

Cortico-thalamocortical operations of multi-target spatial working memory

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October 2002

Neurocomputing

Abstract

Representation and manipulation of multiple target locations would be important aspects of spatial working memory [Tanaka 2002a, b]. It is, however, unknown how such processes are performed in the prefrontal cortical, corticocortical, and cortico-subcortical circuits. We here propose a model of the prefrontal cortical and cortico-thalamocortical circuits that represent and manipulate multiple targets. The simulation with this model shows that transient inputs to the thalamic relay cells increase the signal transmission of the thalamocortical afferents. This eliminates one or more of the targets represented in the prefrontal cortex. The number of the eliminated targets depends on the width of the directional tuning of the inputs to the relay cells.

Keywords: Mediodorsal nucleus; Multi-target; Selective; Spatial working memory; Thalamocortical

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1. Introduction

There are intensive computational studies of the characteristics of the prefrontal cortical (PFC) circuits for working memory [1-3,7-12]. Tanaka [10,11] has suggested that the PFC circuit can perform fundamental cognitive operations of multiple targets. Although the PFC, especially the dorsolateral part, plays central roles, other cortical areas and subcortical structures are considered to be involved in working memory processing. The computer simulation by Tabuchi and Tanaka [6] shows that thalamocortical inputs interact with the cortical circuits to cause interesting phenomena, such as elimination of working memory representation by excitatory thalamocortical inputs. It would, therefore, be interesting to investigate how the cortico-thalamocortical system manipulates multi-target representation of working memory. This article shows computer simulation of a model cortico-thalamocortical circuit. The PFC in this model loads six targets simultaneously and the representation is maintained during the delay period. The representation is manipulated by transient inputs to the thalamic relay cells at the end of the delay period.

2. Model

Circuitry

The cortical model has three layers (the superficial, intermediate, and deep layers) and contains 1080 pyramidal cells and 240 interneurons [4,5,7-11,13]. The MD contains 36 relay cells and 36 inhibitory interneurons. 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 excitatory conductance ratio is $g_{\text{NMDA}}/g_{\text{AMPA}} = 0.0575$. The intracortical inhibitory circuits are assumed to have two subtypes: the isodirectional and the cross-directional [9-11]. The conductance ratio of these circuits is $g_{\text{GABAA,cross}}/g_{\text{GABAA,iso}} = 0.31$. Fig. 1A shows the architecture of the model. The pyramidal cells in the deep layer send feedback projections to the MD relay cells and the 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 and the interneurons of the PFC with the same synaptic weights. The pyramidal cells in the intermediate layer of the PFC receive the cue-

related inputs. The inputs cue the location of the six targets to load and maintain during the delay period (Fig. 1B). The MD relay cells receive the transient excitatory inputs at the end of the delay period. These inputs are directionally tuned.

/ Fig. 1 /

3. Results

The activity of the MD relay cells is transmitted to the cortical pyramidal cells in the intermediate layer. The cortical neurons respond to the transient thalamocortical inputs. The activity is processed intracortically in the PFC, then the pyramidal cells in the deep layer feedback the signal to the MD neurons. Although the pyramidal cells in the deep layer send feedback projections to the relay cells as well as the interneurons in the MD, the projections to the relay cells are assumed to be weak in this model. To clarify the roles of the thalamic interneurons, we show below the simulation under the condition that only the interneurons receive the feedback signals.

Simultaneous loading of multiple targets

Six targets were loaded successfully by receiving cue-related inputs. That is, six different populations of the cortical neurons were activated at the same time and the activity was sustained during the delay period. At the end of the delay period, the MD relay cells received transient excitatory inputs. Depending on the sharpness of the directionally tuned transient input to the MD relay cells, some of the represented targets were eliminated.

Selective elimination of target representation

The transient inputs to the MD with sharp directional tuning selectively eliminated one of the six targets represented in the PFC (Fig. 2). The target eliminated in this simulation is in the direction of 180 deg because the transient inputs had the peak at 180 deg in the directional space. The remaining five targets were continuously represented after the termination of the transient inputs.

/ Fig. 2 /

Non-selective elimination of target representation

As the directional tuning of the transient inputs to the MD increases, more targets were eliminated by the inputs. When it was 90 deg, all of the six targets were eliminated as soon as the transient inputs were given (Fig. 3). During this inputs, the MD relay cells increased their firing rates transiently (Fig. 3F). Before that, the MD relay cells fired at low rates. The firing rates of the MD relay cells after the transient inputs became higher than those before. This is due to disinhibition of the MD relay cells (see the raster of the MD interneurons in Fig. 3G). The interneurons fired at higher rates in the delay period because they received stronger feedback from the PFC representing the six targets. The firing rates of the MD interneurons became lower after the elimination of the target representation due to weaker feedback inputs from the PFC to the MD interneurons.

/ Fig. 3 /

4. Discussion

The PFC can represent multiple targets as working memory. However, how the representation is manipulated is unknown yet. This article studied the capability of the cortico-thalamocortical system to manipulate multi-target spatial working memory. The simulations showed that transient inputs to the MD relay cells eliminate some of the targets represented in the PFC. The selectivity depends on the sharpness of the directional tuning of the inputs. Sharply tuned inputs can eliminate only one of the six targets represented in the PFC. Broadly tuned inputs, on the contrary, eliminate all of the targets. These selective/non-selective processes of the spatial working memory would be generally used in cognitive operations.

This study suggests three important issues on the inhibitory actions in multi-target working memory processes. First, multiple target representation owes to the regulation of the local inhibition because there is competition between targets [10,11]. The cross-directional inhibition mediates this competition in this model. The regulation of the inhibition becomes more and more critical as the number of representing targets increases.

Secondly, it is the intracortical inhibition that extinguishes one or more of the targets represented in the PFC. This is interesting because the thalamocortical afferents convey excitatory signals to the pyramidal cells and the interneurons in the PFC. For the selective elimination, the isodirectional inhibition works predominantly because the inputs are given to the population of neurons representing the target to be eliminated. For the non-selective elimination, on the contrary, both the iso- and the cross-directional inhibition work concurrently to eliminate all of the targets represented. The summated effects are so strong that the elimination of the representation is very quick as Fig. 3 shows.

Thirdly, the MD interneurons play important roles in this mode of the operation of the circuit. By receiving the feedback signals from the deep layer of the PFC, these interneurons tonically inhibit the MD relay cells in this model. As a result, the MD relay cells fire at low rates during the delay period. This is necessary because, otherwise, the thalamocortical inputs destroy the working memory representation in the PFC. After the elimination, the feedback to the MD interneurons becomes lower, then the interneurons become less active. This disinhibits the MD relay cells, then the thalamocortical afferents send stronger inputs (Fig. 3). The PFC neurons thus show noticeable background activity after the elimination of the working memory. At this stage, the PFC becomes ready to load another working memory into itself.

Acknowledgement

This work was supported by the Grants-in-Aid for Scientific Research on Priority Areas (#13210123 and #14017083) from the Japanese Ministry of Education, Science, and Technology.

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Figure legends

Fig. 1. **A**: The circuit diagram of the model. Triangles in the PFC: the pyramidal cells, filled circle in the PFC: the inhibitory interneurons, triangle in the MD: the relay cells, filled circle in the MD: the inhibitory interneurons. See the text. **B**: Six targets represented in the model PFC. The directions of these targets are equally spaced.

Fig. 2. Raster plots of the neuronal spikes in the model. The cue-related inputs were given during 200-300 ms, followed by the delay period. The transient inputs to the MD were given during 1100-1200 ms. The inset shows the directional profile of the inputs, whose width was 10 deg (standard deviation). The figure shows transient activity at the beginning of the simulation ($0 < t < 50$ ms), which is irrelevant to the processes studied here.

Fig. 3. Raster plots of the neuronal spikes in the model. The cue-related inputs were given during 200-300 ms, followed by the delay period. The transient inputs to the MD were given during 1100-1200 ms. The inset shows the directional profile of the inputs, whose width was 90 deg (standard deviation). The figure shows transient activity at the beginning of the simulation ($0 < t < 50$ ms), which is irrelevant to the processes studied here.

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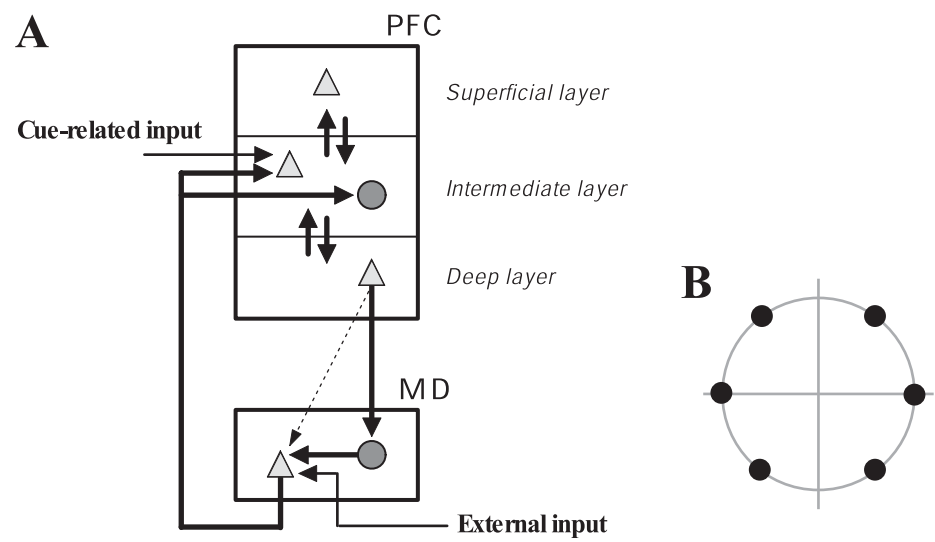


Fig. 1. Miyashita et al. (full width)

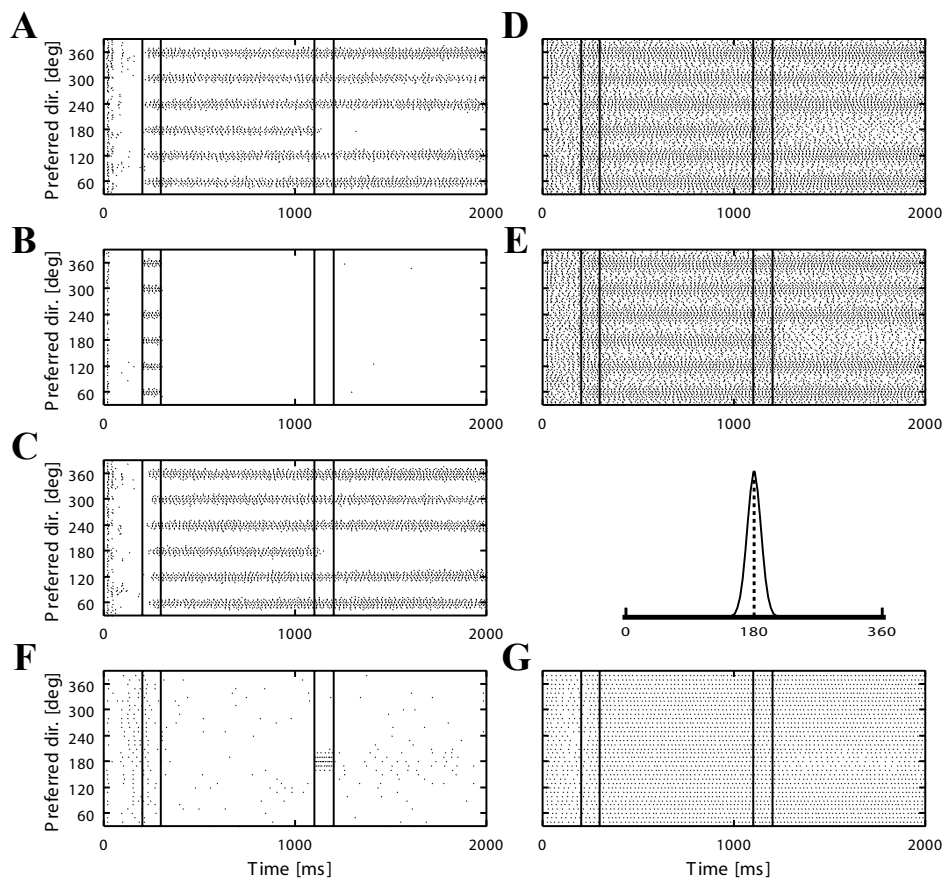


Fig. 2. Miyashita et al. (full width)

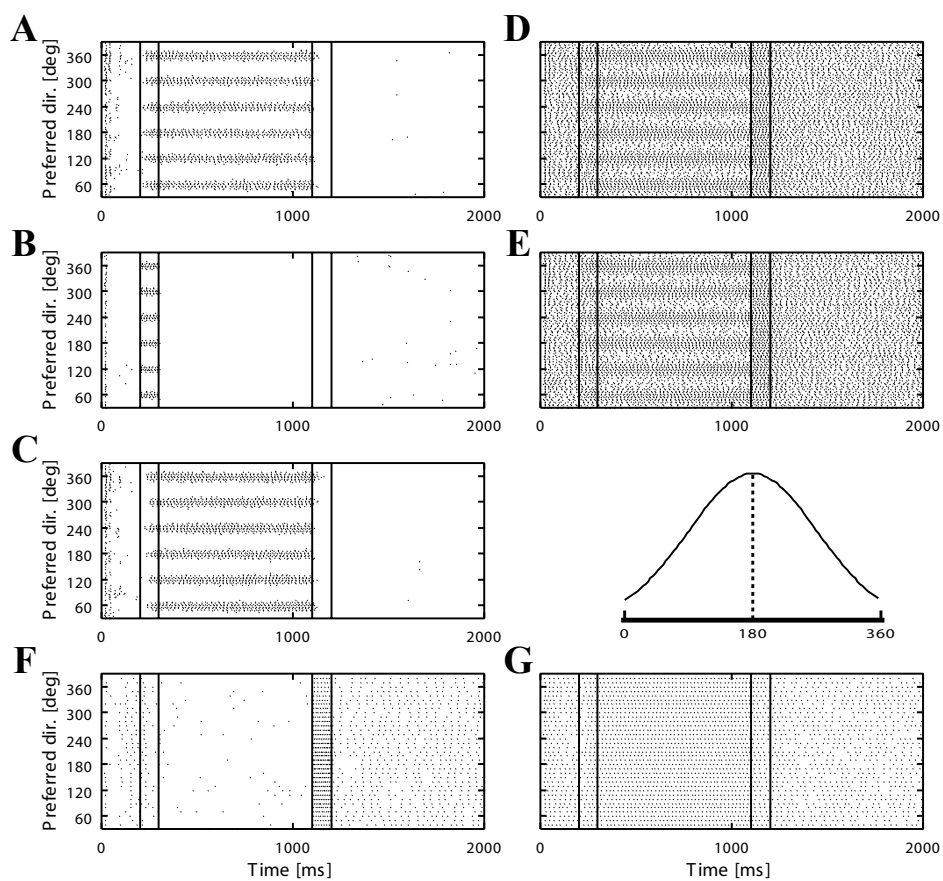


Fig. 3. Miyashita et al. (full width)