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Sequence disambiguation and pattern completion by cooperation between autoassociative and heteroassociative memories of functionally divided hippocampal CA3

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ABSTRACT

The hippocampus memorizes event sequences and some events are shared by a few sequences. When a sequence is retrieved from the linked sequences, ambiguity of sequences becomes a serious problem because the shared events have some possible ways to retrieve other events. We have focused on location dependency elucidated from the hippocampus and suggested that CA3 is functionally divided into autoassociative and heteroassociative memories. Computer simulation results show that the functionally divided CA3 concurrently enables both sequence disambiguation and pattern completion. Consequently, it demonstrates that cooperation between both memories of CA3 brings out the abilities of sequence disambiguation and pattern completion in the hippocampus.

1. Introduction

A promising hypothesis supporting many hippocampal processes has been suggested by Eichenbaum [6,5]. On the hypothesis, daily episodes are memorized as a relational network (previously called memory space) in the hippocampus. In the relational network, an episode is expressed by a sequence of events that are primitive elements of memory. Episodes are associated with each other by events shared among the episodes. For example, let us consider that the hippocampus memorizes two episodes, one is composed of the following events: A, B and C ($A \rightarrow B \rightarrow C$). The other is composed of the events: X, B and Y ($X \rightarrow B \rightarrow Y$), where event B associates the two episodes. As a result, we can find out a new way from event X to event C by associating these episodes. Therefore, the relational network, that can flexibly associate episodes acquired, supports inference that derives new ways to deal with memory. Recent studies have suggested that the hippocampus relates to a flexible representation [17,9] used for inference. It follows that these suggestions support Eichenbaum's hypothesis that leads to the inference. In the relational network, it is difficult to decide which pattern (C or Y) should be retrieved from event B. The ambiguity of sequences becomes a problem for retrieval. Thus, the sequence disambiguation is an essential function for retrieving the original episode from the relational network. Agster et al. have suggested that the hippocampus is required to accomplish sequence disambiguation [1]. In the hippocampus, the CA3 region has unique recursive axons which are called recurrent collaterals (RCs). Because of its uniqueness, many researchers focused on it and proposed many computational models of CA3. Several of the models contribute to solving the sequence disambiguation problem by creating a code [14,8]. In those models, however, CA3 has been homogeneously modeled in spite of its heterogeneous anatomical properties [11]. Thus, we have suggested the importance of the model based on the heterogeneous properties that are elucidated from the location dependency of RCs and spike-timing dependent plasticity (STDP) [18]. On the basis of the location dependency, we have suggested that CA3 is functionally divided into autoassociative and heteroassociative memories [18]. In this paper, using computer simulations, we show that the functionally divided CA3 can disambiguate the overlapped sequences and enables pattern completion that is the already perceived ability of CA3 [16] to recall complete memory from incomplete set of cues. Consequently, it demonstrates that a cooperation mechanism between autoassociative and heteroassociative memories of the functionally divided CA3 brings out the abilities of the sequence disambiguation and pattern completion in the hippocampus.

2. Related works

In this section, we review conventional CA3 models solving the sequence disambiguation problem. Levy et al. have focused on CA3 and proposed a simplified CA3 model composed of

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McCulloch–Pitts neurons [15]. The model has the ability to create a local code for temporal context used for recognizing a subsequence of a large sequence. Since the model solves sequential problems including the sequence disambiguation with the context code, they have suggested the importance of the context for hippocampal functions. Moreover, they have proposed that fundamental properties to create the codes agree to the properties of CA3 [14]. In their study, McCulloch–Pitts neurons model spike rate, but not spike timing. However, STDP that is a rule of changing synaptic weights depending on spike timing exists in the hippocampus [3]. Hayashi et al. have proposed the hippocampal model [8] including CA3 and CA1 receiving from CA3. The synaptic weights of the model are updated by STDP. This model can also create context-like information by transforming temporal information to spatial information in CA3 and this context of CA3 leads to the sequence disambiguation in CA1. Hayashi's model corresponds to the review that cooperation between CA3 and CA1 achieves the sequence disambiguation [13]. However, the spatial pattern completion function of CA3 is undescribed in this model. Furthermore, although heterogeneous anatomical properties that are the subregional local dependency of RCs have already been found in CA3, it was modeled homogeneously in their models. On the other hand, Samura et al. [18] have focused on the anatomical findings. Moreover, they have focused on the location dependency of STDP [20] and suggested that CA3 is functionally divided into autoassociative and heteroassociative memories. So, it seems plausible that the autoassociative memory leads to pattern completion and that the heteroassociative one which can reflect temporal information in synaptic weights leads to the transformation for creating a context. That is, the functionally divided CA3 may exist for the abilities of pattern completion and the creation of a context for the sequence disambiguation.

3. Anatomical backgrounds of hippocampus

3.1. Structure of hippocampus

Fig. 1 shows the structure of the hippocampus. The hippocampus is divided into three regions: Dentate gyrus (DG), CA3 and CA1. Information is transmitted from DG to CA1 via CA3. Entorhinal cortex (EC) works as an interface between the cortex and the hippocampus and transmits information to all hippocampal regions. CA3 has RCs which recursively connect CA3 neurons to other CA3 neurons. Furthermore, CA3 is segmented into three subregions: CA3a, CA3b and CA3c (Fig. 1).

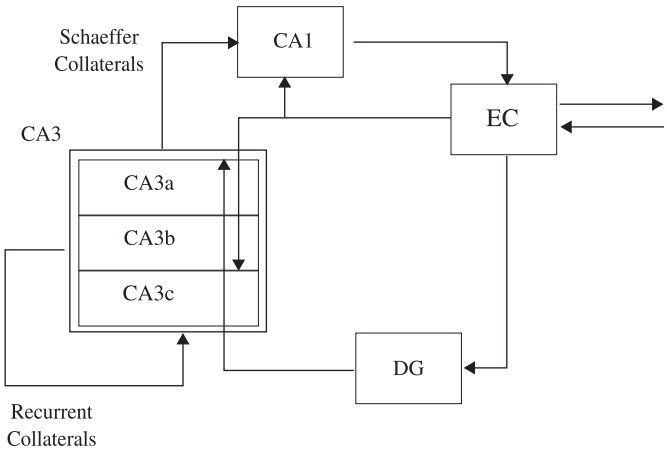

Fig. 1. Connections between the hippocampal regions.

3.2. Connections within CA3

CA3 neurons are connected recursively to other neurons by RCs. Fig. 2(a) shows the relationship between the location of a neuron and the projection zone of its RCs [11]. First, the RCs of CA3c neurons are limited to the area surrounding them. Second, the RCs of CA3b neurons are widely spread. Projection onto CA3c becomes a more temporal location than the position of its source and that onto CA3a becomes a more septal location. Finally, the RCs of CA3a neurons are limited to CA3a and CA3b. Projection onto CA3b becomes a more temporal location. In addition to the location dependency of the projection zones, the dendritic locations of RCs depend on where neurons receive RCs in the CA3 [11] (Fig. 2(b)). CA3c neurons receive RCs at a distance from a soma, while CA3a and CA3b receive RCs near a soma. Additionally, we review projection toward CA3 from other hippocampal regions [10]. Fig. 2(b) shows connections to CA3 from two regions: EC and DG. As shown in this figure, DG connects to all CA3 subregions and EC connects only to CA3a and CA3b. It was suggested that the connections from DG to CA3 contribute to memorization, while those from EC to CA3 are required for retrieval [19].

4. Physiological backgrounds of hippocampus

4.1. Spike-timing dependent plasticity

A neural network memorizes information from the outside world by changing synaptic weights between neurons. In the hippocampus, STDP is observed as a rule of changing synaptic weights [3]. STDP determines the magnitude of a synaptic change and its polarity (potentiation or depression) according to the interval between pre- and postsynaptic spikes. Furthermore,

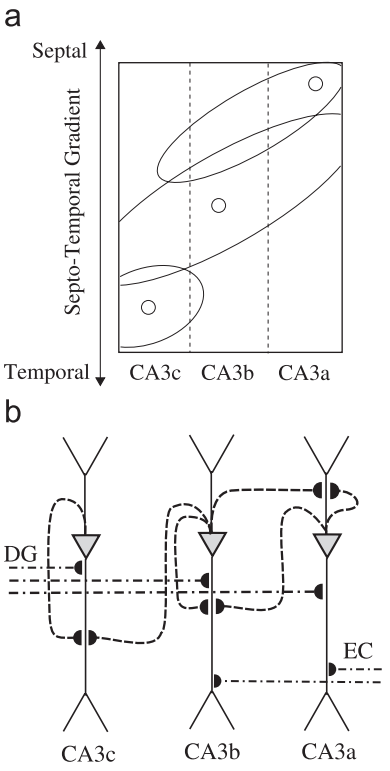

Fig. 2. Connections within CA3. (a) Projection zone of RCs (circle: source neuron, ellipse: projection zone of the circled neuron in it). (b) Dendritic locations of RCs (inverse triangle: soma, forked line: dendrite, dashed line: RCs, chain line: external input).