mixing different pairs of phosphors in turn. The CIE(1931) chromaticity coordinates of the stimulus set are given in the Supplemental Data in [4,5]. In Figure 1, Stoughton and Conway's stimuli are re-plotted in the MacLeod-Boynton (1979) chromaticity diagram [6,7]. To perform this conversion, I have used the transform of Golz and MacLeod [8], which is appropriate for CRT monitors. It is a telling coincidence that the three peaks in Stoughton and Conway's [4] histogram fall close to the apices of the obtuse triangle formed by the red, green and blue phosphors of the monitor.

To understand the physiological significance of this coincidence, consider how the MacLeod–Boynton diagram is constructed. The horizontal axis of the diagram corresponds to one of the chromatic signals present in the early visual pathway; this signal represents the ratio of the photon catches of the long-wave (L) and middle-wave (M) cones, and is carried by cells in the parvocellular laminae of the lateral geniculate nucleus (LGN) [2]. The vertical axis represents the ratio of short-wave cone (S) excitation to the sum of L and M excitation, and corresponds to the signal carried by a subset of cells in the koniocellular layers of the LGN [2,9].

It is immediately clear from Figure 1 that the construction of the stimulus set must distort Stoughton and Conway's [4] polar histogram. The bins of their histogram correspond to very unequal angles in the physiological space, and in fact will be especially narrow near the blue and red guns. But why should there be clusters of cells that are maximally excited by either the blue or the red gun?

Consider the horizontal arrows in Figure 1. They show the projection of the stimulus triangle onto the horizontal axis. They thus represent the range of excitations that the experimental stimuli will produce in LGN cells that extract the ratio M/L or the ratio L/M, cells for which the short-wave cone signal is invisible. Clearly, it is the blue phosphor that will produce the strongest response in cells that are excited by M cones and it is the red phosphor that will produce the strongest response in cells that are excited by L cones.

The vertical arrows show the range of modulation that the experimental stimuli would produce in the S cone signal. So it is the blue phosphor — and not the cardinal axis running vertically through the white point — that would maximally stimulate those cells in the LGN that are excited by S cones and inhibited by L and M cones. A further, heterozygous type of LGN cell is excited by a reduction in the short-wave cone signal [3]: Such cells would plot in the broad distribution that forms the upper right quadrant of Stoughton and Conway's [4] polar plot, and would fall along the lower side of the stimulus triangle in Figure 1.

In sum, Stoughton and Conway's [4] polar distribution of cell preferences is not qualitatively different from what might be expected for LGN cells. To show convincingly that the sensitivities of temporal lobe cells clustered around unique hues, it would be necessary to use not the triangular configuration of Figure 1 but a set of stimuli that lay on a circle in chromaticity space and were uniformly spaced in a defensible metric. For now, it remains the case that no one has shown a cortical origin for the unique hues. Their special status may derive from the outside world [10].

Acknowledgments

I thank J. Bosten, S. Shevell and H. Smithson for discussion.

References

1. Mollon, J.D., and Jordan, G. (1997). On the nature of unique hues. In John Dalton's Colour Vision Legacy, C. Dickinson, I. Murray and D. Carden, eds. (London: Taylor and Francis), pp. 381–392.
2. Derrington, A.M., Krauskopf, J., and Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. J. Physiol. *357*, 241–265.
3. Tailby, C., Solomon, S.G., and Lennie, P. (2008). Functional asymmetries in visual pathways carrying S-cone signals in macaque. J. Neurosci. *28*, 4078–4087.
4. Stoughton, C.M., and Conway, B.R. (2008). Neural basis for unique hues. Curr. Biol. *18*, R698–R699.
5. Conway, B.R., Moeller, S., and Tsao, D.Y. (2007). Specialized color modules in macaque extrastriate cortex. Neuron *56*, 560–573.
6. MacLeod, D.I.A., and Boynton, R.M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. J. Opt. Soc. Am. *69*, 1183–1186.
7. Smith, V.C., and Pokorny, J. (1996). The design and use of a cone chromaticity space: a tutorial. Color Res. Appl. *21*, 375–382.
8. Golz, J., and MacLeod, D.I.A. (2003). Colorimetry for CRT displays. J. Opt. Soc. Am. A *20*, 769–781.
9. Dacey, D.M. (2003). Colour coding in the primate retina: diverse cell types and cone-specific circuitry. Curr. Opin. Neurobiol. *13*, 421–427.
10. Mollon, J.D. (2006). Monge. Vis. Neurosci. *23*, 297–309.

Department of Experimental Psychology, Cambridge University, Downing Street, Cambridge CB2 3EB, UK.
E-mail: jm123@cam.ac.uk

Response: Towards a neural representation for unique hues

Bevil R. Conway and Cleo M. Stoughton

We recently reported that a population of color-tuned neurons in posterior inferior temporal cortex of macaque monkey represents all colors and that this population shows a bias towards certain colors: we found that many cells were tuned to red, followed by peaks to green, blue, and an indistinct peak corresponding to yellow [1]. This appears to be the closest explicit neural representation of unique hues found in the primate. John Mollon suggests that the distribution is what one would expect of neurons found earlier in the visual pathway, in lateral geniculate nucleus (LGN), if tested with the colors we used to measure tuning. Previous work has shown that LGN cells respond linearly to changes in cone contrast and do not represent unique hues. While we acknowledge that our stimuli would constrain the population's color-tuning distribution if the neurons were linear, the recorded cells have narrow nonlinear color tuning, quite unlike LGN cells. Thus, the population tuning is consistent with our initial interpretation.

Retinal and LGN cells that likely contribute to color respond in a linear fashion to increasing differences in activity of different classes of cones — stimuli that elicit the most difference in cone activity will elicit the maximal response. But color perception is not linear: the familiar color circle, composed of a continuous series of colors, is perceived as discontinuous, punctuated by four unique hues — red, green, blue, and yellow. These categories are universal in both humans and macaque monkeys [2], yet there is no neurophysiological account for them. The unique hues may relate to natural light sources like the sun and blue sky, as described by Mollon, but even so, this information must

be represented by the brain. So, somewhere along the visual pathway, the cone signals are presumably transformed from linear responses typical of the LGN into nonlinear responses corresponding to color perception. Combined functional magnetic resonance imaging and single-unit recording has revealed regions in macaque visual cortex, dubbed globs, that are chock full of color-tuned neurons [3]. Could these extrastriate cells, the focus of our recent report, participate in this transformation?

To assess the color properties of glob cells, we initially used cone-isolating stimuli, which are effective in eliciting responses from neurons in LGN and primary visual cortex [4,5]. But few glob cells responded well to these stimuli. The set of cone-isolating stimuli consists of six pastel colors, which do not include optimal examples of the unique hues (or any focal colors). If a cell were narrowly tuned, say to orange, it would simply not respond to this stimulus set. The paltry response of many glob cells to cone-isolating stimuli would be predicted if the cells were narrowly color-tuned. This explanation seems plausible because the proportion of nonlinear neurons increases as one progresses along the visual pathway from the retina through extrastriate cortex [6].

In order to obtain responses to assay color selectivity we therefore used as stimuli a large range of equiluminant colors of maximum saturation, which fell on a triangle when plotted in C.I.E. coordinates (Supplemental Figure S1 in [1]). Such a triangular stimulus set has been used in previous physiological studies of areas V4 and IT [7–9] because of its efficacy at eliciting responses in extrastriate regions. But as Mollon points out, there is a cost associated with having a stimulus set consisting of maximally vivid colors: the magnitude of cone contrast measured against the adapting background will vary considerably from one color to the next, with red and blue generating the highest cone contrast. We agree with Mollon that this stimulus set would produce major peaks in the population tuning, to the red and blue monitor primaries, if glob cells responded as LGN cells do.

Do glob cells respond linearly like LGN cells? The poor response of glob cells to cone-isolating stimuli, along with the direct observation that glob cells have narrow color tuning, suggests otherwise. The vast majority of LGN cells respond to L-cone activity pitted against M-cone activity; for a population of LGN cells tested using the triangular color set, one would therefore expect only two peaks, at red and blue. A population of nonlinear color-tuned cells, on the other hand, would have cells with optimal tuning to various colors besides red and blue — cells narrowly tuned to orange, for example, would not respond strongly to red even though red has higher cone contrast. It is telling that the measured population of glob cells contains many cells with peak tuning to colors not located at the apices of the stimulus triangle (Supplemental Figure S1 in [1]; several single-cell examples are given in Figure 6 of [3]), showing that glob cells have narrow, nonlinear color tuning unlike LGN cells. Moreover, the population clearly contains a prominent peak at green, which is also not predicted for the population of LGN cells. At minimum, one can conclude that the globs reflect the dimensions of color perception better than the LGN.

The peaks in the color tuning of the population of glob cells correspond roughly to the unique hues, and as we initially pointed out [1], also to the most saturated colors in the stimulus set. Curiously there seems to be a correlation between the unique hues and the colors within the Munsell system — used widely in industry — that also display the highest levels of chroma, or saturation, at intermediate luminance (or value). In any event, the coincidence that the population peaks correspond to both unique hues and peaks in saturation may indicate not a bug introduced by vagaries of cone contrast, but rather a feature of these neurons: that they encode not only hue but also saturation, two key components of color.

We acknowledge the importance of a stimulus set defined by a uniform color space, as suggested by Mollon, to disentangle the relative contribution of saturation and hue. The challenge is to identify a space that is both defensible and effective. Any uniform space inevitably will be less than fully adequate because the dimensions of color are non-Euclidean. Controlling for any one of the dimensions of color — hue, saturation or luminance — will eliminate some colors. For instance, a uniform equiluminant color space will not encompass both a vivid yellow and vivid blue: if there is a vivid blue, the space will extend to ochre not yellow, as in the triangular stimulus set. And maintaining equal cone contrast, as obtained in DKL color space [10], has the added disadvantage that it does not yield colors of high, or even equal, saturation. It remains unclear how the brain encodes the inter-connectedness and nonlinearity of these dimensions. With their nonlinear color-tuning properties, glob cells may ultimately hold the key to resolving this puzzle.

Acknowledgments

We are grateful to Thorsten Hansen for very productive discussions, to Anya Hurlbert and Kit Wolf for MATLAB code, and to David Hubel, Alexander Rehding and Mike Wiest for comments on the manuscript.

References

1. Stoughton, C.M., and Conway, B.R. (2008). Neural basis for unique hues. Curr. Biol. *18*, R698–R699.
2. Sandell, J.H., Gross, C.G., and Bornstein, M.H. (1979). Color categories in macaques. J. Comp. Physiol. Psychol. *93*, 626–635.
3. Conway, B.R., Moeller, S., and Tsao, D.Y. (2007). Specialized color modules in macaque extrastriate cortex. Neuron *56*, 560–573.
4. Conway, B.R., and Livingstone, M.S. (2006). Spatial and temporal properties of cone signals in alert macaque primary visual cortex. J. Neurosci. *26*, 10826–10846.
5. Reid, R.C., and Shapley, R.M. (2002). Space and time maps of cone photoreceptor signals in macaque lateral geniculate nucleus. J. Neurosci. *22*, 6158–6175.
6. Gegenfurtner, K.R. (2003). Cortical mechanisms of colour vision. Nat. Rev. Neurosci. *4*, 563–572.
7. Komatsu, H., Ideura, Y., Kaji, S., and Yamane, S. (1992). Color selectivity of neurons in the inferior temporal cortex of the awake macaque monkey. J. Neurosci. *12*, 408–424.
8. Matsumora, T., Koida, K., and Komatsu, H. (2008). Relationship between color discrimination and neural responses in the inferior temporal cortex of the monkey. J. Neurophysiol. *100*, 3361–3374.
9. Kusunoki, M., Moutoussis, K., and Zeki, S. (2006). Effect of background colors on the tuning of color-selective cells in monkey area V4. J. Neurophysiol. *95*, 3047–3059.
10. Derrington, A.M., Krauskopf, J., and Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. J. Physiol. *357*, 241–265.

Program in Neuroscience, Wellesley College, 106 Central Street, Wellesley, MA 02481, USA.
E-mail: bconway@wellesley.edu