Effects of luminance contrast on the color selectivity of neurons in the monkey visual cortex

Tomoyuki Namima

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Department of Physiological Sciences

School of Life Science

The Graduate University for Advanced Studies

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Abstract

Color perception is influenced by the luminance information in various situations. The most notable example is the change in appearance of color stimulus due to the change in luminance contrast against the background. For example, when the luminance of stimulus becomes higher than the background, the appearance of achromatic color is shifted from black to white, and brown also changes to orange.

In the monkey visual cortex, color information is processed along the ventral visual pathway that originates from V1 and consists of areas V2, V4 and the inferior temporal (IT) cortex, and area V4 and IT cortex have been thought to play important roles in color perception. Several recent studies have examined the effect of luminance contrast on the color selective responses in V4 and IT but the results are divergent. Some study reported little effect of luminance contrast on the responses of color selective neurons in posterior IT cortex (PIT) and V4, but other study has found large effects in V4. One possible cause of the discrepancy is the range of colors tested: in the former study, only color stimuli with high saturation at the edge of the gamut were employed while colors with low saturation were used as well in the latter study. So far, no study has compared the effect of luminance contrast across the whole range of colors with both high and low saturation between V4 and PIT. Furthermore, there has been no study that examined the effect of luminance contrast on the color selective responses in anterior IT cortex (AIT).

In this study, I aimed to fully understand the effect of the luminance contrast on the responses of color selective neurons in V4, PIT color area (PITC) and AIT color area (AITC) in a systematic way. For this purpose, I compared the responses of neurons to color stimuli with different luminance contrast using stimuli that evenly distributed across the entire color gamut of the display. While the macaque monkey was performing a fixation task, neuron activities were recorded from V4, PITC and AITC. I examined the effect of luminance contrast on the color selectivity of each neuron as well as the effect of luminance contrast on the representation of color in the population responses of neurons in each area. Two color stimulus set were used to test the color selectivity of neurons. Both color stimulus set contained 16 colors that consisted of 15 chromatic colors whose chromaticity coordinates were evenly distributed on the chromaticity diagram and one achromatic color whose chromaticity coordinate was equal to the gray background. In one set (bright set), the luminance of the stimuli (20 cd/m^2) was higher than the background (10 cd/m^2), and in the other set (dark set), the luminance of the stimuli (5 cd/m^2) was lower than the background.

To examine the effect of the luminance contrast on the color selectivity of each neuron, Pearson's correlation coefficient was calculated between the responses to stimuli in the bright set and those to stimuli in the dark set for each neuron. I found that correlation coefficient for AITC neurons was on average significantly higher than those for neurons in V4 and PITC. This indicates that the patterns of color selective responses in AITC neurons are stable to the change in the luminance contrast of

stimuli than those in V4 and PITC neurons.

Next, to examine how the population responses of color selective neuron varied depending on the luminance contrast, Pearson's correlation coefficient was calculated between the responses of a population of color selective neurons recorded from each area to a color stimulus in the bright set and that in the dark set with the same chromaticity. In V4, the correlation between the population responses to bright stimuli and dark stimuli was lower for cyan to blue colors and higher for magenta to red colors. In PITC, the correlation was lower for colors with low saturation around neutral color. In AITC, in contrast to V4 and PITC, the correlation was high for all colors.

These results indicate that the effect of the luminance contrast on the color representation is markedly different between V4, PITC and AITC. Of these three areas, the pattern of the effects of luminance contrast on the population responses in PITC is most similar to the effect of luminance contrast on the perceptual color appearance. This suggests that population responses of PITC neurons are closely related to the formation of color appearance. In addition, this study shows that the separation between color signal and luminance signal takes place in a stage higher than PITC.

Introduction

Color processing in the ventral visual pathway

In the monkey visual cortex, color information is transmitted through the ventral visual pathway, and it is well known that this pathway plays important role in the processing of color information (Komatsu, 1998; Conway et al., 2010). Ventral visual pathway originates from V1 and consists of areas V2, V4 and the inferior temporal (IT) cortex. Many physiological studies have been conducted to examine the color selectivity of neurons in the areas in the ventral visual pathway. Studies that identified color selective neurons in area V4 have played an important role in the elucidation of functional specialization in the extrastriate cortex. Although it was initially thought that color selectivity is an universal property of V4 neurons, subsequent studies have suggested that the distribution of color selective neurons was not uniform across area V4 (Zeki, 1983a; Conway and Tsao, 2006; Tanigawa et al., 2010). More recently, detailed examination of the property of color selective neurons in IT cortex was initiated (Komatsu et al., 1992; Komatsu and Ideura, 1993), and imaging studies using techniques such as 2DG, PET and fMRI have shown that multiple small regions exist in IT cortex that are strongly activated by color stimuli (Takechi et al., 1997; Tootell et al., 2004; Conway and Tsao, 2006; Harada et al., 2009). An electrophysiological study in the posterior IT cortex (PIT) has reported a region around the posterior-middle-temporal sulcus (PMTS) where a crude retinotpic map exists and where

color selective neurons are clustered and named this area as PIT color area (PITC) (Yasuda et al., 2010). In the anterior IT cortex (AIT), a region that richly contains neurons with sharp color selectivity was identified in the cortical region around the posterior end of the anterior-middle-temporal sulcus (AMTS) and this region is called AIT color area (AITC) (Komatsu et al., 1992; Koida and Komatsu, 2007; Matsumora et al., 2008; Banno et al., 2010).

Involvement of color selective neurons in different aspects of color vision

Lesion studies of monkeys have shown that damage in area V4 caused deficit in color constancy (Walsh et al., 1993) and the damage in IT caused deficit in color discrimination (Heywood et al., 1995; Huxlin et al., 2000). These previous studies suggested that area V4 and IT cortex are involved in the neural basis underlying different aspects of color perception. Color selective neurons in V4 have been shown to possess properties that can be associated with color constancy (Zeki, 1980, 1983b; Schein and Desimone, 1990; Kusunoki et al., 2006). On the other hand, AITC color selective neurons have been shown to exhibit responses that correlate with the color discrimination behavior of the monkey (Matsumora et al., 2008). Response properties of color selective neurons reported in these electrophysiological studies seem to correspond to the results of lesion studies in V4 and AIT. With respect to the categorical perception of color that is another basic property of color perception, color selective responses that may be associated with color category have been reported in each area

from V1 through AIT (Komatsu et al., 1992; Yoshioka et al., 1996; Stoughton and Conway, 2008). However, a recent study (Koida and Komatsu, 2007) has reported that task-dependent modulation of color selective activities in AITC is stronger when the monkey performs color categorization, suggesting that AITC plays an important role in color categorization.

Effect of luminance contrast on color perception

One important problem of color vision that was not been addressed in the above studies is the relationship between color and luminance. Although color information and luminance information are processed through parallel pathways in early visual stages, it is well known that color perception is influenced by the luminance information in various situations. The most notable example is the change in appearance of color stimulus due to the change in luminance contrast against the background. For example, when the luminance of stimulus becomes higher than the background, the appearance of achromatic color is shifted from black to white, and brown also becomes orange. Although at which stage of the visual processing and how the effect of luminance contrast takes place and forms the appearance of color stimuli that depends on the luminance contrast are important questions in color vision, it is not well understood where and how the interaction between color and luminance signals occur in the ventral visual pathway.

Several recent studies have examined the effect of luminance contrast on the color selective responses

in V4 and IT. In one study, Conway and colleagues (2007) found little effect of luminance contrast on the responses of color selective neurons (glob cell) in PIT and V4. In this study, only color stimuli with high saturation at the edge of the gamut were employed. However, V4 neurons that prefer colors with lower saturation have been also reported (Kusunoki et al., 2006; Kotake et al., 2009), and large effects of luminance contrast on the color selective responses in some V4 neurons have also been reported (Yoshioka et al., 1996; Bushnell et al., 2011). Presumably, the difference might result from whether the stimulus set included colors with low saturation and achromatic color (Yoshioka et al., 1996; Bushnell et al., 2011) or did not include such stimuli (Conway et al., 2007), because the effect of luminance contrast on the color perception tends to be large for these colors. Therefore, in order to understand the effect of luminance contrast on the responses of color selective neurons in a systematic way, it should be important to examine the effect of luminance contrast on the color selectivity by using stimuli across as wide range of chromaticity as possible that include both colors with low saturation and those with high saturation.

In the present study, I aimed to systematically examine how the color selectivity of neurons in V4, PITC and AITC are affected by the luminance contrast of the color stimuli. To study this problem, I compared the responses of neurons to color stimuli with different luminance contrast using stimuli that evenly distributed across the entire color gamut of the display. Neuron activities were recorded from V4, PITC and AITC, and I compared the effect of luminance contrast on the color selectivity of

each neuron as well as the effect of luminance contrast on the representation of color in the population responses of neurons among three areas. I found that the effect of luminance contrast on the color representation was markedly different between V4, PITC and AITC. In particular, the effect was especially large for neutral colors (white, gray, black) and for colors with low saturation in PITC that resembles the effect of luminance contrast on the perceptual phenomena of color appearance. These results suggest that population responses of PITC neurons are closely related to perception of color appearance.

Materials and methods

Four adult male macaque monkeys (Macaque fuscata) (weighing 5.1~7.7 kg) and two adult female macaque monkeys (weighing 5.0~6.3 kg) were used for the experiments. All procedures for animal care and experimentation were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and were approved by Institutional Animal Care and Use Committee of National Institute of Natural Sciences.

Surgery

Prior to electrophysiological recording, under the general anesthesia, sterile surgery was conducted to attach a head holder (metal or plastic) and a plastic recording chamber to the skull using dental cement and cortical screw. After surgery, the monkeys was allowed to recover for several weeks before the electrophysiological recordings began. During a week after the surgery, antibiotic (Cefazolin sodium) was given every 12 hours.

Recording sites

In the present study, we determined the recording sites based on the stereo coordinates and sulcal landmarks using MRI images as references. Before surgery, the position of the lunate sulcus (LS),

the superior temporal sulcus (STS), the inferior occipital sulcus (IOS), the posterior middle temporal sulcus (PMTS), and the anterior middle temporal sulcus (AMTS) were identified on MRI images.

We recorded neuron activities from AITC in two hemispheres of two monkeys (monkeys CO and KM), from PITC in two hemispheres of two monkeys (monkeys KM and LW), and from area V4 in four hemispheres of three monkeys (monkeys AL, SI and SK) (Figure 1A).

The recording chamber for AITC was placed above the position corresponding to posterior end of the AMTS, so that the electrode is vertically penetrated through the brain to reach the IT gyrus. The recording chamber for PITC was placed on the lateral surface of IT gyrus so as to cover the regions dorsal and ventral to the PMTS. The recording chamber for area V4 was placed so as to cover the positions corresponding to the dorsal V4 on the prelunate gyrus. For PITC and V4, electrodes were penetrated directly to these areas through the dura.

To precisely locate the electrodes, we used plastic grids. Electrodes were advanced through a stainless steel guidetube situated within a plastic grid in which holes were placed at an interval of 1 mm. We used two types of grids in which the positions of holes were shifted 0.5 mm vertically and horizontally with respect to one another so that a minimum interval of 0.7 mm between holes was attained.

The penetration sites of V4 were identified based on the grid coordinates of MRI images and the depth profiles of the electrode penetrations. These identified recording sites in V4 in two

hemispheres are illustrated in Figure 2. The recording sites of PITC neurons were confirmed by the histological observation under microscopic examination after all recording session. Detailed histological procedures and recording sites in PITC have been previously described (Banno et al., 2010; Yasuda et al., 2010). The results of the recordings from PITC are partially reported in a previous paper (Yasuda et al., 2010). The recording sites in AITC were located around the posterior end of the AMTS on IT gyrus (Monkey CO: A13-A22, L16-L22, and Monkey KM: A16-A24, L14.5-L24.5). The recording sites of AITC neurons in monkey KM were checked by the histological observation. We identified the recording sites of AITC in monkey CO on the MRI image based on the depth profile of the electrode track and by superimposing the X-ray image (Toshiba TR-80A-ES-L, 70 kV, 20 mA, and 0.4 s) of the electrode on the MRI image.

Visual stimuli

Visual stimuli were generated using a graphics board (VSG2/3, Cambridge Research Systems) in the computer and displayed on a cathode-ray tube (CRT) monitor (Sony GDM-F500R, TOTOKU CV921X). The chromaticity coordinates and the luminance of the visual stimuli were calibrated using a spectrophotometer (PR650) or a colorimeter (CS200, Konica Minolta). Visual stimuli were presented on a neutral gray background (10 cd/m^2 unless otherwise noted, x=0.3127, y=0.3290) (Fig. 1B, color#16). The main question I address in this study is how the polarity of luminance contrast

of stimulus affects the responses of color selective neuron. To study this problem, we used 2 color stimulus set to test the color selectivity of neurons whose luminance were either brighter (bright set) or darker (dark set) than the gray background.

Both color stimulus set contained 16 colors (color#1~16, Fig. 1B) that consisted of 15 chromatic colors whose chromaticity coordinates were evenly distributed on the chromaticity diagram (color#1~15, Fig. 1B) and one achromatic color whose chromaticity coordinate was equal to the gray background (color#16, Fig. 1B). Stimulus colors were defined on the basis of the CIE 1931 xy chromaticity diagram (Fig. 1B).

In bright set, all stimuli were brighter than the background (10 cd/m^2) and had the same luminance (20 cd/m^2) except for the blue color (#15, 11~12 cd/m^2). In dark set, all 16 stimuli were darker than the background (10 cd/m^2) and had the same luminance (5 cd/m^2). Luminance contrast of bright and dark sets were equalized in terms of Michelson contrast. Because the luminance of blue color (color #15) in bright set was different from other colors, we omitted the responses to blue colors (color#15) for both bright and dark set from the quantitative analysis.

In the recording from PITC and V4, we mapped the receptive fields (RF) for each neuron by presenting the preferred stimulus at various positions in the visual field and determined the horizontal and vertical extents of the RF. Visual stimuli to test the color selectivity were smaller than the RF and were presented within the RF. In the recording from AITC, visual stimulus was presented at the

foveal center at an adequate size. Stationary flash stimuli were used in all the experiments.

When we tested color selectivity, the shape of the stimuli was fixed and chosen from seven to 19 geometrical shapes (Fig. 1C; square, oblique square, circle, star, cross, oblique cross, triangle, vertical bar, and oblique bar in the clockwise direction, horizontal bar and oblique bar in the counterclockwise direction, narrow diamond and broad diamond (vertical, oblique in the clockwise direction, horizontal and oblique in the counterclockwise direction). Many V4 neurons and PITC neurons exhibited selectivity to both color and shape (V4, Fig. 2BC; PITC, Figs. 3 and 10 in Yasuda et al., (2010)), and after a single unit was isolated, we attempted to find the optimum combination of the color and shape to which the neuron most strongly responded in each neuron. In V4, we used all 19 shapes (95 neurons) or 11 shapes (48 neurons) other than diamonds. In PITC, we used 11 shapes (82 neurons) other than diamonds or seven shapes (2 neurons) other than both diamonds and bars. In AITC, we used 11 shapes (125 neurons) other than diamonds or seven shapes (23 neurons) other than both diamonds and bars. Each of these shape stimuli was painted homogeneously with a single color.

Behavioral task

During the experiment, monkeys were seated on a primate chair and faced a CRT monitor at a distance of 56 cm. The monkeys were trained to fixate on a small white dot (0.1 degree in diameter) presented at the center of the monitor. Monkeys were required to maintain eye position within an

eye window (1.5×1.5~3.0×3.0 degree for recording from IT and 1.5x1.5～1.85x1.85 degree for recording from V4) throughout the trial. If the monkey maintained fixation until the fixation spot disappeared, a drop of water or juice was given as a reward. If the monkeys' gaze deviated from the eye window, the trial was aborted, and an intertrial interval (ITI) immediately started. Eye position was monitored using an eye coil or an infrared eye camera system (ISCAN).

A trial started when the fixation spot turned was on, and color stimulus was presented one to five times within a trial. In recording from IT of monkeys KM and LW, visual stimulus was presented once in a trial for 500ms duration. In recording from IT of monkey CO, visual stimuli were presented three times for 300ms duration each with 300 ms interstimulus intervals. In recording from V4, stimuli were presented two to five times for 300ms duration each with 200 or 300 ms interstimulus intervals. When the visual stimulus was presented at the foveal center in the IT recording, the fixation spot was turned off for a period extending from 350 or 300 ms before visual stimulus onset until 260 or 300 ms after stimulus offset, respectively. Otherwise, the fixation spot was turned on during the entire trial. A stimulus was chosen randomly from the stimulus set in each trial regardless of the recording site.

Electrophysiology

A varnish-coated tungsten microelectrode (200μm in diameter, Frederick Haer) was penetrated

through a stainless steel guide tube fixed within a grid hole, and neuron activities were recorded. The electrode was advanced by a hydraulic microdrive (Narishige). In recording from the PITC and V4, tip of a stainless guide tube was fixed to contact with dura mater, and we advanced the electrode through the dura mater. In the recording from the AITC, we first identified regions where color selective neurons were clustered by systematic mapping, and inserted the guide tubes into the brain and then sampled neuron activities from these regions extensively using a thinner tungsten microelectrodes (125μm in diameter, Frederick Haer). The tips of the guide tubes were positioned approximately 5~10mm above the targeted cortical regions. Recordings through a guide tube inserted in the brain continued for up to three weeks.

Neuronal signals were amplified, sampled at 25 kHz, and stored on a computer for off-line analysis. Behavioral events were recorded at 1 kHz. To inspect the visual responses, neuronal signals were discriminated on the basis of spike amplitude, converted to pulses, and displayed online as rasters and peristimulus time histograms (PSTHs). Neuronal signals and discriminated pulses were also fed to a speaker for audio monitoring.

Data analysis

Off-line quantitative data analysis was conducted only for single neurons. For off-line analysis of neuronal data, we first used a template-matching algorithm to isolate spikes with temporal resolution

of 1ms. We then computed the average firing rate of the isolated spikes during 50-350 ms after stimulus onset, taking into account a response latency of 50 ms. From this average, we subtracted the firing rate before stimulus presentation (300-0 ms before stimulus onset, baseline activity), and the resultant rate was taken as a measure of the neuronal response to the visual stimulus. Neural responses were analyzed only for correct trials, and the minimum number of repetition of each stimulus accepted for analysis was five.

Only neurons whose response to the optimal color was larger than 10 spike/s and whose discharge rates during presentation of the optimal color were significantly different from baseline (Student's t-test, $P < 0.05$) were included in the sample for analysis. In the following text, 'significant responses' means that the responses to a given stimulus set satisfied above two criteria.

To quantify the strength of the color selectivity of each neuron, a selectivity index was calculated as 1 – (minimum response)/ (maximum response). We also used one-way analysis of variance (ANOVA) to evaluate whether the variation in the responses to stimuli within a set of test stimuli was significant. When the selectivity index was larger than 0.6 (i.e., the maximum response was more than 2.5 times the minimum response) and response variation was significant (ANOVA, $P < 0.05$), the neuronal responses were regarded as stimulus selective. To quantify the sharpness of the stimulus selectivity, we calculated a sparseness index (Rolls and Tovee, 1995; Vinje and Gallant, 2000), which was defined as

$$\text{Sparseness Index} = \left[1 - \frac{\left(\sum_{i=1}^{n} \frac{r_i}{n}\right)^2}{\left(\sum_{i=1}^{n} \left(\frac{r_i^2}{n}\right)\right)}\right] / (1 - 1/n)$$

where r_i is the firing rate to the i th stimulus in the set of n stimuli. If r_i was a negative value, it was replaced to zero. This index indicates the degree to which responses are unevenly distributed across the set of stimuli. We used this modified version of the sparseness index (Vinje and Gallant, 2000) because it should be more intuitive if sharper selectivity yields a larger value of the index. When all stimuli evoke the same response amplitude, the sparseness index is minimum and has a value of 0. As the stimulus selectivity sharpens, the index becomes larger. If only one stimulus among the set evokes a response, the index value is at a maximum and is equal to 1.

Comparison between the responses to the bright set and those to the dark set was conducted for neurons in which both bright and dark set generated significant responses and selectivity index to at least one of bright or dark set was >0.6. In the following text, these neurons will be referred to as "color selective neuron" (V4, n=71; PITC, n=58; AITC, n=82. Table 1). Neurons that exhibited significant response only one of either bright or dark set were not analyzed even if they exhibited color selectivity to responsive set (V4, n=31; PITC, n=17; AITC, n=32. Table 1). As the primary measures of color selective responses, maximum response, average response, selectivity index and sparseness

index were calculated for bright set and for dark set separately based on the responses to 14 chromatic colors except for blue (color#15) and an achromatic color (color#16).

A color selective neurons whose sparseness index was larger than 0.3 for at least one stimulus set was defined as a “sharply color selective neuron”. On the other hand, a color selective neurons whose sparseness index was smaller than 0.3 for both bright and dark set was defined as a “broadly color selective neuron”.

Test of the effect of the luminance contrast

We quantitatively examined the effect of polarity change of luminance contrast on the response properties of color selective neurons in several ways. First, we computed four measures of response properties, namely maximum response across a stimulus set, mean response across a stimulus set, selectivity index and sparseness index, for both bright and dark set and compared each measure between two stimulus sets statistically (Two-sample Wilcoxon signed-rank test).

Secondly, to examine the effect of polarity change of luminance contrast on the color selectivity of each neuron, we calculated Pearson’s correlation coefficient (r) between responses to 15 colors of bright set (colors except for bright-color#15) and responses to 15 colors of dark set (colors except for dark-color#15) for each neuron. If correlation coefficient is equal to unity, this means that there is no effect of luminance contrast on the color selectivity of a neuron. When the pattern of the color

selectivity was different between bright set and dark set, correlation coefficient decreases. If the responses to bright set and those to dark set exhibited opposite pattern, correlation coefficient will take negative value.

To examine how the population responses of color selective neuron varied with respect to the polarity of luminance contrast, we calculated Pearson's correlation coefficient (r) between the responses of a population of color selective neurons recorded from each area to bright set and those to dark set for each color with the same chromaticity coordinate. If a population of neurons exhibited the same pattern of responses to a color in the bright set and the same color in the dark set, the correlation coefficient (r) becomes unity. As the pattern of population responses to a color becomes dissimilar between the bright and dark set, the correlation coefficient (r) decreases.

Multi-dimensional scaling analysis

To understand how the color selective neurons in each area carry the information of color and luminance contrast, we conducted multi-dimensional scaling (MDS) analysis for quantitative examination of the dissimilarities of population neural responses across the stimuli in bright and dark set in each area.

To do this, first, Pearson's correlation coefficients (r) between the responses of the population of color selective neurons to all possible pairs of stimuli in bright and dark set (a total of 30 stimuli except

for blue (color#15)) were computed. We regarded 1 – r as the neural distance between two stimuli, and we generated distance matrix based on the neural distances across all pairs of stimuli. We applied nonmetric MDS to the distance matrix, and the resultant dissimilarity between each stimulus was plotted on a two-dimensional plane.

Results

In AITC, 155 well isolated visually responsive neurons were recorded. Of these visually responsive neurons, 107 neurons showed visual responses to both bright set and dark set (CO: 60 neurons, KM: 47 neurons) (Table 1). Eighty-two of them were classified as color selective neurons (CO: 40 neurons, KM: 42 neurons) (Table 2). Forty-eight visually responsive neurons responded to only one of either bright set or dark set. Of these 48 AITC neurons, 32 neurons showed color selective responses, but these neurons were excluded from the analysis in this paper (2-1, Table1).

In PITC, 90 well isolated visually responsive neurons were recorded. Of these, 69 neurons showed visual responses to both bright set and dark set (KM: 29 neurons, LW: 40 neurons) (Table 1). Fifty-eight of them were color selective neurons (KM: 29 neurons, LW: 29 neurons) (Table 3). Twenty-one visually responsive neurons responded to only one of either bright set or dark set. Of these 21 neurons, 17 neurons showed color selective responses, but these neurons were excluded from the analysis in this paper (2-1, Table1).

In V4, 149 well isolated visually responsive neurons were recorded. Of these, 108 neurons showed visual responses to both bright set and dark set (AL: 59 neurons, SI: 30 neurons, SK: 39 neurons) (Table 1). Seventy-one of them were color selective neurons (AL: 40 neurons, SI: 19 neurons, SK: 12 neurons) (Table 4). Forty-one visually responsive neurons responded to only one of either bright

set or dark set. Of the 41 neurons, 31 showed color selective responses, but these neurons were excluded from the analysis in this paper (2-1, Table1). Similar color selective neurons that selectively responded to bright or dark stimuli were reported in area V4 and were referred to as 'Bright cell' and 'Dark cell' in previous studies (Yoshioka et al., 1996; Bushnell et al., 2011).

In the following, I present the results of examining the effect of the polarity change of luminance contrast on the color selectivity of color selective neurons that responded to both bright set and dark set. To start with, Figures 3, 4, 5 show the results of comparison between neural responses to bright set and those to dark set in three example color selective neurons from each of AITC, PITC, and V4.

Examples of AITC color selective activities

Figure 3 shows the responses of three representative color selective neurons recorded from the AITC. Cell 1 whose responses are illustrated in Figure 3A showed color selective responses sharply tuned for red color to both bright set (left panel, Fig. 3A) and dark set (middle panel, Fig. 3A). In the left and middle panels, time course of the responses is shown by rasters and peristimulus time histograms (PSTHs), and response magnitudes to color stimuli are represented by the diameters of circles and are plotted at positions that correspond to their chromaticity coordinates in the insets (bubble plot). As can be seen in the bubble plot, the pattern of color selectivity was similar between bright and dark set, but the response magnitude were different: responses were stronger for bright set

(maximum responses: color#5, 54.2spk/sec) than for dark set (maximum responses: color#5, 25.8spk/sec). In the right panel, scatter plot shows the relationship between responses to bright set (horizontal axis) and those to dark set (vertical axis) (right panel, Fig. 3A). To quantitatively compare the patterns of the neural responses to bright set and dark set, I calculated the Pearson's correlation coefficient (r) between responses to bright set and responses to dark set. Large correlation coefficient (r=0.992) was obtained and this indicates that color selectivity between responses to bright set and dark set were highly similar for this neuron. Cell1 is a neuron that showed the highest correlation coefficient (r) among the sample of AITC neurons.

Cell 2 showed similar color selective responses to blue colors for both bright and dark set (left panel, Fig. 3B). If this neuron, correlation coefficient between the pattern of neural responses to bright set and dark set was 0.925 (right panel, Fig. 3B).

Cell 3 showed sharply color selective responses that were strongest to green color (color #1) for bright set and to green-yellow color (color#2) for dark set, respectively. Color selectivity and response magnitudes were similar between bright set and dark set, although the preferred color is slightly shifted between two sets. Correlation coefficient between the neural responses to bright set and dark set was 0.810. This value was representative among the population of AITC neurons as shown later in Figure 6A. In most of AITC, color selectivity was analogous between responses to bright set and those to dark set.

Preferred colors of these example AITC neurons shown above were different. Similarly, color selective neurons that were tuned to a variety of colors were recorded in both PITC and V4.

Examples of PITC color selective activities

Figure 4 shows the responses of three representative color selective neurons recorded from the PITC. Cell 1 showed sharply color-tuned responses to colors ranging from green to blue for both bright set (left panel, Fig. 4A) and dark set (middle panel, Fig. 4A). Response amplitudes, strength of color selectivity and sharpness of color selectivity for bright set were analogous to those for dark set. Correlation coefficient between the responses to two sets of stimuli was 0.970 (right panel, Fig. 4A). Cell 1 is a neuron that showed the highest correlation coefficient among the sample of PITC neurons.

Cell 2 showed selective responses to red color for both bright set (left panel, Fig. 4B) and dark set (middle panel, Fig. 4B). Strength of color selectivity and the maximum response amplitudes were similar between responses to bright set and dark set, but the sparseness of the color selectivity markedly differed between two stimulus set. Correlation coefficient between responses to bright set and dark set was 0.717. In PITC, many neurons showed the degree of correlation similar to that of Cell 2 (Fig. 6B).

Although Cell 3 showed sharply color selective responses to both bright set and dark set, responsive region in the chromaticity diagram clearly shifted between the responses to bright set and those to dark

set (left panel and middle panel, Fig. 4C). For bright set, the largest response was obtained by purple (color#14, left panel, Fig. 4C). By contrast, this neuron exhibited selective responses to colors from magenta to red (color#12 and 9, middle panel, Fig. 4C) for dark set. Response magnitude also differed between two stimulus set: maximum response amplitude for dark set was less than half of that for bright set. Correlation coefficient between responses to bright set and dark set was 0.150 (right panel, Fig. 4C), which was relatively low in PITC (Fig. 6B).

Examples of V4 color selective activities

Figure 5 shows the responses of three representative color selective neurons recorded from area V4. Cell 1 selectively responded to colors from red to magenta for both bright set and dark set with strongest response to magenta for bright set (color#12, left panel, Fig. 5A) and to red for dark set (color#9, middle panel, Fig. 5A), respectively. Strength and sharpness of color selectivity were similar between responses to bright set and dark set, and correlation coefficient between the responses to two sets was 0.853 (right panel, Fig. 5A).

Cell 2 responded to a range of colors from white, cyan to blue with the strongest response to cyan for bright set (color#10, left panel, Fig. 5B) while it responded to more greenish colors around green-yellow with low saturation (color#7) for dark set (middle panel, Fig. 5B). In this neuron, both response amplitude and preferred color differed between responses to bright set and dark set, and

correlation coefficient between the responses to two sets was 0.477 (right panel, Fig. 5B). Many V4 neurons showed similar degree of correlation as cell 2.

In cell 3, the pattern of color selectivity considerably changed between responses to bright set and dark set. Cell 3 showed broad and bimodal color selective responses peaked at green and purple for bright set (left panel, Fig. 5C). On the other hand, this neuron showed broad color selective responses that was strongest around purple to red for dark set (middle panel, Fig. 5C). Correlation coefficient between the responses to two sets was -0.172 (right panel, Fig. 5C).

Effect of luminance contrast on the color selectivity of a neuron

As can be seen in Figures 3 to 5, the effect of luminance contrast on the color selective responses varied across neurons, and it appears that the effect of luminance contrast on color selectivity tends to be relatively small compared in AITC with other areas.

To compare the effect of the luminance contrast on the color selective responses across three areas, I calculated Pearson's correlation coefficient (r) between responses to bright set and responses to dark set for each neuron, and compared the distribution of the correlation coefficients (r) across three areas (Figs. 6ABC).

In all three areas, correlation coefficients of neurons ranged from negative value to values close to unity, but the distribution of the correlation coefficient was different across three areas. The

distributions appears gradually more skewed to large values in the order from V4, PITC to AITC. In particular, the distribution was skewed to high values around unity in AITC. The difference in the distribution of correlation coefficient is more clearly seen in the cumulative histogram (Fig. 6D). When I compare the cumulative histogram of the correlation coefficient across three areas, that for AITC was clearly shifted rightward compared with those in V4 and PITC, and that in PITC seems slightly shifted rightward compared with that in V4.

The medians of correlation coefficient of V4, PITC, and AITC were 0.477, 0.557, and 0.781, respectively. Correlation coefficients significantly differed between V4 and AITC ($p< 0.001$) and between PITC and AITC ($p< 0.01$) (Mann Whitney U test, Bonferroni corrected), respectively, but the difference between V4 and PITC was not significant. These results indicate that the effect of luminance contrast on the pattern of color selective responses in AITC was smaller than those in V4 and PITC.

I next examined the effect of luminance contrast using the same analysis separately for sharply color selective neurons and broadly color selective neurons. To do this, I classified color selective neurons in each area into sharply color selective neurons (solid bar, Fig6A: V4; n= 42, PITC; n= 43, AITC; n= 62) and broadly color selective neurons (open bar, Fig6A: V4; n= 29, PITC; n= 15, AITC; n= 20) based on the sparseness index (see Materials and Methods).

In V4, median of the correlation coefficients of sharply color selective neurons (0.508) was larger

than that of broadly color selective neurons (0.29) but the difference was not significant (two sample Mann-Whitney U test, $p \geqq 0.1$).

In PITC and AITC, medians of the correlation coefficients of sharply color selective neurons (0.605 in PITC, 0.831 in AITC) were significantly larger than those of broadly color selective neurons (0.198 in PITC and 0.445 in AITC) (two sample Mann-Whitney U test, $p<0.01$), indicating that the effect of luminance contrast on color selectivity was larger for broadly color selective neurons than sharply color selective neurons in PITC and AITC.

I then compared the distribution of the correlation coefficient between the responses to bright set and dark set across three areas separately for sharply color selective neurons and broadly color selective neurons (bottom, Figs. 6EF). For sharply color selective neurons, the cumulative histogram for AITC was shifted rightward compared with V4 and PITC, and there was significant difference in median of the correlation coefficient between V4 and AITC ($p<0.001$) as well as between PITC and AITC ($p<0.001$) (Fig. 6E, two sample Mann-Whitney U test, Bonferroni corrected). For broadly color selective neurons, although the cumulative histogram tended to shift rightward in the order from V4, PITC to AITC, correlation coefficients were not significantly different across three areas (Fig. 6F, two sample Mann-Whitney U test, Bonferroni corrected, $p \geqq 0.05$).

These results indicate that the effect of luminance contrast on the color selectivity of color selective neurons were smaller in AITC than PITC or V4, and that this tendency was more obvious in sharply

color selective neurons than broadly color selective neurons.

Effect of luminance contrast on the response properties of neurons

In the above section, I have shown how the luminance contrast affects the pattern of color selectivity of a neuron. As seen in the example neurons in Figures 3 to 5, response magnitude, strength of color selectivity (color selectivity index) and sharpness of color selectivity (color sparseness index) of individual neurons can be also affected by the luminance contrast, so I examined how these basic response properties were affected by the luminance contrast of stimuli.

Figures 7A-D showed the relationships between an index of each of these basic response properties obtained for bright set and dark set in a scatter plot for each area. Figure 7A shows the relationship between the maximum response of each neuron to bright set (horizontal axis) and that to dark set (vertical axis) for V4 (left), PITC (middle) and AITC (right). Each dot corresponds to one neuron. Diagonal line connects the points where the maximum responses of a neuron were identical between bright set and dark set. While several dots are located near the diagonal line, majority of dots are deviated from the diagonal line, indicating that the maximum responses tended to differ between bright set and dark set. A gray circle indicates the median of the maximum response across the population of neurons in each area. Medians of the maximum response were 31.5spk/s for bright set and 25.6spk/s for dark set in V4, 28.1spk/s for bright set and 30.3spk/s for dark set in PITC, and 22.8spk/s

for bright set and 23.6spk/s for dark set in AITC, respectively. There was no significant difference in the maximum response between bright set and dark set for all of three areas (two sample Wilcoxon signed-rank test, $p \geqq 0.1$). This indicates that, as a population, these was no clear bias in the maximum response that depends on the polarity of the luminance contrast.

I also compared the relationship between mean responses for bright set and dark set for each of V4, PITC and AITC (Fig. 7B). In V4, median of the mean response for bright set (14.2spk/s) was significantly larger than that for dark set (9.3spk/s) (two sample Wilcoxon signed-rank test, $p<0.05$). Medians of the mean response were 10.7spk/s for bright set and 12.1spk/s for dark set in PITC, and 8.3spk/s for bright set and 8.0spk/s for dark set in AITC, respectively. There was no significant difference in the mean response between bright set and dark set (two sample Wilcoxon signed-rank test, $p \geqq 0.1$). These results indicate that there was slight but significant increase in the mean response to bright stimuli compared with those to dark stimuli in V4, but not in PITC nor AITC.

I then examined whether the strength or sharpness of the color selectivity of color selective neuron were affected by the luminance contrast of the visual stimuli. First, I compared the color selectivity index between the responses to the bright set and dark set. Figure 7C shows the relationship between the selectivity index of each neuron to bright set (horizontal axis) and that to dark set (vertical axis) for V4, PITC and AITC. This figure shows the data for all color selective neurons in each area. Some of them exhibited color selectivity to both bright set and dark set (dot symbol, Fig. 7C), but

others exhibited color selectivity either only to bright set (cross symbol, Fig. 7C) or only to dark set (triangle symbol, Fig. 7C), (Tables 2-4). There was no significant difference in the proportion of neurons that showed color selectivity to both bright and dark sets (46/71 = 64.8% in V4, 44/58 = 75.9% in PITC, 68/82 = 82.9% in AITC) or neurons that showed color selectivity to only one of the bright or dark set (25/71 = 35.2% in V4, 14/58 =24.1% in PITC, 14/82 = 17.1% in AITC) across three areas (chi-squared test, $p>0.05$). Evaluation of the difference in the magnitude of the color selectivity index between bright set and dark set was conducted only for neurons that showed color selectivity to both bright and dark sets (dot symbol, Fig. 7C). Medians of the selectivity index were 0.998 for bright set and 0.972 for dark set in V4, 1.030 for bright set and 1.032 for dark set in PITC, rand 1.045 for bright set and 1.030 for dark set in AITC, respectively. There was no significant difference in the selectivity index between bright set and dark set in all three areas (two sample Wilcoxon signed-rank test, $p \geqq 0.1$).

When I compare the distribution of color selectivity index across three areas, I realized that the distribution tended to elongate along the diagonal line and it became narrower in the direction perpendicular to the diagonal line progressively from V4, PITC to AITC. This suggests that the effect of luminance contrast on the strength of color selectivity among the proportion of color selective neurons becomes gradually smaller in the order from V4, PITC to AITC.

Lastly, I examined how the sharpness of the color selectivity is affected by the luminance contrast

of the stimuli. Figure 7D shows the relationship between the sparseness index for the responses to the bright set (horizontal axis) and dark set (vertical axis) for color selective neurons that exhibited color selectivity to both bright and dark sets.

Medians of the sparseness index were 0.342 for bright set and 0.330 for dark set in V4, 0.396 for bright set and 0.416 for dark set in PITC, and 0.529 for bright set and 0.520 for dark set in AITC, respectively. There was no significant difference in the sparseness index between bright set and dark set in all three areas (two sample Wilcoxon signed-rank test, $p \geqq 0.1$).

These results indicate that as a population of color selective neurons, the basic response properties (e.g. response amplitude, strength of color selectivity, sharpness of color selectivity) were little affected by the polarity of luminance contrast of visual stimuli in any of V4, PITC and AITC, except that mean response amplitude is slightly stronger for bright set than dark set in V4.

Effect of luminance contrast on the representation of color

So far, I have examined the effect of luminance contrast on the color selectivity of individual neurons. Another important issue is how the representation of color is affected by the luminance contrast of the stimuli. This problem can be studied by comparing the population neural response to a color stimulus brighter than the background and that to a stimulus with the same chromaticity but which is darker than the background.

I therefore calculated the Pearson's correlation coefficient (r) between population responses of color selective neurons recorded from each area to a color stimulus in the bright set (e.g. color#5) and that to a color stimulus in the dark set with the same chromaticity coordinate (e.g. color#5). I did this for each of the 15 colors in the stimulus set.

I found that the correlation coefficient of the population responses varied depending on the color and the area recorded. Figure 8 shows the relationships between population responses to stimuli in the bright set and those to stimuli in the dark set for three example colors (color#2: green-yellow color with high saturation, Fig. 8A; color#5: red color with high saturation, Fig. 8B; color#16: achromatic color, Fig. 8C). For color#2 and color#5, correlations of the population responses were moderate to high in all three areas: the correlation coefficient for color#2 was 0.528 for V4, 0.782 for PITC, and 0.833 for AITC, respectively, and that for color#5 was 0.600 for V4, 0.743 for PITC, and 0.864 for AITC, respectively. For color#16 that is an achromatic color, while correlation of the population responses for AITC neurons was moderate (r=0.589), that for V4 neurons (r=0.257) and PITC neurons (r=0.052) were quite low.

Figure 9 shows the correlation coefficient between the population responses to a bright stimulus and those to a dark stimulus for each of 15 colors in the stimulus set for V4 (Fig. 9A, n=71), PITC (Fig. 9B, n=58) and AITC (Fig. 9C, n=81). Correlation coefficient for each color is indicated by the height of each bar in the top row, and the diameter of circles that is plotted at the position corresponding to

the chromaticity coordinate of each color in the bottom row (bubble plot).

In V4, there was significant positive correlation between the population responses to a bright stimulus and those to a dark stimulus for 11 colors other than four colors (color#6,#10,#11,#13) in which the correlation coefficients were lower than 0.25 (Fig. 9A). These four colors form a contiguous region in the chromaticity diagram, and as can be seen in the bubble plot (Fig. 9A bottom), the correlation coefficients tended to be lower for cyan and blue color regions and they became gradually higher for other colors such as magenta, red, and orange colors (Fig. 9A).

In PITC, correlation coefficient between population responses to a bright stimulus and those to a dark stimulus considerably varied across colors (Fig. 9 B) as was observed in V4, but the pattern of variation across colors was markedly different from V4. In PITC, correlation coefficient was especially low for neutral color (color#16) and color#11 that is cyan color with very low saturation. Consequently, contour lines that reflect the tendency of correlation coefficient across chromaticity diagram formed concentric circles around neutral color.

In contrast to V4 and PITC, in AITC, correlation between population responses to a bright stimulus and those to a dark stimulus was high for all colors (top, Fig. 9C), and, there was little bias in the magnitude of the correlation coefficient across the entire range of the chromaticity diagram examined (bottom, Fig. 9C).

As shown in Figure 6, effects of luminance contrast on the color selective responses were associated

with the sharpness of the color selectivity of neurons. Therefore, I conducted the same analysis as shown above to the population of sharply color selective neurons and the population of broadly color selective neurons separately. In all three areas, the pattern of the effect of luminance contrast on the population responses of neurons across the chromaticity diagram was similar between sharply color selective neurons (Figs. 10ABC) and broadly color selective neurons (Figs. 10DEF). In V4, the correlation coefficients were lower for cyan and blue colors and higher for magenta to red colors (Figs. 10AD) for both sharply color selective neurons (n=42) and broadly color selective neurons (n=29), and the pattern was analogous to that for all color selective neurons (n=71, Fig. 9A bottom).

In PITC, correlation coefficients for sharply color selective neuron (n=43, Fig. 10B) were lower for colors with low saturation around neutral color, and this pattern is very similar to the pattern obtained by the population responses of all color selective neurons (n=68, Fig. 9B). Correlation coefficients for broadly color selective neurons (n=15, Fig. 9E) were also lower for colors with low saturation, but low correlation coefficients were observed in wider range of the colors for broadly color selective neurons than those for sharply color selective neurons (Fig. 9B). In AITC (Figs. 10CF), while broadly color selective neurons (n=20) showed somewhat low correlation coefficients around yellow color and colors with low saturation, positive correlation coefficients were observed across the entire range of colors tested for both sharply color selective neurons and broadly color selective neurons, and these patterns were analogous to the patterns of correlation for all color selective neurons (n=81,

Fig. 10C).

Next, I examined how the population activities of color selective neurons in each area represent the information of color as well as luminance contrast. One way to answer to this question is to know which pairs of colors were well differentiated and which pairs were not well differentiated by the population neural responses, and this can be evaluated by computing the correlation coefficient between the population neural responses to one color and those to another color. For example, as shown in Figs. 8 and 9, the correlation coefficient between the population responses of PITC neurons to color#16 in the bright set (bright color#16) and those to color#16 in the dark color set (dark color#16) was markedly low. This indicates that bright color#16 and dark color#16 were separately located in the space that represents the similarity of population responses of PITC neurons. In contrast, when I calculated the correlation coefficient between the population neural responses to bright color#16 and those to bright color#7 by using the same procedure, correlation coefficient was pretty high (0.881), that indicates that bright color#16 and dark color#7 were nearly located in the space that represents the similarity of population responses of PITC neurons. I can regard 1-r as the neural distance between two colors that represents the dissimilarity of the pattern of population neural responses to two colors.

To visualize the dissimilarities of population neural responses for all pair of colors, I computed correlation coefficients for the population neural responses in each area to all possible pairs of the 30

colors that consist of 15 colors in the bright set as well as 15 colors in the dark set. I constructed a dissimilarity matrix in which neural distance for all pair of colors were arranged in a matrix form, and non-metric multi dimension scaling (MDS) analysis was applied to the resultant dissimilarity matrix. I visualized the dissimilarities of population neural responses across 30 colors in terms of the distance on two-dimensional plane by using the results of the MDS analysis (V4, Fig. 11A; PITC, Fig. 11B; AITC, Fig. 11C). In these figure, population neural responses to color stimuli were projected onto two-dimensional plane such that the neural distances were preserved as accurately as possible in the arrangement of the 30 colored symbols. Circle and diamond represent the colors in the bright set and those in the dark set, respectively. Colors in the two sets with the same chromaticity coordinate are connected by a line. A number beside the circle corresponds to the color ID in the stimulus set (Fig. 1B), and the symbols are also painted by colors of the stimuli for visualization purpose.

Figure 11A shows the dissimilarities of colors in V4 population neural responses (n=71) which were plotted on two-dimensional plane. Bright colors and dark colors were clearly separated even when two colors had the same chromaticity coordinates, and clustering of color stimuli with the same luminance was clearly observed. This indicates that the information of the luminance contrast of color stimuli was clearly represented in the population activity of color selective neurons in V4.

Spatial arrangement of different colors with the same luminance contrast was in accordance with the order of hue circle, but the neural distance did not accurately reflect the structure of hue circle and

shrank in the direction connecting green-yellow and purple colors. In other words, the distance between green-yellow color (color#2) and purple color (color#14) in Fig. 11A was very small while the distance between red color (color#9) and cyan color (color#10) that were located along the direction approximately perpendicular to the former pair of colors on the chromaticity diagram was large. I also found that neural distances between pairs of colors with the same luminance contrast tended to be larger for colors in the bright set than those in the dark set.

Likewise, population neural responses in PITC were arranged in the order of hue for both colors in the bright set and dark set (Fig. 11B). Furthermore, similar to V4, bright colors and dark colors were clearly separated even when two colors had the same chromaticity coordinates and clear boundary existed between bright colors and dark colors (Fig. 11B). Moreover, neural distances between bright color#16 and dark color#16 (neutral color: white or black) and that between bright color#11 and dark color#11 (Purple with low saturation) were especially longer than neural distances of colors with high saturation.

Arrangement of dissimilarities of colors in AITC neural population was dramatically different from those in PITC and V4. In population responses of AITC neurons (n=82), the effect of luminance contrast was smaller than those in V4 and PITC, and neural distances between two colors that have the same chromaticity coordinates but with different luminance contrast were very small in AITC (Fig. 11C). As a results, these two colors are located side-by-side in Fig. 11C.

With regard to hue, similar to PITC and V4, colors with similar hue are located close to each other. On the other hand, neural distances became longer for pairs of colors that were separately located on the chromaticity diagram (e.g. pair of color#5 (red) and color#10 (cyan), or pair of color#2 (green-yellow) and color#14 (purple)). Therefore, population responses to chromatic colors were arranged roughly in a circular array which resembled the hue circle.

In the MDS analysis described above, I employed neural distance matrix that was based on the correlation coefficient (r) computed using the raw (un-normalized) firing rate. Since Pearson's correlation coefficient tended to be affected by samples with extreme values, in this case, neurons showing very strong responses, there is possibility that the results of the above MDS analysis may be biased by the neurons showing very strong responses.

To examine the dissimilarities of population neural responses across 30 colors after removing the influence of the effect of the difference of responses amplitude across neurons, I normalized neural responses of each neuron that was normalized by the maximum response among 30 stimuli, and I calculated correlation coefficient using the resultant normalized responses. I then conducted MDS analysis by using the correlation coefficient based on normalized responses.

The results of the MDS analysis using normalized responses plotted on two-dimensional plane (Fig. 11D-F) were overall very similar to those of the MDS analysis using raw (un-normalized) neural responses. Nevertheless, I realized several differences between the results of MDS analysis using

normalized responses and those using raw responses. One difference is that, in V4, dark colors are more clearly clustered in Fig. 4A compared with Fig. 4D. This is likely due to the difference in mean response magnitudes between bright colors and dark colors in V4 as shown in Fig. 7B. Mean response magnitudes were significantly smaller for dark colors than bright colors, and this may have caused closer clustering of dark colors in the two-dimensional plot of the MDS analysis when raw responses were used. However, this does not occur when normalized responses were used, and the dark colors becomes less closely clustered in the two-dimensional plot of the MDS analysis.

In PITC, neural distances for the pair of neutral colors, and that for colors with low saturation tended to be smaller for normalized population responses than raw population responses (Fig. 11E). In AITC, when normalized responses were used for MDS analysis, neutral colors came to be plotted about the center of the hue circle, and the color representation became more similar to the arrangement of colors in the chromaticity diagram (Fig. 11F).

Results of the MDS analysis shown in Figures 11A-F indicate that there were large effects of luminance contrast on the population responses in V4 and PITC but, at the same time, systematic arrangement of hue is observed, suggesting that hue representation resides in the population responses of color selective neurons in V4 and PITC.

In order to visualize this possibility more explicitly, we constructed 15×15 distance matrix based on the correlation coefficients that were computed using population normalized responses at 15

chromaticity coordinates: In this analysis, only chromaticity of the stimuli were considered, and the luminance contrast of the stimulus was completely disregarded. I conducted MDS analysis by using the resultant distance matrix. This is in contrast with the analysis described above in which variation across stimuli in chromaticity as well as luminance contrast was considered. For example, in Figure 11D, I have computed the correlation coefficient between the population normalized responses of 71 V4 neurons to 30 pairs of colors that were different either in chromaticity or luminance contrast, and MDS analysis was applied to the resultant 30×30 distance matrix made with the computed correlation coefficients.

To study representation by population of neurons considering only variation across stimuli in chromaticity, I divided responses of one neuron to a bright color and those to a dark color with the same chromaticity as if these responses are obtained from two different neurons to a single color stimulus. Therefore, in this analysis, number of colors becomes 15, and that of neurons is doubled (142 for V4). I then applied MDS analysis to the resultant 15×15 distance matrix. Figure 11G shows that result of this MDS analysis which was conducted to visualize how 142 normalized V4 neural responses represent 15 chromaticities.

I examined the dissimilarity of the population normalized responses across 15 chromaticities when luminance contrast of the stimulus was completely disregarded, in each of V4, PITC and AITC. In all three areas, different chromaticity was circularly arranged in the order of hue on two-dimension

plane. Furthermore, colors with low or no saturation were located inside the hue circle. As a result, color representation which was analogous to the arrangement of colors with variable hues and saturations on the chromaticity diagram was observed. This result indicates that information of hue and saturation of color resides in the activities of neural population in all three areas in a systematic way.

Nonetheless, some difference was observed across areas. In V4 (Fig. 11G) and PITC (Fig. 11H), circular arrangement was compressed in a direction connecting green-yellow color (color#2) and purple color (color#14) so that neural distance between these colors was shorter than the neural distance between red color (color#9) and cyan color (color#10). This anisotropy corresponds to the variation of neural distance between colors as seen in Figs.11A, B, D, and E. In contrast to V4 and PITC, no clear anisotropy was observed in the arrangement of colors in AITC, and hue was represented by clear circle.

The results of the MDS analysis indicate that, in V4 and PITC, population neural responses of color selective neurons were affected by luminance contrast of the color stimuli, and, in PITC, the effect of luminance contrast was especially large for neutral colors (white, gray, and black) and for colors with low saturation, whereas there was little representation of the luminance contrast in AITC.

Effect of stimulus position

The results described so far indicated that the effects of the luminance contrast differed among V4, PITC, and AITC. However, receptive field (RF) positions of the neurons recorded in each area were not the same, and I have to consider a possibility that the difference in the stimulus position in the visual field may have affected the results.

When I recorded from AITC, stimulus was always presented at the foveal center. On the other hand, RF center of V4 neurons resided within 2 to 12 degree in eccentricity, and RF center of PITC neurons resided within 0 to 13 degree in eccentricity.

To study whether the difference in the RF center where the stimuli were presented has affected the difference in the effects of luminance contrast, I examined the relationship between the eccentricity of RF center and the magnitude of the effect of luminance contrast that was evaluated in term of the correlation coefficient between the responses to the stimuli in the bright set and those to the stimuli in the dark set, in V4 and PITC (Fig. 12AB).

I found that there was no significant correlation between the eccentricity of RF center and the effect of luminance contrast in both V4($r=0.185$, $p=0.123$) and PITC($r=-0.113$, $p=0.357$). This suggests that there is no systematic relationship between the stimulus position in the visual field and the magnitude of the effect of luminance contrast.

I next examined whether the pattern of the variation in the effect of luminance contrast across colors

depended on the stimulus position in the visual field (Figs. 12C-F). To study this problem, I compared the effect of luminance contrast on the population responses of neurons to each color between two areas with matched eccentricity of RFs. First, I compared the effect of the luminance contrast on the population responses to colors obtained by V4 neurons (n=51) and PITC neurons (n=22) that were matched with regard to the range of eccentricity of RF center (5-10 degree) (Figs. 12C-D).

There was a considerable difference in the effect of luminance contrast on the population responses to colors between V4 and PITC, even when the ranges of eccentricity of RFs were matched. Correlation coefficient between the population responses to bright stimuli and dark stimuli tended to be low for colors from cyan to blue in V4 and that tended to be low for the range of colors including neutral color and magenta color in PITC. These pattern were similar to those obtained for the entire population of neurons in V4 and PITC (Fig. 9 A and B, bottom), and the difference in the patterns could not be explained by the difference in the stimulus positions.

I also compared the effect of the luminance contrast on the population responses to colors obtained between PITC neurons (n=33) and AITC neurons (n=82). PITC neurons used for this analysis had RFs whose eccentricity was within 0-5 degree that were close to the stimulus position employed for AITC neurons (0 degree eccentricity) (Figs. 12E-F). Again, there was a considerable difference in the effect of the luminance contrast on the population responses to colors between PITC and AITC,

even though the ranges of eccentricity of RFs were similar. In PITC, large effect of the luminance contrast was observed for colors with low saturation, as was seen for the entire PITC neurons.

These results indicate that difference in the stimulus positions could not fully explain the difference in the effect of the luminance contrast among V4, PITC and AITC.

Dissociation of the effect of luminance and luminance contrast

When I tested the effect of luminance contrast in the experiments described above, the luminance of the stimuli in the bright set was 20 cd/m^2 and that in the dark set was 5 cd/m^2 (Figs. 13 A. a, c), thus these two sets of stimuli had different value of luminance as well as luminance contrast. So, I examined whether the cause of the difference in the neural responses between bright set and dark set is due to the difference in luminance contrast or the difference in stimulus luminance itself.

To test this, for ten V4 neurons, I presented stimulus on the background whose luminance (either 40 cd/m^2 or 2.5 cd/m^2) was different from the original condition (10 cd/m^2), while the luminance contrast was the same as either one of bright set or dark set in the original condition.

I recorded the responses of eight neurons to stimulus set with 5 cd/m^2 luminance that were displayed on the 2.5 cd/m^2 background (Fig. 13A b), and the responses of three neurons to stimulus set with 20 cd/m^2 luminance that were displayed on the 40 cd/m^2 background (Fig. 13A d). One neuron was recorded in both conditions. All ten neurons were also tested in the original condition. The logic

underlying this test is as follows.

If the difference in the neural responses between the bright set and dark set was due to the difference in the stimulus luminance itself, I can expect that the pattern of the color selectivity should be similar between the conditions when the luminance of the stimulus was the same (e.g. responses to 5 cd/m^2 stimuli presented on either 10 cd/m^2 (Fig. 13A c) or 2.5 cd/m^2 (Fig. 13A b) background). On the other hand, if the difference in the neural responses was due to the difference in the luminance contrast of the stimulus, I can expect that the pattern of the color selectivity should be similar between the conditions when the luminance contrast of the stimulus was the same (e.g. responses to 20 cd/m^2 stimuli presented on the 10 cd/m^2 background (Fig. 13A a) and those to 5 cd/m^2 stimuli presented on the 2.5 cd/m^2 background (Fig. 13A b)). So, by examining whether the pattern of color selectivity is more similar between the conditions when the stimulus luminance is the same or the condition when the luminance contrast is the same, I can determine which factor is involved in making the difference in the neural responses between the bright set and dark set.

Figure 13A schematically shows the luminance of the background and luminance of visual stimulus in four conditions included in this test: 'a' and 'c' represent the original conditions (background, 10 cd/m^2: stimulus, 20 cd/m^2 or 5 cd/m^2) that were used in the original experiment. On the other hand, 'b' and 'd' represent the test conditions.

A dashed line connects a pair of conditions that had the same luminance but had a different

luminance contrast (‘a’ vs ‘d’, ‘b’ vs ‘c’), and a solid line connects a pair of conditions that had a different luminance but had the same luminance contrast (‘a’ vs ‘b’, ‘c’ vs ‘d’). Figures 13B, C and D show the color selectivity of one example neuron recorded under three different condition and Figure 13B, Figure 13C and Figure 13D show neural responses recorded under the conditions ‘a’, ‘c’, and ‘b’, in Fig.13A respectively.

As can be seen, the pattern of color selectivity was more similar between B and D that were recorded in the conditions with the same luminance contrast than between C and D that were recorded in the conditions with the same stimulus luminance. This suggests that the luminance contrast but not luminance itself was the important factor determining the color selectivity in this neuron.

To quantitatively examine which one of luminance contrast and stimulus luminance affected more significantly on the pattern of color selective responses, I compared the correlation coefficient computed from responses to conditions with the same luminance contrast (‘a’ vs ‘b’, ‘c’ vs ‘d’, solid line, Fig. 13A) and the correlation coefficient computed from responses to conditions with the same stimulus luminance (‘a’ vs ‘d’, ‘b’ vs ‘c’, dashed line, Fig. 13A) (Fig. 13E).

If the pattern of color selective responses of neurons depended more on the stimulus luminance, correlation coefficient of responses will become larger for the pair of conditions lying on the dashed line (e.g. ‘b’ and ‘c’ in Fig. 13A) than the pair of conditions lying on the solid line (e.g. ‘a’ and ‘b’ in Fig. 13A). On the other hand, if the pattern of color selective responses of neurons depended more

on the luminance contrast, correlation coefficient of responses will become larger for the pair of conditions lying on the solid line than the pair of conditions lying on the dashed line.

Figure 13E summarized the results of the above analysis for ten neurons tested. Abscissa indicates correlation coefficient between responses in conditions that had a different luminance but had the same luminance contrast (‘a’ vs ‘b’, ‘c’ vs ‘d’). Ordinate indicates correlation coefficient between responses in conditions that had the same luminance but a different luminance contrast (‘a’ vs ‘d’, ‘b’ vs ‘c’). Open circle and filled circle represent neurons recorded under the background whose luminance was 2.5 cd/m^2 (condition ‘b’, Fig. 13A) and those recorded under the background whose luminance was 40 cd/m^2 (condition ‘d’, Fig. 13A), respectively. An open circle with thick contour represents the neuron depicted in Fig.13B, C, and D. A pair of open and solid circles connected with a dotted line represents a neuron that was recorded under both background conditions.

For nine out of ten neurons tested, correlation coefficient was larger for a pair of conditions with the same luminance contrast than a pair of conditions with the same stimulus luminance and the circles were plotted under the diagonal line.

Neurons plotted near the upper right of this diagram tended to exhibit similar color selectivity for all conditions tested, and correlation coefficient under the original condition (‘a’ vs ‘c’) exceeded 0.67 for three out of four neurons.

The results of this control test clearly showed that V4 neurons whose color selectivity differed

between responses to bright set and responses to dark set varied their color selective responses according to the change in luminance contrast but not to the change in stimulus luminance itself.

Discussion

In the present study, I systematically examined the effect of the luminance contrast of the stimuli on the color selectivity of individual neurons and the population responses of neurons in V4, PITC and AITC by comparing the responses to the color stimuli brighter than the background and those darker than the background. The effects of luminance contrast differed considerably across V4, PITC and AITC. First, the effect of luminance contrast on the color selectivity of individual neurons was smaller for AITC than for both V4 and PITC. Secondly, I found there was remarkable difference in the effect of luminance contrast on the color representation in the population responses of color selective neurons across areas: in V4, the effect of the luminance contrast gradually changed along the direction of L-M axis on the chromaticity diagram and the size of the effect was larger for blue and cyan colors. In PITC, the effect of luminance contrast gradually increased with lowering the saturation and was especially large for neutral colors. In AITC, there was little effect of luminance contrast regardless of color.

Comparison with the previous studies

It has been shown that the luminance contrast of visual stimulus affects responsiveness of color selective neurons in the visual cortex. In V1 and V2, it has been reported that many color selective

neurons represent both color contrast and luminance contrast (Lennie et al., 1990; Kiper et al., 1997).

Several studies have been conducted to examine the effect of luminance contrast on the activities of color selective neurons in higher areas such as V4, PIT and AIT. Conway and colleagues found little effect of luminance contrast on the color selectivity of neurons in 'glob' regions that reside within V4 and PIT (Conway et al., 2007). On the other hand, in one study that directly compared the responsiveness of neurons for color and luminance contrast between V1, V2 and V4 by using common stimuli that consist of different combinations of luminance and color (Yoshioka et al., 1996), it was reported that the effect of luminance in V1 and V2 tended to be larger for neurons tuned for middle-spectral colors than those tuned for end spectral colors. A recent study also reported that many V4 neurons exhibit large effects of the luminance contrast (Bushnell et al., 2011). However, in these previous electrophysiology studies that examined the effect of the luminance contrast on the color selective responses, the effect was not quantitatively analyzed, or the effect was not examined across the entire range of gamut of the display.

In the present study, I have quantitatively examined the effect of the luminance contrast on the color selective responses using stimuli that evenly distributed across the entire range of gamut of the display, and found a large effect of the luminance contrast on the color selectivity of neurons recorded from V4 and PIT. This result is consistent with those in previous studies that reported the responses of V4 neurons tended to vary due to the change in luminance contrast (Yoshioka et al., 1996; Bushnell et al.,

2011). However, our results differed from those in a previous study (Conway et al., 2007) that reported that there is little effect of luminance contrast on the color selective responses of neurons in the globs that reside within PIT and V4.

A plausible cause of this discrepancy is the difference in visual stimuli used. Because Conway and colleagues used only colors with high saturation, they might have missed the large effect of luminance contrast on the responses to colors with low saturation. Another possible reason of the discrepancy is the difference in the recording sites. Conway and colleagues identified 'globs' as cortical regions including V4 and PIT that exhibited strong activation for color stimuli than luminance stimuli by means of fMRI in monkeys, and conducted electrophysiological recording from some of the globs. On the other hand, in this study, we did not attempt to pre-select recording sites by fMRI or other imaging studies, so it is likely that sample of V4 neurons in the present study include both their 'glob' neurons and 'interglob' neurons. Nonetheless, we found some clustering of color selective neurons in V4 (Fig.2) that may correspond to some of their 'globs' and the region strongly activated by color stimuli in optical imaging experiment (Tanigawa et al., 2010). Conway and colleagues also noted that 'glob' cells tend to have sharp color selectivity, therefore it is most likely that sharply color selective neurons in V4 in the present study were recorded from the region where Conway and colleagues called 'globs'.

They also reported there exists negative correlation between the sharpness of color selectivity and

the effect of luminance contrast on the responses of neurons. This is consistent with the observation in the present study that the effect of luminance contrast on color selectivity tended to be slightly smaller for sharply color selective neurons than broadly color selective neurons. However, when we analyzed the effect of luminance contrast on the color representation in the population responses of sharply color selective neurons separately from broadly color selective neurons, the results were very similar between these two population of neurons and both exhibited large effects of luminance contrast that depend on the color. So, it is unlikely that the selective sampling from 'glob' can explain all the difference between the results of Conway and colleagues and the present study.

Possible factor other than luminance contrast

When we analyzed the effect of luminance contrast on the population responses of neurons for each color, we found large effects in both V4 and PITC, but the pattern of the effects across the chromaticity diagram is quite different between V4 and PITC. The pattern in PITC suggests that the magnitude of the effect depends on the saturation of color that is one of perceptual color attributes. Then what is the factor determining the pattern observed in V4?

One possible factor is the difference in cone contrast between bright set and dark set. Cone contrast is defined as the ratio between the increment (or decrement) of cone activity for the stimulus relative to the cone activity for the background. Even when the chromaticity is the same between a

bright stimulus and a dark stimulus, cone contrast can be different, and this may explain the pattern of the effect of luminance contrast observed in V4. If the neuron activities are more tightly related to cone signals than the perceptual color attributes, we may observe a systematic relationship between the pattern of the effect of luminance contrast and the pattern of the differences in cone contrast between bright set and dark set across the chromaticity diagram.

To examine this possibility, we calculated the pooled cone contrast for each of the 15 stimuli in the bright set and dark set using the following equation:

$$\text{Pooled cone contrast} = \sqrt{\left(\frac{\Delta L}{L}\right)^2 + \left(\frac{\Delta M}{M}\right)^2 + \left(\frac{\Delta S}{S}\right)^2}$$

where, L, M and S represent L-cone, M-cone and S-cone activity based on cone fundamentals (Stockman and Sharpe, 2000) for the background, respectively, and, ΔL, ΔM and ΔS represent the differences in L-cone, M-cone and S-cone activity between a stimulus and the background.

Figure 14A shows the normalized difference in pooled cone contrast between a bright stimulus and a dark stimulus across 15 colors. The differences in pooled cone contrast between bright stimuli and dark stimuli tended to be larger for blue colors (color#13, #14) and they became gradually smaller for other colors such as green, yellow, and red colors.

If the correlation between the population neural responses to a bright stimulus and that to a dark stimulus decreased when the difference in pooled cone contrast increased, the pattern of the effect of luminance contrast will exhibit a pattern as illustrated in Fig. 14B in which 1 – (the difference in

pooled cone contrast for each stimulus) is depicted. As can be seen, this simulated pattern based on the pooled cone contrast across 15 colors is clearly different from the actual pattern of correlation coefficient across 15 colors observed in V4. This implies that the effect of luminance contrast on the population responses to each color observed in V4 cannot be explained by the difference in the cone contrast between the bright set and dark set.

Implication of the effects of luminance contrast on the function of each area on color vision

In the present study, I have analyzed the effect of luminance contrast on the color selective activities in three areas, namely V4, PITC and AITC, and found that the effects are different across three areas. In the following, I will consider how the present results can be interpreted in relation to the function of each area in color perception.

Area V4

Lesion studies have shown that the bilateral ablation of V4 caused deficit in color constancy, although the ability of color discrimination was spared (Walsh et al., 1993; Heywood et al., 1995). It has also been shown that V4 neurons exhibited response properties that may be related to color constancy (Zeki, 1983a; Schein and Desimone, 1990; Kusunoki et al., 2006).

In the natural environment with changeable illumination, the functions of brightness constancy and

color constancy play important roles to maintain the appearance of objects stable. When the illumination becomes darker, brightness of both environment and objects decrease, simultaneously. Therefore, when the illumination changes in the natural environment, it should be rare that the polarity of luminance contrast of an object against the background is reversed.

In this study, the results of the control test showed that V4 neurons whose color selectivity differed between responses to bright set and responses to dark set varied their color selective responses according to the change in luminance contrast but not to the change in stimulus luminance itself (Fig13). The response properties of V4 neurons observed in this control test is consistent with the brightness constancy and that V4 plays some roles in this function as well as color constancy. It is likely that similar response property will be observed for PITC neurons whose color selective responses were affected by the luminance contrast of the stimuli.

PITC

It was noted that categorical color discrimination of four primary colors (red, yellow, green, blue) was not affected by the V4 lesion (Walsh et al., 1992), and it is suggested that neural basis of perception of four basic color categories reside in visual areas earlier than V4. Yoshioka and colleagues have reported that proportion of neurons preferring non-primary colors increase in V4 compared with V1, and that color selective neurons in V4 exhibited responses than combine luminance and color information to represent 11 basic color categories. These authors suggested that sophisticated color

category that corresponds to our color perception is formed by the neural processing between V1 and V4 (Yoshioka et al., 1996).

However, in the present study, the results of the correlation analysis and MDS analysis using the population responses indicates that there was clear discrimination between white and black in PITC but the results in V4 is more complicated and the strongest effects were observed for cyan and blue. This indicates that the organization of color space (e.g. color sphere, Munsell color space) that is associated with color perception is more similar to the color representation in PITC than that in V4. Because sophisticated color categories are systematically arranged in these color space, these results suggest sophisticated color category is formed at a stage later than V4 and presumably in PITC.

AITC

AIT has bi-directional anatomical connection with prefrontal cortex (Webster et al., 1993). Task-dependent modulation of color-selective neuron activity observed in AITC (Koida and Komatsu, 2007) may be due to top-down signal from the prefrontal cortex to AITC. Although lesion in PITC alone did not cause clear deficit of the ability in color discrimination, lesion of IT including both PIT and AIT caused severe deficit in the ability of color discrimination (Huxlin et al., 2000; Cowey et al., 2001). These studies suggest that AITC plays an important role in the association between color information and cognitive tasks such as color discrimination or color categorization, and it is possible that the signals of color selective neurons in AITC may be sent to the PFC or other brain regions to

perform these color related behaviors. On the other hand, these neurons may be the target of top-dawn signals to efficiently perform behavior using color information or to select objects based on their colors.

Information of hue and saturation of objects isolated from luminance are thought to be an important cue to recognize particular object in the natural environment that is crowded with many object. In such an environment, interaction between the spatial distribution of illumination light and 3D shape of objects generate complicated change in shading and shadow on the object's surface, and even if an object has a uniform color over its surface, luminance varies across the surface. On the other hand, even in such a situation, hue and saturation are less influenced and are roughly maintained. As seen in the results, AITC neurons represent the hue and saturation independent of luminance contrast. This property should be useful for selection of objects in a crowded environment because AITC neurons can signal precise color information specific to each object. This implies that AITC neurons play the important rule in the discriminate of colors isolated from luminance and contribute to achieve our object perception.

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Figure Legends

Figure 1. Recording sites and color stimuli.

A, Approximate recording sites on the lateral view of the right hemisphere of a monkey (top, V4; middle, PITC; bottom, AITC) (top) and connection of areas involved in color processing (bottom). *B,* Chromaticity coordinates of the stimuli in the color stimulus set plotted on the CIE-xy chromaticity diagram. A color stimulus set contained 16 colors that consisted of fifteen chromatic colors whose chromaticity coordinates were evenly distributed on the chromaticity diagram (color#1~15) and one achromatic color whose chromaticity coordinate was equal to the gray background (color#16). Fifteen stimuli except for color #15 were presented at two different luminances (bright set, 20cd/m^2; dark set 5cd/m^2). Because the luminance of blue color (color #15) in bright set was different from other colors, we omitted the responses to blue colors for both bright and dark set from the quantitative analysis. White triangle depicts the gamut of the display used for the experiments. *C,* Nineteen geometric shapes used to test the shape selectivity (V4, 19 or 11 shapes; PITC and AITC, 11 or 7 shapes). These shapes include, from top left to bottom right, square, oblique square, circle, star, cross, oblique cross, triangle, vertical bar, oblique bar in the clockwise direction, horizontal bar, oblique bar in the counterclockwise direction, narrow diamonds and broad diamonds (vertical diamond, oblique diamond in the clockwise direction, horizontal diamond and oblique diamond in the counterclockwise

direction, respectively). Each of these shape stimuli was painted uniformly with a single color. LS, lunate sulcus; IOS, inferior occipital sulcus; STS, superior temporal sulcus; PMTS, posterior middle temporal sulcus; AMTS, anterior middle temporal sulcus; PITC, posterior IT color area; AITC, anterior IT color area.

Figure 2. Recording sites in area V4 and the distribution of color-shape selectivies

A, Lateral view of the right hemisphere of monkey AL. A white rectangle indicates the area covered by the recording chamber. A red rectangle indicates approximate range of penetration sites that corresponds to the region depicted in *B*. *B,* Stimulus selectivity of neurons across the surface of the V4 of monkey AL (magnification of red rectangle in *A*). The stimulus selectivity of each neuron is indicated by a symbol plotted at the grid coordinates of the electrode penetration site. An open circles with black contour indicate the holes in the grid used for electrode penetrations. Red symbols indicate color-selective neurons; black symbols indicate neurons that are not color selective. Stars indicate shape-selective neurons; circles indicate neurons that are not shape selective. Open circles and open stars indicate that the stimulus selectivity was tested either one of color or shape, respectively. *C,* Stimulus selectivity of neurons across the surface of the V4 of monkey SI. A, anterior; P, posterior; D, dorsal; V, ventral. Other abbreviations are the same as in Fig. 1.

Figure 3. Responses of three example color selective neurons recorded from AITC

A, Responses of a neuron (cell 1) to 15 stimuli in the bright set (left) and those to 15 stimuli in the dark set (middle). Response to each color is shown by rasters and peristimulus time histograms (PSTHs). Stimulus presentation period is indicated by a thick horizontal line below each histogram. The number at the bottom left of each histogram indicates the color number that corresponds to the number of each color in Fig. *1B*. Response magnitude to each color stimulus is represented by the diameter of a circle and is plotted at a position that corresponds to their chromaticity coordinate of that color in the inset (bubble plot). Open and solid circles indicate response increase and decrease, respectively. Contour lines in the bubble plots indicate 75%, 50%, 25%, and 0% of the maximum response, respectively. In the right panel, scatter plot shows the relationship between the responses to the bright set (horizontal axis) and those to the dark set (vertical axis). Each circle corresponds to one color. The correlation coefficient and its p-value between responses to the bright set and those to the dark set are shown at the upper left of the scatter plot. *B* and *C*, Responses of two other example neurons (cell 2 in *B*, cell 3 in *C*) to the bright set and dark set, and the relationship between responses to the two sets (scatter plots). B, bright set; D; dark set.

Figure 4. Responses of three example color selective neurons recorded from the PITC

A-*C*, Responses of three neurons (cell 1 in *A*, cell 2 in *B*, cell 3 in *C*) are plotted using the same format

as in Fig. *3A*. Cell 1 (*A*) showed the highest correlation, cell 2 (*B*) showed the representative correlation, and cell 3 (*C*) showed relatively low correlation among the sample of PITC neurons.

Figure 5. Responses of three example color selective neurons recorded from the V4

A-C, Responses of three neurons (cell 1 in A, cell 2 in B, cell 3 in C) are plotted using the same format as in Fig. *3A*. Cell 1 (*A*) showed the highest correlation, cell 2 (*B*) showed the representative correlation among the population of V4 neurons, and cell 3 (*C*) showed negative correlation.

Figure 6. Distribution of the correlation coefficients between responses to bright set and those to dark set

A-C: Bar graphs show the correlation coefficient between responses to the bright set and those to the dark set for V4 (*A*), PITC (*B*) and AITC (*C*) neurons. Solid bars represent neurons that were classified as sharply color selective neurons and open bars represent neurons that were classified as broadly color selective neurons (see Materials and Methods). Triangle indicates median of the distribution. *D-F*: Cumulative histograms of the correlation coefficient between responses to the bright set and those to the dark set are shown for all neurons (*D*), sharply color selective neurons (*E*) and broadly color selective neurons (*F*). Red line represents V4 neurons, blue line represents PITC neurons and black line represents AITC neurons, respectively. Triangle indicates median. **,

$p<0.001$; *, $p<0.01$; n.s., non-significant (two sample Mann-Whitney U test).

Figure 7. Relationships between an indices for four basic response properties obtained by bright set and dark set

Each column represents the data for V4 (left), PITC (middle) and AITC (right). *A*, Relationship between the maximum response of each neuron to the bright set (horizontal axis) and that to the dark set (vertical axis). Each dot corresponds to one neuron. Diagonal line connects the points where the maximum responses of a neuron were identical between the bright set and the dark set. A gray circle indicates the median of the maximum response across the population of neurons. Number of neurons included in the sample is shown at the inset. *B*, Relationship between the mean response to the bright set (horizontal axis) and those to the dark set (vertical axis). Format is the same in *A*. *C*, Relationship between color selectivity index to the bright set (horizontal axis) and that to the dark set (vertical axis). Dot represents a neuron that exhibited color selectivity to both bright set and dark set. Cross represents a neuron that exhibited color selectivity only to bright set. Triangle represents a neuron that exhibited color selectivity only to dark set. Other formats are the same as in *A*. *D*, Relationship between sparseness index to the bright set (horizontal axis) and those to the dark set (vertical axis). Format is the same in *A*. Only neurons that showed color selectivity to both bright and dark sets (dot symbol in *C*) are included in the sample of this analysis.

Figure 8. Relationships between population responses to a color stimulus in the bright set and those to a color stimulus in the dark set for three example colors

Each row shows the results in V4 (top), PITC (middle) and AITC (bottom). *A*, Scatter plots show the relationship between the population responses of color selective neurons in each area to color#2 in the bright set (horizontal axis) and those to color#2 in the dark set (vertical axis). Each dot corresponds to one neuron. Diagonal line connects the points where the responses to the stimuli were identical between the bright set and the dark set. The correlation coefficient between the population responses is shown above each scatter plot. *B* and *C*, Relationship between the population responses to color#5 (*B*) and color#16 (*C*). Other formats are the same as in *A*.

Figure 9. Correlation coefficient between the population responses to a bright stimulus and those to a dark stimulus for each of 15 colors in the stimulus set

A-C, In the top row, correlation coefficient between the population responses to each of 15colors in the bright set and those to the same color in the dark set is indicated by the height of each bar (top row). Color ID is shown below each bar. Solid bar and open bar indicate significant and non-significant correlation, respectively. In the bottom row, correlation coefficient is indicated by the diameter of a circle that is plotted at the position corresponding to the chromaticity coordinate of each

color (bubble plot). Scale of the circle is shown at the inset. Contour lines indicate where the correlation coefficient is 0.75, 0.50, and 0.25 in the order of thickness of the line. Number of neurons included in the sample is shown at the bottom.

Figure 10. Relationship between the sharpness of the color selectivity of a neuron and the magnitude of the effect of luminance contrast

Correlation coefficients between the population responses of sharply color selective neurons (*A*, *B*, *C*) and broadly color selective neurons (*D*, *E*, *F*) to each of 15 colors in the bright set and those to the same color in the dark set are shown in the bubble plot. Correlation coefficient was calculated for neurons recorded from V4 (*A*, *D*), PITC (*B*, *E*) and AITC (*C*, *F*). Other conventions are the same as in the Fig. 9 bottom.

Figure 11. Neural representation of bright and dark colors in the activities of color selective neurons

Two-dimensional plot of the results of the MDS analysis that was conducted for neurons recorded from V4 (*A*, *D*, *G*), PITC (*B*, *E*, *H*) and AITC (*C*, *F*, *I*). *A*, Results of the MDS analysis based on the neural distance matrix computed from the raw (un-normalized) responses of the 71 V4 neurons to 30 color stimuli (15 bright stimuli and 15 dark stimuli) were projected onto two-dimensional plane such that the neural distances (1 - r) were preserved as accurately as possible. Circle and diamond

represent the colors in the bright set and those in the dark set, respectively. Colors in the two sets with the same chromaticity coordinate are connected by a line. The scree plot at the right of each panel shows the relationship between the number of dimensions and the stress in the MDS analysis. *B, C,* Results of the MDS analysis based on the raw (un-normalized) responses of the population of neurons in PITC (n=58) (*B*) and AITC (n=71) (*C*), respectively. Conventions are the same as in *A*. *D-F,* Results of the MDS analysis based on the normalized responses of the population of neurons in V4 (*D*) PITC (*E*) and AITC (*F*) to 30 color stimuli (15 bright stimuli and 15 dark stimuli), respectively. Conventions are the same as in *A*. *G-I,* Results of the MDS analysis based on the normalized responses of the population of neurons in the V4 (*G*) PITC (*H*) and AITC (*I*) to 15 chromaticity coordinates while disregarding the luminance contrast of stimuli. Colors with high saturation or low saturation and those with separately connected by a line.

Figure 12. Relationship between the stimulus position and the magnitude of the effect of luminance contrast

A, B, Relationships between the eccentricity of RF center (horizontal axis) and the magnitude of the effect of luminance contrast (vertical axis) in neurons recorded from V4 (*A*) and PITC (*B*), respectively. *C, D,* Correlation coefficient between the population responses to a bright stimulus and those to a dark stimulus across colors for sub-population of V4 neurons (n=51) (*C*) and PITC neurons (n=22) (*D*) that

had receptive field whose center ranged between 5-10 degree in eccentricity. *E,* Correlation coefficient between the population responses to a bright stimulus and those to a dark stimulus across colors for AITC neurons (n=82) (*E*) and sub-population of PITC neurons (n=33) (*F*) that had receptive field whose center ranged between 0-5 degree in eccentricity. Format for *C-E* is the same as in Fig. 9 bottom.

Figure 13. Control test to dissociate between the effect of luminance and the effect of luminance contrast

A, Combinations of the background luminance (horizontal axis) and the stimulus luminance (vertical axis) in four conditions used in the control test. 'a' and 'c' correspond to 'bright set' and 'dark set' used in the original experiment, respectively. 'b' and 'd' represent the conditions introduced for the control test. Conditions that have the same luminance but have different luminance contrasts are connected by a dashed line. Conditions that have different luminances but have the same luminance contrasts are connected by a solid line. *B-D,* Color selectivity of one example neuron recorded under the conditions 'a' (*B*), 'c' (*C*), and 'b' (*D*), depicted in *A* respectively. Format is the same as in Fig. 3 inset. *E,* Relationship between the effect of luminance and the effect of luminance contrast. Abscissa indicates correlation coefficient between responses in conditions that had different luminances but had the same luminance contrast ('a' vs 'b', 'c' vs 'd'). Ordinate indicates correlation

coefficient between responses in conditions that had the same luminance but different luminance contrasts (‘a’ vs ‘d’, ‘b’ vs ‘c’). Open circle represents a neuron recorded under the condition ‘b’. Filled circle represents neuron recorded under the condition ‘d’. An open circle with thick contour represents the neuron depicted in *B-D*. A pair of open and solid circles connected with a dotted line represents a neuron that was recorded under both background conditions.

Figure14. Simulated pattern of the difference in the responses between bright and dark stimuli derived from pooled cone contrast

A, Differences in pooled cone contrast between bright stimuli and dark stimuli across 15 chromaticities (see Discussion). *B*, Simulated pattern of the difference in the responses between the bright and dark set derived from the 1 – (difference in the pooled cone contrast).

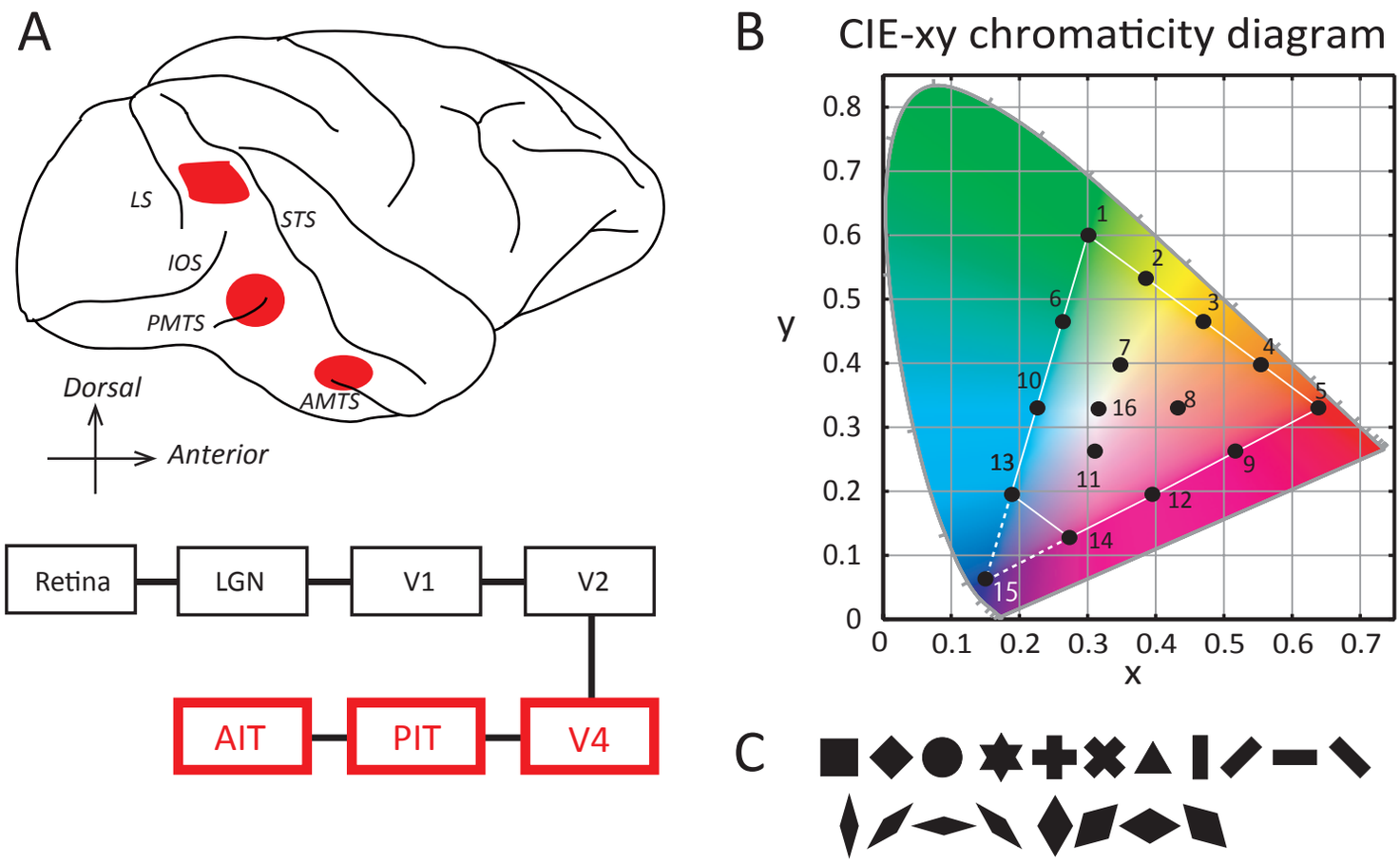
A
LS
STS
IOS
PMTS
AMTS
Dorsal
Anterior
Retina
LGN
V1
V2
AIT
PIT
V4
B
CIE-xy chromaticity diagram
y
x
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
C

Figure 1

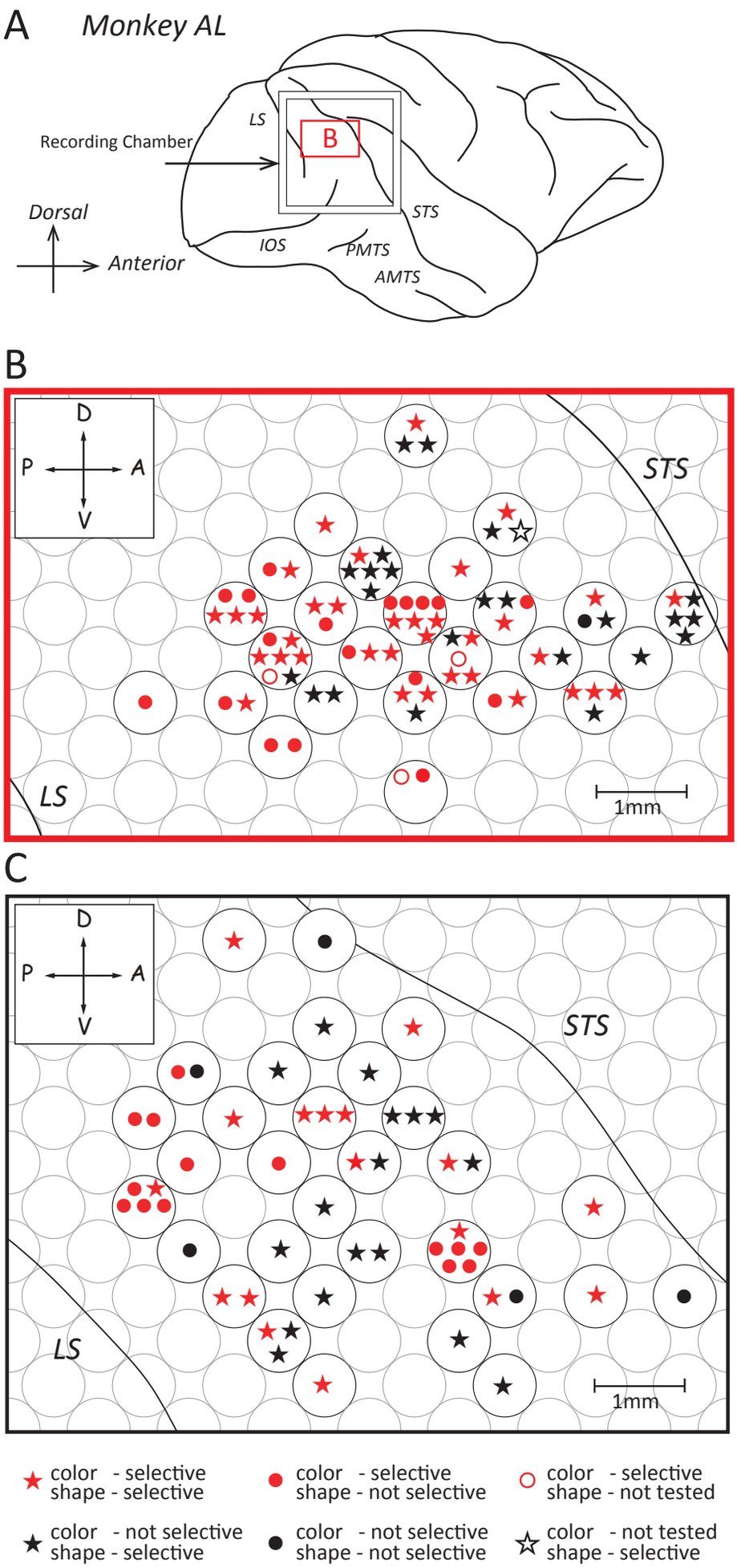
A
Monkey AL
Recording Chamber
LS
B
STS
IOS
PMTS
AMTS
Dorsal
Anterior
B
D
P
A
V
STS
LS
1mm
C
D
P
A
V
STS
LS
1mm
color - selective shape - selective
color - selective shape - not selective
color - selective shape - not tested
color - not selective shape - selective
color - not selective shape - not selective
color - not tested shape - selective

Figure 2

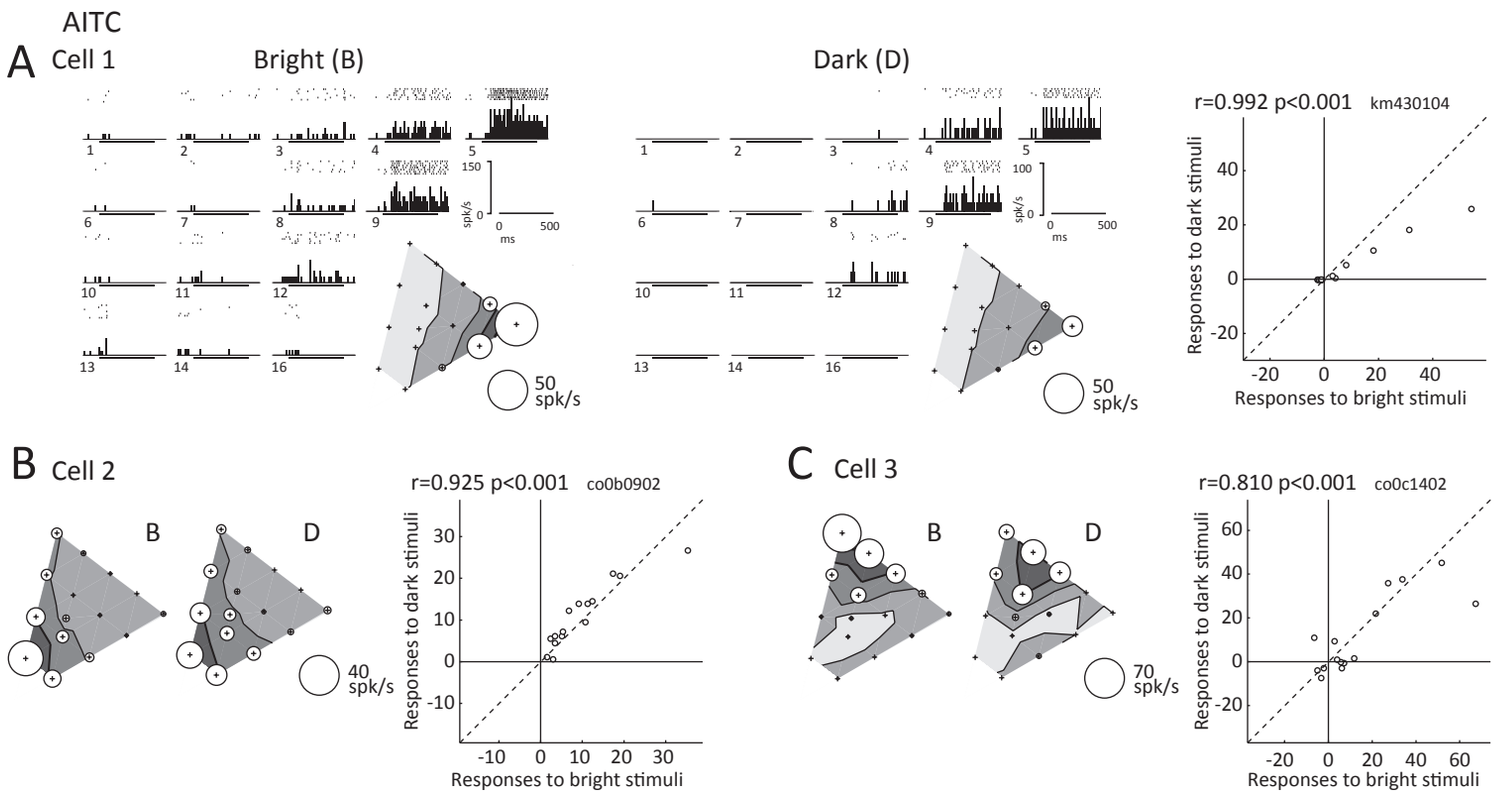
AITC
A
Cell 1
Bright (B)
Dark (D)
r=0.992 p<0.001
km430104
Responses to dark stimuli
Responses to bright stimuli
50
spk/s
B
Cell 2
r=0.925 p<0.001
co0b0902
40
spk/s
C
Cell 3
r=0.810 p<0.001
co0c1402
70
spk/s
ms
spk/s

Figure 3

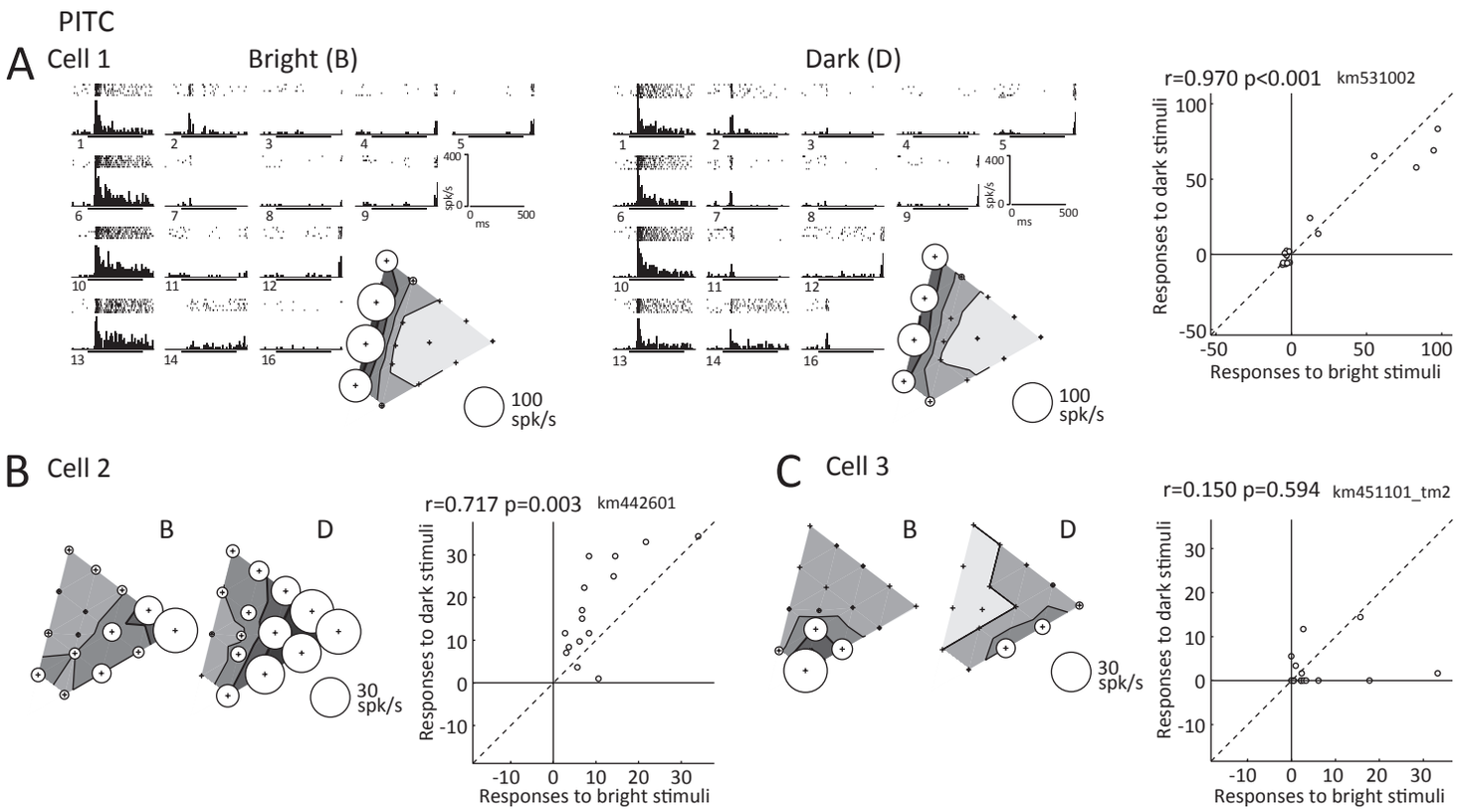
PITC
A
Cell 1
Bright (B)
Dark (D)
100
spk/s
r=0.970 p<0.001
km531002
Responses to dark stimuli
Responses to bright stimuli
B
Cell 2
B
D
30
spk/s
r=0.717 p=0.003
km442601
C
Cell 3
r=0.150 p=0.594
km451101_tm2

Figure 4

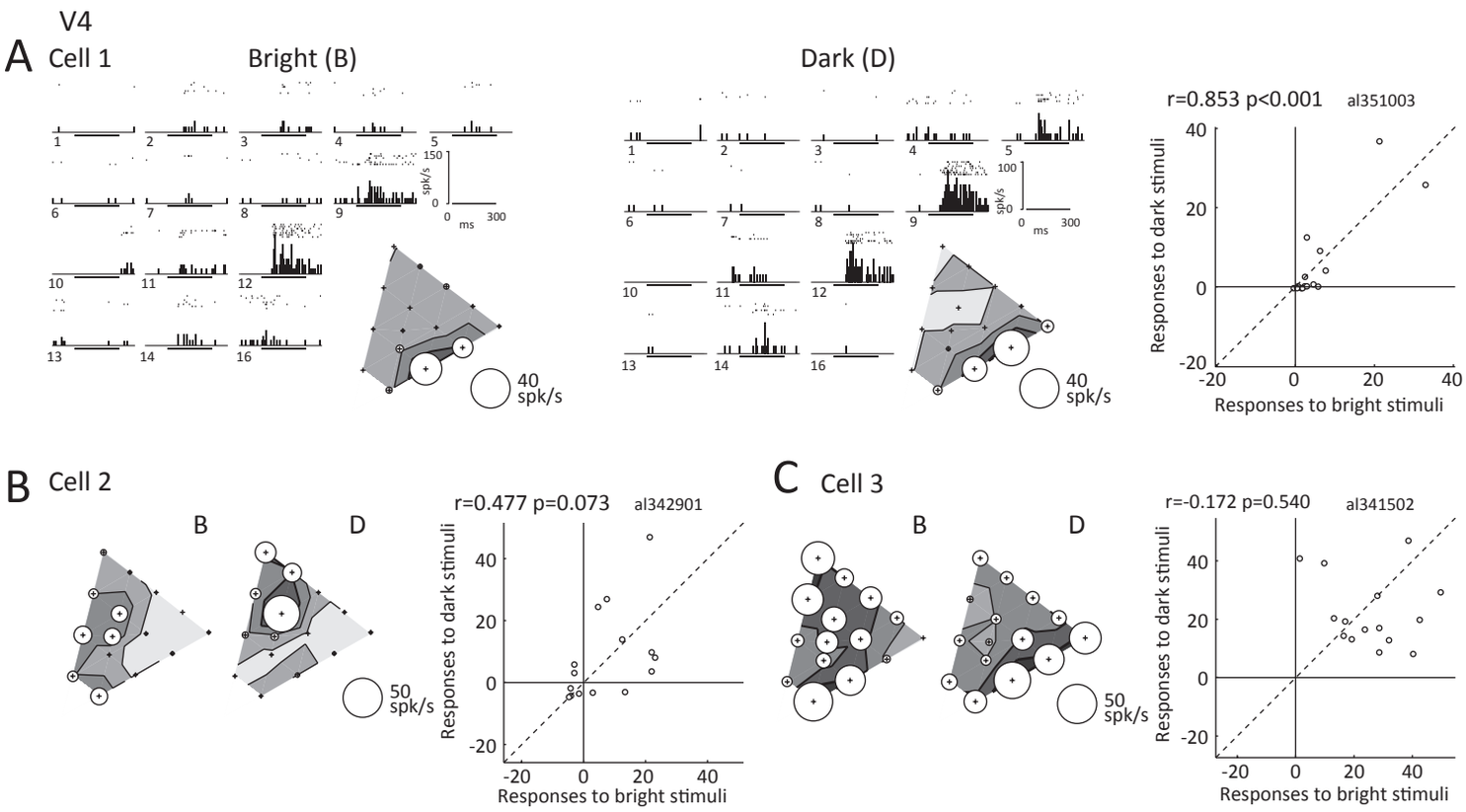
V4
A
Cell 1
Bright (B)
Dark (D)
spk/s
ms
40
spk/s
r=0.853 p<0.001
al351003
Responses to dark stimuli
Responses to bright stimuli
B
Cell 2
B
D
50
spk/s
r=0.477 p=0.073
al342901
C
Cell 3
r=-0.172 p=0.540
al341502

Figure 5

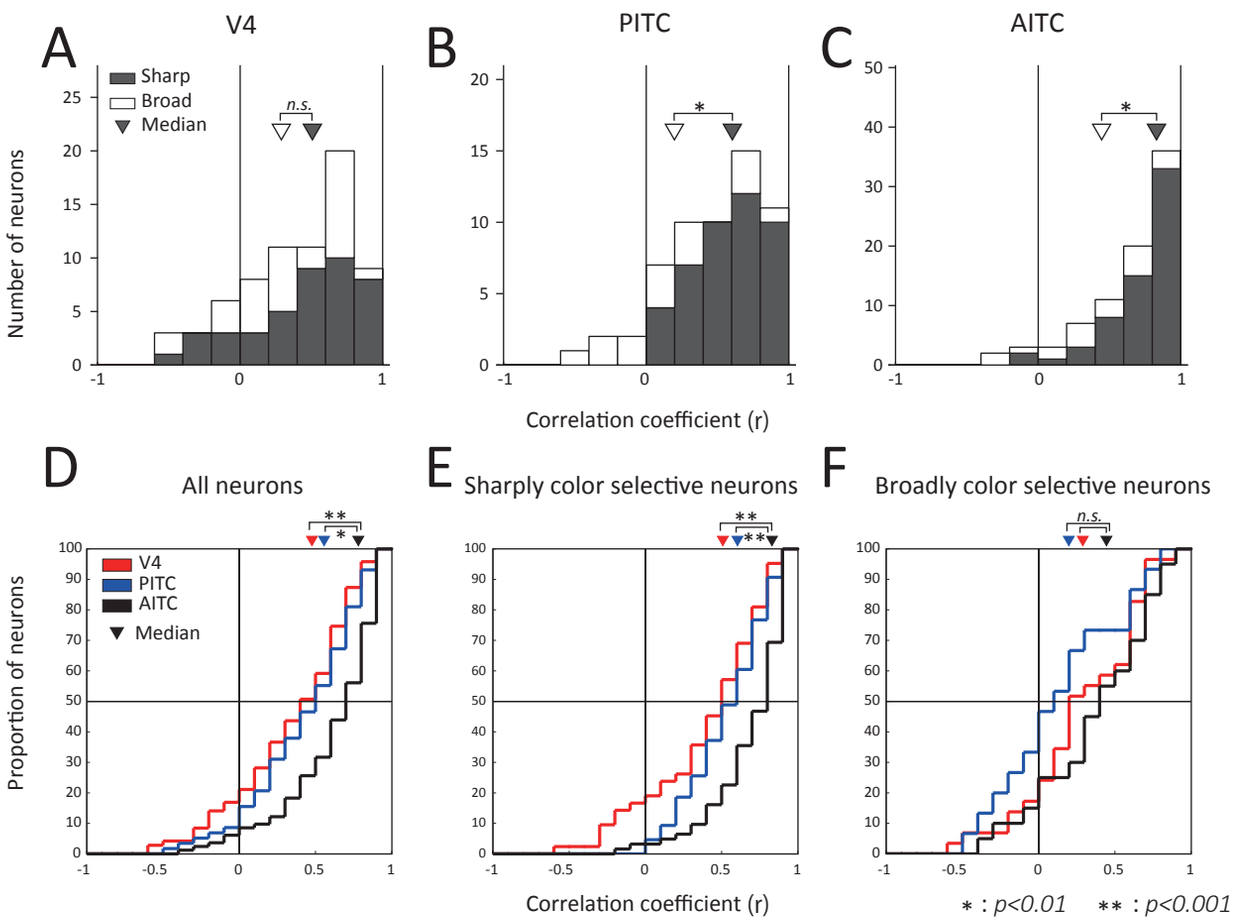
A
V4
Sharp
Broad
Median
n.s.
Number of neurons
B
PITC
*
C
AITC
*
Correlation coefficient (r)
D
All neurons
**
*
V4
PITC
AITC
Median
Proportion of neurons
E
Sharply color selective neurons
**
**
F
Broadly color selective neurons
n.s.
Correlation coefficient (r)
∗ : p<0.01 ∗∗ : p<0.001

Figure 6

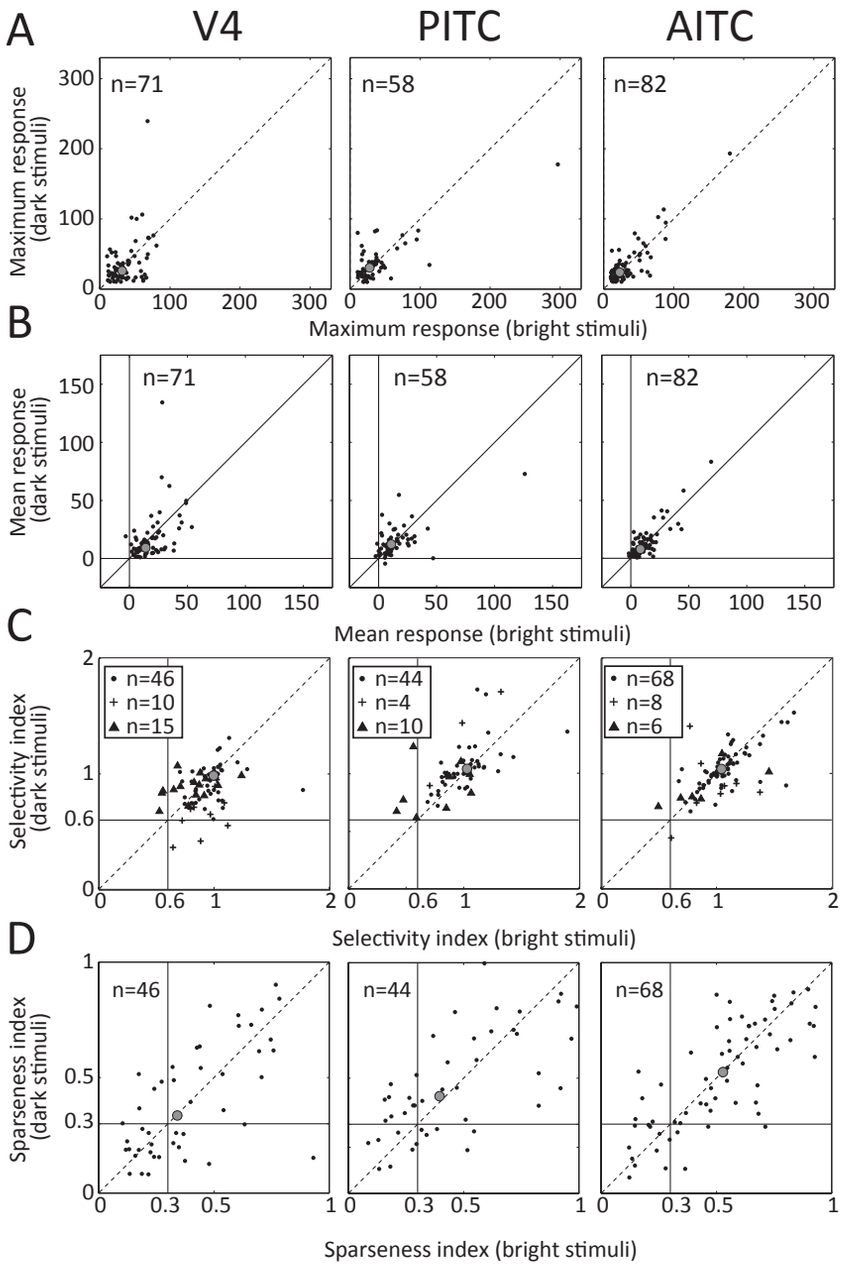
A
V4
PITC
AITC
n=71
n=58
n=82
Maximum response (dark stimuli)
Maximum response (bright stimuli)
B
Mean response (dark stimuli)
Mean response (bright stimuli)
C
n=46
n=10
n=15
n=44
n=4
n=10
n=68
n=8
n=6
Selectivity index (dark stimuli)
Selectivity index (bright stimuli)
D
Sparseness index (dark stimuli)
Sparseness index (bright stimuli)

Figure 7

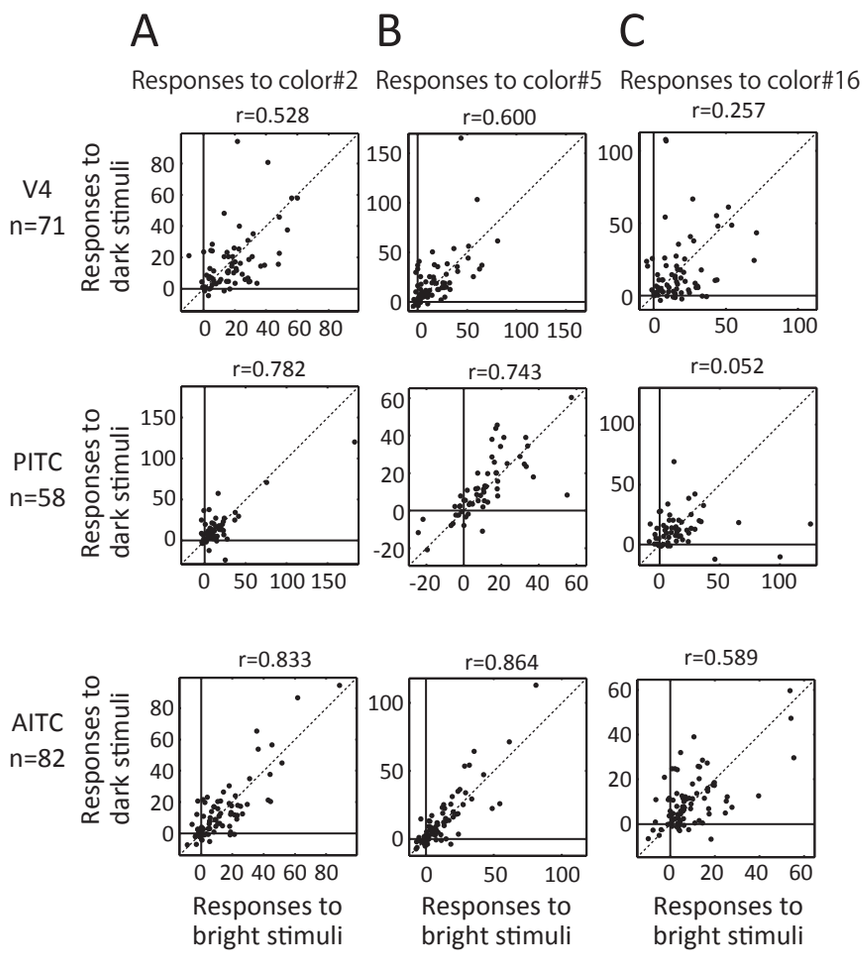
A
B
C
Responses to color#2
Responses to color#5
Responses to color#16
r=0.528
r=0.600
r=0.257
V4
n=71
Responses to
dark stimuli
r=0.782
r=0.743
r=0.052
PITC
n=58
Responses to
dark stimuli
r=0.833
r=0.864
r=0.589
AITC
n=82
Responses to
dark stimuli
Responses to
bright stimuli
Responses to
bright stimuli
Responses to
bright stimuli

Figure 8

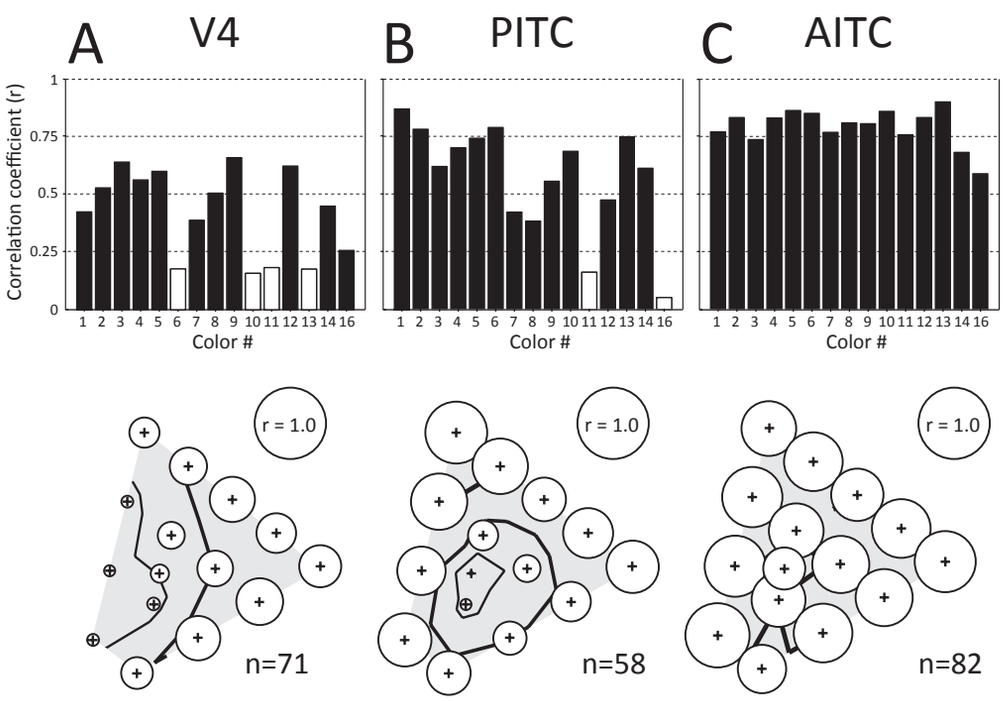
A
V4
B
PITC
C
AITC
Correlation coefficient (r)
1
0.75
0.5
0.25
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 16
Color #
r = 1.0
n=71
n=58
n=82

Figure 9

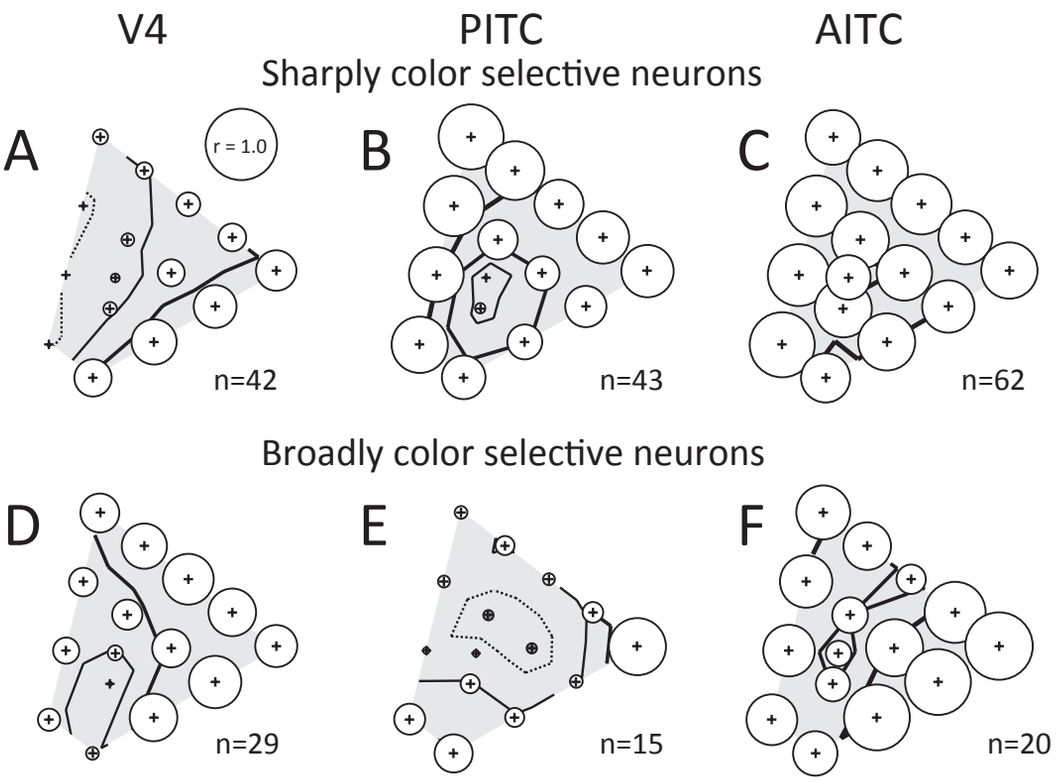
V4
PITC
AITC
Sharply color selective neurons
A
r = 1.0
n=42
B
n=43
C
n=62
Broadly color selective neurons
D
n=29
E
n=15
F
n=20

Figure 10

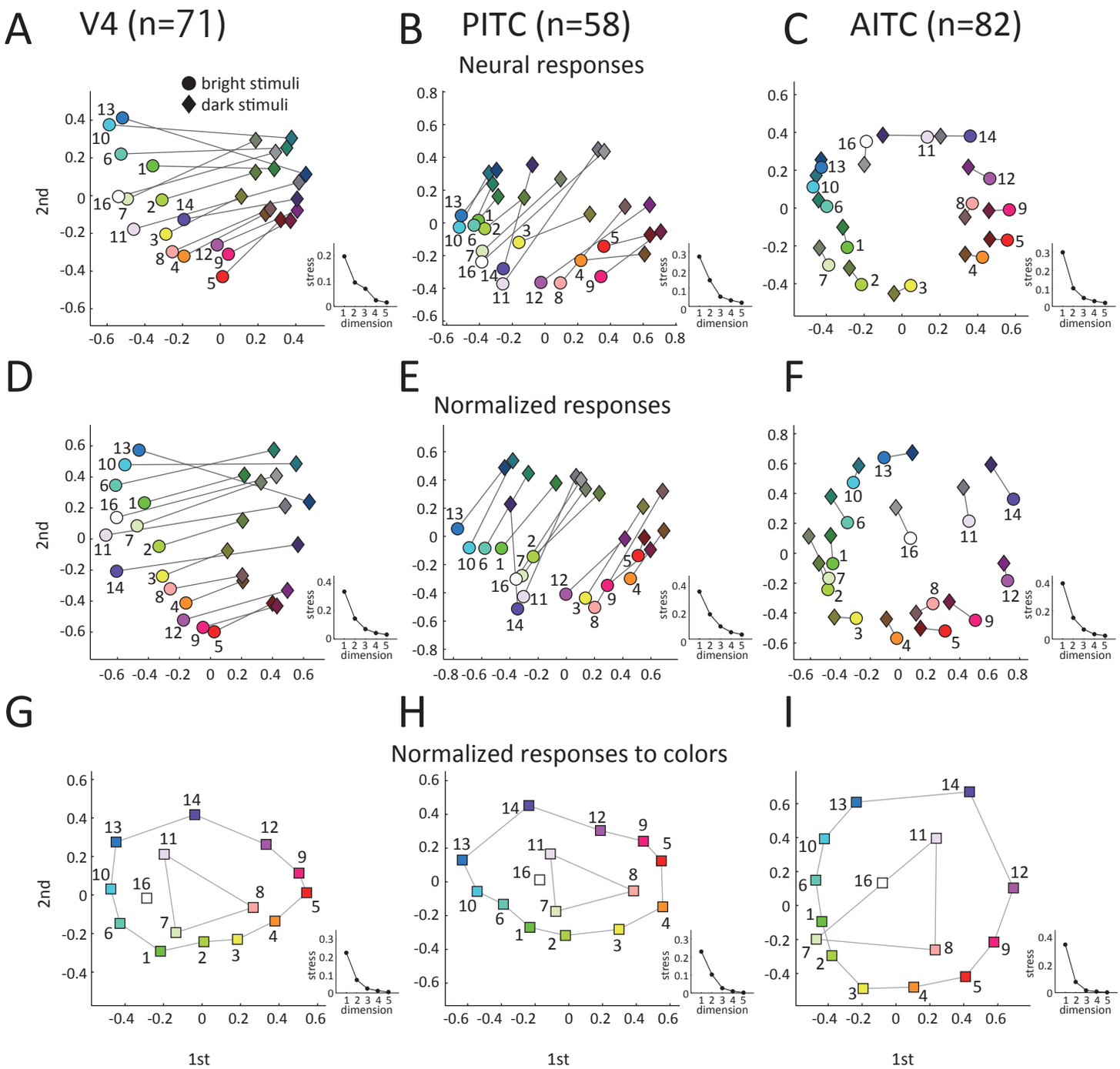
A
V4 (n=71)
B
PITC (n=58)
C
AITC (n=82)
Neural responses
bright stimuli
dark stimuli
D
E
F
Normalized responses
G
H
I
Normalized responses to colors
2nd
1st
stress
dimension

Figure 11

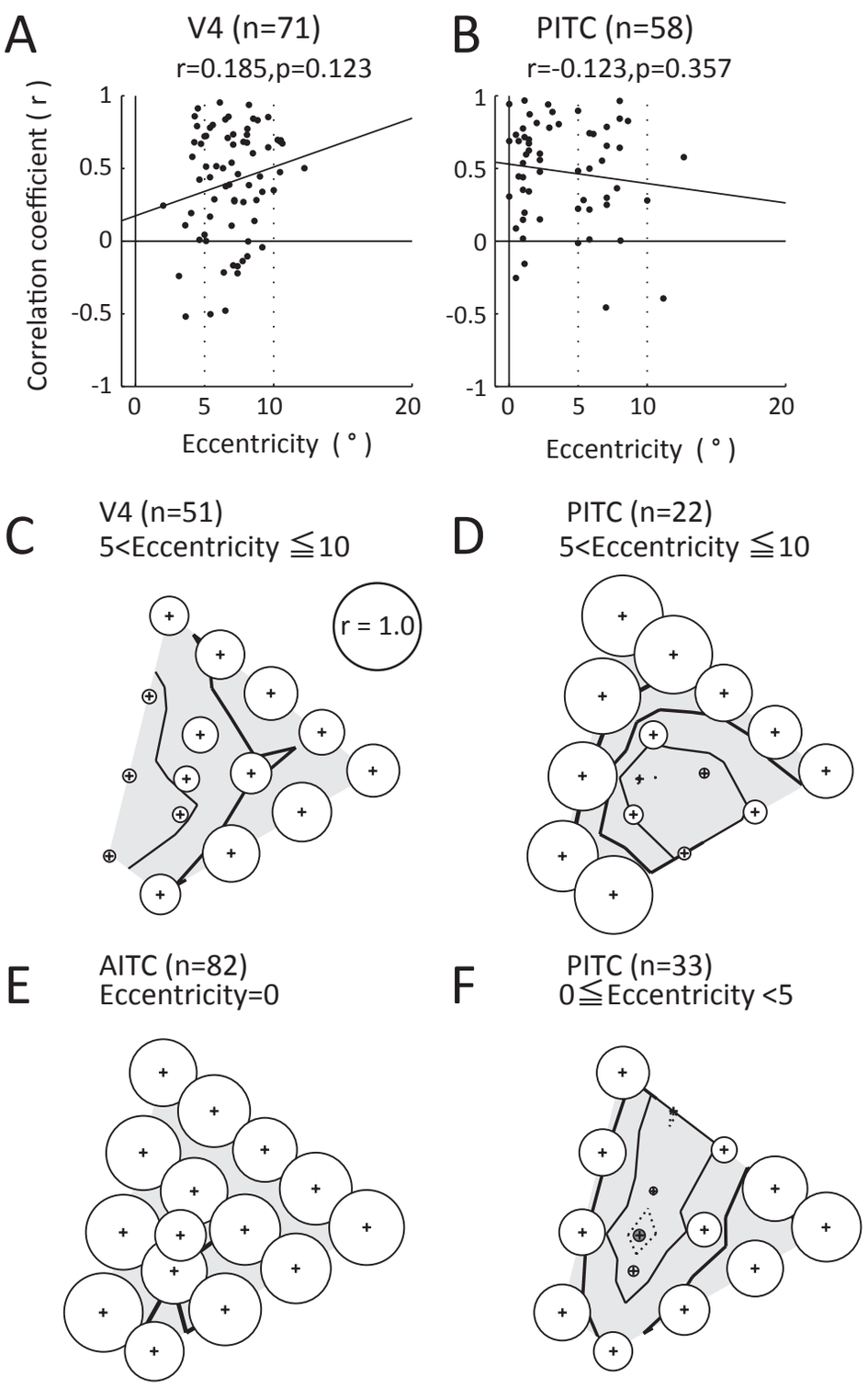
A
V4 (n=71)
r=0.185,p=0.123
Correlation coefficient (r)
Eccentricity (°)
B
PITC (n=58)
r=-0.123,p=0.357
Eccentricity (°)
C
V4 (n=51)
5<Eccentricity ≦10
r = 1.0
D
PITC (n=22)
5<Eccentricity ≦10
E
AITC (n=82)
Eccentricity=0
F
PITC (n=33)
0≦Eccentricity <5

Figure 12

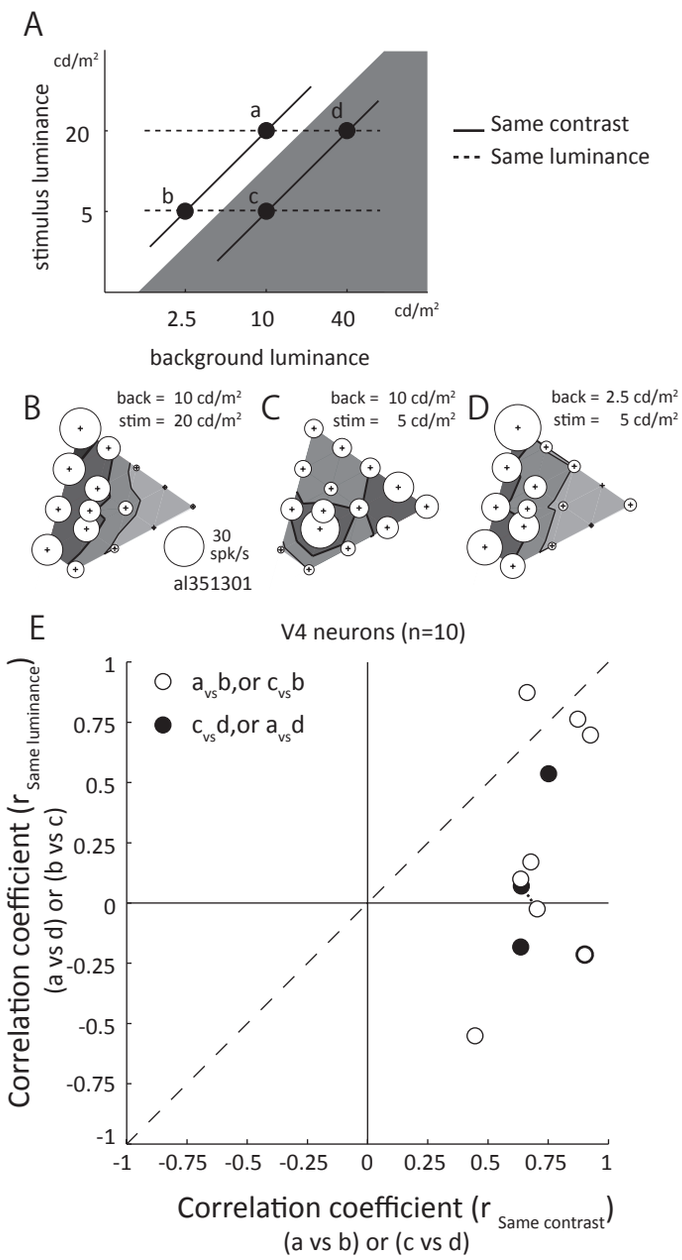
A
cd/m²
stimulus luminance
20
5
a
b
c
d
Same contrast
Same luminance
2.5
10
40
cd/m²
background luminance
B
back = 10 cd/m²
stim = 20 cd/m²
C
back = 10 cd/m²
stim = 5 cd/m²
D
back = 2.5 cd/m²
stim = 5 cd/m²
30
spk/s
al351301
E
V4 neurons (n=10)
a_vs b,or c_vs b
c_vs d,or a_vs d
Correlation coefficient (r Same luminance)
(a vs d) or (b vs c)
1
0.75
0.5
0.25
0
-0.25
-0.5
-0.75
-1
-1 -0.75 -0.5 -0.25 0 0.25 0.5 0.75 1
Correlation coefficient (r Same contrast)
(a vs b) or (c vs d)

Figure 13

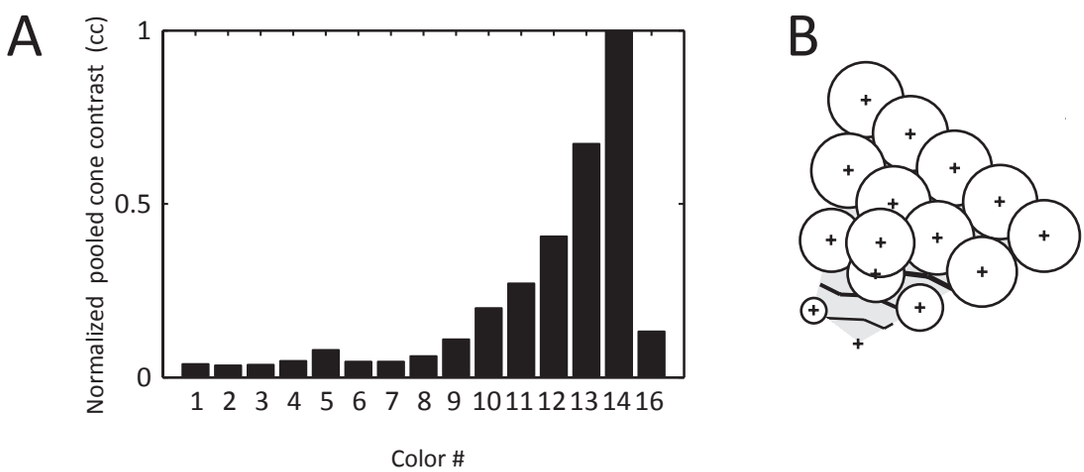
A
Normalized pooled cone contrast (cc)
1
0.5
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 16
Color #
B

Figure 14

Table 1　Proportion of the color selective neurons in each area

Comparison between three areas	V4		PITC		AITC	
Visually responsive neurons	149	(100)	90	(100)	155	(100)
1. Visually responsive neurons to both	108	(72.5)	69	(76.7)	107	(69.0)
1-1. Color selective neurons	71	(47.7)	58	(64.4)	82	(52.9)
1-2. Color selective to both	46	(30.9)	44	(48.9)	68	(43.9)
1-3. Color selective to either one	25	(16.8)	14	(15.6)	14	(9)
2. Visually responsive to either one	41	(27.5)	21	(23.3)	48	(31)
2-1. Color selective	31	(20.8)	17	(18.9)	32	(20.6)

Table 2 Responsiveness to two color stimulus set in the sample of AITC neurons

Samples of neurons from AITC	Monkey CO	Monkey KM	Total
Visually responsive neurons	89	66	155
bright set	73	55	128
dark set	76	58	134
Both bright and dark	60	47	107
Color selective neurons	40	42	82
bright set	35	40	74
dark set	36	41	76
Both bright and dark	29	39	68

Table 3　Responsiveness to two color stimulus set in the sample of PITC neurons

Samples of neurons from PITC	Monkey LW	Monkey KM	Total
Visually responsive neurons	51	39	90
bright set	46	37	83
dark set	45	31	76
Both bright and dark	40	29	69
Color selective neurons	29	29	58
bright set	27	27	54
dark set	21	27	48
Both bright and dark	19	25	44

Table 4 Responsiveness to two color stimulus set in the sample of V4 neurons

Samples of neurons from V4	Monkey AL	Monkey SI	Monkey SK	Total
Visually responsive neurons	78	48	23	149
bright set	68	45	22	135
dark set	69	33	20	122
Both bright and dark	59	30	19	108
Color selective neurons	40	19	12	71
Bright set	35	16	10	61
dark set	34	13	9	56
Both bright and dark	29	10	7	46