Intracortical vs thalamocortical processing of spatial working memory

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Abstract

Working memory processes contain not only its maintenance but manipulation of the contents. The thalamocortical system of the mediodorsal nucleus and the prefrontal cortex could contribute to some aspects of working memory processing. This article studies computationally the characteristics of the integrated cortical and thalamocortical system. We propose here that this system has two modes for the operations of working memory. In the intracortical mode, the recurrent excitation works effectively to maintain working memory. The representation is robust against the thalamocortical inputs. On the contrary, the thalamocortical mode would be useful to change the working memory representation.

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

Introduction

The characteristics of the prefrontal cortical (PFC) circuits for working memory have been investigated intensively (Brunel 2000; Compte et al. 2000; Tanaka 1999, 2000, 2001, 2002; Wang 2001). However, working memory would not be processed only in the PFC circuits. Other cortical areas and subcortical structures are 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 with glutamate transmission. This closed-loop circuit could contribute to the formation and maintenance of working memory. It is, therefore, interesting to investigate how this system contributes to working memory. To do so, we have recently proposed a model cortico-thalamocortical system (Tabuchi and Tanaka, submitted). This model contains the intracortical circuits, the corticothalamic feedback connections, the intrathalamic local circuits, and the thalamocortical 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.

Model

Circuitry
The cortical model has three layers (the superficial, intermediate, and deep layers) and contains pyramidal cells and interneurons (Iida and Tanaka 2002; Morooka and Tanaka 2002; Tanaka 1999, 2000, 2001, 2002; Yamashita and Tanaka 2002). The neurons are described by a leaky integrate-and-fire neuron model. The ion channels include: AMPA, NMDA, Nap, GABAA, K(Ca), and leak. 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 superficial layer of the PFC.

Directional selectivity of MD cells
This model assumes either directional selectivity or non-directional selectivity of the MD neurons. Unit recording from macaque brains reported that there are significant numbers of MD cells with omni-directional properties (Watanabe and Funahashi 2002). It is, therefore, interesting to see if the circuit has beneficial properties for both cases.

Circuit-specific modulation of synaptic transmission
Our model with variable ionic conductances takes into account the circuit-specific modulations of the synaptic transmission. Both the AMPA- and NMDA-channel conductances are assumed to be modulated. When these conductances in the intracortical circuit are increased, the dynamics tends to be switched to the intracortical mode. Increasing the conductances in the thalamocortical circuit tends to switch the dynamics to the TC thalamocortical mode.

Results

Omni-directional inputs to MD cells
We tested four types of transient, omni-directional inputs to MD cells: (1) excitatory input to the MD relay cells, (2) inhibitory input to the MD relay cells, (3) excitatory input to the MD interneurons, and (4) inhibitory input to the MD interneurons. Because of local circuit 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.

Intracortical mode
The cortical neurons respond to the transient thalamocortical inputs (of four types, defined in the last subsection). The activity of the MD relay cells is transmitted to the cortical pyramidal cells in the superficial layer. However, the responses of the cortical neurons to the thalamocortical inputs are weak and transient because, in the intracortical mode, the intracortical signal transmission dominates over the cortico-thalamocortical transmission. In this case, the cortical working memory representation remains unchanged with slight perturbation just after receiving the thalamocortical input.

Thalamocortical mode
The cortical neurons tend to accept the thalamocortical inputs in the thalamocortical mode. As a result, the working memory representation changes significantly by receiving the inputs. In general, the inputs tend to terminate the sustained activity in the PFC. Excitatory input to the MD relay cells increases briefly the activity of virtually of all the cortical neurons that receive the inputs. Then all the cortical neurons suddenly stop firing. Inhibitory input to the MD relay cells, on the contrary, suppresses the activity of the cortical cells. But the suppression is incomplete. In this case, the sustained activity of the cortical neurons

terminates after receiving the thalamocortical input without significantly affecting the activity of the cortical neurons that are not representing the working memory.

Discussion

Mode switching

We have suggested that there exist two modes of the dynamics of the PFC interacting with the MD. The intracortical mode is robust against thalamocortical inputs. It well maintains the working memory representation. On the other hand, the thalamocortical mode accepts thalamocortical inputs. This mode is useful when the working memory content is to be changed or erased. There could at least be four types of input to the MD, all of which have anatomical possibilities. Moreover, one of the possible sources of the excitatory input would be a cortical area (the cortico-thalamocortical system), while the inhibitory input would come form the globus pallidus (the pallido-thalamocortical system). Both the cortical areas and the basal ganglia (Floresco et al. 1999; Kalivas et al. 2001) would contribute to working memory processing.

AMPA vs NMDA receptors

Recently, the change in this ratio was suggested to change fundamental operation modes for multi-target spatial working memory (Tanaka 2002; Yamashita and Tanaka 2002). It is, however, uncertain whether the intracortical synapses and the thalamocortical synapses have different ratios of the NMDA-channel conductance to the AMPA-channel conductances. This issue is to be studied.