The Isthmo-Optic Nucleus: 
A Possible Neural Substrate for Visual Competition

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Abstract

Birds have a well-developed centrifugal pathway from the optic tectum to the retina via the isthmo-optic nucleus (ION). Receptive fields of the isthmo-optic (IO) neurons have a wide suppressive field extending to, at least, two-thirds of the entire visual field of a single eye. Such wide suppressive fields indicate that the IO neurons may compete with each other for activity in a very long-range scale. Simulations using a simple dynamic model of the ION, based on the primitive competition model, suggests that the ION may be a neural substrate for visual competition.

Keywords: winner-take-all circuit; isthmo-optic nucleus; visual attention; visual competition

1 Visual attention and visual competition

Because of limited processing resources in the brain, only a small fraction of the information preprocessed by the retina can be further processed by the brain [1, 2]. Visual attention is a neural process which selects objects for further processing and/or visual orientation. This selection process has been metaphorically expressed as an attention spotlight [3]. It remains unknown how this selection process is biologically implemented by neuronal circuits, although competitive networks, such as the primitive competition model and/or winner-take-all networks have been postulated as mechanisms for attentional object selection, or visual competition [4-7]. The avian centrifugal visual system may be one of the most promising candidates for neural substrate for visual competition, as described below.

2 Centrifugal visual system and isthmo-optic nucleus

Although centrifugal innervation of the retina is widespread among vertebrates, origins of the projections are different [8]. In birds, who possess the most well-developed centrifugal pathway to the retina, neurons in a midbrain nucleus (the isthmo-optic nucleus; ION) project to the contralateral retina [8]. The isthmo-optic (IO) neurons of the Japanese quail send their axons to the contralateral retina, where they make contact with single association cells of Cajal [9, 10]. In turn, the IO neurons receive input from the optic tectum. The tectal neurons projecting to the ION (tecto-IO neuron) may make contact with single IO neurons [11]. Therefore, the tecto-isthmo-retinal (TIR) system may be regarded as a neural structure composed of parallel and discrete modules (= TIR modules; Fig. 1) composed of three serially-connected neurons (tecto-IO neuron, IO neuron and association cell of Cajal). Such a very local and discrete organization may enable single TIR modules to enhance the responses of retinal ganglion cells in a localized region of the retina.

Receptive field properties of the IO neurons and suppressive effect of remote stimuli far beyond the "classical" receptive fields were examined electrophysiologically in the Japanese quail [12]. Receptive fields emitting more than half the maximal on-off response to a small spot of light measured 4.3 ± 1.9 deg. (n = 37) in diameter. A stationary spot of light was presented at a remote point (35-76 deg.) away from the receptive field center, besides a stimulus for the receptive field center, with various onset time difference. The peripheral spot, when turned on 50-100 ms before the center spot, maximally suppressed the on and off responses to the center spot. In most of the IO neurons, even small remote stimuli (2-5 deg. in diameter) significantly suppressed the on-off responses to the center stimulus. The suppressive effects of remote stimuli were seen to be extended to, at least, two-thirds of the entire visual field of a single eye. Such wide suppressive fields indicate that the IO neurons may compete with each other for activity in a very long-range scale (Fig. 2). Thus the ION may be a neural substrate for visual competition.
The ION is a small nucleus (approximately 0.7 mm x 0.4 mm x 0.6 mm), containing approximately 8000-10,000 IO neurons, almost the same number as there are the tecto-IO terminals in the same volume. Given the small size of the nucleus, the small number (< 180) of GABA-immunoreactive neurons within the ION [13] may make mutual inhibition among the IO neurons possible.

3 ION model based on the primitive competition model of Amari and Arbib

A simple dynamic computational model for the TIR system was used to simulate the consequences of the three basic principles of the system; topographical input, long-range competition and focal gain enhancement, as a whole (Fig. 3). Long-range competition was implemented by the primitive competition model of Amari and Arbib [5] with slight modification. In this model, each IO neuron reciprocally connects with 4 retinal output neurons (= retinal ganglion cells). The IO neurons receive visual inputs from retinal ganglion cells. Long-range competition takes place among the IO neurons through an intrinsic inhibitory neuron that has reciprocal connections with all the IO neurons. Membrane potentials of \( i \)-th IO neuron \( (u_i) \) and the inhibitory neuron \((v)\) can be described by the following differential equations:
where

\[ f(u) = \begin{cases} 
  u, & u > 0 \\
  0, & u \leq 0 
\end{cases} \]

\( w_1 \) and \( w_2 \) are synaptic weights, and \( h_1 \) and \( h_2 \) are thresholds. \( s_i \) is input to \( i \)-th IO neuron.

Based on temporal properties of competition between real IO neurons, time constants of model neurons were determined: \( \tau_1 = 20 \text{ ms} \) and \( \tau_2 = 120 \text{ ms} \). Using a real-world movie of rolling tennis balls, competitive process of 48 model IO neurons was observed. The 1-sec-long movie consisted of 21 frames of 60-by-80 pixels gray-level images (Fig. 4A). Absolute values of differences between two consecutive frames were calculated at each pixel. The values of 10 by 10 pixels were summed. Forty eight sets of the 50-ms-step discrete values were temporally interpolated using a spline method. The interpolated values were fed into each IO neuron. Only 1-3 IO neurons with higher input survived the competition, and active neurons moved along with the highest input (Figs. 4B and 5). As a whole, it looked as if the ION system follows the most salient object in the visual field.

4 Conclusion

Simulation of the model based on three principles of the ION system; topographical input, long-range competition and focal gain enhancement, indicates that the ION may be a neural substrate for visual competition. Such principles could be features common to all neural systems for visual competition.
Fig. 4 a. Input images. b. Output of the IO neurons.
Fig. 5  Competition process among the IO neurons.

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References