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Representation of Hue and Saturation of Color in the Visual Cortex of the Monkey

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We can summarize the transformation of color signals in the early stages as follows. First, color is represented by the relative activities of three types of cone photoreceptors. Secondly, linear combination of cone signals occurs in regular manners and color is represented by two axes, namely L–M and S axes (two-axes representation). Finally, signals tuned to various directions in the chromaticity diagram starts to be formed in V1 resulting in hue selective neurons as well as neurons selective for saturation. We can call this third stage as having "multi-axes representation of color". Color representation based on hue and saturation seems a principle way ubiquitous across different areas in the cortical visual areas.

1. Color selectivity in the inferior temporal cortex

A fundamental question on color vision is how in our visual system, color signal is transformed from the set of cone signals to represent perceptual color attributes such as hue and saturation. Color signal is transmitted through the lateral geniculate nucleus (LGN) and sent to the primary visual cortex (V1). In the cerebral cortex, color signal is transmitted along several areas along the ventral visual pathway. In the macaque monkey, this pathway includes sub-regions of area V2, area V4 and the inferior temporal (IT) cortex[4]. When we studied color selectivity of IT neurons, we found that many neurons were sharply tuned to a particular range of hue and saturation[5]. It has been shown that removal of IT cortex severely disrupts the color discrimination in monkeys[4]. These studies suggest that in the IT cortex, the highest stage of visual processing that plays an important role in color discrimination, color is represented by the combination of hue and saturation that may correlate with our color perception.

When we analyzed the color selectivity of IT neurons, we used color stimuli that was defined on the CITE-xy chromaticity diagram. An important feature of the color selective neurons in IT cortex was that the selectivity was formed by the curved response contours on the chromaticity diagram. Because CIE XYZ space is a linear transformation of the cone space, the response contour of any neuron whose activity can be represented as a linear sum of cone signals deem to be straight line on the chromaticity diagram. In other words, the fact that the response contour is curved implies that these neurons receive non-linear combination of cone signals[3]. If the response contour is a straight line, such neurons cannot restrict the response within a small range of colors along the edges of the spectrum locus such as yellow region or purple region. Instead, the color selectivity necessarily becomes broad along the edges of the spectrum locus. However, if the response contour is curved, the neuron can selectively respond to whatever small region at any place in the chromaticity diagram. Such process should be essential for the formation of selectivity to hue and saturation. Then, where does this happen? To obtain clues about this question, we recorded neuron activities from LGN and V1 and examined color selectivity of neurons in these early stages[2].

2. Color selectivity of LGN neurons

When we analyzed the color selectivity of LGN neurons using color stimuli defined on the CIE-xy chromaticity diagram, we encountered three types of neurons. One type of neurons showed excitatory response to red colors and suppressive response or no response to blue or cyan colors. Another type exhibited responses that is opposite to the neuron described above; they showed excitatory response to blue to cyan colors and suppressive response to red colors. These two types of neurons undoubtedly correspond to red-green (R–G) color opponent neurons previously reported[4]. Another type of neurons showed excitatory response to blue colors and suppressive responses to yellow colors. This type of neuron should correspond to blue-yellow (B–Y) color opponent neuron. A notable feature of the color selective LGN neurons is that the response contours are basically straight lines on the chromaticity diagram implying that the responses of these neurons can be in principle represented as the linear sum of cone signals. Quantitative analysis of the tuning directions of each neuron computed after the response distributions are converted to that in the MacLeod-Boyton (M–B) chromaticity diagram indicates that former two groups of neurons are activated by the difference between L cone and M cone signals, and the third type of neurons by the difference between S cone signal and the sum of L and M cone signals. These results are consistent with previous reports employing different methods to characterize color selectivity of neurons[1]. So, at the level of LGN, colors are represented by two cardinal axes, namely L–M axis and S- axis. Color signals represented by these two axes are sent to V1. Then what happens in V1?

3. Color selectivity of V1 neurons

We examined the color selectivity of V1 neurons using the same set of color stimuli used in LGN, and found that color selectivity of V1 neurons differs from that in LGN in two important aspects[2]. One difference is that, in contrast to LGN, neurons tuned to various directions in the chromaticity diagram were observed in V1, an observation that is consistent with other reports[6,7]. This indicates that V1 neurons are activated by various combination of cone signals. Another difference between LGN and V1 is that, in contrast to LGN, considerable number of V1 neurons had clearly curved response contours and exhibit sharp selectivity to hue and saturation. This suggests that V1 neurons are activated by non-linear combination of cone signals. As a result of non-linear combination of cone signals, color selectivity restricted to any direction in the chromaticity diagram became possible. These results suggest that V1 is the first stage where color representation based on hue and saturation starts to occur. Considering the results from V1 and IT cortex and other recent studies together, we believe color representation based on hue and saturation is a principle way ubiquitous across different areas in the cortical visual areas.

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