Modeling the interplay of short-term memory and the basal ganglia in sequence processing

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Abstract

In this paper, the cortico-basal ganglia-thalamic neural circuitry is modeled for sequence processing. Inspired by some experimental observations, a cortical memory system is assumed to encode the serial order of components by using its temporal activity patterns. An actual sequence can be decoded by cortico-subcortical loop neural circuits. It is suggested that the timing of decoding each component is arbitrarily adjusted by the subthalamic input to the internal globus pallidum. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

In a sequential movement, different actions are generated in an appropriate order. Moreover, each component can be generated at an arbitrary rate, whether the sequence has been learned extensively or not. In this study, a possible mechanism is proposed for the basal ganglia which are engaged in sequence processing [1–3]. Information on the serial order of actions, i.e., a motor plan, may be most conveniently represented by the temporal order of neuronal discharges. Therefore to store motor plans temporarily, this model employs a short-term memory system (STM) that shows dual oscillations [4]. In fact, there is evidence for the occurrence of dual oscillations in the cortical areas projecting to the basal ganglia. Plenz and Kitai [5] found in cortex-striatum-mesencephalon organotypic cultures that brief electrical stimulation...
stimulation of supragranular layers induces theta-nested gamma-frequency oscillations in local cortical neural networks. These activity patterns were very similar to those observed in corticostriatal neurons of anesthetized rats [6]. These experimental results encourage us to consider the possibility that dual oscillations are utilized in organizing behavior.

2. Network model

The neural circuitry of this model represents an array of closed loops connecting the striatum, internal globus pallidum (GPi) or substantia nigra pars compacta (SNr), thalamus and cortex. For simplicity, the activities of thalamic and cortical parts are represented by single units (Fig. 1). The striato-GPi/SNr and GPi/SNr-thalamic projections are inhibitory, while the thalamo-cortico-striatal projection is excitatory. The activities of $M$ basal ganglia-thalamo-cortical loops are described as

$$\tau_x \frac{dx_i}{dt} = -x_i + f_p(J_{ts}(z_i - z_0)),$$

$$\tau_y \frac{dy_i^{(l)}}{dt} = -y_i^{(l)} + I^t(I_p^{(l)} - J_{st}^{(l)}x_i - J_{st}^{(l)}y_i^{(l)} - I_I + I_{SN}),$$
using a sigmoid function $f_\beta$ with slope $\beta$ and a threshold-linear function $I^+$. In the above equations, $x$, $y^{(e)}$, $y^{(i)}$ and $z$ describe activities of striatum, internal globus pallidum, external globus pallidum and thalamic/cortical part, respectively. We call $x$’s $M$-cells. Eqs. (1)–(3) are analogue of the Wilson–Cowan equation, whereas Eq. (4) describes the winner-take-all competition [7] in the thalamus. As suggested by recent anatomical studies [8], direct inhibitory GPe–GPi projection is incorporated. On the other hand, the so-called indirect pathway of the basal ganglia is not incorporated, since its action may be similar to that of the direct GPe–GPi projection. It was suggested that subthalamo-striatal projection is diffusive rather than topographic [8].

In the present study, the simplest case that GPi neurons receive a common subthalamic input is considered. This, of course, does not mean to deny the existence of other arrays receiving different subthalamic inputs. Constant inputs $I^{in}$ make pallidal neurons tonically active in the absence of striatal inputs. $I^{in}$ represents the subthalamic input to GPi. The loops are assumed to be driven by the STM output which is relayed by another kind of striatal projection cells, S-cells (Fig. 1), modeled as integrate-and-fire neurons:

$$
\tau_y \frac{dV^S_i}{dt} = -V^S_i + V^S_{rest} + V^{in}_i, \quad i = 1, \ldots, M, \tag{5}
$$

$$
V^{in}_i(t) = \frac{V_i(t)}{\tau_x} (e^{-\frac{t - t_{j}}{\tau_x}} - e^{-\frac{t - t_{j}}{\tau_x}}), \tag{6}
$$

where $t_i$ stands for the time at which the ensemble of pyramidal cells projecting to the $i$th S-cell synchronously fires. If the $i$th S-cell fires at $t = t_i$, the efficacies of cortico-striatal synaptic transmissions at other S-cells are suppressed by the activation of presynaptic GABA$_B$ receptors as follows [9]:

$$
r_j(t) = 1 - e^{-\frac{t - t_j}{\tau_{GABA}}}, \quad j \neq i, \tag{7}
$$

where $\tau_{GABA} \approx 150$ ms. As a result, S-cells show a temporal competition [10] to select the earliest input spike in every theta cycle. The S-cell’s firing gives the following input to the corresponding loop circuit:

$$
I_i(t) = \frac{t - t_i}{\tau_x} e^{-\frac{t - t_i}{\tau_x}}, \quad i = 1, \ldots, M. \tag{8}
$$

The present model of STM essentially follows that proposed by Lisman and Idiart [4]. Therefore the mathematical details are not shown here.
3. Sequencing by the cortico-subcortical mutually inhibiting loops

The loops exhibit a bistable switching if $\beta$ is greater than a certain critical value which depends on the size of $M$. In a resting state, pallidal neurons are tonically active and suppress the thalamic activity. In a self-active state, the output of a $M$-cell continuously inhibits the GPi/SNr neuron that disinhibits the thalamic/cortical unit projecting to the same $M$-cell. A loop can enter the self-active state if the $S$-cell projecting to the loop is innervated by STM. Owing to the competition among $z$, more than one loop cannot be activated simultaneously. For a certain range of firing frequencies of $S$-cells, the self-activation within an active loop overwhelms the competitive effects from other loops. In this case a winner loop is unchanged with the changes in the $S$-cells’ activity patterns. The value of $v_{in}$ is adjusted so that this dynamical property is ensured. Thus, the subcortical activity for controlling the motor mechanisms of sequence generation can be dissociated from the changes in the cortical activity for planning and storing a sequence. A next loop can be activated only after $I_{STN}$ raises the global GPi/SNr activity to reset the thalamic competition (Fig. 2). Thus, the single subthalamic input determines the timing of switching components in sequence decoding.

Fig. 3a shows typical results of simulations for the model consisting of four loops. The loops are sequentially activated in the order specified by the STM activity. Once a component is introduced into the corresponding loop by firing of a pyramidal-cell ensemble, the ensemble is inhibited to eliminate the component from STM. This is because the component is of no further use. With the above prescription, STM always maintains the list of future components and, accordingly, $S$-cells prepare for the next component. As seen from the figure, active loops are switched according to this preparatory activity, when $I_{STN}$ signals the basal ganglia-thalamo-cortical loops to renew their state.

To show that components can always be decoded in the correct order, simulations were repeated while changing the phase of theta oscillation relative to the fixed times of subthalamic signals (Fig. 3b).
4. Summary

A flexible scheme of sequence processing through the cortico-subcortical interplay was described. In this scheme, only the serial order is stored cortically and the timing of decoding components is adjusted when they are actually decoded [11]. It is noted that the short-term memory proposed originally for the hippocampus [4] requires a decoding system such as described here, since the serial order is represented in the temporal range which is much shorter than the behaviorally relevant time scale. The proposed functions of the basal ganglia as a time translator possibly concern a wide class of sequence processing in higher cognitive functions.
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References


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