

A prefronto-parietal network model with feedforward and feedback connections

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Abstract

The cortical network of the prefrontal cortex (PFC) and the posterior parietal cortex (PPC) has been suggested to play central roles in visuospatial working memory processing and attention. However, how these areas contribute to such processes remains obscure. To investigate this, I here propose a layered network model of the prefrontal and posterior parietal cortices with feedforward/feedback-type corticocortical connections. Computer simulation with this model shows that the feedback and feedforward connections critically control the time course of the neuronal activity of the PFC and the PPC.

Keywords: Corticocortical; Feedback; Posterior parietal cortex; Prefrontal cortex;

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Introduction

The prefrontal cortex (PFC), with the assistance of neuromodulators, is considered to play central roles in cognition and working memory. The memory fields of spatial working memory in the PFC are modulated biphasically by dopamine over a wide range of the receptor activity [7,11]. This has been analyzed further by computer simulation [12]. However, how slight deviation of the dopamine level in the normal range alters the PFC circuit dynamics is unknown yet. Recently, Tanaka [10] addressed this issue via computer simulation of a model PFC circuit with dopamine effects. The results suggest the possibility that the PFC circuit performs several different modes of cognitive operations of multi-target spatial working memory, such as “replacement”, “addition”, “rejection”, and “elimination”. The study further suggests that these modes are switched from one to another by slightly changing the dopamine level.

For visuospatial working memory processing in general, both the PFC and the posterior parietal cortex (PPC) are activated. However, how these two areas contribute to the processing remains obscure. Chafee and Goldman-Rakic [3,4] observed very similar neuronal activities of these areas of macaque monkeys during performing a visuospatial working memory task. It is, therefore, interesting to know if the two areas contribute equally to visuospatial working memory processing or if each area has distinct roles in the processing. To answer these questions, the circuit properties of the PFC-PPC network have to be studied. This article proposes a network model of the PFC and the PPC that are connected with each other. Computer simulation with this model investigates how the feedforward and feedback connections between the PFC and the PPC contribute to spatial working memory loading and representation.

Model

The PFC and the PPC are connected intimately with each other by the corticocortical fibers [6]. Earlier anatomical studies in the sensory areas have proposed at least two typical

types of the corticocortical connectivity; i.e., the feedforward/feedback type and the lateral type [5]. Recently, this kind of study has extended to examine the connectivity between association areas, and has proposed a general rule of the laminar specificity of the corticocortical connections [2]. In this model, with some simplifications, the feedforward projections originate from the superficial layers of the PPC and terminate in the intermediate layer of the PFC and the feedback projections originate from the deep layers of the PFC and terminate in the superficial and deep layers of the PPC. Each of the model cortical area has three layers (the superficial, the intermediate, and the deep) and contains pyramidal cells and interneurons. The circuitry in each area is based on the earlier model developed by Tanaka [9,10].

The model contains 2160 pyramidal cells and 720 interneurons (2880 in all). The neurons are described by a single compartment, leaky integrate-and-fire neuron model, which contains the following types of conductance: AMPA, NMDA, Nap, GABA_A, K(Ca), and leak. The model neuron is identical to the previously developed model [9,10] but with several different parameter values: The transmission and synaptic delay is chosen randomly from 2.0 - 10.0 ms for the intracortical connections and 10.0 – 20.0 ms for the corticocortical connections. The ratio of the NMDA conductance to the AMPA conductance [9,10,12] is $g_{NMDA,max} / g_{AMPA,max} = 0.05$. The ratio of the cross-directional inhibition to the isodirectional inhibition [8, 9,10] is $g_{GABA_A(cross),max} / g_{GABA_A(iso),max} = 0.1$.

Results

The visual input conveying the target location is given to the neurons in the intermediate layer of the PPC. The input has a Gaussian directional profile with the standard deviation of 10° and transient increase in the probability of the arrival of Poisson-distributed action potentials [9,10]. The PPC neurons in the intermediate layer exhibit transient response to the input. This activity is transmitted through the intracortical circuit to the superficial layer and

then to the deep layers in the PPC. The activity is then transmitted to the intermediate layer of the PFC via the feedforward connections. The PFC neurons in the superficial and the deep layers exhibit tonic activity when the target information is successfully transmitted to the PFC.

The simulation was performed for the three cases with different strengths of the (feedforward, feedback) connections = (0.86, 1.0) in Case 1, (1.0, 0.65) in Case 2, and (1.0, 1.0) in Case 3. In Case A, the cue-related input caused only transient responses in all layers in the PPC and PFC. In this case, the weak feedforward connections make the PFC off-line from the sensory system. The time course of the neuronal activity and the activity profiles are shown in [Fig. 1A and B](#), respectively.

Increasing the strength of the feedforward connections allows the target information flow to reach the PFC, so that the PFC neurons exhibit prolonged activity ([Fig. 1C and D](#)). In Case 2, however, the PPC neurons receive insufficient feedback influences from the PFC because the relative strength of the feedback connections was decreased to 0.65. Then, the activity of the PPC neurons are weak especially for $t > 1200$ ms. The delay-period activity of the PFC neurons is also weak due to the insufficient reverberation of the signal between the PFC and the PPC in this case.

When the both corticocortical connections are strong enough, in Case 3, the neurons in both the PFC and the PPC show sustained activity in the delay period ([Fig. 1E and F](#)). Due to the strong recurrent excitation, the firing rates are increasing. But, being regulated by the local inhibition, the sustained activities of the PFC neurons have well-tuned directional selectivity, which is well-fitted by the Gaussian function. The onset of the tonic firing of the PFC cell lags behind the cells in the PPC by about 100 ms. The pyramidal cells in the intermediate layer of the PPC still exhibit phasic activity by directly receiving the cue input. The time course of the pyramidal cells in the intermediate layer of the PPC (dash-dot lines in [Fig. 1](#)) remains similar across the cases. This is because these neurons directly receive the external (cue-related) input and do not receive the feedback input so that the activity reflects direct response to the external input without being affected by the corticocortical processing.

Discussion

The rule proposed by Barbas and Rempel-Clower [2] predicts the layer specificity of the corticocortical connections between the areas whose laminar organization is specified. It predicts that, if the PPC in this model has sharper laminar borders than the PFC, the feedforward connections would originate mainly from the layers 2-3 of the PPC and terminate mainly in the layers 4-6 of the PFC. The feedback connections would originate mainly from the layers 5-6 of the PPC and terminate mainly in the layers 1-3 of the PPC. For simplicity, this model assumed that the corticocortical connections originate from either the superficial or the deep layer in this three-layer model. As for the termination of the corticocortical connections, the feedforward connections were assumed to terminate in the intermediate layer of the PFC. On the contrary, the feedback connections were assumed to terminate in both the superficial and the deep layers. This model is, therefore, compatible with both the ascending/descending scheme proposed by Felleman and Van Essen [5] and the rule proposed by Barbas and Rempel-Clower [2]. However, there are several reports that do not fit this model: (i) LIP neurons projecting to the PFC are predominantly in layer 3. They terminate in the superficial (or middle and deep) layers of the PFC [1]. (ii) Ipsilateral prefronto-parietal projections originate from mostly the layer 2/3 [8]. The actual corticocortical connections may depend on the subareas more specifically. Or they may differ across species to some extent. Because the model proposed here specifies neither the subareas (in the PFC and the PPC) nor the species, further arguments on the corticocortical connectivity is beyond the scope of this model.

An interesting notion suggested by this study is the capability of the cortical network to switch the activity pattern of the neurons between tonic and phasic by changing the strengths of the corticocortical connections. In its simplest view, the tonic activity with directional selectivity of PFC neurons is a substrate for the spatial working memory. Then keeping the activity of the PFC neurons tonic is necessary for loading spatial working memory in the PFC. In contrast, the switching of the activity from tonic to phasic can make the network not load spatial working memory. This is mediated by the feedforward connections in the network.

Weak feedforward connections make the PFC off-line from the sensory system. The feedback connections can have different roles. By boosting the activity of the PPC, both the PFC and the PPC exhibit concurrent working memory activity. Because the actual PFC is connected not only with the PPC but with downstream areas, this concurrent mode would be necessary for the PFC to exert top-down control of downstream areas. Taken together, changing the strengths of the feedforward and feedback connections alters the activity patterns or cortical dynamics modes of the PFC and the PPC qualitatively. It can further change the overall magnitudes of the activities of these areas quantitatively. The feedforward and feedback connections would thus change the signal flow in the cortical network to achieve cognitive control.

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Figure legend

Fig. 1. Time course of the neuronal activity and the activity profiles. **A** and **B**: Case 1; **C** and **D**: Case 2; **E** and **F**: Case 3 (see text). The time course was obtained by averaging the firing rates of the neurons whose preferred directions are close to the target direction (the difference being $<15^\circ$). The activity profiles were obtained by averaging the firing rate of each neuron during the delay period ($500 \text{ ms} \leq t \leq 2000 \text{ ms}$). Thick solid line: the pyramidal cells in the superficial layer of the PFC; solid line: the pyramidal cells in the superficial layer of the PPC; dash-dot line: the pyramidal cells in the intermediate layer of the PPC. The horizontal bars in the figure indicate the duration in which the input cueing the target direction was given.

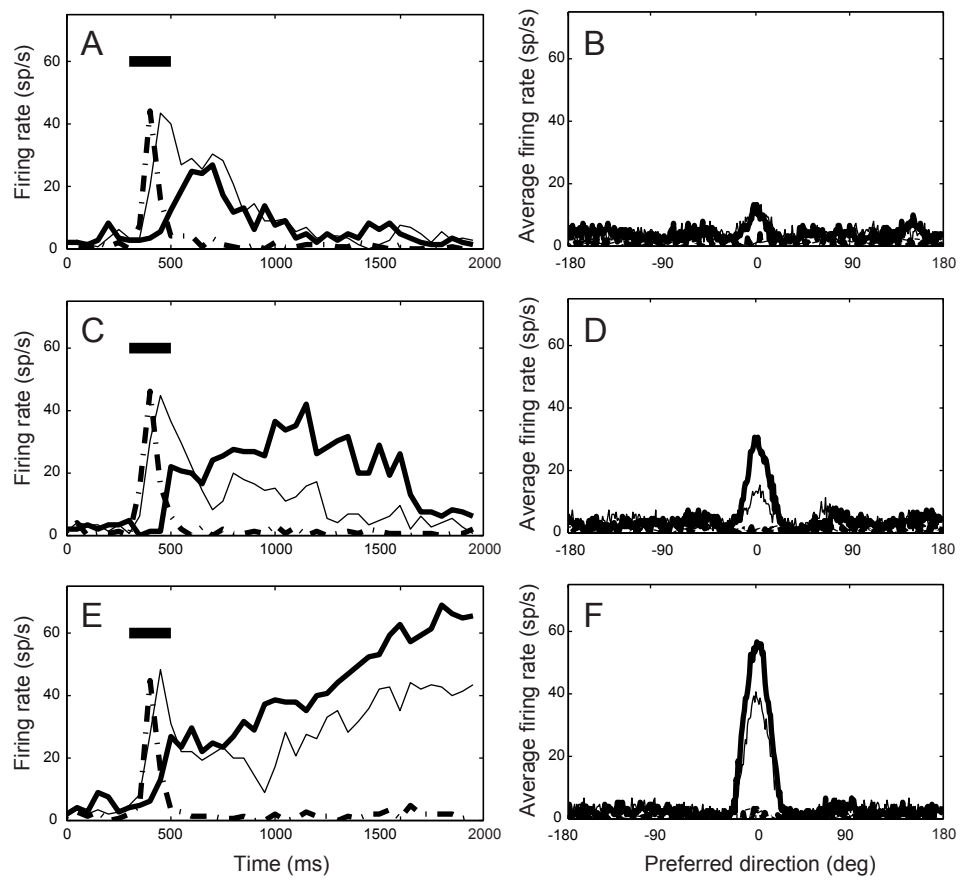


Fig.1. Tanaka