Color Information Processing in the Human Brain

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ABSTRACT

The photoreceptors of human yield red-green and yellow-blue color signals in addition to luminance. If these triplets did not directly represent colors in which we perceive millions of shades of differences, which signal would do? In the talk, some of the front-end studies on this issue will be introduced.

1. Introduction

The display technology is based on various aspects of study on human visual system, and color is one of those features. The color management technology was based on a phenomenon, in which human visual system can not discriminate rays that evoke same responses to photoreceptors in the eye, called *metamerism*. The CIE color coordinates was first established from this metamerism. Since the Euclidean distance in the CIE xyY 1931 system doesn't reflect perceptual difference, CIE decided to recommend two additional color spaces in 1976; they are CIE LAB and CIE LUV. CIE LUV was based on the color discrimination threshold [1]. At the level of discrimination threshold, two rays evoke just barely discriminable differences, but qualitative differences are not questioned. CIE LAB was based on Munsell color system, which is established by color differences at supra-threshold level. The reason why they recommended two color spaces was that it was impossible to unify these two requirements at a time. It means, color mechanisms for discrimination and appearance are distinct.

After the level of cone photoreceptors, the neural signals for color are derived by taking differences of responses between different cones. Difference between long-wavelength selective (L-) and medium-wavelength selective (M-) cones mediates roughly red-green (r/g) difference, and difference between short-wavelength selective (S-) cones and two other cone types mediates roughly blue-yellow (b/y) difference. However, these cone-opponent signals do no represent *color appearance*. Several psychophysical studies reported that colors along cone-opponent axes do not match *unique hues,* each of which yields pure red, green, blue, or yellow [2,3]. Then, what mechanisms represent our color appearance experience? This has been an unsolved question over decades.

Neurophysiological studies in monkeys have reported the presence of neurons in visual cortex that are selective to individual hue [4]. It implies that color representations in visual cortex are different from color opponent signal. Previously, we made an attempt to map hue tunings in human visual cortex by using fMRI technique [5], but it was impossible to find their correspondence with color perception. Here, I will introduce our latest attempt to reveal the neural basis of color appearance by using electroencephalograhy (EEG), which partly reflects a property of our color appearance [6].

2. Method

Participants were healthy undergraduate students, graduate students, and faculties of Tohoku University (N = 18). The entire procedure of the experiment was approved by the ethics committee of RIEC Tohoku University, and informed consent was obtained from all participants.

We used a component of visual evoked potential (VEP) called *steady-state VEP*, hereafter *SSVEP*. The SSVEP is evoked as a cortical response to periodically presented visual stimulus. For example, a visual stimulus presented at 200 ms per cycle will evoke SSVEP at 5 Hz in temporal frequency domain. Therefore, we have conducted a recording of SSVEP response by presenting visual stimulus at 5 Hz and varied its hue in time. It took 24 seconds for a cycle to vary hues along an entire hue circle in the cone-opponent space [6].

The color space was defined by the Weber contrast of L and S cone responses, with respect to those for the background gray (x, y, Y) = (0.333, 0.333, 30). Under the constraint of isoluminance (i.e., weighted sum of L- and M-cone response is constant) M-cone responses were uniquely defined. The extent of color stimulation along L- and S-cone are scaled by the multiples of color discrimination threshold; $\Delta L/L_w$ = 8%, $\Delta S/S_w$ = 80% at the maximum, where ΔL, ΔS represent increment of L-, S-cone responses, respectively, and L_w, S_w represent those to the background gray. To ensure that SSVEP responses are responses to color, we recorded those to three different levels of chromatic saturation; that were *Full* ($\Delta L/Lw$, $\Delta S/Dw$) = (0.08, 0.80), *Half* (0.04, 0.40), and *Quarter* (0.02, 0.20).

The stimulus was a checkerboard pattern whose check size = 0.76º and the outer diameter of the stimulus area was 6.5º, and the background was filled with a uniform gray. The pattern alternated between a color and the background gray at 100 ms per frame, and its alternation took 200 ms per cycle. The participant was asked to fixate the center of the stimulus while conducting a cognitive (Go/No-go) task by responding to either circle or cross presented within the area of color stimulus.

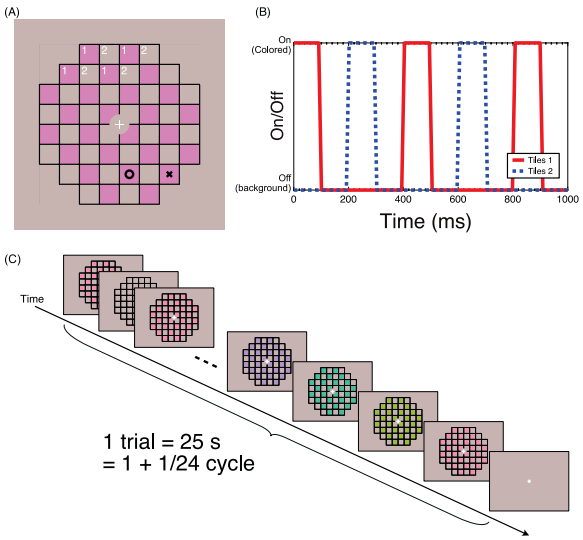

Fig.1 Visual stimulus [6]

Visual stimulus was presented on a CRT display GDM-G520 (SONY, Japan) via a visual stimulus generator ViSaGe (Cambridge Research Systems, U.K.), driven by a desktop computer (HP, U.S.A.). SSVEP was recorded by 32ch whole-head electrodes by BrainAmp plus amplifier (Brain Products, Germany) at the sampling frequency of 250 Hz. All VEP data was preprocessed by EEGLab software on MATLAB (Mathworks, U.S.A.) followed by temporal frequency analyses with our in-house software on MATLAB. Data from two participants were rejected for low signal-to-noise ratio and were not included in main results.

3. Results

The temporal frequency spectrum exhibits a prominent peak at 5Hz, mostly from the occipital electrodes. The amplitude of the 5Hz component varied with the contrast of color stimulus (Fig.2).

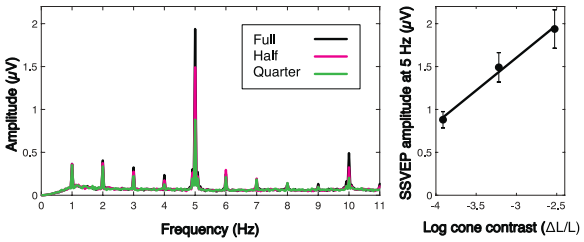

Fig. 2. Spectrum and SSVEP amplitude of 5Hz component for 3 contrast conditions [6].

The grand average of SSVEP amplitude shows modulations with hue changes, which has a unique elongation in an oblique direction of cone-opponent space: magenta-green direction (Fig.3). If the cone-opponent or color discrimination mechanism was the only cause of the neural responses, the shape of SSVEP amplitudes should be line symmetric with respect to the L/M (horizontal) and S (vertical) axes. Therefore, this oblique elongation in the SSVEP amplitude profile includes something other than responses of cone-opponent mechanism and/or color discrimination mechanism. The axis of elongation systematically varied with the contrast of color stimulus; the angle of oblique axis becomes smaller for the smaller contrast stimuli.

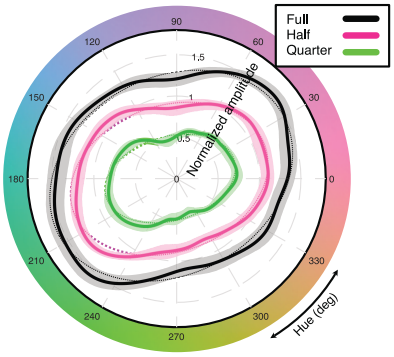

Fig. 3. Hue selectivity profile of SSVEP [6]

Next, we fitted several numerical models to estimate what could be the mechanism behind this hue selective profile of SSVEP response [6]. The primary candidate of the SSVEP component is the cone opponent mechanisms. It is known that the SSVEP responses are mainly reflecting the activity of primary visual cortex (V1) and the population of color selective neurons are known to exhibit prominent peaks at hues corresponding to the cone opponent axes [4]. Therefore, the SSVEP response must include responses of cone opponent mechanisms. However, it is necessary to introduce mechanisms selective to the intermediate directions of the cone-opponent axes.

To evaluate purely color selective responses, we used the difference of SSVEP amplitudes between Full and Quarter conditions, to fit various models. The precision vs efficiency trade-off of model fittings was evaluated by AIC/BIC measures [6].

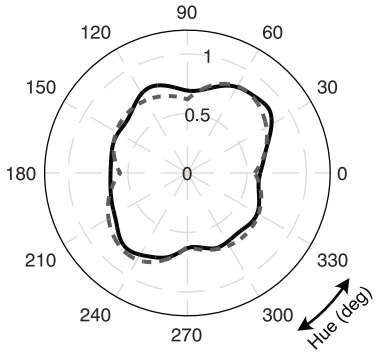

Fig.4 Fitted result (dashed line) [6]

Finally, we found that the combination of cone-opponent responses and deviation from iso-chroma contour of Munsell color space best describes our result (Fig.4). The Munsell color space is designed to represent a perceptually equal-step color system; three parameters (Hue, Chroma, and Value) defines a color in this space. The iso-Chroma contour defines an extent in each hue direction as a distance from the origin of cone-opponent space (gray), at which color contrast appear constant across hues.

The relative contributions of cone-opponent and Munsell Chroma-based mechanisms' responses were approximately 40% and 60%, respectively [6]. This implies that responses of perceptual mechanisms that define Munsell Chroma play a significant role in our SSVEP response amplitude. It also means, we have succeeded in measuring a

part of perceptual color responses by the SSVEP technique.

4. Discussions

Although our numerical model analysis revealed partial contribution of perceptual (Munsell Chroma like) mechanisms, there's no direct evidence that show correspondence between actual perception and SSVEP properties. One possibility is to measure psychophysical property hue selectivity of, and another possible attempt is to introduce the effect of adaptation or simultaneous masking. If the neurons selective to the intermediate hues actually exists and contributed the SSVEP amplitude, it is expected that the response to the intermediate hue would be systematically reduced by adaptation or masking. A recent study has shown the presence of meta-contrast masking effect in the oblique directions of cone-opponent space by the SSVEP recording [7], but they used a bidirectional stimulus which stimulates both sides of neutral gray at a time; it stimulates, e.g., both red- and green-sensitive mechanisms simultaneously. But we believe it is important to test with a unidirectional stimulus.

Another possibility is the analysis of results by using individual differences in the SSVEP responses. It may be possible to apply numerical analyses that decompose factors that commonly underly in each individual and differ in their contribution to the SSVEP responses, like the factor analysis in a psychophysical study on hue selective mechanisms [8].

Acknowledgments

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References

[1] D.L. MacAdam. "Visual sensitivities to color differences in daylight." Journal of the Optical Society of America, Vol. 32, No.5, pp. 247-274 (1942).

[2] R.L. De Valois, K.K. De Valois, E. Switkes, & L. Mahon. "Hue scaling of isoluminant and cone-specific lights," Vision Research, Vol. 37, No. 7, pp. 885-897 (1997)

[3] M.A. Webster, E. Miyahara, E., G. Malkoc, G., & V.E. Raker. "Variations in normal color vision. II. Unique hues." Journal of the Optical Society of America A, Vol. 17, No.9, pp. 1545-1555. (2000)

[4] A. Hanazawa, H. Komatsu, & I. Murakami "Neural selectivity for hue and saturation of colour in the primary visual cortex of the monkey," European Journal of Neuroscience, Vol. 12 No. 5, pp. 1753-1763 (2000).

[5] I. Kuriki, P. Sun, K. Ueno, K. Tanaka, & K. Cheng. "Hue selectivity in human visual cortex revealed by functional magnetic resonance imaging," Cerebral Cortex, Vol.25, No.12, pp. 4869-4884 (2015).

[6] S. Kaneko, I. Kuriki & S.K. Andersen, "Steady-state visual evoked potentials elicited from early visual cortex reflect both perceptual color space and cone-opponent mechanisms," Cerebral Cortex Communications, Vol. 1, No.1, tgaa059 (2020).

[7] J. Chen & K.R. Gegenfurtner, K. R. "Electro-physiological evidence for higher-level chromatic mechanisms in humans," Journal of Vision, Vol. 21, No.8, pp.12-12 (2021).

[8] K.J. Emery, V.J. Volbrecht, D.H. Peterzell, M.A. Webster. "Variations in normal color vision. VI. Factors underlying individual differences in hue scaling and their implications for models of color appearance." Vision Research, Vol.141, pp.51-65 (2017).