Intracortical vs thalamocortical processing of spatial working memory

Yoshinori Tabuchi, Shoji Tanaka*

Department of Electrical and Electronics Engineering, Sophia University

7-1 Kioicho, Chiyoda-ku, Tokyo 102, Japan

October 2002

Abstract

Working memory processes contain not only maintenance but manipulation of the working memory contents. The system of the mediodorsal (MD) nucleus and the prefrontal cortex is considered to contribute to some aspects of the working memory processes. This article studies computationally the characteristics of the integrated cortical and thalamocortical system. The model circuit is operated in the "thalamocortical mode", in which the thalamocortical inputs can control the cortical working memory representation. Our simulation shows that transient excitatory inputs to the MD relay cells can erase the working memory representation through the intracortical processes, especially the cross-directional inhibition.

Keywords: Corticothalamic; Delay-period activity; Intracortical; Spatial working memory; Thalamocortical

---

* Tel: +81-3-3238-3331, Fax: +81-3-3238-3321

E-mail address: tanaka-s@sophia.ac.jp

1. Introduction

The characteristics of the prefrontal cortical (PFC) circuits for working memory have been investigated intensively [1-3,8-12,14]. However, working memory would not be processed only in the PFC circuits; other cortical areas and subcortical structures are also considered to be involved in working memory processing. Among these, the cortico-thalamocortical system of the PFC and the mediodorsal nucleus (MD) would be important because these areas are reciprocally connected [4]. It is, therefore, interesting to investigate how this system contributes to working memory. To do so, we have constructed a model cortico-thalamocortical system. This model contains the intracortical circuits, the corticothalamic feedback connections, the intrathalamic local circuits, and the thalamocortical feedforward connections. In this article, the characteristics of these circuits are investigated by computer simulation of the model circuit. This article focuses on spatial working memory, so that neuronal activities in the model have selectivity in the directional space.

2. Model

The cortical model has three layers (the superficial, intermediate, and deep layers) and contains 1080 pyramidal cells (360 in each layer) and 240 interneurons [5,7,8-12,15]. The MD model contains 36 relay cells and 36 interneurons. The architecture of the model is shown in Fig. 1. The pyramidal cells in the deep layer send feedback projections to the MD relay cells and interneurons. The interneurons have local inhibitory connections with the relay cells. The relay cells, in turn, send the thalamocortical projections to the pyramidal cells in the intermediate layer of the PFC. The neurons are described by a leaky integrate-and-fire neuron model. The ion channels include: AMPA, NMDA, Nap, $GABA_A$, K(Ca), and leak. The ratio of the NMDA conductance to the AMPA conductance is $g_{NMDA}/g_{AMPA} = 0.05$ and the ratio of the cross-directional inhibition to the isodirectional inhibition [10-12] is $g_{GABAA,cross}/g_{GABAA,iso}$

= 0.36.

/ Fig. 1 /

3. Results

Omni-directional inputs to MD cells

We tested four types of transient, omni-directional inputs to the MD cells: (1) an excitatory input to the MD relay cells, (2) an inhibitory input to the MD relay cells, (3) an excitatory input to the MD interneurons, and (4) an inhibitory input to the MD interneurons. Because of the local connections in the MD, inputs to the MD interneurons influence the activity of the MD relay cells. For example, the inhibitory input to the MD interneurons disinhibits the MD relay cells. In general, both the excitatory and inhibitory inputs tend to terminate the sustained activity in the PFC. But the dynamics responding to the thalamocortical inputs are significantly different. We report, in the following, the case of (1) because it contains interesting but somewhat paradoxical results.

Cortical and thalamic activity

The MD relay cells respond to the transient input (Fig. 2). The activity of the MD relay cells is transmitted to the cortical pyramidal cells in the superficial layer. As a result, the working memory representation changes significantly by receiving the input. The excitatory input to the MD relay cells increases briefly the activity of all the cortical neurons that receive the inputs. That is, the intermediate layer exhibits omnidirectional activity by reflecting the thalamocortical input. This activity turns off the sustained activities in the superficial and the deep layers. This is due to the intracortical inhibition, because the cortical interneurons show transient increase in the firing rates during the thalamocortical-input period (1200-1300 ms). The activity profiles of the model neurons are shown in Fig. 3.

/ Fig. 2 /

/ Fig. 3 /

4. Discussion

Thalamocortical mode

This cortical model has strong excitatory projections from the intermediate layer to the superficial layer [8-13]. These projections amplify the activity, by which the transient activity in the intermediate layer is converted to the sustained activity in the superficial layer. This study suggests two interesting features in the processing of the cortical neuronal activity. First, the thalamocortical inputs assist the sustainment of the delay-period activity. We call this mode of operation the "thalamocortical mode". In this mode, the thalamic neurons, receiving sustained inputs from the cortical neurons in the deep layer, are activated tonically and forward the tonic inputs to the intermediate layer of the cortex. Although the firing rates of the neurons in the intermediate layer are fairly low during the first delay period, there is transmission of signals from the intermediate to the superficial layer. When blocked the thalamocortical inputs, the activity of the cortical neurons does not sustain any longer.

Intracortical inhibition

The second interesting feature is that the intracortical inhibition works effectively when the cortex receives omni-directional excitatory inputs. In this model, the thalamocortical projections terminate on the pyramidal cells in the intermediate layer and the interneurons. Then, the thalamocortical inputs activate both the excitatory and inhibitory circuits. Note, however, that the strength of the thalamocortical projections to the interneurons is 0.21 relative to that to the pyramidal cell. Nevertheless, the intracortical inhibition terminates the sustained activity. Slight change in the strength of the intracortical inhibition alters the

4

cortical dynamics significantly (not shown). This suggests that the regulation of the intracortical inhibition is critical to the control of the cortical dynamics [6,10-13]. In the case presented here, the cross-directional inhibition plays more important roles in the termination of the sustained activity because many neurons activated during the MD-input period exert inhibitory influences through the cross-directional inhibitory circuits. The intracortical inhibition and the intrathalamic inhibition contributing to multi-target spatial working memory processes are argued by Miyashita et al. [6].

Acknowledgement

References

[1]   N. Brunel, X.-J. Wang, Effects of neuromodulation in a cortical network model of object working memory dominated by recurrent inhibition, J Comput Neurosci 11 (2001) 63-85.

[2]   A. Compte, N. Brunel, P.S. Goldman-Rakic, X.-J. Wang, Synaptic Mechanisms and Network Dynamics Underlying Spatial Working Memory in a Cortical Network Model., Cereb Cortex 10 (2000) 910-923.

[3]   D. Durstewitz, J.K. Seamans, T.J. Sejnowski, Neurocomputational models of working memory, Nature Neurosci. 3 (2000) 1184-1191.

[4]   M. Giguere, P.S. Goldman-Rakic, Mediodorsal nucleus: areal, laminar, and tangential distribution of afferents and efferents in the frontal lobe of rhesus monkeys, J Comp. Neurol. 277 (1988) 195-213.

[5]   M. Iida, S. Tanaka, Postsynaptic current analysis of a model prefrontal cortical circuit for multi-target spatial working memory, Neurocomputing 44-46 (2002) 855-861.

[6]   S. Miyashita, Y. Tabuchi, S. Tanaka, Cortico-thalamocortical operations of multi-target spatial working memory, Neurocomputing, this issue.

[7]   K. Morooka, S. Tanaka, Correlation analysis of signal flow in a model prefrontal cortical circuit representing multiple target locations, Neurocomputing 44-46 (2002) 541-548.

[8]   S. Tanaka, Architecture and dynamics of the primate prefrontal cortical circuit for spatial working memory, Neural Networks 12 (1999) 1007-1020.

[9]   S. Tanaka, Post-cue activity of prefrontal cortical neurons controlled by local inhibition, Neurocomputing 32-33 (2000) 563-572.

[10]   S. Tanaka, Computational approaches to the architecture and operations of the prefrontal cortical circuit for working memory [Review], Prog. Neuro-Psychopharm. Biol. Psychiat. 25 (2001) 259-281.

[11]   S. Tanaka, Multi-directional representation of spatial working memory in a model

prefrontal cortical circuit, Neurocomputing, 44-46 (2002) 1001-1008.

[12] S. Tanaka, Dopamine controls fundamental cognitive operations of multi-target spatial working memory, Neural Networks, 15 (2002) 573-582.

[13] S. Tanaka, A. Yoshida, Signal flow in a prefrontal cortical circuit model for working memory loading, Neurocomputing 38-40 (2001) 957-964.

[14] X.-J. Wang, Synaptic reverberation underlying mnemonic persistent activity, Trends Neurosci. 24 (2001) 455-463.

[15] K. Yamashita, S. Tanaka, Circuit simulation of memory field modulation by dopamine D1 receptor activation, Neurocomputing 44-46 (2002) 1035-1042.

Figure legends

Fig. 1. Model architecture with the spatio-temporal profiles of the neuronal activities. The pyramidal cells in the deep layer of the PFC send feedback projections to the MD cells (both the relay cells and the interneurons). The MD relay cells send feedforward projections to the pyramidal cells in the intermediate layer and the inhibitory interneurons of the PFC. The thalamocortical projections to the interneurons is weaker than those to the pyramidal cells (the ratio is 0.21). The input, cueing the target location, is given to the pyramidal cells in the intermediate layer of the PFC. A transient, omnidirectional input is given to the MD relay cells.

Fig. 2. Raster plots and the population activities of the neurons in the PFC and the MD. **A**: the pyramidal cells in the superficial layer of the PFC, **B**: the pyramidal cells in the intermediate layer of the PFC, **C**: the pyramidal cells in the deep layer of the PFC, **D**: the isodirectional inhibitory interneurons, **E**: the cross-directional inhibitory interneurons, **F**: the MD relay cells, **G**: the MD inhibitory interneurons. The input, cueing the target location, is given to the pyramidal cells in the intermediate layer of the PFC during 200-300 ms. The MD relay cells receive a transient omnidirectional during 1200-1300 ms. The time bin for the population activity is 10 ms. The figure shows transient activity at the beginning of the simulation ($0 < t < 30$ ms), whish is irrelevant to the processes studied here.

Fig. 3. Activity profiles of the neurons in the PFC and the MD. **A**: the pyramidal cells in the superficial layer of the PFC, **B**: the pyramidal cells in the intermediate layer of the PFC, **C**: the pyramidal cells in the deep layer of the PFC, **D**: the isodirectional inhibitory interneurons, **E**: the cross-directional inhibitory interneurons, **F**: the MD relay cells, **G**: the MD inhibitory interneurons. Thick solid lines: the activity profiles averaged over the first delay period (300-1200 ms), thin solid lines: the activity profiles averaged over the MD-input period (1200-1300 ms), broken lines: the activity profiles averaged over the second delay period (1300-2000 ms).

Author biosketch

Yoshinori Tabuchi

received B.E. from Sophia University, Tokyo, in 2002. He is a graduate student at Sophia University. He is currently studying neuroscience and electrical engineering.

Shoji Tanaka

received B.E., M.E., and Ph.D. degrees from Nagoya University, Japan. He is Professor at Department of Electrical and Electronics Engineering, Sophia University. During 1998-1999, he was a Visiting Science at the Section of Neurobiology, Yale University School of Medicine, USA.

Pyramidal cells in the superficial layer

Isodirectional inh. Interneurons

Pyramidal cells in the intermediate layer

Cross-directional inh. Interneurons

Cue

Pyramidal cells in the deep layer

PFC

MD relay cells

MD interneurons
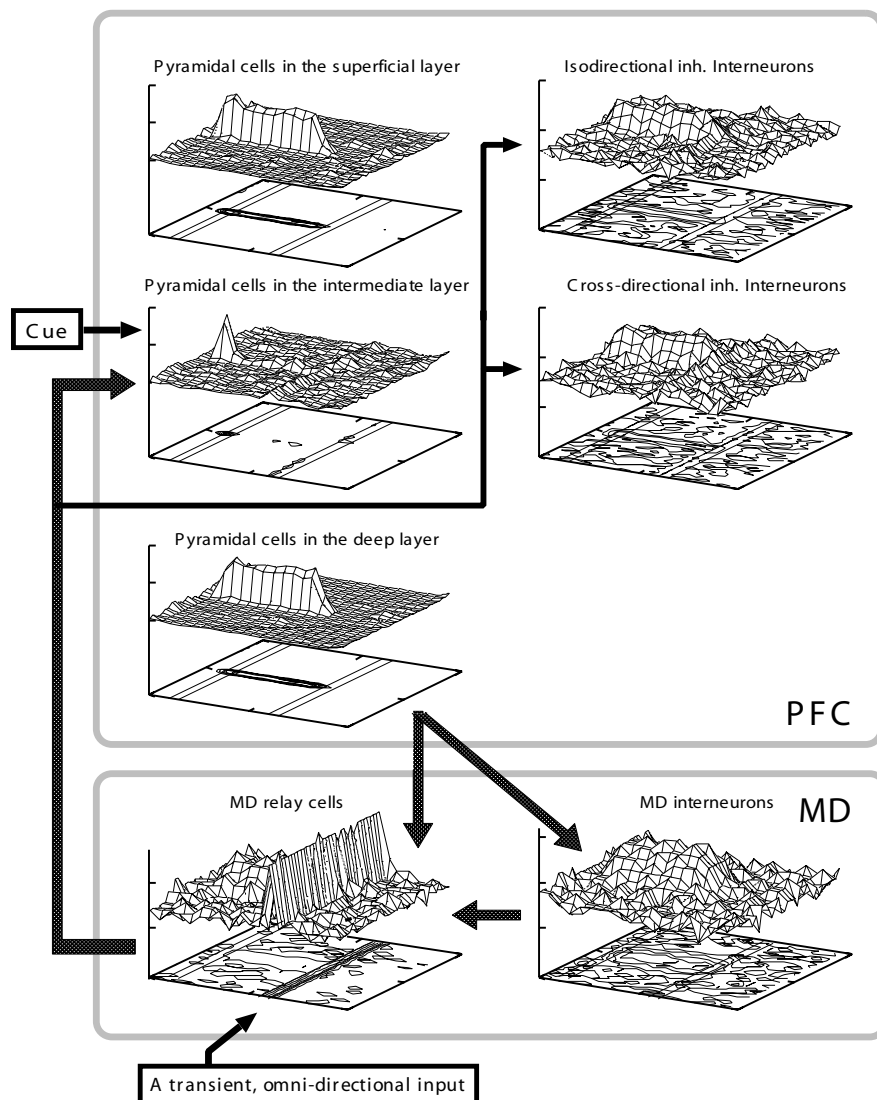
MD

A transient, omni-directional input
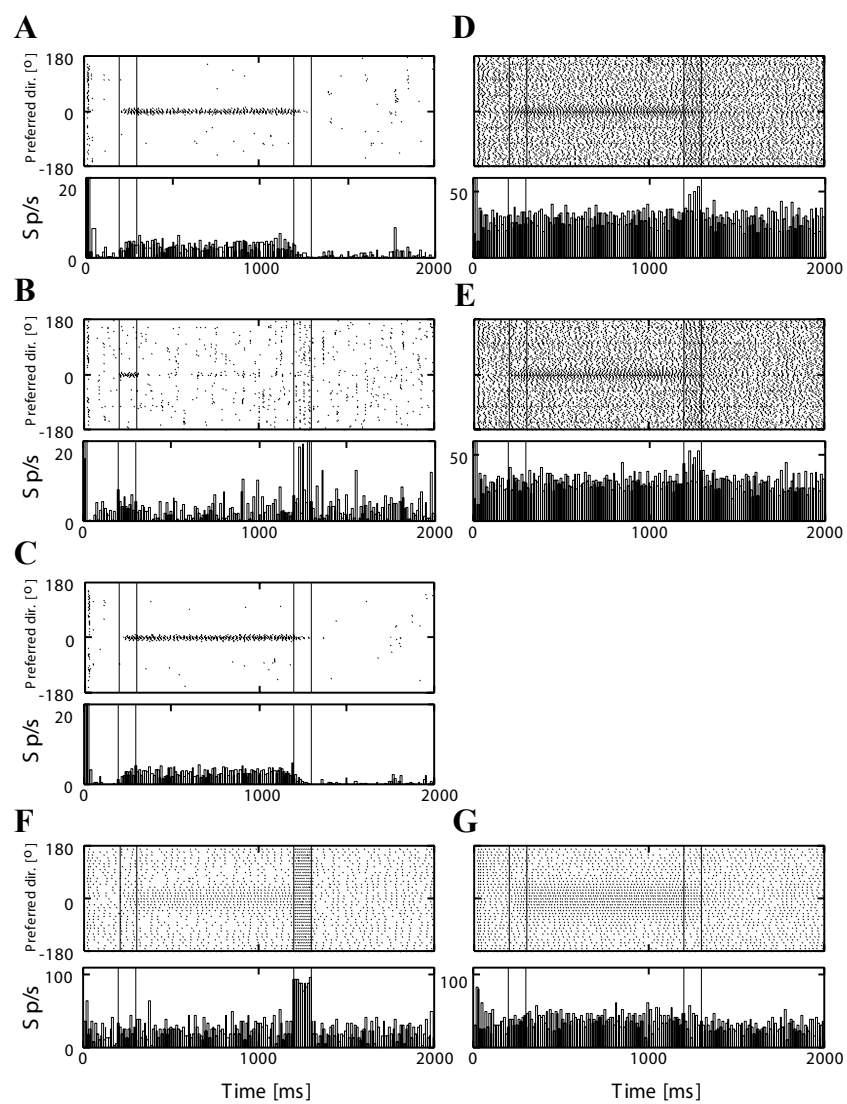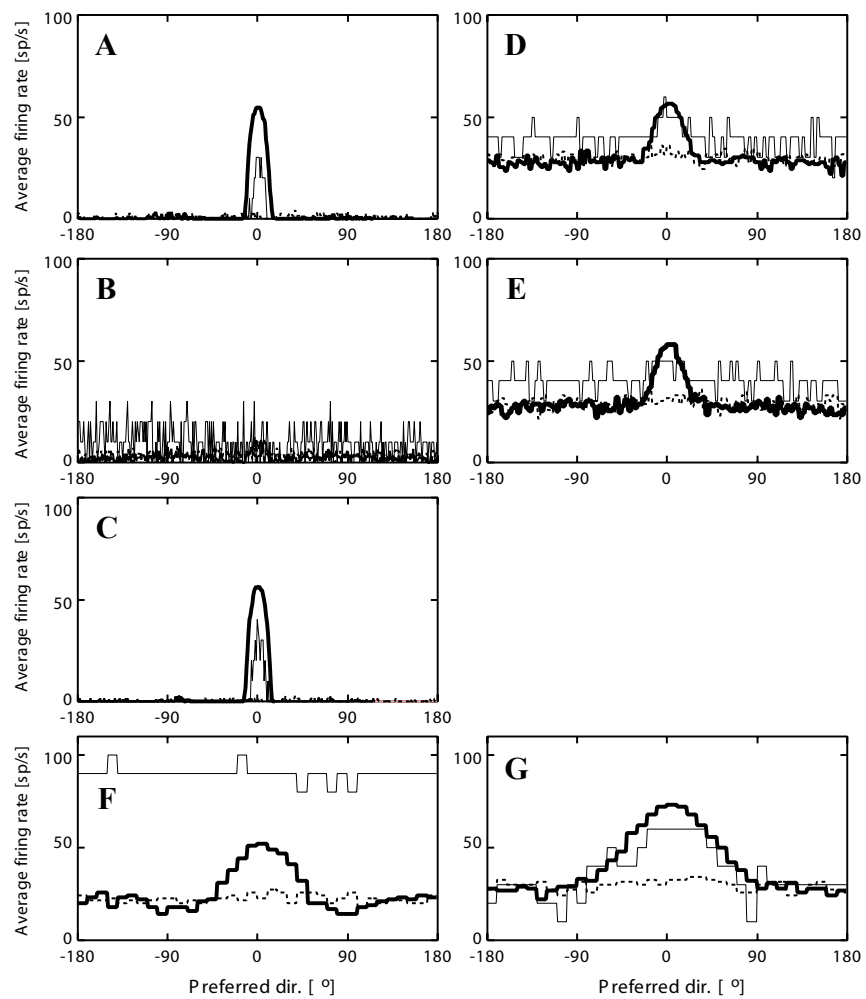
Fig.1 Tabuchi & Tanaka (fill width)

Fig.2. Tabuchi & Tanaka (full width)

Fig.3. Tabuchi & Tanaka (full width)