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Colour Vision: Primary Visual Cortex Shows Its Influence

Dispatch

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New results have revealed that neurons in visual area V1 are influenced by chromatic context, in a way consistent with colour constancy. Other studies have mapped the internal cone–input structure of V1 receptive fields. Put together, these findings suggest important dual roles for V1 in colour perception.

In a landmark statement, Crick and Koch [1] argued against primary visual cortex (V1) being the site for consciousness, citing the fact that V1 neurons did not display the properties necessary for colour constancy, a cornerstone of our conscious experience. Colour constancy is what makes the redness of a red apple stable under changing illumination. All proposed mechanisms for colour constancy require comparisons between lights reflected from different surfaces of the scene, to discount the overall effects of the light source spectrum. The general view until recently has been that neurons capable of making such comparisons do not occur until area V4 or beyond, where the receptive fields are sufficiently large [2]. This view is now challenged by new studies which have revealed that V1 neurons may be influenced by light outside their receptive fields [3,4] and that, within their receptive fields, they perform important steps in computing colours [5–7].

In his pioneering study twenty years ago, Zeki [8] specifically searched for cells whose responses mirrored our perception of colour: cells which, for example, would continue to signal 'red' as long as a surface appeared 'red', regardless of the illumination upon it. He found such cells only in V4, and termed them 'colour-only', as opposed to the 'wavelength-only' cells in V1, whose responses changed with changing wavelength, regardless of the perceived colour. In a new search, Wachtler *et al.* [3] instead looked for neurons whose responses were influenced by changes in the background colour, well outside of their classical receptive fields [9]. By definition, stimuli presented on their own outside the classical receptive field provoke no response from the cell, but, crucially, they may modulate the response to stimuli within the classical receptive field. This non-classical 'contextual modulation' has been demonstrated for a variety of visual attributes, for example, binocular disparity and texture orientation [10], and now luminance [4] and colour [3].

Colour contrast is, of course, a prime example of contextual modulation in perception: a bluish disk against a blue background appears less blue than when against a grey background (Figure 1, left). Colour contrast is also one of the most basic mechanisms by which colour constancy may be achieved, because factoring out the colour of the background is likely to factor out the illuminant colour. The latest search for colour-constant neurons has revealed a population of V1 neurons that report colour contrast, over a large scale [3].

These cells display several properties. When presented with a large patch of uniform colour entirely covering its receptive field against a grey background, each has a preferred colour but also responds well to nearby colours, some with tuning widths as broad as half the entire hue wheel. For most cells, a background of the preferred colour suppresses its response to the preferred colour, as well as, less strongly, to nearby colours. For some cells, a background opposite in colour to the preferred colour enhances its response. (To ensure that the background effects were not due to stray light falling in the receptive field itself, Wachtler *et al.* [3] adjusted each stimulus to be at least twice as large as the classical receptive field, and also verified that the background changes alone did not activate the neuron.) Thus, a cell that fired vigorously in response to a bluish patch against a grey background would respond less well when confronted with the same bluish patch against a blue background, as if it were signalling the reduction in chromatic contrast — or correcting for an overall bluish cast of the illumination, thereby reserving its best response for true-blue surfaces.

Individual cells do not perfectly encode chromatic contrast: on average, the reduction in any one cell's response is about two-thirds the reduction in contrast. Yet, over the whole population of 94 cells tested by

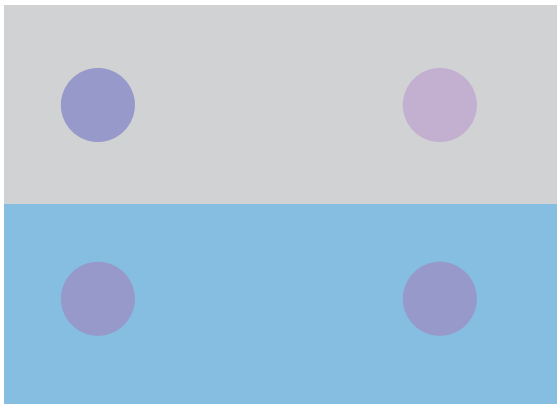

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Figure 1.

The two disks on the left are printed with identical ink, but appear different in colour against the upper and lower backgrounds, because of colour contrast. The two disks on the right are printed with different inks, but appear similar in colour. The pattern of responses of V1 colour-context-modulated neurons would match for the two disks on the right (against their respective backgrounds) but not for the two disks on the left.

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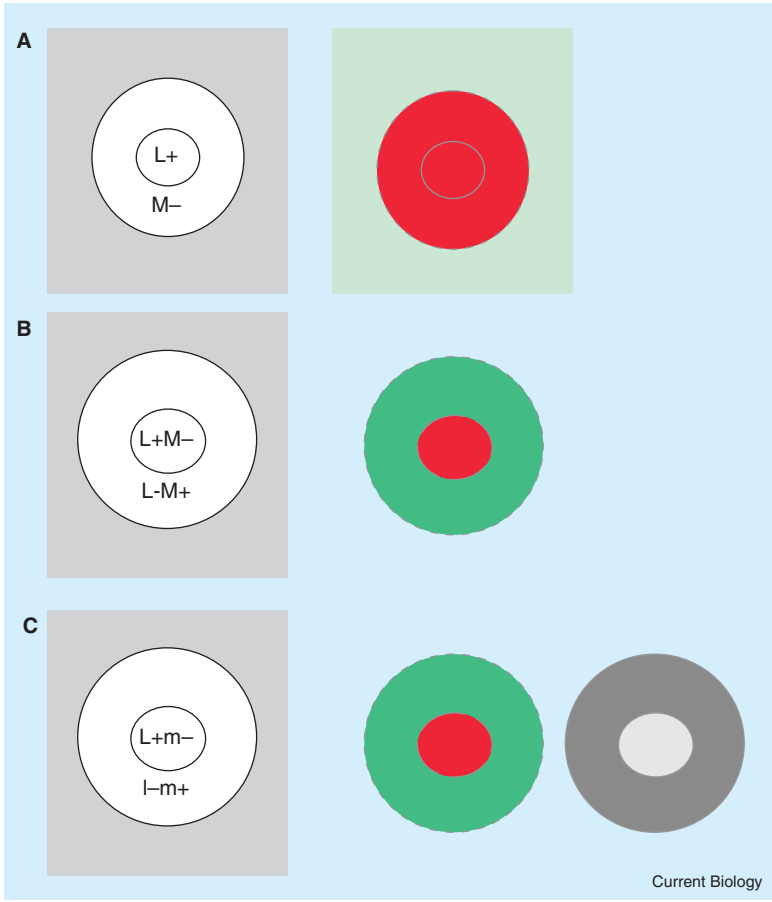

Figure 2. Receptive fields of colour-selective cells (left) and their optimal stimuli (right).

Shaded areas are outside the classical receptive field, where contextual modulation may occur. (A) 'Single-opponent' type receptive field. 'L+' denotes excitatory L-cone input; 'M–' denotes inhibitory M-cone input. The cell thus prefers 'red' in the centre — maximally stimulating the L cone — and a lack of 'green' in the surround. If it were a context-modulated cell, its response may be further enhanced by an extra-classical background of 'green', opposing its preferred colour. (B) Ideal 'double-opponent' type receptive field. (C) Real 'double-opponent' type receptive field. Given unequal weights of cone inputs within and between its centre and surround — denoted by mixed cases of 'L' and 'M' — the cell will respond equally well to colour contrast and luminance contrast within its receptive field.

Wachtler *et al.* [3], the pattern of responses to a particular patch against a bluish background matches the pattern of responses to a slightly pinker patch on a grey background. Thus, as a population, their behaviour mirrors our perception (Figure 1, right).

There remain two pressing questions. First: what is the origin of the extra-classical-receptive field contextual influence? Does it come from below, within or above primary visual cortex? The suppressive effect of the chromatic background typically peaks within 100 milliseconds, allowing just enough time for higher areas such as V4 or IT to feedback their own activation [10]. The paradigm minimises the potential contribution from lower levels by maintaining long-term adaptation to a neutral grey background, interrupting this only very briefly and occasionally with the coloured background. Nonetheless, fast chromatic adaptation of the retinal cones exposed to the new background, coupled with microsaccades and lateral interactions that spread the gain adjustment to nearby cones [11], may weaken the cone input to the receptive field itself. These arguments do not, though, exclude the possibility that lateral interactions within primary visual cortex itself perpetrate the background effects.

The second question is: how do these context-modulated cells fit into the historical taxonomy of colour-selective cells? Traditionally, colour-selective cells have been classified by the spatial distribution of cone inputs within the receptive field (Figure 2): 'single-opponent' cells are fed by one cone type to the center, and by the opponent cone type to the concentric surround, with opposite sign. 'Center-only' cells are fed by opponent cone types, with opposite signs, and have no antagonistic surround. 'Double-opponent' cells have centers like 'center-only' cells, but also have antagonistic surrounds, where the cone types are opposite in sign to the center.

Correctly categorising the context-modulated V1 cells is difficult because the taxonomy itself is under challenge. We now know that 'single-opponent' cells are probably not a distinct type at all, but rather one end of a parvocellular continuum, ranging from pure cone-opponent weightings to non-opponent weightings in which the center and surround have identical spectral sensitivities [11,12]. The 'double-opponent' cell, following its initial discovery thirty-odd years ago [13,14], disappeared under further scrutiny, and has only recently been revived [5,6,16]. Conway *et al.* [5,6] explicitly demonstrated its opponent cone inputs with small high-colour-contrast spots presented in rapid succession throughout the receptive field, using the technique of reverse correlation to map the cell's response. But the real 'double-opponent' cell also proves to be less than ideal.

While the ideal 'double-opponent' cell, with perfectly balanced opponent subunits, would respond neither to a large white spot covering its receptive field, nor to a pure luminance difference between

its center and surround, the real 'double-opponent' cell often responds to both. Yet, crucially, like the ideal, it does respond to colour contrast within its receptive field, as Conway et al. [5,6] showed using adjacent red and green bars against a grey background. In this way, the real 'double-opponent' cell behaves much like the 'colour-luminance' cell of Johnson *et al.* [7], defined by its equal response to low-contrast modulations of colour and luminance over its receptive field. Conway's data [5] provide the explanation for this behaviour: for most of his 'double-opponent' cells, the cone inputs to the opponent subunits are not perfectly balanced, with the surround responses generally weaker than the center strength. And a slight imbalance in weights is enough to convert a pure 'double-opponent' cell into a 'colour-luminance' cell (see Figure 2). The conclusion is that the two types overlap, despite the differences in terminology and techniques.

None of these newly described cells has been tested for response modulation by the background colour; conversely, the context-modulated cells have not been probed for their internal receptive field structure. Nonetheless, we may conclude that the context-modulated cells are likely to be of the 'colour-preferring' variety christened by Johnson *et al.* [7], a group that likely includes the 'centre-only' and 'single-opponent' types from the traditional taxonomy. The reasoning is that 'the cells you find are the cells you look for', and Wachtler *et al.* [3] screened only for cells that responded to relatively large color squares (4 degrees in size), equivalent to the very low spatial frequencies that elicit their best response in structural studies [7]. 'Double-opponent' cells, which prefer colour contrast on a smaller scale, should remain silent to the touch.

It also makes computational sense that the 'colour-preferring' cell should be the one that shows contextual modulation. Because it is the one that responds best to large patches of colour, its response must be calibrated from the outside if it is to remain constant when signalling a constant surface under changing illumination. 'Double-opponent' cells, which compute within-receptive-field contrast, will in theory find material edges — intrinsic surface reflectance differences — regardless of changing illumination [17]. Both cell types therefore contribute to finding the constant colour of surfaces, and therefore breathe new life into the role of V1 in colour constancy.

Intriguingly, the rise of V1's role in colour constancy parallels a rise in consciousness of the animal brains under study. Three of the new studies [3,5,6] were performed in awake macaque monkeys trained to hold their gaze. Yet the luminance-modulated or 'lightness-constant' neurons were found in V1 of anaesthetised cats [4], and there are preliminary reports of 'colour-contrast' neurons in V1 of anaesthetised marmoset [18]. Humans with intact V1 but higher cortical lesions may be conscious of colours but lack colour constancy [19]. Definitive knowledge of the role of V1 in colour perception in any one species therefore awaits the opportunity to interrogate both V1 neurons and the conscious animal itself.

References

1. Crick, F. and Koch, C. (1995). Are we aware of neural activity in primary visual cortex? Nature *375*, 121–123.
2. Schein, S.J. and Desimone, R. (1990). Spectral properties of V4 neurons in the Macaque. J. Neurosci. *10*, 3369–3389.
3. Wachtler, T., Sejnowski, T.J. and Albright, T.D. (2003). Representation of color stimuli in awake macaque primary visual cortex. *Neuron 37*, 681-691.
4. MacEvoy, S.P. and Paradiso, M.A. (2001). Lightness constancy in primary visual cortex. Proc. Natl. Acad. Sci. U.S.A. *98*, 8827–8831.
5. Conway, B. (2001). Spatial structure of cone inputs to color cells in alert macaque primary visual cortex (V1). J. Neurosci. *21*, 2768–2783.
6. Conway, B.R., Hubel,D.H. and Livingstone, M.S. (2002) Color contrast in macaque V1. Cerebral Cortex *12*, 915-925.
7. Johnson, E.N., Hawken, M.J. and Shapley, R. (2001). The spatial transformation of color in the primary visual cortex of the macaque monkey. Nat. Neurosci. *4*, 409–416.
8. Zeki, S. (1983). Colour coding in the cerebral cortex: The reaction of cells in monkey visual cortex to wavelengths and colours. Neuroscience *9*, 741–765.
9. Lennie, P. (2003). Primer: Receptive fields. Curr. Biol, *13*,R216–R219.
10. Zipser, K., Lamme, V.A.F. and Schiller, P.H. (1996). Contextual modulation in primary visual cortex. J. Neurosci. *16*, 7376–7389.
11. Shady, S. and MacLeod, D.I.A. (2002). Color from invisible patterns. Nat. Neurosci. *5*, 729–730.
12. Calkins, D.J. and Sterling, P. (1999). Evidence that circuits for spatial and color vision segregate at the first retinal synapse. Neuron *24*, 313–321.
13. Derrington, A.M., Krauskopf, J. and Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. J. Physiol *357*, 241–265.
14. Daw, N.W. (1968). Colour-coded ganglion cells in the goldfish retina: Extension of their receptive fields by means of new stimuli. J Physiol *197*, 567–592.
15. Michael, C.R. (1978). Color vision mechanisms in monkey striate cortex, Dual-opponent cells with concentric receptive fields. J. Neurophysiol. *41*, 572–588.
16. Shapley, R. and Hawken, M. (2002). Neural mechanisms for color perception in the primary visual cortex. Curr. Opin. Neurobiol. *12*, 426–432.
17. Hurlbert, A. and Poggio, T. (1989). A network for image segmentation using color. In Neural Information Processing Systems I. D.S. Touretzky, ed. (Morgan Kaufmann Publishers, CA), pp 297–304.
18. Hurlbert, A.C., Gigg, J., Golledge, H. and Tovee, M. (2001). Neurons are selective for local cone-contrast in Marmoset V1. Soc. Neurosci. Abstr.
19. Ruettiger, L., Braun, D.I., Gegenfurtner, K.R., Petersen, D., Schoenle, P. and Sharpe, L.T. (1999). Selective color constancy deficits after circumscribed unilateral brain lesions. J. Neurosci. *19*, 3094–3106.