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Input-dependent learning rule for the memory of spatiotemporal sequences in hippocampal network with theta phase precession

Zhihua Wu[1], **Yoko Yamaguchi**[1,2]

[1]Dynamics of Emergent Intelligence Lab., RIKEN Brain Science Institute, 2-1 Hirosawa, Wako, Saitama 351-0198, Japan
[2]CREST Japan Science and Technology Agency

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Abstract. Theta phase precession in rat hippocampal place cells is hypothesized to contribute to memory encoding of running experience in the sense that it provides the ideal timing for synaptic plasticity and enables the asymmetric associative connections under the Hebbian learning rule with asymmetric time window (Yamaguchi 2003). When the sequence of place fields is considered as the episodic memory of running experience, a given spatial route should be accurately stored in spite of differing overlap extent among place fields and varying running velocity. Using a hippocampal network model with phase precession and the Hebbian learning rule with asymmetric time window, we investigate the memory encoding of place field sequences in a single traversal experience. Computer experiments show that place fields cannot be stored correctly until an input-dependent feature is introduced into the learning rule. These experiments further indicate that there exists an optimum value for the saturation level of synaptic plasticity and the speed of synaptic plasticity in the learning rule, which are correlated with, respectively, the overlap extent of place field sequence and the running velocity of animal during traversal. A comparison of these results with biological evidences shows good agreement and suggests that behavior-dependent regulation of the learning rule is necessary for memory encoding.

1 Introduction

Theta phase precession was first described by O'Keefe and Recce (1993) as a phase relationship between the activity of pyramidal cells in the CA1 region of the rat hippocampus and the hippocampal theta rhythm. They found that a place cell's spike activity advances to earlier phases of the theta cycle as the rat passes through the cell's place field. Further experimental findings (Skaggs et al. 1996) indicate that the theta phase precession is a very robust effect, distributed across the entire hippocampal population.

A naturally arising question concerns the functional role of theta phase precession. Although the answer remains unclear, some existing hypotheses have generated considerable interest. For example, theta phase precession was thought to help hippocampus realize spatial navigation (Burgess et al. 1994). The inspiration for this hypothesis derives from the basic fact that the place field of those cells firing at late phases in the theta cycle lies ahead of rat, whereas the field of cells earlier in the theta cycle is behind the rat. Another hypothesis suggested that theta phase precession could serve as a tool for anticipating the future location of rat on a time scale of about 1 s, based on previous experience (Tsodyks et al. 1996). In addition, Jensen and Lisman (1996) proposed a theta/gamma model in which they suggested that theta phase precession occurs and takes effect in recall mode when animal moves through the place fields on a well-known path. They did not show that theta phase precession was related to the learning process. Their hypothesis interpreted theta phase precession as a prediction of sequential upcoming positions along a well-known path, which is similar to the hypothesis in Tsodyks et al. (1996).

In this work, we focus on the hypothesis proposed by Skaggs et al. (1996) and further supported by Yamaguchi et al. (2002). When the rat passes through a sequence of place fields, phase shift leads to compressed representation of temporal structure (Skaggs et al. 1996). Portions of this sequence will be replicated, in a compressed form, within individual theta cycles. Each portion of the sequence is repeated several times as the rat moves along, which provides proper conditions for synaptic plasticity. Therefore, Skaggs et al. (1996) proposed that theta phase precession may play an important role in episodic memory of rat's experience. Specifically, they thought that the compression of place field sequence within individual theta cycles induced by phase precession may make it possible to use long-term

Correspondence to: Z. Wu (e-mail: wuzh@brain.riken.jp, Fax: +81-48-4676938)

potentiation (LTP) to memorize the temporal structure of rat's experience. This possible mechanism was also realized by Wallenstein and Hasselmo (1997) in which they pointed out that the timing properties observed in phase precession might play an important role in the way synaptic modifications take place in the hippocampus. Such a hypothesis was supported by the results of bimodality analysis of theta phase precession in hippocampal place cells in Yamaguchi et al. (2002). More importantly, this hypothesis was shown by Yamaguchi (2003) to be feasible in neural dynamics.

To elucidate the neural mechanism of memory storage of temporal sequences, Yamaguchi (2003) proposed a theory of hippocampal memory based on theta phase precession. This theory is about the neural dynamics of the theta phase precession in freely running rat. It consists of three assumptions: (i) Phase locking of individual neurons by mean field interactions results in phase precession at the entorhinal cortex (EC); (ii) the temporally structured pattern of activities in EC is transmitted along the hippocampal circuit, leading to asymmetric connections in CA3 network based on an LTP mechanism with asymmetric time window; and (iii) in the final stage of the circuit, the deeper layers of EC is considered to have activities with a phase difference of about a quarter theta cycle from that of layer II of EC. It endows selective potentiation in synapses projecting from CA3 to CA1, so that the loop along the hippocampus circuit is closed in the neural module at EC. Assumptions (i) and (ii) work for encoding of memory, while assumption (iii) applies to memory retrieval. A part of the dynamics was briefly reported by Yamaguchi and McNaughton (1998).

The advantage of theta phase precession in the encoding and storage of temporal sequence has been shown in this model (Yamaguchi and McNaughton 1998; Yamaguchi 2003). Moreover, by using this model, Sato and Yamaguchi (2003) clarified that theta phase precession can encode memory of temporal sequences by a behavior time scale that is theoretically impossible by firing rate encoding. However, these studies were only focused on temporal sequences. Complete memory about running experience on a spatial route should involve not only temporal order of place fields but also the extent of spatial overlap between these fields. How to exactly encode the spatiotemporal sequence in hippocampal network, even given varying running velocity, remains an open question. It is this that we focus on in this paper. We will show that an input-dependent learning rule is critically necessary for this purpose, in particular, that the ability to accurately memorize information about the extent of overlap between place fields strongly depends on such a learning rule.

The hippocampus model with theta phase precession proposed by Yamaguchi (2003) as well as the Hebbian learning rule with asymmetric time window are described in Sect. 2. The method of computer experiments is explained in Sect. 3. Section 4 describes computer experiments on the rat when exposed to sequences with varying overlap extent between place fields and running with varying velocity. The biological meaning of the input-dependent learning rule obtained in Sect. 4 is discussed in Sect. 5, and a comparison of this model with other models is also given in this final section.

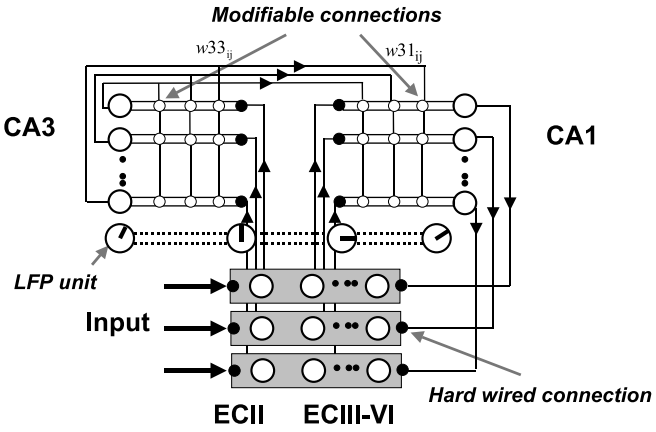


Fig. 1. Neural network model of the closed hippocampal circuit

2 Model and learning rule

2.1 Closed hippocampal circuit

As illustrated in Fig. 1, this model consists of four layers that respectively simulate layer II of the entorhinal cortex (ECII), CA3, CA1, and layers III $\sim$ VI of the EC (ECV) (Yamaguchi 2003). It begins at ECII. Along the circuit, connections between layers are feedforward except for a backward projection from ECV to CA1.

The dynamics of the dentate gyrus can be considered similar to that of ECII. For simplicity, the dentate gyrus is abbreviated in the model.

The input signal is fed to the ECII and ECV layers. A one-to-one connection is assumed between ECII and CA3 and between ECV and CA1. There is no coupling among units in each layer except CA3. Memory is proposed to be stored in a CA3 recurrent network, where the initial all-to-all homogeneous connections will be pruned by learning. From CA3 to CA1, one-to-all forward projections simulate the role of Schaffer collaterals. Besides recurrent connections in CA3, forward projection from CA3 to CA1 is also assumed to have plasticity during running experience. A phase difference of about a quarter theta cycle between activities of ECV and that of ECII helps to induce selective potentiation in synapses projecting from CA3 to CA1. While the plasticity of recurrent connections of CA3 serves as memory encoding, the plasticity in projection from CA3 to CA1 plays a role in transferring replayed memory from CA3 to CA1 during the retrieval stage.

Each unit is considered as a representative of the population of neural elements and comprises a feature of the place cell. Each unit is represented by one oscillator. The network is described by the following dynamics:

$$\dot{\phi}_{\mathrm{ECII}i}(t) = \omega_i(t) - \Big[-\beta(1 - I_i(t)) + \alpha_0^{\mathrm{ECII}} \cos\phi_{\mathrm{ECII0}} \Big] \sin\phi_{\mathrm{ECII}i} \quad (1)$$

$$\dot{\phi}_{\mathrm{CA3}i}(t) = \omega - \Big[-\beta + \alpha_0^{\mathrm{CA3}} \cos\phi_{\mathrm{CA30}} + \alpha_1 P(\phi_{\mathrm{ECII}i}) + \alpha_2 \sum_{j=1}^{N} w33_{ij} P(\phi_{\mathrm{CA3}j}) \Big] \sin\phi_{\mathrm{CA3}i} \quad (2)$$

$$\dot{\phi}_{\mathrm{CA1}i}(t) = \omega - \Big[-\beta + \alpha_0^{\mathrm{CA1}} \cos\phi_{\mathrm{CA10}} + \alpha_3 P(\phi_{\mathrm{ECV}i}) + \alpha_4 \sum_{j=1}^{N} w13_{ij} P(\phi_{\mathrm{CA3}j}) \Big] \sin\phi_{\mathrm{CA1}i} \quad (3)$$

$$\dot{\phi}_{\mathrm{ECV}i}(t) = \omega_i(t) - \Big[-\beta(1 - I_i(t)) + \alpha_0^{\mathrm{ECV}} \cos\phi_{\mathrm{ECV0}} + \alpha_5 P(\phi_{\mathrm{CA1}j}) \Big] \sin\phi_{\mathrm{ECV}i} \ , \quad (4)$$

where variable ϕ_i represents the phase of the i-th oscillator unit whose membrane potential is simulated by $\cos\phi_i$, N is the number of oscillator units in each layer, ω denotes native angular frequency whose value simulates the theta rhythm, the quantity β represents the stabilization coefficient, and $I_i(t)$ is the behavior-dependent input that simulates a sensory input carrying the information about rat's location on the track. A detailed description of $I_i(t)$ will be given in Sect. 3. $w33_{ij}$ denotes the synaptic weight connecting presynaptic unit j and postsynaptic unit i in CA3, while $w13_{ij}$ is the weight connecting presynaptic unit j in CA3 and postsynaptic unit i in CA1. Function $P(x)$ denotes the output of neural unit and is defined as

$$P(x) = \begin{cases} (\cos x - \mu)/(1 - \mu) & \text{if } (\cos x \geq \mu) \\ 0 & \text{(otherwise)} \ , \end{cases} \quad (5)$$

with a firing threshold μ. $P(x)$ possesses the meaning of firing rate and ranges from 0 to 1.

Local field potential (LFP) with a characteristic frequency of theta rhythm dominates all layers, as described by the terms related to α_0^{ECII}, α_0^{CA3}, α_0^{CA1}, and α_0^{ECV} in (1)–(4). The LFP theta of each layer is described by a single oscillator whose phase is denoted by, respectively, ϕ_{ECII0}, ϕ_{CA30}, ϕ_{CA10}, and ϕ_{ECV0}. The LFP theta of each layer couples with another LFP theta as follows:

$$\dot{\phi}_{\mathrm{ECII0}} = \omega \quad (6)$$

$$\dot{\phi}_{\mathrm{CA30}} = \omega - \alpha_6(\cos\phi_{\mathrm{ECII0}} + \cos\phi_{\mathrm{CA10}}) \sin\phi_{\mathrm{CA30}} \quad (7)$$

$$\dot{\phi}_{\mathrm{CA10}} = \omega - \alpha_7(\cos\phi_{\mathrm{CA30}} + \cos\phi_{\mathrm{ECV0}}) \sin\phi_{\mathrm{CA10}} \quad (8)$$

$$\dot{\phi}_{\mathrm{ECV0}} = \omega - \alpha_8 \cos(\phi_{\mathrm{ECII0}} + \pi/6) \cos\phi_{\mathrm{ECV0}} \ . \quad (9)$$

$\omega_i(t)$ in (1) and (4) is the native angular frequency of units in the ECII and ECV layers during input. It is assumed that $\omega_i(t)$ obeys the following change when rat enters the i-th place field:

$$\omega_i(t) = \begin{cases} \omega_S + \omega_A(t - t_i)/D_i & \text{if } (t_i < t < t_i + D_i) \\ \omega & \text{(otherwise)} \ , \end{cases} \quad (10)$$

where t_i is the time when animal enters the i-th place field, and D_i is the duration of place field that imitates the time spent in this place field by the animal.

According to the hypothesis in Yamaguchi (2003), theta phase precession is generated in the EC by phase locking between LFP theta and neural units. When rat enters a place field (on-state), the native frequency of the corresponding neural unit in EC undergoes a gradual increase because of some intrinsic physiological process that is simulated by (10). When rat traverses a sequence of place fields having overlap, a number of neural units are activated sequentially and their frequencies are ordered according to the priority of activation. According to the property of coupled nonlinear oscillators, the phase locking among neural units in (1)–(4) and LFP theta in (6)–(9) leads to theta phase precession, i.e., the relative phase difference between each neural unit and LFP changes monotonically and slowly when rat passes through the place field. Simultaneously, relative phase differences between neural units in the on-state are generated instantaneously and kept stable. Thus the temporal order of place field sequence with behavior time scale is kept in each theta cycle, which makes the synaptic plasticity possible.

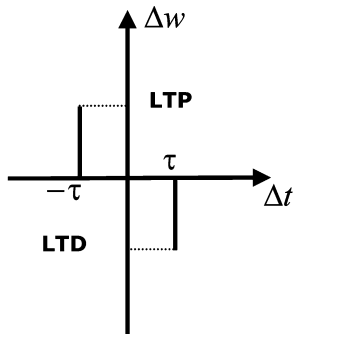
2.2 Hebbian learning rule with asymmetric time window

Learning and memory are considered to occur in recurrent connections in CA3 and connections projecting from CA3 to CA1. Experimental evidence supported the idea that a critical time window between pre- and postsynaptic action potentials determines the fate of synapses. Synapses will be strengthened if presynaptic spikes precede postsynaptic firing by no more than about 50 ms, whereas presynaptic activities that follow postsynaptic spikes will produce long-term weakening of synapses (Markram et al. 1997; Bi and Poo 1998; Debanne et al. 1998; Zhang et al. 1998a). Since the activity of each unit is described by the instantaneous firing rate in this model, we employ a firing-rate-timing-dependent learning rule instead of a spike-timing-dependent one. The learning rule is proposed to have the following form:

$$\dot{w33}_{ij}(t) = A\{\mathrm{LTP}(x_i, x_j, \tau) + \mathrm{LTD}(x_i, x_j, \tau)\} \times (R - w33_{ij}(t)^2) w33_{ij}(t) \quad (11)$$

$$\dot{w13}_{ij}(t) = (A + \Delta A_{13})\{\mathrm{LTP}(x_i, x_j, \tau) + \mathrm{LTD}(x_i, x_j, \tau)\} \times (R + \Delta R_{13} - w13_{ij}(t)^2) w13_{ij}(t) \ , \quad (12)$$

where x_i is the firing rate of the i-th unit. The learning rate is denoted by parameter A, and parameter R determines the saturation level of synaptic plasticity. ΔA_{13} and ΔR_{13} are small amounts that control the



Δt : The time of the presynaptic firing rate minus the time of the postsynaptic firing rate

Δw : The change of the synaptic weight

Fig. 2. Scheme of the critical time window for firing rate-timing-dependent learning rule

possible difference in learning rate and saturation level between CA3 and projection from CA3 to CA1. Whether there exists such a difference between CA3 and Schaffer collaterals is beyond the scope of this paper. The value of ΔA_{13} and ΔR_{13} in simulations is chosen empirically according to the maximum similarity between replayed sequence in ECV and the learned pattern.

Experimental results showed that a continuous time window ranging from 0 to about 50 ms exists for spike-timing-dependent synaptic plasticity. To simplify the problem, only one critical time window with delay τ is used in this learning rule, as illustrated by Fig. 2. The specific learning rule is described as

$$\begin{aligned}\dot{w}33_{ij}(t) = A\Big[&x_i(t)x_j(t-\tau_1)(\gamma_{33}^1 + \cos\phi_{\mathrm{CA30}}(t)) \\ &- \gamma_{33}^2 x_i(t-\tau_1)x_j(t) - \gamma_{33}^3 x_i(t) - \gamma_{33}^4 x_j(t-\tau_1)\Big] \\ &\times \left(R - w33_{ij}(t)^2\right) w33_{ij}(t) \qquad (13)\end{aligned}$$

$$\begin{aligned}\dot{w}13_{ij}(t) = (A + \Delta A_{13})\Big[&x_i'(t)x_j(t-\tau_2) \\ &\times (\gamma_{13}^1 + P(\phi_{\mathrm{ECV}i}(t))) - \gamma_{13}^2 x_i'(t-\tau_2)x_j(t) \\ &- \gamma_{13}^3 x_i'(t) - \gamma_{13}^4 x_j(t-\tau_2)\Big] \\ &\times \left(R + \Delta R_{13} - w13_{ij}(t)^2\right) w13_{ij}(t) \ , \qquad (14)\end{aligned}$$

where $x_j(t) = P(\phi_{\mathrm{CA3}j}(t))$, $x_i(t) = P(\phi_{\mathrm{CA3}i}(t))$, and $x_i'(t) = P(\phi_{\mathrm{CA1}i}(t))$. Coefficients γ_*^1 and γ_*^2 separately determine the amplitudes of LTP and LTD effects. In addition, LTD induced by noncorrelated pre- and postsynaptic firing is also considered in this model, as described by terms relating to γ_*^3 and γ_*^4.

The modulation effect of theta rhythm on synaptic plasticity is emphasized in this learning rule. An important modulatory role of the hippocampal theta rhythm in synaptic plasticity has been reliably observed not only in vitro (Huerta and Lisman 1993, 1995) but also in vivo (Hölscher et al. 1997; Orr et al. 2001). Early in 1993, Huerta and Lisman (1993) found that theta-frequency oscillations induced in hippocampal slices selectively enhanced synaptic efficacy of CA1 neurons in a phase-dependent way. Even in vivo, a single burst given on the positive phase of tail-pinch-triggered theta rhythm reliably induced LTP in the CA1 of urethane-anesthetized rats, while brief burst stimulation had no effect when given on the negative or zero phase or in the absence of theta (Hölscher et al. 1997). A recent study went a further step. The effects of theta phase on the magnitude of LTP was found in awake rats running on a linear track for a food reward (Orr et al. 2001). The results confirmed that LTP can be modulated by locomotion-induced theta. Our computer experiments show that theta rhythm modulation, as illustrated in (13) and (14), is important for ensuring correct learning in this model, which is consistent with the above experimental facts.

Whether the sequence is correctly encoded in memory is checked by a retrieval process after one-trial learning.

Retrieval is triggered by short cue input incident on the EC layer. An important feature of the retrieval process is that the LFP theta rhythm in every layer is stopped, i.e., $\alpha_0^{\mathrm{ECII}} = \alpha_0^{\mathrm{CA3}} = \alpha_0^{\mathrm{CA1}} = \alpha_0^{\mathrm{ECV}} = 0$, which is meant to simulate the state of slow wave sleep. Another feature is that association synaptic modification, defined by (11)–(14), is disabled during retrieval. The network is allowed to freely recall the sequence after experiencing a short cue input. Moreover, a remarkable enhancement of input from CA1 to ECV simulated by increased α_5 is conventionally introduced to imitate the effective activation of ECV in the retrieval stage.

Experimental results showed a significant increase in the spiking activity of the cells that had place fields in the environment, i.e., those that had strengthened connections, in the subsequent slow wave sleep compared with cells without place fields (Pavlides and Winson 1989; Wilson and McNaughton 1994). The physiological basis can be traced to the dramatic decrease in acetylcholine level during slow wave sleep. Studies by computational modeling proposed that low acetylcholine levels allow strong feedback transmission for retrieval and consolidation (see Hasselmo 1995 for review). Consequently, recurrent feedback through intrinsic fiber synapses dominates the dynamics during retrieval stage in contrast to the learning process in which LFP theta and sensory afferent input has an advantage. To simulate this, the stable coefficient β is slightly lowered in the retrieval process to reduce the firing threshold or increase the excitability of the most recently active units. Note that a similar effect was realized in Yamaguchi (2003) by increasing the associative connection coefficients α_2 and α_4 while keeping β constant.

2.3 Memory encoding difficulty with spatiotemporal sequences

The learning rule defined by (11)–(14) was shown to be successful in memory encoding of temporal place field sequences based on theta phase precession (Yamaguchi 2003). However, a serious difficulty arises in this learning rule when spatiotemporal sequences are presented to the

network. The overlap extent between place fields cannot be encoded correctly, which is reflected in the very low similarity between the retrieved sequence and the learned pattern. After many computer experiments, we found that an input-dependent learning rule was critically important for memory encoding. This means that to store the sequences of place fields correctly, parameters R and A in (11)–(14) should be adjusted in an input-pattern-dependent manner. The specific effect of R and A on learning will be thoroughly examined below.

By applying simple mathematical analysis to (11)–(14), it can be understood that R determines the saturation level of synaptic plasticity in the sense that $\sqrt{R}$ controls the maximum synaptic weight of recurrent connections in CA3 during learning. Correspondingly, $\sqrt{R+\Delta R_{13}}$ controls maximum synaptic weight of projecting connections from CA3 to CA1. The learning rate A determines the speed of synaptic plasticity, which is related to the firing rate of place units. The neurobiological meaning of these two parameters will be discussed in the following sections.

3 Method of computer experiment

3.1 Spatiotemporal content carried by place field sequence

A complete memory of spatial route includes not only the temporal order of place fields but also the overlap extent among these fields. We consider a simple situation in which animal traverses a linear track unidirectionally at a constant running velocity. Behavior-dependent input $I_i(t)$ in (1) and (4) is assumed to have the form:

$$I_i(t) = \begin{cases} 1 & \text{if } (t_i < t < t_i + D_i) \\ 0 & \text{(otherwise)} \end{cases}, \tag{15}$$

where t_i and D_i have the same meaning as those in (10). $S_i = t_{i+1} - t_i$ is defined as the shift. The smaller the shift S_i, the larger the overlap degree between the i-th and $(i+1)$-th place fields. Duration D_i is directly proportional to the ratio of field width to rat's running velocity.

For simplicity, it is assumed that all the place fields have the same duration $D_i = D$ and the same shift $S_i = S$. Then the spatiotemporal sequence of place fields has a uniform distribution, as shown in Fig. 3.

For convenience, another parameter K, defined as $K = D/S$, is also used to describe the extent of sequence overlap. It denotes the number of place fields that overlap instantaneously. In other words, K gives the number of place units that encode an instantaneous location in the stationary state of running experience. Note that, of the parameters D, S, and K, only two are independent.

Input sequences are expressed in a unified way as $\{D, S, K\}$ below. D and S are measured in terms of theta cycle T with $T = 2\pi/\omega$. For example, $\{10T, T, 10\}$ represents an input pattern with duration $D = 10T$, shift $S = T$, and $K = 10$.

3.2 Analysis method of similarity between retrieved sequence and learned pattern

To quantify the similarity between retrieval sequence and the learned pattern, the correlation coefficient, denoted by C_r, is calculated. We employ the correlation analysis method described in Louie and Wilson (2001). As shown in Fig. 4, two sequences are separately divided into bins of equal number along the time axis. C_r is defined as

$$C_r = \frac{\frac{1}{B \cdot M} \sum_{m=1}^{M} \sum_{b=1}^{B} \left(\frac{x_{bm}}{X_m} - \bar{x}\right)\left(\frac{y_{bm}}{Y_m} - \bar{y}\right)}{\sigma_x \sigma_y}, \tag{16}$$

where x_{bm} and y_{bm} express lengths for the active period $(P(\phi) > 0)$ of the m-th unit in the b-th bin in, respectively, the retrieval sequence and the learned pattern. M is the unit number and B the bin number. Note the only difference of our definition (16) from that in Louie and Wilson (2001) is the meaning of x_{bm} and y_{bm}. In their definition, x_{bm} and y_{bm} express the binned spike counts of unit m. Other quantities are given by the following

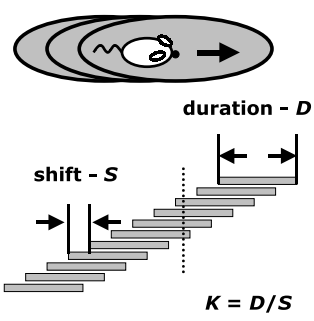


Fig. 3. Spatiotemporal content of rat's place field sequence. The *vertical dashed line* is used to easily estimate the value of K, which is roughly equal to the number of place fields crossed by this line

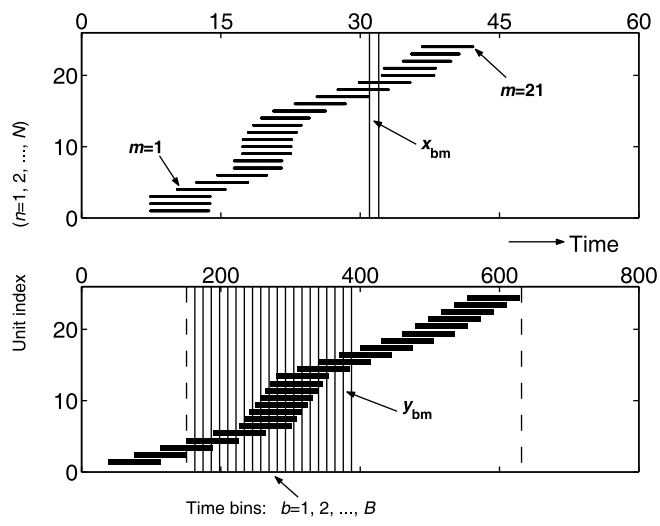


Fig. 4. Correlation coefficient analysis. The *top panel* shows the retrieval sequence, and the the input pattern is displayed in *bottom* panel. *Dashed lines* give the range of units selected for analysis. See text for the meaning of quantities

formulas whose meaning can be found in Louie and Wilson (2001):

$$X_m = \sqrt{\frac{1}{B}\sum_{b=1}^{B} x_{bm}^2} \tag{17}$$

$$\bar{x} = \frac{1}{B \cdot M}\sum_{m=1}^{M}\sum_{b=1}^{B}\frac{x_{bm}}{X_m} \tag{18}$$

$$\sigma_x = \sqrt{\frac{1}{B \cdot M}\sum_{m=1}^{M}\sum_{b=1}^{B}\left(\frac{x_{bm}}{X_m} - \bar{x}\right)^2} \ . \tag{19}$$

To check the memory effect in the CA3 and ECV layers, respectively, two coefficients C_{r_CA3} and C_{r_ECV} are given together for each learned pattern. C_r ranges between -1 and $+1$.

3.3 Values of parameters

Equations defined in previous sections are numerically solved by the Runge-Kutta method. The integration time step in the simulation is chosen to be 0.01. None of the parameters in this model has any units. Although their values are chosen empirically based on Yamaguchi (2003), values of those parameters relating to time are chosen carefully to establish a possible consistency in time scale among them. For instance, the time window size in the learning rule should be much less than theta cycle, i.e., $\tau \prec\prec T$. And the duration D of place field in various input patterns should range around $10T$ according to behavior experimental data.

Parameters along with their meaning and values are summarized in Table 1.

4 Results

4.1 One example for learning and retrieval

The sequence $\{10T, T, 10\}$ is taken as a typical input pattern to investigate the network's dynamics. The learning process in one trial is displayed in Fig. 5, in which activity of each unit is expressed as one short bar whose length corresponds to the time period for

Table 1. Parameters used in computer simulations

Parameter	Interpretation	Value
N	Number of units in each layer	24
ω	Native frequency of unit in theta rhythm	1.0
T	Cycle of theta rhythm	2π
ω_S	Lowest native frequency	0.5
ω_A	Largest increment of native frequency within one place field	1.3
α_1	Coefficient for excitatory input from ECII to CA3	3.0
α_2	Coefficient for recurrent connections in CA3	0.4
α_3	Coefficient for excitatory input from ECV to CA1	2.0
α_4	Coefficient for excitatory input from CA3 to CA1	1.0
α_5	Coefficient for excitatory input from CA1 to ECV	0.1 (R: 1.0)[a]
α_6	Coupling coefficient of LFP theta between neighboring layers and CA3	0.1
α_7	Coupling coefficient of LFP theta between neighboring layers and CA1	0.1
α_8	Coupling coefficient of LFP theta between ECII and ECV	0.3
α_0^{ECII}	Coefficient of LFP theta in ECII	1.0 (R: 0.0)[a]
α_0^{CA3}	Coefficient of LFP theta in CA3	0.6 (R: 0.0)[a]
α_0^{CA1}	Coefficient of LFP theta in CA1	0.3 (R: 0.0)[a]
α_0^{ECV}	Coefficient of LFP theta in ECV	1.0 (R: 0.0)[a]
β	Stabilization coefficient	1.9 (R: 1.4)[a]
μ	Threshold of unit firing	-0.5
A	Learning rate	0.5–2.5
R	Saturation level of synaptic plasticity	0.21–6.00
ΔA_{13}	Difference in learning rate between CA3 and projections from CA3 to CA1	0.0
ΔR_{13}	Difference in saturation level between CA3 and projections from CA3 to CA1	-0.2
τ_1	Time window in the learning rule for CA3	0.4
τ_2	Time window in the learning rule for projections from CA3 to CA1	0.6
γ_{33}^1	Amplitude coefficient of LTP for CA3	0.28
γ_{13}^1	Amplitude coefficient of LTP for projections from CA3 to CA1	0.25
γ_{33}^2	Amplitude of LTD for CA3	0.15
γ_{13}^2	Amplitude of LTD for projections from CA3 to CA1	0.15
γ_{33}^3	Amplitude of LTD by noncorrelated firing for CA3	0.1
γ_{13}^3	Amplitude of LTD by noncorrelated firing for projections from CA3 to CA1	0.1
γ_{33}^4	Amplitude of LTD by noncorrelated firing for CA3	0.15
γ_{13}^4	Amplitude of LTD by noncorrelated firing for projections from CA3 to CA1	0.15
$w(0)$	Initial value of connection weights	0.1
D	Duration of place field	$3T$–$30T$
S	Shift between two fields	$0.5T$–$6T$
K	Overlap extent of sequence	2–15

[a] The value in parentheses denotes the value of the corresponding parameter during retrieval stage

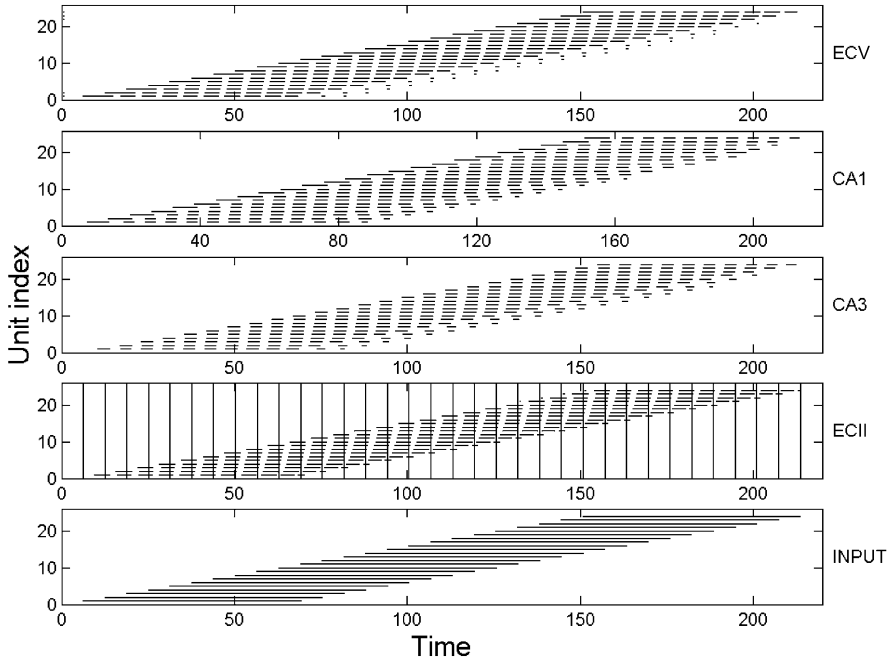


Fig. 5. Learning process for input pattern $\{10T, T, 10\}$ with parameters $A = 1.0$ and $R = 0.57$. Layer name is indicated on *right*. *Vertical lines* in ECII panel are ticks of theta rhythm cycle. Apparent asymmetry appears in synaptic connections

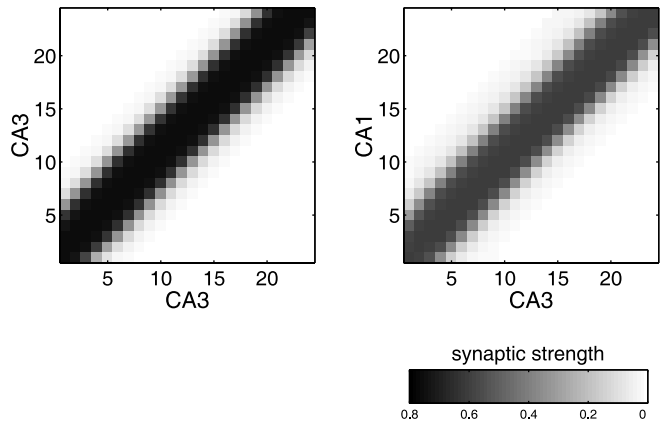


Fig. 6. Synaptic weight matrix after learning in Fig. 5. The horizontal and vertical axes are, respectively, the presynaptic and postsynaptic unit indices. The *left panel* displays recurrent connections in CA3, and the *right panel* shows projecting connections from CA3 to CA1. The *color bar* marks the strength of synaptic connections

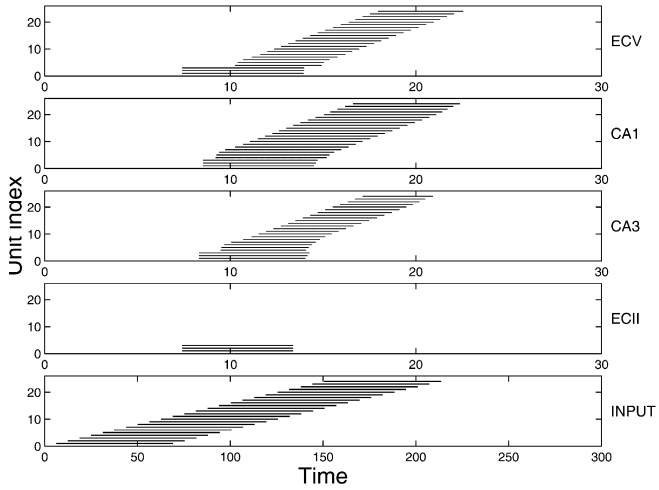


Fig. 7. Retrieval process after learning in Fig. 5. The *lowermost panel* illustrates the input pattern during learning

$P(\phi_i) > 0$. Theta phase precession occurs in ECII and ECV and then is transferred to CA3 and CA1. It can be seen that firing of each unit advances gradually from the end to the beginning of theta cycles. Sequence structure is compressed within individual theta cycles by phase precession. Portions of compressed sequence are repeatedly replicated within theta cycles, causing the ideal timing for LTP and LTD.

The weight matrix after one trial learning is shown in Fig. 6. Note that before learning, $w33_{ij}$ and $w13_{ij}$ were initialized to a very low homogeneous distribution with weight $w(0)$.

Figure 7 displays the corresponding retrieval process. It is performed at a quite fast time scale with the same order as theta cycle, which is the major feature of slow wave sleep. Because units 1 to 3 are involved in the transient process for receiving cue input, only $M = N - 3$ units are used to estimate C_r, as shown by the dashed lines in Fig. 4. Results show a high correlation coefficient: $C_{r_\mathrm{CA3}} = 0.95$ and $C_{r_\mathrm{ECV}} = 0.92$. This means that the learned spatiotemporal sequence can be retrieved with considerable accuracy in this model.

Further computer experiments reveal that memory encoding is not always as good as above example. For a given input pattern, different values of R and A actually lead to different C_r. Moreover, the relationships between R and C_r (or A and C_r) are very different from those with different input patterns. Figure 8 displays two typical examples with fixed A. The result implies that, although the relation between C_r and R is not simple, there is an optimum value of R for correct learning. For almost all

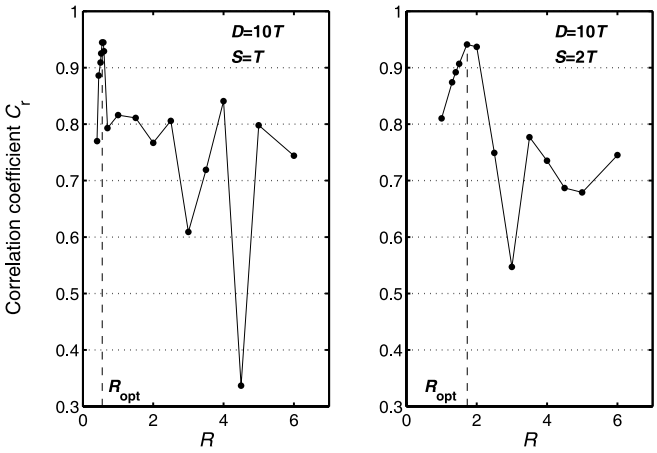


Fig. 8. R-dependent correlation coefficient for, respectively, two input patterns $\{10T, T, 10\}$ (left) and $\{10T, 2T, 5\}$ (right). The learning rate is fixed at $A = 1.0$

input patterns the first peak of the $R - C_r$ curve usually corresponds to the maximum C_r; therefore, the value at this peak is selected as the optimum value, denoted by R_{opt}. By exploring the optimum values under various conditions, we try to elucidate below how the parameter R is regulated by the input pattern.

4.2 Storage of uniform spatiotemporal sequence of place fields

This section presents a thorough investigation into the relationship between R_{opt} and input pattern. Results show that both duration D and shift S of sequence strongly regulate R_{opt}. Figure 9a displays an example of how R_{opt} depends on S when D is fixed, while Fig. 9b shows how R_{opt} is regulated by D with fixed S.

Interestingly, a general rule appears if the above two curves are redrawn with respect to parameter K. As shown in Fig. 9c, the two curves conform to each other very well. It reveals that the optimum saturation level R_{opt} decreases with the overlap degree of sequence except when $K < 3.33$.

According to experimental data in Hampson et al. (1996), the cross correlation between activities of neuron pairs were very small for pairs of neurons with no or less overlap in their place fields up to around 50% overlap. Applying the definition of overlap degree in Hampson et al. (1996) to this model, we have the formula of field overlap degree as

$$\frac{D-S}{D+S} \times 100\% = \frac{K-1}{K+1} \times 100\% \quad . \tag{20}$$

Based on (20), the overlap extent $K < 3.33$ in Fig. 9c corresponds to an overlap extent of less than 55% according to Hampson et al.'s (1996) definition. Therefore, we propose that only the part $K > 3.33$ of the curve in Fig. 9c is reasonable in rat's experience.

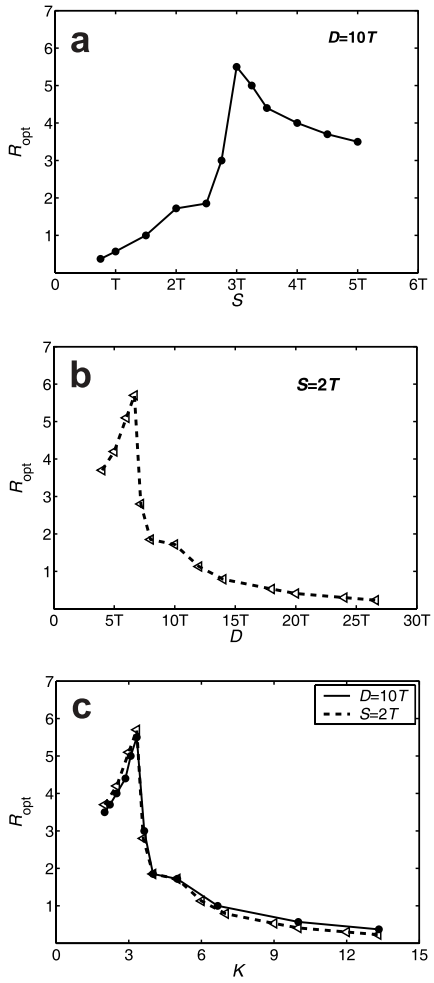


Fig. 9. **a** Relation between shift S and optimum saturation level R_{opt} while duration D remains constant at $10T$ and $A = 1.0$. **b** Relationship between D and R_{opt} while S remains constant at $2T$ and $A = 1.0$. **c** Two *curves* in **a** and **b** after being scaled by overlap extent $K = D/S$

Consequently, results from Fig. 9c propose a necessary condition for memory encoding of place field sequences: saturation level of synaptic plasticity should decrease with overlap degree. The related biological meaning will be discussed at the end of this paper.

Furthermore, two common properties are found to be tenable for memory encoding with uniform spatiotemporal sequences (Fig. 10). One is that asymmetric connections in CA3, i.e., $w33_{ij} \neq w33_{ji}$. The asymmetry reflects the unidirectional traversal of place fields in running experience. Another is that place units encoding an instantaneous location during running experience are bound together by strengthened synaptic weights. The number of place units in the bound population is proportional to the overlap extent of place field sequence. Results suggest that the temporal order of place fields of a sequence is encoded by the asymmetry of weight connections, while the structure of network weight connections encodes the spatial information about overlap extent among place fields. This model realizes the accurate memory encoding of spatiotemporal sequences.

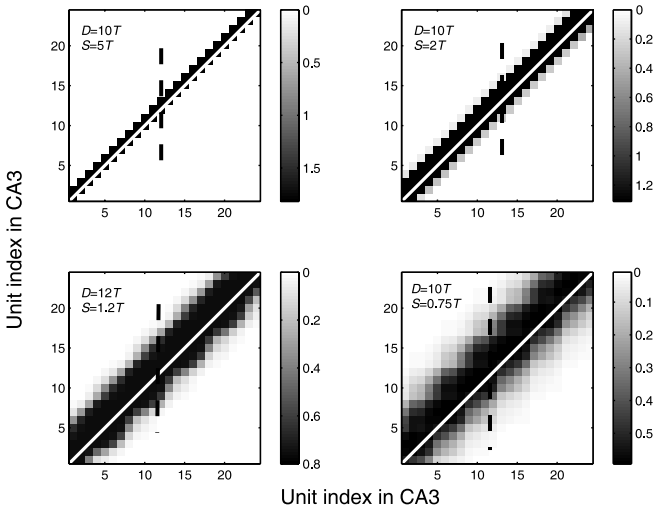


Fig. 10. Structure of synaptic weight matrix in CA3 after one trial learning. Each *panel* corresponds to one uniform input pattern. R_{opt} takes 3.5 (*top left*), 1.72 (*top right*), 0.58 (*bottom left*), and 0.37 (*bottom right*). *White diagonal lines* are used for checking the asymmetry of connections, and *dashed vertical lines* are used to help count the number of place units bound by the enhanced weights

4.3 Storage of place field sequence with varying running velocity

Since rat usually may not move at constant speed, memory encoding with varying running velocity is investigated in this section.

There is a complex correlation between the animal's running speed and the frequency of the hippocampal theta rhythm, as analyzed in Muir and Bilkey (2003). In a previous study in which the location of the animal was space-clamped on a running wheel, it was shown that theta frequency remained constant with increasing running velocity. But other previous studies showed a weak linear relationship between running velocity and theta frequency in freely moving animals (Shen et al. 1997; Slawińska and Kasicki 1998). Considering that the increment of theta frequency is not so large, for instance the frequency was only raised by less than 15% when running speed became six times as fast as before for both young and old rats (Shen et al. 1997), it is simply assumed in this work that the theta frequency is not modulated by running velocity.

Rat is assumed to keep constant velocity for any individual traversal but to run with varying velocity among different traversals on a fixed route. The problem is simplified as to how the same uniform spatiotemporal sequence of place fields is accurately stored with varying running velocity by one trial experience. Input patterns with different velocities can be described by a series of sequences possessing a constant overlap extent K and different duration D, as shown in Fig. 11. Note that running velocity is directly proportional to the reciprocal of duration D, i.e., velocity $\propto 1/D$.

Imagine that a group of rats is running along a fixed track with varying velocities. Does running velocity affect the memory encoding of sequences? What kind of changes will happen in pyramidal neuron activities so that every rat can correctly memorize this running experience by only one single traversal?

Computer experiments revealed a definite answer to the first question. Memory encoding of place fields worsens pronouncedly with increasing running velocity, even under the condition of R_{opt}. This is reflected in a decreased similarity between the retrieved sequence and the learned pattern (data not shown). As the most plausible explanation, we propose that the synaptic weight connecting any two place cells could not have enough time to be sufficiently enhanced due to decreased time spent within each place field. And such a decrease in similarity cannot be made up for through modulation of R_{opt} because K remains constant for all trials with varying running velocity (Fig. 11).

To achieve a level of memory that is as good as before, our computer experiments have revealed that an adjustable learning rate can compensate this loss. An advantage of this learning rule lies in the fact that it enables the analysis of relationship between learning rate and running velocity.

The learning rate A controls the speed of synaptic plasticity. The neurophysiological meaning of learning rate in this model is proportionally related to the firing rate of place units, which can be understood through a transformation of the basic Hebbian learning rule $\Delta W_{ij} = AX_jX_i$ to another form $\Delta W_{ij} = (\sqrt{A}X_j)(\sqrt{A}X_i)$. X_j and X_i denote, respectively, the activities of presynaptic neuron j and postsynaptic neuron i that are usually measured by firing rate. The degree to which the learning rate is changed is commensurate with altering the firing rate of neurons. Because of this commensurateness, we

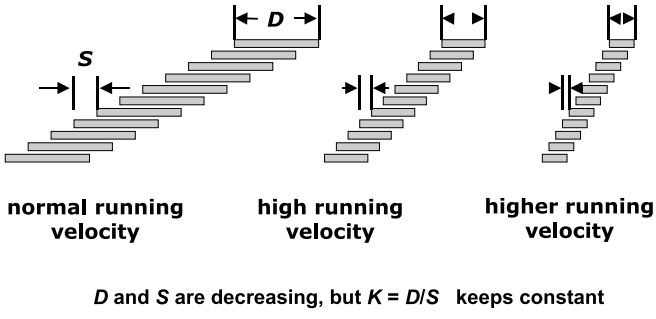


Fig. 11. Scheme of input patterns with increasing running velocity

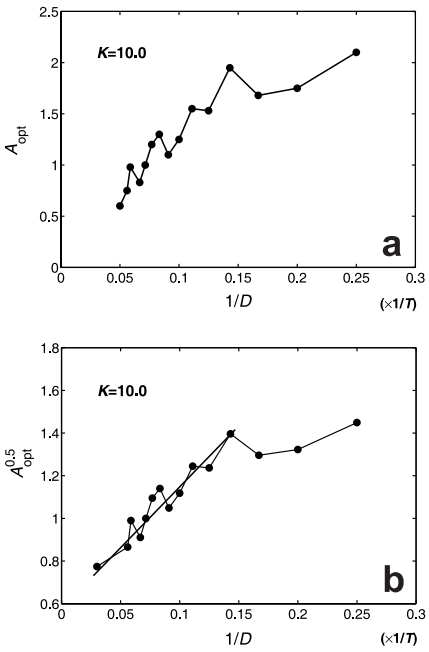


Fig. 12. **a** Relationship between $1/D$ and learning rate A_{opt} for a given track with $K = 10.0$. Saturation level $R = 0.5$. **b** Same curve as in **a** except vertical axis is replaced by $\sqrt{A_{\text{opt}}}$

can investigate the change of firing rate through parameter A.

As with parameter R, there also exists an optimum value for learning rate (denoted as A_{opt}) at which the maximal similarity C_r occurs. Our computer experiments show that A_{opt} should monotonically increase with velocity so that the maximal C_r can be obtained. A typical result is illustrated in Fig. 12a. Considering that firing rate is directly proportional to the square root of learning rate A, the curve in Fig. 12a was redrawn according to $\sqrt{A_{\text{opt}}}$ vs. $1/D$, as shown in Fig. 12b. Further analysis suggested that the linear relationship between $1/D$ and $\sqrt{A_{\text{opt}}}$ holds until around $1/D = 0.15$, as shown by the regression trend line in Fig. 12b.

Based on these results, our model suggests that the velocity-dependent tuning of firing rate is necessary for the correct memory encoding of running experience. At the same time, our computer experiments show that the linear tuning relation breaks down when running velocity is too high. This simulation result is consistent with the experimental facts that the firing rate of hippocampal pyramidal neurons is remarkably related to the velocity at which rat traverses the place field and that the velocity-frequency relationship was linear except at a very high velocity (McNaughton et al. 1983; Wiener et al. 1989; Zhang et al. 1998b; Czurko et al. 1999; Ekstrom et al. 2001). Our results make a successful prediction, which in turn emphasizes the reasonableness of this model.

Experimental facts showed a robust linear relationship between the firing rate of place cells and running velocity except at the highest speeds, which occurred only rarely (McNaughton et al. 1983; Wiener et al. 1989; Zhang et al. 1998b; Czurko et al. 1999; Ekstrom et al. 2001). And experimental observations suggested that when running velocity fell outside the linear range, the effect of running velocity on firing is unique for each neuron and depends on factors other than running velocity (Czurko et al. 1999). Our results also show that at very high running speeds, the linear relationship between learning rate (or firing rate) and running velocity is broken, as shown in Fig. 12b, where the linear curve stops at around $\frac{1}{D} = 0.15$. The underlying network and neural mechanism need further investigation.

5 Discussion

This work elucidated how an input-dependent learning rule is necessary for memory encoding in rat's hippocampal network for spatiotemporal sequences through theta phase precession. Results strongly support the idea that theta phase precession assisted by an input-dependent learning rule provides a biologically plausible way of storing sequences necessary for episodic memory.

Learning by theta phase precession leads to asymmetry of synaptic connections in this model. This is contrary to the previous idea that asymmetry of synaptic connections contributes to the mechanism of phase precession (Jensen and Lisman 1996; Tsodyks et al. 1996; Wallenstein and Hasselmo 1997; Lisman 1999; Lisman and Otmakhova 2001). To resolve this contradiction, we should first address an interesting question. Which comes first, asymmetry of synaptic connections or phase precession? Previous models suggested phase precession occurs only in retrieval mode and is induced by asymmetry of synaptic connections formed through mechanisms other than phase precession. However, recent experimental results (Rosenzweig et al. 2000) revealed that robust phase precession is present at the first experience of a novel route in rats' place cells. What's more, phase precession exists with or without NMDA-receptor blockade. These facts suggested that phase precession is a phenomenon intrinsic in hippocampal pyramidal cells and need not depend on LTP processes or significant experience in a given environment. It supports the basic idea of this model that phase precession happens and plays an important role in learning.

There are several features of this model that merit comparison with other hippocampal models of learning and retrieval. First, the entire sequence of place fields can be easily retrieved by initial cue input. However, in other models recall must be activated by updated external stimuli about present location, which is realized through continuous traversal of rat (Jensen and Lisman 1996; Tsodyks et al. 1996; Wallenstein and Hasselmo 1997). Another principal difference is that our model can realize accurate memory encoding of place field sequence, which is strictly confirmed by correlation analysis between retrieved sequence and learned pattern. This means that not only the temporal structure but also the spatial information of place field sequence can be

stored and retrieved with considerable accuracy. In contrast to our model, only the temporal order of place fields was considered in previous work, whose models usually were not concerned with whether or how much the spatial overlap extent among place fields is memorized.

An input-dependent learning rule is found to be critical for ensuring accurate memory encoding in this model. What kind of neurophysiological mechanism underlies the overlap-dependent adjustment of saturation level of synaptic plasticity? Although it remains unclear, we suspect that the answer lies somehow in heterosynaptic plasticity.

Due to overlap among place fields, an instantaneous location is actually encoded by a population of place units. These units are bound together by the strengthened synaptic weights during learning. From the point of view of population coding, overlap-dependent adjustment of the synaptic saturation level implies that the instantaneous synaptic saturation level depends on the number of place cells in the coding population. We think that such an adjustment of the synaptic saturation level may be a natural property of population coding according to the following experimental evidence. Besides the Hebbian learning rule featuring homosynaptic activity-dependent plasticity, heterosynaptic plasticity also takes place in the learning process (for a review see Bailey et al. 2000). A synapse between a presynaptic and a postsynaptic neuron could be strengthened or weakened as a result of the firing of a third, modulatory, interneuron, and this process has no requirement of activity of either the pre- or postsynaptic neurons. Furthermore, the effect of the modulatory neuron is further enhanced if the firing of modulatory input is associated in time with the firing of a presynaptic cell. This implies that there exists a form of learning rule that combines features of homosynaptic and heterosynaptic plasticity mechanisms (Bailey et al. 2000). In hippocampal pathways, it is found that the late phases of LTP have a further requirement for a heterosynaptic modulatory input that recruits the cAMP cascade. These studies raise the possibility that homosynaptic action alone may not be sufficient to produce long-lasting plasticity in hippocampus (for a review see Bailey et al. 2000). One synapse between two place cells could be weakened through the heterosynaptic modulation of other place cells in the same population that encodes an instantaneous location. And the weakening effect of associative heterosynaptic modulation could be increased with the number of place cells whose place fields overlap each other, then lead to a decrease in the synaptic saturation level described by parameter R_{opt}.

Another important feature of this learning rule involves running-velocity-dependent tuning of learning rate. When sequence is considered as the episodic memory of running experience, a given spatial route must be accurately stored despite varying running velocity. From the viewpoint of neurocomputation, our results revealed that there is a running-velocity-dependent learning rule for this purpose. Specifically, it is proposed that in the one-trial running experience, there exists a linear relationship between the firing rate of place units and animal's running velocity. Our theoretical result is consistent with experimental facts (McNaughton et al. 1983; Wiener et al. 1989; Zhang et al. 1998b; Czurko et al. 1999; Ekstrom et al. 2001). More interestingly, from this result we can deduce a hypothesis: running velocity has a selective facilitatory effect on place cells, i.e., pyramidal neurons that are not involved in memory encoding of spatial routes should not have the feature of velocity-dependent tuning in firing rate. This hypothesis is supported by experimental evidence that a dependence relationship between firing rate and running velocity was only observed in pyramidal cells associated with rat's position, while running velocity did not correlate with increased firing rate in pyramidal neurons whose discharge was not specific to the animal's location (Czurko et al. 1999).

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