Chapter 82
Superior Colliculus and Basal Ganglia Control the Saccadic Response in Motion Discrimination Tasks

Jiaxiang Zhang and Rafal Bogacz

Abstract Recent physiological studies suggest that in motion discrimination tasks, neurons in the lateral intraparietal (LIP) area integrate sensory evidence during decision making process by carrying persistent response selective to the saccadic response. LIP neurons also discharge at high frequency shortly before the saccade onset. We propose that the later response is due to the activity form the bursting neurons in the Superior Colliculus (SC). To test the hypothesis we developed a decision making model with populations of neurons in LIP, Basal Ganglia (BG) and SC where BG and SC process the threshold detection and action generation. The model successfully describes the LIP activity from the experiment, and is also consistent with the behavioral measurements.

Keywords LIP · basal ganglia · superior colliculus · decision making

Introduction

During perceptual decision making tasks a motor response is generated on the basis of sensory stimuli. Neurophysiological studies suggest that certain cortical areas integrate noisy sensory information over time to provide a more accurate decision, and once the accumulated evidence satisfies certain decision threshold, the integration process terminates and the decision is made by behavioral response [1]. Neural correlates of decision making are typically investigated in a two-alternative motion discrimination task [2, 3]. Subjects are shown a display of randomly moving-dots in which a fraction of dots move coherently to one direction (left or right). The task is to identify the direction of the majority of dots and make a saccadic eye movement towards this direction. The required time of response can be controlled by the experimenter or the subject itself, yielding two versions of the task: fixed-duration (FD) and free-response (FR), respectively, as illustrated in Fig. 82.1.

J. Zhang
Department of Computer Science, University of Bristol, Bristol BS8 1UB, UK
e-mail: Jx.Zhang@bristol.ac.uk

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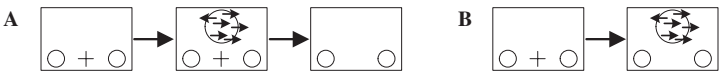

Fig. 82.1 Versions of the motion discrimination task: (a) fixed-duration (FD) and (b) free-response (FR). At the beginning of a trial a monkey is presented with a fixation point (cross) and two targets (circles). In FD the monkey has to fixate during stimulus presentation until the cross disappears, in FR it is free to make a saccade at any time

In single neuron recording data from both FD and FR tasks [2], most neurons in the lateral intraparietal (LIP) area exhibit persistent activity during motion viewing period, whose magnitude correlates with the motion strength. Indeed, LIP neurons accumulate information from sensory area (i.e., extrastriate visual cortex) to form the decision [3]. LIP neuron response also presents a stereotyped increase that is independent of motion strength in the final epoch ($\sim$ 100 ms) before the saccade. In RT task, it is thought to be a reflection of decision threshold crossing by many decision making model proposed so far. However, in FD task, since subjects have to render their decision during pre-fixed delay and keep it in the working memory, the final phase of LIP activity cannot be explained by threshold crossing.

In this work we describe the hypothesis that the increasing activity of LIP in FD task before saccade onset is a reflection of downstream activity from subcortical areas, i.e., basal ganglia (BG) and superior colliculus (SC). We design a population model involving cortical areas, BG and SC based on the existing knowledge of their connectivity. The model is consistent with both behavior and physiological data.

Proposed Decision Making Model

Our model describes three proceeding stages: accumulation of decision evidence from sensory input, threshold detection, and motor response generation. Each stage is mainly controlled by one cortical/subcortical area (Fig. 82.2a). In the first stage, two populations of LIP neurons implement a leaky-competing-accumulator network [4]. I.e., each population integrates input supporting one of the two alternatives, and competes with each other by lateral inhibition. Since the sensory information is biased to the correct alternative, the decision is determined by the winning LIP population which has higher mean firing rate.

The second stage is a mechanism that can detect whether the amount of evidence in LIP in favor of one alternative reaches a threshold and is ready to render a decision. The model applies a common concept that BG is involved in threshold detection [5]. Substantia nigra pars reticulate (SNr), the output nucleus of BG, sends high tonic inhibition to downstream areas to suppress any action response. When the striatum (STR) receives sufficient large excitatory input (e.g., from LIP), it inhibits SNr, and hence SNr decreases its inhibitory output to release downstream activity. In the model, a working memory (MEM) is proposed to effectively receive input from both LIP and SNr (possibly via the thalamus). When LIP activity reaches the threshold, the inhibitory input from SNr is removed and MEM caches the temporal

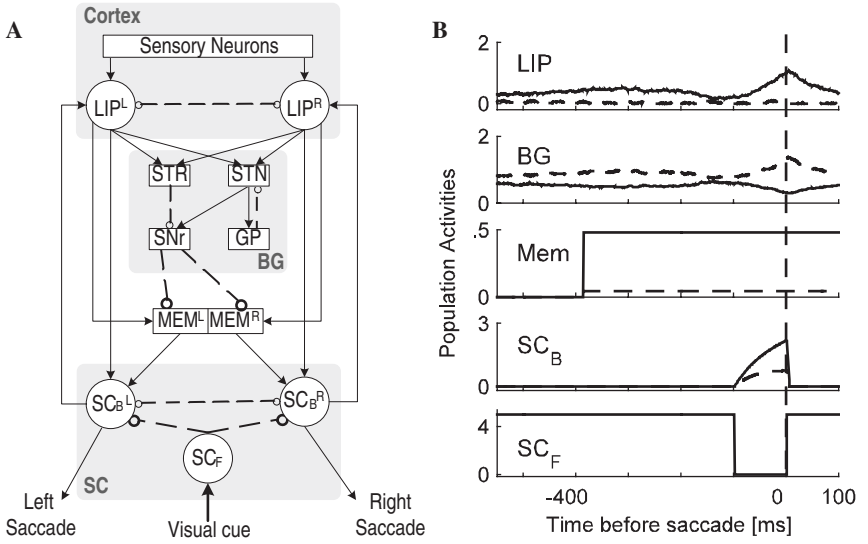

Fig. 82.2 Proposed model and its responses. (a) Schematic architecture. LIP populations send excitatory projections to BG, MEM, and SC_B. The bypass circuit in BG between subthalamic (STN) and globus pallidus (GP) nucleuses are required to implement asymptotically optimal threshold detection mechanism [8]. When decision threshold is reached in BG, SNr opens the gates of MEM by disinhibition to cache the preferred choice from LIP. LIP and SC_B units are modeled as leaky integrators with bounds at baseline zero to avoid negative firing rate. The superscripts on the units indicate the population's selectivity to left (L) or right (R) stimulus. Solid and dash lines represent excitatory and inhibitory connections, respectively. Strong outputs are shown in thicker lines (i.e., outputs from SNr and SC_F). (b) Responses of populations on a sample simulated FD trial, aligned to initiation of the saccade (denoted by the vertical dashed line). Motion viewing time is 1000 ms. Solid and dashed curves respectively denote the activity of population selective to R and L stimulus when the correct choice is R

LIP activity (i.e., the decision result) to guide later response. As we proposed before such working memory is critical in FD task. However the neural mechanism of working memory for saccade movement is still an open question. Some studies suggest it would be implemented in the BG [5] or prefrontal cortex [6].

In the final stage, the decision results stored in the working memory are passed down to motor center (SC) to generate saccade command. SC includes two types of neurons: the fixation (SC_F) and burst neurons (SC_B). SC_F generates tonic inhibition during visual fixation and suppress most saccades, as a "No-Go" signal [7]. SC_B is normally silent but have high firing rates ($\sim$ 200 Hz) just before saccade onset, as a "Go" signal [7]. In FD task the subject was trained to gaze on the fixation point while it is present during stimulus viewing (Fig. 82.1a) hence we assume SC_F is active and inhibits saccades during this period. When the fixation point disappears, the inhibition of SC_F is removed allowing the saccade. In FR task, during stimulus viewing, there is no fixation point (Fig. 82.1b) and hence no inhibition from SC_F, allowing a saccade as soon as the threshold in BG is exceeded.

Simulation Results and Conclusion

Stimulations are performed to illustrate the dynamics of the model's response in FD task. On a sample trial (Fig. 82.2b), threshold crossing happens $\sim$ 380 ms before saccade onset in BG. Then the MEM starts to maintain the preferred choice from LIP by increasing MEM^R. Due to the high inhibition from SC_F, SC_B are inactive until 100 ms before saccade, when the disappearance of fixation point induces a sharp drop in SC_F activity. The burst response in SC_B before saccade also increases LIP activity via excitatory connections. This effect is more obvious in average LIP activity across trials (Fig. 82.3a). During motion viewing period LIP activity depends on the motion strength, followed by a stereotyped increase in the final 100 ms before saccade onset. The model predictions are consistent with experiment data [2, 3]. Moreover, the model is naturally consistent with behavioral measurements [2, 3] (Fig. 82.3b) as it extends the model [4] previously shown to capture these data. The model can be also simulated in FR task [9] by neglecting the effect of fixation point.

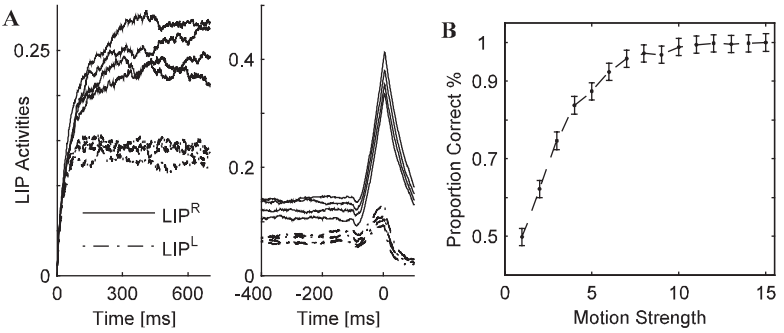

Fig. 82.3 (a) Time course of LIP activity under different motion strengths. On the left panel LIP responses are aligned to the motion onset. On the right panel responses are aligned to the saccade time. Each line is averaged over 200 trials. (b) The accuracy from 500 trials against different motion strengths with error bars showing standard error. The logarithmic increasing of accuracy is consistent with the experiment observations [2, 3]

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