pathogens. Experimental studies crossing the presence/absence of the bacteria with the presence/absence of a specialized garden pathogen — a fungus in the genus *Escovopsis* — have shown that ants with antibiotic-producing bacteria are better able to protect their fungal gardens from disease. These studies are among the best evidence that at least some antibiotics suppress infections in nature.

The ant–fungus–bacteria mutualism is an ancient system whose evolutionary histories can be deduced by traditional molecular phylogenetic studies. Once these histories have been established and the associated antibiotics have been identified, there will be a wealth of data to trace both the evolution of these small molecules and their function. These studies could also reveal how the ant-bacteria system has maintained itself over tens of millions of years without running out of antibiotics to combat the inevitable development of antibiotic resistance by their microbial pathogens. In short, we can learn a lot from bugs — both the six-legged and microbial varieties.

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A neural basis for unique hues?

J.D. Mollon

The four perceptually simple colors — red, green, yellow and blue — are a challenge to neuroscience, because no one has found cortical cells that represent color in terms of these ‘unique hues’ [1]. The chromatically selective cells at early stages of the primate visual system do not map on to the unique hues [2,3]. Recently, however, Stoughton and Conway [4] have reported that the peak sensitivities of color cells in posterior inferior temporal cortex do cluster near the unique hues. The authors plot their results as a polar histogram: at each position on a hue circle, they show the number of cells that are maximally excited by that hue. There are three peaks in the histogram: one (the largest) falls close to unique red and another falls close to unique blue, while the third (less well-defined) lies in the yellow-green region. In fact, however, if the stimuli used in the experiment are plotted in a physiological color space, they form not a circle but an obtuse triangle. The peaks identified by Stoughton and Conway [4] fall at the apices of this triangle. Because these stimuli maximize the ratios of cone signals, they would maximally excite cells earlier in the visual system. So Stoughton and Conway’s polar plot does not in itself show that cells of the posterior inferior temporal cortex represent unique hues, nor that they differ qualitatively in their behavior from chromatic cells at an earlier level.

The stimuli were presented to the monkey on a CRT and the individual chromaticities were obtained by

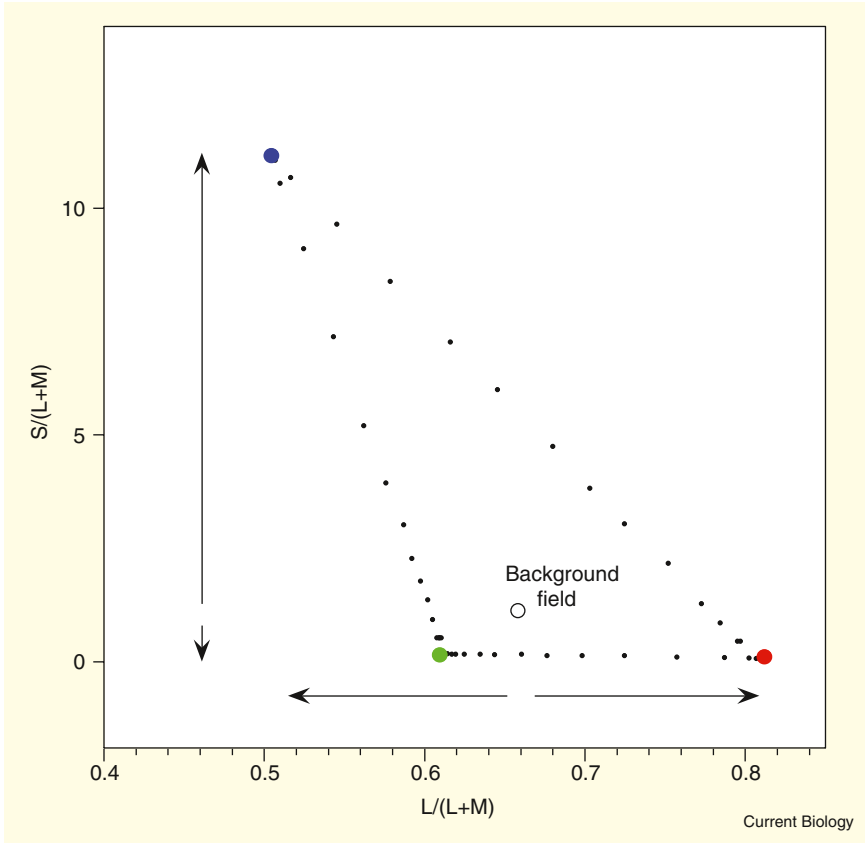

Figure 1. Stoughton and Conway’s [4] equiluminant stimulus set (small black points) re-plotted in the chromaticity diagram of MacLeod and Boynton (1979).

The colored dots show the chromaticities of the three phosphors of the CRT used in the experiments. Open circle: chromaticity of the white background present during the measurements. The arrows indicate the maximum available modulations on the two axes of the diagram. Scaling of S axis as in [8].

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].

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Response: Towards a neural representation for unique hues

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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