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Color Representation at the 'Mid-Level' of Human Visual System

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Color spaces based on cone-response opponency (including CIE system) are useful for photometry. However, several psychophysical and physiological studies have suggested that they do not represent color appearance. Color signals for color appearance should exist somewhere in between the opponent and categorical levels: 'mid-level' of color-vision system. In this text, we would like to introduce some of our attempt on investigating color information processing systems at the mid-level by using psychophysical method and functional brain imaging technique (fMRI).

1. Introduction

It has been pointed out for a long time that major axes of color systems based on cone-response opponency (L−M and S−(L+M)) are not corresponding to the appearance of four major unique hues, such as red, green, blue and yellow[1,2]. Therefore, it is slightly misleading to estimate two cone-opponency channels as the physiological correspondence for the mechanisms of opponent color perception.

Several physiological studies reported that color selectivity of LGN neurons is limited to hue directions defined by the two cone-opponency channels[2,3]. Also, psychophysical and electro-physiological studies suggested that the higher order visual system treats color signal in a categorical manner[4]. It may be natural to assume that there are some 'mid-level' mechanisms between the LGN and higher order visual cortex, which plays a significant role in the representation of color appearance. The results of recent physiological studies reported that the color signal is transformed to multiple hue-selective systems at the level of primary visual cortex[3,5]. These results imply that activities of such neurons could code color appearance. The primary purpose our study is to clarify the color coding at the 'mid-level' by using human observers.

It must be noted that a color-coding system with multiple channels does not conflict with opponent color theory, which stresses the exclusiveness of opponent color in terms of perception, if the selectivity of a neuron which responds mostly to a hue (e.g., red) have little or no sensitivity to its opponent hue (green).

2. Psychophysical study[7]

Because of the multiple-stage structure of the color vision mechanisms, it requires elaborated technique to stimulate the 'mid-level' exclusively by psychophysical method. We used contrast-adaptation technique[6] to bypass the lower level visual system, and we used color-appearance matching task to avoid stimulating the categorical system at the higher level of visual cortex. The contrast-adaptation stimulus was a two-dimensional tessellated pattern of 50 colors, which lack a particular hue within a hue circle, arranged randomly. This missing hue is aimed to retain a hue-selective system intact while other hue-selective systems are desensitized. The color was also alternated in time at the rate of 20 frames per second.

Subjects adapted to this notched-noise stimulus at the beginning of every trial and then they were asked to match color appearance of target color chips in adapted- and un-adapted-visual fields. The result of color matches show systematic hue shifts and the chromatic saturation of the aftereffect was neither point nor line symmetric in cone-opponent color space. Such a nonlinear adaptation can not be ascribed to the desensitization of either of two cone-opponent channels or the linear combinations of their outputs.

We used a numerical model of multiple hue-selective channels, and optimized the number of channels, most selective hue direction, and bandwidth of each channel to best fit the data. The result of fitting showed that at least five channels are necessary to explain the data.

3. fMRI study

As a more straight forward method to investigate the color selectivity of neurons in the 'mid-level' of human visual system, we used a functional MRI technique[8]. We presented a visual stimulus whose color changed slowly along the circumference of a hue circle in an isoluminant plane. We recorded BOLD signal changes from two blocks of stimulus presentation in a session. In block A, the color of stimulus started from +L−M direction in the color space, and in block B, the color started from −L+M direction and changed in the same order as block A. At each time point of stimulus presentation, BOLD signals from blocks A and B are of neural response to opposite colors. By taking difference of BOLD signal changes between blocks B and A, it enables to remove response common to both blocks (onset and offset response) and maximize the BOLD response difference between opponent colors. By this continuous and differential response mapping technique, we obtained a hue direction to which each voxel shows the maximum BOLD signal increase.

The population histogram of color selectivity in the human visual cortex is similar to those in the monkey electrophysiological studies[3,5], suggesting that the human visual system have similar color selective neurons in the visual cortex.

4. Summary

These two studies has just demonstrated the possible variability of color selectivity in neurons at the 'mid- level' of human visual system. In future studies, we would like to clarify how the responses of multiple-color channels represent color appearances, including the neural basis of unique hues.

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