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Neural Correlates and Effective Connectivity of Subjective Colors during the Benham's Top Illusion: A Functional MRI Study

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Benham's top is a rotating black-and-white pattern that fuses to form concentric rings of different colors (Prevost–Fechner–Benham subjective colors [SCs]). The underlying mechanism has been explained as resulting from local retinal cell interactions, yet the cortical processing of this illusion is largely unknown. We used rapid event-related functional magnetic resonance imaging to investigate the neural mechanisms of this SC illusion. The SCs induced when Benham's top rotated at 5 Hz were compared with perceptually matched physical color (PC) stimuli to reveal differences in both the neural substrates and their dynamic interactions by means of effective connectivity. Subjects ($n = 7$, all with normal vision) were required to judge whether or not they perceived color in each stimulus. The activation patterns for each condition were almost identical, but the effective connectivity from V4 to V2 and V2 to V1 was stronger during SC perception than when viewing perceptually matched PCs. All subjects perceived SC when the rotation speed of Benham's top was greater than or equal to 3 Hz, which was coupled with enhanced effective connectivity between V4 and V1. These results indicate that modulation from V4 to V2 to V1 plays a significant role in SC perception during the Benham's top illusion.

Keywords: backward connection, color perception, dynamic causal modeling, ventral visual pathway, visual illusion

Introduction

Color perception is elicited primarily by the neural processing of the wavelength composition of the light that reaches the eyes. This process consists of a series of steps such as wavelength discrimination, color opponency, local color contrast, elaboration of hue, global color constancy, and the experience of color (Conway 2009). Many previous studies demonstrated that color processing is found at multiple levels of the visual system, and recent studies have shown that the ventral visual pathway deals with color processing through a connected network involving V1, V2, V4, and the posterior inferior temporal cortex (reviewed by Bartels and Zeki 2000; Conway 2009). These anatomically distinct regions seem to have different roles: the cells in V1 are most sensitive to changes in wavelength composition (Zeki 1983b), the double opponent cells in V1 are deeply involved in local color contrast (Conway 2001), V2 is involved in hue processing (Xiao et al. 2003), the responses of some cells in V4 correlate with global color constancy (Zeki 1983a), and the posterior inferior temporal cortex is responsible for the integration of signals (Conway and Tsao 2006). Although some cortical chromatic properties are still controversial (Gegenfurtner and Kiper 2003), it is widely believed that each region has a different role in color processing and that all regions work together as a system to generate color perception.

Although all color perception is subjective, the term "subjective color" (SC) is used to describe the perception of color from an achromatic stimulus, which does not contain the variations in wavelength that would be expected from the colors that are perceived. SCs can be generated when the stimulus has particular spatial and temporal properties. Because Benham demonstrated SCs using the "artificial spectrum top" (Anonymous 1894; Benham 1894), many scientists have tried to explain how the perception of SCs is generated (von Campenhausen and Schramme 1995). The Benham top illusion is produced by temporally modulating a pattern that has a fixed-phase relationship to a flickering background. As the visual system is sensitive to phase shifts between stimuli, the phase difference of the rings causes the perception of different colors. von Campenhausen thought that a phase-sensitive lateral interaction between neurons explained this phenomenon and stressed that it takes place prior to binocular fusion (von Campenhausen 1968, 1973).

Many studies suggest that this lateral interaction occurs in the retina (Zrenner 1983; von Campenhausen and Schramme 1995), yet there are several phenomena that cannot be explained solely by retinal processing. For example, if the interaction occurs only in the fovea of the retina, phase-sensitive coupling should be generated only within a limited distance ($<1°$ of the visual angle), but this influence acts over large distances (3°–40°) (Le Rohellec et al. 1992; Schramme and Supply 1997). Furthermore, Billock et al. (2006) examined whether cortical processes are involved in Benham's SCs using McCollough's colored aftereffect, which is thought to be produced cortically (Dodwell and Humphrey 1990). They reasoned that if the origin of Benham's SCs was retinal, then Benham's top could induce McCollough's aftereffect; however, Benham's top did not induce McCollough's colored aftereffect. These findings indicate that the origin of Benham's SCs is not restricted to the retina but also involves visual cortical regions. That said, its neural mechanisms are still unknown.

The organization of the visual cortex can be considered as a hierarchy of cortical levels with reciprocal cortico-cortical connections among the component regions, and the hierarchy depends on an anatomically asymmetric distinction between the forward and backward connections of these distinct regions (Felleman and Van Essen 1991; Hegdé and Felleman 2007). As for functional asymmetry, Friston argued that the connections from lower to higher areas are predominantly driving in nature, whereas backward connections are capable of exerting modulatory influences and mediating top-down influences (Friston 2007; Chen et al. 2009). Kawato claimed that forward connections from lower to higher visual areas provide an approximated inverse model of the imaging process (i.e., optics), whereas backward connections provide a forward model of the optics (Kawato et al. 1993). Edelman (1989) advocated that reentrant signaling plays an important role in conscious visual perception based on his model and model simulations. Hochstein and Ahissar (2002) proposed the reverse hierarchy theory of visual perception. According to their theory, feedforward processing follows the bottom-up hierarchical pathway, whereas explicit visual perception begins when processing reaches higher cortical levels and proceeds in a top-down fashion to encompass detailed information available from other cortical areas. Lamme and Roelfsema (2000) also demonstrated that the feedforward sweep of information processing is mainly involved in unconscious vision, whereas recurrent processing is required for conscious visual perception. These perspectives emphasize the importance of the backward connections for conscious perception. Direct evidence for the modulatory effect of backward connections has been obtained from reversible deactivation studies in nonhuman primates (Sandell and Schiller 1982; see review by Bullier et al. 2001) and humans (see Bullier 2001). Hupé et al. (1998) showed that cortical feedback from higher-order area V5 to lower-order areas (V1, V2, and V3) improves discrimination of figure/ground differentiation, particularly in the case of low-visibility stimuli. They concluded that backward connections act in a nonlinear fashion to boost the control (gain or suppression) of the response in lower-order areas (Bullier et al. 2001). In humans, several studies have used transcranial magnetic stimulation to show the importance of backward connections to the lowest stage of the visual hierarchy for conscious visual perception (Pascual-Leone and Walsh 2001; Juan and Walsh 2003). Based on the anatomical and functional data described above and previous studies of color processing (Bartels and Zeki 2000; Conway 2009), it is conceivable that color perception emerges from recurrent top-down and bottom-up processes in the ventral visual cortical system, even in the case of SCs induced by Benham's top.

To investigate the cortical involvement of the SC perception generated by Benham's top, we conducted 2 types of experiments. The first experiment was designed to elucidate the difference between subjective and perceptually matched PC perception (Color Benham experiment). This experiment was intended to differentiate the color generation mechanism in the visual cortex between the SC and PC conditions. In this experiment, the physical properties of the input (i.e., stimulus) differed, but the output (i.e., perception) was very similar. As Benham's SCs are generated automatically and are dependent upon spatiotemporal patterns rather than concrete objects, its neural substrates likely include lower-level color-processing regions, and/or direct connections to these regions, rather than higher-level color-processing areas. We hypothesized that the neural representations of the SCs and perceptually matched PCs differ with regard to V1/V2 activation and/or the connections between V1/V2 and other regions.

Another important characteristic of the SCs induced by Benham's top is frequency dependency: color perception is induced only when the rotation speed is in an adequate range. Therefore, we designed the second experiment to examine the neural substrates of the perception of Benham's top at various rotation speeds (Speed Benham experiment). In this experiment, the physical properties of the stimuli were the same for all conditions, but the rotation speed varied, resulting in changes in the SC percept. This experiment enabled us to differentiate the regions involved in rotation speed-dependent SC perception and those involved in motion perception. We hypothesized that SC perception is related to the activation of the ventral visual areas and also to the strength of the connectivity between V1/V2 and other ventral regions such as V4.

Materials and Methods

Subjects

Seven healthy subjects (4 females and 3 males; aged 23–39 years) participated in the present study. Five of the 7 subjects were naive to the stimuli used in the study; these subjects were provided with monetary compensation. All subjects had normal or corrected-to-normal visual acuity and passed a color vision examination including the Ishihara test (Ishihara 1993) and the Farnsworth–Munsell 100-Hue test (Farnsworth 1943). The protocol was approved by the ethical committee of the National Institute for Physiological Sciences, Okazaki, Japan. The experiments were undertaken in compliance with national legislation and the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki). All subjects provided written informed consent.

Apparatus for Visual Presentation

Presentation 0.98 software (Neurobehavioral Systems) implemented on a personal computer (Dimension 9250; Dell Computer Co.) was used for the presentation of visual stimuli for retinotopic mapping and for response collection for the experiments. In all other experiments, a Delphi 6.0 was used for visual stimuli presentation. An LCD projector (DLA-M200L; Victor) located outside and behind the scanner projected the stimuli through a waveguide to a translucent screen, which the subjects viewed via a mirror attached to the head coil of the magnetic resonance imaging (MRI) scanner. The spatial resolution of the projector was 1024 × 768 pixels, with a 60-Hz refresh rate. The distance between the screen and each subject's eyes was approximately 60 cm, and the visual angle was 18.9° (horizontal) × 14.2° (vertical). Responses were collected via an optical button box (Current Design Inc.).

Experimental Design and Task Procedures

Experiment 1: Color Benham Experiment

In Experiment 1, we used 5 types of tops: a Benham's top to induce SCs; physically colored red, blue, and green tops; and a physically colored top, the colors of which were matched perceptually to the SCs (Fig. 1*a*). Benham's top spinning at 5 Hz was used as the SC stimulus, whereas a static Benham's top was used as a control. Because of limitations due to the functional magnetic resonance imaging (fMRI) experiment, parameters such as disk size, arc thickness, arc position, the number of arcs, and the distance between arcs were determined based on when subjects clearly perceived the SCs with Benham's top in the MR scanner. Therefore, the design parameters of the Benham's top were different from the optimal settings proposed by Jarvis (1977). Because we aimed to minimize activity related to eye movements, which was of no interest in the present study, we used a disk size of 6° in diameter in order to avoid eye movements. The arc thickness was 3.3 min and the distance between arcs was 0.12°, which was adjusted so that there was a set of 5 arcs between 0.8° and 3.0° (excluding the fovea). These parameters induced the clearest SC perception in the MR scanner in the present study.

To emphasize SC perception and compare this with the physically colored stimuli, the Benham's top was designed as follows: the disk was half black and half white, and the white side had a series of 3 sets of 5

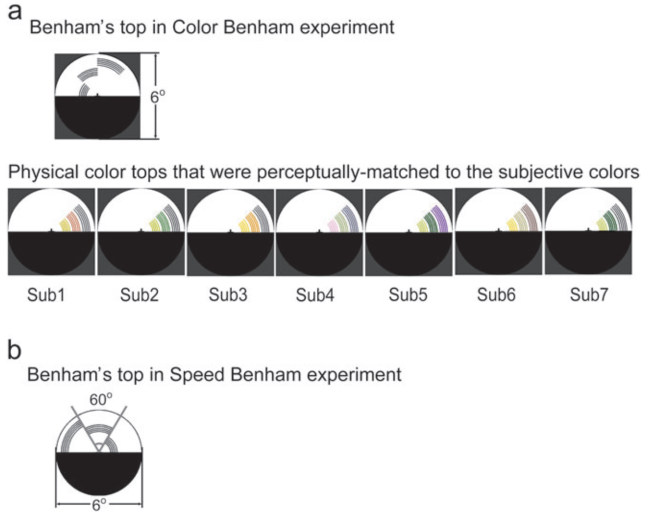

Figure 1. Visual stimuli used in the Benham's top experiments. (*a*) Tops used in the Color Benham experiment. All tops were rotating at 5 Hz. Upper, Benham's top; bottom, the PC top that was perceptually matched to the SC top for each individual. (*b*) Benham's top used in the Speed Benham experiment. This top rotated at 0, 0.5, 1.5, 3, 4, or 5 Hz.

concentric black arcs. Each set was placed with a central angle of 45° and 3 different phases (0°, 45°, and 90° from the black-to-white boundary) (Fig. 1*a*, Benham's top). The PC stimuli were produced as follows: the disk was also half black/half white, and the white side had a series of 3 sets of 5 concentric black or color arcs. Each set was placed with a central angle of 45° with 125° phases from the black-to-white boundary. When the disk with black arcs was spun at 5 Hz, the subjects either did not see any colors (dark gray or black) or saw a very dark navy blue color. Therefore, we decided to use this pattern as the baseline. For the PC stimuli that were perceptually matched to the SCs, the perceptually matched PCs were determined for each set of arcs with the following approach. The subjects entered the MR scanner before the actual MRI experiment. They saw 2 rotating tops presented on the screen in the MR scanner. One was Benham's top rotating at 5 Hz, and the other was the baseline top described above. The subjects were then required to adjust the colors of both tops by communicating vocally with the experimenter via an intercom (Siemens). During the online adjustment, the experimenter changed the mixing ratio of RGB parameters (0–255 in each parameter) in each set of arcs by communicating with the subject inside the scanner and tried to achieve the SCs perceived by the subject wherever possible. This top was used for the perceptually matched PC stimuli in each individual (Fig. 1*a*, PC tops that were perceptually matched to the SCs). We also used red, green, and blue tops for the PC stimuli; these will not be discussed further in the article.

In the actual experiment, the experimental design was based on a rapid event-related paradigm, in which the efficiency of the design was highly dependent upon the temporal pattern of the stimulus presentations (Dale 1999; Friston, Zarahan et al. 1999). The detailed method required to obtain a highly efficient experimental design is described elsewhere (Morita et al. 2008). There were 6 conditions in this experiment: SCs, perceptually matched PCs, 3 nonmatched PCs, and the static Benham's top. The condition and rotation direction (clockwise or counterclockwise) was switched every 4 s. The subjects were required to press a button with the right index finger when they perceived color and to press a button with the right middle finger when they did not perceive color. Therefore, button presses occurred every 4 s. There were 60 trials of each condition per session, and 10 sessions were conducted in the present study.

Experiment 2: Speed Benham Experiment

A typical Benham's top with 6 rotation speeds was used in this experiment. The disk was half black and half white, and the white side had a series of 3 sets of 5 concentric black arcs. Each set of arcs was placed with a central angle of 60° in 3 different phases (0°, 60°, and 120° from the black-to-white boundary) (Fig. 1*b*). The disk was 6° in diameter, the arc thickness was 3.3 min, and the distance between arcs was 0.12°. There were 6 conditions with various rotation speeds. In each condition, the rotation speed was 0 (static), 0.5, 1.5, 3.0, 4.0, or 5.0 Hz, respectively. The experimental design was based on a rapid event-related paradigm, and the rotation speed (6 conditions) and direction (clockwise or counterclockwise) were switched every 4 s. The structure of the design was the same as in Experiment 1. The subjects were required to press a button with the right index finger when they perceived color and with the right middle finger when they did not perceive color, so that button presses occurred every 4 s. There were 60 trials of each condition per session, and 10 sessions were conducted.

The detailed experimental procedure and analysis methods for the functional localizer mappings are described in the Supplementary Notes and Figures (Supplementary Fig. 1).

MRI Data Acquisition

All images were acquired using a 3-Tesla MR scanner (Allegra; Siemens). To acquire a fine structural whole-brain image, magnetization prepared rapid acquisition gradient echo (MP-RAGE) images were obtained (time repetition [TR], 2500 ms; time echo [TE], 4.38 ms; flip angle = 8°; field of view [FoV], 230 mm; 1 slab; number of slices per slab = 192; voxel dimensions = 0.9 × 0.9 × 1.0 mm). For functional imaging, an ascending T_2^*-weighted gradient-echo echo-planar imaging (EPI) procedure was used. Oblique scanning was used to exclude the eyeballs from the images and cover the entire cerebrum. The parameters of each experiment were as follows: retinotopic and color region mapping (TR, 2500 ms; TE, 30 ms; flip angle, 80°; 40 slices; FoV, 192 × 192 mm; 64 × 64 matrix; slice thickness, 3 mm; slice gap, 0.45 mm), motion region mapping, Speed Benham experiment, and Color Benham experiment (TR, 2000 ms; TE, 30 ms; flip angle, 75°; 34 slices; FoV, 192 × 192 mm; 64 × 64 matrix; slice thickness, 3 mm; slice gap, 0.45 mm). The number of volumes obtained in each session of retinotopic mapping was 106; color region mapping, 104; motion region mapping, 136; Color Benham, 136; and Speed Benham, 136 volumes. These volumes included the baseline measurements obtained before the first trial and after the last trial.

Image Preprocessing

We analyzed the fMRI data using SPM5 revision 1111 (The Wellcome Trust Centre for Neuroimaging; http://www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB 2007a (MathWorks). After discarding the first 2 (retinotopic mapping and color region mapping) or 4 (motion region mapping, Color Benham, and Speed Benham) volumes of each session to allow for stabilization of the magnetization, the remaining images were used for analysis. The images were realigned to correct for head motion, then corrected for differences in slice timing within each volume. The whole-head MP-RAGE image volume was coregistered with the image volume of the first EPI volume. The whole-head image volume was normalized to the Montréal Neurological Institute T_1 image template using a nonlinear basis function. The same parameters were applied to all the EPI volumes, which were spatially smoothed in 3 dimensions using a 4-mm full-width at half-maximum Gaussian kernel.

Analysis for the Benham's Top Experiments

Experiment 1: Color Benham Experiment

As the neural activity for color attenuates rapidly, we adopted a rapid event-related design for the Benham's top experiments. Six regressors (PC, SC, 3 PCs, and the control static Benham's top) were modeled. These regressors were convolved with a canonical hemodynamic response function. The data were high-pass filtered with a cutoff period of 128 s to remove low-frequency signal drifts. A first-order autoregressive model (AR(1)) was used to remove serial correlations in the data. To compare the subjective and perceptually matched PC condition, contrast images (SC − PC, PC − SC) were created and estimated.

We used both voxel-level and cluster-level inferences to determine the activated regions (Friston et al. 1996). Both these procedures control familywise type 1 error (FWE) but differ in terms of statistical and localizing power (Friston, Worsley, et al. 1994, Friston et al. 1996). Using a theoretical power analysis of distributed activations, cluster-level inference is more sensitive than voxel-level inference in fMRI data; however, this increased sensitivity reduces localizing power. Because we aimed to identify the regions active during a specific condition (localizing power), but also wanted to emphasize detection of differences between conditions with higher statistical sensitivity, we used voxel-level inference to depict the regions active in each condition (e.g., SC, PC), whereas cluster-level inference was used to detect the differences between the conditions (e.g., SC – PC, PC – SC). To be more precise, in order to depict regions induced by the SC or the PC condition, we set the threshold at $P < 0.05$ with an FWE correction at the voxel level for the entire brain. To detect differences between the SC and the PC conditions, we set the height threshold to $P < 0.001$ at the voxel level and $P < 0.05$ with an FWE correction at the cluster level for the entire brain (Friston et al. 1996). Analyses were first performed at the individual level. Then, the contrast images of SC – PC or PC – SC for each subject were used for the group analysis with a random-effects model, to make inferences at the population level (Friston, Holmes et al. 1999) with the same statistical thresholds as described above.

Experiment 2: Speed Benham Experiment

We employed the same experimental design as that used in the Color Benham experiment. In this experiment, we modeled 6 regressors (Benham's top rotating at 0, 0.5, 1.5, 3, 4, and 5 Hz). Two contrast images were created to identify the regions related to SC perception and those involved in motion perception: the contrast image of [3 + 4 + 5 Hz] – [0 (static) + 0.5 + 1.5 Hz] was used for the former and [0.5 + 1.5 + 3 + 4 + 5 Hz] – [0 (static) Hz] for the latter. The resulting set of voxel values for each contrast constituted an SPM of the *t*-statistic (SPM$\{t\}$). To depict the regions active during SC perception or motion perception, we used a statistical threshold of $P < 0.05$ with an FWE correction at the voxel level for the entire brain.

Effective Connectivity Using Dynamic Causal Modeling

Effective connectivity is defined as the influence that one neural system exerts over another (Friston, Tononi, et al. 1994). Determining effective connectivity requires a causal model of the interactions between the elements of the neural system of interest (Stephan, Harrison, et al. 2007). Dynamic causal modeling (DCM) is an approach used to analyze effective connectivity with experimentally designed inputs and blood oxygen level–dependent (BOLD) responses (Friston et al. 2003). DCM is based on a bilinear model of neural population dynamics that is combined with a hemodynamic forward model describing the transformation of neural activity into a measured BOLD response (Friston et al. 2003). The aim of DCM is to estimate parameters at the neuronal level, such that the modeled BOLD signals are maximally similar to the experimentally measured BOLD signals. DCM for fMRI combines the model of neural dynamics with an experimentally validated hemodynamic model including the "balloon model" (Buxton et al. 1998), which describes the transformation of neuronal activity into a BOLD response. It consists of a set of differential equations that describe the relationships between the 4 hemodynamic state variables using 6 parameters (Friston 2002; Stephan, Weiskopf, et al. 2007). The combined neural and hemodynamic parameter set is estimated from the measured BOLD data, using a fully Bayesian approach with empirical (for hemodynamic) and conservative shrinkage (for neural) priors for the coupling parameters. At the neural level, 3 sets of parameters are estimated: the direct input to a region (i.e., the direct influence of stimuli on regional activity), the intrinsic connectivity between regions (i.e., the interregional influences in the absence of a modulating experimental context), and the modulation of connectivity between regions (i.e., the changes in connectivity between regions induced by the experimental context).

Systems of Interest, Definition of the Models, and Data Extraction from Regions

In our evaluation of the effective connectivity between regions, the system of interest consisted of 5 regions within each hemisphere: primary visual cortex (V1); the cortical entry node of visual input; the color-related regions V2, V4, and V4α, which are involved in elaboration of hue, global color constancy, and integration of color processing, respectively; and the visual motion–sensitive region V5. These regions fulfilled the minimum requirements for the system of interest in the present study and comprised the constituent elements of the simplest possible circuit diagram (Aertsen and Preßl 1991) because the major elements of the perception of the rotating Benham's top are visual inputs, color perception, and motion perception.

By referring to a previous anatomical study in nonhuman primates (Hegdé and Felleman 2007), we defined a model comprising: the system-driving input to V1; the reciprocal connections between V1 and V2, V2 and V4, V2 and V5, and V4 and V4α regions (intrinsic connectivity); and all the connections influenced by the modulation effect. Modulation of connectivity was determined based on the SCs, the perceptually matched PCs, the 3 PCs in the Color Benham experiment, and the SCs and the rotation speed (i.e., 0.5, 1.5, 3, 4, and 5 Hz) in the Speed Benham experiment.

In order to construct suitable driving and modulatory inputs in the DCM analysis, the design matrix was reorganized as follows. For the Color Benham experiment, we determined the regressor that indicated the system-driving input to V1 (all combined conditions) and the regressors that indicated modulatory inputs (SC, PC, and 3 color conditions, respectively) to the connections between regions. For the Speed Benham experiment, we determined the regressor that indicated the system-driving input to V1 (all combined conditions) and regressors that indicated modulatory inputs (0.5, 1.5, 3, 4, and 5 Hz conditions, respectively) to the connections between regions. In addition, we concatenated all 10 sessions with some modifications in order to extract session-concatenated time series data; in this way, we tried to avoid deformation of the time series data due to inadequate high-pass filter, session effects, and AR model between sessions.

Subject-specific time series were extracted from voxels within a 3-mm radius centered on the local maxima as follows. For V1 and V2, we first detected the local maxima around the calcarine sulcus based on the results of the Color or Speed Benham experiments, and the coordinates were then transformed into Talairach space. Next, the transformed coordinates were located in the flattened map containing the V1/V2/V3 boundaries and eccentricity boundaries generated by the retinotopy mappings. We selected the local maximum that was within or nearest to the region in V1 or V2 and the 0.8°–3° eccentric field (Table 1). For V4, V4α, and V5, we first detected the local maximum of each region using the color (V4 and V4α) or motion (V5) localizer mapping results and determined the coordinates of each region. Then, we searched and selected the local maxima in the results of the Color or Speed Benham experiments and selected those that were closest to the coordinates of the regions of interest (ROIs; V4, V4α, and V5) derived from the localizer mappings described above. Because we were not always able to find bilateral activity based on localizer mappings in individual subjects, either the left or right hemisphere coordinates were used in the present study (Table 1).

The time series data were high-pass filtered, whitened using an AR(1) model, and adjusted with the effect of interest of all experimental conditions. We used the first eigenvariate of the adjusted time series across all voxels within the ROI using principal component analysis and entered these data into the DCM. All parameters of the DCM were estimated for each subject using Bayesian estimation schema.

Evaluation of Effective Connectivity

The values of the modulation of connectivity were extracted for each subject and entered into summary statistics (between subject) using a *t*-test. One-sample *t*-tests were used to evaluate the modulation of connectivity in each condition. To compare the difference between the SCs and PCs in the Color Benham experiment, the SC and the PC conditions were compared using parametric paired *t*-tests. In the Speed Benham analysis, in each individual, we calculated the correlation between the SC perception (percentage of perceived colors) and the modulation of the connectivity parameters at the 5 rotation speeds. The *r* values were transformed to *z*-scores, and summary statistics using 1-sample *t*-tests were performed for each connection. The same strategy was applied to the correlation analysis between the SC perception and the neural activity in each region.

Results

Functional Localizer Mapping

Representative results of the retinotopic mapping (Fig. 2*a*), color mapping (Fig. 2*b*), and visual motion mapping (Fig. 2*c*) are shown. The regional coordinates were determined together with the coordinates of the local maxima in the present study, along with information provided by previous studies. Based on these local maximum coordinates, the coordinates of the extracted data in the Color and Speed Benham experiments were determined individually (Table 1).

Behavioral Results of the Color Benham Experiment

In the Color Benham experiment (Experiment 1), all subjects perceived the color in all conditions except the static (0 Hz) condition (data not shown). In the debriefing session following the experiment, they reported that they did not notice a difference between the subjective and PC stimuli in the MR scanner because the stimuli switched rapidly every 4 s for 360 trials in each session.

Imaging Results of the Color Benham Experiment

In each condition, the areas of activation were restricted to the occipital cortex. The active areas included both the ventral and dorsal visual pathways. The activation patterns were very similar between the SC and perceptually matched PC conditions in all subjects. Representative results are shown in Supplementary Figure 2. To compare the SC condition with the PC condition, contrast images were created and estimated. Individual contrast images were combined for group analysis. In all the individual analyses, there were no statistical differences between the 2 conditions based on a height threshold of $P < 0.001$ (voxel level) and FWE-corrected $P < 0.05$ at the cluster level for the entire brain. This result was confirmed by

Table 1

Coordinates of the data extraction for DCM analysis

ROI	Sub1			Sub2			Sub3			Sub4			Sub5			Sub6			Sub7		
	x	*y*	*z*	*x*	*y*	*z*	*x*	*y*	*z*	*x*	*y*	*z*	*x*	*y*	*z*	*x*	*y*	*z*	*x*	*y*	*z*
Color Benham experiment																					
V1	−16	−100	−2	−12	−98	−4	10	−100	−4	10	−102	2	−14	−102	−6	14	−102	2	14	−98	4
V2	−24	−96	−4	−20	−92	−4	24	−96	−2	24	−98	−2	−26	−96	−6	28	−98	−2	22	−100	2
V4	−32	−76	−16	−32	−72	−18	28	−76	−16	32	−80	−14	−34	−70	−18	38	−78	−20	36	−72	−16
V4α	−32	−62	−18	−38	−56	−16	34	−56	−20	32	−52	−22	−36	−58	−16	30	−46	−20	44	−52	−12
V5	−44	−74	2	−54	−76	0	50	−78	2	54	−68	8	−54	−76	6	44	−70	−4	46	−78	6
Speed Benham experiment																					
V1	−12	−100	−2	−10	−98	−4	10	−100	−4	10	−102	0	−12	−100	−6	14	−102	0	14	−98	4
V2	−24	−94	−6	−20	−92	−4	24	−98	0	26	−98	−2	−26	−94	−6	28	−98	−2	24	−100	4
V4	−32	−74	−18	−36	−80	−20	28	−72	−20	32	−78	−18	−34	−70	−18	36	−78	−20	34	−76	−12
V4α	−36	−58	−22	−32	−56	−20	34	−52	−16	30	−48	−22	−36	−58	−16	30	−46	−20	30	−54	−20
V5	−44	−80	2	−52	−72	−6	50	−72	2	54	−68	8	−54	−76	8	48	−72	−4	48	−74	6

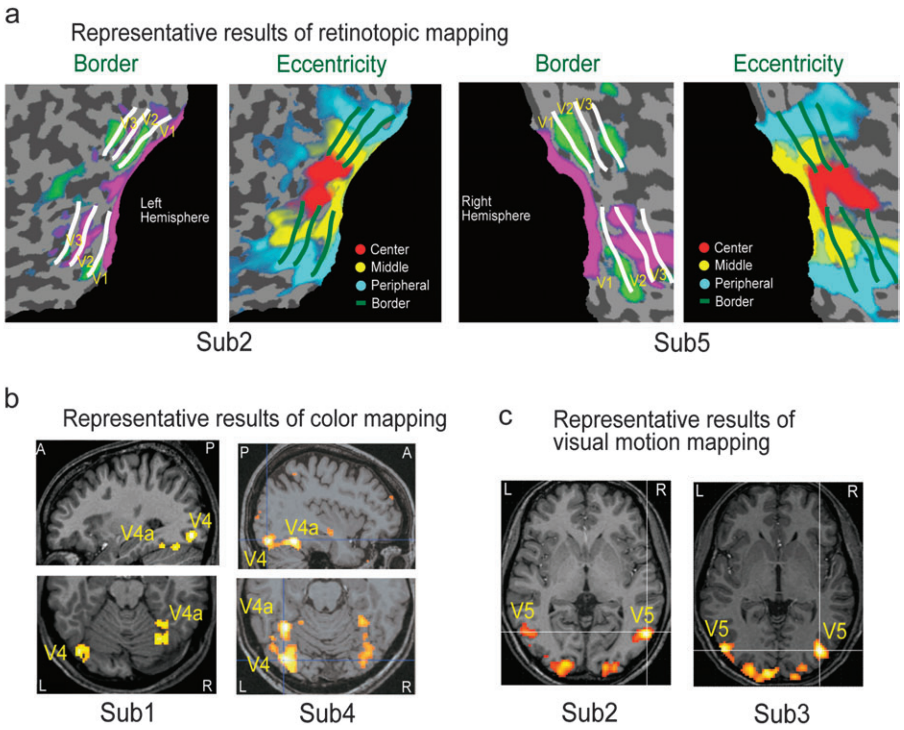

Figure 2. Representative results of the functional localizer mappings. (*a*) Representative results of retinotopic mapping. (*b*) Representative results of the color region mapping. (*c*) Representative results of rotating visual motion mapping.

the group analysis with the same statistical thresholds described above.

We compared the activation between the SC and PC conditions in each ROI (V1, V2, V4, V4α, and V5) that constituted the system of interest for the DCM analysis (Fig. 3). There were no statistically significant differences between the conditions in any of the regions (V1, t_6 = 1.92, P = 0.103; V2, t_6 = 1.99, P = 0.094; V4, t_6 = –0.31, P = 0.766; V4α, t_6 = –0.96, P = 0.373; V5, t_6 = –0.31, P = 0.768). Activation during the nonmatched color conditions did not statistically differ from the activation during the SC condition.

DCM in the Color Benham Experiment

Figure 4 illustrates the modulating effects of the SC condition (left arrows) and the perceptually matched PC condition (right arrows). Using a classical random-effects analysis (P < 0.05), the modulating effect was statistically significant during the SC condition (orange arrows) for V1 to V2, V2 to V1, V2 to V4, V4 to V2, and V4 to V4α and for V1 to V2, V2 to V1, V2 to V4, V4 to V2, V4 to V4α, V2 to V5, and V5 to V4 during the PC condition (blue arrows).

To examine the difference in the modulating effect on the connections between the SC and the PC conditions, a classical paired t-test was conducted. The results showed that there was a statistically significant difference in the modulating effect for the V4 to V2 (t_6 = 3.56, P = 0.012) and V2 to V1 connections (t_6 = 4.92, P = 0.003). More specifically, the V4 to V2 and V2 to V1 modulating effect values for the SC condition were higher than those during the PC condition. The modulating effects from V1 to V2 and from V2 to V4, which were statistically significant with 1-sample t-tests during the PC and the SC conditions, were not significantly different between the PC and the SC conditions when compared using paired t-tests (V1 to V2, t_6 = –1.44, P = 0.200; V2 to V4, t_6 = –1.21, P = 0.227).

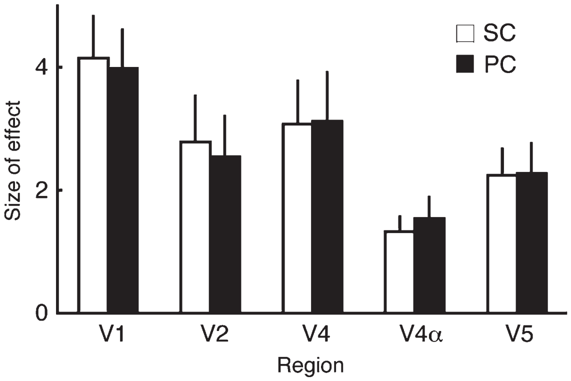

Figure 3. Responses of V1, V2, V4, V4α, and V5 in the Color Benham experiment. Effect sizes (activation) for the SC and PC conditions are plotted in each region. The data were averaged across subjects. Error bars indicate the standard error of the mean.

Behavioral Results of the Speed Benham Experiment

In the Speed Benham experiment (Experiment 2), there were 6 rotation speeds (0, 0.5, 1.5, 3, 4, and 5 Hz). As expected, almost all subjects perceived colors when the Benham's top was rotated at a speed greater than or equal to 3 Hz (Fig. 5). Two of the subjects perceived colors at 1.5 Hz in about one-fifth of the trials. However, during the debriefing session following the Speed Benham experiment, these subjects stated that the color sensation was faint during the 1.5 Hz condition compared with speeds greater than 1.5 Hz.

Imaging Results of the Speed Benham Experiment

Based on the behavioral results, the contrast [(3 + 4 + 5 Hz)] – [(0 + 0.5 + 1.5 Hz)] was used to visualize the areas involved in SC perception. We used a threshold of P < 0.05 with an FWE correction at the voxel level for the entire brain to depict activated regions. The results showed activation in bilateral regions of the ventral visual pathway (lingual gyrus and part of the fusiform gyrus; representative results are shown in Fig. 6, red regions). In contrast, bilateral dorsal visual pathway areas (the lateral side of each hemisphere, V1 to V5 regions) were activated when we examined the main effect of motion [(0.5 + 1.5 + 3 + 4 + 5 Hz)] – [0 Hz] (Fig. 6, cyan regions). This tendency was observed in all 7 participants in the present study.

The averaged activation pattern of each region (V1, V2, V4, V4α, and V5) comprising the system of interest for the DCM is shown in Figure 7. The averaged correlation among subjects between the activity level and the perception of SCs was: in V1 (r_{average} = 0.87; t_6 = 7.74, P < 0.001, 1-sample t-test of the random-effects analysis), V2 (r_{average} = 0.73; t_6 = 18.4, P < 0.001), V4 (r_{average} = 0.85; t_6 = 9.03, P < 0.001), V4α (r_{average} = 0.85; t_6 = 6.61, P < 0.001), and V5 (r_{average} = –0.01; t_6 = –0.12, P = 0.91). The results showed that performance (color perception) was highly correlated with activity in the ventral visual pathway regions.

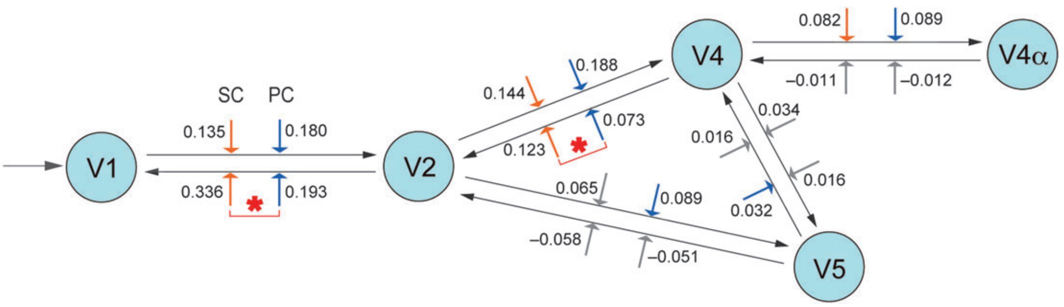

Figure 4. Summary of the DCM results in the Color Benham experiment. The averaged connectivity values of the modulating effects are shown. The arrows perpendicular to the connection between the regions indicate the modulating effect. The left-sided arrows are for the SC condition, whereas the right-sided arrows represent the PC condition. The orange and blue arrows indicate statistically significant findings based on the 1-sample t-test ($P < 0.05$) in the SC and PC conditions, respectively. Red asterisks denote statistically significant differences between the SC and PC conditions ($P < 0.05$ in the paired t-test).

DCM in the Speed Benham Experiment

Figure 8*a* shows a summary of the results of the modulating effect of rotation speed. The modulating effects from V1 to V2, V2 to V4, V4 to V2, and V2 to V1 were greater with increasing rotation speed, whereas the modulating effect from V2 to V5 decreased with increasing rotation speed (thick lines). In the other connections, the modulating effect was not affected by changes in rotation speed. Correlation analyses were conducted to examine the relationships between the modulating effect of each connection and the perception of SCs as a function of disk rotation speed (Fig. 8*b*). The results showed strong positive correlations between SC perception and the modulating effect observed in the V1 to V2 connection ($r_{\text{average}} = 0.83$; $t_6 = 7.04$, $P < 0.001$, 1-sample *t*-test, random-effects analysis); the V2 to V4 connection ($r_{\text{average}} = 0.83$; $t_6 = 7.15$, $P < 0.001$); the V4 to V2 connection ($r_{\text{average}} = 0.93$; $t_6 = 11.04$, $P < 0.001$); and the V2 to V1 connection ($r_{\text{average}} = 0.87$; $t_6 = 6.38$, $P < 0.001$). In contrast, a statistically significant negative correlation was observed in the V2 to V5 connection ($r_{\text{average}} = -0.90$; $t_6 = -7.91$, $P < 0.001$). There were no statistically significant correlations ($P < 0.01$, 1-sample *t*-test, random-effects analysis) with any of the other connections.

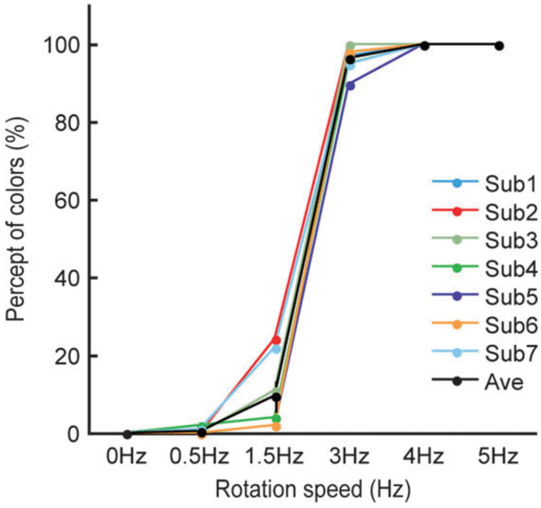

Figure 5. Behavioral results during the Speed Benham experiment. The perception of SCs as a function of the rotation speed of the top is shown for each subject (colored lines). The black line shows the average for all 7 subjects. Error bars indicate the standard deviation.

Discussion

Task-Related Activation Patterns for Benham's Top

During the Color Benham experiment, we matched not only the conscious perception of color but also the rotation speed (5 Hz) of the top. The activation patterns were similar between the SC perception and perceptually matched PC conditions (Supplementary Fig. 2 and Fig. 3). These results suggest that SC perception shares common neural mechanisms with real-color perception.

In the Speed Benham experiment, we focused on the activation correlated with the rotation speed of the top because Benham's top induces color perception only when the rotation speed is in an adequate range. By introducing various rotation speed conditions, we could separate the SC-related activity from the motion-related activity because slow rotation speeds such as 0.5 and 1.5 Hz do not induce color perception but do produce motion perception. The activation corresponding to the SC perception induced by Benham's top rotating at ⩾3 Hz was observed mainly in the ventral visual areas (Fig. 6, red regions; Fig. 7*a*–*c*). This activation pattern was distinct from the motion-related activity that was observed in the dorsal visual pathway (Fig. 6, cyan regions; Fig. 7*d*). Debriefing following the Speed Benham experiment revealed that all subjects experienced motion perception in all conditions except during the static stimulus (0 Hz); however, the

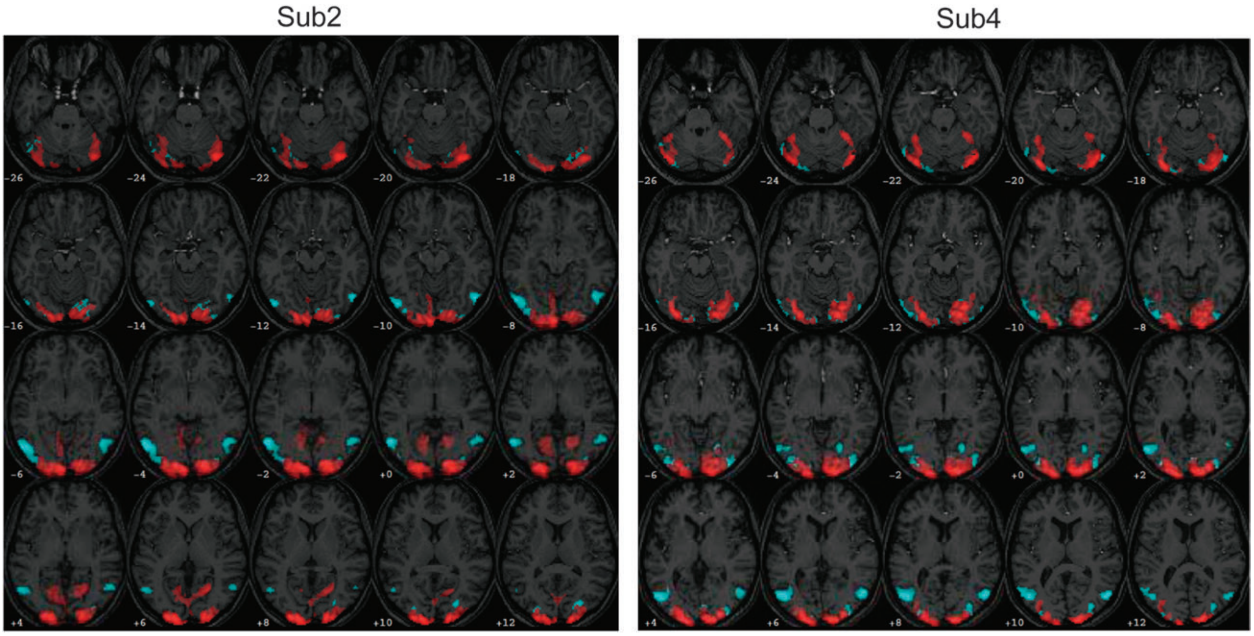

Figure 6. Activated areas during the Speed Benham experiment. Activation results are shown for 2 representative individuals. Red, activation areas correlated with SC perception; cyan, activation areas related to visual motion perception. Activation areas are superimposed on normalized high-resolution T_1 axial slice images of the *z*-axis from $z = -26$ to $z = 12$ mm in 2-mm steps. The threshold was set at $P < 0.05$ with an FWE correction at the voxel level for the entire brain.

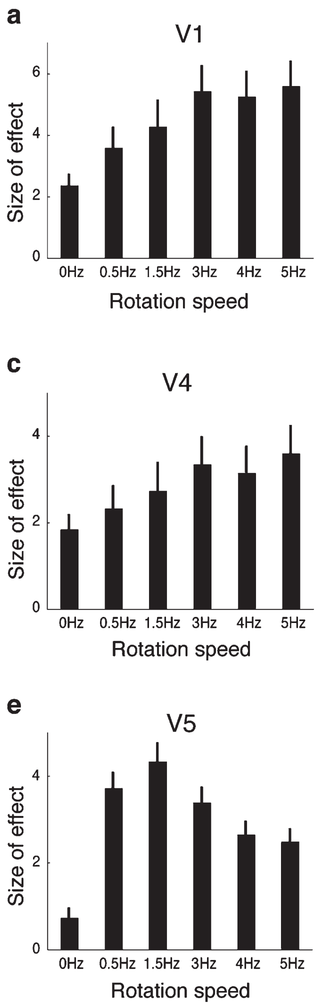

Figure 7. Responses of V1, V2, V4, V4α, and V5 during the Speed Benham experiment. The size of the effect (activation) is plotted as a function of rotation speed (conditions). (*a*) V1 region, (*b*) V2 region, (*c*) V4 region, (*d*) V4α region, and (*e*) V5 region. The data were averaged across subjects. Error bars indicate the standard error of the mean.

strongest motion perception was induced at 1.5 Hz. Consistent with these subjective ratings, the strongest activation in V5 was during 0.5 or 1.5 Hz in almost all subjects (see Supplementary Fig. 3). The same tendency was observed at the local maxima near the V5 region in the Speed Benham experiment (Fig. 7*e*). Thus, the activation corresponding to visual motion was located in the dorsal visual pathway, distinct from SC perception, which involved the ventral visual pathway.

Many anatomical, electrophysiological, and neuroimaging studies have shown that the ventral visual pathway, including V1, V2, V4, and V4α, is strongly involved in color perception (Lueck et al. 1989; Corbetta et al. 1991; Zeki et al. 1991; McKeefry and Zeki 1997; Zeki and Marini 1998; Beauchamp et al. 1999; Conway and Tsao 2006; Conway et al. 2007; see reviews by Bartels and Zeki 2000; Conway 2009). In the present study, we confirmed that color perception was highly correlated with the activity of the ventral visual areas. Our findings suggest that, even during SC perception, the ventral visual pathway is involved in a similar manner as during real-color perception. SC perception (McCollough's colored aftereffect) also involves the color-responsive areas V4 and V4α (Morita et al. 2004), and thus, achromatic stimuli can activate color-processing regions. Other previous studies support these findings (Sakai et al. 1995; Humphrey et al. 1999). However, based on the correlations between color perception and brain activity, we could not clarify the way in which these regions interact as a system to bring about color perception. Consequently, we evaluated the effective connectivity among these regions using DCM.

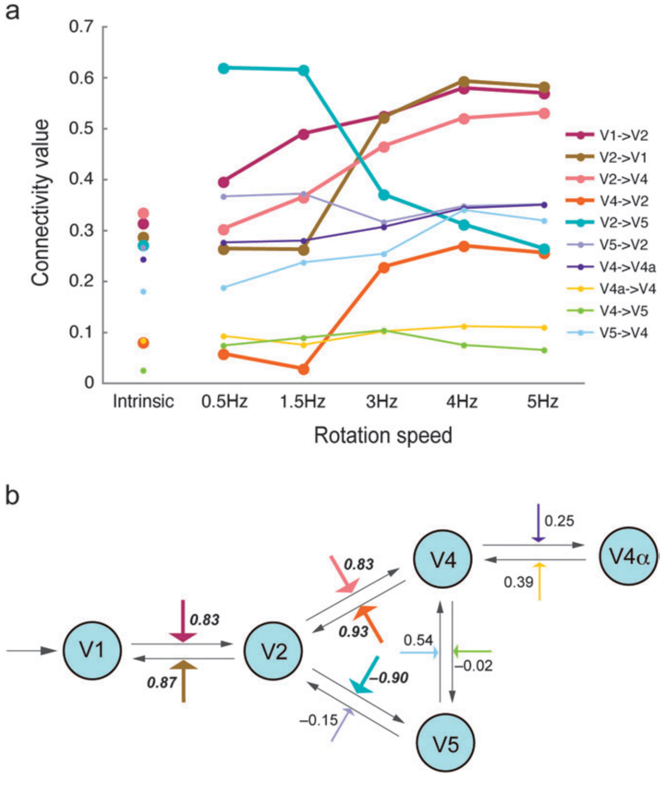

Figure 8. Summary of the DCM results for the Speed Benham experiment. (*a*) The modulating effect in each condition for each connection is shown. (*b*) Correlations between the connectivity value of the modulating effect and the perception of colors as a function of rotation speed. The values indicate the averaged correlation value *r*. Thick arrows denote statistically significant correlations ($P < 0.001$, 1-sample *t*-test).

Effective Connectivity for Benham's Top

DCM of the data from the Color Benham experiment showed differences between the SC and perceptually matched PC conditions in the modulating effect on the backward connectivity from V4 to V2 and V2 to V1 (Fig. 4). Thus, V1 is receiving different information from V4 via V2 in the SC condition compared with the PC condition. This observation supports our hypothesis that the neural representations of the subjective and PCs differ in the connections between V1/V2 and other regions. Considering these results, the stronger effective connectivity from V4 to V2 to V1 in the SC condition could be caused by the SCs induced by an achromatic stimulus, which does not contain the variations in wavelength that would be expected from the colors that are perceived. As we adjusted the output (perception of colors) of the PC condition to match that of the SC condition in the Color Benham experiment, it is conceivable that modulation of the backward connectivity from V4 to V2 to V1 caused the ventral visual system to represent the color percepts in a similar way to the representations evoked by PCs.

Moreover, in the Speed Benham experiment, DCM indicated that the modulating effect increased as a function of rotation speed in the connections between V1 and V4 (i.e., V1 to V2, V2 to V4, V4 to V2, and V2 to V1) (Fig. 8*a*). This change in the modulating effect was highly correlated with the perception of SCs (Fig. 8*b*). These connectivity results suggest that the ventral visual regions, especially V1, V2, and V4, work together as a system to generate color perception and are consistent with our prediction that lower-level color-processing regions and/or the direct connections to these regions play a significant role in SC perception while viewing Benham's top. Although the activation of the regions (V1, V2, V4, and V4α) and some of their connections (i.e., between V1 and V4) showed significant positive correlations with the percept of SCs, the highest correlation was observed from V4 to V2, and the second highest correlation was in the V2 to V1 connection. This indicates that the backward connection from V4 to V2 to V1 might play an important role in the SC perception induced by Benham's top.

As noted in the Introduction, previous psychophysical experiments using a modified Benham's top demonstrated that the SC percept was influenced by stimulus properties over large distances (Le Rohellec et al. 1992; Schramme and Supply 1997) and was generated only under adequate spatiotemporal conditions. This finding implies that additional cortical processing is necessary for the SC percept of Benham's top. It has been suggested that additional phase-sensitive lateral interactions might occur within the parts of the brain that receive retinotopic visual information (von Campenhausen 1968; von Campenhausen and Schramme 1995). Increased connectivity between V1 and V4 is well suited to this prediction because V1, V2, and V4 all conserve retinotopy, and the smallest estimated receptive field sizes near the fovea were in V1, with those in V2 intermediate in size, and those in V4 were large in humans (Smith et al. 2001). According to Zeki and Marini (1998), V1 is concerned with registering the presence and intensity of different wavelengths, whereas V4 is concerned with color constancy operations. As Conway (2009) summarized, each visual cortical region might have a different role in color processing: V1 deals with local color constancy, V2 is involved with hue processing, and V4 processes global color constancy. Importantly, statistically significant differences in modulatory effects were found only in the V4 to V2 to V1 direction in the model. Hence, the modulatory effect of the V4 to V2 to V1 backward connections during SC perception can be interpreted as the top-down augmentation of the recurrent processes in the ventral visual cortical system that usually operate when PC perception emerges.

Color Perception as a Representation of a Neural Ensemble

In the present study, we showed that the effective connectivities between V1 and V2 and between V2 and V4 are highly correlated with color perception, and the V4 to V2 to V1 backward connections play a significant role in the generation of SCs. These results illustrate that color perception is based on the neural ensemble of the ventral visual areas and provide evidence for the claim that each region in the ventral visual cortex has a different role in color processing and that all regions work together as a system to generate color perception.

Conclusion

The present study showed that the ventral visual cortex was activated during SC perception induced by Benham's top spinning at 3–5 Hz. The effective connectivity between V1 and V4 highly correlated with the perception of SCs. The difference in the modulating effect between subjective and PCs was detected in the V4 to V2 and V2 to V1 backward connections, although no differences in activation were seen. These results indicate that effective connectivity from V4 to V1 plays a significant role in generating the SCs induced by Benham's top at particular rotation speeds. This finding supports the notion that color perception emerges from recurrent top-down and bottom-up processes in the ventral visual cortical system.

Supplementary Material

Supplementary Figures 1–3 and other Notes can be found at: http://www.cercor.oxfordjournals.org/.

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Notes

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