A neural mechanism of dynamic gating of task-relevant information by top-down influence in primary visual cortex

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ARTICLE INFO

ABSTRACT

Visual recognition involves bidirectional information flow, which consists of bottom-up information coding from retina and top-down information coding from higher visual areas. Recent studies have demonstrated the involvement of early visual areas such as primary visual area (V1) in recognition and memory formation. V1 neurons are not passive transformers of sensory inputs but work as adaptive processor, changing their function according to behavioral context. Top-down signals affect tuning property of V1 neurons and contribute to the gating of sensory information relevant to behavior. However, little is known about the neuronal mechanism underlying the gating of task-relevant information in V1. To address this issue, we focus on task-dependent tuning modulations of V1 neurons in two tasks of perceptual learning. We develop a model of the V1, which receives feedforward input from lateral geniculate nucleus and top-down input from a higher visual area. We show here that the change in a balance between excitation and inhibition in V1 connectivity is necessary for gating task-relevant information in V1. The balance change well accounts for the modulations of tuning characteristic and temporal properties of V1 neuronal responses. We also show that the balance change of V1 connectivity is shaped by top-down signals with temporal correlations reflecting the perceptual strategies of the two tasks. We propose a learning mechanism by which synaptic balance is modulated. To conclude, top-down signal changes the synaptic balance between excitation and inhibition in V1 connectivity, enabling early visual area such as V1 to gate context-dependent information under multiple task performances.

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1. Introduction

The dominant view of cortical sensory processing is that as one proceeds along the visual pathway from primary visual cortex (V1) to higher-ordered visual areas, neurons become sensitive to progressively more complex stimuli-'complexification'. Early areas are thought to analyze simple attributes, such as orientation, direction of movement, and color. But visual processing also involves countercurrent streams of information flow, and the operation between bottom-up information coding from retina and feedback information coding from higher-ordered visual areas (Engel et al., 2001; Gilbert and Li, 2013; Lamme and Roelfsema, 2000). Visual recognition involved in memory, prediction, and attention is processed in distributed cortical and subcortical networks which include the subcortical structures and V1. However, the involvement of early

visual areas in cognition has been often underestimated (Gilbert and Sigman, 2007). V1 neurons are not passive transformers of sensory inputs but rather their activity is influenced by attention, task, training, and expectation (Muckli, 2010; Muckli and Petro, 2013; Tong, 2003). V1 receives considerably more feedback than feedforward thalamic afferents and 10 times more axons from V2 than from the lateral geniculate body (LGN) (Budd, 1998). Consequently, information processing in V1 includes top-down influence. However, it is poorly understood how V1 and higher-ordered visual areas concurrently form visual recognition leading to behavior.

Several studies on perceptual learning have demonstrated that V1 neurons can function as adaptive processor, changing their function according to behavioral context, and their responses reflect the demands of the perceptual task being performed (Gilbert and Li, 2013; Gilbert and Sigman, 2007; Li et al., 2004, 2006). In the study on two discrimination tasks with five-bar arrays (Li et al., 2004), it was demonstrated that V1 neurons exhibited the changes of tuning curves depending on these tasks. Further study by Ramalingam et al. (2013) showed the differences in the temporal correlations of spikes and local-field potential (LFP) coherence, caused by the two

tasks. Their study pointed out the importance of dynamic control in top-down influence, suggesting that the intracortical connections of V1 network could be dynamically organized so as to gate information critical for the relevant tasks. However, it remains unclear how task-relevant information is gated by the dynamic interplay of the connection change of V1 network and the top-down signals reflecting task behavior.

To address this issue, we developed a neural model of the V1, which receives feedforward inputs from LGN and top-down signals from a higher-ordered area such as V2. V1 neurons interact with each other via a balanced connection of excitation and inhibition. We made two assumptions. One is that a synaptic balance between excitation and inhibition in the V1 network is modulated in a different way, depending on which task is relevant. This assumption is based on the evidence that the circuitry in the V1 has long-range horizontal connections linking columns of similar orientation specificity (Gilbert and Wiesel, 1989; Stettler et al., 2002). Another is that top-down signal has a temporal correlation reflecting behavior relevant to each task. The temporal correlation is supported from the experimental results by Ramalingam et al. (2013). We show that a balance between excitation and inhibition in the V1 connectivity is modulated to gate task-relevant information. The balance change well accounts for the modulations of tuning curves and dynamic properties of V1 responses. We also show that the balance change is caused by top-down signals with temporal correlations reflecting the perceptual strategies of the two tasks. We propose a learning mechanism of the balance change. The results provide a neural mechanism of how V1 is associated with visual recognition and behavior.

2. Model

2.1. Five-bar discrimination task

In the five-bar discrimination tasks (Li et al., 2004), the visual stimuli consisted of five bar segments, a central bar fixed in receptive field (RF) center and four additional flanking bars surrounding the RF, paralleled side-by-side and end-to-end, as shown in Fig. 1a and b. The left and right bars have always the same offset and the top and bottom flanking bars are shifted in the similar way. Two referenced arrays were defined to represent the offsets of side and end flanks: the offsets of side flanks were defined by a referenced array, in which the central bar was equidistant from two side flanks, whereas the offsets of end flanks were measured based on a referenced array, in which the central bar was collinear with two end flanks. These offsets of side and end flanks were represented by the values in the range of −2 to +2, depending on the deviations from each reference array, as shown in Fig. 1c. The five-bar stimuli used were 5 × 5 arrays, in each of which the central bar was fixed and two side flanks and two end flanks were placed on different positions (see Fig. 1a in the paper by Li et al. (2004)). Monkeys were trained to perform two visual tasks based on different attributes of the five bar stimuli. In bisection task, task-relevant components were the central bar and the side-flaking bars (the three bars in the ellipse zone in Fig. 1a). The monkeys had to decide to which flanks of the two side ones the center bar was closer. In vernier task, task-relevant components were the central bar and the end-flanking bars (the three bars in the ellipse zone in Fig. 1b). The monkeys had to determine to which side of the end flanks the center bar was displaced. The animals were cued to the tasks by color difference, with the task-relevant components shown in green and task-irrelevant components shown in white. The animals were trained by repeating the bisection and vernier tasks, with the combination of the 5 × 5 stimulus arrays and two colored cues.
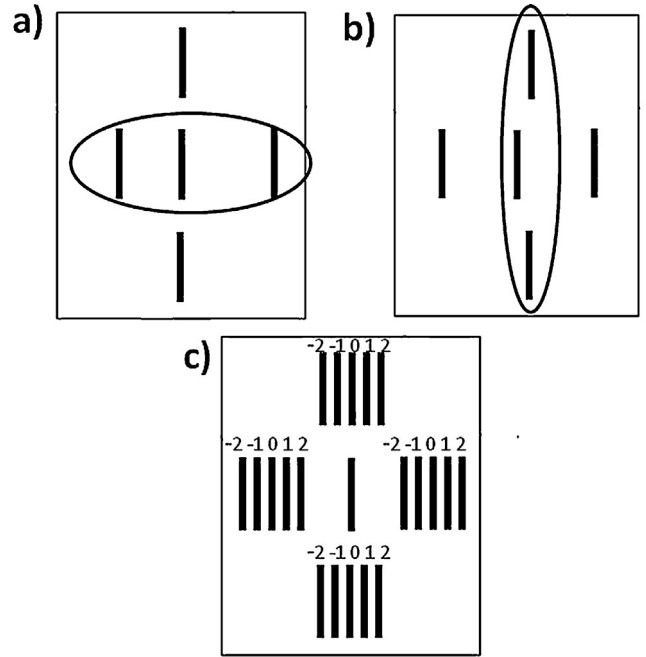

Fig. 1. Five-bar discrimination task. Stimuli presented are designed by five bars that consist of a central bar and four bars surrounding it. The four bars are paralleled side-by-side and end-to-end. (a) The bisection task requires the animal to judge whether the central bar is closer to the right or left flanks. The bars which the animal should judge in the bisection task are shown by the ellipse. (b) In the vernier task, the animal has to judge whether the central bar is above or below the collinear flanks. The bars which the animal should judge in the vernier task are shown by the ellipse. (c) The stimuli used have 5 × 5 arrays with the offset values of −2 to +2. The offsets of the side-flanks and end-flanks are defined by two reference arrays. In the bisection task, the offset is measured by a reference array in which the central bar is equidistant from the side flanks, defined by the value of 0. The offsets of the vernier task require a reference array where the central bar is collinear with the end-flanks, define by the value of 0. For a five-bar stimulus, the left and right bars have the same offset and the top and bottom flanking bars are shifted in the similar way, as shown in the panels, (a) and (b).

2.2. Model of the V1

The model of V1 network consists of a two-dimensional array of V1 neurons, with the size of $N \times N$, where $N = 20$. The V1 network contains only V1 neurons sensitive to the vertical line being the stimulus component of five-bar tasks. Fig. 2a shows the spatial array of V1 neurons, with the array of bar components. Each bar is encoded by four neurons. V1 neurons receive feedforward input from LGN at the location of corresponding bar component. They also receive top-down signal from a higher visual area, or V2, as shown in Fig. 2b. V1 neurons in the network are fully connected with balanced synapses of excitation and inhibition. V1 neuron was modeled with the leaky integrated-and-fire neuron (LIF) model (Tuckwell, 1988). The membrane potential of the (i, j)th V1 neuron, V_{ij}, is given by

$$\tau_V \frac{dV_{ij}}{dt} = -V_{ij} + \sum_{kl} w_{ij,kl}^{\text{exc}} X_{kl}(t) + \sum_{kl} w_{ij,kl}^{\text{inh}} X_{kl}(t - t_d) + I_{ij}^{\text{LGN}} + I_{ij}^{\text{FB}}.$$

(1)

The neuron model evokes a spike when the membrane potential reaches a threshold θ, and is then reset to $V_{ij} = 0$. The evoked spike has the refractory period of 3 ms. The synaptic weights, $w_{ij,kl}^{\text{exc}}$ and $w_{ij,kl}^{\text{inh}}$, are those of the excitatory and inhibitory connections from the (k, l)th neuron to the (i, j)th one, respectively. The inhibitory synapse, with the time delay t_d, really works through an inhibitory interneuron but the interneuron is not included in the model, for simplicity. τ_V is the time constant of V_{ij}. $X_{kl}(t)$ is the postsynaptic