A neural circuit model for changing the amount of information maintained in short-term memory depending on stimuli relationships

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Abstract

We propose a neural circuit model of changes in amount of information maintained in short-term memory depending on stimuli relationships. The relationships between stimuli are represented by the synchronous firings of overlapping neuronal groups for semantically related stimuli and the excitatory mutual connections for semantically unrelated but simultaneously presented stimuli. We conduct computer simulations to confirm our proposed neural circuit model. The resultant numbers of stored informational input patterns are almost consistent with the maximum numbers in the psychological experiments for both semantically related and unrelated stimuli. This agreement with the psychological experiments suggests that the structure and informational representation of the proposed model are appropriate.

Key words:
neural circuit model; short-term memory; number of stored patterns; stimuli relationship

1 Introduction

Memory plays an important role in higher-order human functions such as recognition, reasoning, and thinking. These higher-order functions cannot be

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performed in the absence of memory. Memory has been classified into two major forms by duration: short-term memory (STM) and long-term memory (LTM) (Waugh and Norman, 1965; Atkinson and Shiffrin, 1971). STM plays an essential role in such functions as sentence comprehension and mental arithmetic, although LTM is also required. Miller (1956) suggested that the capacity of STM is 7 ± 2 chunks, independent of the information contained in each chunk. The chunk is a unit of memory organization formed by bringing together a set of already-formed elements, which might be chunks themselves in certain cases. Examples of the chunks in an article include character, word, phrase, sentence, and so on.

Since the chunk is a variable unit, the amount of information that can be maintained in STM is not always fixed. The more information gathered into a chunk, the greater the amount of information that can be memorized. The results of previous psychological experiments (Miller, 1956; Hunt and Seta, 1984; Miyake and Uchida, 1923; Lupien et al., 1994) suggest that the amount of information maintained in STM changes depending on relationships between the units of information themselves.

The biologically plausible model network simulating seven-chunk capacity of STM was proposed by Lisman and Idiart (1995). This model network consists of after-depolarization (ADP) and rapid feedback inhibition onto pyramidal model neurons. The model network can encode information in gamma cycles oscillatory subcycles within main theta cycles. This phenomenon leads to the magical number seven. Based on the model proposed by Lisman and Idiart (1995), Usher et al. (2001) proposed a competitive model network explaining the new magical number 4 ± 1 presented by Cowan (2001, 2005). The new magical number 4 ± 1 is the capacity limit for working memory, which is a theoretical framework referring to the processes used for STM and for manipulating information. The working memory capacity is generally restricted by attention, time, interference, and other factors. Although the two aforementioned model networks (Lisman and Idiart, 1995; Usher et al., 2001) can show some aspects of STM capacity, they cannot explain how the amount of information maintained in STM increases.

Some neurophysiological experiments (Tsunoda et al., 2001; Freedman et al., 2001; Gray et al., 1989) suggest that semantic relationships having common features are represented by the oscillatory synchronous firings of overlapping neuronal groups. On the other hand, the relationship of semantically unrelated but simultaneously presented stimuli (Miyake and Uchida, 1923; Lupien et al., 1994) also plays a role in changing the amount of maintained information available. It is thought that the neuronal groups corresponding to such stimuli are excitedly connected with each other.

We propose a neural circuit model of STM with changes in the amount of

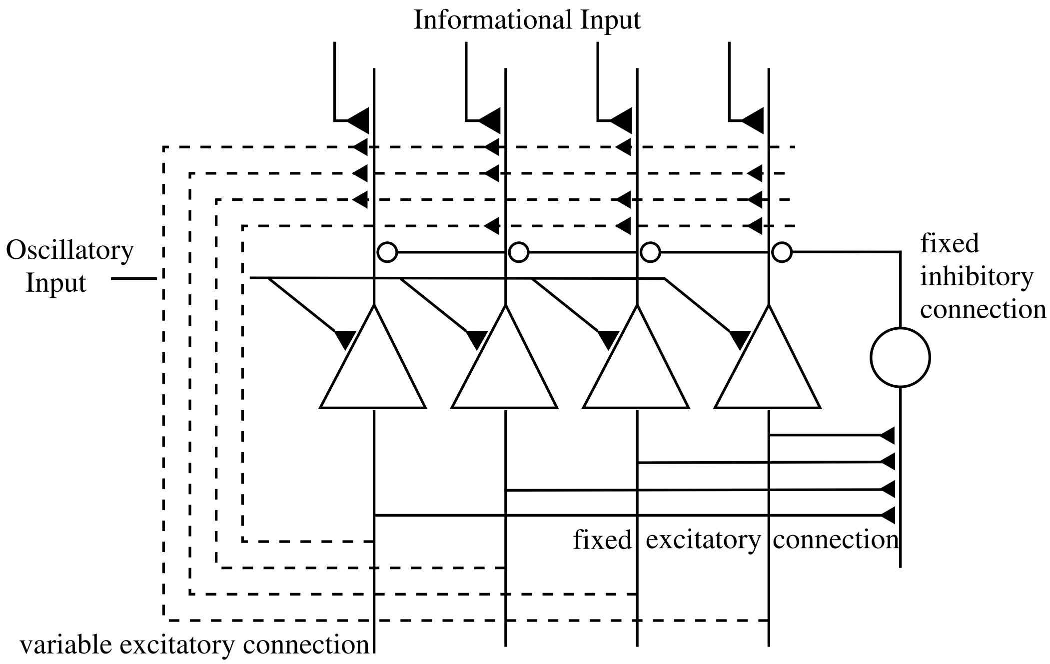

Fig. 1. Proposed model.

maintained information depending on the same relationships indicated by the psychological experiments. In the proposed model, the relationships between stimuli are represented by the synchronous firings of overlapping neuronal groups for semantically related stimuli and the excitatory mutual connections for semantically unrelated but simultaneously presented stimuli. Mutual connections between excitatory model neurons are learned by spike-timing-dependent synaptic plasticity (STDP), because these relationships are not intrinsically obtained. To evaluate the proposed model, we conduct computer simulations. We compare the amounts of maintained information in computer simulations with the results of the previous psychological experiments.

The remainder of this paper is organized as follows. In Section 2, we propose a neural circuit model of STM with changes in the amount of maintained information depending on the relationships between stimuli. Section 3 shows the results of our computer simulation to confirm our proposed model. Section 4 presents our conclusions.

2 Proposed Model

Our proposed model network is shown in Fig. 1. The proposed model consists of informational input, θ-band oscillatory input, excitatory pyramidal neurons, and feedback inhibitions, same as the model proposed by Lisman and

Idiart (1995). However, mutual excitatory connections between the excitatory pyramidal neurons are newly added. The mutual excitatory connections are very similar to the extended model (Jensen and Lisman, 1996) of the base model (Lisman and Idiart, 1995). The difference between the extended model and the proposed model is that the mutual excitatory connections are variable by the STDP learning rule.

The remainder of this Section is organized as follows. In Section 2.1, we denote the dynamics of a model neuron. Section 2.2 explains how to encode the relationships between stimuli. Section 2.3 and 2.4 present the excitatory and inhibitory connections, respectively, that enable the encoding of the relationships.

2.1 Dynamics of the Model Neuron

When an object to be stored in memory is presented, the corresponding model n-neurons are injected with a 15 mV pulse current. We call this pulse current, simultaneously injected to the model n-neurons, an informational input pattern. When the entire set of corresponding model n-neurons fires simultaneously, the informational input pattern for the object can be stored in STM.

The membrane potential $V_i(t)$ of the i-th excitatory model neuron at time t is given by the following equations:

$$\tau_v \frac{dV_i(t)}{dt} = -V_i(t) + V^{rest} + V^{OSC}(t) + V_i^{ADP}(t) + V^{inh}(t) + r_m I_{ext}, \tag{1}$$

$$V^{inh}(t) = \sum A^{inh} \frac{t - t_k}{\tau^{inh}} \exp\left(\frac{1-(t-t_k)}{\tau^{inh}}\right), \tag{2}$$

$$V_i^{ADP}(t) = \sum A^{ADP} \frac{t - t_k}{\tau^{ADP}} \exp\left(\frac{1-(t-t_k)}{\tau^{ADP}}\right), \tag{3}$$

$$V^{OSC} = B \sin(2\pi f t), \tag{4}$$

$$I_{ext} = \sum_j^N w_{ij} g(i), \tag{5}$$

where V^{inh} and V_i^{ADP} are the voltage affected by the inhibitory connections and ADP, respectively, I_{ext} is the external input current, r_m is the membrane resistance, and N is the total number of excitatory model neurons. τ_v, τ^{inh}, and τ^{ADP} are the time constants for the membrane potential, inhibition, and ADP, respectively. A^{inh} and A^{ADP} are the maximum amplitudes of the inhibition and ADP, respectively. t_k is the time of the k-th spike in the network. f is the frequency of the θ-wave, and B is the amplitude of the θ-wave. If $V_i(t)$ exceeds the threshold V^{thresh}, the model neuron fires and $V_i(t)$ is reset to V^{rest}. $g(\cdot)$ is the function that outputs 1 when the model neuron fires; otherwise, the model neuron outputs 0. w_{ij} is the weight from the i-th model neuron to the j-th model neuron.

2.2 Encoding of Relationships

We encode two types of relationships: semantically related stimuli and semantically unrelated but simultaneously presented stimuli. The former relationship is encoded by the oscillatory synchronous firings of overlapping neuronal groups while the latter relationship is encoded by mutual excitatory connections among neuronal groups. The encoding of these two types of relationships is illustrated in Fig. 2, where a neuronal group consists of four neurons.

In storage of objects A and B, the two central neurons are the common components that represent the common features (semantically related stimuli) of the two objects. For instance, when A is human and B is monkey, polyphagia and viviparity are examples of common features. The greater number of common components, the more the two objects are similar to each other. As the similarity increases, the amount of information maintained in STM will increase depending on the ratio of the number of common components to the number of neurons in a group.

In storage of objects C and D, the two neuronal groups corresponding to the objects are excitedly connected each other. In this case, the stronger the mutual excitatory connections, the stronger the relationship between the two

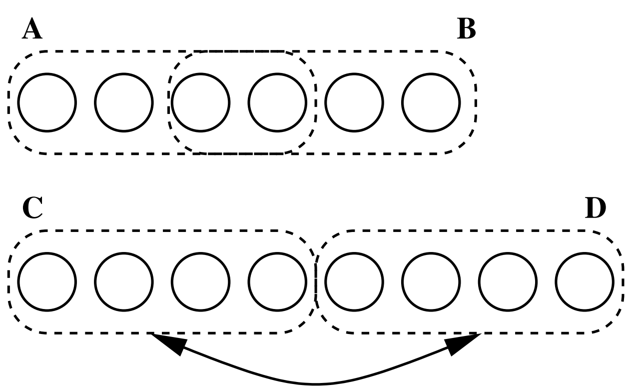

Fig. 2. Encoding of two types of relationships: overlapping neuronal groups (top) and mutual excitatory connections among neuronal groups (bottom).

objects. As the relationship is strengthened, the amount of information maintained in short-term memory will increase depending on the weight strength among the neuronal groups.

2.3 Excitatory Connections

The excitatory connections for the informational input and the oscillatory input are fixed. The excitatory connections from the excitatory model neurons to the inhibitory neurons are also fixed. On the other hand, the mutual excitatory connections are variable; that is, they are learned by STDP.

STDP is a minute time resolution version of the well-known Hebb learning rule. The profile of STDP has been observed electrophysiologically (Markram et al., 1997; Bi and Poo, 1998; Froemke and Dan, 2002). From the profile, postsynaptic potentials arriving after presynaptic potentials induce long-term potentiation, and postsynaptic potentials arriving before presynaptic potentials induce long-term depression. Froemke and Dan (2002) have derived a numerical description of the increase and decrease rates of synaptic plasticity $w(\Delta t)$ % from electrophysiological data as follows:

$$\Delta w(\Delta t) = \begin{cases} 1.02 \exp \frac{-|\Delta t|}{15.5} & (\Delta t > 0) \\ -0.52 \exp \frac{-|\Delta t|}{33.2} & (\Delta t < 0), \end{cases} \quad (6)$$

where Δt [ms] is the temporal difference from a postsynaptic spike to a presynaptic spike.

2.4 Inhibitory Connections

In the original model proposed by Lisman and Idiart (1995), the firings of the excitatory neurons are separated by feedback inhibition. In our proposed method, since one object to be stored is represented by the n-neurons as an informational input pattern, the inhibitory weight strength is divided by n.

3 Simulation

We conducted computer simulations to confirm our proposed neural circuit model of STM for changes in the amount of maintained information depending on stimuli relationships. The membrane potential was calculated by the Euler

Table 1
List of parameters.

Parameter	Value
Total simulation time, T (ms)	32,000
Total number of neurons, N	128
Number of neurons for an object, n	8
Interval between input patterns (ms)	2,000
Propagation delay of excitatory neurons (ms)	0.35
Propagation delay of inhibitory neurons (ms)	0.05
Maximum excitatory weight strength	0.4
Initial value of excitatory weight strength	0.01
Inhibitory weight strength	0.5
Membrane resistance, r_m	2.0
Membrane time constant, $\tau_v (ms)$	0.1
Threshold, $V^{thresh}(mV)$	-50
Resting membrane potential, $V^{rest}(mV)$	-60
Time constant for inhibition, τ^{inh} (ms)	5
Amplitude of inhibition, $A^{inh}(mV)$	-4
Time constant for ADP, $\tau^{ADP}(ms)$	200
Amplitude of ADP, A^{ADP} (mV)	10
Frequency of θ-wave, f (Hz)	6
Amplitude of θ-wave, B (mV)	5

method with a time step of 0.05 ms. The parameters used in these simulations are shown in Table 1.

In both types of relationships, each informational input pattern has to be learned by STDP before conducting the simulations that investigate the number of informational input patterns that may be stored in STM. Before learning of each informational input pattern, the mutual excitatory weight strengths were initialized to a small value. Here, an object consisted of the corresponding model 8-neurons. During learning of each informational input pattern, the corresponding model 8-neurons were activated periodically with a frequency of θ, f, at random timing. Each informational input pattern was learned in this manner for 70,000 ms. For simplicity, we used 8 pairs of informational input patterns, making the total number of learned informational input patterns 16.

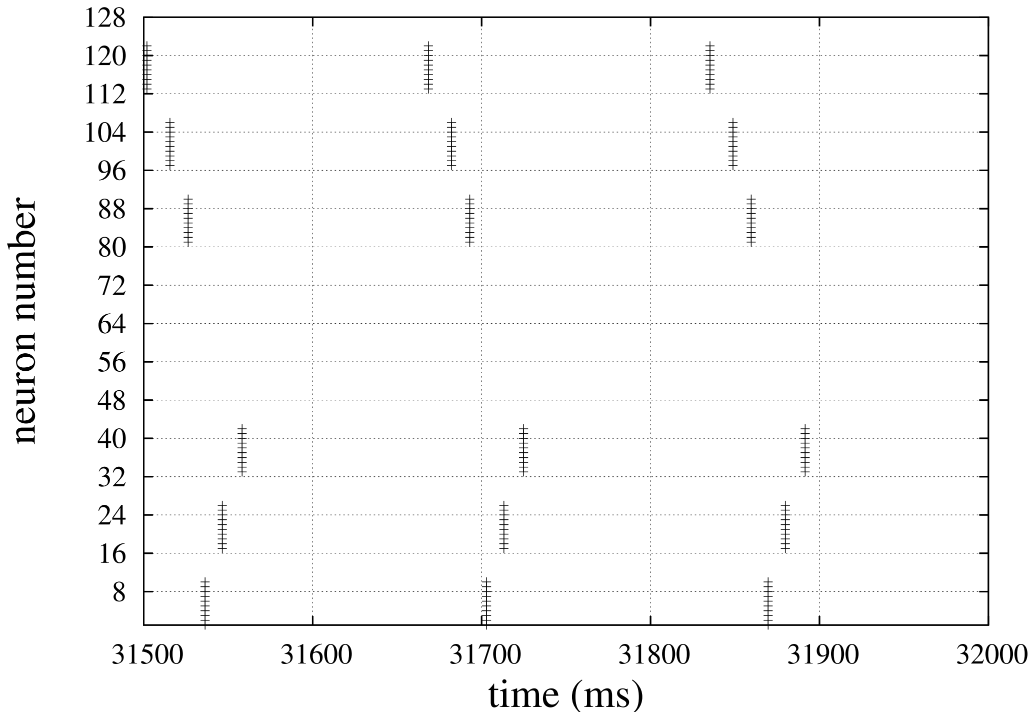

Fig. 3. Example of firing patterns.

We considered an informational input stored in STM when the entire model 8-neurons for the informational input fired within 1 ms, in consideration of neurophysiologically accurate firing time (Mainen and Sejnowski, 1995).

3.1 Semantically Related Stimuli

We simulated storage in STM to investigate how many informational input patterns are stored in STM depending on the semantical strength between related stimuli, that is, the ratio of the number of common components to the number of neurons in a group. After learning each informational input pattern separately, 8 pairs of informational input patterns were presented to the proposed model successively, with a 2,000 ms interval between individual pairs in the various number of common components.

Figure 3 shows an example of results with 6 common components in each pair. In this case, the number of stored informational input patterns is 12. We show the summary results in Fig. 4. The vertical axis is the number of stored informational input patterns and the horizontal axis is the number of common components.

When the number of common components is zero, the number of stored in-

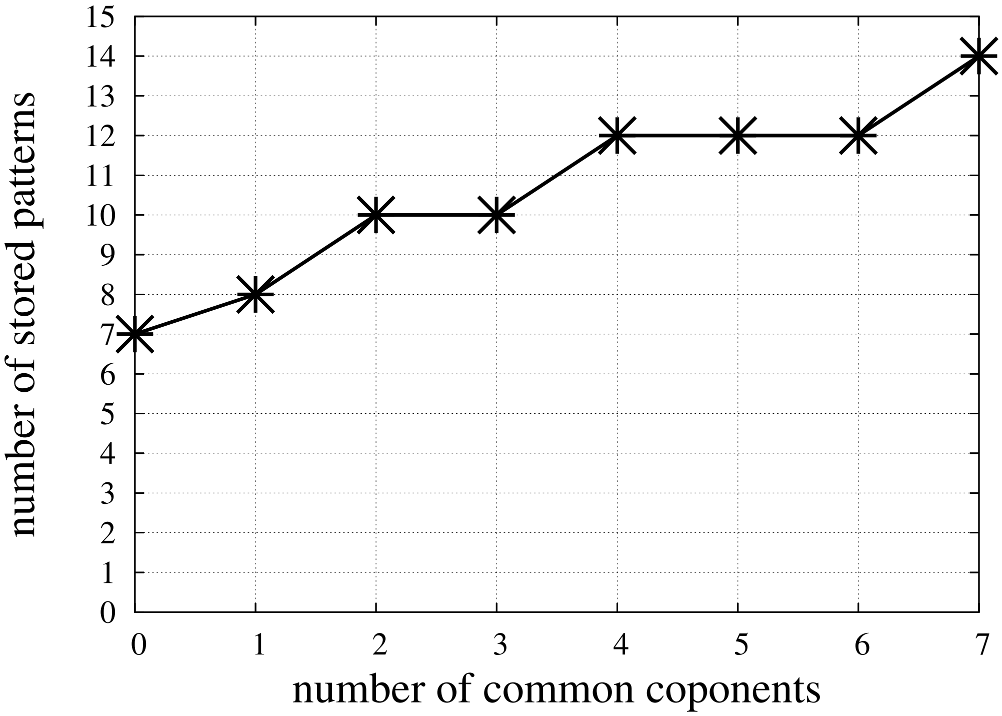

Fig. 4. Number of stored informational input patterns versus number of common components.

formational input patterns is 7. This is consistent with the magical number 7 suggested by Miller (1956). The number of stored informational input patterns increases with increase in the number of common components. The maximum number of stored informational input patterns is 14. The number 14 is consistent with the maximum number in the psychological experiments for semantically related pairs (Miyake and Uchida, 1923; Lupien et al., 1994).

3.2 Semantically Unrelated but Simultaneously Presented Stimuli

We simulated storage in STM to investigate the number of informational input patterns that can be stored in STM depending on the simultaneous presented frequency of unrelated stimuli, that is almost proportional to the weight strength between the informational input patterns. After learning each informational input pattern separately, 8 pairs of informational input patterns were presented to the proposed model successively, with a 2,000 ms interval with individual pairs in the various weight strength between the informational input patterns.

Figure 5 shows the number of stored informational input patterns versus weight strength between informational input patterns. When the weight strength

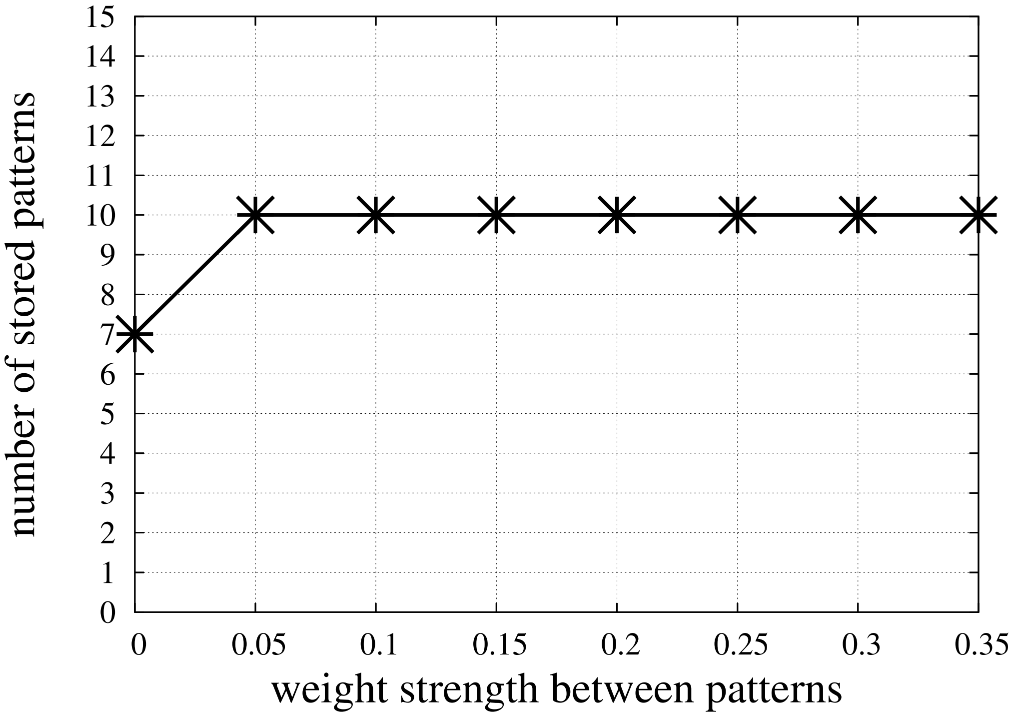

Fig. 5. Number of stored informational input patterns versus weight strength between informational input patterns.

is greater than 0.05, the number of stored informational input patterns is saturated, that is, a value of 10 is achieved. The number 10 is almost consistent with the maximum number in the psychological experiments for semantically unrelated pairs (Miyake and Uchida, 1923; Lupien et al., 1994).

4 Conclusions

We propose a neural circuit model of STM in which the amount of maintained information changes depending on relationships of the stimuli. The relationships between stimuli are represented by the synchronous firings of overlapping neuronal groups for semantically related stimuli and the excitatory mutual connections for semantically unrelated but simultaneously presented stimuli. We conducted computer simulations to confirm the proposed neural circuit model. The numbers of stored informational input patterns are almost identical to the maximum number in the psychological experiments for both semantically related and unrelated pairs (Miyake and Uchida, 1923; Lupien et al., 1994). This agreement with the psychological experiments suggests that the structure and informational representation of the proposed model are appropriate.

For simplicity, the current simulation results were only for the case of restoring pairs of input at the same time. We believe our proposed model also predicts the results for the case of restoring more than three inputs at the same time.

A wide variety of tasks concerning STM are possible. Note that the current results show only the upper limit of the amount of maintained information, because this issue focuses on how the amount of information maintained in STM increases. The memory capacity is generally restricted by factors such as attention, time, interference, and other considerations. The restricted memory capacity was discussed by Usher et al. (2001), Cowan (2005), and others.

In our current work, for simplicity, we deal with the inhibitory connections – important for the functions of storing STM – as fixed. Because some types of STDP of inhibitory synapses were physiologically observed (Holmgren and Zilberter, 2001; Woodin et al., 2006; Haas et al., 2006), we will introduce a STDP model of inhibitory synapse into our proposed method in the future work. Finally, we hope to verify the coding methods of stimuli relationships suggested in this study through actual biological experiments.

References

Atkinson, R., Shiffrin, R., 1971. The control of short-term memory. Sci. Am. 225, 82–90.

Bi, G.-Q., Poo, M.-M., 1998. Synaptic modifications in cultured hippocampal neurons: Dependence on spike timing, synaptic strength, and postsynaptic cell type. J. Neurosci. 18, 10464–10472.

Cowan, N., 2001. The magical number 4 in short-term memory: A reconsideration of mental storage capacity. Behav. Brain Sci. 24, 87–185.

Cowan, N., 2005. Working Memory Capacity. Psychology Press, New York.

Freedman, D. J., Riesenhuber, M., Poggio, T., 2001. Categorical representation of visual stimuli in the primate prefrontal cortex. Science 291, 312–316.

Froemke, R. C., Dan, Y., 2002. Spike-timing-dependent synaptic modification induced by natural spike trains. Nature 416, 433–438.

Gray, C. M., Kőnig, P., Engel, A. K., Singer, W., 1989. Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. Nature 338, 334–337.

Haas, J. S., Nowotny, T., Abarbanel, H. D. I., 2006. Spike-timing-dependent plasticity of inhibitory synapses in the entorhinal cortex. J. Neurophysiol. 96, 3305–3313.

Holmgren, C. D., Zilberter, Y., 2001. Coincident spiking activity induces long-term changes in inhibition of neocortical pyramidal cells. J. Neurosci. 21, 8270–8277.

Hunt, R. R., Seta, C. E., 1984. Category size effects in recall: The roles of relational and individual item information. J. Exp. Psychol. Learn. Mem. Cogn. 10, 454–464.

Jensen, O., Lisman, J. E., 1996. Novel lists of 7 ± 2 known items can be reliably stored in an oscillatory short-term memory network: Interaction with long-term memory. Learn. Mem. 3, 257–263.

Lisman, J. E., Idiart, M. A. P., 1995. Storage of 7 ± 2 short-term memories in oscillatory subcycles. Science 267, 1512–1515.

Lupien, S., Lecours, A. R., Lussier, I., Schwartz, G., Nair, N., Meaney, M. J., 1994. Basal cortisol levels and cognitive deficits in human aging. J. Neurosci. 14, 2893–2903.

Mainen, Z. F., Sejnowski, T. J., 1995. Reliability of spike timing in neocortical neurons. Science 268, 1503–1506.

Markram, H., Lübke, J., Frotscher, M., Sakmann, B., 1997. Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs. Science 275, 213–215.

Miller, G. A., 1956. The magical number seven, plus or minus two: Some limits on our capacity for processing information. Psychol. Rev. 63, 81–97.

Miyake, K., Uchida, Y., 1923. Clinical experimental result concerning memory I (in japanese). Shinkeigaku Zashhi 23, 458–488.

Tsunoda, K., Yamane, Y., Nishizaki, M., 2001. Complex objects are represented in macaque inferotemporal cortex by the combination of feature columns. Nat. Neurosci. 4, 832–838.

Usher, M., Haarmann, H., Cohen, J., Horn, D., 2001. Neural mechanism for the magical number 4: competitive interactions and non-linear oscillations. Behav. Brain Sci. 24, 151–152.

Waugh, N., Norman, D., 1965. Primary memory. Psychol. Rev. 72, 89–104.

Woodin, M. A., Ganguly, K., Poo, M.-M., 2006. Coincident pre- and postsynaptic activity modifies GABAergic synapses by postsynaptic changes in Cl^- transporter activity. Neuron 39, 807–820.