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Colour Vision: A Clue to Hue in V2

Dispatch

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Where do our brains encode all the colours of the rainbow? We know the neural basis for colour opponency and colour contrast, and recent studies have now provided evidence for the representation of hue in cortical visual area V2.

Almost everybody knows that colour perception begins with the three cone types — L, M and S, or loosely, red, green and blue (Figure 1A,B) — but what most people do not know is that each cone type does not represent a single colour. If cones did, then we would be able to see a continuous mixture of impossible colours, such as reddish-greens and bluish-yellows. How cone responses are translated into our perception of hue has been a difficult nut to crack, but a recent study [1] suggests it happens in V2, the second cortical visual area.

Colour perception involves an opponent process whereby single cells in the retina and the lateral geniculate nucleus (LGN) — the relay station between the eye and the brain — compare by subtraction the activity of different cone types. Some cells are excited by L cones and suppressed by M cones — so these are referred to as 'red ON/green OFF' cells [2–4] — which may explain why red is exclusive of green. In the LGN there are three categories of 'colour' cells (Figure 1B): red–green, or 'L versus M', cells; blue–yellow, or 'S versus L+M', cells; and black–white, or luminance, cells (yes! as Matisse showed us, black and white *are* colours). These presumably connect to specialized red–green, blue–yellow and black–white cells in primary visual cortex (V1), the first cortical stage of visual processing.

Together, these are the building blocks for colour vision. This explains why colour television sets get away with stipulating just the red-green-blue (RGB) phosphor values at each point to achieve a given colour and can be represented as a three-dimensional chromatic-opponent colour space (see Figure 1C). But where and how does your brain integrate the information from the different LGN and V1 cells to give you your perception of specific hues? Where are cyan, orange, magenta and pink represented? And why do we perceive red and orange as more similar in hue than red and yellow? Why does very short-wavelength light look 'reddish'? It is, after all, as far from long-wavelength red light as it can be. In a provocative new paper, Xiao *et al.* [1] propose some answers.

Xiao *et al.* [1] studied V2, the cortical visual area adjacent to V1, which receives and integrates information directly from V1 (Figure 1A). Like V1, V2 has a distinctive pattern of staining for the metabolic enzyme cytochrome oxidase. In V1, such staining reveals small scattered 'blobs' of tissue, resembling polka dots, which presumably represent regions with particularly high cytochrome oxidase activity. With V2, cytochrome oxidase staining reveals stripes, not blobs, and these consist of alternating darkly-staining thick and thin stripes, separated by pale-staining stripes (Figure 1). What is more, blobs and thin stripes in V1 and V2 are specialized, or at least strongly biased, to process colour.

This apparent bias has been tricky to confirm, however, because it is very difficult to compare physiology and anatomy in the same chunk of tissue. Recently, Landisman and T'so [5] have managed to do this in V1 using optical imaging. They confirmed Livingstone and Hubel's [6] landmark finding that cone-opponent 'colour' cells in V1 are clustered in blobs. Hubel and Livingstone [7] had also claimed that colour cells cluster in the thin stripes in V2, a finding that has been disputed [8]. Using optical imaging, Xiao *et al.* [1] and Ts'o *et al.* [9] have nicely demonstrated that this finding is also true. But Xiao *et al.* [1] have gone further and made an observation that will prove to be remarkable if it holds up.

Xiao *et al.* [1] measured the activity in V2 using a very sensitive camera which detects activity-dependent changes in the optical density of tissue [10,11]. They subtracted the responses to black–white grating stimuli from those to red–green grating stimuli and concluded that the differential regions coincided with V2 thin stripes. They then measured the responses to different colours — red, orange, yellow, lime, green, aqua, blue and purple — presented as isoluminant colour-and-gray gratings (isoluminant gratings appear roughly a uniform gray in a black-and-white reproduction). The locations of peak activity for each colour were sequentially shifted, so that red was next to orange, orange was next to yellow, yellow was next to lime, and so on (Figure 2A).

The peak activities to 'secondary' colours — lime, aqua and purple — were found to be weaker than those to the other colours. There was also a bit of scatter in the maps when the same colour was measured on separate trials, and often the peak response to red and green did not overlap with the differential response to the red–green grating used to identify the thin stripes. The statistical significance of the spatial shift of the different hue regions was assessed for only two colour bands, and some of the colour peaks in these two bands were not significantly shifted. So we anxiously await a more thorough study, but in the meantime we have something tantalizing to chew on, because if it is true, then we can begin to see how the brain solves the problem of translating the chromatic axes — each represented by different populations of cells in the LGN and V1 — into a representation of specific hues. Quite simply, the location within a given V2 colour band would represent the perceived hue.

It remains a mystery how saturation and brightness, two other values critical for colour, are encoded. But for the meantime, we might have a reason why red

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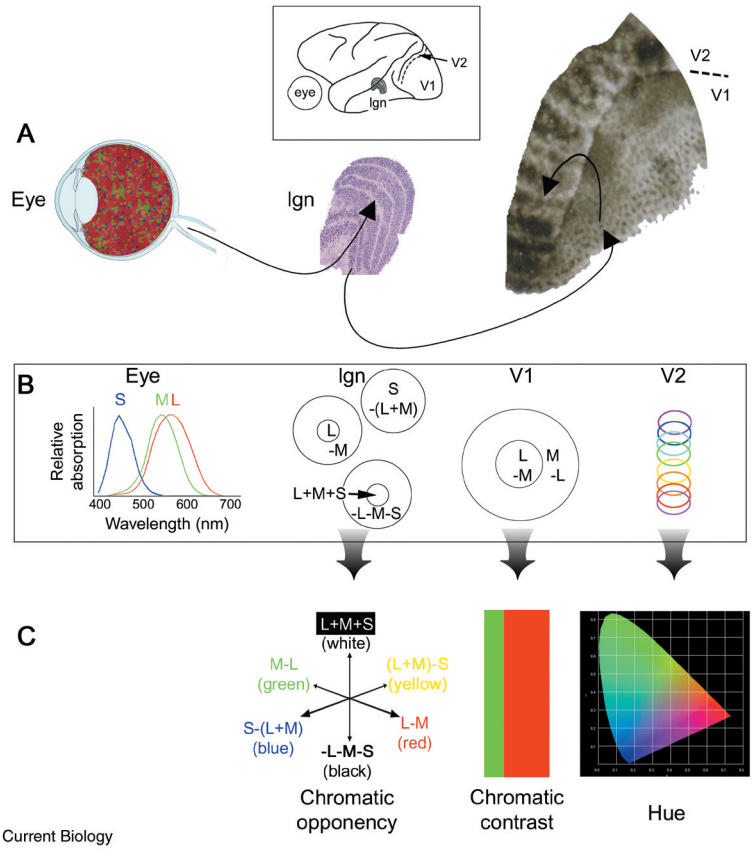

Figure 1. A summary of colour processing in the visual system.

The panels illustrate the anatomy (A), physiology (B) and perception (C) of colour vision. Light activates the three cone classes — L, M and S — according to their relative absorption ('eye' in B). Cone signals are compared by cells in the lateral geniculate nucleus ('LGN' in B). Some cells have receptive fields excited by L cones and suppressed by M cones ('red–green' cells); others have receptive fields excited by S cones and suppressed by (L+M) cones ('blue–yellow' cells). These underlie chromatic opponency evident perceptually: red is exclusive of green, and blue is exclusive of yellow (C). Specialized 'double-opponent' cortical cells compare cone ratios in one part of visual space with those in an adjacent part of visual space ('V1' in B); these are presumably constructed from LGN colour cells and enable chromatic contrast calculations – red looks redder next to green ('chromatic contrast' in C). Colour signals are transmitted to the thin stripes of V2 (A, right), where specific hues are represented in colour bands (B, right) that span the V2 thin stripes. These might subserve our perception of hue (C, right). The picture of V1 and V2 (A, right) is of unfolded squirrel monkey cortex that has been stained for the metabolic enzyme cytochrome oxidase. Note the blobs in V1 and the thick-inter-thin-inter-thick stripe pattern in V2. The arrow points to a thin stripe. (Adapted from [17].)

appears closer in hue to orange than to yellow: the peak red activity is adjacent to orange, not yellow (Figure 2A). In some of their maps, Xiao *et al.* [1] found two representations for purple at opposite ends of a single band, one next to red and one next to blue (Figure 2A). This might help explain why short-wavelength light appears both reddish and bluish.

The V2 thin stripes receive inputs from V1 blobs [6,12] (Figure 1), but how are the cells within the colour bands connected with the blob inputs and to each other? There are about 1,000 cells in a 'red' region in Xiao *et al*.'s study [1]. Surely all of these cells are not doing the same thing. Using microelectrodes to record single cell responses in V2 [9] and V1 (see [16], and my own observations), red-ON/green-OFF cells have been recorded so close to green-ON/red-OFF cells that the two would not be distinguishable with optical imaging, which is relatively coarse. Does this contradict Xiao *et al*.'s [1] finding that separate regions within V2 colour bands are specialized for a given hue? Or does it simply argue that the 'red' regions have more red-ON/green-OFF cells but not red-ON/green-OFF cells exclusively? Xiao *et al*. [1] attempted to address this question with multiunit recordings and found, not surprisingly, a rather weak correlation between optical signal and neuronal response (Figure 2B).

Thirty years ago, Edwin Land [13] showed that two regions reflecting very different spectral distributions could be made to appear the same colour just by changing chromatic context. Thus spatial context is critical to our judgment of colour, as any Christmas-tree decorator knows — red bows look much redder when they are against a green tree. The neural mechanisms responsible for this also give us 'colour constancy' [14], which refers to the way, under varied illumination conditions, the colour of an object does not change that much (most cameras are not colour constant, which is why a photograph of a tungsten-lit room has an orange cast).

One wonders if two different stimuli that produce the same colour percept, like the ones Land used, would activate the same region of the V2 thin stripe, as presumably they must if the spatial maps in V2 thin stripes actually represent hue. If so, this implies that colour-constant calculations take place in or *before* V2 — maybe even in V1 — and not in higher areas (like V4 or V8) as previously suspected [15]. A role for V1 is corroborated by recent studies showing that specialized cells in this region have spatially structured cone-opponent receptive fields (Figure 1B) [16–18] that respond better to chromatic borders [19] and take into account broad chromatic context [20]. Perhaps V1 is more involved in the 'conscious' aspects of colour vision, such as colour constancy, than previously thought.

A spatial representation of hue in V2 is interesting, but one might ask: is it necessary for colour vision? Perhaps this spatial pattern arises during development because of a Hebbian circuit: red and orange are close in hue, and so cells representing them are more often active at the same time and would therefore

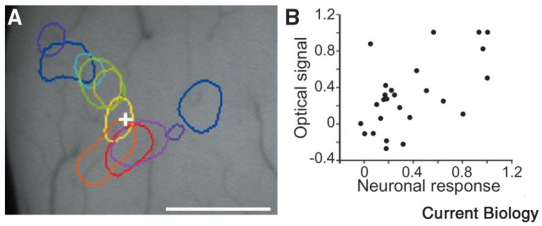

Figure 2. Colour specific band in the second cortical visual area (V2).

(A) Regions corresponding to the peak activity to different coloured stimuli, each tested separately, are outlined on the surface picture of the brain (note the darkly-imaged blood vessels). Scale bar is 0.5 mm. (B) Correlation between multiunit electrode recording and optical signals in V2 colour bands. (Adapted from [1].)

tend to wire together or in close proximity. Or perhaps there is a developmental wiring constraint: the three V1 chromatic axes presumably feed multiple populations of V2 cells. Having the related hues next to each other would reduce the amount of axon, or 'wire', lengths required. But these sorts of explanations beg the question: does hue *need* to be represented spatially for us to have colour vision? If so, why is it critical? These questions prompt us to ponder fuzzy, unsettling, philosophical questions like 'what does a neural representation of colour actually mean?' For now, we have to satisfy ourselves by describing patterns of brain activity as rigorously and precisely as we can. This has the advantage, at least, of offering us hope that we will be able to make artificial brain-stimulation interfaces to help restore colour vision in those with impaired early visual systems.

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