Neural Networks 81 (2016) 39–51

Contents lists available at ScienceDirect

Neural Networks

journal homepage: www.elsevier.com/locate/neunet

A neural model of the frontal eye fields with reward-based learning

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ARTICLE INFO

Article history:
Received 30 May 2015
Received in revised form 3 May 2016
Accepted 6 May 2016
Available online 24 May 2016

Keywords:
Decision-making
Task switching
Reward-based Hebbian learning
Direction-preferred population

ABSTRACT

Decision-making is a flexible process dependent on the accumulation of various kinds of information; however, the corresponding neural mechanisms are far from clear. We extended a layered model of the frontal eye field to a learning-based model, using computational simulations to explain the cognitive process of choice tasks. The core of this extended model has three aspects: direction-preferred populations that cluster together the neurons with the same orientation preference, rule modules that control different rule-dependent activities, and reward-based synaptic plasticity that modulates connections to flexibly change the decision according to task demands. After repeated attempts in a number of trials, the network successfully simulated three decision choice tasks: an anti-saccade task, a no-go task, and an associative task. We found that synaptic plasticity could modulate the competition of choices by suppressing erroneous choices while enhancing the correct (rewarding) choice. In addition, the trained model captured some properties exhibited in animal and human experiments, such as the latency of the reaction time distribution of anti-saccades, the stop signal mechanism for canceling a reflexive saccade, and the variation of latency to half-max selectivity. Furthermore, the trained model was capable of reproducing the re-learning procedures when switching tasks and reversing the cue-saccade association.

1. Introduction

Decision-making in the presence of multiple choices requires more than sensory signaling and motor response. Information accumulation and processing are also necessary for decision-making (Noorani, 2014; Salinas, 2004; Savine & Braver, 2010). Decision-making is a flexible process of integrating various forms of information, such as past experience and learning rules (Chaumon, Kveraga, Barrett, & Bar, 2014; Cutsuridis, Kumari, & Ettinger, 2014; Drugowitsch, Moreno-Bote, Churchland, Shadlen, & Pouget, 2012; Kan, Niel, & Dorris, 2012; Pleger et al., 2006). In an anti-saccade testing paradigm, which is an important tool for estimating frontal lobe dysfunction, trial-by-trial training can alter the visuomotor mapping of macaques and make them saccade to the opposite side against the reflexive response (Munoz & Everling, 2004). Based on this kind of flexibility, humans and other animals are capable of responding to a specific stimulus in different ways (Drea & Wallen, 1999; Platt & Glimcher, 1999).

The visuomotor choice tasks, such as the anti-saccade task and no-go task, have been widely used to investigate the cognitive process of decision-making, because a saccadic eye movement can readily represent the behavioral outcome (Hutton, 2008; Leathers & Olson, 2012; SchlagRey, Amador, Sanchez, & Schlag, 1997). These experiments study the process of accumulating experience and integrating information. The goal of these tasks is to perform planned eye movements in response to learned stimuli, and the decision is signaled to be correct by reward. At the end of a trial, rewards can be given based on the performance of this sensory-triggered activity, instructing animals to learn the “correct” visuomotor mappings and suppress the “erroneous” choices (Baldassarre et al., 2013; Blank, Biele, Heekeren, & Philiastides, 2013; Munoz & Everling, 2004). In other words, the brain will re-establish the link between the ongoing sensory signals and behavioral results, under the guidance of rewards (Brown, Bullock, & Grossberg, 2004; Luhmann, Chun, Yi, Lee, & Wang, 2008). Some experimental findings have emphasized the role of synaptic plasticity in the functional neural circuits in the frontal eye fields (FEF), which play a key role in oculomotor control of saccadic eye movements and visual attention. For example, Chen and Wise (1995b) observed learning-dependent and learning-selective activities in FEF. Bichot, Schall, and Thompson (1996) discovered a type of experience-dependent

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http://dx.doi.org/10.1016/j.neunet.2016.05.001
0893-6080/

plasticity that mediated the learning of arbitrary stimulus-action associations. Recent results present more evidence that learning in oculomotor behaviors involves FEF (Lee & Keller, 2008; Lewis, Baldassarre, Committeri, Romani, & Corbetta, 2009; Tseng et al., 2013). All these findings provide support for synaptic plasticity in FEF.

In this study, we extended the layered FEF model introduced by Heinzle, Hepp, and Martin (2007) into a learning-based model, shedding more light on the cognitive process of choice tasks. The modification of the model includes four aspects: (1) The recognition module and layer 6 were removed and the model could initially only cause a reflexive saccade (pro-saccade). (2) Two rule modules were added to the fixation input layer. These modules not only reserved the function of fixation neurons, but could also transform the color signal from V4 into rule-based control. Meanwhile, two functional units were divided out of layer 2/3 to represent the rule-dependent neurons that are controlled by the rule modules. Interestingly, the rule-preferred activity has been observed in FEF and other parts of the frontal cortex (Asaad, Rainer, & Miller, 2000; Everling & DeSouza, 2005; Everling & Munoz, 2000; Ferrera, Cohen, & Lee, 1999; Hasegawa, Peterson, & Goldberg, 2004; Hoshi, Shima, & Tanji, 1998; Johnston & Everling, 2006; Johnston, Levin, Koval, & Everling, 2007; White & Wise, 1999). In the work of Johnston, DeSouza, and Everling (2009), a mechanism based on two functional populations has been proposed to account for task selectivity in the prefrontal cortex. All these evidence support the rule module in our model. (3) The populations had direction preference, i.e. different populations in a layer preferred specific directions. Orientation selectivity in FEF has been extensively researched (Douglas, Martin, & Whitteridge, 1991; Hansel & van Vreeswijk, 2012; Hubel & Wiesel, 1959; Li & Creutzfeldt, 1984; Nowak, Sanchez-Vives, & McCormick, 2008; Ringach, Shapley, & Hawken, 2002; Schiller, Finlay, & Volman, 1976). Additionally, an increasing number of models have applied this property to distinct functional modules to simulate various physiological experiments (Ardid & Wang, 2013; Engel & Wang, 2011; Shushruth et al., 2012; Wu & Guo, 2011; Zirnsak, Beuth, & Hamker, 2011). (4) We assumed that the connections from layer 4 to layer 2/3 were plastic, employing reward-based Hebbian learning (Ardid & Wang, 2013; Engel & Wang, 2011; Pfeiffer, Nessler, Douglas, & Maass, 2010). In the present model, the connection between E4 and I23 which did not exist in the original model was considered to be weakly linked and plastic. These plastic synapses simulated the varying inputs to the neuronal population that was involved in the accumulation of sensory information, allowing decision-making to be guided by the associated values of the choices (Connolly, Bennur, & Gold, 2009; Gold & Shadlen, 2002, 2003; Gottlieb, Hayhoe, Hikosaka, & Rangel, 2014; Law & Gold, 2009).

In order to gain insight into the effect of the plasticity on controlling the oculomotor behaviors in FEF, we trained the extended model to simulate three different choice tasks: an anti-saccade task, a no-go task, and an associative task. The simulation results successfully accounted for the learning processes, and quantitatively exhibited the cognitive procedure of decision-making. They also could explain the relearning processes when tasks switched without an explicit cue. The extended model generalizes the learning mechanism to the saccade control in FEF so that it can choose or switch between multiple sensory-motor maps, suggesting that the plasticity plays an important role in flexibly controlling the saccade movements.

2. Method

2.1. Network architecture

The architecture of the learning-based FEF model is illustrated in Fig. 1(A). This extended model consists of interacting layers contributing to different functions: sensory processing in layer 4 (L4), attention allocating in layer 2/3 (L23), fixation input layer (FIX) and motor output in layer 5 (L5). L4 neurons process orientation-preferred visual input from early visual areas. L23 serves as an attention allocator as it transforms the sensory signal from L4 into the attention signal at a direction-preferred position. The activities of L23 neurons are similar to those of visuomotor neurons in FEF classified by Bruce and Goldberg (1985). Visuomotor neurons discharge both in response to visual signals and after the visual targets disappear. The response of visuomotor neurons can persist until the monkey makes a saccadic eye movement. Based on the winner-take-all competition and strong recurrent excitation, L23 neurons are able to reproduce these activities of visuomotor neurons. Strong synaptic weights from the excitatory pool in L5B to the inhibitory pool in L23 are required to suppress the L23 neurons when a saccade is made in the present model. L23 is divided into two task-relevant units L23L and L23R which are controlled by the rule neurons in FIX. In addition, we use two populations to simulate the rule neurons which transform the green and red color information from V4 into a rule signal in FIX (Fig. 1(C)). The third population in FIX only processes fixation input without color information. For the sake of simplicity, we have designed the network so that E23L and E23R are inhibited by the red and green rule neurons through connecting FIX to I23L and I23R, respectively. L5 is comprised of two types of neurons: ramping motor neurons (L5R) and burst motor neurons (L5B), which integrate attention signals and signal the motor output, respectively. The ramping activities of L5R are inhibited by FIX. Except FIX, each layer has 13 retinotopic positions which have their own preferred direction (Fig. 1(B)). It is noteworthy that a retinotopic position consists of a different number of neurons in different layers. In L4 and L23, each position contains 100 excitatory neurons and 25 inhibitory neurons, while L5 is composed of 40 excitatory and 25 inhibitory neurons. FIX has 100 neurons in each of the three excitatory populations, and 75 inhibitory neurons.

2.2. Neuronal dynamics

Each neuron is modeled as an integrate-and-fire model which is described by

$$\tau_m \frac{dV}{dt} = -V - g_{exc}(V - V_e) - g_{inh}(V - V_i) + I_{ext} \tag{1}$$

where V represents the membrane potential, τ_m is the membrane time constant, $\tau_m = 20$ ms in excitatory neurons and $\tau_m = 12$ ms in inhibitory neurons, and $V_e = 74$ mV, $V_i = -10$ mV denote the excitatory and inhibitory reversal potentials. The conductance g_{exc} and g_{inh} consist of three distinct parts $g_{e,i}$, g_{noise} and $g_{plastic}$ which represent synaptic conductance, noise input and the plastic synapse. The spiking threshold is 20 mV, and reset value is 10 mV. The absolute refractory period of excitatory and inhibitory neurons are 1.8 ms and 1.2 ms, respectively. First, the synaptic conductance is given by

$$\begin{aligned} g_{e,i}^{k\to j} &= \sum_{l} g_{kj} s_{e,i}^{k\to j} \\ \tau_{e,i} \frac{ds_{e,i}}{dt} &= -s_{e,i} \end{aligned} \tag{2}$$

where $s_{e,i}$ is the activation variable and $\tau_{e,i}$ is the time constant of excitatory and inhibitory synapses. Different connections are given different time constants: $\tau_{e,i} = 50$ ms in the connection E5R → E5R, $\tau_{e,i} = 10$ ms in the connections E23L → E23L, E23R → E23R, I5B → E5R, and $\tau_{e,i} = 5$ ms in the other connections. g_{kj} denotes the direction preference factor between neurons with preferred