V1 mechanisms underlying chromatic contrast detection

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Abstract

To elucidate the cortical mechanisms of color vision, we recorded from individual V1 neurons in macaque monkeys performing a chromatic detection task. Roughly 30% of the neurons we encountered were unresponsive at the monkeys’ psychophysical detection threshold. The other 70% were responsive at threshold, but on average, were slightly less sensitive than the monkey. For these neurons, the relationship between neurometric and psychometric threshold was consistent across the four isoluminant color directions tested. A corollary of this result is that neuronal thresholds were roughly four times lower for L–M stimuli than S-cone isolating stimuli. Nearly half of the neurons that responded to chromatic stimuli at the monkeys' detection threshold also responded to high contrast luminance modulations, suggesting a role for jointly color-luminance tuned neurons in chromatic detection. Analysis of neuronal contrast-response functions and signal-to-noise ratios yielded no evidence for a special set of “cardinal color directions” for which V1 neurons are particularly sensitive. We conclude that at detection threshold – as shown previously with high contrast stimuli – V1 neurons are tuned for a diverse set of color directions and do not segregate naturally into red-green and blue-yellow categories.

Keywords

Color vision, Visual cortex, Detection psychophysics, Electrophysiology
Introduction

Understanding vision requires understanding the signal processing that supports visual detection. Visual detection is often investigated with two complementary approaches: psychophysics and neurophysiology. Psychophysicists infer a set of theoretical visual “mechanisms” that parsimoniously explain a body of behavioral data, whereas neurophysiologists measure the neuronal responses that are presumably the biological basis of these mechanisms. Forging links between these two bodies of work has greatly improved our understanding of signal processing in the visual system. For example, many aspects of achromatic contrast detection can be explained on the basis of the spatiotemporal contrast sensitivity of neurons in the primary visual cortex (V1) (Tolhurst et al. 1983; Geisler and Albrecht 1997; Boynton et al. 1999; Hawken and Parker 1990; Palmer et al. 2007). Whether the same is true for chromatic contrast detection is unknown.

Substantial psychophysical evidence supports the idea that chromatic detection is mediated by two cardinal mechanisms: a red-green mechanism that receives antagonistic signals from L- and M-cones, and a blue-yellow mechanism that receives strong S-cone input opposed to a combination of L- and M-cones (Cole et al. 1993; Sankeralli and Mullen 1996; Sankeralli and Mullen 1997; Krauskopf et al. 1982; LeGrand 1949; Nagy et al. 1987). Under the cardinal mechanisms model (Figure 1), stimulus modulations in the two mechanism-isolating directions are detected by distinct populations of neurons. Stimuli in intermediate color directions are detected by both populations, and could be detectable via probability summation even if neither population reaches detection threshold individually (Sachs et al. 1971; Graham 1977).

We asked whether signals measured in V1 at psychophysical detection threshold are consistent with the cardinal mechanisms model. Although V1 neurons are not tuned to the
cardinal color directions when tested with high contrast stimuli (Lennie et al. 1990; Johnson et al. 2004; Solomon and Lennie 2005; Horwitz et al. 2007), the responses of V1 neurons have not previously been measured at chromatic detection threshold, and nonlinearities in neuronal responses to high contrast stimuli complicate extrapolations to a low-contrast regime (Conway and Livingstone 2006; De Valois et al. 2000; Hanazawa et al. 2000; Solomon and Lennie 2005; Horwitz et al. 2005; Horwitz and Hass 2012). The possibility remains that, near detection threshold, individual V1 neurons are preferentially sensitive to modulations in the cardinal color directions, as would be the case if only L–M or S-cone dominated LGN afferents were active at threshold. Such a result would indicate that chromatic detection is mediated by distinct populations of red-green and blue-yellow V1 neurons.

We recorded the responses of V1 neurons to near-threshold chromatic stimuli in awake behaving monkeys to test a prediction of the cardinal mechanisms model: responses of individual neurons to intermediate colors should be determined by the magnitude of the stimulus component in the preferred cardinal color direction. This was the case for the only the minority of the V1 neurons we tested. Instead, we found a close relationship between the sensitivity of individual V1 neurons and the monkeys’ behavioral sensitivity that generalized across cardinal and intermediate color directions. Additionally, using high contrast stimuli, we identified a population of neurons that responded preferentially to chromatic modulations and a population that was equally responsive to chromatic and luminance modulations. These populations were similarly sensitive to near-threshold chromatic modulations, a result that supports a role for jointly color-luminance tuned neurons in chromatic detection. We conclude that the chromatic contrast sensitivity of individual V1 neurons is well matched to that of the monkey, and that even at low contrasts, a privileged status for a set of cardinal color directions is not evident.
Materials and Methods

Animal preparation

Two female *Macaca mullata* participated in this study. Each monkey was surgically implanted with a stabilization head-post and scleral search coil. Neuronal recordings were obtained via surgically implanted recording chambers (Crist Instruments, MD) which were centered over the posterior occipital cortex adjacent to the longitudinal fissure. Surgical procedures were performed under sterile conditions using isoflurane or sevoflurane anesthesia. Following surgery, monkeys were administered the following analgesics: buprenorphine (0.01-0.03 mg/kg BID for 2 days) and ketoprofen (5 mg/kg BID for 3 days). All animal procedures, including those related to surgery, housing, and behavioral training, were conducted in accordance with the National Institute of Health’s Guide for Care and Use of Laboratory Animals as well as the University of Washington’s Institutional Animal Care and Use Committee.

Behavioral task and stimuli

Monkeys were trained to perform the spatial two alternative forced choice (2AFC) detection task illustrated in Figure 2A. Monkeys viewed a computer monitor at a distance of 100 cm while seated in a primate chair in an otherwise dark room. Each trial began when the monkey fixed its gaze on a 0.1° black square located at the center of the monitor. Five hundred milliseconds later, a Gabor stimulus appeared in one of two mirror symmetric locations about the fixation point and disappeared after 666 ms. Following a brief delay (100 to 600 ms), the fixation point disappeared and two choice targets appeared. Choice targets were 0.2° black squares
positioned between the fixation point and the two possible stimulus locations. Monkeys were given juice rewards for making an eye movement to the choice target located in the direction of the Gabor stimulus. No feedback was given for incorrect choices. All stimuli were presented binocularly. Trials were aborted if, at any time before the onset of the choice targets, the monkey’s gaze deviated from an electronically defined 1° square window centered on the fixation point. Event timing and eye position monitoring was controlled by routines written in REX (Laboratory of Sensorimotor Research, National Eye Institute). Stimuli were generated using custom software written in Matlab (The MathWorks, MA) that used routines from the Psychophysics Toolbox (Brainard 1997).

To avoid high temporal-frequency cues, which might favor detection via luminance-tuned mechanisms, stimulus contrast ramped up and down smoothly (Wandell 1985). Contrast increased linearly for 167 ms, remained constant for 332 ms, and then decreased linearly for 167 ms (Figure 2B). The sinusoidal component of the Gabor stimulus drifted at 3 Hz, and the Gaussian envelope had a standard deviation of 0.4°. The orientation and spatial frequency of the Gabor stimulus were optimized for each neuron as described previously (Horwitz and Hass 2012). The time course, Gaussian envelope, and drift rate of the Gabor stimulus were held constant across all psychophysical and neurophysiological experiments.

Stimuli were displayed on a cathode ray tube computer monitor (Sony Trinitron, 760x1400 pixels, 75 Hz refresh rate) whose phosphor emission spectra were characterized with a spectroradiometer (PR650, Photo Research Inc, CA). The color depth of each channel of the monitor was increased from 8 to 14 bits using a digital video signal processor (Bits++, Cambridge Research) at the expense of spatial resolution: each pixel was twice as wide as it was tall.
Gamma correction was performed in software. All stimuli were presented on a uniform gray background (CIE coordinates: \(x = 0.33, y = 0.33, Y = 100 \text{ cd/m}^2\)).

Stimuli were generated using the method of silent substitution (Estévez and Spekreijse 1982) and were based on the Stockman, McLeod, and Johnson 1993 cone fundamentals (Stockman et al. 1993). For 78 neurons, stimuli were based on the 2° fundamentals, and for 30 neurons, stimuli were based on the 10° fundamentals. Results from these two sets of experiments were similar and thus have been pooled together in this report. Most importantly, the main conclusion of this study – that the signal-to-noise ratio of individual V1 neurons at psychophysical detection threshold does not depend on color direction – was unaffected by this manipulation. A more thorough analysis of the differences between the two stimulus sets and their impact on our results can be found in the Discussion. Unless otherwise stated, contrast was defined as the vector norm of the stimulus in L, M, S cone-contrast space:

\[
\text{Contrast} = \sqrt{\left(\frac{\Delta L}{L}\right)^2 + \left(\frac{\Delta M}{M}\right)^2 + \left(\frac{\Delta S}{S}\right)^2}
\]

Eq. 1

Recording procedures

Recordings from individual V1 neurons were attained via glass-tipped transdural tungsten microelectrodes (FHC Inc.) with impedances of 1 to 2 MΩ measured at 1000 Hz. The raw voltage signal was amplified, bandpass filtered (100 Hz to 8 kHz), and digitized at 40 kHz using the Multichannel Acquisition Processor (Plexon Inc.). Single unit isolation was assessed by stability in the action potential waveform over the duration of the recording and the absence of inter-spike-intervals < 1 ms.
During an initial characterization procedure, we estimated each neuron’s color tuning using circularly apertured drifting sinusoidal gratings of a preferred orientation, size, and spatial frequency. Chromaticities were selected from an isoluminant plane defined by two axes (Figure 2C): one in which L- and M-cones modulated out of phase (L–M or 0°), and one in which only the S-cones were modulated (S-cone isolating or 90°). The plane spanned by L–M and S-cone axes consists of stimuli that are isoluminant for the Stockman-MacLeod-Johnson standard observer. Stimuli in this plane are not perfectly isoluminant for the monkeys, but are expected to be approximately so. During the initial neuronal characterization procedure, stimulus contrasts in the L–M and S-cone isolating color directions were roughly matched for detectability (~13x threshold) and presented in four color directions (two cardinal and two intermediate). Thus, modulations in the intermediate color directions (45° and 135°) produced roughly equal changes in the detectability of their S- and L–M components. Had we equated the S and L–M components for cone contrast, the S-cone component would have been sub-threshold when the L–M component was clearly visible. The suprathreshold appearance of intermediate colors was distinct from that of the cardinal colors. The 45°/225° intermediate appeared lime/magenta and the 135°/315° intermediate appeared orange/cyan.

During the detection task, behavioral performance and neuronal responses were measured simultaneously in the preferred cardinal and intermediate color directions using the method of constant stimuli. We identified each neuron’s preferred cardinal and intermediate color direction on the basis of mean firing rates to the suprathreshold sinusoidal gratings used during the initial characterization procedure. Gabor stimuli were presented at 7 contrasts spanning the monkey’s psychophysical detection threshold. Presentations of 15 stimuli were randomly interleaved across trials: 2 color directions x 7 contrasts + 1 zero contrast (blank).
Contrast selection procedure

Measuring psychometric functions via the method of constant stimuli required a judiciously selected range of contrasts. If contrasts were too high or too low, or the contrast range too wide, then the informative (steep) portion of the psychometric function would have been poorly sampled. This problem was exacerbated by the fact that we tailored the spatial frequency and color direction of the stimuli to maximize each neuron’s response and thus presumably their relevance to behavioral performance. Because psychophysical thresholds vary by as much as 2 orders of magnitude across the color directions and spatial frequencies we tested (Mullen 1985; Burr et al. 1994), using the same contrast range for each neuron would have undoubtedly lead to poor sampling of the psychometric function.

To facilitate selecting appropriate contrast ranges for the detection task, we first measured behavioral detection threshold for 32 Gabor stimuli (each combination of 4 color directions and 8 spatial frequencies). Thresholds were determined using the QUEST adaptive procedure for each subject (Watson and Pelli 1983). Contrast sensitivity functions in each color direction were fit independently with a second order polynomial (Figure 3). The fits were then used to determine the contrasts used during neuronal recordings. Contrasts were typically chosen to span a range from 0.25 to 2x the detection threshold estimated by the fit, but in rare cases were adjusted manually to ensure adequate sampling.

To confirm that the monkeys were performing the task near threshold difficulty levels for humans, the first author performed the QUEST version of the 2AFC detection task using the same display that was used in the monkey experiments. Eye position was not measured in these experiments and psychophysical reports were indicated with button presses. Written, informed
consent was obtained from the human observer, and the experimental procedures conformed to the policies of the University of Washington Human Subjects Division.

Fitting contrast-response functions

A linear neuron tuned to a cardinal color direction will respond to modulations in intermediate color directions simply by virtue of the fact that intermediate colors have a component in the preferred cardinal direction. Expressed rigorously, the response of such a neuron depends on the projection of a stimulus onto its preferred cardinal color direction. To ask whether V1 neurons behave this way, we measured contrast-response functions (CRFs) in each neuron’s preferred cardinal and intermediate color directions and fit them simultaneously with the following model:

\[
\text{Spike counts}_{\text{card}} = \beta_0 + \beta_1 \times \max[\text{Contrast} - \beta_2, 0]^2
\]

(Eq. 2)

\[
\text{Spike counts}_{\text{int}} = \beta_0 + \beta_1 \times \max[(\text{Contrast} \times \beta_3) - \beta_2, 0]^2
\]

(Eq. 3)

In this model, CRFs in the two color directions are modeled as horizontally-scaled versions of each other. \(\beta_0, \beta_1, \) and \(\beta_2\) are fitted parameters that represent the background discharge, contrast gain, and spike threshold, respectively. \(\beta_3\) is a fitted parameter that determines the scaling between the cardinal and intermediate CRFs. If the CRF in the cardinal direction is steeper than in the intermediate direction, \(\beta_3 < 1\). If the CRF in the intermediate color direction is steeper than in the cardinal color direction, \(\beta_3 > 1\). Parameters were fit using maximum likelihood estimation assuming Poisson error. Contrast was defined as the projection of each stimulus onto the preferred cardinal color direction for Figure 4C&D, and defined as multiples of psychophysical threshold in Figure 4F&G.
The basis of the fit, half-squaring, has been used to describe the contrast-response functions of V1 neurons before (Anzai et al. 1999; Heeger 1992), but we found that the addition of a non-zero baseline firing rate ($\beta_0$) and a contrast threshold ($\beta_2$) improved the quality of many fits. The $\beta_3$ parameter was included to allow us to test the hypothesis that contrast-response functions in the cardinal and intermediate directions were horizontally scaled versions of each other (that is, $\beta_3 = 1$). The model does not include response saturation because none of the neurons showed signs of saturation over the contrasts we tested.

We considered quantifying neuronal activity differently for simple and complex V1 neurons (viz. F1 and F0 components of the response, respectively), but results obtained this way were nearly identical to those obtained using raw spike counts. Although we encountered simple cells with robust F1 components during our initial characterization procedure, the time course of the Gabor stimulus in the 2AFC task often dominated the neural response more so than the F1 component of the drifting Gabor. We thus quantified neuronal activity as spike counts during the stimulus interval for all analyses.

Quantification of psychometric and neurometric sensitivity

A primary objective of this study was to quantify the signals present in V1 at chromatic detection threshold and to relate these signals to behavioral sensitivity. We quantified behavioral sensitivity by fitting a cumulative Weibull function to the psychophysical data:

$$P(\text{correct}) = 1 - 0.5e^{-\left(\frac{x}{a}\right)^\beta}$$

(Eq. 4)

where $P(\text{correct})$ is the probability of a correct detection and $x$ is the stimulus contrast. The fitted parameters, $a$ and $\beta$, correspond to the threshold (i.e., the contrast necessary to support 82% correct detection) and slope of the psychometric function, respectively.
To quantify the reliability of neuronal signals in a way that is directly comparable to behavioral thresholds, we used an ideal observer analysis based on the responses of each neuron (Tolhurst et al. 1983; Britten et al. 1992; Palmer et al. 2007). For each color direction and contrast, we calculated an ROC curve based on the distribution of spike rates in response to a stimulus inside the RF (signal) and no stimulus presented (noise). The performance of the ideal observer was calculated as the area under the ROC curve, which gave rise to a single point on a neurometric function (e.g., Figure 5A&B).

This method assumes a model of detection in which, on each trial, the ideal observer receives a draw from a signal distribution (which represents the information available from the neuron at the tip of the electrode) and a draw from the noise distribution (which represents the information available from a theoretical but identical neuron whose receptive field is in the mirror symmetric location opposite the fixation point) (Britten et al. 1992). The ideal observer’s choice is based on whichever draw is larger, and is correct when the larger draw came from the signal distribution. We quantified the performance of the ideal observer by fitting equation 4 to the neurometric data, where the fitted parameters $\alpha$ and $\beta$ describe the neurometric threshold (NT) and slope, respectively. To compare neuronal and behavioral thresholds directly, we calculated the neurometric to psychometric threshold ratio (TR) separately for each color direction. Although we routinely tested only contrasts within 0.25 to 2 times the QUEST estimate of detection threshold, threshold ratios varied over a wider range because psychometric and neurometric thresholds were occasionally at the upper and lower ends of this range.

To assess differences in neuronal sensitivity across color direction statistically, we performed a permutation test based on an F-statistic:
where $\bar{i}$ is the mean neuronal sensitivity (NT or TR) for the $i_{th}$ color direction, $\bar{Y}$ is the mean across all color directions and neurons, $k$ is the number of color directions, $n_i$ is the number of observations for the $i_{th}$ color direction, $Y_{ij}$ is the sensitivity of the $j_{th}$ neuron in the $i_{th}$ color direction, and $N$ is the total number of observations. Next, we calculated F-statistics for 5000 datasets that were permuted by randomly reassigning neuronal sensitivity values (NT or TR) to color directions subject to two constraints: 1) the two values for any given neuron were reassigned to a cardinal direction and an intermediate direction (consistent with our experimental design) and 2) the number of values within each color direction was the same as in the original dataset. The permuted data sets thus maintained the statistical dependence within cells that was observed in the real dataset but randomly shuffled the association between neural sensitivity values and color. The p-value was calculated as the percentage of permuted F-statistics that exceeded the observed F-statistic.

**Choice probability**

For each neuron, we converted firing rates to z-scores within each stimulus condition (color direction x contrast x stimulus location), and then pooled z-scores according to the choice the monkey expressed at the end of the trial. We calculated an ROC curve from these two distributions of z-scores, and defined choice probability as the area beneath the curve (Britten et al. 1996). Choice probability equals 0.5 when the monkey’s choice is unrelated to the variations in the neuronal response. Choice probability $> 0.5$ indicates that the monkey more often reported
the stimulus to be inside the RF on trials in which the firing rate was unusually high. Firing rates were z-scored to remove effects of the color direction and contrast of the stimulus in the RF.

Inclusion criteria

We recorded from 96 V1 neurons in two monkeys performing the 2AFC chromatic detection task (51 from monkey K, 45 from monkey S). Receptive fields were located between 3° and 8° from the fovea (mean ± SD: 5.14 ± 0.88°). A minimum of 16 trials per color contrast condition was collected from each neuron. For the purposes of fitting contrast-response functions, we included neurons for which one or more ROC areas exceeded 0.8 (n= 67). We used the same inclusion criteria for the analysis of threshold ratios. For the analysis of choice probability, we included only those color/contrast conditions in which the monkey made ≥ 5 choices to each target.

Results

Preliminary psychophysical results

In order to test the appropriate contrast ranges during our neurophysiology experiments it was critical that we first measure psychophysical detection thresholds in the cardinal and intermediate color directions and across the range of spatial frequencies preferred by parafoveal V1 neurons. In these preliminary measurements, psychophysical thresholds were estimated using the QUEST adaptive procedure (Watson and Pelli 1983). Stimuli were centered at [-5°, -3.5°] or [5°, 3.5°] with respect to the fixation point. Consistent with psychophysical results from humans, contrast sensitivity functions for isoluminant stimuli were spatially lowpass (Figure 3 A-C) and sensitivity for achromatic stimuli was bandpass (Mullen 1985). Note that the Gaussian envelope
(SD = 0.4°) renders stimuli of nominal spatial frequency < ~1 cycles/deg artifactually similar. Nevertheless, we were able to observe an attenuation of achromatic contrast sensitivity below this value. Spatial frequencies > 4 cycles/deg were not tested to avoid complexities introduced by chromatic aberrations. The qualitative and quantitative similarities between the human (Figure 3C) and monkey observers demonstrate that the monkeys were under behavioral control. Under the cardinal mechanisms model, stimulus modulations in intermediate color directions are detected on the basis of pooled signals from the cardinal mechanisms. As shown in Figure 1, this should cause detection thresholds in the intermediate directions to be lower than detection thresholds mediated by either of the cardinal mechanisms individually. We tested this prediction by plotting detection thresholds for intermediate colors in threshold units along the cardinal color directions (Figure 3D-F). Points that lie on the interior of the gray shaded square are qualitatively consistent with the cardinal mechanisms model (i.e., probability summation between cardinal mechanisms). This was the case for detection of the 135º/315º intermediate across all the spatial frequencies we tested, but not for the 45º/225º intermediate at > 1 cycle/degree. These psychophysical results are agnostic to the color tuning of individual neurons, an issue that we turn to next.

Testing the cardinal mechanisms model in V1

We asked whether individual V1 neurons were tuned to the cardinal directions at psychophysical detection threshold. For two example V1 neurons (Figure 4A&B) spike counts in response to the L–M cardinal color direction were greater than responses to the intermediate color direction at every contrast tested. This tuning is consistent with a preference for the cardinal direction, but this interpretation depends critically on how stimulus contrast is defined.
Implicit in our definition of contrast (Eq. 1) is the equality of contributions from the L-, M-, and S-cone types. Changing the relative weights on the three cone types changes the contrast values, which in turn can scale contrast-response functions along the contrast axis.

To determine whether V1 neurons conform to the cardinal mechanisms model, we tested a prediction that it makes: spike counts in intermediate color directions should be determined by the projection of the stimulus onto the neuron’s preferred cardinal axis. For example, a neuron tuned to the L–M color direction would respond equally well to stimulus modulations in the L–M+S and L–M color directions if their L–M components are equal. To test this prediction, we quantified stimulus contrast as the projection onto the preferred cardinal axis and fit CRFs using a model which represents the difference between the CRFs as a scaling of the contrast axis (Equations 2 and 3). If V1 neurons respond like the psychophysical cardinal mechanisms, the two contrast-response functions should overlay each other, and the scale factor that relates cardinal and intermediate CRFs ($\beta_3$ in Eq. 3) should equal one. The CRFs for some neurons were consistent with the linear cardinal model (Figure 4C), but the majority of neurons had CRFs that were inconsistent with the cardinal model (Figure 4D). $\beta_3$ was significantly $> 1$ for 82% of the neurons individually (Wald tests, $p < 0.05$) and across the population (geometric mean = 1.50; $t$-test on $\log(\beta_3)$, $p < 0.001$; Figure 4E).

As a control analysis, we randomly partitioned responses to cardinal colors into two groups and then fit them with Eqs. 1 and 2. The average $\beta_3$ parameter from this control analysis was not significantly different from one ($t$-test on $\log(\beta_3)$, $p = 0.24$), which demonstrates that the tendency we observed in the data for $\beta_3 > 1$ is not a trivial consequence of the model fitting procedure. We conclude that individual V1 neurons respond more strongly to modulations in intermediate color directions than predicted by the cardinal model.
Comparing contrast-response functions equated for stimulus detectability

The qualitative similarity between neuronal and behavioral chromatic sensitivity led us to ask whether CRFs in cardinal and intermediate color directions might match quantitatively if stimulus intensity were represented in units of detection threshold. We scaled the contrast values so that an intensity of “1” in any color direction was detectable 82% of the time, and then re-fit Eqs. 2 and 3 to the data. For the few neurons that were well described by the cardinal model, this rescaling necessarily forced a discrepancy between cardinal and intermediate CRFs (Figure 4F). For most neurons, however, this manipulation yielded a closer correspondence in the CRFs (e.g., Figure 4G). The average $\beta_3$ (Eq. 3) for the entire population was not significantly different from 1 (geometric mean = 0.97, $p = 0.59$, t-test on $\log(\beta_3)$, Figure 4H). We conclude that the CRFs of V1 neurons are more closely related to psychophysical detection thresholds than to the S and L–M components of cone contrast modulations.

Neurometric sensitivity

Chromatic detection depends on the amplitude and variability of neural responses to low-contrast chromatic stimulation. To compare neuronal sensitivity across colors, we performed an ideal observer analysis that incorporates measurements of neuronal signal and noise (see Methods). Specifically, neuronal sensitivity was quantified as the neurometric threshold (NT) derived by fitting a cumulative Weibull function to the performance of a theoretical ideal observer with access to neuronal responses (Figure 5A&B; see Methods). Every neuron was tested in two color directions during the detection task, and NTs were calculated for each color direction separately.
An analysis of neurometric thresholds showed that V1 neurons were preferentially sensitive to some colors directions relative to others (permutation test on NTs p < 0.001; Figure 5C). Neurometric thresholds in the L–M color direction were lower than in any other color direction, and were 4.1 times smaller than in the S-cone isolating color direction (unpaired t-test \( t(56) = 5.5, p < 0.001; \) mean for L–M = 0.029, mean for S-cone isolating = 0.12). This analysis demonstrates that individual neurons are capable of producing reliable signals to near-threshold chromatic stimuli, and that the contrast (as defined by Eq. 1) necessary to evoke a reliable response depends on color direction.

**Neurometric-to-psychometric threshold ratios**

To quantify the relationship between neuronal sensitivity and behavioral performance we calculated neurometric-to-psychometric threshold ratios (TR) for each neuron in both color directions tested. A TR of 1 means that the neuron and monkey are equally sensitive. A TR > 1 means that the monkey is more sensitive than the neuron. On average, monkeys were 1.5 times more sensitive than V1 neurons (geometric mean TR = 1.5, 95% CI [1.38, 1.63]; Figure 6A). 30% of the neurons in our sample did not respond above baseline over the range of contrasts tested (i.e., at psychophysical detection threshold), and their threshold ratios were undefined. These neurons are unlikely to contribute to processing chromatic signals at detection threshold.

To determine if the relationship between neurometric and psychometric sensitivity depended on color direction, we compared TRs across the four color directions tested. This analysis was necessarily limited to those neurons for which neurometric thresholds were measureable given the contrast range that we used (see Methods). For this sub-population of
neurons, the distributions of TRs were highly overlapping (Figure 6B) and the geometric mean threshold ratio did not differ significantly across color direction (permutation test on log(TRs) p = 0.42; see Methods). Note that under the cardinal mechanisms model we would expect TRs to be higher in the intermediate directions than in the cardinal directions (Figure 1), which we did not observe.

Consistency between neurometric and psychometric sensitivity was also observed within cells. Threshold ratios measured in each neuron’s preferred cardinal and intermediate color directions were not significantly different (paired t-test, p = 0.60; Figure 6C). Moreover, the within-cells analysis demonstrated that TRs in the cardinal and intermediate color directions were well correlated (Spearman’s r = 0.84, p < 0.01). We conclude that V1 neurons differ widely in their sensitivity relative to the monkey, but that the relationship between neuronal and psychophysical sensitivity does not depend on color direction.

A potential explanation for the consistency of TR across color directions is that we tested too narrow a range of color directions: each neuron was tested in only two neighboring color directions of the four we considered. To control for this possibility, we tested 11 neurons in two orthogonal color directions: L–M and S-cone isolating. Only 4 of these 11 neurons were sensitive to one of the cardinal color directions and insensitive to the other. The remaining 7 neurons were sensitive to both color directions and were often more sensitive than the monkey (Figure 7A). For these neurons, TRs in response to L–M were slightly smaller than in response to S-cone isolating stimuli (geometric mean TR for L–M = 0.8 and for S-cone isolating = 1.05, paired t-test, p = 0.043; Figure 7B). Thus, S-cone isolating and L–M stimuli produce similarly reliable signals in V1 at the monkeys’ detection threshold, both across neurons and within the subpopulation that is sensitive in both color directions.
Choice probability

V1 neurons that contribute to chromatic detection must be responsive at the monkey’s chromatic detection threshold, however the converse is not true: not all chromatically sensitive neurons must contribute to psychophysical contrast detection. To identify V1 neurons that are most likely to contribute to the monkey’s psychophysical judgments, we performed an analysis of choice probability (CP). This analysis hinges on the logic that neurons that are causally linked to behavior may produce responses that are correlated with the monkey’s behavior on a trial by trial basis (Britten et al. 1996; Palmer et al. 2007; but see Nienborg and Cumming 2009).

By this analysis, neuronal responses were correlated with the monkeys’ choices only weakly. The average choice probability was $0.52 \pm 0.008$ s.e.m., which is slightly but significantly greater than 0.5 (t-test, $p < 0.05$). Very few individual V1 neurons had significant choice probabilities ($n = 4$ of 67, Wilcoxon, $p < 0.05$), and those that did were not obviously unusual in any other way. Specifically, they were not unusually sensitive compared to neurons with insignificant CP (t-test on log(TR), $p = 0.44$). Nevertheless, to designate a population of V1 neurons that were the best candidates for contributing to task performance, we extracted the subset of 32 neurons that had a choice probability $> 0.51$ (the median value). This subpopulation was neither particularly sensitive (t-test on log(TR), $p = 0.71$) nor differentially sensitive across color direction (ANOVA on log(TR) $F(3,27) = 0.84$, $p = 0.48$). Choice probability thus appears to provide little leverage into the question of which V1 neurons mediate performance on our task.

Suprathreshold response properties of chromatically sensitive V1 neurons
The degree to which a V1 neuron participates in color vision has traditionally been inferred from its responses to suprathreshold chromatic stimuli (Lennie et al. 1990; Johnson et al. 2001; Solomon and Lennie 2005), but the extent to which these suprathreshold measurements predict near-threshold sensitivity is unknown.

Following Johnson et al. (2001), we computed a color sensitivity index (CSI) based on responses to the high-contrast chromatic gratings used in our initial characterization procedure:

\[
\text{CSI} = \frac{\text{FR}_{\text{Pref Isolum}}}{\text{FR}_{\text{L+M}}} \tag{Eq. 5}
\]

where \(\text{FR}_{\text{Pref Isolum}}\) is the average firing rate in response to the preferred isoluminant stimulus and \(\text{FR}_{\text{L+M}}\) is the average rate in response to a 13% contrast L+M stimulus. Neurons with CSIs \(\leq 0.5\) were classified as luminance preferring (\(n = 19\)). Neurons with CSIs between 0.5 and 2 were classified as color-luminance cells (\(n = 46\)), and neurons with CSIs \(\geq 2\) were classified as color-preferring cells (\(n = 31\)). The prevalence of color-preferring neurons in our data set is higher than reported previously (32% vs. 11% Johnson et al. 2001; Johnson et al. 2008; Conway 2001) and the prevalence of luminance-preferring neurons is lower (20% vs. 60%). This outcome likely reflects our use of 4 chromatic stimuli (three of which robustly modulate the S-cones) instead of a single red-green isoluminant stimulus. When we redefined color sensitivity as the ratio of responses to the L–M and L+M color directions, the proportion of color-preferring neurons (13%) was closer to those of previous studies (Johnson et al. 2001; Johnson et al. 2008; Conway 2001).

A comparison of CSI and TR (Figure 8) showed a weak but significant relationship (Spearman’s \(r = -0.28, p = 0.005\)); neurons that were particularly sensitive during our detection task (i.e., those with the lowest TRs) tended to be color-preferring whereas neurons that were insensitive tended to be color-luminance or luminance-preferring. As expected, luminance
preferring neurons had higher TRs than color-luminance or color-only cells (Wilcoxon tests: p < 0.05), but many (n = 8 of 19) had TR ≤ 3, indicating non-negligible sensitivity to isoluminant modulations. Threshold ratios of color-luminance and color-only neurons were statistically indistinguishable (Wilcoxon test, p = 0.17). This result supports a role for color-luminance neurons in chromatic detection and argues against the idea that they can be considered “miscalibrated photometers” whose sensitivity to chromatic stimuli is small and has no behavioral significance (Gegenfurtner et al. 1994; Billock 1995).

Color-luminance V1 neurons, unlike color-preferring neurons, tend to have bandpass spatial frequency tuning (Johnson et al. 2001). Our observation that color-luminance neurons are sensitive at chromatic detection threshold thus implies bandpass spatial frequency tuning among the most chromatically sensitive V1 neurons. Consistent with this prediction, neurons that were sensitive at the monkeys’ detection threshold had a range of spatial frequency preferences and tuning bandwidths when measured with achromatic gratings (Figure 9A-F). Bandwidths calculated by fitting a difference of Gaussians model to the raw data (Johnson et al. 2001) were poorly correlated with threshold ratios (Spearman’s r = 0.14, p = 0.25; data not shown), and the population spatial frequency tuning function of neurons sensitive at detection threshold (TR ≤ 3) was similar to the tuning function for insensitive neurons (Figure 9J). For most neurons, spatial frequency tuning was measured with achromatic gratings, but a similar result was obtained from a subset of neurons (n = 14) whose spatial frequency tuning was measured using gratings of the preferred isoluminant color direction (Figure 9G-I). The existence of chromatically sensitive, spatially bandpass V1 neurons is consistent with psychophysical observations (Bradley et al. 1988; Losada and Mullen 1994; Mullen and Losada 1999), and argues against the view that
strongly color-opponent, lowpass, unoriented neurons are the sole mediators of color processing in V1.

Discussion

Detection psychophysics has been instrumental in developing models of contrast sensitivity on the basis of neural detection mechanisms (Blakemore and Campbell 1969; Mullen 1985; Tolhurst et al. 1983; Boynton et al. 1999; Geisler and Albrecht 1997; Cole et al. 1993; Sankeralli and Mullen 1996). Simultaneous measurement of neuronal responses and psychophysical performance offers a powerful method of testing these models. Using this approach, we showed that individual V1 neurons are responsive at chromatic detection threshold but their tuning is inconsistent with the linear cardinal mechanisms model. Contrast-response functions did not match when contrast was defined as the projection of a stimulus onto the preferred cardinal axis but were better matched when contrast was defined in units of detection threshold. An ideal observer analysis showed that neurometric thresholds were on average 1.5 times greater than the monkeys’ psychometric thresholds, and this result was consistent across the 4 color directions we tested. In contrast to the independence between the cardinal mechanisms demonstrated psychophysically (Krauskopf et al. 1982; Krauskopf and Farell 1990; Sankeralli and Mullen 1997) and supported by the physiology and anatomy of the visual system prior to V1 (De Valois et al. 1966; Derrington et al. 1984; Chatterjee and Callaway 2003), some V1 neurons were sensitive at detection threshold in both L–M and S-cone isolating color directions. Lastly, we found that many V1 neurons that responded to high contrast luminance stimuli were also well driven by isoluminant stimuli at the monkey’s psychophysical threshold. This suggests a role for jointly color-luminance tuned neurons in chromatic detection.
Relationship to psychophysically defined detection mechanisms

Psychophysical experiments have demonstrated that chromatic detection is mediated by multiple visual mechanisms, but the tuning and number of these mechanisms is controversial (for review see Eskew 2009; Stockman and Brainard 2009). Evidence in favor of the cardinal mechanisms model comes from a variety experimental techniques including color matching (LeGrand 1949), detection (Cole et al. 1993; Sankeralli and Mullen 1996), chromatic habituation (Krauskopf et al. 1982), noise masking (Sankeralli and Mullen 1997; Giulianini and Eskew 1998; Eskew et al. 2001), and motion coherence judgments (Krauskopf and Farell 1990). Using essentially the same techniques, other experiments have acknowledged a dominant role for the cardinal mechanisms in chromatic detection but suggest the existence of an unknown number “higher-order” mechanisms that also contribute to color vision (Krauskopf et al. 1986; Krauskopf and Gegenfurtner 1992; Webster and Mollon 1994; Krauskopf et al. 1996; Stoughton et al. 2012). A third group of experiments found evidence of higher-order mechanisms and argued against a dominant role for the cardinal mechanisms (Gegenfurtner and Kiper 1992; D'Zmura and Knoblauch 1998; Hansen and Gegenfurtner 2006).

The higher-order chromatic detection mechanisms revealed psychophysically may result, in part, from cone signal processing in V1. Many previous studies have documented non-cardinal color tuning in V1 (Lennie et al. 1990; Johnson et al. 2004; Horwitz et al. 2007). Our study confirms and extends these previous studies in three ways. First, we studied neurons in a low-contrast regime most appropriate for revealing detection mechanisms. Second, we analyzed the signal and noise components of neuronal responses in a way that is directly comparable to the psychophysical performance of the observer. Third, we measured neuronal responses directly,
thereby obviating the need for stimulus manipulations to isolate detection mechanisms (e.g., habituation and noise masking) which can have complex effects on the responses of individual V1 neurons (Tailby et al. 2008) and may affect task strategy (D’Zmura and Knoblauch 1998; Gegenfurtner and Kiper 1992). We conclude that even under these conditions, V1 neurons do not conform to the cardinal mechanisms model.

One potential concern with this conclusion is that detection might be mediated exclusively by the subset of neurons tuned to the cardinal color directions (e.g., those with $\beta_3$ near 1, see Eqs. 2&3). While this possibility is consistent with our data, it is not strongly supported by them: neurons tuned to the cardinal axes were uncommon and only moderately sensitive to chromatic contrast. TRs of neurons with $\beta_3$ within $\pm 1$ SD of 1 were not significantly different than TRs of neurons with $\beta_3$ outside of this range (t-test, p = 0.78). Similarly, $\beta_3$s were not significantly correlated to TRs (Spearman’s r = 0.02, p = 0.85). We thus find no evidence that V1 neurons tuned to the cardinal axes have a special role in chromatic detection.

An additional concern is that our main conclusion – that V1 neurons do not behave as the cardinal mechanisms at detection threshold – is dependent on the spatial properties of the stimulus we used. Indeed, color tuning is not, in general, separable from spatial tuning (Lennie et al. 1990; Johnson et al. 2001). For example, LGN neurons are tuned to the cardinal color directions when tested with full field stimuli but not when tested with stimuli that are spatially band-limited such as sinusoidal gratings (Lennie et al. 1990; De Valois et al. 2000). Although it is possible that we might have obtained a different result by using a different spatial stimulus, we found that restricting our analysis to neurons with a preferred spatial frequency < 1 cycle/deg did not change our main conclusion (data not shown).
Our use of spatially band-limited stimuli was motivated by two factors: First, neurophysiological investigations have shown that some V1 neurons are chromatically and spatially opponent. For example, Johnson, Hawken, & Shapley (2008) showed clear examples of double-opponent V1 neurons that appear to behave in accordance with the cardinal mechanisms model (e.g., Johnson et al. 2008 their Figure 1). Spatially band-limited stimuli drive these cells more strongly than full-field stimuli and are thus presumably a better choice for revealing the a contribution of these cells to visual processing. Second, we wanted to compare fairly the neurometric sensitivity of color-only and color-luminance V1 neurons. Neurons in these two groups tend to be tuned for different ranges of spatial frequency (Johnson et al. 2001), and their respective contribution to color vision is a matter of debate. Fixing the spatial frequency of the stimulus would likely have biased the result in favor of one group or the other (lower spatial frequencies favoring the color-only group). By tailoring the spatial frequency to the neuron under study, we found that neurons in both categories were approximately equally sensitive. Our results suggest a role for band-pass V1 neurons in the detection of isoluminant stimuli and is consistent with psychophysical evidence postulating spatial frequency selective mechanisms for chromatic detection (Bradley et al. 1988; Losada and Mullen 1994; Mullen and Losada 1999; Webster et al. 1990).

We presented all stimuli binocularly, but had we occluded one eye, we expect that psychometric thresholds would have increased by a factor of ~1.5 (Legge, 1984; Simmons and Kingdom, 1998). How this manipulation would affect neuronal sensitivity is unclear and we did not measure ocular dominance. For monocular neurons, this manipulation would not have affected neurometric thresholds. Because psychometric thresholds would increase, the neurometric to psychometric threshold ratio for monocular neurons would be closer to one.
However, binocular, color-sensitive neurons are common in V1 and likely have higher
neurometric thresholds under monocular stimulation (Landisman and Ts'o, 2002; Pierce et al,
2008).

We looked for trial-to-trial covariations between neuronal and psychophysical behavior
(CP) but did not find compelling evidence for this relationship among the V1 neurons we
studied. Although one study of V1 (Palmer et al. 2007) has reported significant CP for the
population of V1 neurons taken as a whole, CP has not been solidly established as a
characteristic of individual V1 neurons. Another notable study failed to find significant choice
probability in V1 (Nienborg and Cumming 2006). Another reason that we may have failed to
find significant CP in this study is that Z-scoring distributions of low spike counts can corrupt
CP measurements (Kang and Maunsell 2012). Improved methods of measuring weak
relationships between neuronal responses and behavior might reveal such a pattern in our data,
but for our purposes, such a method would have to be sufficiently sensitive at the level of
individual neurons to be useful for identifying those that are tightly linked to behavior.

Small signal linearity

A motivation to study color vision at detection threshold is that the complexities of
adaptation and gain control are minimized, potentially leading to a closer-to-linear color vision
system (Solomon and Lennie 2005; Tailby et al. 2008; Solomon et al. 2004). This is undoubtedly
true at many levels of the visual system, but we were surprised by clear nonlinearities in V1
responses even in the low contrast regime.

One nonlinearity that all V1 neurons exhibit is a spike threshold which naturally exerts a
strong effect at low contrasts. This nonlinearity was expected, and was thus included in the
model we used to fit contrast-response functions (Eqs. 1 and 2). The model also assumes that CRFs in pairs of color directions can be equated by scaling the contrast axis. This would be the case for a linear neuron with a static output nonlinearity (e.g. spiking threshold), but was demonstrably untrue for 39% of the neurons we recorded. For these neurons, an analysis of deviance rejected the simple contrast scaling model in favor of a more complex model in which the spiking threshold and contrast gain parameters were allowed to differ between color directions (data not shown).

An additional nonlinearity was the width of color tuning observed for some V1 neurons. 7 of the 11 neurons we tested in the L–M and S-cone isolating directions were sensitive to both color directions at detection threshold. A linear-model fit to the TRs for these neurons predicts an average intermediate color direction TR of 0.65, which is lower than any of the TRs we measured when we directly tested each neurons’ preferred intermediate color direction.

We have previously shown that the responses of many V1 neurons to high chromatic contrast are poorly described by a linear model (Horwitz and Hass 2012), and the current data suggest that this observation extends to near-threshold contrasts. Some V1 neurons in the current study were sensitive at psychophysical threshold to both L–M and S-cone isolating color directions. These neurons may have had isoresponse surfaces that resemble ellipsoids or hyperboloids of one sheet. A few neurons (n = 17) were sensitive at psychophysical threshold to one of the colors we tested but not the neighboring color direction (45° away in the color space of Figure 2). These neurons may have had hyperbolic isoresponse surfaces. Unfortunately, we were unable to draw stronger connections between these two data sets despite the fact that we tested 20 neurons in both experimental paradigms. Isoresponse surfaces measured at near-threshold contrasts were too noisy to be interpreted, and isoresponse surfaces measured at higher
contrasts (those described in Horwitz and Hass 2012) were insufficient to infer neural responses at detection threshold.

Effects of stimulus eccentricity

Most chromatic detection experiments in humans have been performed at the fovea, but our experiments were performed at ~5° eccentricity. At this eccentricity, V1 receptive fields are often cone opponent but are large with respect to fixational eye movements. The spatial distribution of cones and their convergence onto downstream neurons depends critically on eccentricity, leaving open the possibility that our results could change if we had performed our study at a different eccentricity. A decisive test of this idea would require repeating our experiment, recording from a different region of V1. However, psychophysical evidence from humans suggests that the cone inputs to the detection mechanisms that operate 18° in the periphery are similar to those at the fovea (Newton and Eskew 2003) although the relative sensitivity of these mechanisms depends on eccentricity (Mullen and Kingdom 1996; Mullen and Kingdom 2002).

We controlled the activity of the L-, M-, and S-cones using the method of silent substitution. Our use of human cone fundamentals in the silent substitution calculations is justified by the similarity in photopigment absorption spectra between monkeys and humans (Baylor et al. 1987). Nevertheless, it is likely that the 2° cone fundamentals we used in the majority of our experiments resulted in incomplete cone-isolation due to the relatively large eccentricity of the neurons we recorded (mean RF eccentricity = 5.14° SD = 0.88°). The 10° fundamentals presumably provided better cone isolation.
The major difference between the 2° and 10° cone fundamentals is that the 2°
fundamentals implicitly assume a higher density of macular pigment. Macular pigment is dense
in the fovea but is largely absent > 5° from the fovea (Snodderly et al. 1984). Because it absorbs
short wavelength light preferentially, macular pigment affects the shape of the S-cone
fundamental. As a result, high-contrast nominally S-cone isolating stimuli based on the 2°
fundamentals can have appreciable luminance artifacts when presented outside of the fovea
(Cottaris 2003; Sun et al. 2006).

The impact of this error on the results of our experiments is minimal because stimulus
contrasts were low. The highest psychometric threshold for S-cone isolating stimuli
corresponded to the point [0, 0, 0.17] in L-, M-, S-cone contrast space when represented using
the 2° fundamentals, but corresponds to the point [0.0029 0.0072 0.172] when calculated using
the 10° fundamentals. This introduces an L+M artifact of 0.71% cone contrast and an L–M
artifact of 0.30% cone contrast. These contrasts were below detection threshold for both
monkeys across all spatial frequencies we tested (see Methods: Spatial contrast sensitivity, and
Figure 3). Moreover, the error in S-cone contrast (0.20% cone contrast) is small relative to the
standard deviation of detection thresholds for S-cone isolating lights based on 2° cone
fundamentals (average SD across spatial frequencies and monkeys = 0.93% contrast). As an
extra precaution, we used the 10° fundamentals (Stockman et al. 1993) in a subset of
experiments. The data from these experiments (n = 30) were neither qualitatively nor
quantitatively different than the data collected using the 2° fundamentals. Future studies of color
processing in the macaque cerebral cortex will benefit from accurate measurements of corneal
cone fundamentals specifically for these animals.
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Disclosures

The authors declare that they have no competing interests.
References


Figure Captions

Figure 1

Relationship between neuronal and psychophysical detection thresholds under the cardinal mechanisms model. 

A: Under the cardinal mechanisms model, V1 neurons are tuned to either the L–M or S-cone isolating color direction. The response of a neuron to intermediate stimuli is determined by the projection of the stimulus onto its preferred cardinal color direction. Thus, neuronal detection thresholds (NT) can be represented by lines in the isoluminant plane (red and blue dashed lines for an L–M and S-cone tuned neuron, respectively). Psychophysical threshold (PT) is assumed to result from pooling across all responding neurons, and is lower than the neurometric threshold in either of the cardinal color directions. Due to probability summation, psychophysical thresholds trace out an arc in the interior of the square formed by the cardinal neurometric thresholds. 

B: Under the cardinal model, individual V1 neurons respond robustly to one of the two cardinal color directions but weakly to the intermediate color directions.

Figure 2

A: Display geometry B: Event timing of the chromatic contrast detection task. C: The four color directions represented as vectors in the isoluminant plane. For each neuron, only two color directions were tested during the detection task: the neuron’s preferred cardinal and intermediate colors as identified during an initial characterization procedure.

Figure 3

A, B, and C: Spatial contrast sensitivity functions for two monkeys and one human subject in the four isoluminant color directions shown in Figure 2C and the achromatic color direction. Data
points represent the average sensitivity (1/threshold) estimated with the QUEST adaptive procedure. Curves are the best fitting 2nd order polynomials. Error bars represent ±1 s.e.m. D, E, and F: Data from A, B, and C replotted in threshold units along the L–M (abscissa) or S-cone isolating (ordinate) cardinal color directions. Points that lie on the interior of the gray shaded square are qualitatively consistent with the cardinal mechanisms model (i.e., probability summation among the cardinal mechanisms). Individual points are color coded according to color direction, and are joined together in ascending order of spatial frequency. The point corresponding to the highest spatial frequency stimulus in the 45°/225° color direction is labeled in each panel.

Figure 4

Analysis of contrast-response functions (CRFs) measured during the detection task. A and B: CRFs for two example neurons in response to stimulus modulations along their preferred cardinal (black) and intermediate color directions (gray). Contrast was quantified as the vector norm of the stimulus (Eq. 1). C and D: CRFs for the same neurons in A and B but recalculating contrast as a stimulus’ projection onto the preferred cardinal axis. Fits are half-squaring functions (Eqs. 2 and 3). Under the linear cardinal mechanisms model, the two CRFs should be identical. E: Histogram of scale factors (β3 in Eq. 3) across the population of neurons tested (n = 67). F and G: CRFs for the neurons in A and B but quantifying contrast in units of psychophysical detection threshold. H: Histogram of scale factors (β3 in Eq. 3) after redefining contrast in units of psychophysical detection threshold. Error bars represent ±1 s.e.m.

Figure 5
Ideal observer analysis of neuronal responses. \( A \) and \( B \): Example psychometric (black) and neurometric (blue and red) functions from a single neuron in response to modulations in the preferred cardinal (\( A \)) and intermediate (\( B \)) color directions. Black points represent the raw psychophysical data. Blue and red points represent the performance of an ideal observer with access to the neuronal responses (i.e., area under the ROC curve). Neurometric thresholds (NT) and psychometric thresholds (PT) were obtained from the best fitting cumulative Weibull distribution (curves). \( C \): Distributions of neurometric thresholds for each color direction. The top and bottom of each box represent upper and lower quartiles respectively, and the horizontal line inside each box represents the median. Vertical lines indicate the range. The dashed gray line represents the median neurometric threshold calculated across cells and color directions. The number of neurons measured in each color direction is indicated in parentheses. The total number of cells included in the analysis was 67 (each neuron contributes a TR to one cardinal and/or one intermediate color direction).

**Figure 6**

Comparison of threshold ratios within and between cells. \( A \): Neurometric to psychometric threshold ratios (TR) across the population of neurons (\( n = 96 \)) combined across color directions. Neurons were tested in two color directions, but only contribute a single TR to the population histogram (the minimum of the two). Threshold ratios were considered undefined (Und) when the neurometric threshold could not be measured (no points on the neurometric function > 0.8). Triangle represents the geometric mean. \( B \): Distributions of threshold ratios for each color direction across neurons that were responsive at psychophysical threshold. The number of neurons measured in each color direction is indicated in parentheses. The total number of cells...
included in the analysis was 67 (each neuron contributes a TR to one cardinal and/or one intermediate color direction). C: Threshold ratios measured in each neuron’s preferred cardinal and intermediate color direction (black: monkey K, gray: monkey S).

Figure 7
Sensitivity of individual neurons to modulations in the L–M and S-cone isolating color directions. A: Example psychometric (black) and neurometric (blue or red) performance and the best fitting cumulative Weibull distributions (solid curves). This neuron was slightly more sensitive than the monkey in response to modulations in either of the cardinal color directions. B: Threshold ratios of the subset of neurons that were tested in the L–M and S-cone isolating color directions and were responsive at psychophysical threshold to both colors.

Figure 8
The relationship between color sensitivity index and threshold ratio. Color sensitivity indices were calculated on the basis of mean firing rates in response to suprathreshold sinusoidal gratings. Threshold ratios were calculated from responses in the chromatic detection task. The smaller of the two threshold ratios from each neuron is shown here, but results were qualitatively similar when we used the larger one (see Figure 6C).

Figure 9
Spatial frequency tuning of neurons that were sensitive (i.e., threshold ratio ≤ 3) at the monkey’s chromatic detection threshold. A–F: Data from six individual neurons illustrating low-pass (A and D) and band-pass (B,C,E,F) tuning in response to achromatic sinusoidal gratings. G–I: Data
from three example neurons illustrating band-pass tuning in response to isoluminant sinusoidal gratings. Curves are the best fitting difference of Gaussians. The threshold ratio (TR) and color sensitivity index (CSI) are provided for each neuron. Population average spatial frequency tuning curve for neurons that were sensitive (black) and insensitive (gray) at chromatic detection threshold. Individual tuning functions were normalized by their maximum value and then averaged across neurons. Error bars represent ±1 s.e.m.
A

Cardinal mechanisms model

B

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<tr>
<th>S-iso</th>
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NT_{S-iso}
A

Fixation 500 ms

Stimulus Presentation 666 ms

Delay 100-600 ms

Decision and Reward

B

Fixation Point

Gabor Targets

Time (ms)

0 500 1000

C

135° / 315°

45° / 225°

S-iso

L–M

Cardinal

Intermediate
Neuron 1

A

L – M

45° / 225°

Spike Count

Contrast (vector norm)

0 1 2 3

Scale Factor

B

L – M

135° / 315°

Spike Count

Contrast (vector norm)

0 0.005 0.01 0.02

Scale Factor

C

β₃ = 1.09

Spike Count

Contrast (projection onto cardinal axis)

0 0.01 0.02 0.03

E

Count

Scale Factor

D

β₃ = 1.79

Spike Count

Contrast (projection onto cardinal axis)

0 0.005 0.01 0.02

Neuron 2

B

L – M

135° / 315°

Spike Count

Contrast (vector norm)

0 0.002 0.004

Scale Factor

E

Contrast (vector norm)

0 0.02 0.04

Neuron 2

F

β₃ = 0.74

Spike Count

Contrast (threshold units)

0 1 2

Neuron 2

G

β₃ = 1.11

Spike Count

Contrast (threshold units)

0 1 2

Neuron 2

H

Count

Scale Factor

0 0.2 0.5 1 2 4
A  S-Iso  

Monkey  
Neuron  

Cone Contrast  

p(Correct)  

0.05  0.1  

0.02  0.05  0.1  

135° / 315°  

NT = 0.11 CC  
PT = 0.08 CC  
TR = NT/PT = 1.38  

135° / 315°  

NT = 0.065 CC  
PT = 0.042 CC  
TR = NT/PT = 1.55  

C  

Cardinal  
Intermediate  

Neurometric Threshold  
(cone contrast)  

S-Iso  
L-M  
135°/315°  
A5/1225  

(37)  (21)  (40)  (17)
Cardinal TR

Intermediate TR

Und

Threshold Ratio

S-iso

45º /225º

135º /315º

Intermediate

Cardinal

(37) (21) (40) (17)

Threshold Ratio

Count

0 5 10 15 20 25 30

0 1 2 3

0.5 1 1.5 2 2.5 3 3.5 4

Cardinal TR

Intermediate TR

Und

(37) (21) (40) (17)
Color Sensitivity Index

Threshold Ratio

$r = -0.283$

$p = 0.005$