A Model of Hippocampal Learning with Neuronal Turnover in Dentate Gyrus

Yuko Wakagi and Motonobu Hattori

Abstract— Recent studies have revealed that neurons are replaced in the dentate gyrus of the adult hippocampus. Although it is believed that the hippocampus is essential to store some kinds of memory, the role of neuronal turnover in the hippocampus have not been understood yet. In this paper, we examine the effect of neuronal turnover by using a hippocampal model. Computer simulation results show that the similarity of patterns to be stored is reduced by neuronal turnover, and this contributes to storing similar patterns easily and increasing the storage capacity. Moreover, we show that the number of learning epochs required to store all patterns can be reduced as the neuronal turnover rate becomes large.

Keywords— Dentate gyrus, hippocampus, neural networks, neurogenesis, neuronal turnover.

I. Introduction

Our high level information processing such as thinking, inference and so on is based on the declarative memory which can be recalled consciously. Recent studies show that the hippocampus plays a vital role in acquisition of the declarative memory. Therefore, in order to construct an intelligent information processing system like human brain, it is very important to clarify how memory is formed in the hippocampus.

The hippocampus is a bilateral structure located in the temporal lobes of the hemispheres (Fig. 1). In the hippocampus, Dentate Gyrus (DG) and Cornu Ammonis (CA) constitute the so-called trisynaptic circuit, the entorhinal cortex (EC)→DG→CA3→CA1, which is known as an important path in the hippocampus [1]. Adult hippocampal neurogenesis has been found in DG where the first station of the trisynaptic network. That is, some granule cells in DG are replaced by new born cells every day. A lot of researchers have focused on this phenomenon to reveal its role in the hippocampus [2]. So, there is a lot of literature on neurogenesis in DG, and there are several hypotheses on the role of neuronal turnover [3], [4]. For example, Kempermann has suggested that new born neurons do not add memory, but are inserted strategically to a network to increase in the complexity that can be processed by the network [5]. Nottebohm has suggested that new neurons are used for storing new memories, thereby protecting old memories from interference [6]. The other hypotheses and suggestions on neurogenesis are found in the review [7]. Among them, Becker has suggested that newly born neurons may be used to generate novel codes for highly similar events by using computational model of the hippocampus [8].

However, the role of neurogenesis in the hippocampus is still not clear.

In this paper, in order to examine the role of neurogenesis, we construct a computational model of the hippocampus and simulate the process of neuronal turnover in the model. By using the model, we examine how the similarity of input patterns changes in each region of the hippocampus with/without neuronal turnover and its relation to the storage capacity of the model, and its influence on the number of learning epochs.

In Section II, we briefly review anatomical background of the hippocampus and neurogenesis. In Section III, the computational model of the hippocampus is explained. Then, computer simulation results are shown in Section IV.
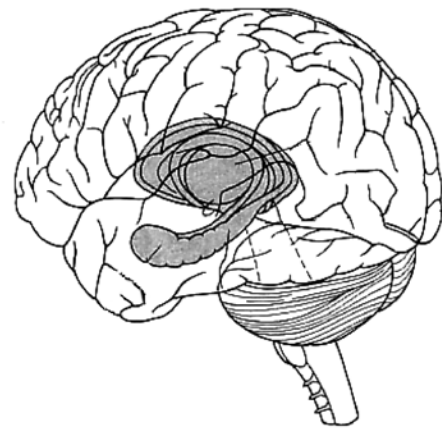

Fig. 1: The hippocampus (gray part) of the human brain.

II. Anatomical Background

Here, we briefly review the hippocampal architecture and neurogenesis in DG.

A. Structure of Hippocampus

As shown in Fig. 2, the hippocampus consists of DG and CA, and CA is divided mainly into CA1 and CA3. DG consists of granule cells, while CA3 and CA1 consist of pyramidal cells. Entorhinal Cortex (EC) which is adjacent to the hippocampus works as an interface to the hippocampus. External input is given to the hippocampus from the second layer of EC, and output of the hippocampus is given to the fifth layer of EC. Neurons of each region are connected with each other. The connection between EC and every region is called Perforant Path (PP). The connection from CA3 to CA1

is called Schaffer Collateral (SC), and that from DG to CA3 is Mossy Fiber (MF). This connection is known as very sparse and powerful. CA3 has recurrent connection from CA3 to itself, which is called Recurrent Collateral (RC).
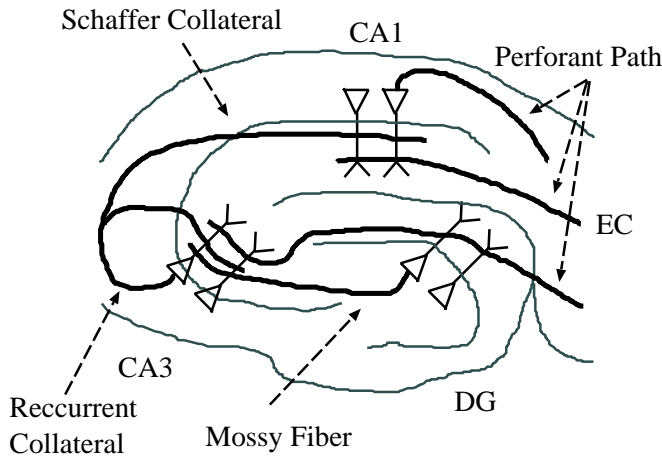

Fig. 2: Hippocampal circuitry.

External input is given to the hippocampus via EC, and it is sent to each region through PP, MF, SC and RC. Electrophysiological experiment has revealed that the dominant path in learning and that in recall is different [9]. The path, EC→DG→CA3→CA1 is dominantly used during learning. In contrast, the path, EC→CA3→CA1 is dominantly used during recall. Therefore, DG becomes dominant only when learning. In addition, neurogenesis occurs only in this region of the hippocampus.

B. Neurogenesis

Neurogenesis in DG of the human hippocampus was discovered in 1998 by Erikson and Gage [10]. Fig. 3 shows the process of neurogenesis in DG. DG consists of the granule cell layer and the subgranular zone. First, precursor cells in the subgranular zone divide asymmetrically. Following division, one cell remains in the subgranular zone and retains the capacity to proliferate, and the other cell moves the granule cell layer of DG and grows up. Most of the newly born cells that enter the granule cell layer acquire neuronal characteristics [10]. Therefore, some time is necessary until a new cell can be used as a neuron in DG.
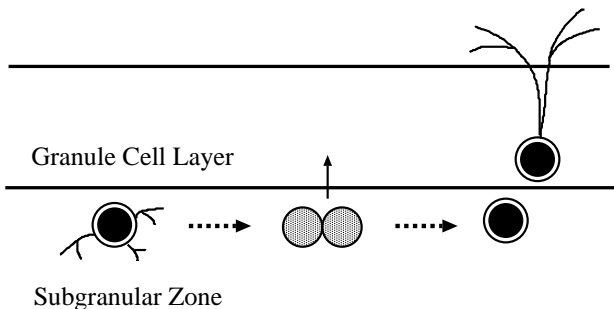

Fig. 3: Neurogenesis in DG.

According to the investigation of Cameron and McKay, about 9,000 new cells are generated per day in the adult rat DG, and the survival rate of generated cells is about 50% with 5-12 days [11]. Since the number of granule cells in the rat DG can be estimated about a million, the rate of neuronal turnover is about 0.45% per day. While, according to the data of young adult rats (35-days-rats), new cells were born about 10,000 per day, and 70% survive two weeks, suggesting a daily neuronal turnover rate of about 1% [8].

III. HIPPOCAMPAL MODEL IN CONSIDERATION OF NEURONAL TURNOVER

Here, we describe the hippocampal model for this study. First, we show the architecture of our hippocampal model, and then describe process of learning, recall and neurogenesis.

A. Architecture of Hippocampal Model

The hippocampal model for this study is shown in Fig.4. The model consists of EC, DG, CA3 and CA1. EC is used as input layer to the hippocampus, and CA1 is used as output layer. Table I shows the number of neurons and the firing rate in the hippocampal model. These data are based on physiological findings and as same as those shown in [12].
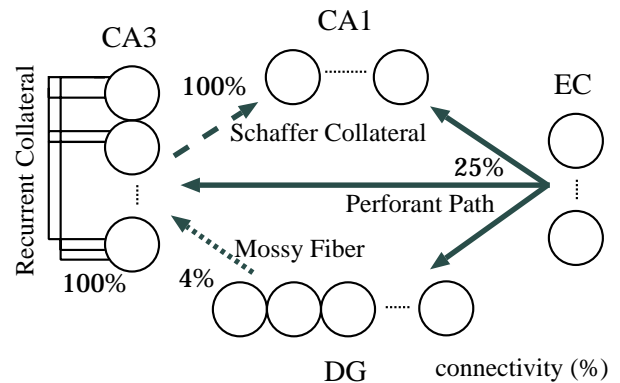
Fig. 4: A hippocampal model.

In the model, we use McCulloch and Pitts neuron model in each region. Therefore, each neuron in the hippocampal model takes 0 or 1 as its output:

$$Y_j = \phi(\sum w_{ij} X_i), \qquad (1)$$

where X_i shows the output of a neuron in a layer, Y_j shows that in the subsequent layer, w_{ij} denotes the connection weight between these neurons. ϕ is the output function:

$$\phi(x) = \begin{cases} 1 & \text{for winner neurons} \\ 0 & \text{otherwise.} \end{cases} \qquad (2)$$

The number of neurons firing in each region is decided by the k-winner-take-all manner [12] based on the firing rate of each region. The rates of connection between two regions are as follows: 25% for PP, 4% for MF, and 100% for RC and SC. For example, in the case of PP, one neuron in DG connects to 25% of neurons in EC. Input from DG to CA3 is assumed 25

times stronger than other input because there is physiological evidence that the connection from DG to CA3 is very strong.

TABLE I: Details of each region in the hippocampal model.

Region	EC	DG	CA3	CA1
Number of neurons	240	1600	480	240
Firing rate (%)	10.0	1.0	4.0	10.0

B. Flow of Data

The flow of data in the hippocampal model is as follows:

1) A pattern is inputted to EC.
2) DG receives input from EC, and a pattern is formed by using the k-winner-take-all manner.
3) CA3 receives input from EC, DG, and CA3 itself, and a certain number of neurons become active by the k-winner-take-all rule.
4) CA1 receives input from EC and CA3. We regard the pattern formed in CA1 as an output of the hippocampal model.

C. Learning

All of connection weights in the model are learned by Oja's rule [13]. Although Hebbian learning was used in the model [8], we have employed Oja's learning rule because it can constrict the divergence of weights. Oja's rule is expressed by

$$\Delta w_{ij} = \eta Y_j (X_i - Y_j w_{ij}), \tag{3}$$

where X_i shows the output of a neuron in a layer, Y_j shows that in the subsequent layer, w_{ij} denotes the connection weight between these neurons, and η is the learning rate.

In learning, we examine the pattern formed at CA1. When all patterns appeared at CA1 are different from each other, we have regarded it as successful learning.

D. Recall

Based on an evidence from electrophysiological experiment, only the path, EC →CA3→CA1 is used in recall. Therefore, DG is not used in recall. When recall, we examine the pattern formed at CA1 for each input. If it is as same as the pattern formed in learning, we have regarded it as successful recall.

E. Neuronal Turnover

Neuronal birth and extinction, namely neuronal turnover has been modeled as follows. Assume that the rate of neuronal turnover is set to α%. First, α% of neurons are chosen randomly in DG. Then the connection weights of those neurons are initialized according to the connection rate of PP and MF.

IV. COMPUTER SIMULATION RESULTS

A. Storage Capacity

Here, we examined the relation between the similarity of patterns and the storage capacity under various neuronal turnover rates.

Fig. 5: An example of input patterns when the direction cosine was set to 0.42. A white square shows an inactive neuron, and others show active neurons. Gray neurons are common in all patterns.

In this experiment, we made a set of 10 different patterns in which every two patterns have the same value of the direction cosine. In order to construct such patterns, a random pattern was generated according to the firing rate of EC first. That is, a pattern which has 24 active neurons was randomly generated. Then, we let a certain number of the active neurons inactive and choose substitute active neurons randomly again. Repeating this process, we can produce a set of patterns which has given similarity. In our experiments, the similarity was measured by the averaged direction cosine between two patterns. The direction cosine between two patterns, $\boldsymbol{P}^{(i)}$ and $\boldsymbol{P}^{(j)}$ ($j \neq i$) is defined as follows:

$$\frac{\boldsymbol{P}^{(i)} \cdot \boldsymbol{P}^{(j)}}{||\boldsymbol{P}^{(i)}||||\boldsymbol{P}^{(j)}||}, \tag{4}$$

where $\boldsymbol{P}^{(i)}=\{p_1^{(i)},p_2^{(i)},\cdots,p_{240}^{(i)}\}$, $\boldsymbol{P}^{(j)}=\{p_1^{(j)},\ p_2^{(j)},\cdots,\ p_{240}^{(j)}\}$ and $p_k^{(i)}=\{0,1\}$ ($i=1,2,\cdots,10$, $k=1,2,\cdots,240$).
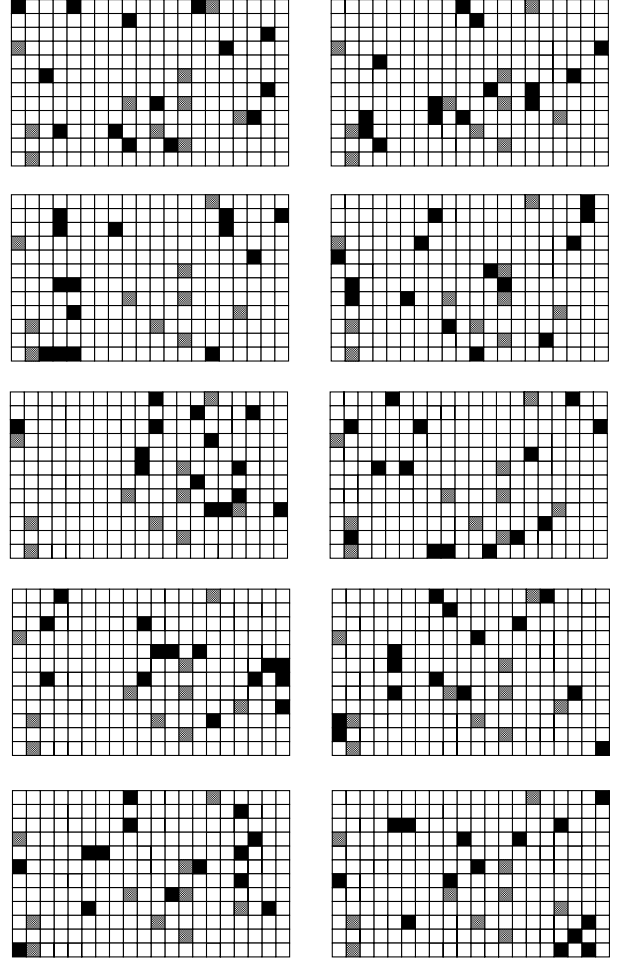
Fig. 5 shows an example of input patterns when the direction cosine was set to 0.42. White squares show inactive neurons and others denote active neurons. Gray neurons were common in all patterns.

Input patterns were given to EC one by one. A pattern was learned by the model for 20 times (20 epochs), then the next pattern was given to the model and learned. Namely, each pattern was learned in an additional or incremental fashion. Neuronal turnover occurred between learning. We examined the number of patterns which could be successfully learned and recalled in the model under various neuronal turnover rates and similarity of patterns. Fig. 6 shows the results of the experiment based on 20 trials.
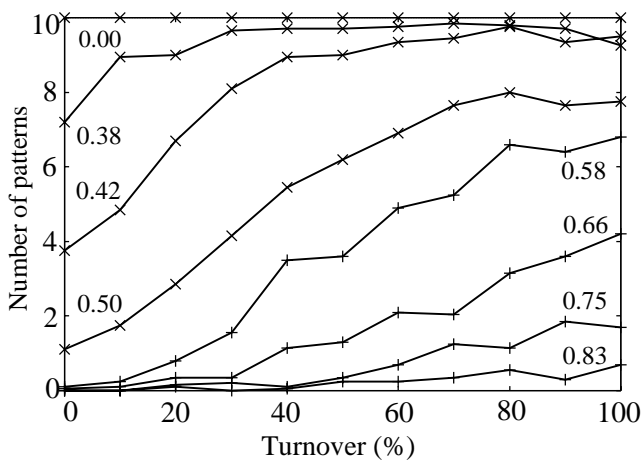

Fig. 6: Storage capacity based on 20 trials. The numbers in the figure show the similarity of patterns measured by the direction cosine.

In general, when patterns to be stored are very similar (that is, the direction cosine is close to 1), it is very difficult to learn them. As seen in the figure, as the similarity of patterns becomes large, the storage capacity decreases. However, we can see that the rise of neuronal turnover can much improve the storage capacity. Namely, neuronal turnover makes it easier to learn similar patterns.

B. Similarity of Patterns in Each Region

In this experiment, we examined how the similarity of patterns changes in each region during learning. Tables II, III and IV show the similarity of every two patterns appeared at DG, CA3 and CA1, respectively. In the tables, each pattern is represented by an alphabet. In this experiment, the similarity of input patterns and the neuronal turnover rate was set to 0.42 and 0%, respectively.

TABLE II: Similarity of patterns in DG. Neuronal turnover rate: 0%.

	B	C	D	E	F	G	H	I	J
A	.21	.22	.22	.22	.22	.21	.21	.20	.22
B		.36	.39	.39	.39	.39	.38	.38	.39
C			.44	.47	.44	.44	.44	.42	.45
D				.52	.50	.51	.51	.49	.53
E					.54	.55	.55	.55	.56
F						.55	.56	.54	.57
G							.57	.57	.61
H								.57	.61
I									.60

TABLE III: Similarity of patterns in CA3. Neuronal turnover rate: 0%.

	B	C	D	E	F	G	H	I	J
A	.04	.04	.05	.06	.06	.06	.07	.06	.07
B		.11	.15	.17	.18	.20	.18	.18	.19
C			.18	.25	.20	.23	.23	.23	.23
D				.33	.31	.34	.29	.30	.35
E					.45	.49	.47	.47	.47
F						.54	.52	.47	.53
G							.55	.56	.62
H								.60	.62
I									.61

TABLE IV: Similarity of patterns in CA1. Neuronal turnover rate: 0%.

	B	C	D	E	F	G	H	I	J
A	.00	.00	.00	.00	.00	.00	.00	.00	.00
B		.01	.00	.03	.03	.03	.03	.01	.02
C			.01	.07	.05	.04	.06	.05	.05
D				.10	.12	.15	.05	.07	.16
E					.30	.32	.31	.32	.32
F						.46	.48	.39	.52
G							.52	.54	.62
H								.61	.68
I									.64

TABLE V: Similarity of patterns in DG. Neuronal turnover rate: 60%.

	B	C	D	E	F	G	H	I	J
A	.09	.04	.02	.02	.01	.01	.00	.00	.01
B		.14	.06	.03	.02	.01	.01	.01	.01
C			.16	.06	.03	.02	.02	.02	.01
D				.12	.06	.02	.02	.01	.01
E					.13	.05	.02	.02	.01
F						.11	.04	.03	.01
G							.12	.06	.02
H								.12	.05
I									.12

TABLE VI: Similarity of patterns in CA3. Neuronal turnover rate: 60%.

	B	C	D	E	F	G	H	I	J
A	.03	.02	.02	.03	.02	.03	.03	.02	.02
B		.04	.01	.01	.01	.03	.01	.02	.03
C			.03	.03	.03	.03	.03	.03	.01
D				.01	.03	.04	.03	.03	.02
E					.04	.03	.03	.02	.01
F						.05	.04	.02	.03
G							.05	.02	.03
H								.02	.02
I									.04

TABLE VII: Similarity of patterns in CA1. Neuronal turnover rate: 60%.

	B	C	D	E	F	G	H	I	J
A	.00	.00	.00	.00	.00	.00	.00	.00	.00
B		.00	.00	.00	.00	.00	.00	.00	.00
C			.00	.00	.00	.00	.00	.00	.00
D				.00	.00	.00	.00	.00	.00
E					.00	.00	.00	.00	.00
F						.00	.00	.00	.00
G							.00	.00	.00
H								.00	.00
I									.00

TABLE VIII: Similarity of patterns in DG. Neuronal turnover rate: 100%.

	B	C	D	E	F	G	H	I	J
A	.01	.02	.01	.01	.02	.01	.01	.01	.01
B		.01	.01	.02	.01	.01	.01	.01	.01
C			.00	.01	.01	.01	.01	.01	.00
D				.01	.01	.01	.01	.00	.02
E					.01	.01	.01	.01	.01
F						.01	.01	.01	.01
G							.01	.01	.01
H								.02	.01
I									.01

TABLE IX: Similarity of patterns in CA3. Neuronal turnover rate: 100%.

	B	C	D	E	F	G	H	I	J
A	.03	.03	.02	.03	.02	.01	.03	.03	.02
B		.02	.02	.02	.02	.05	.02	.03	.02
C			.02	.01	.02	.02	.03	.03	.03
D				.04	.01	.03	.02	.03	.02
E					.01	.02	.03	.04	.03
F						.02	.04	.03	.03
G							.02	.03	.02
H								.01	.02
I									.02

TABLE X: Similarity of patterns in CA1. Neuronal turnover rate: 100%.

	B	C	D	E	F	G	H	I	J
A	.00	.00	.00	.00	.00	.00	.00	.00	.00
B		.00	.00	.00	.00	.00	.00	.00	.00
C			.00	.00	.00	.00	.00	.00	.00
D				.00	.00	.00	.00	.00	.00
E					.00	.00	.00	.00	.00
F						.00	.00	.00	.00
G							.00	.00	.00
H								.00	.00
I									.00

We can see that the connection from EC to DG can reduce the similarity of patterns when the number of patterns to be stored is small. Namely, the similarity was less than 0.42 before D was learned by the model. The similarity of CA3 was generally lower than that of DG.

Although similar results can be seen in CA1 as shown in Table IV, the similarity of patterns was much reduced: the similarity was less than 0.42 before G was learned. Note that the neuronal turnover rate of this experiment was set to 0%. Therefore, we can say that the hippocampal model has an inherent function that can reduce the similarity of input patterns.

Tables V–VII show the result under the same condition, except that the neuronal turnover rate was set to 60%. As seen in these tables, the similarity of patterns were much reduced owing to neuronal turnover. In this case, the patterns formed at CA1 became completely orthogonal.

Tables VIII–X show the result when the neuronal turnover rate was set to 100%. In these tables, the similarity of DG was even lower than the other results.

As shown in these results, the hippocampal model reinforces the reduction of the similarity of input patterns with neuronal turnover in DG. This may contribute to store a lot of similar patterns in the hippocampal model.
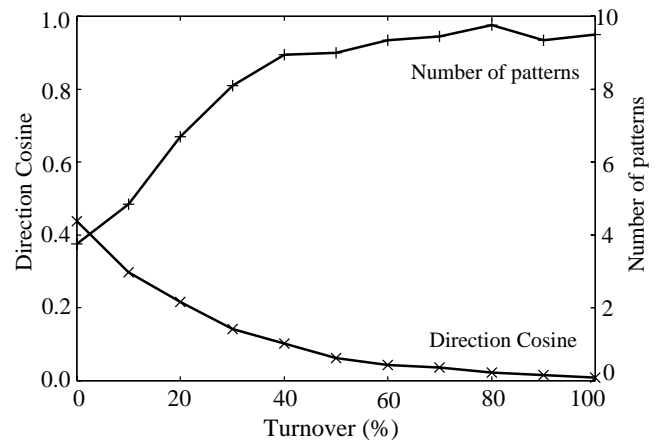

Fig. 7: Relation between the neuronal turnover rate and the similarity of patterns in DG (left axis) and the storage capacity (right axis). The similarity of input patterns was set to 0.42.

Fig. 7 shows the relation between the neuronal turnover rate and the average of the similarity in DG when the similarity of input patterns was set to 0.42. As seen in this figure, the larger the neuronal turnover rate is, the lower the similarity of patterns is. Besides, the storage capacity becomes larger as the neuronal turnover rate becomes larger.
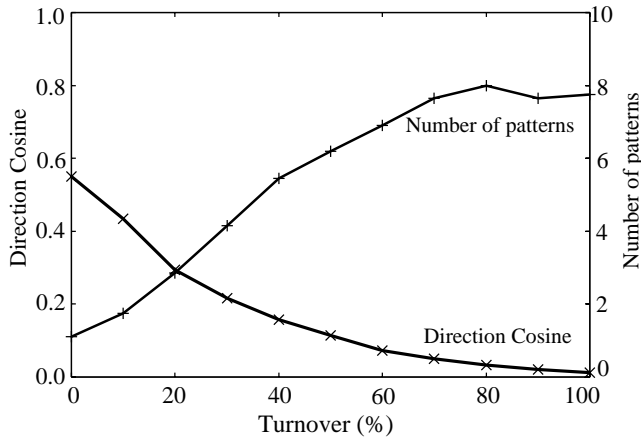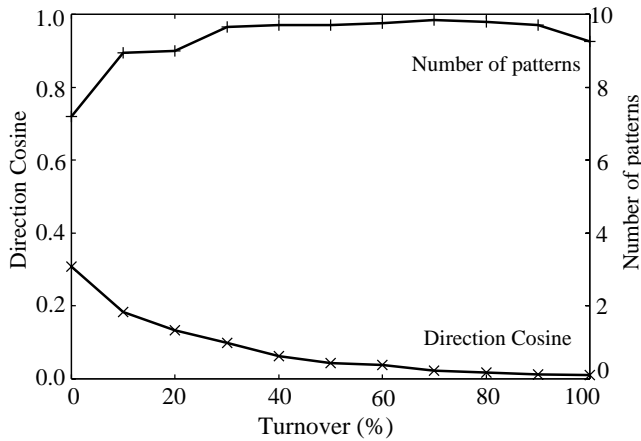

Fig. 8: Relation between the neuronal turnover rate and the similarity of patterns in DG (left axis) and the storage capacity (right axis). The similarity of input patterns was set to 0.50.

Fig. 9: Relation between the neuronal turnover rate and the similarity of patterns in DG (left axis) and the storage capacity (right axis). The similarity of input patterns was set to 0.38.

Figs.8 and 9 show the results when the similarity of input patterns was set to 0.50 and 0.38, respectively. As seen in Figs.7–9, neuronal turnover becomes more effective when the similarity of input patterns is large.

C. Learning Epochs

In this experiment, we examined the relation between neuronal turnover and the number of learning epochs required for successful learning. First, we made 5 different patterns so that every two patterns have the direction cosine. Then, these patterns were incrementally learned by the hippocampal model one by one. We varied the learning epochs from 1 to 100, and examined the minimum learning epoch to store all patterns successfully. We regarded it as unsuccessful learning if learning did not succeed within 100 epochs.
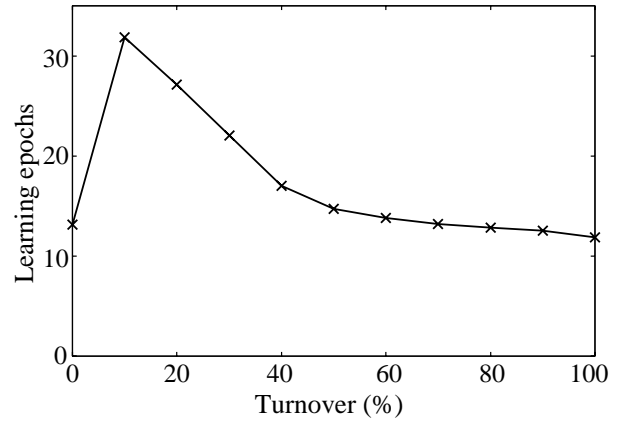

Fig. 10: Relation between the neuronal turnover rate and learning epochs. The similarity of input patterns was set to 0.50.
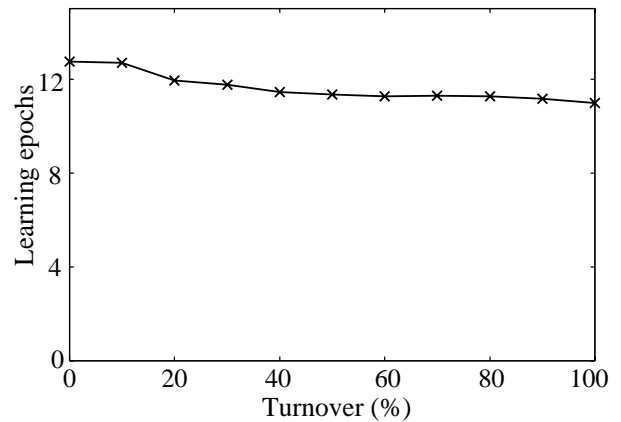

Fig. 11: Relation between the neuronal turnover rate and learning epochs. The similarity of input patterns was set to 0.42.

TABLE XI: The number of successful learning based on 400 trials. The similarity of input patterns was set to 0.50.

Turnover(%)	Number of successes
0	15
10	183
20	325
30	384
40	393
50	394
60	394
70	394
80	394
90	394
100	396

TABLE XII: The number of successful learning based on 400 trials. The similarity of input patterns was set to 0.42.

Turnover(%)	Number of successes
0	261
10	394
20	396
30	386
40	396
50	396
60	396
70	396
80	396
90	396
100	396

Figs.10 and 11 show the results when the similarity of input patterns was set to 0.50 and 0.42, respectively. These results are based on 400 trials. As shown in the figures, neuronal turnover is more effective when the similarity of input patterns is large (Fig.10): the larger the neuronal turnover rate is, the smaller the number of learning epochs to store all patterns is.

Tables XI and XII show the relation between the neuronal turnover rate and the number of successful trials in the experiment. We can see that the number of successful learning out of 400 trials is extremely small without neuronal turnover when the similarity of input patterns is large: the number of successful learning was 15 without neuronal turnover when the similarity was 0.50 (Table XI), while it was 261 when the similarity was 0.42 (Table XII). In other words, patterns difficult to learn (without neuronal turnover) can be learned by using neuronal turnover.

The reason why the number of learning epochs without neuronal turnover is very small in Fig.10 is due to the small number of samples, 15 (see Table XI).

V. CONCLUSIONS

In this paper, we have examined the role of neuronal turnover in dentate gyrus (DG) by using an abstract model of the hippocampal network. Neuronal turnover was modeled by choosing neurons in DG arbitrarily and initializing their weights randomly. Computer simulation results show the following features of the hippocampal model:

1) The storage capacity can be much improved as the neuronal turnover rate becomes large, especially when the similarity of input patterns are large.

2) The similarity of input patterns is reduced by the hippocampal model even without neuronal turnover. It seems that the hippocampal model has an inherent function so that the similarity of input patterns can be reduced.

3) The similarity of input patterns is much reduced with neuronal turnover, and this contributes to enlarge the storage capacity of the hippocampal model.

4) Owing to neuronal turnover, patterns difficult to learn can be successfully stored. Moreover, when the similarity of input patterns is large, the larger the neuronal

turnover rate is, the smaller the number of learning epochs is.

In our experiments, we have varied the neuronal turnover rate from 0 to 100%, which is clearly too high in comparison with the biological turnover rate. However, a more biologically realistic neuronal turnover rate did not produce a detectable effect in the scale of our model. In [8], Becker have varied the neuronal turnover rate from 25 to 100% in the almost same scale of the model. In the future research, we enlarge the scale of our model and employ a more biologically realistic neuron model and recent biological findings so that we can examine the features of the hippocampal network more precisely.

REFERENCES

[1] G. Kempermann, *Adult Neurogenesis*, Oxford University Press, 2006.
[2] F. H. Gage, "Neurogenesis in the Adult Brain," *The Journal of Neuroscience*, Vol.22, No.3, 2002, pp.612-613.
[3] J. B. Aimone, J. "Wiles and F. H. Gage, Potential role for adult neurogenesis in the encoding of time in new memories," *Nature Neuroscience*, Vol.9, No.6, 2006, pp.723-727.
[4] E. Gould, A. Beylin, P. Tanapat, A. Reeves, and T. J. Shors, "Learning enhances adult neurogenesis in the hippocampal formation," *Nature Neuroscience*, Vol.2, No.2, 1999, pp.260-265.
[5] G. Kempermann, "Why New Neurons? Possible Functions for Adult Hippocampal Neurogenesis," *The Journal of Neuroscience*, Vol.22, No.3, 2002, pp.635-538.
[6] F. Nottebohm, "Why Are Some Neurons Replaced in Adult Brain?," *The Journal of Neuroscience*, Vol.22, No.3, 2002, pp.624-628.
[7] B. Leuner, E. Gould, and T. J. Shors, "Is There A Link Between Adult Neurogenesis and Learning?," *HIPPOCAMPUS*, Vol.16, 2006, pp.216-224.
[8] S. Becker, "A Computational Principle for Hippocampal Learning and Neurogenesis," *HIPPOCAMPUS*, Vol.15, 2005, pp.722-738.
[9] M. F.Yeckel, and T. W. Berger, "Feedforward excitation of the hippocampus the trisynaptic pathway," *Proceedings of the National Academy of Sciences of the USA*, Vol.87, 1990, pp.5832-5836.
[10] P. Andersen, R. Morris, D. Amaral, T. Bliss, and J. O'Keefe, *The Hippocampus Book*, Oxford University Press, 2007.
[11] H. A. Cameron, R. D. McKay, "Adult Neurogenesis Produces a Large Pool of New Granule Cells in the Dentate Gyrus," *The Journal of Comparative Neurology*, Vol.435, 2001, pp.406-417.
[12] K. A. Norman, and R. C. O'Reilly, "Modeling Hippocampal and Neocortical Contributions to Recognition Memory: A Complementary-Learning-Systems Approach," *Psychological Review*, Vol.110, No.4, 2003, pp.611-646.
[13] J. Hertz, A. Krogh, and R. G. Palmer, "Introduction to The Theory of Neural Computation," *Adison-Wesley Publishing Company*, 1991.

Yuko Wakagi was born in Yamanashi, Japan. She received the bachelor degree in Engineering in 2007 from University of Yamanashi. She is now in the master course of Interdisciplinary Graduate School of Medicine and Engineering, University of Yamanashi in Japan.

Ms. Wakagi is a member of IEICE.

Motonobu Hattori was born in Tokyo, Japan on February 11, 1970. He received B.E., M.E. and Ph.D degrees in Electrical Engineering from Keio University in 1992, 1994 and 1997, respectively.

In 1997, he became a research associate of University of Yamanashi, Kofu, Japan. Since 2000, he has been an Associate Professor. From 2003 to 2004, he was a visiting researcher at Center for the Neural Basis of Cognition (CNBC) in Carnegie Mellon University, USA. His current research interest is in neural networks, reinforcement learning and evolutionary computation.

Dr. Hattori is a member of the IEEE, IEICE and IEE. He received Niwa Memorial Award in 1996.