Cortico-thalamocortical operations of multi-target spatial working memory

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Abstract

Working memory and attention are intimately related. Performing visuospatial working memory tasks with multiple targets, for example, requires attentional control, such as focused attention and selective attention, as well as other cognitive operations (Tanaka 2002). This article argues how these operations are performed in the cortical and cortico-thalamocortical circuits. In our model, attentional bias is assumed to be exerted via the thalamocortical system. The computer simulation explored the interaction of the thalamocortical input and the cortical representation of working memory. The results suggest that the circuit dynamics for various multi-target tasks require several different types of the thalamocortical bias.

Keywords: Corticothalamic; Multi-target; Selective attention; Spatial working memory; Thalamocortical

Introduction

There are intensive computational studies of the characteristics of the prefrontal cortical (PFC) circuits for working memory (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 would be important. This article investigates how this system contributes to working memory processing including attention. To do so, we here analyze a model cortico-thalamocortical system, which has been proposed recently (Tabuchi and Tanaka, submitted). This model contains the corticothalamic feedback connections, the intrathalamic local circuits, and the thalamocortical connections. The characteristics of these circuits are investigated by computer simulation with this model. This article focuses on multi-target spatial working memory and attention. Recently, Tanaka (2002) has suggested that the PFC circuit can perform fundamental cognitive operations of multiple targets. It would therefore be interesting to investigate how the cortico-thalamocortical system modifies the cortical representation of working memory.

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; Tabuchi and Tanaka, submitted; 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. Either excitatory or inhibitory input is given to the MD relay cells or interneurons. The inputs are either directionally tuned or untuned. 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.

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.

Multi-target tasks

We employed the following tasks for the simulation (Iida and Tanaka 2002; Morooka and Tanaka 2002; Tanaka 2002):
(a) Single target
(b) Multi target, simultaneous loading
(c) Multi target, sequential loading

Results

The activity of the MD relay cells is transmitted to the cortical pyramidal cells in the superficial layers. The cortical neurons respond to the transient thalamocortical inputs. The activity is processed intracortically in the PFC circuit, then the pyramidal cells in the deep layer feedback the signal to the MD relay cells and interneurons.

Replacement and rejection

Two targets were loaded sequentially in time. The first target was loaded successfully, but the response of the cortical neurons is not stereotyped. We simulated the response for different types of the input to the MD cells. With no bias, the cortical neurons rejected the second target. With omni-directional bias, on the contrary, the cortical neuron accepted the second target to replace the first target under a certain condition. Directionally-tuned bias made the representation more robust against other thalamocortical inputs. Therefore, it switched between the rejection and replacement by changing the time at which it was given.

Simultaneous loading of multiple targets

Six targets were loaded successfully, representing them simultaneously in the circuit. That is, six different populations of the cortical neurons were activated at the same time and the activity was sustained in the delay period. After the loading of six targets, several types of inputs were given to the MD relay cells or interneurons. The inputs were directionally tuned with the gaussian profiles. Both the inhibitory input to the MD relay cells and the excitatory input to the MD interneurons eliminated one or more of the targets (selective elimination). On the contrary, the excitatory input to the MD relay cells eliminated the non-selected targets. The activity of the selected target(s) sustained even after receiving the thalamocortical input.

Discussion

Operations of multiple targets

This study has shown that the model cortico-thalamocortical system performs several different processes of multiple targets. These processes include selective sustainment and selective elimination. Even broader inputs to the MD cells can process a selected target. By shifting the input in the directional space, the system can select any one or more of the targets. Moreover, the system can either accept or reject targets that are successively loaded. As results, the system updates the target information in one condition and sustains the older target information in another condition. These processes are switched by receiving different types of input to the MD cells.

Attentional control

Processing working memory requires attention. This type of attentional control may be exerted by the cortico-thalamocortical system. As the corticothalamic projections, both the monosynaptic one and the disynaptic one via another nucleus, such as the reticular thalamic nucleus, could be possible (Guillery et al. 2001; Montero 1999, 2000). The sources of the input to the thalamocortical system may be some subareas of the PFC. At present, it is unknown whether the source areas are the same with the areas in which the spatial working memory is maintained and processed. This issue is closely relevant to the debate about domain-specific processing vs. process-specific processing of working memory (Goldman-Rakic 1994, 1995; Rao et al. 1997; Rushworth et al. 1997; Ungerleider et al. 1998). More detailed analyses would be necessary for further understanding.