receptor–driven plasticity[14,15]. Alternatively, optogenetic activation may induce plasticity downstream of striatal activation, either in the basal ganglia at subthalamic nucleus, GPe or GPi synapses, or possibly further along in thalamic or cortical areas. Notably, Kravitz *et al.*[1] found an asymmetry in the temporal longevity of stimulation effects, with positive reinforcement effects outlasting the transient punishment effects of activation; such differences provide an intriguing starting point for future studies into the neural locus of reinforcement learning. In a final experiment, the authors show that direct and indirect pathway stimulation also changes behavior in a place preference task, suggesting that striatal activation may provide a reinforcement signal that generalizes to context as well as action.

Overall, the results of Kravitz *et al.*[1] highlight a fundamental point about decision-making: selecting an action is never truly independent of reward learning. Functionally, the learned values of different options is a crucial element of the action selection process. Neurally, action selection and reinforcement learning appear to be implemented in the same striatal circuitry, with distinct functional compartments processing rewarding versus aversive outcomes. Understanding the exact nature and mechanism of this relationship between reinforcement and action will be a critical avenue for further research.

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Squaring cortex with color

Brian A Wandell & E J Chichilnisky

A long-standing puzzle has been the seeming inconsistency between neuronal responses in primary visual cortex to colored stimuli and the elementary perceptual attributes of color vision. Nonlinear analysis resolves this paradox.

Color perception begins with light absorption by three types of cone photoreceptors in the retina. Cone signals are processed by visual system circuitry to produce the familiar perceptual attributes of color appearance. In the past several decades, studies of this circuitry have revealed consistency between perceptual experiments and the responses of neurons in the retina and thalamus. However, responses of neurons in primary visual cortex (area V1) to colored stimuli have been difficult to reconcile with these findings. Now, work by Horwitz and Hass[1] that accounts for certain nonlinear processing characteristics of V1 neurons points the way to a unified understanding.

A fundamental aspect of color vision is that an appearance match can be arranged between any target light and an appropriate combination of three fixed primaries, even though the spectra of the target and combined primaries differ greatly. The detailed and quantitative characterization of this phenomenon, known as color matching, was a great achievement of twentieth century science. Our understanding of color matching is the basis for all technologies relating to color imaging[2]. For example, modern color displays repeat the color matching experiment 60 times a second in millions of pixels to provide realistic scene renditions. Quantitative measurements of the spectral sensitivity of the three types of cones secured the connection between the biology of light transduction and color matching[3].

But color matching does not explain color appearance. We can match the appearance of two lights without saying what either looks like, just as we can match the weight of two objects without knowing what either is made of. Consequently, modern color science has focused on determining how color appearance is derived from the signals in the three types of cones. The first major step was the remarkable discovery of a simple empirical rule of color appearance: certain colors occur in combination, whereas others do not. For example, the color orange appears both reddish and yellowish. But there are no colors that simultaneously appear red and green or that simultaneously appear blue and yellow. These forbidden color pairs were discovered by Hering[4] and developed into the theory of color opponency by Hurvich and Jameson[5] and others[6,7].

What is the neural basis of color opponency? Svaetichin[8] and DeValois[9] discovered that neurons in the retina and the lateral geniculate nucleus (LGN), the subcortical relay station en route to V1, encode color signals as sums and differences of cone signals. For example, certain retinal and LGN neurons are excited by inputs from the cones that are sensitive to long wavelengths and are suppressed by inputs from the cones that are sensitive to middle wavelengths. If increases in the activity of these cells encode red and decreases encode green, such neurons could report red or green, but not both, which is consistent with the observed exclusivity of red and green percepts. A similar situation holds for blue-yellow opponent circuitry. Neural responses in the LGN were grouped into three categories that roughly matched the three categories of color-opponent theory[10]: red-green, blue-yellow and light-dark. Thus, to a first approximation, circuitry in the subcortical visual system implements the perceptual phenomenon of color opponency in physiology and behavior. The agreement between physiology and behavior falls short of the precision of color matching, but it is not so far off as to cause any serious alarm.

Cortical neurons, however, have refused to join the party. Over the past several decades, studies of color processing in visual cortex have produced confusing and seemingly contradictory results. The earliest studies in V1 suggested that there were very few color-opponent cells[11]. Subsequent studies found

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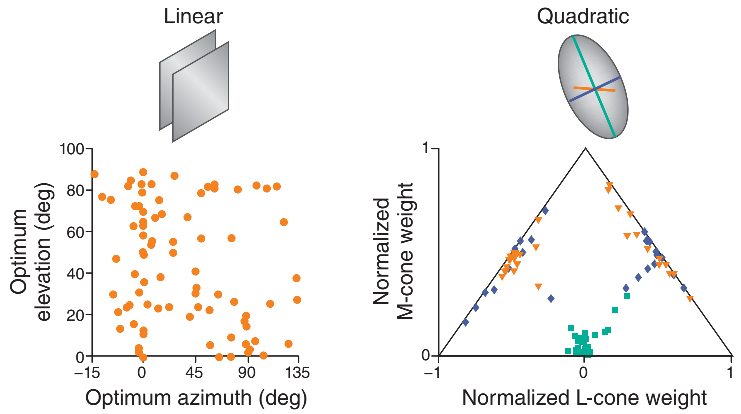

Figure 1 Clustering of V1 neuron color tuning estimated using linear and quadratic models of neural response. Linear models involve fitting pairs of planes (top left) to points in three-dimensional color space that elicit equal neural response. Quadratic models involve fitting quadratic surfaces, such as ellipses (top right), to such data. The left graph shows the distribution of color tunings from neurons in area V1 obtained in a previous study[13] that used linear models to characterize response in a color space defined by behavioral measurements. The optimum response direction in this space (that is, the vector orthogonal to the planes) is a description of color tuning and is summarized by the azimuth and elevation. No clear pattern of color tunings was observed. Using quadratic models, Horwitz and Hass[1] found that color tuning is more orderly. The right graph shows the distribution of principal axes of quadratic surfaces in a color space defined by normalized activation of cones sensitive to long (L) and middle (M) wavelengths, with short-wavelength cone activation given implicitly in the distance from the edges of the triangle. Using the quadratic description, the principal directions of color sensitivity measured in V1 neurons are grouped into clear clusters in this space, and these clusters are similar to the opponent colors revealed by perceptual experiments[4]. Figures are adapted from ref. 13 (left) and ref. 1 (right) with permission.

many more 'color-selective' cells, but did not provide quantitative measurements that could be compared to behavior[12]. More recently, linear systems methods that had been used to quantify cone inputs to neurons in the retina and LGN were applied to cortical neurons. When this was done, the color responses of cortical neurons appeared to span a wide range of sensitivities that showed no systematic organization associated with color opponency (**Fig. 1**)[13]. This left our understanding of the circuitry for color vision in a confused state. Could it be that low-level visual circuits are organized in a color-opponent fashion, but that this organization is discarded at the level of V1? Or could there be something about the measurement scheme clouding the picture?

To clarify the picture, Horwitz and Hass[1] tackled a fundamental problem: the responses of many V1 neurons are markedly nonlinear[14], perhaps more so than in retina or LGN. These nonlinearities were widely appreciated, but the field lacked an approach that could reveal the underlying quantitative structure of color computations in cortical neurons without relying on assumptions of linearity that had worked so well in retina and LGN. Horwitz and Hass[1] applied two innovative approaches to this problem. First, they developed a measurement scheme that could incorporate nonlinearities using classical ideas by means of real-time feedback to identify groups of stimuli that yielded equivalent responses in a given cortical neuron as a signature of its nonlinear behavior. Second, they used both linear and quadratic models to summarize their measurements. One group of the neurons in the V1 sample was reasonably fitted by a linear model, whereas a second group of was much better fit by a quadratic model. The quadratic model is only slightly more complex than the linear model, but is powerful enough to capture important trends in the data that were previously missed.

Now it's party time again. With this improved characterization of the population of V1 color responses, order emerged. Specifically, quadratic models, like linear models, can be associated with a principal direction in color space that reflects the color tuning of a neuron. For example, an ellipsoidal sensitivity contour in color space has a set of directions associated with its three principal axes (**Fig. 1**). Horwitz and Hass[1] show that the color directions defined by the linear and quadratic models fitted to V1 color responses are reasonably consistent with the color opponent directions derived from appearance measurements and with responses in the retina and LGN. In summary, when an appropriate quantitative model and associated measurement approach is adopted, order emerges in the representation of color in the cortex.

Of course, much remains to be understood. First, color appearance is not entirely separable from other stimulus features: changing the size, the motion or the flicker rate of a stimulus influences its color appearance. Because of time restrictions, the color measurements in this study were obtained with a single spatiotemporal pattern. Retinal measurements that characterize the full chromatic-spatial response provide more information[15], suggesting that more complete measurements in cortex may be informative as well. Second, the methods Horwitz and Hass[1] used in cortex focused on single cells, making it difficult to understand how color is represented by the pattern of activity in many neurons. It may be possible to obtain larger and more completely characterized samples using next-generation recording methods.

The good news is that another major part of the visual circuitry for color has been thoughtfully assessed. The new measurements improve the characterization of V1 color responses, and this improvement brings the organizational perception in V1 into better alignment with psychology and peripheral encoding. The new analyses will make it possible to interpret color signals in cortex more accurately and to coordinate these measurements with perception.

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