Hierarchy of Hue Maps in the Primate Visual Cortex

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Many stimulus attributes are represented in the cortex in the form of a map, such as the retinotopic map in the visual cortex and the frequency map in the auditory cortex where nearby cortical locations are associated with similar values of a given stimulus or action attribute. Given the computational advantage of maps for processing information,\(^1\) it is likely that a cortical region with a mapped representation of an attribute plays a much more important role in processing the given attribute than do regions without such mapped representations.

Color is an important attribute for catarrhine primates. A theoretical work has predicted the existence of color maps in primate visual cortex,\(^2\) but no clear evidence for it was present until we carried out an imaging study in the visual area V2 of macaque monkeys.\(^3\) In that study, we first located modules in V2 that were highly sensitive to color stimuli as reported by Roe and Ts’o.\(^4\) Such modules in V2 and other areas are called “highly color sensitive modules” below. We then imaged intrinsic optical signals at these modules to determine the spatial distribution of their responses to various color/gray gratings. Different colors elicited largely overlapping responses across the highly color sensitive modules, but the response peaks shifted systematically as a function of the stimulus color. Most interestingly, the spatial shift of these response peaks followed the perceptual hue order of the stimuli; nearby peaks were associated with perceptually close hues (Figure 1). Therefore, our results suggested the existence of a “hue map” in each highly color sensitive module in V2. Furthermore, we found that these hue maps were located at the cytochrome oxidase (CO) thin stripes. Some previous studies have suggested an important role for CO thin stripes in processing color information,\(^4-6\) although other studies did not find any evidence for this suggestion (see Shipp and Zeki\(^6\) for a review). Those previous studies were largely focused on the behavior of individual neurons and were unable to map the organization of neurons tuned to various colors. Given that we found V2 hue maps only at the highly color sensitive modules and CO thin stripes, and the computational advantage of maps for processing information,\(^1\) our results suggest an important role for these V2 compartments in processing stimulus hue.

Visual signals from the eyes reach area V2 through area V1. To determine whether hue maps in V2 originate in V1, we also imaged the responses to various uniform colors at the highly color sensitive modules in monkey V1. Similar to our findings in V2, the spatial shift in response peaks followed the order of stimulus hue (Figure 2, top image). However, hue maps in V1 were smaller than those in V2 by an order

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**Figure 1.** A hue map in area V2. Left, contours of peak responses to color/gray gratings of various hues. (White cross, peak location of a highly color sensitive module, scale bar, 500 mm). Right, stimulus colors in CIE-xy color diagram. Comparing these two panels suggests that nearby contours were associated with perceptually close hues (Modified from Xiao et al\(^3\)).
of magnitude (~200 µm versus 1.2 mm across), parallel to the difference in size between CO blobs in V1 and thin stripes in V2. These V1 hue maps were largely co-localized with CO blobs in V1 (Figure 2, bottom image), consistent with reports that the highly color sensitive modules in V1 are co-localized with CO blobs.8,9 Taken together, our results support the hypothesis that V1 blobs are more involved in processing color information than inter-blob regions, a highly controversial hypothesis that was first put forth based on single- and multi-unit recordings.5 This hypothesis has been one of the central themes of studies on the cortical mechanisms of color processing.10 Note that since each area contains many hue maps (Figure 2, bottom), each hue map processes information from a small part of the visual field.

Area V4 is one of the two main recipients of projections from V2. It was originally labeled as an area specialized for processing color.11 However, later studies suggested that V4 is also involved in processing information about other attributes.12 Consistent with this view, anatomical studies found regions in V4 that received inputs from either CO thin stripes or inter-stripes.13 With image-guided injection of anterograde tracers into the highly color sensitive modules and other regions in V2, we found that major parts of the projections from different functional compartments innervated different parts of V4, suggesting the existence of highly color sensitive modules in V4.14 Indeed, more recent imaging studies confirmed the presence of these modules in V4 and higher visual areas,15,16 and suggested that these modules also contain hue maps.16

Although hue maps in various visual areas are assumed to play an important role in processing color information from a computational point of view,1,2 direct evidence for this hypothesis is scarce. One piece of such evidence was found in our study that linked activity in V1 hue maps with the semantic division between “warm” and “cool” colors.17 In that study, we found that the warm-cool dichotomy across languages18 can be explained by the polarity of the contrast between long wavelength-sensitive cones (L cones) and middle wavelength-sensitive cones (M cones). Coincidently, the responses in V1 hue maps can also be divided into two groups based on the polarity of the L-M cone contrasts of associated stimulus colors. Our study thus suggests that some features of the activity in V1 hue maps are manifested in our color terms. Since color terms must be based on color perception, our results are consistent with the above hypothesis that links hue maps with color perception.

Another piece of evidence for the above hypothesis came from a study on a seizure patient who had an electrode implanted in a highly color sensitive module in the temporal cortex.19 This module was anterior to area V4 and was presumably located at a high level in the hierarchy of visual processing. The local field potential recorded at the implanted electrode were tuned to blue stimuli, suggesting that cells near the electrode tip were predominantly tuned to blue, which was consistent with the existence of a hue map in the module. Most interestingly, when the region near the electrode tip was electrically stimulated, the patient reported seeing blue even though no visual stimulus was presented. To my

Figure 2. Hue maps in V1. Top, peak locations of responses to uniform colors of various hues at a hue map in V1 (Modified from Xiao et al7 ). Bottom, several hue maps superimposed onto cytochrome oxidase (CO) staining of V1, showing that V1 hue maps were largely co-localized with CO-dense blobs (Unpublished data).
knowledge, this is the only reported case in which cortical stimulation alone elicited a particular color percept in a predictable way.

It is unclear how hue maps in various visual areas process color information differently. It is known that the perceived color of a surface depends not only on the wavelength composition of the reflected light from the surface but also that of its surroundings. This contextual effect on perceived color enables us to perceive more or less the same color for a surface under different levels of illuminations, a phenomenon called “color constancy”. Zeki found some cells in V4 whose responses resembled the perceptual experience of color constancy, and found no such cells in V1. Based on these results, Zeki proposed that the computation for color constancy is not complete until visual signals reach V4. However, more recent studies have found evidence either for or against the above proposal in terms of whether the chromatic contrast effect is present in early visual areas V1 and V2. The chromatic contrast effect is a prominent form of contextual effects presumably underlying color constancy. One possible reason for this discrepancy is that different studies have been biased by cells located in different functional compartments. Given the potential importance of hue maps in processing color information, we have chosen V2 hue maps as a target for finding signs of the chromatic contrast effect in early visual areas.

We used multi-electrode arrays to record local field potentials, multi- and single-unit activities in response to two sets of visual stimuli. In the first set, color was modulated across the entire field of 36x26 degrees, which caused physical modulation in the receptive fields of the recorded neuron population. The modulations were along one of the three cardinal color axes. In the second stimulus set, the same color modulations were presented to the surrounding area of a constant gray square (2x2, 4x4, or 8x8 degrees) that covered the receptive fields. Although not physically modulated, the gray square was perceived as being modulated in color. As a result of the chromatic contrast effect, the perceived modulations in the region that covered the cells’ receptive fields had opposite phases for the corresponding stimulus in the two sets. If the recorded neuronal population mediates the chromatic contrast effect, the recorded responses are supposed to have opposite phases as well for the corresponding stimuli in the two sets. Such anti-phase responses were not present in our results, suggesting a lack of chromatic contrast effect in V2 hue maps. Therefore, our results are consistent with Zeki’s proposal that computation for color constancy is not completed in early visual areas, at least for the stream of hue maps in various areas.

In summary, studies by our group and from other labs have discovered a hierarchy of hue maps along the ventral visual pathway in primates, and this hierarchy likely plays an important role in transforming a wavelength-based representation of color in the early visual areas to a perception-based one in the late areas.

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**Conflicts of Interest**

None.

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