman showed that a rat in the spatial recognition uses not only sensory signals but also a global information of the environment, in term of the cognitive map. O'Keefe et al. discovered that the neural activity representing the place is observed in the hippocampus [3]. They showed that the neural activity in the hippocampus represents the place where the rat is in the environment. The hippocampal study based on the cognitive map theory was well developed in rodents in various spatial and motivational conditions. The results show that the activity of the hippocampus not only represents the space, but also depends on the behavioral motivation [5]. The cognitive map is considered to represents not only the physical environment but also somehow semantic environment. Furthermore, recently it is known that the temporal sequence is represented in the theta dynamics of place cells [6,7]. The collective activities of place cells represent not merely the spatial context but the context as spatio-temporal sequence. It seems important to elucidate the theta dynamics in rat hippocampus in order to enlighten the brain mechanism for the contextual information.

3. SYNCHRONIZATION OF THETA RHYTHM

The hippocampal theta rhythm is a regular field potential oscillation observed in rodents during freely running. Individual pyramidal cells fire robustly when the rat is in specific portions of the environment. These portions are called "place fields", O'Keefe and Recce [6] have shown that the spatially specific firing of pyramidal cells has an temporal correlation with the theta field potential, the phase of the theta cycle at which a pyramidal cell fires advances as the rat passes through the place field. This phase shift effect is called "phase precession". By using large-scale parallel recording, Skaggs et al. [7] showed that the phase precession is robust and coherent across neural populations, They suggested that a functional consequence of phase precession is to represent the temporal sequence of place codes in a compressed form, The firing of place cells in the compressed sequence in each theta cycle represents the current place surrounded by the place in near past and that in near future in order. The activity representing the current space is placed in the temporal stream from past to future, Concurrent sequence gradually changes according to the temporal evolution of running behavior. Thus, theta phase precession in freely running rat seems to show some temporal stream of the spirit,

4. A THEORETICAL MODEL OF NEURAL DYNAMICS OF THETA SYNCHRONIZATION

Yamaguchi and McNaughton [8, 9] proposed a hypothesis on the neural dynamics of the theta phase precession in the freely

running rat. The behavior dependent input considered in the model is shown in Fig.1. Neural oscillators are alternatively activated in an indefinite order according to the behavior in a novel environment Theta phase precession is phenomenologically reconstructed by a kind of synchronization written as follows.

$$\dot{\phi}_i = \omega_i + A\sin(\phi_o - \phi_i), \qquad (1a)$$

$$\dot{\phi}_0 = \sum_{i=1}^{N} \omega_i \equiv \omega_0 \qquad (1b)$$

where ϕ_i denotes the oscillation phase of the ith neural oscillator. The oscillator with $i = 0$ is the mean oscillation of all oscillators or that of local field potential. The magnitude of interaction A is positive only when the ith oscillator is active.
It is easily obtained that the solution at the phase locking state is found as

$$\theta_{si} = \arcsin(\frac{\Delta\omega_i}{A}) \qquad (2)$$

with

$$\phi_i - \phi_0 \equiv \theta_i \quad \text{and} \quad \Delta\omega_i = \omega_i - \omega_0 .$$

It means the oscillators are ordered in phase according to the magnitude of native frequency ω_i, as illustrated in Fig.2. The important assumption for theta phase precession is that the native frequency ω_i increases monotonically during its active period. That is, the magnitude of native frequency represents the history of activation of the ith unit. The older the activation is, the larger the native frequency is. Thus, the ordered sequence in phase encodes the input in a slow time scale.

Based on the neuroanatomical evidence on the hippocampal circuit, we get the hypothesis on the network dynamics as shown in Fig. 3. The hypothesis is proposed for the neural mechanism of the memory storage of the temporal. It consists of three assumptions. 1) Phase locking of individual neurons by mean field interactions results in phase precession at the earliest stage of the hippocampal closed circuit, in layer II of the entorhinal cortex (ECII for short). 2) The temporally structured pattern of activities in ECII is transmitted along the hippocampal circuit, leading to asymmetric connections in CA3 network based on LTP mechanism with asymmetric time window. 3) The final stage of the circuit, the deeper layer of the entorhinal cortex (ECIII~VI) is considered to have activities with a phase difference of 90 degrees from that of ECII. It endows selective potentiation in synapses projecting from CA3 to CA1, so that the loop along the hippocampal circuit is closed in each neural module at EC.
1) and 2) work for encoding of memary, while 3) is assumed for the memory retrieval.

The example of the computer experiments is shown in Fig. 4. The phase shift patter originated in ECII is transmitted to CA3. It should be noted that the temporal sequence experienced only one time is stored in CA3 as asymmetric connections. In the retrieval process, an extermal singal trigger the activation of the temporal sequence in the neural time scale as an associative memory. The spatio-temporal pattern recalled in CA3 is projected through CA1 to the entorhinal cortex.

Suppose there is the feed back pathway from the entorhinal cortex to neocortex,, the collective pattern of neural activities possibly works as top down signals in defferent ways in different stages. One is behavioral stage when theta phase precession is apparent, that is awake or REM state. The other is

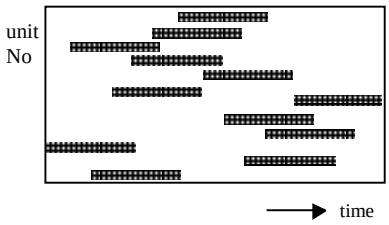

Fig.1 Input pattern of a temporal sequence.

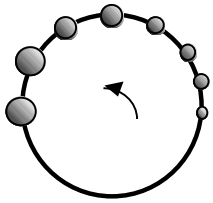
Fig. 2 Ordered sequence in phase is illustrated on the cycle orbit. Each particle shows the neural oscillator, whose size represents the native frequency.

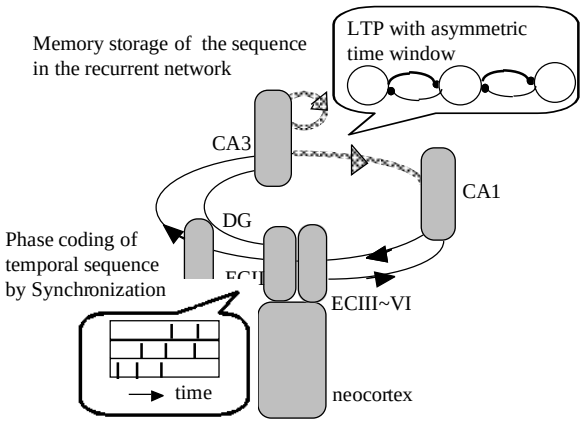

Fig. 3 A hypothesis on the hippocampal dynamics. The behavioral temporal sequence encoded in phase by theta phase precession is transmitted to CA3 and stored in CA3 recurrent network.

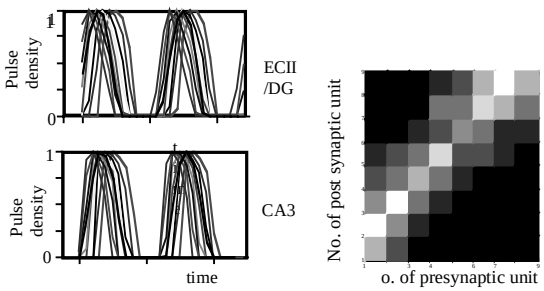

Fig.4 An example of computer experiments. Left: Activities of neural oscillations. Right: The connection matrix obtained after one experience of temporal sequence. Plotted after [8]

in the recall state, corresponding with Slow Wave Sleep state. In the former case, the hippocampus work to give constraints to the sensory or behavioral processing in the neocortex, by the inerplay between the hippocampus and neocortex. The latter concern with the consolidatin of the memory. Let us consider the semantic meaning of the former case in the next chapter.

5. CIRCULATION STRUCTURE OF SYNTHETIC LOGIC

According to Kant [10], the pure reason by Descartes is considered as analytic logic, and another logic is defined as contrary to the analytic one as follows. Any statement is obtained by deductive steps, which are individually given by secure elementary statements. If any doubt could not be avoided in individual steps, the resultant statement must be dismissed as an improper statement. Such type of logic is used in the modern science, obviously seen in mathematics or in computer programming. On the other hand, it is usual to use the statement which cannot be decomposed into secure steps. The other logic used in our life is classified into "synthetic logic", or "a priori synthetic logic". Kant described the importance of the back ground nature of the presupposition in the synthetic logic. That is, the presupposition is available even if it is indefinite. The same statement or word is sometimes true and false, depending on the background of our complex world, as well as the subject's internal situation. Human intelligence has the ability to use the logic without analysis but based on some background premise. Kant considered the ability innate. The property of the back ground premise are litellaly unknown in most cases.

The presupposition could be generalized as context in the sense that it works as constraints in processing of information in background. Holden, a cultural anthropologist, showed that the background rule as context is commonly found in human and animals, depending on the culture or region [11]. The variety of the context is sometimes observed in the motion of body or in communication in a group of people. Thus, the background premise is found not only as philosophy of human entities but also in body and mind as biological properties.

The question is whether the context could be described in an operational way. If one grasps the context definitely, the definite part has further indefinite portion as back ground. The definite description does not converge forever. How the biological organism descrive the context in its finite system?

According to Gestalt psychology [12], the fundamental entity of life is found in the circulation loop between the biological system and environments, called as Gestalt cycle, illustrated in Fig. 5. When the interaction is restricted to the action in one way from the environment to the biological, it is what is called stimulus-response relation in the behaviorism. In this paradigm, the stimulus is given. The circulation loop of life, on the contrary, the stimulus is changed or selected by the subject itself. According to this circulation, the life knows the consistency between the perception and action in a meaningful way. That is, the meaning of the stimulus becomes definite under the background premise of the circulation loop accompanied by its own action. The context is found in the circulation loop as the relation between the biological system and its environment.

On the other hand, in general in higher animals, the circulation loop includes various time scales because of the ability to use long term memory and the highly complex structure of the brain. It seems impossible to describe the circulation loop altogether definitely. It is usually and necessarily decomposed into two, cognition and motion in the research field. In brain research, the brain is analyzed in the recognition process. We actually experience that the brain works in synthetic logic even if the action perception cycle is temporally cut. There must be some circulation loop in the brain.

The information structure in the cognition process is considered to be hierarchical in the brain. When the interaction between the layers is reciprocal the processing in the lower

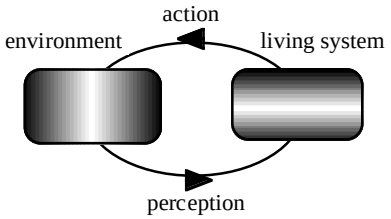

Fig.5 Illustration of Gestalt cycle as a loop between the living system and environment.

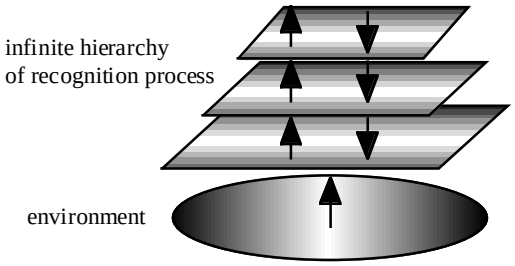

Fig.6 Hierarchical structure considered in the recognition process. Each layer represents functional module or the neural layer in the brain Arrows show the information flow.

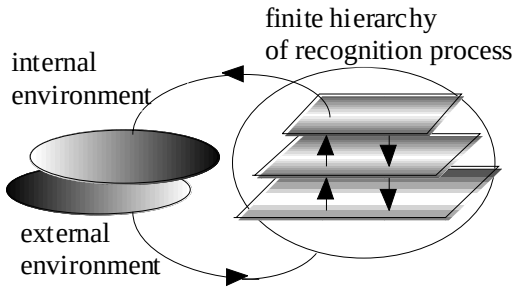

Fig.7 Gestalt cycle in cognition through "internal environment" represented in the hippocampus.

layer depends on control by the upper layer, as is illustrated in Fig. 2. Each layer corresponds to sensory layer for primary feature, sensory layer for further global features, memory layer and so on. This structure is considered as a linear chain of individual circulation loops. Since definite representation in one layer needs constraints from the upper layer, the highest layer has a contradiction. The top constraint has no constraint. Thus, in case of chain structure, the number of chain becomes infinite. The infinite hierarchical system is practically impossible in the finite brain.

It is interesting that brain anatomy suggests the solution of the contradiction. In case of visual system, the linear chain structure is found as the anatomical structure of projections as well as functional relation[13]. When it is followed from V1 toward either temporal area, or parietal area, it arrives to the hippocampus. All sensory systems are known to converge to the hippocampus. Thus, the hippocampus is placed at the top in the information flow of cognition. As shown in Fig. 7, the circulation between the living system and environment is identically found in the figure. The living system is restricted to the cognition system in the brain. The environment is given by dual structure, external environment and internal environment.

That is, the information represented in the hippocampus could be considered as internal environment, as is clearly seen in the cognitive map theory. When the two kinds of environments are consistent with each other, the circulation loop is effectively closed to give Gestalt cycle. The consistency is managed by either emergent dynamics or memory storage in the hippocampus. It should be noted that the internal environment does not mean the copy of the external environment. As is shown in this paper, the hippocampus processes and integrates the information according to the experience and motivation. Then, the internal environment is generated from time to time in a proper way for the living system. The internal environment represented in the hippocampus contributes to the circulation loop as contextual information in the cognition. Thus, the contradiction of the linear chain is solved by the virtual Gestalt cycle.

The difficulty and importance in circulation loop in two hierarchical layers are elucidated in hermeneutics by Wittgenstein [14] and in hierarchical neural dynamics [15]. Shimizu et al. [16] and Yamaguchi and Shimizu [17] proposed synchronization hypothesis in the visual pattern recognition as an interpretation process. They showed that the circulation in visual pattern recognition is synthetically processed in the hierarchical neural network of neural oscillators. The circulation loop between the sensory and memory layers are self-organized by synchronization. Even in the presence of large background activities, the synchronization represents the circulation loop in phase of oscillation, separating from ground activities out-phase. Thus, it shows the ability of synchronization network to complete the circulation loop by evaluating the logical consistency as synchronous dynamics. The indefinite boundary of the external and internal word is autonomously solved leading to definite in dynamics of synchronization. These studies as well as the present study of the hippocampus reveal that synchronization of neural oscillation provide the neural mechanism to evaluate the consistency in the circulation of hierarchical layers in an emergent way. It is important to elucidate the synchronization in the network composed of hippocampus and cortices based on the information structure for the synthetic logic.

6.CONCLUSION

The hippocampus represents the contextual information as spatio-temporal pattern of neural activities generated by synchronization. The information structure necessary for the synthetic logic is found to be a circulation loop between the cognitive system and environment. It is found that the loop includes the hippocampus as a layer to represent the internal environment. Synchronization among these systems provides a possible and important neural principle to evaluate the consistency of the circulation loop,

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