

Research and Teaching Interest of Youping Xiao

My long-term goal is to understand how visual information is represented and processed to guide behavior in primates. I am particularly interested in the neural mechanisms underlying color perception, and the ways by which color perception contributes to visual functions such as scene segmentation, object searching and recognition. My planned project will address two key questions: a) How is color coded in the activity profiles on large groups of neurons in individual visual areas; b) Are color and form processed by separate populations of neurons in different compartments or areas in the ventral visual stream, which is believed to subserve object recognition?. Answers to these questions are prerequisites for understanding how neural coding of different visual attributes makes concerted contributions to visually guided behavior.

Previous studies have established the important functions of color perception, but the neural representation of color is still poorly understood, especially with respect to the neuronal population coding. My research plan is an extension of my postdoctoral works in Dr. Daniel Felleman's lab at the University of Texas, Medical School at Houston, and in Dr. Ehud Kaplan's lab at Mount Sinai School of Medicine. My work in Dr. Felleman's lab using optical imaging and unit recording in macaques showed that V2 responses to different colors peaked at different locations in the thin CO stripes (Xiao *et al.*, *Nature*, 2003). Most significantly, the peak responses to similar colors were located at nearby sites that formed spatially organized color maps. These results suggest that the location of the peak response in a V2 thin stripe may explicitly represent the perceptual color of a stimulus. This work, to our knowledge, was the first one that revealed population coding of individual colors in the primate visual systems. On the website Faculty of 1000, David Fitzpatrick at Duke University commented our paper "*The results of this paper provide convincing optical imaging evidence for an orderly spatial representation of color in monkey visual cortex, an important contribution to one of the more contentious areas of visual neuroscience.*" My recent work in Dr. Kaplan's lab has shown that a subset of V1 blobs contained similarly organized color maps, but on a much smaller scale (~0.25 mm and ~1.3 mm in length in V1 and V2, respectively). To investigate how the population coding of color evolves along the ventral visual stream, and whether the coding underlies conscious color perception, I propose to study color representation in macaque V4.

V4 was originally thought of as an area mainly for color processing because earlier studies by Zeki had found a high concentration of color selective neurons in V4. Other electrophysiological studies showing unique chromatic response properties of V4 neurons and the lesion studies all suggest that V4 play an important role in constructing and/or maintaining the perception of color. However, later studies by other groups found that V4 contained many fewer color selective neurons as well as neurons selective for other visual attributes. The discrepancy over the concentration of color selective neurons may suggest that V4 contains compartments rich in color selective neurons that are surrounded by regions with few such neurons. Other evidence supporting the existence of color compartments in V4 includes: 1) the CO-thin stripes and interstripes in V2 project to largely segregated compartments in V4 (DeYoe *et al.*, 1994; Xiao *et al.*, 1999); 2) Our preliminary results found color-preferring modules in V4 that responded to isoluminant color stimuli more vigorously than did surrounding regions (Xiao and Felleman, 1999); 3) A study using double-label deoxyglucose found similar color-preferring modules in

V4 (Tootell et al., 2004); 4) V4 contains multiple representations of some parts of visual field (Van Essen and Zeki, 1978).

In my planned study, V4 color-preferring modules will be visualized *in vivo* with optical imaging at the beginning of each experiment. Then I shall study the neuronal properties, organization and connectivity of these modules, using the techniques of optical imaging, electrode recording, and anatomy. My project will address the following specific questions:

- 1) Do the V4 color-preferring modules contain spatially organized color maps like those we found in V2 and V1? If so, do the color maps code the *wavelength* or the *perceived color* of the stimulus? The second question can be addressed by examining the effect of background color on the activity of a color map.

Previous electrophysiological studies by Zeki have found some color-selective neurons that were organized to form chromatopic maps in V4. Zeki's studies also suggested that some V4 neurons coded perceived color of stimuli, instead of the wavelengths (Zeki, 1980). This suggestion is supported by studies showing that monkeys with V4 lesions had a color constancy deficit, although their performance of wavelength discrimination was close to normal (Walsh et al., 1993).

- 2) Do color-preferring modules and the surrounding regions differ in the percentage of color selective neurons, or in the way by which these neurons are organized? One specific hypothesis is that neurons in the color-preferring modules cluster according to their selectivity for color, whereas neurons in the surrounding regions cluster according to their selectivity for form. Groups of neurons recorded at each site will be compared for their selectivity for color or form.
- 3) Are the color-preferring modules and surrounding regions connected with V2 thin stripes and interstripes in a largely parallel way? Are they also connected with separate compartments or areas in the inferior temporal cortex, as suggested by our preliminary results (Xiao and Felleman, 1998).
- 4) Are there *two* interdigitating retinotopic maps in V4, one in the color-preferring modules, and one in the surrounding regions?

Answers to the above questions will shed light on the hierarchy of the neural substrates involved in color processing, and the relationship between color and form processing. Based on the outcomes of this project, I will investigate whether the hierarchy of color processing is necessary and/or sufficient for generating conscious color perception, by studying the *behavior of awake monkeys* with targeted lesions or micro-stimulation. To understand how the cortical color maps are involved in visual functions such as scene segmentation, object searching and recognition, I will record electrically and optically (intrinsic signals and/or signals derived from dyes) in behaving monkeys. For this purpose, I have been using the recording chamber and artificial dura that have been developed by Grinvald's group for recording in behaving monkeys. To further prepare myself for these future projects, I have initiated a collaborating project with Dr. Ralph Siegel at Rutgers University to image the color maps in V2 of behaving monkeys.

Overall, my research on the population coding of color and its underlying neuronal organization will not only contribute to our understanding of neural representation of color, but also the representations of other visual or even non-visual modalities. This understanding is the basis of the development of new treatments of perceptual disorders. Therefore, the significance of my research will be far beyond color vision.

I am interested in teaching neuroscience courses, especially on the topics of sensory system. I have given lectures on visual system to graduate students at Mount Sinai School of Medicine. My teaching philosophy is to present the details of each system in the context of its computational goals. This way of teaching helps students to understand and memorize the details in terms of their functional significance. By introducing individual experiments and theories, and by letting students making presentations, I intend to train students on critical scientific thinking including pinpointing specific questions, designing experiments or models, analyzing data and reaching conclusions. I also want graduate students to be exposed to various modern technologies in each research field. I really enjoy interacting with students, which I think benefits both students and myself.

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