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Decoding Color Responses in Human Visual Cortex

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SUMMARY Color percept is a subjective experience and, in general, it is impossible for other people to tell someone's color percept. The present study demonstrated that the simple image-classification analysis of brain activity obtained by a functional magnetic resonance imaging (fMRI) technique enables to tell which of four colors the subject is looking at. Our results also imply that color information is coded by the responses of hue-selective neurons in human brain, not by the combinations of red-green and blue-yellow hue components.

key words: *color, human vision, brain, decoding, fMRI*

1. Introduction

Color information in the human visual system initiates from responses of three cone photoreceptors, such as long-, medium- and short-wavelength sensitive cones (in short, L, M and S cones, hereafter). Therefore, a set of three independent variables is sufficient to represent color signal, and that is why three dimensional color coordinates is often used to describe the color of light. Color spaces used for colorimetry (like CIE XYZ (1931) or CIE LAB (1976)) have an axis for light intensity and two axes to designate colors.

These "2+1" color coordinates *roughly* correspond to the lower level mechanisms of human color vision [1]. The color code is transferred to a luminance and two cone-opponent-color components before the level of retinal ganglion cell; the luminance signal is composed by the sum of L- and M-cone responses ($L + M$). Two color channels are composed by the difference of L- and M-cone responses ($L - M$) or that of S-cone responses and the sum of L- and M-cone responses ($S - (L + M)$): cone-opponent-color channels. Color differences conveyed by the $L - M$ channel roughly correspond to apparent redness vs. greenness component, and those by $S - (L + M)$ channel do to apparent blueness vs. yellowness component.

However, there are two problems to consider this "2+1" type color code as the neural basis of *color appearance*. First of all, it has been frequently reported in psychophysical studies that colors which selectively stimulate each cone-opponent channel ($L - M$ or $S - (L + M)$) do not correspond to *perceptually* pure red, green, yellow and blue, i.e., unique hues [2]–[4].

Secondly, several electro-physiological studies have reported that neurons in the monkey visual cortex show a variety of hue selectivity in addition to four directions in the color space [5]–[7], while the cone-opponent-color code is preserved up to the level of lateral geniculate nucleus (LGN) [5], [6]. It may be natural to consider that neurons in the human visual cortex have color selectivity to intermediate hues in addition to those selectively stimulate cone-opponent channels.

Recent studies in human subjects by psychophysics [8] and by functional magnetic resonance imaging (fMRI) technique [9], [10] showed evidence for the presence of neurons that selectively respond to intermediate hues among cone-opponent-channel selective ones.

Multi-voxel-pattern analysis has been used to assess the color selectivity of cortical neurons in human fMRI studies [9], [10]. If brain activities can be classified between two different color stimuli that evoke identical activation to cone-opponent channels, it will suggest the presence of the neurons that directly code the individual colors. An fMRI study [10] succeeded in classifying brain-activity patterns in correspondence with eight color stimuli that were equally spaced on a hue circle in an isoluminant plane of CIE LAB color space. However, CIE LAB space is defined by nonlinear transformation of cone responses, and therefore, the experiments using colors defined in such a color space do not provide a direct answer to a question about whether color information is coded only with the cone-opponent-response components or not.

The aim of the present study is to assess the presence of neurons that selectively respond to intermediate hues of the cone-opponent axes by classifying fMRI images.

2. Methods

2.1 Apparatus

All experiments were conducted with a 4-Tesla MRI scanner and a 5-inch RF surface coil at RIKEN BSI. Visual stimuli were generated with an MRI-compatible-image projector (AVOTEC, U.S.A.) and rear projected on a diffusion screen. The screen image was carefully calibrated with a spectrophotometer. Subjects viewed the screen through an oblique mirror mounted on a head-support structure. Sub-

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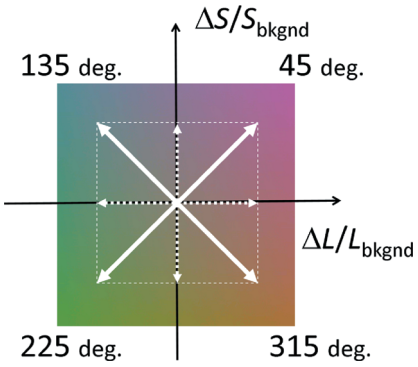

Fig. 1 Cone-contrast-based-color space. Solid arrows in diagonal directions indicate directions of hues used in this study. Dotted lines show orthogonal projection of these colors to the horizontal and vertical axes. Two opponent-color pairs (45–225 deg and 135–315 deg) stimulate two cone-opponent-color systems with the same amount in positive in negative directions, indicated by dotted arrows along the axes.

jects used a bite bar to minimize head motions during MRI scans, and no motion correction was applied to the MR images. Respirations and heartbeats were also measured to reduce biophysical artifacts by removing components corresponding to these factors [11].

2.2 Stimulus Design

A color space composed by a luminance axis and two cone-opponent axes was used for the definition of color stimuli (Fig. 1). Axes in an isoluminant (chromatic) plane are defined by the proportion of increments in L- and S-cone excitations (ΔL and ΔS, respectively) with respect to those for a gray background (L_{bkgnd} and S_{bkgnd}, respectively). Equal-energy gray was used for the background. This color space is compatible with the one proposed previously [12] and Smith & Pokorny cone fundamentals [13] was used. The scale of S-cone-contrast axis ($\Delta S/S_{bkgnd}$) was equated to L-cone-contrast axis ($\Delta L/L_{bkgnd}$) by detection thresholds for each subject.

The hue of colors is represented by the angular direction in the isoluminant plane ($L + \omega M$ = const, where ω is a weight unique to each subject and is around 1.0) of this color space, and 0, 90, 180 and 270 deg correspond to $+L - M$, $+S - (L + M)$, $-L + M$ and $-S + (L + M)$ directions, respectively. Four stimulus colors were selected from diagonal directions, such as 45, 135, 225 and 315 deg, each of which appear magenta, cyan, lime green, and orange, respectively. The magnitude of stimulation in the L-cone contrast ($\Delta L/L_{bkgnd}$) was ±0.05.

Stimulus was a circular check pattern (check size = 0.26 deg) which alternated its color between two colors (experiment 1) or between a test hue and a background gray (experiment 2) at the temporal frequency of 5 frames per second. The diameter of the check pattern was 6 deg to limit the area of stimulation in the area of macular pigmentation (Fig. 2). The luminance uniformity across the stimulus area was obtained for each subject by flicker photometry between

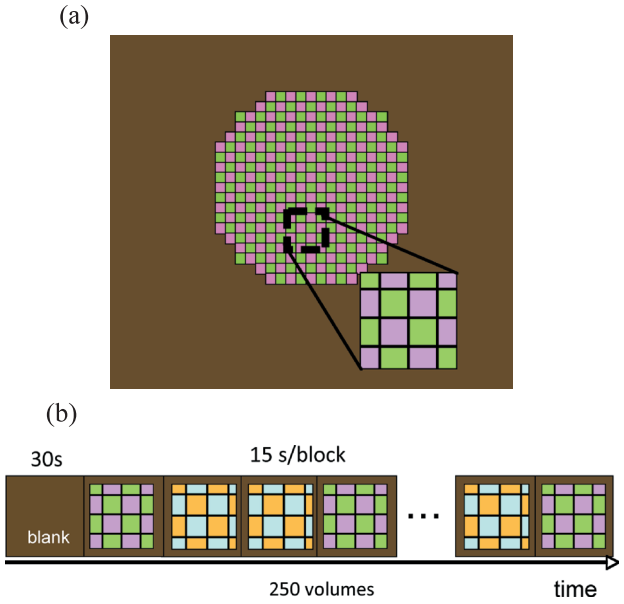

Fig. 2 (a) Schematic view of stimulus in Exp 1. Inset shows enlarged check pattern. In Exp.2, alternations between either of four colors vs. gray were presented. (b) Time sequence of stimulus presentation for a run in Exp1. Two kinds of check patterns represent two stimulus conditions. See text for details. Colors may appear different from actual ones, because of calibration differences.

the background gray and the test color at 13 locations in the stimulus area.

Each stimulus was presented as 15 s of check reversals in a block and stimuli were switched without any blank period to maximize differences (by eliminating BOLD signal drops for blank period) in brain activity between the stimuli. The stimuli were presented in a pseudo-random order to counter balance the effect of preceding stimulus. One run of experiment consisted of eight repetitions for each color (approx. 8 min.), and four runs were conducted for each subject.

We conducted two experiments with these colors. In Experiment 1, pairs of two colors were used: 45 and 225 deg, or 135 and 315 deg. Both pairs excite $L - M$ and $S - (L + M)$ channels to the same extent in both in increment and decrement directions with respect to the background. Therefore, if responses of two cone-opponent channels coded color information in the cortex, it would evoke identical fMRI signals, because of the temporal delay (around 6 s) in the blood-oxygenation-level changes: *hemodynamics*.

Figure 3 shows the rationale of Experiment 1 by simulating hemodynamic responses for each stimulus color. Figure 3(a) shows a typical hemodynamic response (HDR) curve. Let us define $I(t)$ as the time course of blood-oxygenation-level dependent (BOLD) signal change in response to a short impulse of visual stimulation, like Dirac's $\delta(t)$. This $I(t)$ works as an impulse response function to visual stimuli. Let us define $S(t)$ as a function for stimulus time-sequence in a block. As shown in Fig. 3(b), actual stimulus was presented for 15s at the frequency of five frames-per-second. By taking the convolution of $I(t)$ and

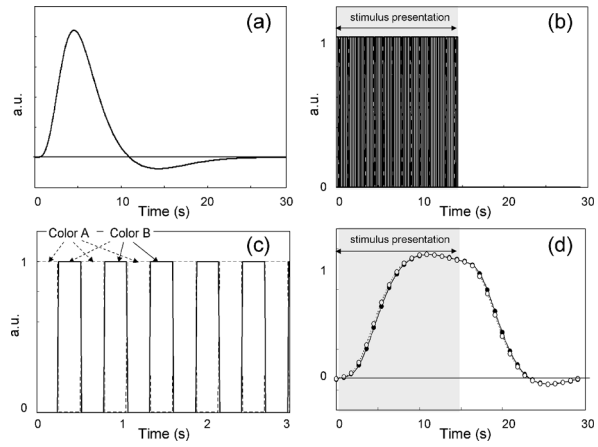

Fig. 3 Simulated hemodynamic response (HDR) curves. (a) A typical time course of HDR curve. (b) and (c) Time sequence of magenta emergence in the check pattern. (c) shows color alternations in an enlarged view. Two colors (color A and B in this figure) are presented alternatively in both space and time (five frames per second) at the duty cycle of 50%. (d) Estimated HDR curve obtained by the convolution of (a) and (b) (see Eq. (1)). Estimated HDRs for two colors in a check pattern, e.g., magenta (45 deg in hue angle) and lime green (225 deg), are shown in solid and open symbols, respectively, but are irresoluble in the figure.

$S(t)$, it will be possible to estimate the HDR for a block of stimulus presentation: $R(t)$.

$$R(t) = I(t) * S(t) \tag{1}$$

Solid line in Fig. 3(d) shows the estimated HDR for a block of stimulus presentation of, e.g., magenta (45 deg), which can be represented by the combination of opponent-channel responses of $+\Delta L/L_{bkgnd}$, $+\Delta S/S_{bkgnd}$. Figure 3(d) shows a comparison of estimated two HDR curves for 45 and 225 deg colors. There is little difference between these two HDR curves, and considering the existence of additional biophysical noise, it would be virtually impossible to differentiate two HDR curves in the experimental results. This is an estimation of HDR curve for a pair of color in a stimulus (45–225 deg), and it is also possible to derive a set of estimated HDR curve for the other pair of colors in the other stimulus (135–315 deg). Since the basic idea of the derivation of estimated HDR is the same, the estimated curves of HDR to the other color pair for the stimulus would be the same as in Fig. 3(d).

Therefore, it would be impossible to expect the successful classification of the BOLD signal responses from the two pairs of color stimuli, if only the cone-opponent channels coded colors in the human brain.

In Experiment 2, four colors are presented independently, with temporal alternations with gray, to check whether cortical color selective neurons respond to each hue.

2.3 Imaging Procedure and Subjects

Six slices of images were taken perpendicular to the calcarine sulcus. The thickness of each slice was 3 mm and the in-plane resolution was $2 \times 2\,\mathrm{mm}^2$. A segmented EPI pulse sequence (TE = 25 ms, TR = 1,500 ms) was used to obtain blood-oxygenation-level-dependent (BOLD)-signal images [14].

Three healthy subjects participated in the experiment. Their color vision was confirmed to be normal by Ishihara-pseudo-isochromatic plates (Handaya, Japan). Preparatory sessions for heterochromatic flicker-photometry were conducted to define ω in each subject for isoluminance ($L+\omega M$ = const.) and to establish luminance uniformity across the stimulus area.

The experimental procedure was approved by the ethics committee of RIKEN, and all subjects gave informed consent in a written form.

2.4 Analysis

All multi-voxel-pattern-classification analyses were conducted with a linear support-vector machine (SVM) [15] programmed on MATLAB (Mathworks, U.S.A.). To reduce the number of dimension for the SVM analysis a general linear model (GLM) analysis was conducted to specify voxels activated by a similar visual stimulus with a statistically significant difference from noise. Then, standard deviation for crude BOLD signal was calculated for each effective voxel (more than 300 in each subject), and 100 voxels from the largest were used for the SVM analysis.

The basic idea of SVM is to classify multi-dimensional data into two classes [15]. The present study uses the BOLD signals from voxels as elements for the multi-dimensional vector in the SVM analysis. A supra surface in the multi-dimensional space constitutes a border for the classifier, and is defined by a weighted sum of the unit vectors. In the training phase, the weights are optimized to classify the training-set vectors as correctly as possible, through iterations. As a consequence, the weights for the vector elements with higher reliability become larger. Therefore, by mapping the weights with voxel (i.e., vector element) locations, it would be possible to map which part of the brain plays significant role in the classification. The classifier performance (hit rate) will be tested by classifying test vectors, which were not included in the training-data set.

The SVM analysis was conducted with a *leave-one-out-validation* procedure. At the beginning of each training-and-test cycle, four test blocks were randomly selected for each stimulus, and the rest of them were used for the training of SVM classifier. 300 times of this cycle was repeated to obtain hit rates. 95% confidence intervals were also calculated by bootstrap analysis.

In the first experiment, a region of interest (ROI) was defined around calcarine sulcus (CS), which includes primary and secondary visual areas (V1/V2).

3. Results

3.1 Experiment 1

Figure 4 shows the result of classification analysis for two subjects. The hit rates were significantly above the chance performance ($p < 0.05$). The classification with CS ROI was sufficient for the classification with an above chance performance. The hit rate for the classification between the color stimuli and luminance stimuli was higher than 90%, when a luminance-defined-check pattern (±7% luminance contrast with background) was used for comparison (not shown). These results imply that the color signal in the visual cortex is not coded solely by cone-opponent-channel responses.

3.2 Experiment 2

Figure 5 shows that the performance of classification analysis was significantly above the chance ($p < 0.05$).

The classification performance was different among hues. Asymmetry between opponent colors (45 vs. 225 deg, 135 vs. 315 deg) may imply that color is coded in a unilateral way in the color space. It may also imply that the hue selectivity of neurons do not match exactly with the diagonal directions in the cone-opponent-color space.

The weight for the contribution of each voxel to the classification was obtained as a map after the training phase (Fig. 6). This map shows that the most significant contribution was obtained from the voxels around the boundary between occipital cortex and cerebellum: ventro-occipital (VO) area, which includes the fourth visual area (V4). This is consistent with other human subject studies, reporting that the VO areas play a significant role in color vision, using PET [16], fMRI [10], [17], [18] and for brain-damaged patients [19].

4. Discussions

4.1 Summary of Results

The results of this study imply that the crude responses of cone-opponent channels may not be used to code color signal in the human visual cortex. The second experiment implies that the cortical color representation is shifting toward the response to individual hue. Also the higher contribution of voxels in VO area (Fig. 6) to the color classification implies the relevance of neurons in the VO area to color appearance.

4.2 Comparison with Previous Decoding Studies

In relation to the similarity in the method of analysis, previous studies by Parkes et al. [9] and by Brouwer and Heeger [10] are closely relevant to the present study.

Parkes et al. [9] tried to insist that unique-hue system is a better model for the cortical code of color than the cone-opponent system, but their experimental design could have been biased to conclude that the unique hue is the better model in the cortex. They showed that classification for cone-opponent stimuli is not successful, while that for four unique hues for each subject are. However, their unique-hue stimuli were not balanced in positive and negative directions, in terms of cone-opponent responses. Therefore,

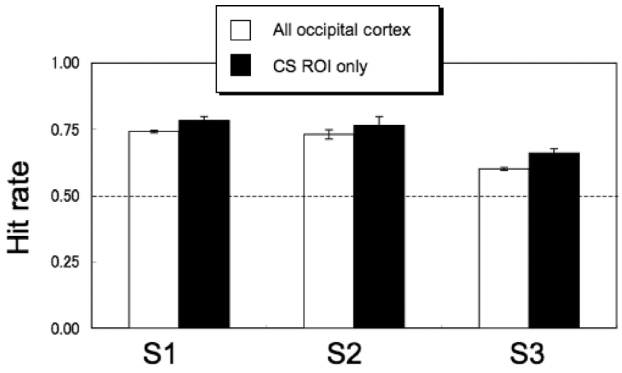

Fig. 4 Results of classification analysis for paired color stimuli. Hit rate of classification analysis with voxels from all occipital cortex (open bars) and with voxels in CS-ROI (filled bars). Error bars indicate 95% confidence intervals. Hit rates are significantly higher than the chance level (50%) indicated by a dotted line.

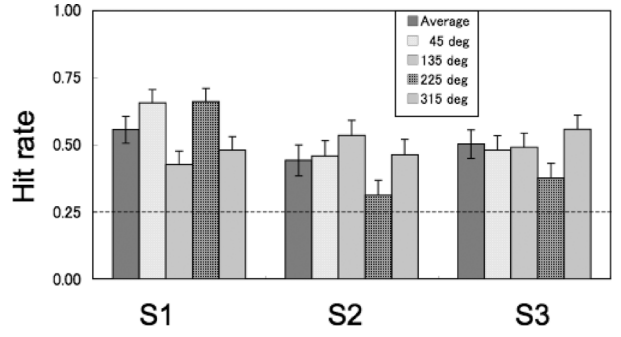

Fig. 5 Results of classification for each hue. Bars indicate results for each hue stimulus: from left, average of all hue, 45, 135, 225, and 315 deg, respectively. A dotted line at 25% indicates chance level and error bars indicate 95% confidence intervals in classification performance for each hue.

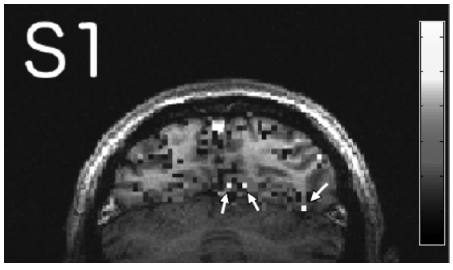

Fig. 6 A contribution weight map among voxels in the classification analysis, overlaid on an anatomical image (subject S1). A gray scale bar in the right indicate the scale of weight that brighter voxel had larger weight. There are voxels with higher contribution from ventro-occipital (VO) area (indicated by arrows and their surrounding darker voxels).

some asymmetry in unique-hue stimuli could have caused in the better classification performance for unique-hue stimuli. Also, the comparison of classification accuracy between unilateral stimulation with unique-hue stimuli vs. bilateral stimulation with cone-opponent-channel stimuli may not be adequate to argue which is better as the model for the cortical color representation, because brain activity from bilateral stimuli could be more complex and more difficult to classify.

Brouwer and Heeger [10] have demonstrated the possibility of classifying neuronal response to eight color stimuli, in more sophisticated manner. They introduced an elaborated hue-selectivity model for the better precision of classification and also to demonstrate that principal components of brain-activity patterns in V4 represent color difference in more efficient way than that in V1. Their study may have succeeded in demonstrating the possibility that the structure of hue circle is better represented as neural activities in V4 than in V1. However, according to the nonlinear relationships between cone responses and CIE LAB space, their results may infer some indirect information about relationships among cone responses, brain activities and color percept.

The results of our two experiments have demonstrated that the classification of multi-voxel-BOLD-signal patterns with a linear SVM is successful for color stimuli. In the Experiment 1, we have used bilateral stimuli that are aligned in diagonal directions in the cone-opponent space and are equated in the magnitude of stimulation for cone-opponent channels. Therefore, our study might be more suitable to reject that color code in human visual cortex is formed only by the cone-opponent responses. The result of the Experiment 2 may imply that color information in the human visual cortex is coded by unilateral hue-selective neurons in a simpler and more direct manner than in the previous studies.

4.3 Neural Basis for Color Appearance in Humans

The higher contribution of voxels in VO area for classifying hues may imply correspondence with recent studies in monkey visual cortex using fMRI and electro-physiological recordings of neural responses [20], [21]. They found many colonies of neurons that respond selectively to colors (they named 'glob') and the other part ('interglob') selectively responded to the tilt of bars. They also insisted that neurons in the color selective chunk are the neural basis of 'unique colors' [21] from a correspondence between some peaks of hue-selectivity histogram for 'glob' neurons in monkeys and unique-hue loci in humans. Although it may call a caveat to consider such a correspondence as a direct evidence for the neural basis of color *appearance*, their study may suggest that the homologue of 'glob' in humans can be the focus of color appearance, because unique-hue loci for a large number of subjects show some systematic convergence in the cone-opponent space [4]. Therefore, the higher contribution of VO-area voxels to color classifications in the present study may be in line with their conclusions, as well as those by previous studies on the relation of VO area with color stimuli in human subjects [10], [15]–[18].

However, none of the previous studies have succeeded in showing a direct evidence for the correspondence between color *appearance* and the brain activities, so far, and we would like to pursue this issue to clarify the neural basis for color appearance.

The present study has demonstrated that the human visual cortex represents color by the activation of neurons selective to each of multiple (no fewer than eight) hues. This color-encoding scheme enabled us to classify brain activity data with the hue in the intermediate directions of cone-opponent axes. However, this result does not conflict with the presence of the cone-opponent color signals in human brain. The stimuli in the first experiment were designed so that the opponent color mechanisms cannot discriminate them, but it does not reject the presence of neurons responding to cone-opponent colors. As it has been reported in the electro-physiological studies of V1 neurons in macaques [5]–[7], there are neurons with hue selectivity in various colors, including cone-opponent hue directions. Another electro-physiological study in macaque reported that the color selectivity of neurons become categorical at the level of inferior temporal cortex [22], and some of the color categories were similar to those based on human psychophysics [23]. In addition, the neurons in the inferior temporal cortex (after V4) are estimated to play a preparatory role in visual memory, and a psychophysical study in humans has shown that color memory for natural scene had categorical characteristics [24]. Altogether, the results of the present study may support a hypothesis that the color representation in human visual cortex changes progressively from the cone-opponent-color system to the categorical-color system.

5. Conclusions

The present study demonstrated that the color information is not coded with the combinations of cone-opponent-channel responses, but with responses of neurons selective to each hue.

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