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Color Vision: Decoding Color Space

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A new study has used magnetoencephalography to track cortical responses to color as they emerge in time. Similarities and differences within these neural responses parallel characteristics of the perceptual experience of color.

It is still common to describe color vision in terms of two stages. In the first, the light spectrum is sampled by three classes of retinal cone receptors with different spectral sensitivities. In the second, the cone signals are compared within post-receptoral channels that encode perceptual attributes like the hue and saturation of the light. But dividing the neural machinery of color vision in this way — between the initial receptors and the rest of the brain — is a bit like saying that the two main parts of a dissertation are the signature page and the thesis. It may feel that way to students during their defense, but this dichotomy hides an intricate story with many chapters, most of which are still unread. A new study reported in this issue of *Current Biology* by Rosenthal *et al.*[1] sheds further light on this story by probing the cortical responses to color as they emerge over time.

One way nervous systems represent information is through different populations of neurons tuned to different properties of the stimulus. These tuning preferences are typically arranged systematically in the brain. For example, many areas of the visual system are arranged retinotopically, so that nearby cells respond to nearby locations in space (and thus to nearby locations in the image falling on the mosaic of receptors in the retina)[2]. These retinotopic 'maps' can provide a representation of visual space, linking processing stages. However, the maps are highly distorted — many more neurons are devoted to sampling our central foveal vision than the visual periphery, and the receptive field size or spatial area captured by individual neurons also increases with eccentricity. This is why we see more clearly at the center of gaze: spatial discriminations are better in the fovea because the same stimulus difference produces larger differences in the neural response when shown in central *versus* peripheral vision. For some spatial judgments the falloff in sensitivity with eccentricity corresponds reasonably to the changes in cortical sampling, so that performance can be equated by scaling the stimulus size to stimulate a constant number of neurons — the cortical magnification factor[3]. Thus, the distortions in the neural representation impact our perception, and raise the exciting possibility that we could reverse engineer aspects of our percepts from the properties of the neural code.

Within and beyond these retinotopic maps, there are further arrangements of neuronal populations with preferences for different inputs, such as eye dominance or subpathway, or for image features such as edge orientation, size, or color[4]. For example, for color, different combinations of the cone signals are carried by distinct cell types in the retina, and course through different layers of the lateral geniculate nucleus[5]. Many studies have explored how the geniculate inputs are further transformed within visual cortical areas, from V1–V4 to VO, to form new representations of color. These studies have revealed many important properties of cortical color coding and point to a variety of 'maps' of color space that may emerge in different

stages along the visual stream[6,7]. The maps in different visual areas may serve different ends. Could the distortions of color maps in higher visual areas along the ventral stream predict the distortions and biases in our perceptual experience of color[8] (Figure 1)?

In their new study, Rosenthal *et al.*[1] examined cortical responses to four hues at two luminance levels, uniformly sampled in terms of the retinogeniculate representation, and then analysed how similar or different the neural responses were for the samples. This work follows a long tradition of exploring the neural mechanisms of color using a variety of techniques: from recording activity in individual cells to the population activity measured by noninvasively monitoring the electrical (EEG/ERG) or related hemodynamic (fMRI, for example) responses of the brain. These studies have revealed color-specific responses throughout the visual pathway, although with differing representations in different visual areas[8,9]. However, the temporal dynamics of — and interplay between — these representations remain poorly understood. In the new work, neural responses were measured with magnetoencephalography (MEG), which measures activity-dependent changes in the magnetic fields of the brain at a high temporal resolution, providing a powerful window into how the representations emerge and change over time[10]. These may include faster responses to luminance than chromatic stimuli, so that the interplay of these dimensions may change with time; the authors explore the interaction of hue and luminance in a separate new paper[11].

Analyses of the responses revealed a number of features in the neural representation that parallel prominent features of our color perception. This is important because identifying the neural substrates of color appearance has proven difficult. One interesting parallel is the interaction between hue and lightness: while these are often treated as independent dimensions — and appear largely separable in the retinogeniculate signals — some hues appear to change markedly depending on whether they are brighter or darker than the surround. In particular, yellow exists only as an increment, but becomes brown as a decrement[12] (Figure 1B). This difference

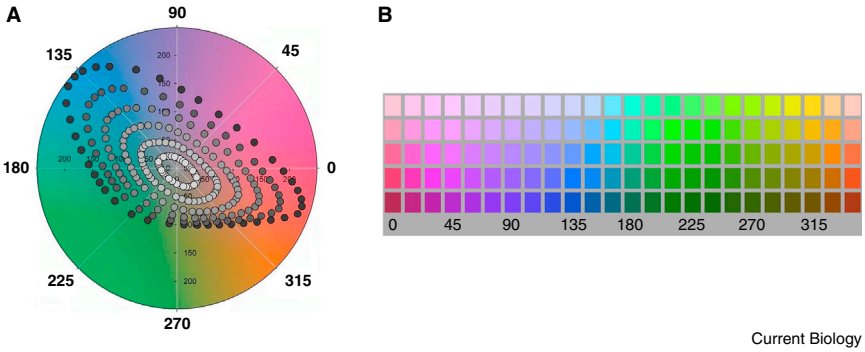

Figure 1. Representations of color.
(A) The circle of hues correspond to hues evenly sampled by the two cardinal axes along which color is carried in the retina and geniculate. However, perceptually equal samples, as in the Munsell color system (symbols), show strong biases relative to the geniculate representation. (Panel reproduced with permission from Webster[20].) (B) Hues also interact with lightness. Some hues appear similar regardless of lightness, while yellows change to browns when they are darker than the surround[12].

was revealed as dissimilar neural responses to dark and light versions of the orange/yellow hue, while the other responses (particularly to blue) remained similar with light level. While it is striking that such perceptual differences are reflected in the patterns of neural activity, we do not know whether it is the structure of the brain, or the structure of the visual environment, that causes us to experience color in this way.

In addition to identifying neural analogs of color percepts, the Rosenthal *et al.*[1] study is notable for a number of other intriguing findings. One is that the pattern of color responses across participants appeared to reverberate in time after 275 milliseconds, potentially reflecting a late role of recurrent networks in the representation. Another is that the responses to color stimuli could predict the responses to color words, but only at very long delays (~900 ms), while the responses to words did not predict the color responses, thus failing to support a close association between perceptual *versus* conceptual neural representations of color. The relationship between perception and cognition is actively debated[13,14], and it would be interesting to see how the neural responses might differ across languages that, unlike English, do treat light and dark blues as separate color categories[15].

Could we work back from the neural responses to build a perceptual metric for color? Many attempts have been made to create a uniform color space, in which equal distances in the space correspond to equal differences in perception[16]. What is equal depends on the percept, however, and different scalings are required for different judgments, such as just noticeable differences or the salience of large color differences. Color information is also involved in many different visual tasks, from segmenting the scene to judging surface materials or even the expression on a face. The processes underlying different visual analyses involve different pathways and areas, and how color contributes to these can vary widely. Moreover, reports of color percepts — for example, which stimulus is pure red — can be very different from one person to the next[17]. Thus, identifying which aspects of color perception a given neural measure reveals is challenging. Consider again retinotopic maps: the magnification required to equate performance across the visual field also varies with the task[18]. Moreover, despite the distortion in resolution, we do not experience the world to be compressed in the periphery. Similarities in the retinotopic responses across the map(s) therefore do not predict a single perceptual geometry of space.

A further question is to what extent the neural representation of color is like a 'space'. The initial sampling by the three classes of cones constrains color coding to be three-dimensional or trichromatic, and encourages the idea that the brain might represent colors in terms of their coordinates, however these might be transformed at different stages. The conceptual framework of an

underlying geometry has considerable explanatory power. We clearly experience stimuli with nearby cone coordinates as more similar, and can order hues continuously in terms of their similarities[19]. Yet for untrained observers, it is not intuitive what the opposite of a given hue is, let alone what is orthogonal[20]. These are relationships we can readily compute for visual space, and which we often need to. But the utility of experiencing such relationships for color is uncertain, and it may be that we represent colors more like distinct objects or categories than computable vectors. In this sense, it could be that the representation of purples and oranges is like apples and oranges.

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Microbiomes: Infant Chimps Crawling with Bacteria

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Human guts are colonized at birth by a limited set of microbes that gradually increases in diversity throughout infancy. A new study reports the opposite pattern in infant chimpanzees, raising questions about how host–microbiota relationships have changed during ape evolution.

Humans are largely sterile *in utero*[1], but the guts of newborns are rapidly colonized by microbial communities that affect host health. This gut microbiota gradually grows in complexity throughout infancy[2–5]. Founding microbes facilitate the colonization of later-arriving lineages[6], the addition of complementary foods to the infant's diet creates new metabolic niches[7], and the infant's adaptive immune system is trained to tolerate the presence of a diverse microbial consortium[8]. The accretion of microbial species continues until the gut microbiota reaches an adult-like state, typically within 2–3 years. This pattern of increasing gut microbial diversity during infant development has been observed in multiple human populations, but almost nothing is known regarding gut microbiota assembly in non-human primate species. A remarkable new study by Reese *et al.*[9], published in this issue of *Current Biology*, suggests that wild chimpanzees, our closest living relatives, exhibit the opposite pattern: infant chimpanzees harbor significantly more microbial species than do older individuals. These findings raise intriguing questions about the assembly of gut microbiota in