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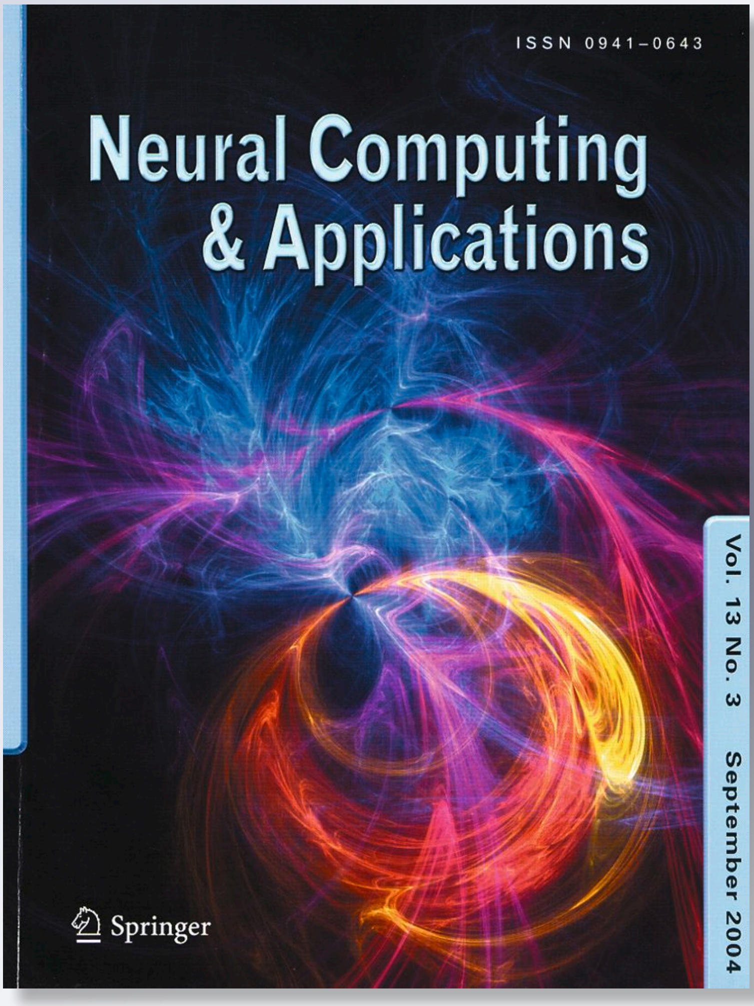

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Learning to memorize input–output mapping as bifurcation in neural dynamics: relevance of multiple timescales for synapse changes

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Abstract When a certain input–output mapping is memorized, the neural dynamics provide a prescribed neural activity output that depends on the external input. Without such an input, neural states do not provide memorized output. Only upon input, memory is recalled as an attractor, while neural activity without an input need not fall on such attractor but can fall on another attractor distinct from the evoked one. With this background, we propose that memory recall occurs as a bifurcation from the spontaneous attractor to the corresponding attractor matching the requested target output, as the strength of the external input is increased. We introduce a neural network model that enables the learning of such memories as bifurcations. After the learning process is complete, the neural dynamics are shaped to generate a prescribed target in the presence of each input. We find that the capacity of such memory depends on the timescales for the neural activity and synaptic plasticity. The maximal memory capacity is achieved at a certain relationship between the timescales, where the residence time at previous learned targets during the learning process is minimized.

keywords Neural network · Bifurcation · Associative reward–penalty · Multiple timescales

1 Introduction

The ability to learn appropriate responses to stimuli from the environment is one of the most important features of the brain. On the basis of the advances made in neuroscience over the past decades, it is now generally accepted that the output responses to input stimuli are memorized by the synaptic plasticity. Various neural network models have been proposed to study how a synaptic strength pattern is formed to memorize given input–output (I/O) mappings. In most of these studies [1–5], inputs are supplied as the initial states for neural activity, whose temporal evolution results in the generation of desired outputs. Thus, a dynamical system without inputs is not taken into account, and spontaneous activity is only considered to be noise. However, recent experimental studies have shown that structured spontaneous neural activity exists even in the absence of external stimuli and that such spontaneous activity is related to the cognitive function [6–9].

Upon external stimuli, such neural activity is modified to provide appropriate response neural activities [10]. Considering these experiments, we proposed a novel perspective for the memorization of I/O mappings [11]. If a neural system memorizes an I/O mapping, the spontaneous dynamics are modulated by a memorized input to provide a required target output. In other words, the input changes the flow structure of the neural dynamical system to generate the corresponding target output. This change in flow is mathematically formulated as the bifurcations of attractor upon input.

In the present paper, we use a layered neural network model to show that this idea of "memories as bifurcations" is indeed realized. In particular, we discuss the dependence of the learning process on the neural and synaptic timescales: the timescales for neural activity and the plasticities of both forward and backward synapses. We find that there is an optimal relation among these timescales, in order for the system to have a maximum memory capacity. This relation states that the timescale for neural activity is

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smaller than that for the backward synaptic plasticity and that the timescale for the backward synaptic plasticity is smaller than that for the forward one. We discuss how this timescale relationship is relevant to the formation of flow of neural dynamical system to achieve appropriate bifurcations for memories.

The structure of this paper is as follows: In the second section, we describe the model used in the paper. We adopt reinforcement learning in a three-layered network, which is composed of two rules, Hebbian (strengthening with "reward") and anti-Hebbian (weakening with "punishment") synaptic changes. We describe the dynamics of neural activity and the synaptic dynamics, i.e., the change in synaptic strength by reinforcement learning. The next section shows the results of the model described in the preceding section; these results include the typical behavior of our model and a demonstration of "memories as bifurcations." In particular, how the neural and synaptic dynamics change depending on the relationship between their timescales is analyzed in depth. In the last section, we discuss the implications of the results for learning and memory in our brain and the significance of the multiple timescales.

2 Model

We construct a neural network model for learning based on the following two conditions that satisfy the biological requirements for the normal process of the brain function. (1) Different error information for each individual neuron should not be required. In other words, individual error information is used commonly for all neurons. In contrast, in the error back-propagation algorithm [5], one of the most popular learning algorithms for neural networks, information corresponding to each of the output neurons is required. In biological learning with a neural system, however, it is difficult to transmit the specified information to each neuron. (2) I/O mappings should be learned sequentially, one-by-one, i.e., a new I/O mapping should be learned only after the previous mapping has been learned, while preserving the previously learned mappings. In contrast, in most learning algorithms for neural networks, numerous mappings are simultaneously and iteratively learned by gradually changing the synaptic strength until all of the mappings are memorized.

To satisfy the above-mentioned requirements, we introduce a layered network model consisting of input, hidden, and output layers, along with a reinforcement learning algorithm known as the associative reward–penalty (ARP) algorithm (Fig. 1) [4, 12]. In this model, several I/O mappings are learned one-by-one using only a single error signal, which is given as the distance between the activity pattern of the output neurons and a prescribed target output pattern. During the learning process, the synaptic strength is changed in accordance with the Hebbian and anti-Hebbian rules, switching based on the magnitude of the error signal (Fig. 1).

To be specific, we adopt the following model with N neurons in each layer. Three types of synapses are considered: forward synapses (FSs), backward synapses (BSs), and mutually inhibiting intralayer synapses (ISs). FSs connect the neurons in the input layer to those in the hidden layer and the neurons in the hidden layer to those in the output layer. BSs connect the neurons in the output layer to those in the hidden layer, while ISs connect the neurons within a given layer (a hidden layer or output layer).

2.1 Neural dynamics

The neural activity in the input layer is determined by an input pattern, I, a vector whose element takes the value 0 or 1; the magnitude of this vector (input strength) is η (1). The neural activities in the other layers change, as shown by the rate coding model (2, 3):

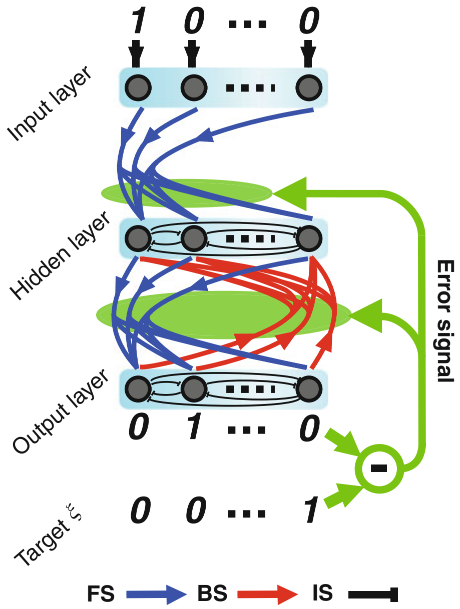


Fig. 1 Schematic representation of network architecture of our model. In this study, we use a three-layered model with input, hidden, and output layers. There are three kinds of synaptic connections in the network: forward synapses (FSs) represented with the *blue lines*, backward synapses (BSs) with the *red lines*, and inhibitory synapses (ISs) with the *gray lines*. FSs and BSs are modified during learning in accord with the error signal (the *green line*) between the output activity and target output activity, while ISs are fixed

$$x_i = \eta I_i \qquad (I \in \{0,1\}) \quad \text{(input layer)} \tag{1}$$

$$\tau^{\mathrm{NA}} \dot{x}_i = 1/(1 + \exp(-\beta u_i^{hid} + \theta)) - x_i \quad \text{(hidden layers)} \tag{2}$$

$$\tau^{\mathrm{NA}} \dot{x}_i = 1/(1 + \exp(-\beta u_i^{out} + \theta)) - x_i \quad \text{(output layers)} \tag{3}$$

where x_i is the firing rate of neuron i, and u_i is the input current applied to neuron i. The input current is given by $u_i^{\mathrm{hid}} = \sum_{j=1}^{N} J_{ij}^{\mathrm{FS}}\, x_j^{\mathrm{in}} + \sum_{j=1}^{N} J_{ij}^{\mathrm{BS}}\, x_j^{\mathrm{out}} + \sum_{j \neq i} J^{\mathrm{IS}}\, x_j^{\mathrm{hid}}$ for the neurons in the hidden layer and $u_i^{\mathrm{out}} = \sum_{j=1}^{N} J_{ij}^{\mathrm{FS}}\, x_j^{\mathrm{hid}} + \sum_{j \neq i} J^{\mathrm{IS}}\, x_j^{\mathrm{out}}$ for the neurons in the output layer. Here, $J_{ij}^{\mathrm{FS}}(J_{ij}^{\mathrm{BS}})$ is the strength of the forward (backward) synapse from a pre-synaptic neuron, j, to a post-synaptic neuron, i. J^{IS} is the strength parameter for the mutually inhibiting IS; this parameter assumes a fixed and identical value for all synapses except $J_{ii}^{\mathrm{IS}} = 0$ for all i. The parameters are set at $\tau^{\mathrm{NA}} = 1$, $\beta = 43$, $\theta = 2.5$, $\eta = 1.0$, $J^{\mathrm{IS}} = -1.0$, and $N = 10$.

For each input pattern, we prescribe a target output pattern, ξ, as an N-dimensional vector whose element takes the value 0 or 1. Sparse input and target patterns, in which only one neuron is activated, are chosen. By describing the neural activity in the output layer as the N-dimensional vector X^{out}, the learning task moves the error, $E = |X^{\mathrm{out}} - \xi|^2/N$, closer to zero, as measured by the Euclidean norm.

2.2 Synaptic dynamics

Synaptic plasticity is necessary for learning in neural network models. We adopt two schemes for the synaptic plasticity: multiple timescales and the ARP algorithm for reinforcement learning [4, 12]. First, the timescale of the plasticity of FSs τ^{FS} is different from that of the plasticity of BSs τ^{BS}. Second, the synapse pattern that generates the target output pattern is strengthened, in accordance with the Hebbian rule; A connection between the active neurons is strengthened, and, otherwise, it is unchanged or depressed. On the other hand, the synapse pattern that does not generate the target output pattern is weakened as per the anti-Hebbian rule; A connection between the active neurons is depressed, and, otherwise, it is unchanged or strengthened. In accordance with the ARP algorithm, the synaptic dynamics depend on the activities of the pre- and post-synaptic neurons as well as on the R determined from error signal E:

$$\tau^p \dot{J}_{ij}^p = R^p (x_i - r) x_j \qquad (J \geq 0) \qquad (p = \text{FS or BS}) \tag{4}$$

$$R^{\mathrm{FS}} = \begin{cases} 1 & \text{for} \quad E \leq \varepsilon \\ -1 & \text{for} \quad E > \varepsilon \end{cases} \qquad R^{\mathrm{BS}} = \begin{cases} 0 & \text{for} \quad E \leq \varepsilon \\ -1 & \text{for} \quad E > \varepsilon \end{cases} \tag{5}$$

Here, r is the spontaneous firing rate (set at 0.1), and ε is the error threshold, set at 10^{-3}. The sign of R changes with the magnitude of the error signal, E, between the output pattern and target pattern. When the output pattern is close to the target pattern, i.e., $E = |X^{\mathrm{out}} - \xi|^2/N \leq \varepsilon$, the synaptic plasticity follows the Hebbian rule, which is derived by substituting $R^{\mathrm{FS}} = 1$ and $R^{\mathrm{BS}} = 0$ in (4). This plasticity stabilizes the ongoing neural activity pattern. Note that during this stabilization process, only the strength of the FS varies, and hence, memories of the I/O mappings are embedded in the FSs. In contrast, when the output pattern is distant from the target pattern, i.e., $E > \varepsilon$, the synaptic plasticity follows the so-called anti-Hebbian rule, and the ongoing neural activity pattern is destabilized. Note that with the above form, $(x_i - r)x_j$, the synapse shows only negligible changes when its pre-synaptic neuron, j, is in a low-firing state. In our model, we require only a single error term for all of the neurons; this is in strong contrast to error back propagation, which requires the computation of a large number of error terms, i.e., as many error terms as output neurons.

In most neural network studies, only two timescales are considered: one for neural activities and the other for synaptic plasticity. In this study, we consider a variety of timescales for synaptic plasticity and introduce two timescales for the plasticities of the FSs and BSs. As will be shown later, I/O mappings are successfully memorized when the difference between the timescales is appropriate.

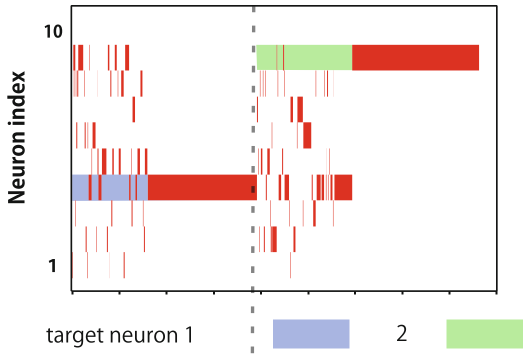
3 Results

3.1 Learning process

We first show that this model can be used to learn I/O mappings. Our learning process is composed of two phases. The neural activity varies to search a desired target when far from it ($E > \varepsilon$) and stabilizes when matching it ($E < \varepsilon$). Figure 2 shows the learning process for two I/O mappings. When the error is large, the present neural activity becomes unstable by the anti-Hebbian rule (5), and hence, the neural activity itinerates among different patterns ($0 < t < 350$). It searches the target pattern during this itineration. We term this period the "search" phase in what follows. At $t \sim 350$, the magnitude of the error decreases to a sufficient extent when the output dynamics are within the neighborhood of ε. Once this occurs, the neural activity is stabilized as per the Hebbian rule (Eq. 5), and the output activity remains close to the target ($350 < t < 800$). In this model, only one neuron in the output layer is active in each of the target patterns (the neurons highlighted by the blue and green bars in Fig. 2a), along with one neuron in the hidden layer. We term such neurons in the output and hidden layer the “target” neuron and “relay” neuron, respectively, corresponding to each input. Note that the relay neurons are not prescribed before the learning process but are determined as a result of the learning process, in contrast to the target neurons.

Thus, the activated synapses are continuously strengthened until a new target is presented, so that the present target is memorized. This period is called the “stabilization” phase, and the process to learn one I/O mapping, which is composed of a single search phase and stabilization phase, is called the “learning step.” At $t \sim 800$, we switch to a new input and the corresponding target pair to learn this. At that time, the distance between the output activity and target pattern increases again, and therefore, the search process progresses on the basis of the anti-Hebbian rule ($800 < t < 1{,}200$). In this manner, the neural activity can reach the target by switching between the anti-Hebbian and Hebbian rules alternately for synaptic plasticity, depending on the error. Now, we successively provide new input–target pairs after the time interval of the stabilization phase, which is sufficiently long for learning an I/O mapping. See [11] for details about the numerical results and analysis of the present model.

(a) Raster plot



(b) Error signal

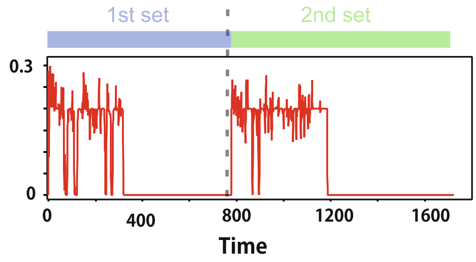


Fig. 2 Dynamics of neural activities during learning for two input–output (I/O) mappings. One learning process for two I/O mappings is shown. I/O mappings are learned in the search phase by the anti-Hebbian rule ($0 < t < 350$, $800 < t < 1200$) and in the stabilization phase by the Hebbian rule ($350 < t < 800$,$1200 < t < 1700$). Here, we set $\tau^{\mathrm{NA}} = 1$, $\tau^{\mathrm{BS}} = 8$, and $\tau^{\mathrm{FS}} = 64$. As initial states for the network, we assign the synaptic strength a random value between 0 and 1, except in the case of the ISs, and the neural variable a random value between 0 and 1. **a** A raster plot of neurons in the output layer. In this model, only one neuron in the output layer is active in each of target patterns, called the “target” neuron. The target neurons for two I/O mappings are highlighted by the blue and green bars. The red bar represents the time in which the neural activity is high ($x_i > 0.9$). **b** Time series of the amplitude of the error signal, E, between the output activity and target pattern. The *blue* and *green bars* above the time series represent a time in which the first and second (I/O) mappings are learned, respectively

3.2 Memories as bifurcations

In the present study, the system learns I/O mappings successively, as stated in the above section. Generally, it is not easy to memorize numerous mappings through successive learning processes, because after memorizing one mapping, the learning process for the next I/O mapping and the resulting synaptic change may destroy the previous memory. We thus check whether the system can memorize several I/O mappings in our model, and if possible, we then analyze how these mappings are memorized in the neural dynamical system.

First, we define “memory” based on the viewpoint that “memories as bifurcations.” From this viewpoint, the input is not initial state, but acts as a control parameter that causes bifurcation in the neural dynamical system (Fig. 3). In this paper, we investigate how the dynamical system is changed as the strength of the input, η, is changed from 0 (corresponding to the spontaneous dynamical system) to 1 (corresponding to the evoked dynamical system). If the system memorizes an I/O mapping, the evoked dynamical system at $\eta = 1$ has a fixed-point attractor that matches the target output pattern and is attracted globally from most initial neural activities. In other words, the attractor of concern in the evoked dynamical system has a sufficiently larger basin. Here, we set the criterion that the basin volume is larger than half of the phase space. Note that this attractor matching the target pattern need not be an attractor in the spontaneous dynamical system. In fact, many of the learned targets in the spontaneous dynamical system are not attractors in our model. The nature of the spontaneous dynamical system is independent of the definition of memory.

By adopting this definition, we analyze the number of memories by successively carrying out the learning processes for the I/O mappings. We find that by setting the parameters in our model appropriately, the number of memories (memory capacity) is near N, which is the maximum possible number for the set of I/O mappings in the sparse coding. In the next subsection, we analyze this dependence of the number of memories on the parameters,

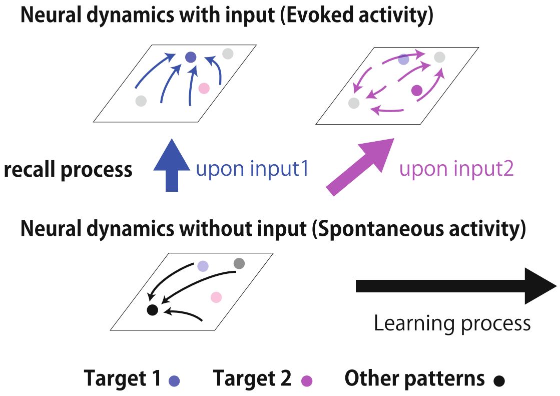


Fig. 3 Schematic representation of "memories as bifurcations." The lower panels represent the neural dynamics without inputs (spontaneous dynamics) whereas the dynamics upon different inputs (evoked dynamics) are given in the upper panels, where fixed-point attractors are selected through bifurcations so that the corresponding output patterns are generated. The learning process changes the neural system both with and without input by the synaptic plasticity. When viewing "memories as bifurcations," there are two types of parameter changes: one for the input strength (recall process) and the other for the synaptic plasticity (learning process). The spontaneous and evoked dynamics are modified through the learning process, so that the adaptive bifurcation from the spontaneous dynamics to a fixed-point attractor matching the target is formed upon the input

especially the timescale parameters, τ^{NA}, τ^{BS}, and τ^{FS} (2–4), to find the optimal values.

In order to understand how memories are embedded, we analyze the dynamical systems after each learning step with a fixed pattern of synaptic strength (i.e., the system is not learning at this time). After learning the given I/O mappings, the neural activity orbits are examined, first in the absence of inputs and then in their presence. Figure 4 displays orbits after learning four and seven I/O mappings. After four I/O mappings are learned (Fig. 4a(i)), the neural activity in the output layer in the absence of any input shows transient itinerant dynamics over three patterns that are close to three of the target patterns, until it finally converges to a fixed point. In general, there can be several attractors in the neural dynamics, and which attractors are reached depends on the initial conditions of the neural activities. However, many orbits from different initial states also come close to each of the learned targets (see [11]).

In Fig. 4a(ii), an example of neural activity orbits in the absence of inputs is displayed after seven I/O mappings are learned. In this case, the attractor is a limit cycle that itinerates over the targets in the cyclic order 2, 6, 3, 4, and 5. In both cases, the target patterns do not exist as fixed-point attractors without inputs. Upon the application of the input, the fixed point or limit cycle collapses, and instead, the corresponding target pattern becomes a stable fixed-point attractor. Hence, a memorized output pattern is generated as a result of bifurcation.

The number of attractors varies through the learning process. As the learning progresses further, the number of fixed-point attractors first increases but then decreases as the learning steps increase beyond three. These attractors are replaced by one or more limit cycle attractors, while the total number of attractors itself decreases. This is because the limit cycle globally covers the phase space, with little room left for other attractors (Fig. 4b).

3.3 Dependence of memory capacity on timescales for synaptic plasticity and neural activity

In this subsection, we discuss the dependence of the memory capacity on the timescale relationships. In our model, there are two timescales for the synaptic plasticity, in contrast to most neural network models, which only use one timescale. We focus on the dependence of the memory capacity on three timescales (including one timescale for neural activity): τ^{NA} for changes in the neural activity, and τ^{BS} and τ^{FS} for the plasticities of the BSs and FSs, respectively. We study the dependence by varying τ^{BS} with fixed τ^{NA} and τ^{FS}. Here, we set $\tau^{NA} = 1$ and $\tau^{FS} = 64$ in the following analysis.

We measure the memory capacity and find that it reaches the maximum possible number, *N*, under the sparse coding case, when the condition $\tau^{NA} \ll \tau^{BS} \ll \tau^{FS}$ is satisfied (Fig. 5). This implies that with a single synaptic timescale ($\tau^{FS} = \tau^{BS}$), as is used with the usual learning models, this high capacity is not realized.

This relationship for the timescales requires the following explanation for the optimal learning. In our model, a smaller value of either τ^{FS} or τ^{BS} determines the timescale of the search phase, because the search for the target is possible only on the basis of the change in the flow structure by the anti-Hebbian rule. Further, τ^{FS} determines the timescale of the memory decay, because the memory information is embedded in the FSs (5). Because the

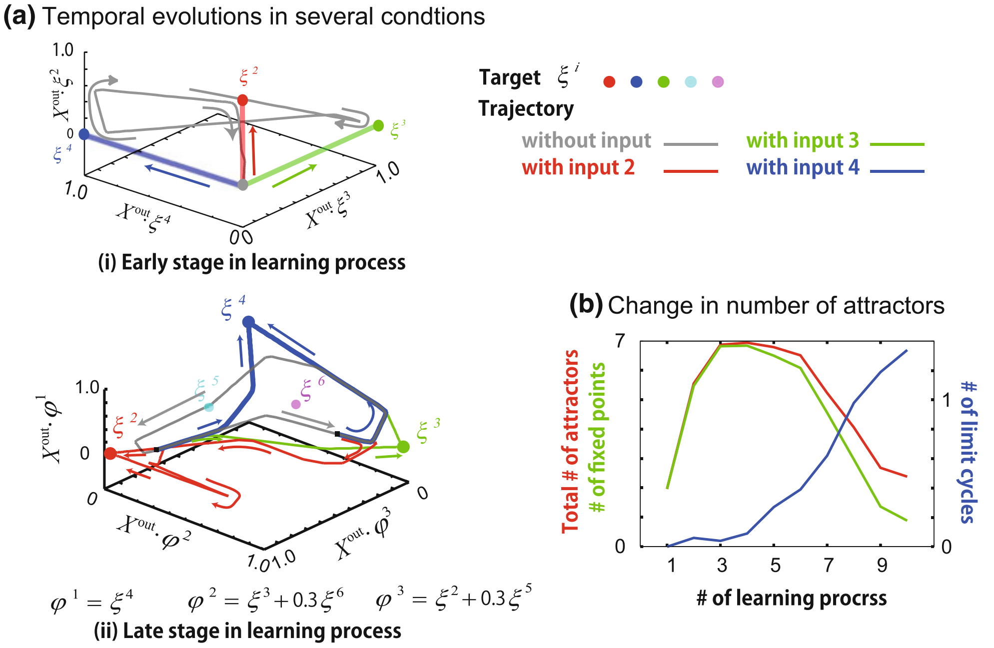


Fig. 4 Analysis of changes in flow structure of spontaneous neural activity during learning process. **a** Temporal evolution of neural activity in the output layer. The neural activity in the output layer is projected from the *N*-dimensional space consisting of the neural activities of the neurons in the output layer to a three-dimensional space by obtaining the products of the output activity and target output pattern. The gray line represents the orbit in the phase space of the dynamical system without inputs, while each colored line represents the orbit in the phase space in the presence of a different input. The circles in the phase space represent the targets. (i) Neural dynamics after learning four I/O mappings. Each axis represents the product of the neural activity and corresponding target output pattern. Each of the targets is stable in the presence of the corresponding input, whereas in the absence of input, it does not exist or is unstable. (ii) Neural dynamics after learning seven I/O mappings. Each axis represents the product of the neural activity and corresponding combined target patterns φ^i in the figure. The limit cycle is an attractor in the absence of inputs (*the gray line*) and is broken in the presence of each input. Each of the targets is stable in the presence of the corresponding input, just as in (i). Some transient orbits with input starting with the initial states on the broken limit cycle are shown. **b** Changes in the number of attractors during the learning process. The numbers of fixed-point attractors (*the green line*), limit cycle attractors (*the blue line*), and total attractors (*the red line*) in the absence of inputs are plotted as a function of the number of learning steps, i.e., the number of learned targets

timescale for the search phase should be sufficiently smaller than the memory decay time, $\tau^{BS} \ll \tau^{FS}$ is required to preserve the previous memory during the search phase.

Next, we consider the relationship between τ^{NA} and τ^{BS}. τ^{NA} determines the timescale for the neural dynamics under a given fixed flow structure. If τ^{NA} was larger than or of the same order as τ^{BS}, the phase structure would be modified before the neural activity changes, which would hinder the approach to the target pattern. In fact, the total search time decreases rapidly with an increase in the timescale of the BS plasticity, as will be shown in the next subsection. Hence, $\tau^{NA} \ll \tau^{BS}$ is required. Accordingly, the relationship $\tau^{NA} \ll \tau^{BS} \ll \tau^{FS}$ is required for an effective search for a new target without destroying the previous memory.

3.4 Dependence of learning process on timescales for synaptic plasticities

We next discuss how the learning process depends on the timescale relationship. Figure 6 shows the neural activity dynamics during the learning process for the fifth I/O mapping. The time series of neural activities are plotted for three different timescale values for the backward synapses: $\tau^{BS}=1$ $(\tau^{NA}=\tau^{BS} \ll \tau^{FS})$, $\tau^{BS}=19$ $(\tau^{NA} \ll \tau^{BS} \ll \tau^{FS}$, near the peak of the capacity curve), and $\tau^{BS}=128$ $(\tau^{NA} \ll \tau^{BS} \approx \tau^{FS})$. Figure 6a displays the raster plot of the output layer neurons. After successive changes in the firing of the neurons, only the fifth output neuron keeps on firing, which corresponds to the target pattern. When the neural activity converges to a target pattern, a single neuron in the hidden layer is activated, which is called a relay neuron, as defined in the above section. To examine the transient process before converging to a target, we plot the neural activity of a target output neuron and the corresponding relay neuron in the hidden layer in Fig. 6b. As shown, there are epochs where both the output and relay neurons are kept activated. During each of these epochs, the neural activity pattern stays close to that of the corresponding learned pattern. As shown in the figure, this residence at the learned pattern lasts longer as τ^{BS} is

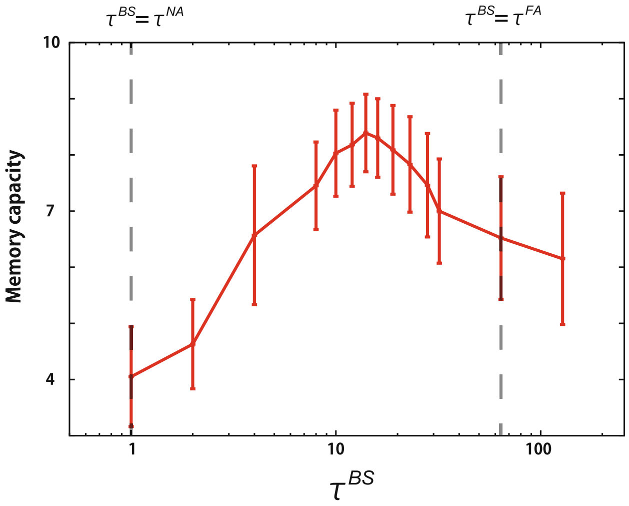


Fig. 5 Memory capacity. Memory capacity is a function of the timescale for the backward synapses, τ^{BS}. The other two timescales, τ^{NA} and τ^{FS}, are fixed at $\tau^{NA} = 1$ and $\tau^{FS} = 64$. The values are computed from the averages for over 100 learning processes for each τ^{BS}. The error bar indicates the standard deviations. For the learning processes computed here, we set the synaptic strengths of the FSs and BSs to 0 as initial conditions for the network for simplicity, in contrast to the case in Fig. 2, and set the neural activities at random values between 0 and 1, just as in Fig. 2. The randomness of the initial state of the neural activities causes the variability of the learning process. We also set such initial values in Figs. 7 and 8

increased, while the frequency of visiting each learned pattern is larger as τ^{BS} is decreased.

Now, we will study how the residence time, i.e., the average time span for the residence at a target pattern, depends on the timescales for the synaptic plasticity. This residence time is related to the memory capacity for the following reason. In the search phase, the output activity changes from one pattern to another, and the activity may come close to one of the previously learned target patterns. Because this pattern differs from the current target pattern, the attraction to this pattern embedded in the synapses may be destroyed by the anti-Hebbian rule. In general, the longer the output pattern stays close to a state corresponding to a previously learned target pattern, the stronger is this destabilization. Hence, the degree of the destabilization of the previous memory increases with the residence time at the corresponding pattern.

The dependence of the residence time on timescale τ^{BS} is plotted in Fig. 7. The residence time at each target is defined as the time span in which the activities of both the output target neuron and relay neuron remain larger than a given threshold, with a value of 0.5 used here (see the caption of Fig. 6). As shown in Fig. 7, this single residence time increases roughly in proportion to τ^{BS}.

Through the learning process, there are many residences at the previous targets. Thus, the accumulated residence time is also dependent on the total search time, which is the time span required for the search phase through the entire learning process. The dependence of the total search time on τ^{BS} is plotted in Fig. 7, which shows that it increases with a decrease in τ^{BS}.

Considering the fact that the accumulated residence time increases with both the (single) residence time and the total search time, the accumulated residence time is expected to increase for both small and large τ^{BS}. We compute this total accumulated time and also plot it also in Fig. 7. As shown, it has a sharp drop at the intermediate value of τ^{BS}, at about 16, which agrees well with the optimal value of τ^{BS} required to achieve the maximum memory capacity. Thus, the timescale relationship for synaptic plasticity for the optimal memory capacity is explained as the minimum accumulated residence time.

The residence time at each target depends on the order in which the target is learned. It is expected that the residence time at an older learned target is short, whereas that at a newer learned one is long. Thus, we analyze this dependence. Figure 8 shows the residence times at each of the learned targets during the learning process of the tenth I/O mapping. This residence time is plotted for three τ^{BS} values. The residence times for the few targets that were memorized most recently are rather high for $\tau^{BS} = 1$ and $\tau^{BS} = 128$. During this long residence time, it is easy for the memories to be destabilized. Thus, only slight traces of the earlier targets remain, which is why the residence time at the earlier learned target is smaller. In fact, the residence times at the previous target patterns decrease rapidly in the case of $\tau^{BS} = 1$ or 128. In contrast, the residence times in the case of $\tau^{BS} = 19$ remain at almost the same level, except for the two latest targets. This result shows that a greater record of a learned target remains in the case of $\tau^{BS} = 19$ than for $\tau^{BS} = 1$ and 128.

4 Discussion and conclusion

In the present paper, we investigated the dependence of the memory capacity on timescales on the basis of a novel dynamical system model for the memory [11]. In this model, the learning process shapes the “appropriate” flow structure of the spontaneous neural dynamics through successive presentations of inputs and their corresponding outputs. Memory recall is achieved as a result of the bifurcation of neural dynamics from an attractor of the spontaneous activity to that evoked by the external input matched with the target pattern. Specifically, we adopted a layered network model with multiple synaptic timescales and the adaptive reward-penalty (ARP) algorithm. As a result, we found that an appropriate relationship has to be satisfied among the timescales of the changes in the neural activity and that of the plasticities of the FSs and BSs, in

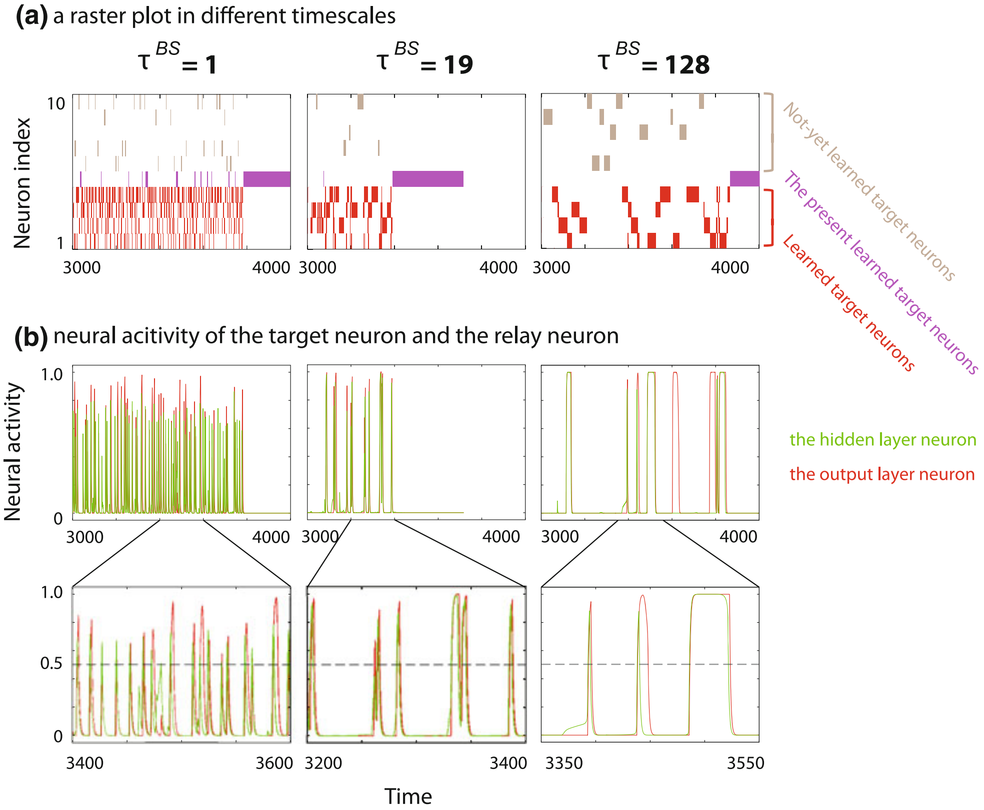


Fig. 6 Neural dynamics for three timescales for synaptic plasticities. The neural dynamics through the learning process of the fifth I/O mapping are shown for the three timescales for the plasticity of the BSs: $\tau^{BS} = 1$, $\tau^{BS} = 19$, and $\tau^{BS} = 128$. **a** A raster plot of all the neurons in the output layer. The *red bar* represents the time during which the neural activity is high ($x_i > 0.5$). The vertical axis represents neuron index i, which is activated at the i-th target, in the order of learning. Here, the fifth neuron on this index is the target neuron for the fifth I/O mapping (*the magenta raster plot*), and the first to fourth neurons in the index are the target neurons of the previously learned I/O mappings (*the red raster plot*). In contrast, the other neurons in the output layer are not yet learned target neurons (*the gray raster plot*). After the transient time, the fifth neuron remains activated, which implies that the learning process of the memory is completed. **b** Neural activities in the hidden and output layers are shown. Plotted are the neural activities of the first output neuron (corresponding to the first target neuron) and the "relay" neuron in the hidden layer, which is the neuron that is kept activated in the stabilization phase of learning the corresponding I/O mapping. (See Sect. 3.1 for a definition of the relay neuron.) In other words, this neuron receives input from the current active input neuron and outputs to the target output neuron. Magnified views of the middle panels are given in the lower panels. We define the residence time as the time in which the activities of both the target and relay neuron are higher than a threshold (we set this at 0.5 here). This threshold is represented by the dashed line in the lowest panel

order to achieve the maximum number of memorized patterns. In this section, we discuss the possible relevance of our results to biological learning: First, the implementation of the present learning mechanism in the biological brain, and second, the functional meaning of the multiple synaptic timescales.

4.1 Biological implementation of learning mechanism

Here, we discuss the possibility of implementing the architectures of our model in the brain.

(1) **Multiple timescales:** The timescales of the synaptic dynamics represent the magnitudes of the synaptic plasticities such as long-term potentiation and long-term depression, and these plasticities depend on the number and/or type of receptors for the neural transmitters in our brain. Hence, the timescales for the synaptic plasticities are related to the number and/or type of these receptors. When two areas (say between the hippocampus and prefrontal cortex) are mutually connected, the forward and backward synaptic connections may have different characteristics, and hence, their plasticities may differ.
Recall that in our model, a proper relationship has to be satisfied among the timescales of the changes in the FSs and BSs and in the neural activity, to achieve the maximum number of memorized patterns. On the basis of the above argument, it is suggested that such a difference in the plasticities may be implemented by the possible difference between the number distribution and/or types of receptors in the neurons for the

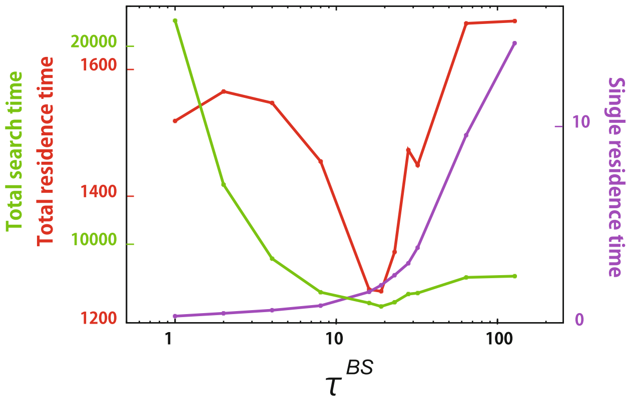


Fig. 7 Total search time, accumulated residence time, and residence time. The total search time (*the green line*), accumulated residence time (*the red line*), and residence time (*the magenta line*) through the entire learning process are plotted as functions of τ^{BS}. The total search time is the time required for the search phase for all of the learned I/O mappings, while the residence time is computed using the average time span for each epoch remaining at a target. The accumulated residence time is computed by summing the residence times at the targets memorized previously. These are computed throughout the entire learning process, averaged over 50 learning processes

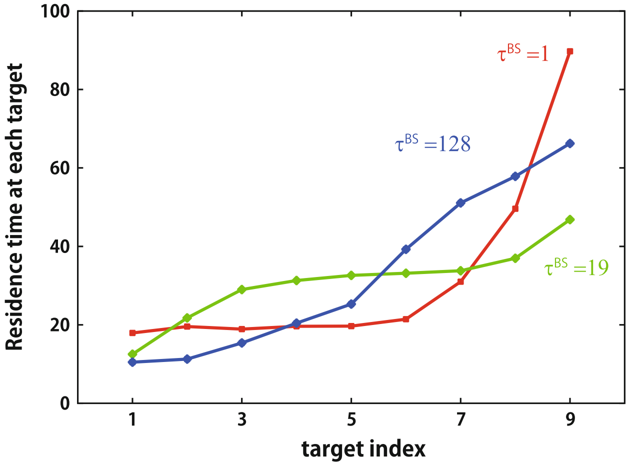


Fig. 8 Residence time at each learned target during learning process for tenth I/O mapping. The residence time during the process to learn the tenth I/O mapping is plotted against the target index for different timescales, which are shown in different colors: $\tau^{BS} = 1$ (*red*), $\tau^{BS} = 19$ (*green*), and $\tau^{BS} = 128$ (*blue*). We measure the residence times at the previous learned targets, i.e., from the first to ninth, during the learning process for the tenth I/O mapping. The target index order is the same as that for the learning. The residence time is computed by averaging over 50 learning processes, in the same way as used in Fig. 7

forward and backward connections between the given areas.

(2) **Adaptive reward-penalty:** In our model, the synaptic plasticity is switched between Hebbian and anti-Hebbian rules by the ARP algorithm, depending on the magnitude of the error signal. In our brain, neural modulators such as dopamine, serotonin, norepinephrine, and acetylcholine may give rise to this error signal. In particular, dopamine modulates the synaptic plasticity at the hetero-synaptic connection [13] and is broadly projected onto the cerebral cortex. Furthermore, the activity of dopamine neurons is related to the extent to which the response matches the request [14]. Hence, dopamine can act as a global error signal carrier. Thus, it is suggested that the switching between positive and negative plasticities, corresponding to that between the Hebbian and anti-Hebbian rules in our model, is regulated by the concentration of dopamine.

4.2 Function of multiple timescales

In general, the timescale for memory decay should be larger than that used when searching for the appropriate neural patterns for a new memory. In our model, the former timescale is given by the plasticity of the FSs, while the latter is given by that of the BSs. Indeed, it is necessary in our model that the timescale for the plasticity of the FSs be much larger than that for the BSs.

We expect that this postulate for such multiple timescales is rather general for successive learning. Recently, Fusi et al. [15] proposed a meta-plasticity-based model, which may involve multiple timescales similar to those in our model. They suggested that a meta-plasticity mechanism would be needed for simultaneous robustness and flexibility.

Generalizing our present results, we propose that the effective plasticity timescales for synapses are different for different roles.

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