Cogn Neurodyn (2007) 1:119–141
DOI 10.1007/s11571-006-9013-6

REVIEW ARTICLE

Neural dynamics of the cognitive map in the hippocampus

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Received: 25 June 2006 / Accepted: 25 October 2006 / Published online: 11 January 2007

Abstract The rodent hippocampus has been thought to represent the spatial environment as a cognitive map. In the classical theory, the cognitive map has been explained as a consequence of the fact that different spatial regions are assigned to different cell populations in the framework of rate coding. Recently, the relation between place cell firing and local field oscillation theta in terms of theta phase precession was experimentally discovered and suggested as a temporal coding mechanism leading to memory formation of behavioral sequences accompanied with asymmetric Hebbian plasticity. The cognitive map theory is apparently outside of the sequence memory view. Therefore, theoretical analysis is necessary to consider the biological neural dynamics for the sequence encoding of the memory of behavioral sequences, providing the cognitive map formation. In this article, we summarize the theoretical neural dynamics of the real-time sequence encoding by theta phase precession, called theta phase coding, and review a series of theoretical models with the theta phase coding that we previously reported. With respect to memory encoding functions, instantaneous memory formation of one-time experience was first demonstrated, and then the ability of integration of memories of behavioral sequences into a network of the cognitive map was shown. In terms of memory retrieval functions, theta phase coding enables the hippocampus to represent the spatial location in the current behavioral context even with ambiguous sensory input when multiple sequences were coded. Finally, for utilization, retrieved temporal sequences in the hippocampus can be available for action selection, through the process of reverting theta rhythm-dependent activities to information in the behavioral time scale. This theoretical approach allows us to investigate how the behavioral sequences are encoded, updated, retrieved and used in the hippocampus, as the real-time interaction with the external environment. It may indeed be the bridge to the episodic memory function in human hippocampus.

Keywords Hippocampus · Place cell · Theta rhythm · Theta phase precession · Asymmetric Hebbian plasticity · Memory-guided behavior

Introduction

The concept of the cognitive map was initially proposed as a global representation of the environmental space by Tolman (1948). It is based on his evidence that rats are endowed with map-like representations of their environments which they use to solve spatial tasks, an opposing theory to the stimulus-response paradigm. In freely moving rats, O'Keefe and Dostrovsky (1971) discovered so-called place cells in the hippocampus, which fire in correlation with the animal's location in space. Thus, the hippocampus has been thought to maintain the cognitive map. O'Keefe and Nadel (1978) proposed the cognitive map theory which posits that the population activity of place cells represents where the animal is in the form of a map. According to this theory, not only is the firing of

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different cells associated with different environmental places, but the spatial relationship between places is also encoded by whole sets of cells (Fig. 1). For the last several decades, the major stream of hippocampal studies was directed towards the elucidation of hippocampal cell activities which are dependent on spatial location and the characteristics of these activities.

The following experimental observations of hippocampal pyramidal cells in behavior have confirmed the fact that the hippocampus is critical in spatial learning and memory; however, the detail learning mechanism is still unclear. In experimental studies of the synaptic plasticity, a temporal asymmetry in the time window of the synaptic change has been reported in the hippocampal circuit (Levy and Steward 1983; Larson and Lynch 1989; Fitzsimonds et al. 1997; Bi and Poo 1998). This suggests that neurons are connected asymmetrically rather than by symmetrical connections, which are formed by the conventional Hebbian plasticity with simultaneous firing. Theoretically the formation of the cognitive map as a network of place cells is considered to form by the conventional Hebbian rule, while the experimental evidence of the asymmetric time window seems to be contradictory to the memory function of the cognitive map.

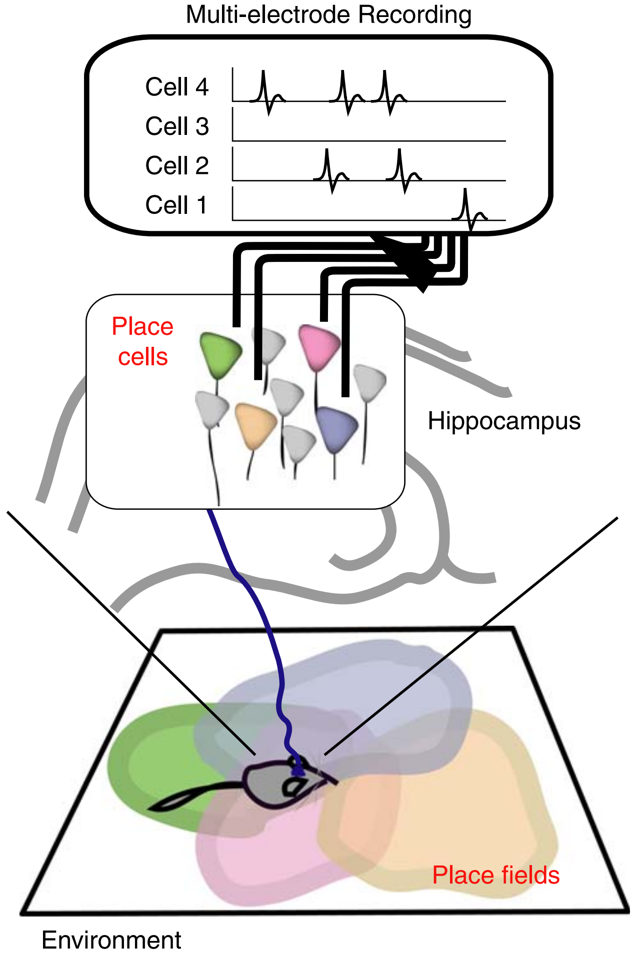


Fig. 1 Schematic illustration of place cells and their place fields. Place cells, which are pyramidal cells in the hippocampus, fire in correlation with the animal's location in space. Different place cells fire when the animal is in different spatial regions of the environment, called place fields, as shown in the figure with corresponding colors

Eichenbaum (Eichenbaum et al. 1999; Eichenbaum 2001) has claimed that the role of hippocampal memory is not restricted to spatial processing and emphasized that the hippocampus predominantly represents sequences of events that compose episodic memories, even in animals. Episodic memory was initially defined in human clinical studies as the ability to remember specific personal experiences and is an essential function maintained by the human hippocampus (Tulving 1972). Episodic memory in animals can be defined as neural responses that correlate past events and behaviors, as is observed in experimental studies of the rodent hippocampus, for instance in olfactory discrimination tasks (Eichenbaum et al. 1987). Interestingly, recent experimental data reported the relevance of the hippocampal temporal firing pattern to the behavioral sequences. Skaggs et al. (1996) showed that the temporal firing pattern of hippocampal cells regularly appears in every theta cycle. The temporal difference in firing of the cells was consistent with the time window of the asymmetric synaptic plasticity, suggesting a temporal coding mechanism (Skaggs et al. 1996; Yamaguchi 2003). By using mice lacking the NMDA receptor in the hippocampal CA3 region, which is the site of dense recurrent connections, the experimental study proved that hippocampal synaptic modifications are crucial for encoding of the one-time experience (Nakazawa et al. 2003). This evidence highlights the importance of the hippocampal memory function for behavioral sequences.

A key question here is whether memory of the environmental geometry, such as that encoded in the cognitive map, and memory of behavioral sequences are derived from distinctive neuronal mechanisms or not. In the classical theory of rate coding, the formation of the cognitive map has been explained as the result of linking different spatial regions, or features in them, independent of the encoding of behavioral sequences. However, if these memory functions are derived from a consistent neuronal mechanism, the better question is what neural mechanism comprehensively organizes both hippocampal memory functions. It could be thought of as the development of memories of behavioral sequences on the cognitive map in the framework of a consistent memory encoding neural mechanism.

Here we review our theoretical approaches to studying the temporal coding mechanism that enables the hippocampal neural network to encode behavioral sequences (Yamaguchi 2003; Sato and Yamaguchi 2003; Wu and Yamaguchi 2004; Yamaguchi et al. 2004), and the hypothesis that cognitive map formation is an extension of memories of behavioral sequences (Wagatsuma and Yamaguchi 1999, 2000, 2004, 2005; 2006). We focused on the biological dynamics underlying memory formation in the hippocampus, which is called theta phase coding. The rate coding theory has attempted to capture a universal form of information represented in the brain and focused what is encoded in the population vector of massive neurons as a stationary state. Here we attempt, as a breakthrough, to consider how biological information emerged in the interaction between the brain and the ever-changing world and focused how behavioral sequences are represented in the temporal sequence of neural events and how they are retrieved and used even with environmental changes.

This theoretical approach would shed light on a developmental process of memory, from a recollection of past experience to a consistent framework. In the behavior of animals, or even in our daily lives, everything happens in the context of the past, present, and future, in a so-called context-dependent manner. Looking back to the history of the developmental psychology, Piaget (1928) describes a cognitive process for how behavioral experiences are developed into operational knowledge when an infant develops into a child. In this sense, our theoretical approaches may bridge between memory of behavioral sequences in the animal case and episodic memory in the human hippocampal study.

Associative memory neural network for the cognitive map

The classical neural network theory assumes that information is coded in the firing rate of neurons, a concept called rate coding. The neural basis of hippocampal memory was theoretically proposed by Marr (1971) as a framework of associative memory with rate coding. The hippocampus has widespread recurrent synaptic connections in the CA3 region, which enable the network to instantaneously encode associations among external stimuli that the animal experiences. This recurrent network then has the ability to retrieve the set of firing patterns, referred to as memory patterns, after the learning. Several theoretical models of hippocampal associative memory were proposed (McNaughton and Morris 1987; McNaughton 1989; McNaughton and Nadel 1989; Rolls 1989; O'Reilly and McClelland 1994) and discussed in terms of quantitative properties, such as memory capacity, the robustness of the memory recall, and the interference of similar memory patterns. Extending to the theoretical studies, two major types of neural network models for the cognitive map were proposed. The first one is the goal-oriented vector map, in which directions toward a single goal from different spatial positions are encoded in the network, and the population vector of place cells, then, represents where the animal should go next to reach the goal in the environment. The other one is the spatial vector map, in which individual spatial positions are encoded in the network, and the population vector of place cells in this case represents where the animal is in the environment at each instance. These models were proposed independent of memory encoding to behavioral sequences.

In the former model, the function of the cognitive map is to guide navigation toward a goal from different spatial locations (Burgess et al. 1994; Blum and Abbott 1996; Gerstner and Abbott 1997; Redish and Touretzky 1998; Trullier and Meyer 2000). In the assumption of place cells in the hippocampus without learning, they focused on the function of a temporal asymmetry in the synaptic plasticity of hippocampal pyramidal cells (Levy and Steward 1983; Larson and Lynch 1989; Fitzsimonds et al. 1997; Bi and Poo 1998; see Abbott and Blum 1996). Burgess et al. (1994) firstly proposed the model of the cognitive map, representing the direction toward a single goal in the environment. The model could learn a shortcut pathway to reach the goal location by the population vector representing where the animal goes next, as schematically shown in Fig. 2A. In this model, goal-oriented vectors are encoded in association between place cells and goal cells, as to not form recurrent asymmetric connections among place cells. This concept was developed into subsequent models with asymmetric connections by using the Hebbian plasticity with an asymmetric time window (Blum and Abbott 1996; Gerstner and Abbott 1997; Trullier and Meyer 2000). This type of models explains how the asymmetric synaptic plasticity contributes to a specific cognitive function, such as spatial navigation. However, it is hardly applicable for spatial tasks with multiple goals, and place cell activities do not always change depending on differences between reward locations (Gothard et al. 1996). Thus, being a single goal-fixed vector map is not likely the fundamental property of place cells.

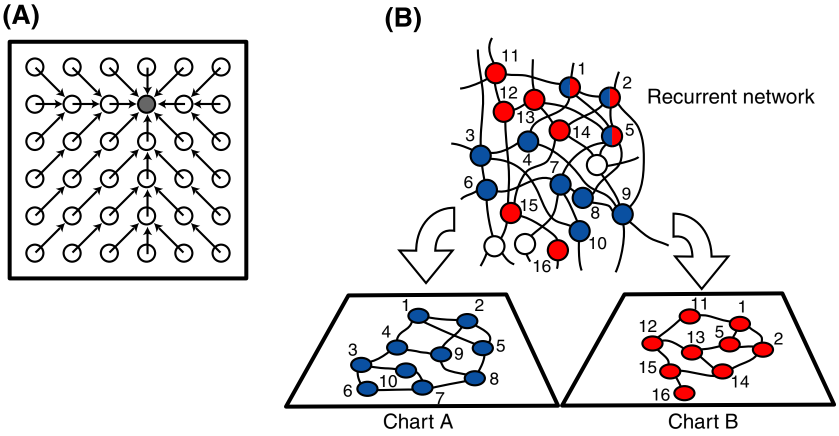


Fig. 2 (**A**) An example of a vector field map, or directional map, representing routes to a single goal that are stored in the recurrent connections of the hippocampal associative network. Open circles denote the individual positions of the place cells, which correspond to individual place fields. A filled circle denotes the goal position. An arrow from one circle to the other represents an effective directional connection between them, guiding a route to the goal. Thus, every connection between neighboring cells is considered to be asymmetric (see Blum and Abbott 1996; Gerstner and Abbott 1997; Trullier and Meyer 2000; Redish and Touretzky 1998). (**B**) Schematic illustration of a multiple chart network. The recurrent network of place cells has anatomically twisted synaptic connections. Blue and red circles, respectively, denote place cells that are active in environment A, called chart A, and the cells that are active in environment B, called chart B. The top figure represents the anatomical position of cells, and the bottom figures represent imaginary arrangements of cells that are aligned according to their place fields in environment A (blue) and environment B (red). Twisted connections in the top figure can be straightened in the bottom figures as neighboring connections among cells. On each chart, neighboring cells are cooperatively active through their mutual connections, generating a concentration of population activity in the cognitive map as a population code of place. Thus, every connection between neighboring cells basically represents the distance; thus, it is considered to be symmetric (see Samsonovich and McNaughton 1997)

In the latter model, the function of the cognitive map is to represent where the animal is in space, even with the lack of sensory information. The basic concept is that mutual connections among neighboring place cells help them to activate together, explaining how the population activity of place cells appears consistently in the same environment. In recent experimental study, the parallel extracellular recording of hippocampal place cells enables the simultaneous recording of a large numbers of place cell activities during the spatial exploration of the animal (Wilson and McNaughton 1993). It clearly demonstrated that population coding of place cells represents where the animal is, in the form of a massive concentration of the firing pattern in a two-dimensional plane that derived from the rearrangement of place cells according to their place field locations. The concentration of the firing pattern is sometime called the place code or self-localization (Redish 1999), which is theoretically considered to be a consequence of the mutual connections among neighboring place cells. In experimental observations, population coding is reorganized drastically depending on changes in the environment, such as the configuration of external cues and task procedures (Muller and Kubie 1987; Bostock et al. 1991; Gothard et al. 1996). Then the same population pattern reappears when the animal is returned in the original environment (Barnes et al. 1997).

In this framework, Muller and his colleagues (Muller et al. 1991, 1996) initially proposed the idea that the simultaneous firing of place cells forms a network where these cells have strong synaptic connections with neighboring place fields. Accordingly, the geometric network of place cells, called a "chart," represents the environment through a spatial relationship among place cells (McNaughton 1996) as schematically shown in Fig. 2B. Such a chart formation was demonstrated by Káli and Dayan (2000). The strength of the connection between a pair of place cells represents the distance between two corresponding locations in the environment, and the connections must be symmetric. Associative connections in the CA3 region serve as the functional basis of a cognitive map during spatial navigation, providing neural activities that are spatially localized in the chart. Recently, Nakazawa et al. (2002) experimentally confirmed that recurrent connections of pyramidal cells in the CA3 region serve as associative memory by using mutant mice with an ablated NMDA receptor gene specifically in the CA3 region. The ability for encoding multiple cognitive maps is demonstrated in the model of Samsonovich and McNaughton (1997). This type of model effectively explained how recurrent connections of place cells work to give the representation of where the animal is in the environment, even with a change of the environment; however these learning mechanisms are proposed independent of experimental evidence for the asymmetric synaptic plasticity.

As intermediate between the two types, Redish and Touretzky (1998) proposed a combination between the spatial vector map and the goal-orientation map. They hypothesized that symmetric connections between place cells are learned to represent the spatial map when the rat explores for the first time, and then the asymmetric property is added into the network to represent the goal-orientation from different places. Their model demonstrated that asymmetric and symmetric connections coexist in the same network, while still in the framework of the single goal-fixed vector map. In contrast, Rolls et al. (2002) hypothesized that episodic memory and spatial memory are distinct representations in the hippocampus and simplified the concept of episodic memory to those memories of non-spatial events that happen at a particular time, independent of temporal sequence. By using the conventional Hebbian learning rule, the model could encode independently the continuous firing pattern of place cells and discrete neural events as episodic memory. Both memories are retrieved cooperatively, either when the animal visits a specific location or when a non-spatial cue is presented. The separation of episodic memory and spatial memory might be plausible, especially in the human hippocampus, but it is not concerned with describing linked temporal sequences of events in episodic memory.

Neural dynamics of memory development in the hippocampus

In the first place, a key question presented here is whether the cognitive map and memory of behavioral sequences are derived from distinctive neuronal mechanisms. We attempt to consider a possible neural mechanism in the hippocampus that provides both memory functions in the consistent theoretical framework. Then we focus on the biological dynamics underlying memory formation in the hippocampus, called theta phase coding. The rate coding theory enlightened on what is represented in the neural network, while theoretical analyses of temporal coding allow us to investigate how biological information is formed, updated and used in relationship with the external environment. In this framework, we hypothesized that memories of behavioral sequences are developed into the cognitive map, as schematically shown in Fig. 3.

Here we review our theoretical approaches with the temporal coding mechanism that we previously reported (Yamaguchi and McNaughton 1998; Yamaguchi 2003; Yamaguchi et al. 2004), focusing specifically on our work on cognitive map formation (Wagatsuma and Yamaguchi 2004), disambiguation of memory retrieval in the spatial alternation task (Wagatsuma and Yamaguchi 2005) and spatial navigation with motion control by using theta phase coding (Wagatsuma and Yamaguchi 2006).

Real-time memory formation with temporal coding

A sequence of neural events can be stored in sequentially ordered synaptic connections or in asymmetric connection among neurons. The Hebbian plasticity with an asymmetric time window of ~50 ms in the hippocampus is considered to be composed of these asymmetric connections; however, the question remains as to how often a pair of neuronal firings within 50 ms happens in the hippocampus? Behavioral events happen on the timescale of several seconds or slower. There is a large gap between timescales of the synaptic time window and the behavioral sequence. Thus, asymmetric synaptic plasticity could not be directly applicable for the encoding of the behavioral sequence.

In the rodent hippocampus, a stable oscillation of the local field potential around 8 Hz is observed during

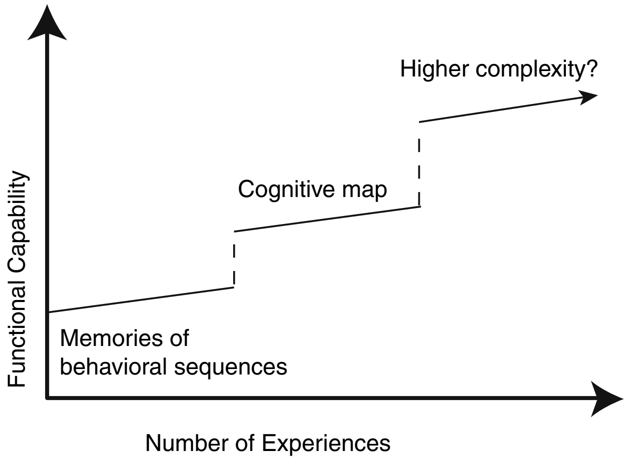


Fig. 3 Schematic illustration of a developmental change of hippocampal representation. In the working hypothesis of theta phase coding, the neural dynamics of memory formation in the hippocampus integrates different memories of behavioral sequences into a consistent framework representing the relationship between the environment and the animal itself, such as a cognitive map. It suggests that the representation would develop in a further representation with some hierarchical structure

running and is referred to as the theta rhythm. O'Keefe and Recce (1993) initially discovered an advancement of the place cell's firing phase relative to the cycle of the theta rhythm when a rat goes through the place field. The phenomenon is called theta phase precession. Parallel recordings of place cells demonstrated that phase precession is not only the phase advancement of individual cells, but also retains the robust phase difference with a sequential order in the firing of a population of cells (Skaggs et al. 1996). The phase difference in place cells regularly preserved in successive theta cycles has a time scale similar to the asymmetric time window of Hebbian plasticity. It is suggested that the phase difference of place cells' firing that highly aligned in every theta cycle represents the behavioral sequence of a series of place fields in which the animal traversed as a compression of behavioral events into theta phases. Thus it enables memory encoding of behavioral temporal events in asymmetric connections among place cells by using Hebbian plasticity with an asymmetric time window (Skaggs et al. 1996; Yamaguchi 2003). This property is supported by experimental observations of the phase precession even in the novel environment or without training (Czurko et al. 1999; Rosenzweig et al. 2000; Ekstrom et al. 2001; Magee 2001).

The neural mechanism has been debated extensively. From early studies, proposed theoretical models can be classified into two groups: theta phase precession caused by existing asymmetric connections (Tsodyks et al. 1996; Jensen and Lisman 1996; Wallenstein and Hasselmo 1997) and phase precession in the absence of asymmetric connections (O'Keefe and Recce 1993; Kamondi et al. 1998; Bose and Recce 2001; Harris et al. 2002, Yamaguchi 2003; Lengyel et al. 2003; Magee 2003; Mehta et al. 2002). In particular, some models focused on the property of phase locking for the mechanism of theta phase precession (Kamondi et al. 1998). Mehta et al. (2002) proposed that the asymmetric increase of firing rate of CA1 place cells causes the phase advancement. The firing rate is slowly increased so that it maximizes just before the end of the place field. They determined that this slow increase is obtained after several trials.

These models raise two significant questions: whether several trials, or some learning property, are necessary for theta phase precession, and where it is originally generated, in the CA1 region of the hippocampus or other regions? Melamed et al. (2004) answered the former question by pointing out that phase precession is seen without training (Czurko et al. 1999; Ekstrom et al. 2001; Magee 2001). Therefore, it is possible that in novel environments, theta precession firstly appears and causes the memory formation (Fig. 4). Answering the latter question, past experimental data reported that theta phase precession is observed in the CA1 region (O'Keefe and Recce 1993; Skaggs et al. 1996), the CA3 region (Harris et al. 2002), the dentate gyrus (Skaggs et al. 1996), and the entorhinal cortex (Hafting et al. 2005, 2006; McNaughton et al. 2006). It may originate in the superficial layer of the entorhinal cortex through the hippocampal closed circuit (Skaggs et al. 1996; Yamaguchi 2003).

In a computational model study, Yamaguchi (2003) has hypothesized that theta phase precession causes the associative memory formation in the hippocampus and that the phase precession is generated in the entorhinal cortex, the entrance of hippocampal network. In the entorhinal cortex, phase locking between the theta rhythm and cells with a gradual increase in natural frequencies is phenomenologically assumed. Under the assumption of sensory inputs in changing environments, this model works for the real-time generation of theta phase precession. Behavioral sensory input is coded in the firing phase in the theta cycle, called "theta phase coding." Yamaguchi and her colleagues presented a series of theoretical models based on theta phase coding (Yamaguchi 2003; Sato and Yamaguchi 2003; Wu and Yamaguchi 2004; Yamaguchi et al. 2004; Wagatsuma and Yamaguchi 2004), which demonstrated that theta phase coding functions in memory encoding of behavioral experience as an online learning system.

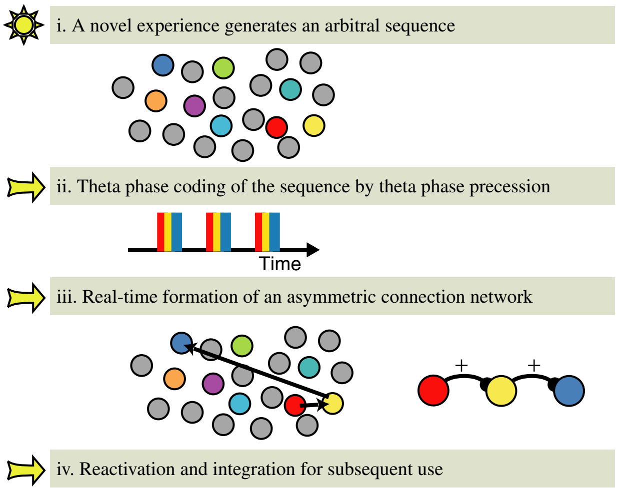


Fig. 4 A minimum function of theta phase coding for novel sequence memory encoding in the hippocampus, based on theta phase precession and asymmetric Hebbian rule

In this model, the neural mechanism of the generation of theta phase precession can be compared to the central pattern generator of animal locomotion, like that in fish when swimming, shown in Fig. 5. Coupled neural oscillators that contain a gradient in natural frequencies generate the periodic bending motion needed for swimming. In theta phase precession, place cell firing in each theta cycle has a similar pattern to the motion of the central pattern generator, while the cell population changes in successive theta cycles, as shown in Fig. 5B.

In the entorhinal–hippocampal network of associative memory, they use a simple phase model to describe the neural oscillator in the entorhinal cortex. The robust phase locking is derived from the coupling between a stable oscillation (LFP theta) and individual oscillators. Assuming an oscillation state continues when it has tonic input, the phase locking pattern is described by

$$\dot{\phi}_i = \omega_i + A\sin(\phi_0 - \phi_i), \quad (i = 1, \ldots, N)$$
$$\dot{\phi}_0 = \frac{1}{N}\sum_{i=1}^{N}\omega_i \equiv \omega_0, \tag{1}$$

where ω_i is ith unit's natural frequency. The phase difference between individual oscillators, ϕ_i, and the stable oscillator, ϕ_0, is defined as $\dot{\theta}_i = \Delta\omega_i + A\sin(\theta_i)$ where $\theta_i = \phi_0 - \phi_i$ and $\Delta\omega_i = \omega_i - \omega_0$, and the solution $\dot{\theta}_i = 0$ is obtained analytically as:

$$\theta_{si} = \arcsin\left(\frac{\omega_i}{A}\right), \quad \left(\text{if } \left|\frac{\omega_i}{A}\right| \leq 1\right) \tag{2}$$

This solution means that this system is the robust phase difference described by a value $\Delta\omega_i = \omega_i - \omega_o$ as shown in Fig. 6A.

Here we assume a gradual change of natural frequencies depending on input. The change is defined as:

$$\omega_i(t) = \begin{cases} \omega_s + (t - i\Delta t)\omega_d & \text{if } I_i(t) = I_0 \\ \omega_0 & \text{if } I_i(t) = 0 \end{cases},$$
$$I_i(t) = \begin{cases} I_0 & \text{if } i\Delta t < t < i\Delta t + t_d \\ 0 & \text{otherwise} \end{cases} \tag{3}$$

where ω_s and ω_d are positive constants, and Δt and t_d, respectively, denote the time difference of input onset and the input duration corresponding to several theta cycles. Since the natural frequency, ω_i, changes slowly, the solution θ_{si} in the Eq. 2 describes phase locking as a quasi-fixed point (Yamaguchi 2003). The different onset timing of inputs gives the different value of theta phases. Equation 3 given by a function of time can be replaced by the distance-dependent function, which gives the phase precession as a function of distance as is observed in experiments (O'Keefe and Recce 1993). This phase locking mechanism, given by Eqs. 1 and 2, was used in the following the entorhinal–hippocampal network model with some modification.

In the model of Wagatsuma and Yamaguchi (2004, 2005, 2006), the phase model in Eq. 1 is rewritten as a neuronal unit with the assumption that the membrane potential is efined by $\cos\phi_i$. The time evolution of the network is described as:

$$\dot{\phi}_i^{\mathrm{EC}}(t) = \omega_i^{\mathrm{EC}}(t) + \left[\beta_0 - I_i(t) - \gamma_1\cos\phi_0^{\mathrm{EC}}(t)\right]\sin\phi_i^{\mathrm{EC}}(t),$$
$$\dot{\phi}_0^{\mathrm{EC}}(t) = \omega_0, \dot{\phi}_i^{\mathrm{CA3}}(t) = \omega_1 + \left[\beta_1 - f_i^{\mathrm{EC}}(t) - \gamma_1\cos\phi_0^{\mathrm{CA3}}(t) - E\cdot\sum\nolimits_j w_{ij}^{\mathrm{CA3}} f_j^{\mathrm{CA3}}(t) + G\cdot\sum\nolimits_j f_j^{\mathrm{CA3}}(t)\Big/N\right]\sin\phi_i^{\mathrm{CA3}}(t),$$
$$\dot{\phi}_0^{\mathrm{CA3}}(t) = \omega_0 - \gamma_2\cos\phi_0^{\mathrm{EC}}(t)\sin\phi_0^{\mathrm{CA3}}(t),$$
$$\dot{w}_{ij}^{\mathrm{CA3}}(t) = \left[\lambda_{\mathrm{LTP}}\left(f_j^{\mathrm{CA3}}(t)\cdot f_i^{\mathrm{CA3}}(t-\tau)\right) - \lambda_{\mathrm{LTD}}\left(f_j^{\mathrm{CA3}}(t) + f_i^{\mathrm{CA3}}(t-\tau)\right)\right]\cdot\lambda_w\left[1 - \left(w_{ij}^{\mathrm{CA3}}(t)\right)^2\right],$$
$$\left(\phi_0^{\mathrm{EC}}, \phi_0^{\mathrm{CA3}} \bmod 2\pi\right), \quad (i = 1, \ldots, N), \tag{4}$$

where $\omega_L, \beta_L (L = 0,1)$ represent the constant parameters of natural frequency and stabilization, γ_1 and γ_2, respectively, represent the effect of the local field oscillation (LFP theta) and the coupling constant between different layers, E and G, respectively, represent effects of the recurrent connection feedback and the global inhibition, and λ_{LTP}, λ_{LTD} and λ_w, respectively, represent constant parameters of LTP, LTD and the learning rate. τ represents the asymmetric time window

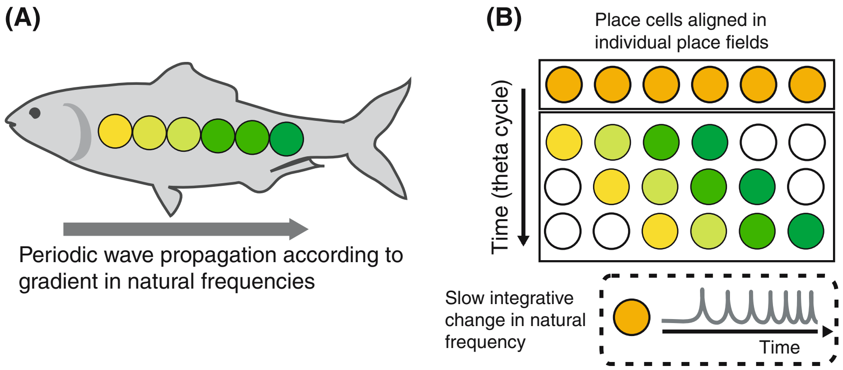


Fig. 5 Comparison between phase locking in the central pattern generator of fish swimming (**A**) and theta phase precession in the rat hippocampus (**B**). Periodic bending motion for swimming is generated by coupled neural oscillators with a gradient in natural frequencies. In theta phase precession, place cell firing in each theta cycle reflects the motion of the central pattern generator, while head-tail roles of place cells change in successive theta cycles. The evolution from tail to head of a cell is given by a slow increase in the intrinsic frequency

in the Hebbian synaptic plasticity, which is given by 0.2 theta cycles in the computer experiment (Wagatsuma and Yamaguchi 2004). N denotes the number of units in every layer. Equations with the suffix "EC" describe the time evolution of the entorhinal unit, which corresponds to Eq. 1. $\omega_i^{\mathrm{EC}}(t)$ and $I_i(t)$ are given by Eq. 3 with some modification of the input's assumption, depending on the model used (Wagatsuma and Yamaguchi 2004). Equations with the suffix "CA3" describe the time evolution of the CA3 unit receiving the temporal firing activity of the EC unit. We simply assume the one-to-one projection between layers, and the firing, or pulse density, $f_i^L(t)$, $(L = \mathrm{EC,CA3})$ is given by a function of the membrane potential with the threshold as:

$$f_i^L(t) = \begin{cases} \cos\phi_i^L(t) & \text{if } \cos\phi_i^L(t) > 0 \\ 0 & \text{otherwise} \end{cases} \tag{5}$$

The CA3 layer only has the modifiable recurrent connections, $w_{ij}^{\mathrm{CA3}}(t)$, and the connections change according to the asymmetric Hebbian rule, which is simply assumed here by the combination of timing specific LTP, to maximize one fifth of the theta cycle (~25 ms), and timing non-specific LTD.

In the EC layer, the unit starts its oscillation when it receives a tonic input that slowly changes over several oscillation cycles, and the gradual change of the natural frequency gives a phase shift under the robust phase locking. The phase model can be considered as a simplified form of mathematical descriptions of neurons with either a limit cycle solution or a fixed-point with excitability, such as the FitzHugh-Nagumo equation (FitzHugh 1961; Nagumo et al. 1962; see Hoppensteadt 1986). In the CA3 layer, the unit is described by the neuronal oscillator similar to the EC unit, but it has no change in the natural frequency and only uses instantaneous excitability given by input onset. In computer experiments, CA3 units inherit the firing pattern of entorhinal units, reproduce the phase precession, and then the temporal pattern leads to a modification of the recurrent connections of CA3 units in accordance with asymmetric Hebbian plasticity (Levy and Steward 1983; Larson and Lynch 1989; Fitzsimonds et al. 1997; Bi and Poo 1998). Ultimately, it enables temporal sequence storage (Fig. 7). In the phase precession, a compressed form of behavioral sequence represented by the firing phase, occurs repetitively in every theta cycle and gives stably asymmetric connections in the CA3 recurrent network by using asymmetric Hebbian plasticity, even for a one-time experience. This result indicates that the neural dynamics are biologically plausible for the memory encoding of novel temporal sequences as episodic events.

Cognitive map formation through sequence integration

The important question here is whether sequence learning based on theta phase precession in the presence of asymmetric synaptic plasticity can be extended to other hippocampal memories. After a brief exploration of an environment of about 10 min, pyramidal cells in the CA3 and CA1 regions of the hippocampus exhibit firing preferences based on the animal's location (Wilson and McNaughton 1993). This means that place cells for a new location are quickly established, and the geometry of the new environment soon becomes familiar. How does the hippocampus acquire the

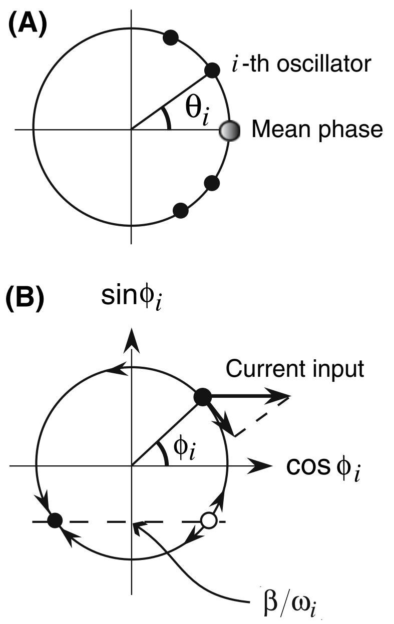


Fig. 6 Phase locking of coupled oscillators. (**A**) N coupled oscillators ϕ_i with different natural frequencies ω_i is given by Eq. 1. The system arrives to a phase locking state where the phase difference between each oscillator and the mean phase, θ_i, depends on the natural frequency. If the natural frequency is larger than the mean value, the phase is advanced i.e. $0 < \phi_i < \pi/2$, but if it is smaller than the mean value, the phase is behind i.e. $-\pi/2 < \phi_i < 0$. (**B**) The ith unit equation in the model is given by Eq. 4. The value cos ϕ_i^L, $(L = \text{EC,CA3})$ represents the membrane potential. The filled and the open circles, respectively, denote the stable point, as the resting state, and the unstable point. The current input appears in the equation with the factor $sin\phi_i^L$, $(L = \text{EC,CA3})$ because of the vector relation in the figure. In the equation with suffix EC, the resting state is replaced by a sustained oscillation, as shown in **A**, when the current input is coming. In the equation with suffix CA3, the equation has both stable and unstable points. When the current is input, the state exceeds the unstable point and then it goes back to the resting state

cognitive map even after such a short running experience? Is it possible to consider that the integration of memories of behavioral episodes develops into a representation of the environmental geometry when the animal explored it freely?

Wagatsuma and Yamaguchi (1999, 2000, 2004) hypothesized that theta phase coding not only provides memory encoding of the temporal sequence of a behavioral experience into asymmetric connections of the CA3 region, but also that the one-dimensional network encoding of the sequence is integrated during the animal's exploration. Computer experiments demonstrated that the memory integration of behavioral experiences during the spatial exploration of the simulated animal, "rat," develops the cognitive map as a chart by using a simplified hippocampal network model with theta phase coding (Fig. 8).

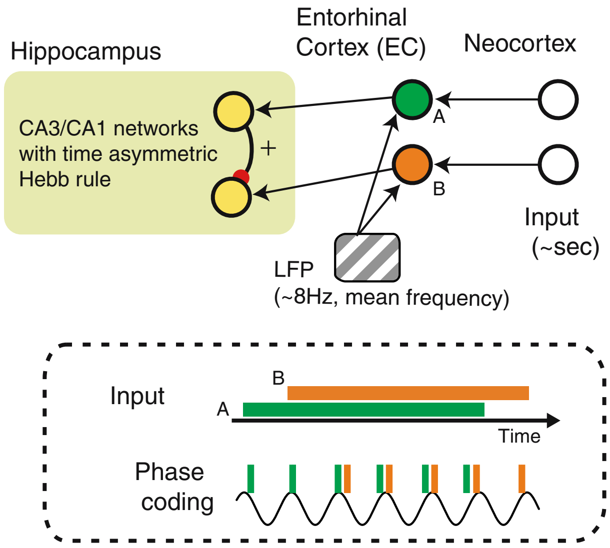


Fig. 7 A working hypothesis on memory formation with theta phase precession in the hippocampus. Theta phase precession is generated at the entrance of the hippocampus, the entorhinal cortex (EC). For phase locking of individual units in the EC, a unit representing local field theta oscillation (LFP theta) is introduced. Phase locking of each unit with LFP theta instantaneously stabilizes the phase at each theta cycle according to the current value of the natural frequency. This results in a constant phase between pair units of successively active inputs (**A** and **B** in the figure). Firing with the phase difference causes selective synaptic plasticity in the hippocampal associative memory network

The environmental space is given by a square field, $1 \times 1\ \text{m}^2$. In the model, the local view input is simply assumed as a set of landmarks that are distributed on the floor in a lattice configuration (Fig. 8A). Each landmark is assumed as rotation-fee object or mark, such as colored paint on the ground. The field of vision with landmarks is restricted in the front of the rat and is given by a semicircle shape of a one-third meter radius. We assumed four hundred landmarks over the environment, and 50 different landmarks in front of the rat's nose are seen at each instance. The local view input is an egocentric view depending on the rat's head direction. The rat runs randomly for one minute with the running velocity, 0.34 m/s. The running direction changes once every 18 theta cycles with a random variable, and walls in edges of the environment force to change the direction as reflection turn. The model simply assumed the projection from landmark-associated inputs to entorhinal units as one-to-one. The input intensity is given by a function of the distance between the landmark and the rat, so that near landmarks give strong input, far landmark give weak input and landmarks out of the visual field give no input. In the simple projection assumption, we visualized population

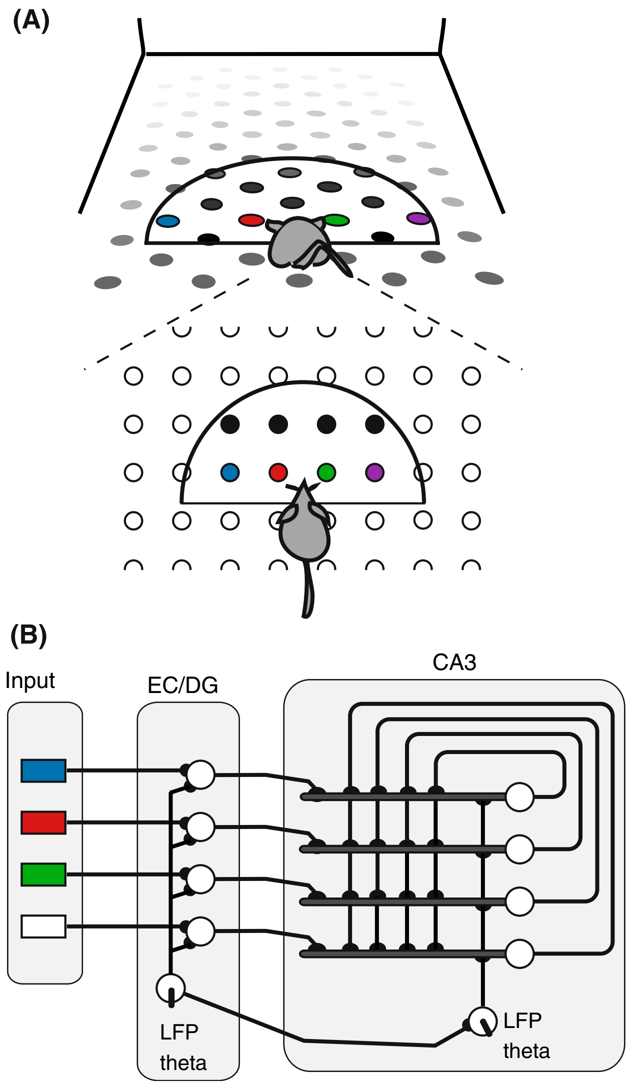


Fig. 8 Schematic illustration of the network structure and local view input in the model of Wagatsuma and Yamaguchi (2004). (**A**) Local view input is given by a set of landmarks. *N* landmarks are assumed to distribute at lattice points in a two-dimensional environment. Landmarks around and in front of the simulated animal, "rat," activate individual units in the Input layer within a semicircle of visual field *V*, which covers *M* landmarks. $N = 400$ and $M = 50$ in the computer experiments. (**B**) The neural network model has three layers, the Input, the EC, and the CA3 layers. Each input derives from a single landmark shown in A. Open circles in the EC and CA3 layers represent neural units. Projections from the Input to the EC and from the EC to the CA3 are assumed to be one-to-one connections. Black half circles represent synaptic connections. Recurrent connections in the CA3 layer are assumed to follow the asymmetric Hebbian rule. The LFP theta units representing the local field theta oscillation are shown at the bottom of the EC and CA3 layers

activities of the entorhinal and the hippocampal units in the two-dimensional plane where the units are aligned in the same arrangement as the landmarks in the environment, which is consistent with the methods of Samsonovich and McNaughton (1997). We call the arrangement of units the expected array, which denotes ideal positions of place fields after leaning.

During the rat's running, population activity as theta phase precession is observed as a wave propagation in the expected array. Within the semicircle of the local view, an instantaneous subpopulation of EC activity appears as a crescent shape. The population activity propagates within the semicircle, from the near to the far, in every theta cycle. This property of wave propagation is in good agreement with the phase precession pattern on a chart reconstructed from experimental data (Samsonovich and McNaughton 1997). The important point in this case is that the current local view, or 50 landmarks, triggers the simultaneous activation of 50 units, while the instantaneous subpopulations differentiate their firing timings, classifying sensory inputs according to the temporal context, the past, the present and the future, along the running direction. The CA3 network receives those activities and reproduces the two-dimensional phase wave as a population activity with a projection delay, and it modifies its recurrent connections according to the relative firing timing by using the asymmetric Hebbian rule (Eq. 4). Thus, the learning rule makes unidirectional connections between subpopulations of units that are sequentially activated with a time delay of 20–25 ms in the phase precession.

In the beginning of spatial exploration, such as a short run without any crossings, the distribution of synaptic connections forms a part of the phase wave pattern, and then it gradually forms a concentric shape during the full exploration (Fig. 9). During chart formation, the strength of recurrent connections decreases monotonically with respect to the distance in the chart (Fig. 10). Thus, the CA3 recurrent network sufficiently establishes the chart property within a minute.

This property is consistent with the results obtained by Muller et al. (1991, 1996) and Redish and Touretzky (1998) using a Hebbian rule for rate coding. In these models, simultaneous firing of neighboring place cells produces symmetric connections proper to the chart, while temporal coding with theta phase precession in our model produces asymmetric connections. We obtained two types of average distribution of the synaptic weights in CA3 recurrent connections: the one is the conventional average distribution and the other is the rotated average distribution. The conventional average distribution is obtained from the superposition of all units' weight distributions, as seen in Fig. 9, after each weight distribution is centralized according to the unit's expected position, or landmark position. The

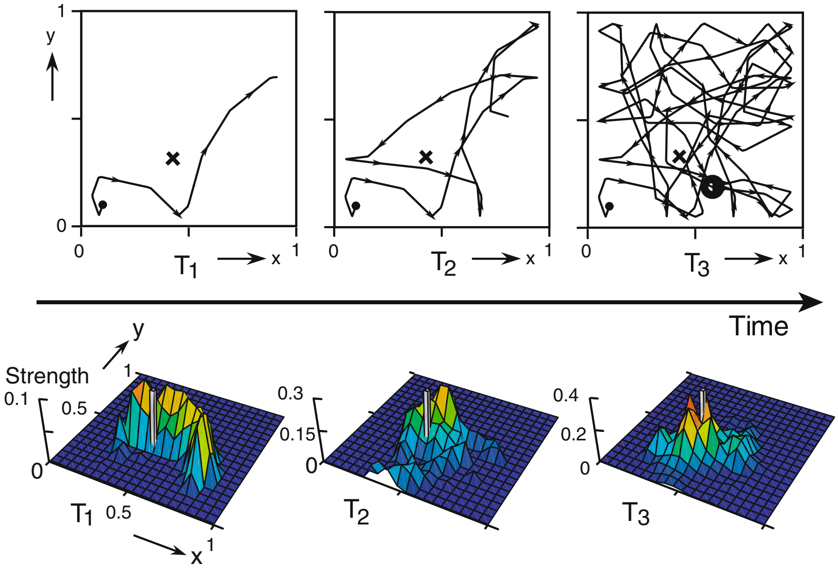


Fig. 9 (Top row) Trajectories in spatial exploration. Three representative points of time, T_1, T_2, and T_3 correspond to 35 cycles (4.375 s), 117 cycles (14.625 s), and 467 cycles (58.375 s), respectively. Solid lines denote trajectories of the rat. The running direction is shown as arrowheads on the line. The closed circle denotes the starting position. The open circle, shown only in T_3, represents the final position of the exploration. The behaviors of periods [0,T_1], [0,T_2], and [0,T_3], respectively, correspond to a simple trajectory, a trajectory with crossings at several points, and well exploration. (Bottom row) Development of the efferent map of an example unit during time T_1–T_3. The efferent map of a pre-synaptic unit, i, is defined as the arrangement of the synaptic weight values, $W_i^E = \{w_{ji} : j = 1, K \ldots, N\}$, so that the values are aligned with the expected array, which is defined as locations of landmarks distributed in the environment, as shown in Fig. 8A. The white bar standing on the expected array indicates the expected position of the pre-synaptic unit to which the cross mark in A corresponds. At time T_1, it is in a crescent form, which is similar to a pattern of population activity observed in theta phase precession. At time T_2, the efferent map is in a circular form in relation to the pre-synaptic unit (indicated by the white bar). A concentric shape of the connection map sharpens at time T_3. As the trajectory crossing points increase, the distribution of the connection weights on the map becomes more concentric around the expected position of the pre-synaptic unit. Figure from Wagatsuma and Yamaguchi (2004)

rotated average distribution is obtained from the superposition of all units' weight distributions after each weight distribution is centralized according to the unit's position and rotated to set its peak position to the same direction, which is shown as the gray line in Fig. 11C. Interestingly, after the spatial exploration the conventional average distribution gives a concentric shape with a central peak position, while the rotated average distribution statistically deviates from the center (Fig. 11C). This result indicates that after spatial exploration individual weight distributions tend to have a single peak with a certain distance from the unit's position and that individual peak positions have a variety of directions so that they are finally canceled out in the conventional average. Therefore, the overall structure of the learned network has a two-dimensional geometry with a two-dimensionally symmetric distribution on the chart, while the asymmetry is significantly preserved in the individual deviations derived from the connection balance between outgoing and incoming synapses.

The reason why asymmetric properties in connections are preserved, even after the formation of the chart, is the presence of an effective positive feedback of CA3 activities through ongoing established recurrent connections. In the classical theory of the hippocampal network, such recurrent feedback in the presence of the theta rhythm is considered to be negligible. This notion derives from experimental evidence using hippocampal slices which showed that acetylcholine (Ach) enhances the synaptic change but suppresses neuronal transmission in intrahippocampal synapses when the theta rhythm is present (Hasselmo and Schnell 1994; Hasselmo 1999; Hasselmo et al. 2002a). However, during in vivo observation, the region of the environment in which place cells fire, the place field, expands when the rat travels repeatedly along a given path (Mehta et al. 1997), which is necessary for synaptic modification in the hippocampus (Ekstrom et al. 2001; Rosenzweig and Barnes 2003). It suggests that the synaptic plasticity sufficiently contributes to the change of the place cells' firing when the animal is running, even with acetylcholine suppression. Therefore, we assumed a certain amount of the positive feedback of CA3 recurrent connections, given by E in Eq. 4, and then the result showed that the

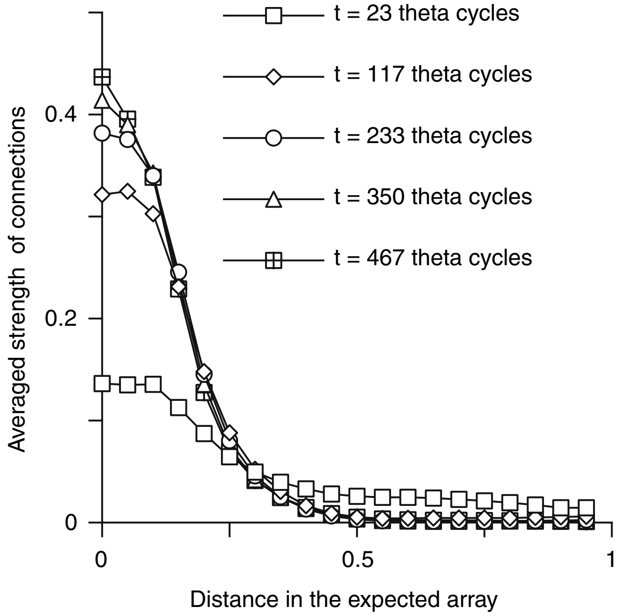


Fig. 10 Averaged connection weights with respect to the distance in the environment. All efferent connections are averaged with respect to the distance from individual presynaptic units. During the spatial exploration, the strength of the efferent connections changes, and the curve is converged to form a monotonical decrease with a high gradient. Thus, the CA3 recurrent network sufficiently establishes the chart property within a minute. Figure from Wagatsuma (2005)

asymmetry in connections always changes during spatial exploration, even when the total synaptic weights are converged (Fig. 12). The obtained distribution of asymmetry in connections is quite different from the vector field map, shown in Fig. 2A, from previous theoretical studies (Blum and Abbott 1996; Gerstner and Abbott 1997; Redish and Touretzky 1998; Trullier and Meyer 2000).

The importance of the investigation on the positive feedback effect was suggested by Redish and Touretzky (1998); however, no hippocampal models deal with it directly. This property is critical for the investigation of how the hippocampal memory develops, and it paves the way for comparison between the results of computer simulation and experimental data on experience-dependent changes. In the present model, experience-dependent place cell activity is successfully observed, as with running memory shown in Fig. 13, and compared with theta rhythm-dependent population activity after a short run and after spatial exploration.

It proceeds to a prediction that the theta rhythm acts as an internal clock, coordinating perception and memory, with the following sub-processes, as schematically shown in Fig. 14.

(1) *Current perception*. Representation of a local view in the current position by the current EC input.
(2) *Pattern completion of place*. Representation of the current place based on the resulting recurrent connections.
(3) *Anticipation*. Coordination between the representations of the current perception and place.

Thus, the above sequence of computation is repeated in every theta cycle during running, which is called theta phase coding. This process emerges from the harmonics between the phase wave of oscillator synchronization and the trigger wave generated by asymmetric recurrent connections.

Memory retrieval avoiding the interference between past memories

The issue of how the hippocampus avoids memory interference is the question we have to consider next. With respect to the theta rhythm, Hasselmo et al. (2002c) presented an interesting idea of the functional difference in theta phases for memory encoding and retrieval. They hypothesized that the former half cycle of theta contributes to the memory encoding while the latter half contributes to the memory retrieval. They were inspired by experimental evidence from the spatial alternation task, which is known to require hippocampal memory. In this task, the animal is trained in a T- or Y-shaped maze to pass through the common pathway and to choose first one of two branches and then the second branch. After the training, there is no cue in the common pathway to distinguish which branch is the correct choice. The problem is how the hippocampus encodes the behavioral sequence of the second choice just after the encoding the first choice. The difficulty that they emphasized is that the memory retrieval of the first choice disturbs the encoding of the second choice, because two alternative choices have an overlap in representing the behavioral sequence for the common pathway. Thus, the first one must enhance itself when the animal passes through the common pathway, preventing the encoding of the second choice. They solved this problem by separating the theta cycle into the encoding and retrieval stages.

Extending the problem, another question arises: how does the hippocampus retrieves the correct choice in the common pathway after the encoding of two similar memories? Wagatsuma and Yamaguchi (2005) tackled this problem and hypothesized the CA3 recurrent feedback, which carries past memories

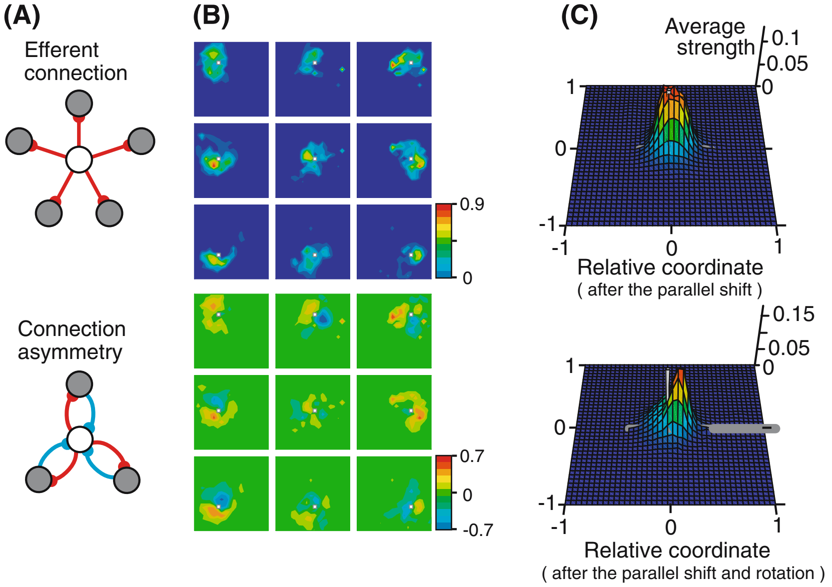


Fig. 11 Comparison between efferent maps and connection-asymmetry maps. (**A**) Schematic illustration of efferent connections and connection-asymmetry. To analyze an asymmetric property in connections, the "connection-asymmetry" of the unit i is defined as the set of differences between the efferent and afferent connection weights, given as $\bar{W}_i = W_i^E - W_i^A = \{w_{ji} - w_{ij} : j = 1, K \ldots, N\}$. In the connection-asymmetry map, these values are aligned in the same way on the efferent map. When every value on the connection-asymmetry map is equal to zero, every pair of connections is symmetric. (**B**) Top: A selected set of efferent maps. Bottom: connection-asymmetry maps of the same set of units as the above. Peak points in efferent maps are consistent with positive peaks in connection-asymmetry maps. (**C**) The conventional average distribution of efferent maps and the rotated average distribution of efferent maps (bottom). Both distributions are obtained in time T_3. The conventional average distribution is obtained from the superposition of all 400 efferent maps (example is shown in **B**) after it is centralized according to the unit's expected position (as the white pixel in the map). The rotated average distribution is obtained from the superposition of all 400 efferent maps after it is centralized according to the unit's position and rotated to set its peak position to the same direction (as the gray line in **C**). Both figures show the coexistence of the symmetric two-dimensional distribution and asymmetric property consistently observed in efferent connections and connection-asymmetry. Figure from Wagatsuma and Yamaguchi (2004)

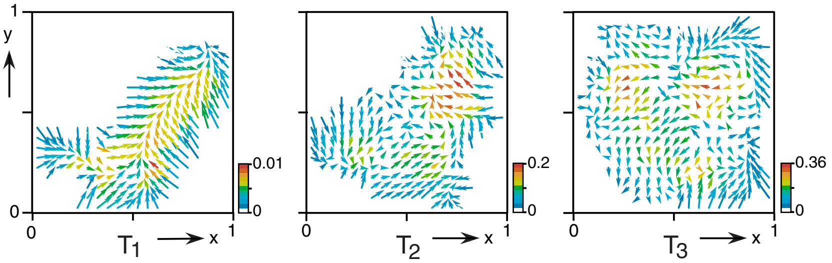


Fig. 12 The time evolution of the directionality map during time T_1–T_3. As shown in Fig. 11B, the directionality of unit i is defined as the direction from the animal's own position to the peak position. The directionality map is obtained as the superimposed image of all the directionalities. At time T_1, arrows are aligned with a short trajectory representing a single behavioral episode. According to the time lapse, the directionality distribution does not disappear but rather spreads out over the environment. The directionality of each unit changes according to the evolution of exploration, and the heterogeneous distribution of the directionalities in the environment is kept as a collective property. The synaptic plasticity with a positive feedback loop through CA3 recurrent connections enhances the preservation of asymmetric properties in connections, even after the formation of the cognitive map. Figure from Wagatsuma and Yamaguchi (2004)

encoded in the synaptic connections and selectively effects the specific range of theta phases for the disambiguation. The difficulty in this case is that even if the correct memory is once retrieved, ambiguous sensory information might reset the ongoing memory retrieval when the rat is running in the common pathway, as is schematically shown in Fig. 15. It is based on the concept of continuous attractor dynamics (Amari 1977; Amit and Tsodyks 1992; Samsonovich and McNaughton 1997), where a behavioral episode,

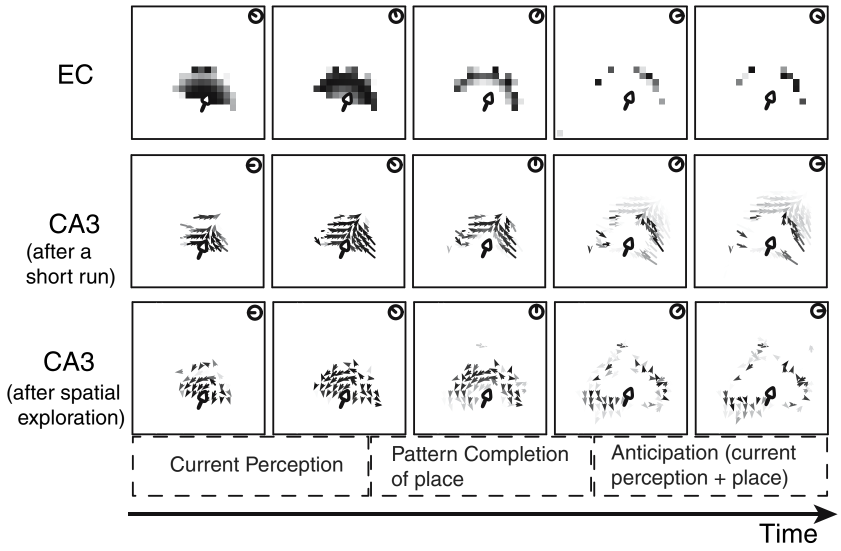
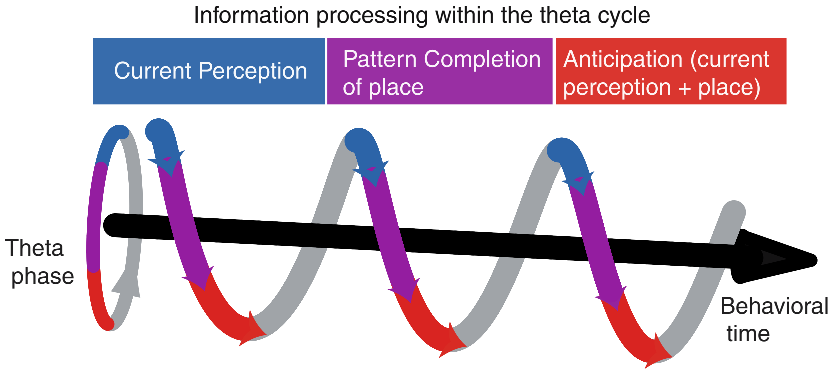


Fig. 13 Temporal evolution of population activities when rats are running on the same trajectory with different preceding experiences, time T_1 and T_3. (Top) The population activity of the EC in the T_1- and T_3-conditions. (Middle) The population activity of the CA3 in the T_1-condition. (Bottom) The population activity of the CA3 in the T_3-condition. Arrows in the middle- and bottom-row figures represent the directionality of the units. The gray-scale of the individual arrow represents the firing rate of the individual unit. The current position is marked by the symbol of the rat at each time. The clock displayed in the top-right corner in each square represents the value of the LFP theta in each layer. Each plot is given in a half theta cycle. Figure from Wagatsuma and Yamaguchi (2004)

Fig. 14 Schematic illustration of information processing by using theta phase coding



or a cognitive map, is represented as a type of combined attractor in which different places are represented as different attractor states, and an attractor state can smoothly shift over neighboring attractors with some input perturbation.

In the model of Wagatsuma and Yamaguchi (2005), different running episodes in the T-maze are represented as different continuous attractors, according to the task procedure shown in Fig. 16. It is consistent with the training procedure of Wood et al. (2000), which experimentally reported the existence of different groups of place cells that represent right-turn and left-turn running episodes independently after the training. In this computer experiment, two factors are necessary for the correct memory retrieval: one is the selection of the correct group, either a right- or left-turn, with respect to the current behavioral context, and the other is the correct place cell activity with respect to the current position of the animal. These factors are evaluated as the retrieval correctness, E_P, and position error, P_E, in the model (Wagatsuma and Yamaguchi 2005; Wagatsuma 2005). How difficult is it for both accuracies to coexist during the running task? As shown in Fig. 17, without the theta rhythm, behavioral episodes of right- and left-turns are easily retrieved by a trigger input at the start position. In this retrieval test, the population activity starts at right or left edges and smoothly propagates along the experienced path. However, if the theta modulation and sensory input change are given, they may disrupt the memory retrieval.

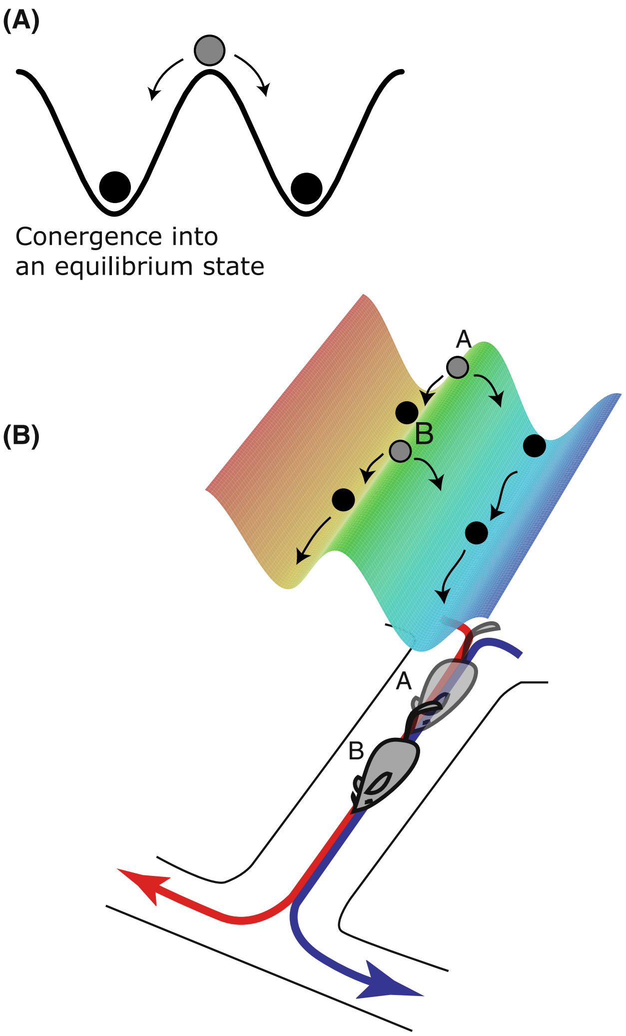


Fig. 15 (**A**) Schematic illustration of memory retrieval in associative memory. Solid line denotes the shape of an energy function that has two attractors. When an ambiguous input pattern (an open circle) is given at the hilltop, a retrieval pattern is obtained as either of two attractors (closed circles) with an equal probability. (**B**) Two continuous attractors corresponding to two behavioral episodes in a spatial alternative task, where the rat is required to retrieve a behavioral episode (right- or left-turn) depending on the context even with the same sensory inputs. When sensory inputs are updated in every theta cycle (**A** and **B** in the figure), memory retrieval also restarts at the hilltop. It is difficult to keep one attractor consistent with a behavioral episode

As Hasselmo et al. (2002c) pointed out, strong past memory retrieval sometimes disturbs the renewal of the current position representation, as in the transition from one place to the next. In contrast, weak memory retrieval might help in the transition to the next place, while it also allows for the transition to another wrong behavioral episode. Thus, both factors should be separated in theta phases; in other words, the sensory update and the preservation of the current behavioral context should alternate in every theta cycle. We investigated the best range of theta phases for the CA3 recurrent feedback by using the same computational model of the cognitive map formation (Wagatsuma and Yamaguchi 2004). For this analysis, we assumed a modulator of the feedback effect as an additional theta rhythm with a certain phase shift from the original LFP theta. In computer experiments, the range of theta phases with high retrieval correctness and low position error is obtained around -0.55π of the theta cycle. It can be suggested that the recurrent feedback that maximizes prior to the LFP theta within a quarter theta cycle enables the hippocampal network to update the proper place cell activity in the correct group. This is because the recurrent feedback preserves the current behavioral context in the previous theta cycle, and it restricts sensory update in the next theta cycle. Interestingly, theta phase precession naturally occurs in the best range (Fig. 18B), and spike count distribution is smoothly modulated according to the LFP theta (Fig. 19), which is consistent with the experimental observation of place cell populations when theta phase precession appears (Skaggs et al. 1996).

An important unsolved problem is how the hippocampus differentiates place cell populations for different behavioral episodes in the same location. This has been a controversial issue, because contradictory experimental results have been reported. Wood et al. (2000) observed the different population activity of place cells on places of the common pathway in the T-maze alternation task. A similar result was observed by Frank et al. (2000) and Ferbinteanu and Shapiro (2003). In contrast, Lenck-Santini et al. (2001) could not observe differential hippocampal activity in the similar alternation task, and observed only conventional place cells independent of the turning directions. Focusing on this inconsistency, Bower et al. (2002, 2005) revealed the essential factor and demonstrated that how the hippocampus encodes is determined by how behavioral sequences are learned. According to their results, the training condition with obstructive blocks to force the animal to run along correct pathways gives a differentiation in the population activity of place cells after the training. In contrast, the training condition without obstacles, such as in the try-and-error procedure, gives a consistent firing pattern of place cells. Bower et al. (2002, 2005) further investigated whether the differentiation in the hippocampal place cells contributes to the performance in the task. Nonetheless, the rat successfully learns in both cases. Thus, the function of the differentiation of behavioral context in the hippocampus is still unclear. It might relate to the animal's strategy to solve the spatial task,

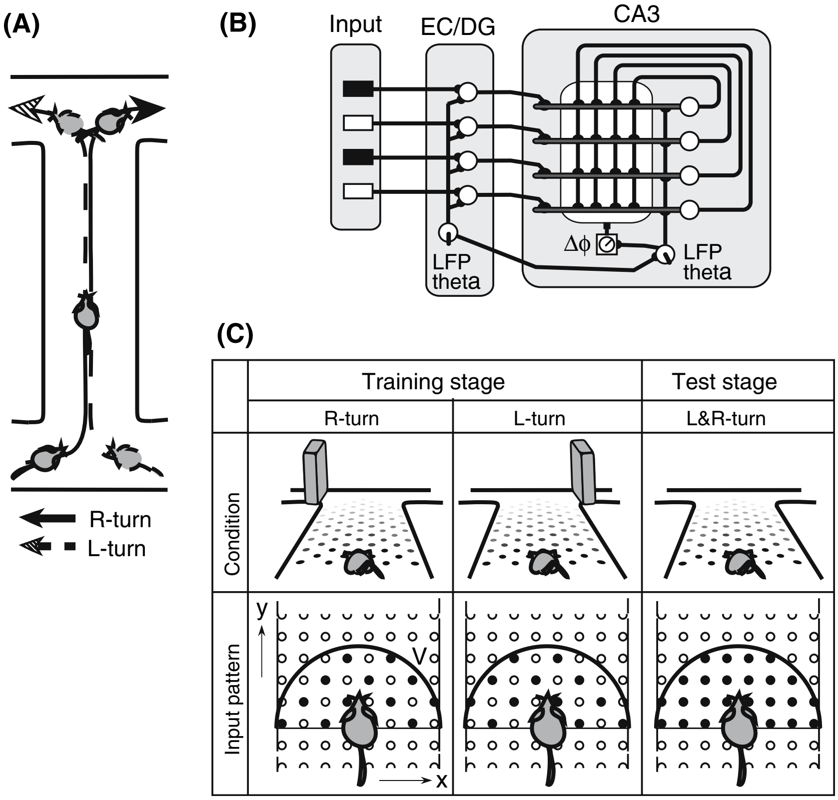


Fig. 16 (**A**) Forced run trajectory in the spatial alternation task. The local view input depends on the rat's position in the running trajectories, as shown in **C**. (**B**) Schematic illustration of the neural network model consisting of three layers. The model is consistent with the model in Fig. 8, with the exception of the modulation of synaptic weights by CA3 LFP theta with a phase shift, shown as $\Delta\phi$ in this figure. (**C**) Input patterns in individual conditions. The conditions in the training stage are characterized by different distal cues in order to discriminate the R- and L-turns. The landmarks are marked on the maze (top). The open and solid circles with the semicircle *V*, respectively, denote the input values 1 and 0 (bottom). In the training stage, the patterns are assumed to be orthogonal to each other in the R- and L-turn trials. In the test stage, the distal cues are removed in the condition, and the input pattern is then given as the full semicircle by assuming a mixed pattern of the R- and L-turns in the training stage. Figure from Wagatsuma and Yamaguchi (2005)

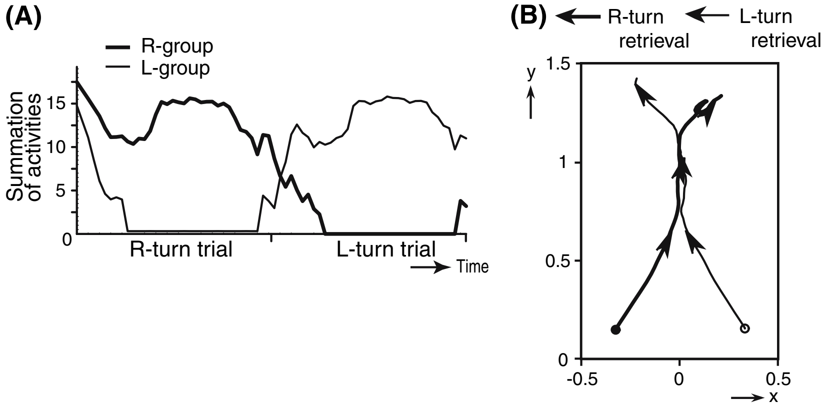


Fig. 17 (**A**) CA3 population activities of the R- and L-groups in the training stage. CA3 units are classified into R- and L-groups by input patterns in the training stage, shown in Fig. 16C. Each line denotes the summation of activities in each group, which are averaged individual theta cycles. The R- and L-groups clearly alternate depending on the trial. (**B**) Trace of the population activity in the retrieval test. The solid circle and open circle represent the trigger input position of the R-turn retrieval and L-turn retrieval. The trace curves are plotted by the center of mass of the retrieval population activity at each instance. Spontaneous activity starts from the trigger input and moves continuously along the trajectories of the R- and L-turn trials, depending on the input position. Figure from Wagatsuma and Yamaguchi (2005)

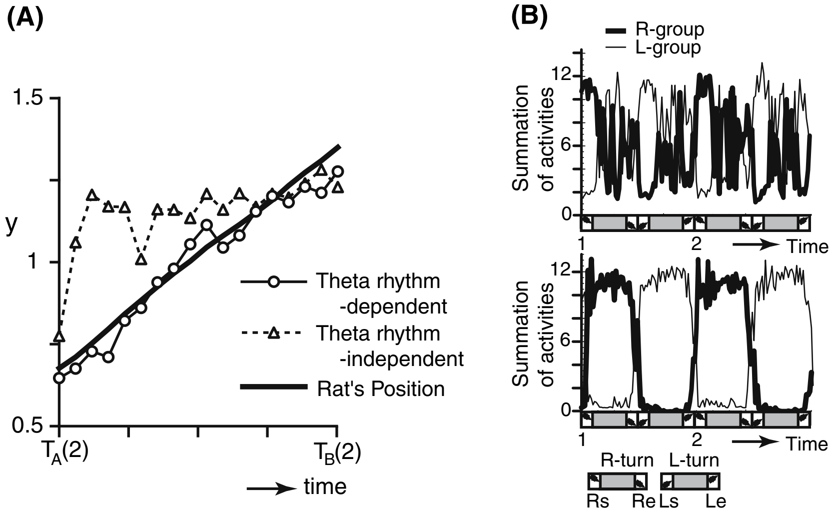


Fig. 18 (**A**) The place representation by CA3 population activities in theta rhythm-dependent and independent conditions. The ordinate and abscissa, respectively, represent the position of *y* in the maze and time. The actual current position and decoded position of the rat are, respectively, obtained by the sensory input pattern and the CA3 population activities. The theta rhythm-dependent condition ($\Delta_\phi = -0.55\pi$) is in good agreement with the current position, while the theta rhythm-independent condition (E_a=0.8) fails to trace the current position. Figure from Wagatsuma and Yamaguchi (2005). (**B**) CA3 population activities of the R- and L-groups in the test stage with various phase shifts in the theta rhythm-dependent modulation of the synaptic weights $\Delta_\phi = -0.55\pi$ (Top) and $\Delta_\phi = -0.55\pi$ (Bottom). Time evolution of CA3 population activities. Each curve denotes the summation of activities in each group, which are the averaged individual theta cycles. In the top, the R- and L-groups irregularly alternate, while in B, the R- and L-groups are alternatively activated depending on the trial. The latter case shows success in behavioral-context dependent retrieval. Figure from Wagatsuma and Yamaguchi (2005)

involving memories of behavioral episodes and the motor learning in the prefrontal cortex and the basal ganglia. It can be replaced with the question of how hippocampal memories are utilized with respect to decision-making. As is seen in the remapping phenomenon, where the drastic change of place cell populations with the change of the environment has been observed (Muller and Kubie 1987; Bostock et al. 1991; Gothard et al. 1996), the hippocampus discriminates context by changing the set of place cells or changing place field locations. If hippocampal memories of behavioral sequences are necessary in the spatial alternation task, the similarity between different behavioral episodes, such as the overlapping length in task, may be an important factor. If so, the result of Wagatsuma and Yamaguchi (2005) suggests that the functional difference in theta phases is useful when the hippocampal network preserves the current behavioral context.

Neural dynamics of action selection in the hippocampal-locomotor system

In previous chapters, we discussed how the hippocampus encodes behavioral episodes and how the hippocampus retrieves these memories while avoiding ambiguity. The next and last question in the present article is how hippocampal memories of behavioral sequences are used for action selection in spatial navigation? Damage to the hippocampal formation is known to impair the ability for spatial navigation, suggesting a contribution of the cognitive map to navigation. However, the cognitive map's contribution to the learning of a sequence of spatial locations remains uncertain.

In the classical rate coding theory, a simple sequence can be uniquely represented by the firing rate of the cell population. This concept is useful for navigation tracing the experienced pathway if the sequence does not have any repeated segments in it. In the case with a repeated segment, this concept causes ambiguity in the space representation on the repeated segment and requires another cell population for different contexts (Levy 1996; Wallenstein and Hasselmo 1997; Sohal and Hasselmo 1998). The hippocampus might need to assign different contexts to different cell populations. This difference in cell population firing is, however, not always observed in experimental observations (Lenck-Santini et al. 2001; Bower et al. 2002, 2005).

In the concept of theta phase coding, localized activity generated on the map in every theta cycle represents not only where one is but also where one

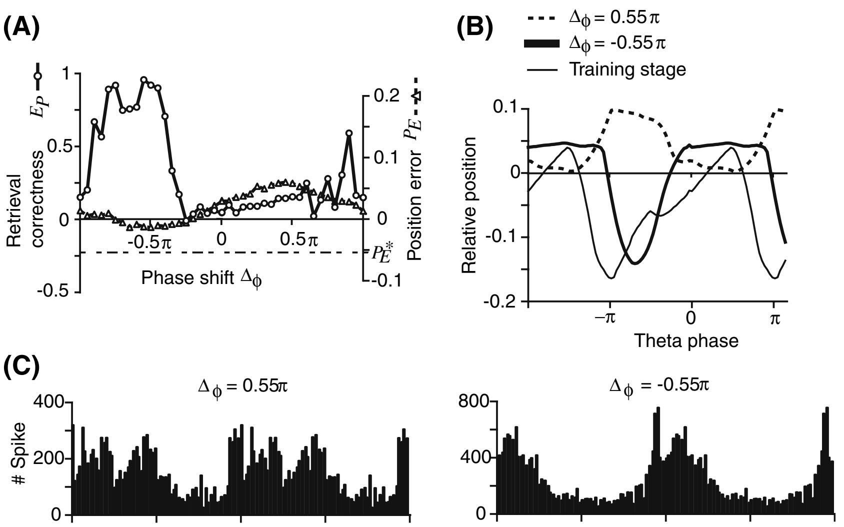


Fig. 19 (**A**) Retrieval correctness (E_P) and position error (P_E). P_E^* denotes the position error in the training stage. Correct retrieval with a small position error is found in the theta-rhythm dependent condition around $\Delta_\phi = -0.55\pi$. (**B**) The propagation of the population activity of CA3 units during theta cycles. The traces of the center of mass of the population are averaged over the entire time in the training or test stage. The ordinate represents the relative position that is defined as the difference between the current position of the rat and the center of mass of the CA3 population in each condition. The abscissa represents the phase of theta rhythm. In the training stage, the relative position advances as much as the length of the local view input. In the condition $\Delta_\phi = -0.55\pi$, the relative position of the population activity advances in the same amount as in the training stage, as the regular phase precession; it moves with a faster velocity, because the asymmetric connections accelerate the propagation of population activities. On the other hand, in the condition $\Delta_\phi = -0.55\pi$, the movement of the relative position is reduced to the half-length and is inconsistent with the result in the training stage. (**C**) Spike counts of the activity of CA3 units with respect to the phase of the LFP theta. A single spike of unit *i* is defined as the theta phase when a unit has a maximum firing rate in each theta cycle. The value in each bin, called the spike count, is obtained by the summation of the firing of all the units over all 10 trials with respect to each phase of the theta cycle. In comparison with the condition of $\Delta_\phi = -0.55\pi$, the envelop of the spike density in the condition $\Delta_\phi = -0.55\pi$ has a smooth oscillatory curve modulated by the theta rhythm. This result suggests that the smoothness of the theta rhythm modulation and the weakly distributed firing bridging components in subsequent theta cycles are necessary for success in behavioral-context dependent retrieval. Figures **A** and **B** are from Wagatsuma and Yamaguchi (2005) and Figure **C** is from Wagatsuma (2005)

goes (Fig. 14). Thus, behavioral context is coded in the firing phase of place cells in a compressed form, which contains the sub-processes of current perception, pattern completion and anticipation. This setup is expected to enable avoidance of ambiguity in spatial navigation. We hypothesized that current sensory input, spatial memory and motion are concurrently coded in the phase of every theta cycle to compute a possible direction of motion (Wagatsuma and Yamaguchi 2006). Memory-guided locomotor behavior in the eight-figure running task was investigated by extending the model of the cognitive map formation (Wagatsuma and Yamaguchi 2004). The model was proposed as a hippocampal-locomotor system with theta phase coding. It consists of five layers: EC, HP, HD, SUB, and LC, as illustrated in Fig. 20.

Extending parts are HD, SUB, and LC. The HD layer is the head direction system, including the anterior thalamus and other related regions, which receives visual and vestibular information and maintains representation of the current allocentric direction of the animal's head, called the head direction. The SUB layer corresponded to the subicular complex, which receives directional and location information as outputs of the HD and HP layers. The LC layer is a locomotor system, which determines the direction of egocentric motion, right- or left-turns, by receiving the SUB output (Fig. 20B). There are two modifiable connections in the learning stage: the recurrent connections in HP representing a sequence of places and connections between HP and SUB layers representing the association of place and the head-direction when the rat was in the place. This network structure is consistent with the model of Samsonovich and McNaughton (1997).

This model of the hippocampal-locomotor system can reproduce a motion of an experienced path in two-dimensional space according to hippocampal memory retrieval. (In the theta phase coding, the important point is that the system provides not only

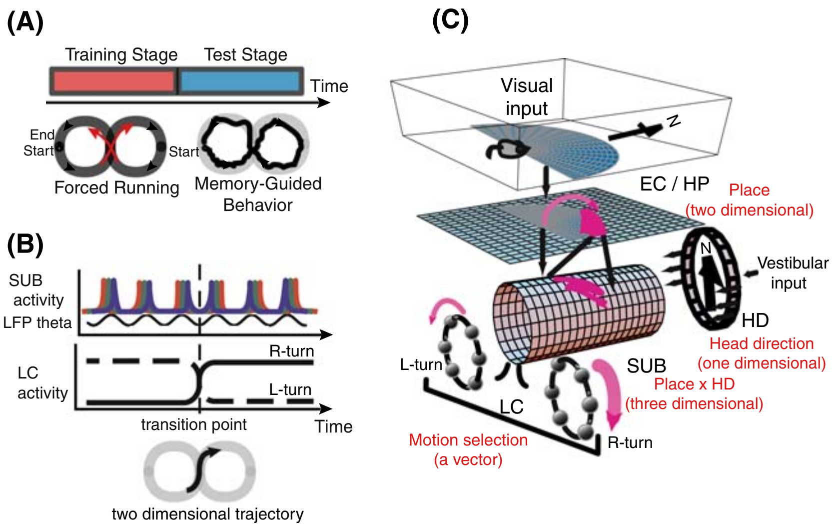
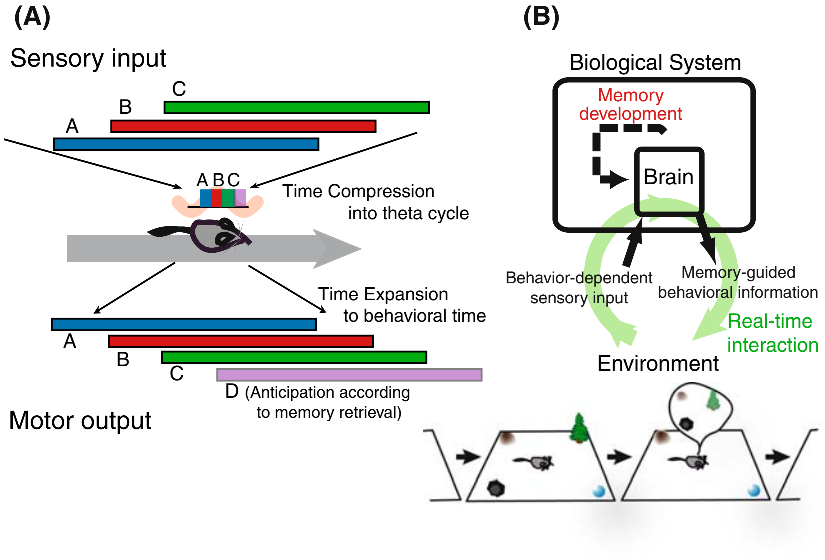


Fig. 20 Schematic illustration of the task procedure and the network structure in the model of Wagatsuma and Yamaguchi (2006). (**A**) The task procedure of the eight-figure task. In the training stage, the rat is forced to run on the eight-figure trajectory and the hippocampal network stores the behavioral sequence in the recurrent connection by using theta phase coding. Memory guided behavior is tested after learning. (**B**) The schematic illustration of the dynamics of signal detection in the LC layer, which transforms temporal sequences of head-directions in SUB to egocentric turning directions as R- or L-turns. The temporal sequence of red, green and then blue spikes in theta cycles before the dashed line enhances the left-turn signal, while the sequence with the opposite order (blue, green and then red spikes) in theta cycles after the dashed line enhances the right-turn signal reversely, as a transition. (**C**) Three-dimensional illustration of a model of the hippocampus-locomotor system with five layers. Black lines denote projections between layers. Red lines denote propagation of population activities within individual layers. In EC/HP layers, wave propagation occurs repeatedly in every theta cycle, as theta phase precession. In the HD layer, a sustained population activity appears, representing the current head-direction. In the SUB layer, location- and head-direction-dependent activity occurs by receiving the output of HP and HD layers, and it makes a temporal sequence of head-directions in every theta cycle, shown in **B**. Finally the LC circuit receives the SUB temporal sequence and determines the current motion by using competitive dynamics between R- and L-turn circuits

Fig. 21 (**A**) Schematic illustration of synthetic coupling of "time compression" and "time expansion" processes in theta phase coding, which are necessary for a real-time interaction between the brain and the environment, as schematically shown in **B**



the transformation of allocentric locational information to egocentric directional information, but also the transformation of the synaptic time scale, 50–100 ms, to the behavioral time scale, several seconds.) The memory of the behavioral sequence is retrieved in every theta cycle in a compressed form. It is then necessary to revert encoded sequences to information in the original time scale to use for behavioral motions, a concept called time expansion (Fig. 21A).

In the computer experiment, after the learning, the rat successfully traced the eight-figure trajectory. In the crossing point of the eight-figure trajectory, the system can generate the behavioral information to go to either the right or left side. In every theta cycle, a sequence of places in HP is transformed to a sequence of head-directions in SUB by using learned associations. The temporal sequence in SUB is finally transformed to a population activity in LC. LC has two parts, R-turn and L-turn circuits, and they competitively activate according to mutual inhibitions. In each circuit, directional connections make a ring structure that is either clockwise or counter-clockwise. Thus, the R-turn circuit responds to SUB activities with a temporal sequence of head-directions in the clockwise direction. In contrast, the L-turn circuit responds to the opposite sequences, as shown in Fig. 20C. In this simple task with a crossing point, the hippocampal-locomotor system with theta phase coding can generate context-dependent behavioral information, while in case of the long overlap in the common pathway, it might require some theta rhythm-modulation of the recurrent feedback as is investigated in the model of Wagatsuma and Yamaguchi (2005).

In the concept of the goal-oriented map (Fig. 2A), or vector field, every position has a unique direction in which to go next, ignoring where the animal came from. Thus, the running direction is determined out of context. The mechanism is effective to guide the animal to a single goal in the environment, even when obstacles exist; however, this is not applicable to navigation with multiple and/or changing goals. To explore how a cognitive map contributes to navigation with multiple goals, the contribution of the deep layer of the entorhinal cortex was recently discussed. Hasselmo and his colleagues (Hasselmo et al. 2002b; Gorchetchnikov and Hasselmo 2002; Koene et al. 2003) proposed that sustained activity in the cortices represents the temporal context and the desired goal and is transmitted to the hippocampal cognitive map through the deep entorhinal cortex. They obtained successful results by using the original large-scale simulation system of the spiking neural network with the virtual rat.

It is still unclear if unique cell populations are necessary for the hippocampus to represent the same location in different contexts. These considerations await further experimental investigation. However, the concept of theta phase coding sheds light on new aspects of the functional roles of theta rhythm-dependent neural dynamics in the hippocampus. It enables the hippocampal network to encode and retrieve the information of multiple contents in every theta cycle in the form of time compression and time expansion. These temporal mechanisms are necessary for real-time interaction with the environment, such as on-line sensory update and action change (Fig. 21B).

Summary and perspective

Here we have briefly reviewed the classical theory for the cognitive map in the framework of rate coding, discussed the potential of memories of behavioral sequences and focused on theoretical approaches to theta phase coding.

In the classical theory, many conventional models contained assumptions of a transient input, on the order of several milliseconds, dealt with output by sustained firing rates of neurons, and investigated neural dynamics independently of the behavioral change that happens in the external environment. Recently several theoretical studies investigated the function of the theta rhythm in memory (Lisman and Idiart 1995; Jensen and Lisman 1996; Fukai 1999) and the contribution of theta rhythm to the memory encoding (Sato and Yamaguchi 2003; Wu and Yamaguchi 2004). Furthermore, a large-scale simulation system of the spiking neuron network with theta rhythm was designed within the system of the virtual rat in the external environment (Hasselmo et al. 2002b; Gorchetchnikov and Hasselmo 2002; Koene et al. 2003).

The research presented here was directed towards real-time computation based on the collective dynamics of non-linear oscillations. The primary finding was that the behavioral context of the environment, not only where I am but also where I go, is represented in a temporal manner in the entorhinal–hippocampal network, which can be described by neural dynamics with oscillator synchronization. In the concept of theta phase coding, a temporal evolutional pattern of the population activity emerges in every theta cycle, resulting in the harmonics between the phase wave of sensory input-driven activity and the trigger wave generated by learned synaptic connections. It works for reorganization of the hippocampal network and enables on-line update of the memory content in accordance with the current perception. Further investigation will focus on a long-term interaction between accumulated memories and the current perception and will enlighten the development of the network structure. This information would provide memories with a higher complexity beyond two-dimensional maps, as shown in Fig. 3 (Sato and Yamaguchi 2005). These computational approaches will pave the way for theoretical study on the cognitive processes behind how individual experiences develop into knowledge, which happens not only in animal cases but also in humans.

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