Measurements of long-range suppression in human opponent S-cone and achromatic luminance channels

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Cortical responses to spatially discrete patches of achromatic luminance contrast can be altered by the presence of high-contrast, spatially remote “surrounds” and this achromatic “surround suppression” has been the subject of much recent research. However, the nature of long-range contrast normalization in chromatic signals has been less studied. Here we use a combination of neuroimaging data from source-imaged EEG and two different psychophysical measures of surround suppression to study contrast normalization in stimuli containing achromatic luminance and S-cone-isolating contrast. In an appearance matching task, we find strong within-channel but little between-channel suppression. However, using a contrast increment detection task, we do find evidence for weak but significant between-channel effects. Our neural measurements agree with the appearance matching data, showing significant within-channel suppression and no significant interactions between signals initiated in different pre-cortical pathways. We hypothesize that appearance judgments and V1 population responses are dominated by neurons with chromatically matched classical and extra-classical surrounds while contrast increment detection tasks rely on a subpopulation of neurons that have extra-classical surrounds sensitive to both chromatic and achromatic contrasts. Our psychophysical and source-imaged EEG results are consistent with a hypothesis based on natural scene statistics that long-range contrast normalization in early visual system is largely driven by signals within the same chromatic channel.

Keywords: color appearance/constancy, color vision, contrast gain, detection/discrimination, functional imaging, receptive fields


Introduction

Texture and object boundaries in visual scenes are defined by changes in the spatial variance of the retinal cone absorption rates. In human trichromats, these signals are often specified in a color space defined by sums and differences of the long-wave, medium-wave, and short-wave-sensitive cone signals, termed “L,” “M,” and “S,” respectively, and the dimensions of this color space correspond, approximately, to anatomically distinct pre-cortical channels (Derrington, Krauskopf, & Lennie, 1984). When scaled appropriately, with reference to a constant background absorption rate, one type of contrast can be defined as a dimension along which the three cone contrast signals covary (L + M + S) leading to a stimulus that stimulates a post-receptoral “luminance” mechanism with a well-defined spectral sensitivity profile similar to the human V(λ) curve but which appears colorless (Lennie, Pokorny, & Smith, 1993). The two other contrast dimensions are constructed from differences as well as sums of cone signals: One channel carries a signal representing the difference between the S-cone and the sum of L- and M-cones (S − (L + M)), the other signals the difference between L- and M-cone absorption rates (L − M). These two “opponent color” channels carry chromatic information but do not contribute significantly to our sense of luminance contrast. In particular, the contribution of the S-cones to the luminance channel is believed to be negligible (Eisner & MacLeod, 1980; Lee & Stromeyer, 1989; Stockman, MacLeod, & DePriest, 1991).

For the visual system to be sensitive to boundaries in visual scenes, differences in local contrast must correspond to changes in neural firing rates. However, the range of contrast levels present in natural scenes far exceeds the coding capacity of any individual post-receptoral neuron. One solution to this is to use a large population of neurons with a range of contrast sensitivities so that at least some neurons will be sensitive at any given contrast level. This system is somewhat wasteful in that most neurons at any moment will be either saturated or unresponsive. A better solution is to adjust the gain of each neuron dynamically to bring its operating range into compliance with the local
scene statistics. Such contrast normalization mechanisms are common throughout the early visual system and are well understood in the domain of achromatic contrast control (Carandini et al., 2005; Heeger, 1992). One natural way to order these mechanisms is in terms of their spatial extent and order of operation in the visual pathway. Most strikingly, the effects of pre-cortical mechanisms can be almost entirely dissociated from the effects of cortical gain control based on their featural tuning, functional order of operation, and spatial extent (DeAngelis, Robson, Ohzawa, & Freeman, 1992; Petrov, Carandini, & McKee, 2006). Here, we adopt the nomenclature from these and subsequent studies and refer to short-range, untuned gain control as “overlay suppression” while effects involving an extended “silent” surround are termed “surround suppression” and are presumed to reflect predominantly cortical phenomena (Petrov, Carandini, & McKee, 2005), although shorter range versions of such effects can be measured as early as the LGN (Bonin, Mante, & Carandini, 2005; Solomon, White, & Martin, 2002).

These two gain control processes differ in many respects. Surround suppression, an umbrella term for at least two long-range normalization processes (Webb, Dhruv, Solomon, Taibby, & Lennie, 2005), exhibits both spatial and temporal tuning. It is strongest when the spatiotemporal characteristics of the surround match those of the probe (Blakemore & Tobin, 1972; DeAngelis, Freeman, & Ohzawa, 1994; Nelson & Frost, 1978). In comparison, spatiotemporal tuning in overlay suppression is generally weak or absent (Bonin et al., 2005; Petrov & McKee, 2006).

One outstanding question is whether long-range suppressive mechanisms in the early visual system also exhibit chromatic tuning at the population level. In other words, do significant normalization effects occur when the surround and probe stimulate different chromatic or achromatic luminance channels? The fact that chromatic and achromatic contrast boundaries are largely decorrelated in natural scenes (Hansen & Gegenfurtner, 2009) would suggest that there is no advantage to the visual system in adjusting neural sensitivity to luminance contrast based on local chromatic contrast. Studies of short-range cross-channel overlay suppression (Chen, Foley, & Brainard, 2000a, 2000b; Medina & Mullen, 2009) indicate that some cross-channel interaction does occur within local contrast normalization mechanisms although it is significantly weaker than within-channel normalization. However, there is also ample evidence that many cells in V1 respond to both luminance and chromatic signals and that the tight segregation of pre-cortical color and luminance channels is lost shortly after these signals enter the cortex (Johnson, Hawken, & Shapley, 2001, 2004; Sincich & Horton, 2005; Webster & Mollon, 1991).

One comprehensive psychophysical study of chromatic contrast induction (Singer & D’Zmura, 1994) speaks to this issue directly. The authors examined the effect of annular surrounds on spatially structured disk using combinations of contrasts defined by excursions along the McLeod–Boynton color axes. Interactions were measured using a modulation nulling task and the authors concluded that while no axes were truly independent, within-channel suppression was significantly stronger than between-channel suppression. In general, however, they found relatively weak induction effects using their foveal stimuli and these effects were not tuned for orientation. Recent work has shown that the magnitude of “surround suppression” increases significantly outside the fovea (Xing & Heeger, 2000) with some researchers (Petrov et al., 2005) reporting little or no long-range suppression for the types of stimuli used by Singer and D’Zmura. It is possible, therefore, that the results reported by this group represent the function of a small and rather specialized retinal location. Because almost all the experiments in Singer and D’Zmura’s paper also used abutting disks and surrounds, the possibility arises that the results conflate the action of what are now believed to be two anatomically separate normalization mechanisms: surround suppression and overlay suppression (Petrov et al., 2005).

Finally, single-unit studies (Solomon, Peirce, & Lennie, 2004) demonstrate the existence of cells in V1 and V2 with a variety of extra-classical tuning preferences, but the contribution of these cells to perception is still unclear.

In this study, we constructed center/surround stimuli with components that isolated the achromatic luminance (L + M + S) and opponent S-cone (S − (L + M)) channels independently. Using these stimuli, we measured the effect of placing iso-oriented and orthogonal gratings around central “probe” regions using all four combinations of S-cone-isolating and pure luminance probes and surrounds. We made these measurements in three ways. First, using source-imaged EEG, we measured the change in V1 neural responses due to a stimulus-locked signal generated by flickering the probe region on and off. Second, using a two-alternative forced-choice psychophysical paradigm, we measured the effect of surrounds on contrast modulation detection thresholds—a task that is thought to engage only a sensitive subpopulation of neurons driven by the probe region (Adams, Courage, & Mercer, 1991; Shadlen, Britten, Newsome, & Movshon, 1996). Finally, we allowed subjects to match the apparent contrast of probe regions presented with and without a surround—a task that was designed to tap processes that pool responses from the entire population of probe-driven neurons (Cavanaugh, Bair, & Movshon, 2002a).

In all three data sets, we found that surround suppression is strongest when the surround and the probe components have the same chromaticities (within-channel) and suppression is largely absent when the components have different chromaticities (cross-channel). For the low spatial frequency stimuli, we found little evidence of orientation dependence but orientation-dependent suppression became clearer when we used stimuli with higher spatial frequencies. We found only one clear example of long-range
cross-channel suppression: surround suppression measured psychophysically using a contrast discrimination task showed weak but significant suppressive interactions between luminance contrast surrounds and S-cone contrast probes. We discuss these findings within a signal detection theory framework and relate them to recent data on the chromatic sensitivities of extra-classical receptive fields in the early visual system.

Methods

Psychophysical methods: Contrast matching

Observers

Seven observers (four females, average age = 31) participated in both the contrast matching and the contrast discrimination experiments. All of the subjects were naive to the purpose of the experiments. All had normal or corrected-to-normal visual acuity and normal color vision. Acuity was measured using the Bailey–Lovie LogMAR chart, which has five letters per line and equal log increments in the letter sizes across lines. Color vision was measured using Ishihara plates book. Informed consent was obtained prior to experimentation under a protocol that was approved by the Institutional Review Board of the Smith-Kettlewell Eye Research Institute.

Stimuli

Figure 1 shows an example of the stimuli used in the appearance matching experiment. The stimulus is composed of a “reference” and “match” region. The reference is always a Gabor grating patch in isolation. The match is composed of a Gabor grating presented either in isolation or with an annular surround containing a high-contrast grating drifting at 5°/s. Both the reference and the match are presented at eccentricity of 5° with matching spatial frequencies of either 1.875 cycles per degree (cpd) or 1 cpd and the probe flickered on and off with a temporal frequency of 3 Hz and a 50% duty cycle. The temporal frequencies of our stimuli were chosen to lie close to those identified as optimal for generating chromatic VEP responses (Crognale, Switkes, & Adams, 1997).

Stimulus contrasts are listed in Table 1. In general, our goal was to use probe contrasts that generated approximately equal, robust, and suppressible responses in the EEG. Matching chromatic and achromatic stimulus contrasts using constant multiples of detection threshold (e.g., Switkes, Bradley, & De Valois, 1988) or superthreshold cross-channel contrast appearance matches (Switkes & Crognale, 1999) did not achieve this aim because pilot studies showed that EEG responses to the scaled achromatic luminance stimuli were too weak to elicit reliable EEG signals. This apparently paradoxical observation may be due to the fact that the waveform elicited by achromatic stimuli are more complex than those generated by S-cone stimuli (Rabin, Switkes, Crognale, Schneck, & Adams, 1994)—possibly because they represent the summed (and partially cancelled) responses of both magnocellular and parvocellular post-receptoral pathways.

Procedure

On each trial, observers were presented with reference and match targets appearing simultaneously on different sides of fixation. The observers’ task was to adjust the contrast of the match Gabor grating to that of the reference while fixating in the center. Observers adjusted

Figure 1. An illustration of the stimuli used in surround suppression appearance matching experiment. The stimulus-grating period shown here (λ) is 0.67° although we also used stimuli with λ = 1°. Probes were presented at an eccentricity of 5° and a radius of 1λ with a Gaussian envelope. The gap width was 1λ, and the annulus width was 2λ. In each trial, the probes were flickered continuously on and off at 3 Hz within a drifting surround in a configuration similar to that used in the EEG. Subjects adjusted the contrast of the probe within the annulus region until it matched the apparent contrast of the probe presented in isolation.
the contrast of the match Gabor by pressing keys on a keyboard and when they were satisfied with the match, they terminated the trial and another one began automatically. Data shown are the average of five such matches at each condition and for each observer.

Within each trial, the chromaticity, spatiotemporal frequency, and relative orientations of the targets and surrounds were constant. Across the trials, we used four different combinations of target and surround chromaticity representing all possible combinations of our S-cone and luminance contrasts (see Table 1) as well as control conditions in which the probe region appeared in isolation. Each of these probe/surround conditions were tested at two different relative orientations (parallel and orthogonal).

Cone isolation and stimulus contrasts

Stimuli were represented in the MacLeod–Boynton color space (MacLeod & Boynton, 1979), whose axes were scaled in cone contrast units. The probe and surrounds were defined by symmetrical contrast modulations along one of two directions in cone contrast space computed using a combination of monitor phosphor spectra measured using a photospectrometer (USB2000, OceanOptics, Florida) calibrated against an NIST-traceable light source and the Stockman 10° cone fundamentals (Stockman, MacLeod, & Johnson, 1993) appropriate for the extra-foveal stimuli we used in these experiments. One direction was computed to stimulate only the S-cones, leaving the quantal catch in the L- and M-cones unaffected, thereby generating a strong and independent signal in the opponent S − (L + M) pathway. The other direction was designed to stimulate all cone classes equally, generating a signal in the achromatic luminance pathway and nulling the S − (L + M) chromatic pathway. We subsequently refer to these stimuli as “S-cone” and “Luminance” stimuli. The former is defined solely by changes in S-cone quantal catches and excites only the opponent S − (L + M) post-receptoral pathway. The latter excites only a luminance-sensitive post-receptoral pathway, leaving the opponent S-cone post-receptoral pathway unaffected (see Table 1 for the contrasts of the S-cone and luminance stimulus components). S-cone isolation was verified by two methods. First, individual subjects adjusted the luminance of a nominally S-cone-isolating stimulus to minimize apparent flicker. Their cone contrast settings were within 1.5% of the stimuli used in the experiments along all cone contrast axes. Second, we ran a small number of additional EEG experiments in which the stimulus was flooded by an additional yellow light source generated by placing a Kodak Wratten 12 filter (Eastman Kodak Company, New York) together with an infrared reflective “hot mirror” in the optical path of a slide projector (Kodak Ektographic III AMT projector, Eastman Kodak Company, New York). This manipulation added another 20 cd/°s² to the luminance of the stimulus, reducing the sensitivity of the L- and M-cones significantly while leaving the S-cones unaffected. We found that the waveform of the S-cone probe stimuli measured with this method was very similar to that in the main experiment. The suppression results we measured using this control system also matched those described in the main series of experiments indicating that the within- and cross-channel S-cone suppression we observed was not simply due to luminance artifacts.

Display device

Psychophysical stimuli were presented on a PowerPC Apple Macintosh (Apple Computers, Cupertino, CA) running OS9 with a 10-bit graphics card (ATI Radeon 9000). They were presented on a Lacie Electron Blue II monitor running at 100 Hz with a resolution of 1024 × 768 pixels. Monitor calibration was performed at 1-nm spectral resolution using a fiber-optic photospectrometer (USB 2000, OceanOptics, Florida). Subjects viewed the stimuli monocularly in a darkened room at a distance of 80 cm from the screen. The background of the screen was maintained at a mean gray luminance of 42 cd/m² and all

<table>
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<td>No surround</td>
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<tr>
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<td>No surround</td>
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<tr>
<td>S/S Col</td>
<td>60%</td>
<td>60%</td>
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<tr>
<td>S/S Orth</td>
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Table 1. Stimuli parameters of conditions used in both psychophysical experiments.
stimuli were calibrated in units of cone contrast relative to this background.

**Psychophysical methods: Contrast discrimination**

**Stimuli**

The stimuli used in the contrast discrimination experiment had the same spatial configurations as those used in contrast matching experiment (see Figure 1). Each trial lasted 1500 ms. In a single trial, the subject first received an auditory cue signaling the start of the trial. The probe location markers (thin gray rings) and the mask annulus (where present) were then presented. The central probe regions were presented 800 ms later for a duration of 200 ms within a raised-cosine temporal window. Finally, the mask and location rings disappeared at the end of the 1500-ms trial and this was the cue for the subject to make a response.

**Procedure**

Instead of adjusting the contrast of the stimuli continuously, in this experiment, we used a single-trial 2AFC task to measure contrast increment detection thresholds. On each trial, the observers’ task was to indicate with a single key press, which Gabor (left or right) had the highest contrast. Probe contrast was adjusted using an adaptive staircase algorithm (QUEST; Watson & Pelli, 1983) until a 78% correct detection threshold was reached. Trials that failed to reach a stable threshold were rejected. The average of all thresholds was taken for each condition and subject.

**Source-imaged EEG methods**

**Observers**

Ten observers (four females, average age = 37) participated the source-imaged EEG experiments. This group included all of the psychophysical observers and the inclusion criteria for the two groups were identical.

**Stimuli**

Our aim was to match the stimuli used in the EEG with those used in the behavioral experiments. The EEG recording paradigm placed some restrictions on the types of stimuli that could be used in these experiments, but nevertheless, we were able to match all the important spatiotemporal and chromatic features across the two experiment types. Just like the contrast matching experiment, the probe flickered continuously at 3 Hz (on/off) and the surround grating drifted at 5°/s. The temporal frequencies of our stimuli were chosen to lie close to those identified as optimal for generating chromatic VEP responses (Crognale et al., 1997). Below, we report the responses at the fundamental of the stimulus flicker frequency (F1 = 3 Hz).

Figure 2 shows the stimulus arrangement for the EEG. The stimuli consist of six probe + annulus regions

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**Figure 2.** An illustration of stimuli used in the EEG experiment. The probe flickers at 3 Hz (on/off); the surround grating drifts at 5°/s. The surround and the probe could be defined by either achromatic or S-cone-isolating contrast. Spatial frequencies for both probe and surround gratings were 1 cpd. During each trial, letter identification task is presented around the fixation point. Contrasts and colors have been adjusted to aid visualization.
connected together in a circle (a “wreath”). This configuration left the central region blank. Each individual stimulus in the wreath consisted of a 1-cpd “probe” Gabor region and an annular surround containing a grating of the same frequency. The probe centers were equally spaced around the perimeter of a 5°-radius circle centered on fixation. The inner radius of the surround was 0.8°, the radius of the probe was 0.7°, and the gap width was 1°. We used the same temporal and spatial frequencies, chromaticity, relative orientation, and contrast conditions for the probe and the surround as we used in the psychophysics experiment above. We also included the isolated S-cone probe and luminance probe without the surround as baseline conditions. To limit subject fatigue during recording sessions, we performed two separate recording sessions on each subject with individual sessions lasting approximately 1 h. The spatiotemporal properties, contrasts, and chromaticities of the probe and the surround of each condition are shown in Tables 2 and 3 of the two experiments.

**Experimental procedure**

To control attention, observers were required to perform a rapid serial letter identification task (to detect “T” among five adjacent “Ls”) in the center blank region in Figure 2. The difficulty of this task was adjusted automatically throughout the experiment to maintain a constant 78% correct performance level. The session began with a block of 8 trials of experimental conditions with random order along with the letter task. Each trial was presented for 10 s and was followed by a blank period with a random duration (3000 ms ± 500 ms) before the next trial began. There were a total of five blocks of eight trials in each experiment lasting approximately 15 min. Subjects were allowed to rest for several minutes before the next experiment started. Each observer completed three sessions.

**Display device**

Stimulus generation and signal analysis were performed by in-house software, running on a Macintosh G4 platform. Details of this software are discussed in previous publications (Appelbaum, Wade, Pettet, Vildavski, & Norcia, 2008; Appelbaum, Wade, Vildavski, Pettet, & Norcia, 2006). Stimuli were presented in a dark and quiet room on a LaCie Electron Blue19IC (Model N2901) monitor at a resolution of 1024 × 768 pixels, with a 60-Hz vertical refresh rate and a mean background luminance of 40 cd/m². Monitor calibration was performed at 1-nm resolution using a fiber-optic spectrophotometer (USB 2000, Oceanoptics, Florida).

**EEG data collection and source imaging procedure**

The source imaging EEG methods including EEG signal acquisition, head conductivity modeling, source estimation, visual area definition, and region of interest (ROI) quantification have been described previously in Appelbaum et al. (2008, 2006) and Busse, Wade, and Carandini (2009).

The electroencephalogram (EEG) data were collected using 128-sensor HydroCell Sensor Nets (Electrical

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Table 3. Stimuli parameters of conditions used in EEG Experiment 2.
Geodesics, Eugene, OR) that utilize silver–silver chloride electrodes embedded in electrolyte-soaked sponges. The EEG was amplified at a gain of 1000 and recorded with a vertex physical reference. Signals were 0.1 Hz high-pass and 50 Hz Bessel low-pass filtered and digitized at 512 Hz with a precision of 4 bits per μV at the input. Following each experimental session, the 3D locations of all electrodes and three major fiducials (nasion, left and right pre-auricular points) were digitized using a 3Space Fastrack 3D digitizer (Polhemus, Colchester, VT). For all observers, the 3D digitized locations were used to co-register the electrodes to their T1-weighted anatomical Magnetic Resonance Imaging (MRI) scans.

Artifact rejection and spectral analysis of the EEG data were performed offline. The raw data were evaluated using a sample-by-sample thresholding procedure to remove noisy sensors, which were replaced by the average of the six nearest spatial neighbors. Additionally, EEG epochs that contained 15% of the samples exceeding an absolute amplitude threshold (25–50 μV) were marked for exclusion on a sensor-by-sensor basis. These noisy epochs were not considered in subsequent analysis steps. The percentage of bad channels is less than 10% for all observers. A time average for each stimulus condition was computed over one stimulus cycle (1000 ms). To avoid onset transients, the first second was excluded from analysis. The time average was then converted to complex-value amplitude spectra at a frequency resolution of 0.5 Hz via a discrete Fourier transform. The resulting amplitude spectra of the steady-state visual evoked potential (SSVEP) were then evaluated using the first harmonic of the input stimulus frequency tag. Although McKeefry, Russell, Murray, and Kulikowski (1996) reported significant asymmetries in their VEP responses to counterphase flickering chromatic gratings, our on/off chromatic and achromatic stimuli generated responses confined almost entirely to the first harmonic. Significance was assessed using the Tcirc2 statistic (Victor & Mast, 1991).

**Head conductivity and geometry models**

As part of the source estimation procedure, head tissue conductivity models were derived for each individual from T1- and T2-weighted MR scans at a resolution of $1 \times 1 \times 1$ mm for each observer. Anatomical MR scans were obtained on a Siemens TIM Trio 3T scanner at the UCSF Neuroscience Imaging Center using a 12-channel whole-head coil and stock manufacturer MPRAGE and T2-weighting pulse sequences. Boundary element models were computed based on compartmentalized tissue segmentations that defined contiguous regions for the scalp, outer skull, inner skull, and the cortex. To begin, approximate cortical tissue volumes for gray and white matters were defined by voxel intensity thresholding and anisotropic smoothing using the FSL toolbox (http://fslsoftware.nimh.nih.gov/). The resulting white matter tissue boundaries were used to extract the contiguous cortical gray matter surface. These approximate segmentations were then used as a starting point for the anatomical segmentation procedure in Freesurfer (http://surfer.nmr.mgh.harvard.edu). This package used an iterative mesh-fitting procedure to generate topologically correct estimates of the white matter surface, the pial surface as well as the inner and outer skull boundaries and the scalp. We used a surface midway between the white matter and the pial surface as our boundary element model cortex.

Finally, all tissue surface tessellations were visually checked for accuracy to assure that no intersection had occurred between concentric meshes. Co-registration of the electrode positions to the MRI head surface was done by alignment of the three digitized fiducial points with their visible locations on the anatomical MR head surface using a least-squares algorithm in Matlab and electrode deviations from the scalp surface were removed.

**Cortically constrained minimum norm source estimates**

Estimates of the underlying cortical activity were derived using a cortically constrained minimum norm implemented in Matlab. This technique assumes that surface EEG signals are generated by multiple dipolar sources that are located in the gray matter and oriented perpendicular to the cortical surface. Cortical current density (CCD) estimates were determined based on an iterative approach that takes a realistic forward model generated by the MNE package (http://www.nmr.mgh.harvard.edu/martinos/userInfo/data/sofMNE.php) and minimizes an L2 cost function to produce an inverse mapping of current density on the cortical surface having the least total (RMS) power while still being consistent with the voltage distribution on the scalp (Hämäläinen & Ilmoniemi, 1994).

**Definition of regions of interest (ROIs)**

Functional magnetic resonance imaging (fMRI) data were collected on the same 3T Siemens scanner used for the anatomical scans. We used standard Siemens EPI functional imaging sequences with a resolution of $1.7 \times 1.7 \times 2$ mm. The general procedures for these scans (head stabilization, stimuli, traveling wave analysis) are standard and have been described in detail elsewhere (Appelbaum et al., 2008, 2006; Busse et al., 2009). Retinotopic field mapping produced regions of interest (ROIs) defined for each participant’s cortical area V1, V3A, and hV4 in each hemisphere (Biswal, DeYoe, & Hyde, 1996; Engel, Glover, & Wandell, 1997; Tootell & Hadjikhani, 2001; Wade, Brewer, Rieber, & Wandell, 2002). ROIs corresponding to each participant’s MT homologue “hMT+” were identified using low-contrast motion stimuli similar to those described by Huk, Dougherty, and Heeger (2002). In this paper, we focus on visual area V1 as it has been the
subject of most of the single-unit work on chromatic surround suppression.

**ROI-based data analysis**

We averaged the cortical current density (CCD) time courses from all mesh points falling within each ROI across both hemispheres. Figure 3A shows one observer’s fMRI-defined visual area V1. Figure 3B shows the mean CCD time course averaged across eleven observers for both the achromatic luminance probe alone and achromatic luminance probe with achromatic luminance surround conditions. The time averages were converted to the complex-valued frequency domain at frequency resolution of 0.5 Hz via a discrete Fourier transform in Matlab. The resulting amplitude spectra of the CCD time courses were then evaluated at frequencies attributable to the first harmonic of the probe grating modulation frequency (3 Hz). Figure 3C shows the mean amplitudes of the F1 (3 Hz) component averaged across all subjects. The sidebars, showing the amplitudes in the neighboring frequency bins (2.5 Hz and 3.5 Hz), give an estimate of the local noise. We performed spectral analysis on individual 1000 ms bins and used coherent averaging to compute the amplitudes of the responses corresponding to each of the frequency-tagged gratings in a single visual area. Within-subject averaging was performed on the complex Fourier components and therefore preserved phase information.

**Suppression index**

In order to compare neural and behavioral measures directly, we report all suppression effects as indices. The surround suppression index (SSI) is defined as the difference between the suppressed and unsuppressed conditions normalized to the unsuppressed condition. In our EEG source imaging data, the SSI is

\[
SSI = \frac{R_{\text{probe+surround}} - R_{\text{probe}}}{R_{\text{probe}}},
\]

where \( R \) is the response amplitude (the norm of the response vector in complex space) at the stimulus frequency of each condition for each observer.

For the contrast matching experiments, the SSI is

\[
SSI = \frac{\text{MatchedContrast}_{\text{probe+surround}} - \text{MatchedContrast}_{\text{probe}}}{\text{MatchedContrast}_{\text{probe}}},
\]

where MatchedContrast is the contrast at which the suppressed probe appears to match the unsuppressed probe.

Finally, for the contrast discrimination experiments, the SSI is

\[
SSI = \frac{\text{TholdAddContrast}_{\text{probe+surround}} - \text{TholdAddContrast}_{\text{probe}}}{\text{TholdAddContrast}_{\text{probe}}},
\]

where TholdAddContrast is the contrast modulation of the 30% pedestal at the 78% correct detection threshold.

**Statistical analysis**

*Four-way repeated-measures ANOVA*

We first performed a four-way repeated-measures ANOVA on both the psychophysics and EEG data using...
the statistical analysis package “R” (http://www.r-project.org/). We tested the effects of surround presence, probe chromaticity, surround chromaticity and orientation on contrast levels and EEG amplitudes. Between-observer differences were treated as random effects. For all experiments (EEG and two psychophysical experiments), we found significant effects of surround presence (Matching: \(p < 0.001\); Discrimination: \(p < 0.02\); EEG: \(p < 0.001\)), probe chromaticity (Matching: \(p < 0.0001\); Discrimination: \(p < 0.01\); EEG: \(p < 0.05\)), and surround chromaticity (Matching: \(p < 0.05\); EEG: \(p < 0.01\); except Discrimination: \(p > 0.2\)). We also found significant interactions of probe chromaticity and surround chromaticity (Matching: \(p < 0.0001\); EEG: \(p < 0.05\); except Discrimination: \(p = 0.12\); Table 4). We did not find significant effects of orientation (Matching: \(p > 0.1\); Discrimination \(p = 0.08\); EEG: \(p > 0.1\)).

**Results**

It has been suggested that different population of neurons contribute to different psychophysical tasks such as detection and appearance matching (Hillis & Brainard, 2007a, 2007b; Hol & Treue, 2001; Itti, Koch, & Braun, 2000; Stockman & Brainard, 2010). To study this in more detail, and in order to compare the behavioral results with neural responses, we conducted two types of psychophysical experiments to measure surround suppression: contrast appearance matching and contrast discrimination. We present the results from each type of experiment separately.

**Psychophysical results**

**Contrast appearance**

Figure 4 shows the mean SSIs measured for our psychophysical contrast appearance matching task. The stimuli were S/S (S-cone probes with S-cone surrounds; Figure 4A), Lum/Lum (luminance probe and luminance surrounds, Figure 4B), S/Lum (S-cone probes with luminance surrounds, Figure 4C), and Lum/S (luminance probes and S-cone surrounds, Figure 4D). The data are averaged across seven observers with 1 SEM error bar. Figures 4A and 4B show very strong within-channel suppression for both S/S and Lum/Lum stimuli (paired \(t\)-test for the matched contrasts of both the parallel conditions and orthogonal conditions for S/S: \(p < 10^{-7}\) and for Lum/Lum: \(p < 10^{-7}\)). Figures 4C and 4D show no evidence of cross-channel suppression (S/Lum and Lum/S conditions, paired \(t\)-test for contrast thresholds of parallel conditions: S/Lum \(p = 0.3\) and Lum/S, \(p = 0.7\)). We note that Figure 4C shows a hint of enhancement instead of suppression with the mean SSI S/Lum being negative for both parallel and orthogonal conditions (mean SSI =

<table>
<thead>
<tr>
<th>Effect</th>
<th>Matching</th>
<th>Discrimination</th>
<th>EEG</th>
</tr>
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<tr>
<td>Surround presence</td>
<td>(p &lt; 0.001)</td>
<td>(p &lt; 0.05)</td>
<td>(p &lt; 0.01)</td>
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<td></td>
<td>(F: 48.5)</td>
<td>(F: 13.63)</td>
<td>(F: 5.35)</td>
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<td>Probe chromaticity</td>
<td>(p &lt; 0.0001)</td>
<td>(p &lt; 0.01)</td>
<td>(p &lt; 0.03)</td>
</tr>
<tr>
<td></td>
<td>(F: 128)</td>
<td>(F: 18.64)</td>
<td>(F: 6.20)</td>
</tr>
<tr>
<td>Surround chromaticity</td>
<td>(p &lt; 0.05)</td>
<td>(p &lt; 0.2)</td>
<td>(p &lt; 0.01)</td>
</tr>
<tr>
<td></td>
<td>(F: 8.7)</td>
<td>(F: 0.3)</td>
<td>(F: 13.5)</td>
</tr>
<tr>
<td>Orientation</td>
<td>(p: 0.46)</td>
<td>(p: 0.08)</td>
<td>(p: 0.8)</td>
</tr>
<tr>
<td></td>
<td>(F: 0.6)</td>
<td>(F: 4.11)</td>
<td>(F: 0.01)</td>
</tr>
<tr>
<td>Surround presence *</td>
<td>(p: 0.36)</td>
<td>(p: 0.01)</td>
<td>(p: 0.57)</td>
</tr>
<tr>
<td>probe chromaticity</td>
<td>(F: 1.06)</td>
<td>(F: 17)</td>
<td>(F: 0.34)</td>
</tr>
<tr>
<td>Probe chromaticity *</td>
<td>(p &lt; 0.0001)</td>
<td>(p: 0.12)</td>
<td>(p &lt; 0.05)</td>
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<tr>
<td>surround chromaticity</td>
<td>(F: 150)</td>
<td>(F: 3.17)</td>
<td>(F: 7.2)</td>
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<td>(p: 0.7)</td>
<td>(p: 0.18)</td>
</tr>
<tr>
<td>surround chromaticity *</td>
<td>(F: 0.05)</td>
<td>(F: 0.13)</td>
<td>(F: 2.06)</td>
</tr>
</tbody>
</table>

Table 4. ANOVAs with repeated measure.
Although suppression was strong in the within-channel conditions, the effect of orientation was not significant (paired \( t \)-test of contrast thresholds of parallel and orthogonal conditions for S/S conditions: \( p = 0.9 \) and for Lum/Lum conditions: \( p = 0.12 \)). Somewhat surprisingly, the effect of the surround in the pure luminance condition is smaller than that for the S-cone stimuli (Figures 5A and 5B, for S-cone parallel conditions, mean SSI = 0.71, and for luminance, mean SSI = 0.22). We also measured cross-channel suppression with this contrast detection task. However, unlike the appearance task (Figure 4C) we measured weak but significant surround suppression for heterogeneous stimuli. Specifically, we found suppressive interactions between S-cone probes and luminance surrounds. In Figure 5C, we show a mean SSI of 0.38 for the parallel conditions and 0.19 for the orthogonal conditions. A permutation test on the condition S/Lum
and the control condition with S-cone probe alone shows a borderline effect ($p = 0.05$) for the parallel surround alone and a significant overall effect of a surround ($p < 0.05$ for data binned across both parallel and orthogonal conditions). High-contrast S-cone surrounds, on the other hand, had no effect on luminance probes (Figure 4D, parallel conditions, mean SSI = $-0.03$ and orthogonal conditions, mean SSI = $-0.04$). Paired $t$-test: $p = 0.18$ and permutation test: $p = 0.8$. This asymmetry may be due to the fact that the luminance surrounds were many times stronger, in terms of detection thresholds, than the S-cone surrounds or because the luminance probes were inherently less suppressible—perhaps because they were driving the underlying neural population closer to saturation. Saturation of the luminance-sensitive neurons may also explain the weaker effect of the Lum/Lum suppression despite the fact that strong suppression using these types of stimuli can be obtained at lower probe contrasts (Petrov et al., 2005) and higher spatial frequencies (Figure 7).

As in the appearance matching experiment, we found little effect of orientation in our suppression profiles (paired $t$-test of the contrast thresholds between two orientations of the within S-cone channel ($p = 0.3$) and of the within-luminance channel ($p = 0.3$)).

### Source-imaged EEG results

Figure 6 shows suppression indices calculated based on source-imaged EEG data extracted from retinotopically defined visual area V1. SSIs were calculated based on the $F_1$ amplitude as described in Equation 2 and averaged over ten subjects. As in the psychophysical data discussed above, we observed significant within-channel surround suppression (Figures 6A and 6B, for pure S-cone stimuli: mean SSI = 0.54 for parallel conditions, mean SSI = 0.46 for orthogonal conditions and $p < 0.01$ for both conditions;...
for pure luminance stimuli: mean SSI = 0.34 for parallel conditions, mean SSI = 0.35 for orthogonal conditions and p < 0.01 for both parallel and orthogonal conditions). For S-cone probe and luminance surround cross-channel conditions, we did not find significant surround suppression (Figures 6C and 6D, for S-cone probe and luminance surround conditions, mean SSI = −0.03 for parallel conditions, mean SSI = −0.04 for orthogonal conditions and p > 0.1 for both parallel and orthogonal conditions, paired t-test; for luminance probe and S-cone conditions, mean SSI = −0.13 for parallel conditions, mean SSI = −0.18 for orthogonal conditions, p > 0.1 for parallel conditions and p = 0.09 for orthogonal conditions). It is interesting to note that we observed weak surround enhancement in the cross-channel EEG conditions, especially the luminance probe with S-cone surround conditions, just as we did in the contrast matching experiment although neither effect reached statistical significance. We did not observe any significant effect of orientation of the pure S-cone and pure luminance surround suppression (p = 0.3 and 0.4, respectively, paired t-test of the amplitudes across conditions with different orientations). Altogether, the EEG data are very similar to the contrast matching data.

Discussion

Main results

The purpose of this study was to characterize the degree of long-range interactions between luminance and S-cone contrast in the early visual system. Our stimuli were carefully designed to generate strong surround suppression comparable to that observed in single-unit experiments. The probe and mask onsets were separated in both space and time and contained persistent cues that
eliminated the effect of spatial uncertainty (Pelli, 1985). To study neural responses, we used electrical source imaging (ESI) to extract current density time courses from early visual cortex. To relate our neural data to perception, we also made two types of psychophysical measurement (contrast detection and contrast appearance matches) using almost identical stimuli.

Across all these methods, we found that long-range surround suppression is strongest when the probe and the surround have the same chromaticity. Although we measured little effect of relative probe/surround orientation in either our behavioral or neural measurements, orientation effects were stronger when we used higher spatial frequencies in our probe and surround regions. When the spatial frequency was increased to 1.875 cpd, we found stronger suppression when the surrounds were parallel with the center compared to when they were orthogonal (Figure 7).

**Multiple sites of surround suppression**

While the neural computations underlying surround suppression are not fully understood, several aspects of it are becoming clear. First, it is not a unitary phenomenon. Suppression from extra-classical “silent” surrounds can be measured as early as the LGN (Bonin et al., 2005; Solomon et al., 2002) although this acts over relatively short distances and lacks strong orientation or spatial frequency tuning. Additional, long-range suppression is also present when measured in primary visual cortex (Angelucci, Levitt, & Lund, 2002; Angelucci & Sainsbury, 2006; Bair & Movshon, 2004; Blakemore & Tobin, 1972; Cavanaugh et al., 2002a; Cavanaugh, Bair, & Movshon, 2002b; Shushruth, Ichida, Levitt, & Angelucci, 2009) and this exhibits tuning for both spatial frequency and orientation. Suppressive surrounds can also be measured in extrastriate cortical areas including V2 (Gegenfurtner, Kiper, & Fenstemaker, 1996; Levitt, Kiper, & Movshon, 1994; Solomon et al., 2004), V4 (Desimone & Schein, 1987; Desimone, Schein, Moran, & Ungerleider, 1985), and MT (Allman, Miezin, & McGuinness, 1985; Born, 2000; Pack, Conway, Born, & Livingstone, 2006). It seems likely that the general principle of normalizing neural responses by a spatially extended gain pool is a canonical computation in visual cortex, and possibly throughout the brain.

In striate cortex, at least two long-range suppressive mechanisms can be identified: an “early” component, originating either pre-cortically or at the input to V1 and a later component that may involve feedback from higher visual areas (Angelucci & Sainsbury, 2006; Bair, Cavanaugh, & Movshon, 2003; Webb et al., 2005). Psychophysical correlates of these two early mechanisms can also be demonstrated by manipulating the timing and duration of the stimuli (Petrov et al., 2005).

We make only weak claims for the cortical site of the surround suppression that we measure in our ESI experiments. Simulations of signal cross-talk in our EEG source imaging computations suggest that the great majority of the signals that we attribute to V1 do, in fact, come from this visual area, but there are small but significant contributions from neighboring regions V2 and V3. We are unable to distinguish between temporally “early” and “late” suppressive mechanisms within striate cortex as we deliberately used a steady-state EEG paradigm in which precise temporal ordering of signal components is lost. Similarly, our psychophysical experiments were designed...
specifically to mirror our EEG stimuli and isolate the effects of a steady-state suppression phenomenon that does not depend critically on the timing of probe and mask onsets (Petrov et al., 2006; Wade, 2009). However, it is intriguing to note that our data are consistent with a suppression mechanism that acts very early in V1—at a point before the signals from the opponent pre-cortical pathways have been combined (Johnson et al., 2004; Sincich & Horton, 2005).

The chromatic tuning of surround suppression

Singer and D’Zmura (1994) found that the long-range modulation they measured was clearly tuned for chromaticity: probes were suppressed most effectively by annuli defined by contrast along the same axis in MacLeod–Boynton space. Both our ESI and psychophysical data agree with this general result.

Our ESI data show that in signals originating primarily from V1, surround suppression has a clear chromatic tuning. It is strongest when the chromaticity of the suppressive surround matches that of the central probe region, and decreases significantly when the chromaticities of the probe and surround are different. In the case when the surround and probe isolate different pre-cortical channels, there appears to be no statistically significant surround suppression in the ESI data or the contrast appearance data. However, our contrast discrimination data do show significant cross-channel suppression under these conditions.

The presence of chromatic tuning in the classical receptive fields of V1 neurons is well-established and both electrophysiological and psychophysical data suggest that V1 cells have a broader variety of chromatic tuning profiles than is measured in the LGN (Conway, Hubel, & Livingstone, 2002; Johnson et al., 2001, 2004; Webster & Mollon, 1991; Xiao, Wang, & Felleman, 2003). However, relatively few studies have examined the chromatic properties of the remote extra-classical receptive field in V1.

Solomon et al. (2004) measured the chromatic tuning of surround suppression with single-unit recording in macaque V1 and V2. They found V1 surrounds to be less chromatically tuned than the center and, in addition, found generally stronger suppression for luminance-tuned CRFs compared to chromatically tuned CRFs. Interestingly, this predicts a relatively high-pass de facto spatial tuning for luminance stimuli because extended luminance-domain patterns tend to self-suppress while extended chromatic stimuli do not. We were unable to probe multiple spatial frequencies using our stimulus configuration, as the resolution of the S-cone system is limited, especially in the periphery. However, at the single spatial frequency we tested extensively (1 cpd), we found equally strong, if not stronger suppression of S-cone isoluminant gratings by S-cone surrounds compared to their luminance counterparts.

A recent fMRI study has also examined the chromatic tuning of long-range suppressive interactions in multiple early visual areas. McDonald, Seymour, Schira, Spehar, and Clifford (2009) reported significant population-level cross-channel suppression in a study using oriented grating stimuli with similar eccentricities and spatial frequencies to those described here (eccentricity of 2–3° and spatial frequency of 1 cpd). Their results for signals in striate cortex are qualitatively similar to ours. They found significant chromatic tuning for surround suppression and little evidence of orientation tuning. There are, however, several differences between the two studies—notably, the apparent absence of cross-channel effects in our data and weak but significant cross-channel suppression in the data of McDonald et al. We note that McDonald et al. used isoluminant red/green gratings to define their chromatic probe, rather than S-cone-isolating Gabors as we did. The chromatic channels carrying these different opponent color signals are anatomically and functionally distinct at the input to V1 and so McDonald et al.’s results are best seen as complementary to our own. One issue that may be important in comparing these data directly is that McDonald et al. used abutting test and probe stimuli so that their responses were, potentially, due to high-level object segmentation effects (Appelbaum et al., 2006) as well as long-range surround suppression. In an earlier fMRI study of achromatic surround suppression, Williams, Singh, and Smith (2003) showed that local border effects were responsible for almost the entire orientation-tuned suppressive effect that they measured.

The relatively high levels of S-cone responses and surround suppression we measured could reflect a combination of several factors including a bias toward chromatically tuned, S-cone-sensitive CRFs caused by the relatively low spatial and temporal frequencies of our stimuli and intrusion of signals from extrastriate visual areas. Another explanation, however, might lie in the differential levels of long-range suppression to be found within the three pre-cortical anatomical visual pathways. Pre-cortical surround suppression is known to be very weak within the parvocellular system but somewhat stronger for koniocellular signals (Solomon, 2002). Because both the magnocellular and parvocellular systems can be driven by achromatic stimuli (Lee, Pokorny, Smith, Martin, & Valberg, 1990), the surround suppression we measure for our achromatic stimuli reflects the sum of a suppressed MC signal and an unsuppressed PC signal. Although some contributions of S-cone signals to the luminance pathway have been demonstrated in the past (Drum, 1983; Stockman, MacLeod, & Lebrun, 1993), these interactions are weak and the S-cone-isolating stimuli that we present against gray, non-saturating backgrounds predominantly drive responses in a single pre-cortical pathway with moderate suppression. This relative purity of the S-cone responses may explain both the relatively high response amplitudes as well as the similar amount of suppression that we see in the two chromatic stimuli directions (McKeefry et al., 1996).
Lack of orientation effect

Like Singer and D’Zmura (1994), we found no significant effect of relative probe/surround orientation in our main experiments. However, unlike them, we believe that this is due in part to the relatively low spatial frequencies of our stimuli. This low spatial frequency was chosen to ensure that both the luminance and the S-cone-isolating gratings were visible in the periphery. When we repeated a subset of our experiments using a higher spatiotemporal frequency, the effect of the relative orientation of surround and the probe became significant only for the luminance stimuli (paired t-test, \( p < 0.02 \), Figure 7). This observation is important because the lack of orientation effect in masking is often taken as an indication of pre-cortical processing (Xu, Ichida, Shostak, Bonds, & Casagrande, 2002). Because it has been shown that orientation tuning and spatial frequency tuning are reasonably well-correlated in a paradigm using long-duration drifting surrounds similar to the ones used here (Xing & Heeger, 2001) and because we are able to generate orientation-dependent effects using versions of our stimuli with slightly higher spatial frequency, we believe that at least some of the mechanisms we have isolated are cortical. For example, they may correspond to the early mechanism proposed by Webb et al. (2005), which has weak, although measurable spatial tuning.

An additional reason for the relative weakness of our orientation effect relative to other studies might be the absence of the transient mask presentations. Psychophysical studies that have reported strong orientation tuning in surround suppression have often used relatively transient stimuli occurring in close temporal proximity (Petrov et al., 2005; Wade, 2009).

Difference between contrast matching and discrimination experiments

Even though the spatial and temporal configurations of our two psychophysical experiments were similar, we found that they yielded slightly different results with respect to the effect of luminance surrounds on chromatic probes. Specifically, the appearance matching data showed no evidence of cross-channel interactions while the contrast detection threshold data indicated a significant effect of high-contrast luminance surrounds on S-cone probes (Figures 4C and 5C).

One explanation for this may be the differences in the temporal structure of the two stimuli. For example, our contrast detection experiments were conducted using a slower, single-trial, two-alternative forced-choice paradigm where we expect little contrast adaptation. However, the appearance measurements were made using a continuous flickering stimulus that was designed to enable the observer to adjust the contrast of the “match” region in real time. It is possible that some contrast adaptation effects occurred in the probe location with this paradigm and that this adaptation predominantly affected cortical cells with untuned- or luminance-tuned suppressive surrounds. There is some evidence (Werner, Sharpe, & Zrenner, 2000; Werner, 2003) that adaptation is driven preferentially by spatially structured stimuli, suggesting that neurons with spatial tuning are more adaptable. Since neurons with tight color tuning tend to have weak spatial frequency tuning (Johnson et al., 2004), it is conceivable that adaptation of the type found in our appearance matching task is sufficient to explain the lack of cross-channel masking. Adaptation (or the lack thereof) may also be responsible for the relative weakness of within-channel Lum/Lum surround suppression and the absence of Lum/S suppression in the contrast discrimination task, which we attribute to the near saturation of the luminance channel at these relatively high probe contrast levels.

An alternative explanation is that subjects may use different populations of cells or different readout strategies to perform these different tasks. In particular, a recent paper (Hillis & Brainard, 2007a) demonstrates that contrast detection and appearance are dissociable within the same stimulus and that top-down influences are more likely to affect appearance judgments than pure detection thresholds. Our demonstration of small differences in the effects of cross-channel surrounds on appearance and detection measurements is therefore not unprecedented.

We expect both appearance matching and the EEG signal to be determined by a population average of activity across many neurons (Cannon & Fullenkamp, 1991; Graham, 1989). This, in turn, will be dominated by neurons responding strongly to the input stimulus, in other words, neurons tuned to the chromaticity of the input. Given the relatively high contrasts that we used in these experiments, many such neurons are likely to be saturating or at least operating within a regime above the accelerating portion of their response functions. On the other hand, contrast discrimination is best performed by attending to neurons at the most sensitive parts of their contrast response functions (Dayan & Abbott, 2001; Itti et al., 2000). The optimal neurons to detect changes in chromatic contrast may, therefore, be those tuned slightly away from the chromatic direction of the stimulus, and even if the CRFs and ECRFs of these neurons are matched, they may still experience significant inputs from achromatic luminance stimuli. This argument is essentially a chromatic version of the off-frequency listening phenomenon in the auditory system (Leshowitz & Wightman, 1971) and similar effects have been demonstrated for discriminating gratings orientation in visual stimuli (Wilson & Regan, 1984).

Finally, we note that while our stimuli are not identical to those of Singer and D’Zmura (1994), our contrast modulation detection paradigm is likely to engage a mechanism similar to the one they probed using a continuous temporal modulation nulling procedure. It is interesting, therefore, to observe that Singer and D’Zmura found weak but significant cross-channel interactions in their data as we do for some stimulus combinations in our contrast detection paradigm.
Conclusions

We are interested in the question of how surround suppression, a type of contrast normalization, extends to the chromatic pathways and where in the cortex it might operate. In this paper, we focused on the opponent S-cone and achromatic luminance systems. Psychophysically, we found that suppression is strongest when both the probe and the surround have the same chromaticity—either S-cone-isolating or luminance contrast. In common with other neuroimaging studies, we found little effect of orientation in our suppression measurements at low spatial frequencies, but our additional experiments suggest that this may be due to the relatively low spatial frequencies that we used. Our neuroimaging data from V1 largely matched those of our behavioral tasks and in particular agreed with our contrast matching data. It did not exhibit the small levels of inter-channel suppression that we observed in our contrast discrimination experiments, possibly because the neural populations underlying the two measures were different. Our data place constraints on the neural computations underlying chromatic surround suppression. Importantly, they indicate that appearance judgments are dominated by neurons with chromatically matched classical and extra-classical receptive fields similar to those dominating the EEG signal from V1. Conversely, contrast discrimination judgments appear to be based on a subset of the neurons driving our EEG responses, and while the suppressive fields of these neurons are driven strongly by the stimuli that drive the CRF, they also respond to contrast along other directions in color space.

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