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Steps towards neural decoding of colors

Qasim Zaidi[1] and Bevil Conway[2]

How we see colors is a great mystery, but also a route to understanding how we experience any quale, because color does not exist in the world outside our brains, and is undetectable by other senses. From photoreception to primary visual cortex, the neural encoding and transmission of color signals is well understood, providing a foundation for understanding cortical computations of color appearance. We describe how probabilistic models coupled with fMRI-guided microelectrode recordings from inferior-temporal macaque cortex (IT) could help us understand color decoding: i.e. how appearance is extracted from the neuronal responses evoked by a stimulus. Neurons in IT respond to a narrow range of colors with their peak responses scattered around the color circle. We discuss how intra-cellular processes and cortical circuits could generate such tuning curves, and how they approximate optimal Bayesian decoders in winner-take-all schemes.

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Introduction

Cezanne, the artist of the visibly corporeal, said, "Color is the place where our brain and the universe meet", reflecting his conviction that we perceive what we construct together with nature. In visual neuroscience, we try to understand how visual appearance is generated from the population of neuronal responses elicited by stimuli [1–4]. Color used to be the preeminent modality for pursing this goal. The first distributed neural population code proposed was Young's [5] trichromatic theory, which postulated that perceived color is determined by the relative activation of three classes of broadly tuned photoreceptors. The first computable model for interpreting a population code was Helmholtz's [6] line-element, which treated three photoreceptor outputs from a light as components of a vector, and proposed that two colors become discriminable when the vector difference reaches some threshold value. Since then, line-element models have been developed to provide explanations for color discrimination [7], but line-elements do not provide a decoded value, so they cannot predict appearance. In its recent history, color science has concentrated on the encoding and transmission of color signals through the retina, LGN and V1 [8,9], but unlike for shape, motion, objects and faces [10–14], not much has been thought about how these signals are decoded to yield color percepts of objects and materials. In this paper, we concentrate on Inferior Temporal (IT) cortex, the last purely sensory stage of visual processing. We consider issues in characterizing color properties of IT neurons, and present proposals for how these properties are generated by neural circuits to support successful decoding of stimulus colors.

Neural hierarchy of color processing

Humans and monkeys have similar spectral sensitivity [15], identical cone types [16], and similar psychophysical chromatic mechanisms [17], so color sensitive neurons have been directly probed in monkey brains as a route to understanding human color perception. Primate photoreceptor sensitivities overlap [16], so every real light activates more than one class of photoreceptors, and color perception requires later neural circuits to compare cone responses. Retinal circuits transform cone outputs to ganglion cell signals that consist of sums and differences of cone responses in accord with concepts of transmission efficiency [18,19], and predominantly fall on the cardinal axes of color space [20,21] with a notable exception [22]. These signals are then relayed by thalamus to primary visual cortex. Cortical cells that respond selectively to particular combinations of different classes of thalamic signals are thus needed to fill up the three dimensional color space formed by axes representing cone responses or their linear transforms. In the absence of cells that signal relative responses along more than one axis, the 'space' reduces to a 'skeleton' composed of only the axes, for example, Mantis shrimp have 12 photopigments but their signals are kept separate, leading to a 12-D skeleton, not a 12-D space, and this is reflected in poor color discrimination [23].

Even though we have incomplete knowledge of how color signals are transformed as they propagate through the cortical circuitry, it is clear that the neural circuits responsible for color perception computations are linked across several different extra-striate cortical regions [24]. At one

time, V4 was considered the 'color area' [25–27], but lesions of V4 cause only mild color deficits [28–31]. By contrast, lesions of IT (a large expanse of cortex anterior to V4) not only impair object recognition but also cause color blindness [32,33], similar to cerebral achromatopsia acquired after certain strokes [34–38].

Microelectrode recordings, guided to fMRI-identified locations, have revealed that V4 contains discrete large regions that primarily contain color-tuned neurons (globs), contributing to the current view that V4 facilitates selective extraction of specific visual domains [39,40]. The functional organization of IT, on the other hand, is still poorly understood. Only a small number of papers have estimated the fraction of color-tuned neurons in IT, and the estimates differ widely [41,42]. A preliminary explanation [43] suggests that like V4, IT is not a homogenous area. Instead, IT appears to be highly organized, comprising four stages of processing, with each stage itself organized by an eccentricity template [43]. Color-biased regions within IT occupy a location between face patches (which show a foveal bias) and place-biased regions (which show a peripheral bias), in both monkeys and humans. It is likely that different IT color-biased regions are engaged in specific computational tasks (Figure 1), but it remains unknown what these differences might be. Recordings from ALc revealed color-tuned neurons with large receptive fields. These neurons appear to make little contribution to color discrimination [44], but may be involved in color categorization [45,46]. fMRI suggests the existence of a color region (AMc) even further anterior, but nothing is known about the response properties of the neurons within it. fMRI-guided microelectrode recordings of color-biased regions in posterior IT, some of which were clearly anterior to the V4 Complex and likely in PVc [40,47], showed many color-tuned neurons with receptive fields that were localized within visual space, suggesting that retinotopy plays a role in organizing posterior IT. Previous recordings showed that interstitial regions between the globs of the V4 Complex/PIT are not enriched for color-tuned neurons, but as a population, interglob cells nonetheless carry some color information [46]. The boundary between the V4 Complex and IT remains murky. But despite gaps in knowledge, a hierarchy of color processing is consistent with the documented differences in receptive-field size and retinotopy, and the putative categorization role of anterior IT. The parallel multi-stage organization of IT discovered in monkeys is also evident in humans, and underscores the importance of understanding how IT works in a behavioral context [48,49].

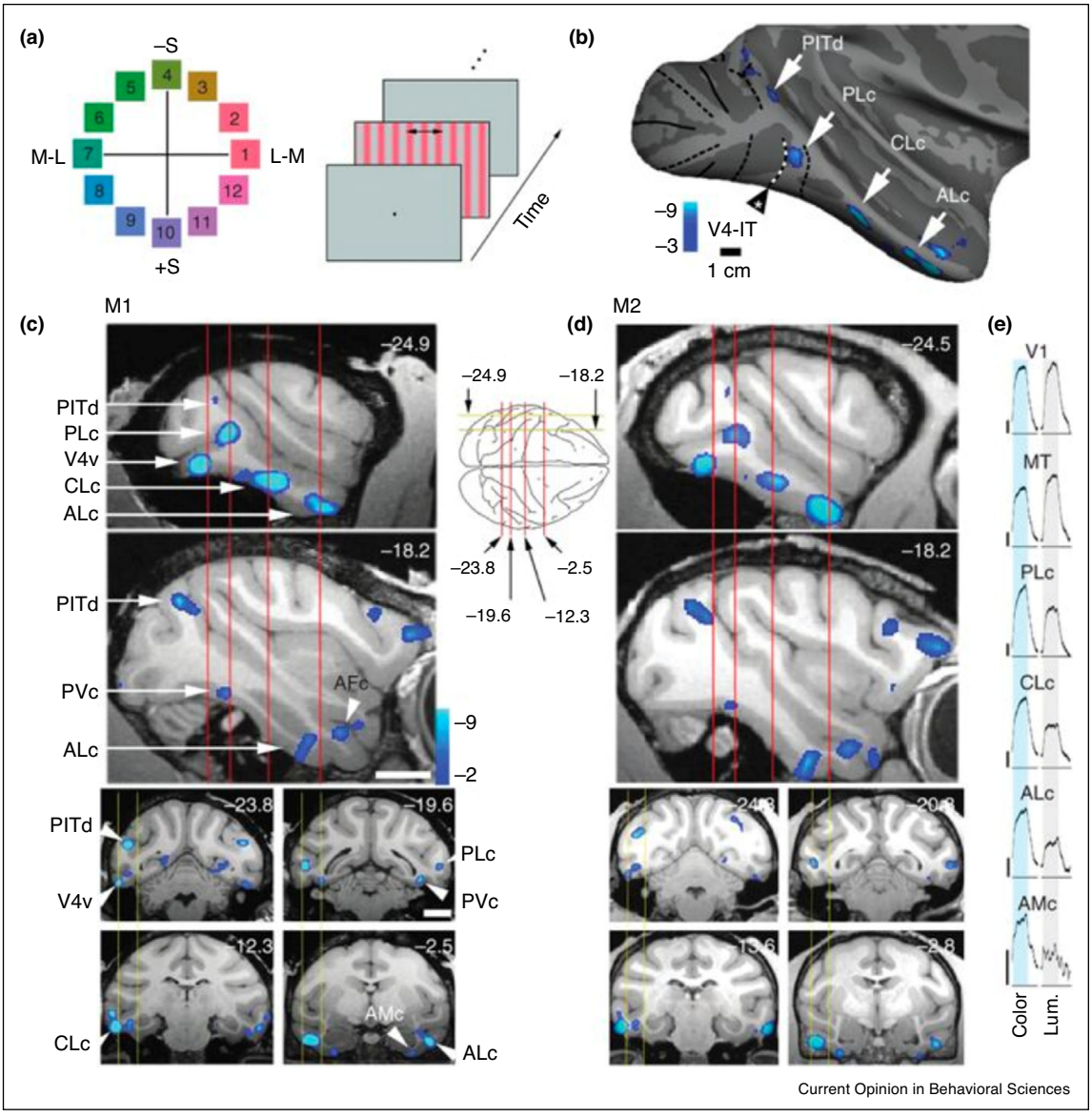
Color properties of IT cells

Of particular relevance to color decoding, neurons in IT have been shown to be remarkably color-specific [40,41], a small sample cells from posterior IT/V4 Complex are illustrated in Figure 2. Stimulated by flashed lights, some cells respond only to red, others to reddish blue, bluish red, violet, and so on. For isolated lights, each of these colors corresponds to a particular combination of more than one of the cardinal thalamic signals transmitted to cortex. We would like to determine whether the peak responses of IT neurons tile the 3D space defined by thalamic color axes, and whether the grain of filling-in is fine enough to underlie human color discrimination.

In decoding models, generally the aim is to recover the physical parameters of the stimulus. The physical parameter that evokes different colors is wavelength, but it is irrelevant in color decoding because multiple combinations of physical wavelengths can be the same color (metamers), and representing stimuli in wavelengths has other drawbacks. In vector-averaging models [50], each class of neurons in the population is represented by a vector pointing in the direction of the peak of that class's tuning curve with length proportional to its activity, and the vector average is the decoded value. If tuning curves are functions of physical wavelengths, the vector average will decode spectral hues, but not non-spectral colors such as purples and unsaturated colors. More frequently used for decoding are Bayesian models that invert the probability function of response given stimulus to obtain the function of stimulus given response [51], but the same drawback applies if the posterior probability is a function of wavelength. Clearly, neural responses to lights that are combinations of physical wavelengths need to be considered. Since neural computations of color begin with cone photoreceptor responses, and information about specific wavelengths is lost, measurements of color properties and physiologically plausible computations of color are better grounded in a 3D space defined by cone responses, or a linear transformation of such space.

To characterize the responses of IT cells over all of 3D color space may seem foolhardy, given limitations of extended recording from an individual cell, but we have found it possible to efficiently measure 3-D color tuning surfaces by using spatiotemporal variants of stimuli that were previously used in retinal electrophysiology [21,22,51,52,53]. Knowing the absorption spectra of the three cone classes (L, M, S), colors are defined in a 3-D space defined by L − M, S, and L + M axes. Modulations of colors along the maximal radius circles in the planes defined by pairs of axes (Figure 3), modulate the inputs to the cones as temporal sinusoids with phases shifted by multiples of 90° [21]. A circular modulation in the L − M versus S plane modulates sinusoidal L and M inputs in opposite phase, with the S input shifted in phase by 90° from both. The responses of IT cells measured with extracellular electrodes can be represented as peri-stimulus time histograms (PSTH). The mid-point between the PSTH peaks to clockwise (CW) and counter-clockwise (CC) circular modulations gives an estimate of the preferred color by removing the response lag. The 3-D preferred

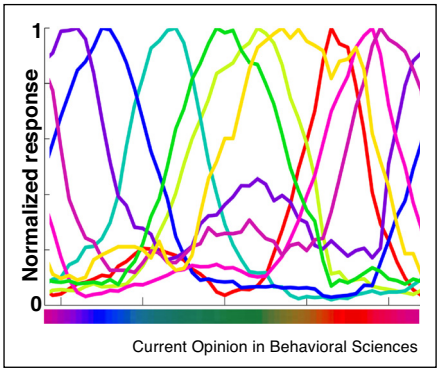
Figure 1



(**a**) Color stimuli and stimulus procedure. (**b**) Regions with greater activation to chromatic gratings than achromatic gratings (PLc: posterior lateral color; CLc: central lateral color; ALc: anterior lateral color; AMc: anterior medial color; PIT: posterior IT; PVc: posterior ventral color). (**c**) Top two: sagittal slices. Bottom four: coronal sections (**d**) Second monkey. (**e**) Average time course traces during color and achromatic blocks (from Ref. [43]).

color gives direct estimates of the cone-weights. Half the distance between the peaks (in time) gives an estimate of the lag, which increases linearly as temporal frequency increases, i.e. hence roughly constant in time. Taking the mean of the CW and CC PSTH at the slowest modulation rate, after shifting for the lag, gives the color-tuning. One cycle of the circular modulation is equivalent to modulating colors simultaneously along every axis passing through the center, but with successively shifted phases, so this method is much more efficient than axis modulations [54–57], and much finer grained tuning curves can be obtained in the same number of trials. For IT, we have found that tuning curves can be measured reliably and efficiently, when the stimuli are presented against a mid-grey background, within an elongated rectangle ascertained as optimal for the cell. The axes represent the principal color inputs to cortex from thalamus [20,21], so shifts of color preference from LGN cells are easily seen, and since cortical inputs are cosine-tuned, narrowing of tuning curves is readily apparent, as in the measurements of the PIT cell shown in Figure 3, recorded using the grid hole indicated by the penetration (Notice the guide-tube for the electrode leading to the fMRI identified color hot-spot in blue). This method confirms the narrow

Figure 2



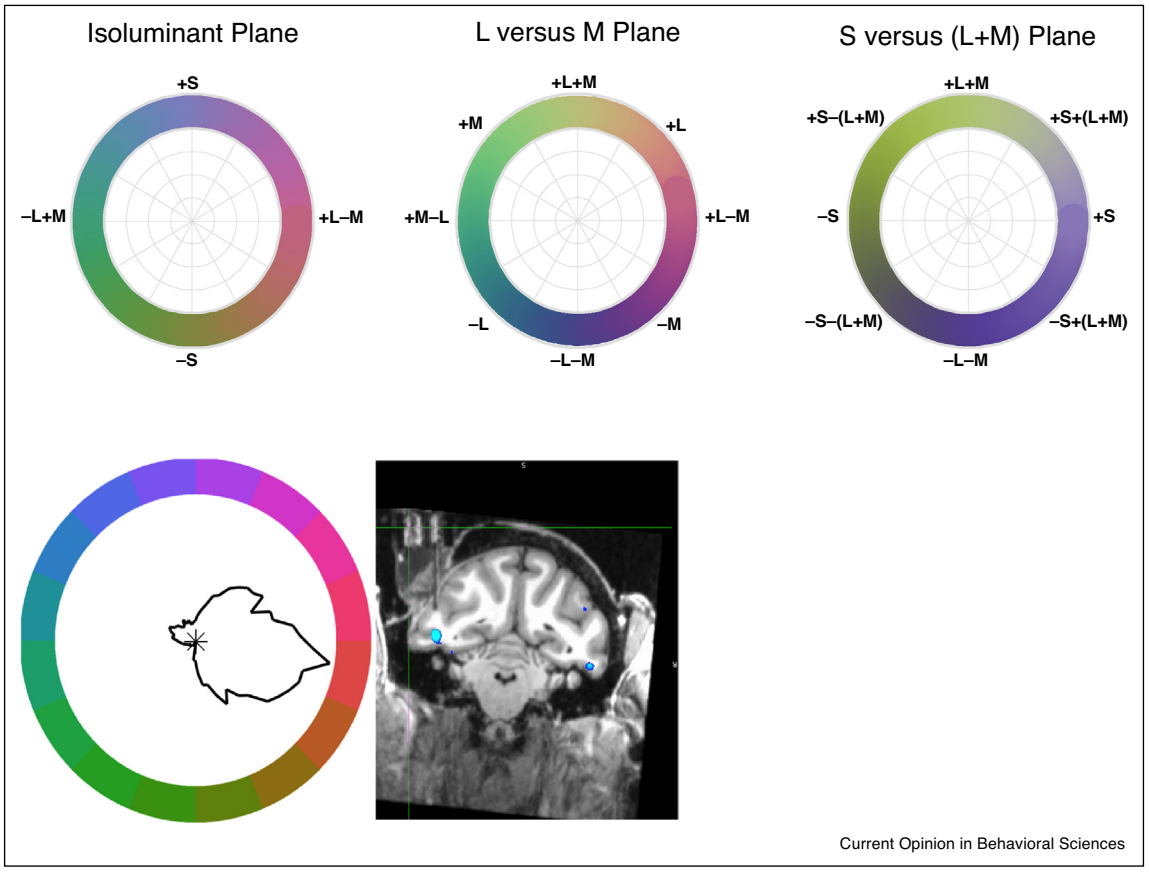
Examples of IT neuronal responses to 45 colors spaced along a triangle in cone space (from Ref. [1]).

hue tuning of IT cells, and the saturation corresponding to peak sensitivity can be measured by responses to modulations along the radial axis defined by the vector of peak sensitivity. The response lag estimated from the circular modulations can be used to correct measured responses to obtain the phase of peak response to the radial modulation, thus locating response peak at any color between the equal energy white at the center of the color space and hue where the radial line meets the circumference of the circular modulation.

Models for IT color tuning

It is possible to model a neuron with a peak location anywhere in color space with a straightforward weighted combination of thalamic inputs, but generating narrow tuning is more involved. There are no published models for how narrow tuning is generated, possibly because its importance for color decoding has not been recognized. What are the neural circuits that make cells in IT cortex much more narrowly tuned than LGN and V1 cells? Mathematically, there are a number of alternatives. Tuning curves could be narrowed progressively from V1 to IT by combining earlier inputs with a multiplicative operation, equivalent to a logical AND. A cell that only fires if it gets spikes from two differently tuned cells within a short synaptic integration interval, will only fire

Figure 3



(Top) Circles representing modulations of maximum radius in three planes of color space. (Bottom) Color tuning (left, normalized responses) of an IT cell lying in a color-biased domain of Posterior IT. The MR image (right) shows the electrode (black vertical line) targeting the color-biased domain (higher fMRI responses to equiluminant colored gratings compared to achromatic gratings is shown with brighter blues).

for stimuli for which the tuning curves of the earlier cells overlap, i.e. therefore the output tuning curve will look like a multiplication of the input tuning curves. With this scheme, the less overlap between the input tuning curves, the narrower the output tuning, and the smaller the output response, because only sparse responses on the flanks of the input tuning curves are combined. A similar relation will hold for a cell that only fires if it receives n spikes in a short interval from an earlier cell, leading to raising the input tuning curve to the power n, thus resulting in a narrower tuning curve [9]. To generate a variety of peak colors in the population along with narrow tuning, both mechanisms would be needed, along with a process to amplify spike rates.

An alternative model involves local cortical interactions. Since recordings show that cells with similar color preferences cluster together [47], excitation from neighboring neurons would differentially increase the response to the preferred color of a cell, thus effectively narrowing the color tuning. This model is motivated by investigations of orientation processing in striate cortex, where width of orientation tuning in striate cortex is narrower in iso-orientation domains and broader at pin-wheels [58], and this can be explained by the gain for orientation selective cells being set by pooled excitation from neighboring cells [59]. If narrowed color tuning is due to similar excitatory interactions as narrowed orientation tuning, that would provide another useful canonical circuit to explore for different functions in the cortex. Note that the divisive normalization proposed as a canonical computation for a number of neural processes [60], would make the wrong predictions for color tuning width, because for neurons surrounded by cells with similar color preference, division by surrounding responses would reduce the response to the preferred color, broadening the color tuning. Shaping the contrast response function may still require divisive normalization [59] from either broadly tuned color cells, or from the pooled responses of widely spread cells with uniformly distributed peaks. Experiments that can critically distinguish between different models for the generation of narrow color tuning would probably require intra-cellular measurements, but simultaneous multi-electrode recordings from neighboring cells could help narrow the possibilities.

Color decoding from neuronal responses

Similar to decoding of other visual qualia, color-decoding models process the whole population of neuronal responses. The first decoding scheme that assumed that IT neurons are tuned to tile color space [4], suggested that color should be understood as encoded in the distribution of activity across IT. However, this population decoding solution was based on a simulation of only 30 IT neurons, with overestimated widths of color tuning in IT, and seriously underestimated number of classes of neurons. Surprisingly, simpler color decoding schemes were not explored until we hypothesized that the decoded color of a stimulus could correspond to the color preference of the IT neuron that produced the largest response to the stimulus, i.e. equivalent to a winner-take-all decision rule [1]. For each of 279 PIT color selective cells, we simulated a model cell based on isolated responses to brief presentations of 45 colors, extracted by spike sorting multi-unit recordings [40]. The probability of eliciting r_i spikes from neuron i to color ω was assumed to be a Poisson distribution:

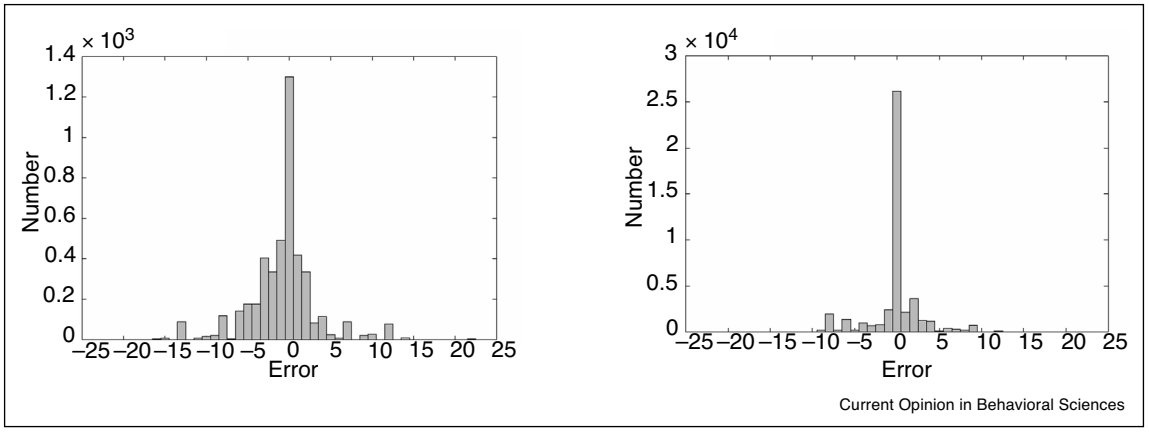
$$p(r_i|\omega) = \frac{e^{-f_{i(\omega)}} \times f_i(\omega)^{r_i}}{r_i!} \quad (1)$$

with the empirically estimated tuning curve $f(\omega)$ giving the mean response for each color ω [9]. We generated trial-by-trial responses of each neuron to each of the colors, and on each of 45 000 simulated trials compared the winner-take-all decoded color (the preferred color of the cell that fired maximally on that trial) to the stimulus color. Videos of the simulations [1] demonstrate the generation of correct and incorrect decoding. The results are summarized in Figure 4 (left) as histograms of the frequency of error magnitudes, and show a marked peak at zero error when expressed as discrete ordinal distance to the wrongly decoded color. So even with this meager number of cells and stimuli, the population supported fairly accurate interval decoding of color under a winner-take-all rule. Since each cortical neuron receives multiple inputs, and color cells are organized into areas of similarly color-tuned cells [47], it may be unrealistic to restrict the decision to a single neuron's response. So we used the average of the responses of all cells with the same preferred color as representative of responses from a local cortical patch, and found that the decoding accuracy improved markedly. The frequency of exact decoding increased by a factor of 20, so that there were very few errors (Figure 4 right). The surprising success of winner-take-all decoding presents a physiologically realistic and computationally efficient alternative to color appearance models based on unique hues [61] that have no physiological support. This decoding scheme is also compatible with the results of color micro-stimulation done on a human brain [62].

Decoding implications of narrow color tuning

The accuracy of the winner-take-all scheme, that uses only the location of the peak response of each cell, needs to be compared to the optimal Bayesian decoder that uses the complete tuning curve of each cell. To optimally decode colors from population responses, the general assumption is that a cell's number of spikes to a color flash is predicted by the tuning curve with some randomness, since the tuning curve is the average firing rate for each color. If the probability of firing is a constant within time intervals of equal length, then the randomness is

Figure 4



Histogram of frequency of decoding errors in winner-take-all rule as a function of ordinal distance between 45 stimulus colors arranged systematically around the periphery of a color triangle (summarizes simulations from Ref. [1]).

governed by a Poisson distribution, and the response can be modeled as a Poisson process (Eq. (1)) with the tuning curve as the parameter [51,63–66]. If neurons can be treated as stochastically independent, with correlated firing attributable to overlap in receptive fields or tuning curves, then the population response to a stimulus is given by the product of the Poisson distributions. Using Bayes' formula, the optimal estimate of the stimulus can be simply decoded from the probability function for the stimulus given the population response [51]:

$$p\left(\omega\middle|r\right) = \frac{p(\omega)}{R} e^{-\sum_i f_i(\omega)} \prod_{i=1}^{n} f_i(\omega)^{r_i} \qquad (2)$$

The maximum of the posterior probability distribution provides an optimal estimate of the stimulus color given the population response on a trial [67]. We have previously used this method to model decoding of orientations in the context of 2-D angles and 3-D shapes [63], using estimates of anisotropy in orientation tuning and preference in mammalian primary visual cortex. Based on mean tuning curves for different orientations, we were able to predict perceived distortions in magnitude of angles based on their orientation, thus demonstrating the power of these models. For decoding colors, the same model could be used with colors tiling the equiluminant plane.

IT cortex has millions of color-tuned cells, sampling color space quite finely with narrow tuning, with a possible bias towards the distribution of colors of objects [49]. In the posterior distribution (Eq. (2)), the only term that depends on the pattern of responses on a trial, represents multiplication of tuning curves raised by the number of spikes, which will give the highest weight to cells tuned to the stimulus, thus essentially creating a narrow population tuning curve for each color. This aspect of decoding will also be true for exponential distributions other than the Poisson [66]. So it is worth testing the hypothesis that narrow tuned IT cells can behave as approximations to the optimal estimators, i.e. and essentially act like 'grandmother cells' [68] for each color, so that the perceived color depends only on the firing of the cells most responsive to that color. This test can be formalized by comparing estimates from the winner-take-all scheme to estimates from the optimal Bayesian procedure.

Decoding color in complex configurations

Isolated lights in aperture mode are a small subset of visual stimuli in the world. Most colors are seen in context and as belonging to objects or materials. Some aspects of color perception can be abstracted from perception of object and material colors. Spatial [69] and temporal [70] neural interactions create contrast colors, for example, dark colors such as Brown, Maroon or Navy, or hues that appear more saturated than spectral lights. In fact, White differs from Grey only as a contrast from a darker preceding or surrounding Grey, and so the key to decoding White may be simpler than previously thought [4], requiring cells that respond only to achromatic increments. For isolated aperture colors, the decoding scheme discussed earlier is restricted to accurately and rapidly estimating position in the three dimensional space of cone outputs. Later cells cannot improve on the estimate from cones, but may be worse because of additional neural noise. This would be compatible with voxel-based discrimination from BOLD responses being better in primary visual cortex than later areas [3]. The main reason to identify a decoding scheme is to model a final sensory stage whose outputs lead to perceived colors directly, and that could also be useful in more complex situations. For contrast

colors, decoding has to go beyond spatially local cone-outputs. Similarly, when a colored transparent layer is perceived over a background of a different color, a decoding model has to generate estimates of two colors at every retinotopic point [71–73]. The simplest scheme for decoding contrast colors, such as Brown, Maroon or Navy could be IT cells that prefer these over the aperture versions of these hues, and we are attacking this question by using the same isoluminant color stimuli but on white backgrounds that generate dark colors from the same physical stimuli, instead of black backgrounds that shift colors to aperture mode. We are also searching for cells that respond to the same overlaid transparency color, irrespective of background colors, and cells that respond to the same background color irrespective of the color of the overlaid transparency. Whether simple winner-take-all rules suffice for decoding dark colors, and separating transparency colors from background colors, remains to be tested. An equally perplexing problem is how colors are decoded as inherently associated with shapes of objects or textures of materials [74–77], and whether that requires signals from pre-frontal brain areas [78], or whether even much smaller brains have evolved simple hard-wired schemes to accomplish such tasks [79,80].

Conflict of interest statement

Nothing declared.

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